



RESEARCH ARTICLE

Seasonal succession of functional traits in phytoplankton communities and their interaction with trophic state

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Abstract

1. Understanding and explaining the structure of communities in response to environmental gradients is a central goal in ecology. Trait-based approaches are promising but yet rarely applied to understand community dynamics in response to changing environmental conditions.
2. Here, we investigate seasonal succession patterns of functional traits in phytoplankton communities and how nutrient reductions (oligotrophication) alter these patterns. We used phytoplankton data from 40 years of observation from the Rappbode Reservoir (Germany), which underwent a strong shift in trophic conditions, and translated taxonomic composition into functional traits by assigning trait values compiled from the literature.
3. All studied traits (morphological, behavioural and physiological traits) responded to changing environmental conditions and showed consistent, reoccurring seasonal developments. The seasonal succession of phytoplankton communities was shaped by a trade-off between small-celled, fast-growing species that are able to rapidly incorporate existing resources (*r*-strategists) and large-celled species with more complex and efficient mechanisms to exploit scarce mineral nutrients or acquire previously unexploited nutrient pools (*k*-strategists). In summer, when nutrients were scarce, the *k*-strategy was prevailing (important traits: phosphate affinity, nitrogen fixation, motility and mixotrophy). During the rest of the year, nutrients and turbulence were high and *r*-strategists dominated (important traits: maximum growth rate and light affinity).
4. A comparison between eutrophic and oligotrophic years revealed that the main features of functional trait succession were largely preserved, but intra-annual fluctuations from spring to summer were stronger during eutrophic years. Nutrient reductions mainly affected functional traits and biomass in spring, while in summer the functional community composition changed little.
5. *Synthesis.* This study provides for the first time a quantitatively supported functional template for trait-based succession patterns in lakes under different nutrient conditions. By translating taxonomic composition into trait information, we

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demonstrate that the quantification of functional characteristics enables ecological interpretation of observed community dynamics and provides not only a testable template but also a powerful tool towards a more mechanistic understanding. The quantification of functional traits further improves the predictability of community shifts in response to changing environmental conditions and thus opens new perspectives for predictive limnology using lake ecosystem models.

KEYWORDS

freshwater ecology, functional groups, oligotrophication, plankton ecology group model, Rappbode Reservoir, seasonal dynamics, trait-based approaches

1 | INTRODUCTION

Understanding and explaining the structure and dynamics of biotic communities in response to environmental gradients is a central goal in ecology. As planktonic organisms in aquatic systems have short generation times (Collins, Rost, & Rynearson, 2014), are very dynamic and are highly influenced by abiotic factors as well as biotic interactions, they are well suited to study the reaction of communities to environmental changes. In temperate lake ecosystems, seasonal changes in environmental factors such as temperature, light intensity, nutrient concentration or grazers induce shifts in phytoplankton abundance and species composition (Bergquist, Carpenter, & Latino, 1985; Stomp et al., 2007; Tilman, Kilham, & Kilham, 1982; Vrede, Vrede, Isaksson, & Karlsson, 1999), referred to as seasonal succession. Seasonality is the presence of regular and periodic changes in a variable that recur on an annual time-scale. Explaining and predicting these distinct, reoccurring seasonal patterns has long been in the focus of freshwater ecologists (Margalef, 1978; Reynolds, 1984a; Sommer, Gliwicz, Lampert, & Duncan, 1986). Early theoretical models describe phytoplankton succession mainly as a consequence of turbulence and nutrient availability (Margalef, 1978; Reynolds, 1988). They predict the occurrence of *r*-strategists, which are characterized by small cell sizes and high maximum growth rates, under high nutrient and high turbulence conditions, as they prevail during spring. In summer, when nutrient availability and turbulence are low, *k*-strategists with larger cells, slow growth, but high nutrient affinities and diverse strategies for nutrient acquisition (e.g. mixotrophy, nitrogen fixation) are expected to dominate (Margalef, 1978; Reynolds, 1988). The most popular and widely cited conceptual model about plankton succession is the verbally formulated plankton ecology group (PEG) model, which provides a standard template to describe dynamics of total biomass and composition of plankton communities in response to specific driving environmental factors in the temperate zone (Sommer et al., 1986, 2012). For example, the PEG model predicts a shift from small, edible algae in spring towards larger, inedible algae in summer as a response to increased grazing pressure from zooplankton. Besides changes along the seasonal development, the species composition of phytoplankton communities has also been shown to vary along nutrient gradients, e.g. during

oligotrophication (Anneville et al., 2002; Gaedke, 1998; Jeppesen et al., 2005). Interestingly, studies about oligotrophication focus mostly on inter-annual changes, while intra-annual changes in succession patterns with trophic status have rarely been addressed.

Community dynamics of phytoplankton along seasonal or along nutrient gradients are traditionally described taxonomically. As the basal level in taxonomy, species can be conceptualized by a characteristic information about morphological and physiological features, however, predictions at species level are notoriously difficult or maybe even impossible to make (Reynolds, 2000). Therefore, higher taxonomic units (e.g. diatoms, cyanobacteria) are widely used to evaluate phytoplankton distributions (Wetzel, 2001). However, phylogenetic classifications of organisms have the disadvantage that their ecological functions are heterogeneous within these higher taxonomic units and hence often do not reflect their ecological niche. For instance, species from the same taxonomic group might show very different ecological adaptations, while species from different taxonomic groups can share similar ecological strategies (e.g. mixotrophy or the ability to form colonies; Salmaso, Naselli-Flores, & Padisák, 2015).

Trait-based approaches are a promising tool to overcome these drawbacks and to better reflect the ecological properties of (and diversity within) a community. While much work has been done on classifying species into functional groups (e.g. Kruk et al., 2017; Kruk, Mazzeo, Lacerot, & Reynolds, 2002; Padisák, Crossetti, & Naselli-Flores, 2009; Reynolds, 1980; Reynolds, 1984a; Reynolds, Huszar, Kruk, Naselli-Flores, & Melo, 2002; Salmaso et al., 2015), the study of individual functional trait dynamics in natural communities and their links to abiotic drivers as well as to fitness and survival (e.g. maximum growth rate or phosphate affinity) is still in its early stages in aquatic ecology (Litchman, Edwards, Klausmeier, & Thomas, 2012; Litchman & Klausmeier, 2008; Litchman, Klausmeier, Schofield, & Falkowski, 2007; Weithoff, 2003). Functional traits can provide a mechanistic foundation for understanding and predicting community structure and dynamics across environmental gradients (Edwards, Litchman, & Klausmeier, 2013b; Thomas, Kremer, Klausmeier, & Litchman, 2012) and bridge from the level of organisms to that of ecosystems (Falkowski, Barber, & Smetacek, 1998; Litchman et al., 2015). However, studies about the seasonal

dynamics of phytoplankton traits are rare, especially for physiological traits requiring detailed laboratory measurements. We are only aware of Edwards, Litchman, and Klausmeier (2013a) and Edwards (2016), who studied the seasonality of maximum growth rate, light and nutrient utilization traits in a marine ecosystem.

To the best of our knowledge there are no studies investigating the seasonal dynamics of eco-physiological traits (i.e. derived from quantitative laboratory measurements, for simple binary traits refer to Weithoff, Rocha, & Gaedke, 2015) in a freshwater habitat. Our study aims at closing this knowledge gap and investigates to which extent eco-physiological traits conceptualize functional changes in phytoplankton communities along inter- and intra-annual environmental gradients in lakes. Additionally, we analyse how the impact of nutrient reductions alters the seasonal patterns of these functional traits. We take advantage of a 50-year-long, seasonally resolved dataset from the German Rappbode Reservoir, which underwent a strong and abrupt shift in trophic conditions in the nineties (Wentzky, Tittel, Jäger, & Rinke, 2018). This allows us to analyse functional trait succession under nutrient-enriched and nutrient-deficient conditions (average TP concentrations: 0.13 and 0.02 mg/L, respectively), without the confounding effects of geographical location and lake morphometry that are problematic when making cross-system comparisons (e.g. Edwards et al., 2013b). In contrast to previous studies (Edwards et al., 2013a, 2013b; Klais et al., 2017; Kruk, Martínez, Nogueira, Alonso, & Calliari, 2015; Weithoff & Gaedke, 2016), we describe phytoplankton communities by a variety of relevant traits from independent categories, including morphological, behavioural and physiological traits (cell size, silica use, mixotrophy, motility, nitrogen fixation, buoyancy, ability to form chains and colonies, edibility for *Daphnia*, maximum growth rate, phosphate affinity and light affinity). With our trait-based approach we intend to achieve an understanding of the composition and dynamics of freshwater phytoplankton communities in response to seasonal and long-term environmental changes. Moreover, our goal is to generalize the existing patterns in order to provide a functional template for trait-based succession patterns in temperate lake ecosystems, which is quantitative and therefore largely extends the verbally formulated PEG model. Such a trait-based, quantitative approach will push forward research about seasonal phytoplankton developments, since it allows for a predictive community ecology that can be statistically tested and is capable of making comparisons across different environments.

2 | MATERIALS AND METHODS

2.1 | Study site and sampling

The Rappbode Reservoir is Germany's largest drinking water reservoir and is located in Harz Mountains, a mid-mountain reach in central-northern Germany. Three pre-dams discharge their water into the Rappbode Reservoir. The inflow volume is $120 \times 10^6 \text{ m}^3$ and the residence time 344 days. It has an elongated shape with a length of

8 km, a maximum surface area of 3.95 km^2 , a mean depth of 28.6 m and a maximum depth of 86 m. The Rappbode Reservoir is a mono- to dimictic water body, which underwent a re-oligotrophication process around 1990. Within a very short time period of 2–3 years, total phosphorus concentrations in the epilimnion declined from approximately 0.12 to 0.02 mg/L (Wentzky et al., 2018). The day when stratification set on decreased over the years and the stratification duration increased (for details on calculation of stratification see Wentzky et al., 2018): From 1980 to 1990 (eutrophic period), the stratification period started on average at day 130 (± 8 days), while the mean stratification onset was already at day 114 (± 9 days) between 1996 and 2016 (oligotrophic period). The stratification offset increased from on average day 322 (± 9 days) during the eutrophic period to day 336 (± 20 days) during the oligotrophic period. As a result of earlier stratification onset and later stratification offset the mean stratification duration increased from 192 days (± 10 days, eutrophic period) to 223 days (± 25 days, oligotrophic period). For more details about the Rappbode system, we refer to Rinke et al. (2013), Friese et al. (2014) and Wentzky, Frassl, Rinke, and Boehrer (2019). The sampling point was located close to the dam wall. For this study, we used water samples collected at 0, 5 and 10 m depth between 1970 and 2016 approximately six times a year in monthly intervals during the growing season (March until October). Additionally, mixed samples were taken in the water layer from 0 to 10 m depth every week between 1980 and 2016 for environmental abiotic parameters and between 1980 and 2008 for phytoplankton. Therefore, no samples between November and February were available from 2009 onwards. More details about sampling methods and sample analysis are given in Wentzky et al. (2018). For further analysis, we calculated depth-weighted average values from the data collected at 0, 5 and 10 m depth in order to make them comparable with the mixed water samples collected at 0–10 m depth and both datasets were merged. These measurements cover most of the epilimnetic layer. In this study, we used data for phytoplankton community composition, soluble reactive phosphorus (SRP), water temperature, nitrate (NO_3), silica (Si), oxygen, pH and secchi depth (for details on measurement methods, see Wentzky et al., 2018).

2.2 | Trait selection

For this study we selected functional traits that are considered crucial for survival, growth or reproduction of phytoplankton (see Table 1): Size of individual cells, phosphate affinity, light affinity, maximum growth rate, silica use, motility, buoyancy, mixotrophy, nitrogen fixation, ability to form chains/colonies and edibility for *Daphnia*. Detailed descriptions of the selected phytoplankton traits and their importance for fitness are given in Table 1 and in Weithoff (2003), Litchman and Klausmeier (2008), Litchman, Tezanos Pinto, Klausmeier, Thomas, and Yoshiyama (2010) and Klais et al. (2017). For each species in the dataset ($n = 131$), the mentioned functional trait values were assigned. Cell sizes were taken from local measurements conducted on the organisms present in the Rappbode Reservoir. The

TABLE 1 Overview about phytoplankton functional traits used in this study, including their trait type, range and categories, definition and ecological function. Trait type and ecological function are assigned according to Litchman and Klausmeier (2008)

Trait	Trait type	Range and categories	Definition	Ecological function
Cell size	Morphological	8–200,000 μm^3	Volume of a single cell	Reproduction, resource acquisition and predator avoidance
Phosphate affinity	Physiological	1.52–1,504.98 $\text{L } \mu\text{mol}^{-1} \text{ day}^{-1}$	Ratio of maximum growth rate to half-saturation coefficient. Phosphorous uptake ability. Competitive ability under phosphate limitation	Resource acquisition
Light affinity	Physiological	0.004–0.07 $\mu\text{mol quanta}^{-1} \text{ m}^2 \text{ s day}^{-1}$	Initial slope of the growth-irradiance curve. Growth ability under light limitation. Ability to tolerate low irradiances	Resource acquisition
Maximum growth rate	Physiological	0.20–10.18/day	Ability for fast uptake of nutrients and fast growth. Competitive ability under high nutrient concentrations	Resource acquisition
Silica use	Physiological	Presence or absence	Need to use silica as cell wall material	Resource acquisition
Motility	Behavioural	Presence or absence	The possession of flagella. Ability to actively move in the water column to position with optimal conditions	Resource acquisition and predator avoidance
Mixotrophy	Physiological and behavioural	Presence or absence	Ability to perform photosynthesis (phototrophy) and ingest bacteria or algae through phagotrophy	Resource acquisition
Buoyancy	Behavioural	Presence or absence	Possession of gas vacuoles. Ability to adjust position in the water column to depth with optimal conditions	Resource acquisition and predator avoidance
Nitrogen fixation	Physiological	Presence or absence	Potential to fix atmospheric nitrogen. Competitive advantage under nitrogen limitation	Resource acquisition
Chain and colony	Morphological	Presence or absence	The potential to form colonies or chains	Resource acquisition and predator avoidance
Edibility for <i>Daphnia</i>	Behavioural	0.07–2.5	Susceptibility against predation by <i>Daphnia</i> . The rate of prey consumption relative to the rate at which the favourite prey is consumed	Predator avoidance

cell size always refers to the volume of one single cell, even when organisms form chains or colonies, and hence does not exactly represent grazing resistance of algae. Trait values for morphological and behavioural traits (motility, mixotrophy, buoyancy, nitrogen fixation, silica use and chain and colony formation) were assigned based on available trait compilations (e.g. Klais, 2018: <https://www.riinaklais.com/phytotraits> & Weithoff, 2003) and additional literature review and web search. These latter traits are binary, where a value of 1 means possession of this trait and 0 means absence. While information about morphological and behavioural traits was relatively easy to compile, physiological trait values only exist for a subset of species, since they are measured on cultures in the laboratory. Hence, to be able to assign trait values to every member of the community we took advantage of a method developed by Bruggeman, Heringa, and Brandt (2009) and Bruggeman (2011) allowing to estimate the missing values for the traits maximum growth rate, phosphate affinity, light affinity and edibility for *Daphnia*. Missing trait values were inferred from available laboratory measurements on related species with the help of phylogenetic relationships and morphology-based

power-law relationships. For this study, Bruggeman's model was extended to estimate the light affinity trait, since it was originally not included. For more details on the model see Supporting Information S1. The proportion of species (incl. genus level where species did not match) in Rappbode Reservoir that had measured trait values for maximum growth rate was 38%, while the remaining 62% were estimated using the methods of Bruggeman (2011). For phosphate affinity 26% of the species had measured values, for edibility 24% and for light affinity 27%. For the remaining species the trait values were estimated.

2.3 | Phytoplankton community data

To compare the seasonal development between nutrient-rich and nutrient-poor years, the dataset was split into two periods of equal length based on TP concentrations: The eutrophic period covered the nutrient-rich years between 1970 and 1990. During the eutrophic period the annual mean TP concentration was on average

0.13 mg/L and ranged from 0.11 to 0.20 mg/L. The oligotrophic period covered the nutrient-poor years from 1996 till 2016, with an average annual mean TP concentration of 0.022 mg/L, a minimum of 0.006 mg/L and a maximum of 0.048 mg/L. The number of phytoplankton samples (after aggregation of vertically resolved samples into vertically averaged values between 0 and 10 m) was 555 for the eutrophic period and 596 for the oligotrophic period. For environmental parameters, 557 samples were available for the eutrophic period and 1,050 samples for the oligotrophic period.

To compare different seasons (see Section 2.3.3), the dataset was further divided into spring, clearwater, summer and winter phase. The spring phase covered the months March, April and May (day of year: 60–151); summer was defined as the period from July until October (day of year: 182–304) and winter from November until February (day of year: 305–359); in June usually the clearwater phase appeared (day of year: 152–181). The number of available samples during the eutrophic period was 158 for spring, 67 for clearwater phase, 215 for summer and 115 for winter season. For the oligotrophic period 161 samples were available for spring, 63 for clearwater phase, 238 for summer and 134 for winter months. The most abundant species during the different seasons in the Rappbode Reservoir are presented in Table 1 in Supporting Information S2.

2.3.1 | Ecological trait space of the phytoplankton community

After assigning trait values to each species, we transformed this trait matrix of species into a distance matrix using principal components analysis (PCA) based on Euclidean distances, which is an ordination technique used for visualization of multivariate data. The PCA result can be interpreted as a functional trait space, where the species are separated according to their ecological traits. This trait space gives information about the location of species in relation to their traits and shows how close different traits are related. There were 87 species with unique trait combinations present in the dataset. Species in the PCA plot were phylogenetically aggregated into one of the following groups: diatoms, cyanobacteria, chlorophytes, dinoflagellates, cryptophytes, chrysophytes, euglenophytes and desmids. To visualize the abundance of different taxa in the Rappbode dataset within the PCA, the total biovolume of each species in the dataset over the entire observation period was calculated and log transformed. The point size in the PCA plot was then rescaled to reflect the average abundance of the different taxa in the dataset. To evaluate the number of components retained in the PCA, Horn's parallel analysis from the R package `PARAN` was used. In this method components with adjusted eigenvalues >1 are retained. Of the 11 PC axes 4 were non-random. For easier visualization of the results only the first two axes were used. However, the trait scores for the first four axes are presented in Table 3 in Supporting Information S2.

To address co-variation between traits, a correlation matrix was calculated, using the Pearson correlation coefficient. The correlation

matrix was visualized using the `corrplot` function from the R package `CORRPLLOT` (see Figure 1b).

2.3.2 | Seasonal development of environmental parameters, phytoplankton biomass and traits

The taxonomic composition of each sample in our dataset was translated into a matrix of trait values by adding the characteristic combination of traits to each species. This converted the list of species and their corresponding biovolumes into a matrix of biovolumes and trait

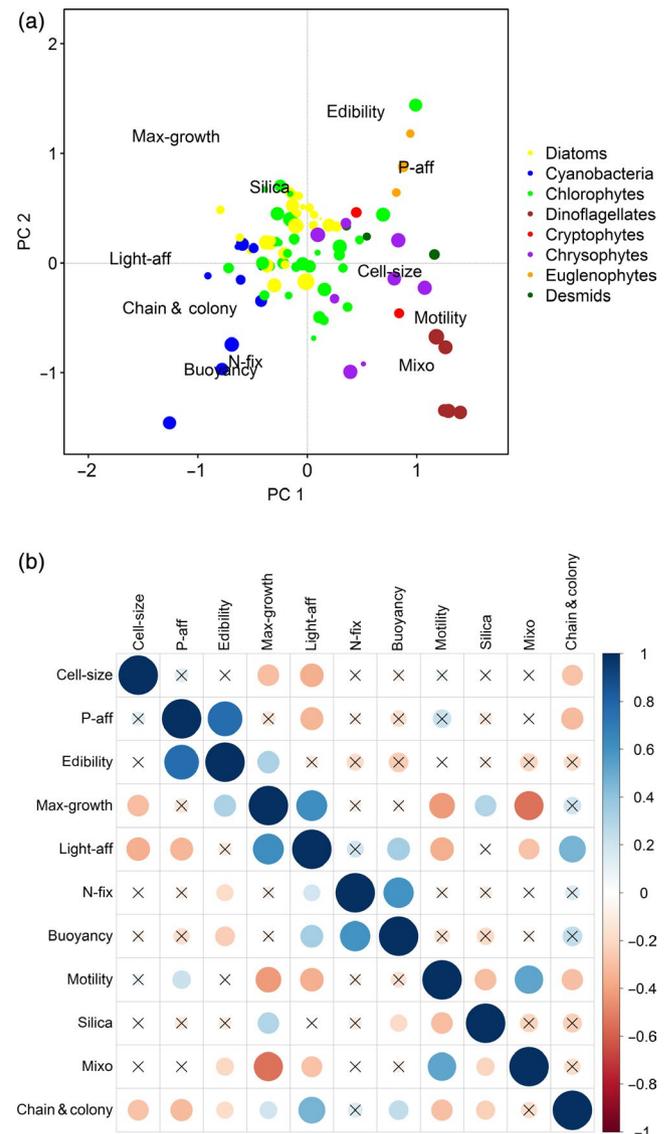


FIGURE 1 (a) Trait-based ordination (PCA) of phytoplankton species along the two main axes, representing the two-dimensional trait space. The different colours represent the algal group, where the species belongs to. The point size represents the average abundance of the different taxa in the Rappbode dataset (on a logarithmic scale). (b) Correlation matrix between traits. The areas of the circles show the absolute value of the corresponding correlation coefficient. The crossed-out points are insignificant correlations. The significance level was set to $p = 0.05$

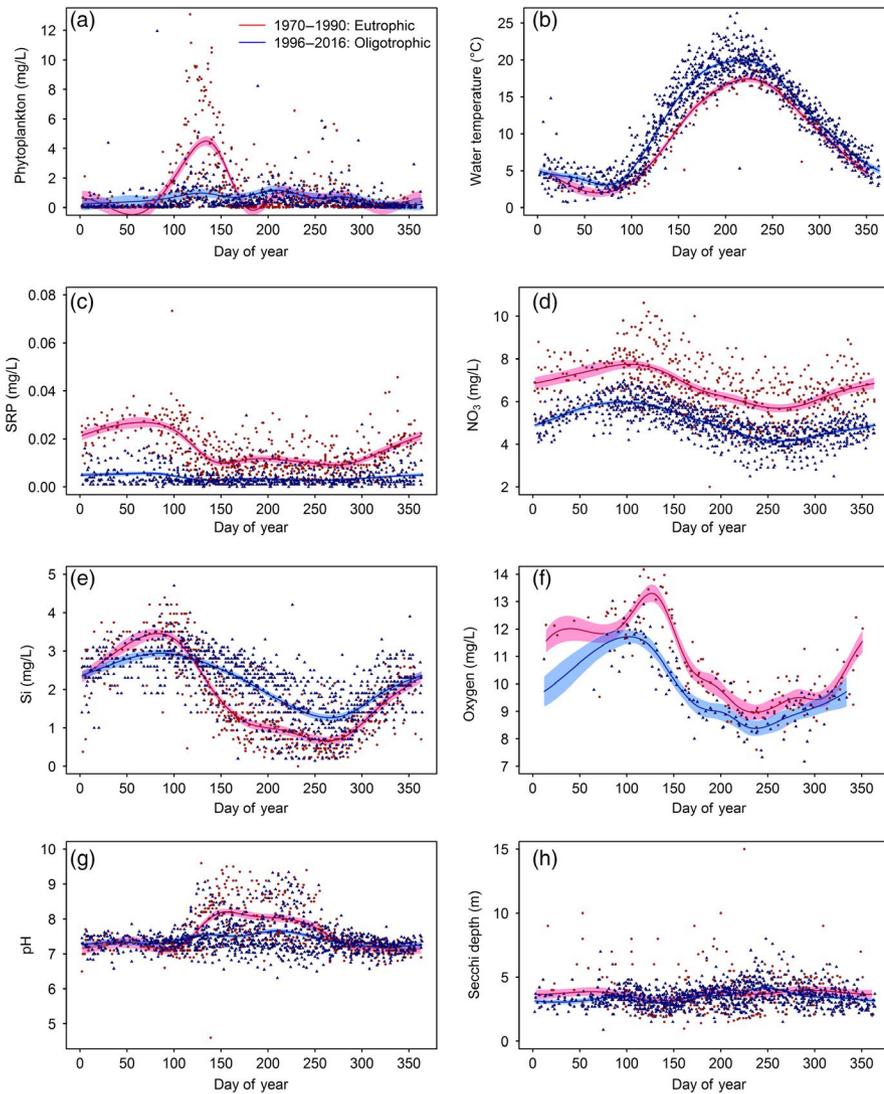


FIGURE 2 Seasonal development of (a) phytoplankton biomass and environmental parameters, including (b) water temperature, (c) soluble reactive phosphorus, (d) nitrate (NO_3), (e) silica (Si), (f) oxygen, (g) pH and (h) light conditions (secchi depth), during the eutrophic (red) and oligotrophic (blue) period in the Rappbode Reservoir. The points are the measured data. The solid lines are the smooth terms from the generalized additive models fitted to the data; the shades indicate the confidence intervals of these fits

values. Subsequently, community-weighted mean (CWM) values were calculated for each sample and each functional trait, in order to describe temporal variability of the individual traits. For quantitative traits and cell size, the CWM is the biomass-weighted mean trait value (or mean cell size, respectively) of organisms in the sample. For the qualitative traits, the CWM represents the biomass proportion of species possessing the trait value 1, hence the CWM will have a value between 0 and 1.

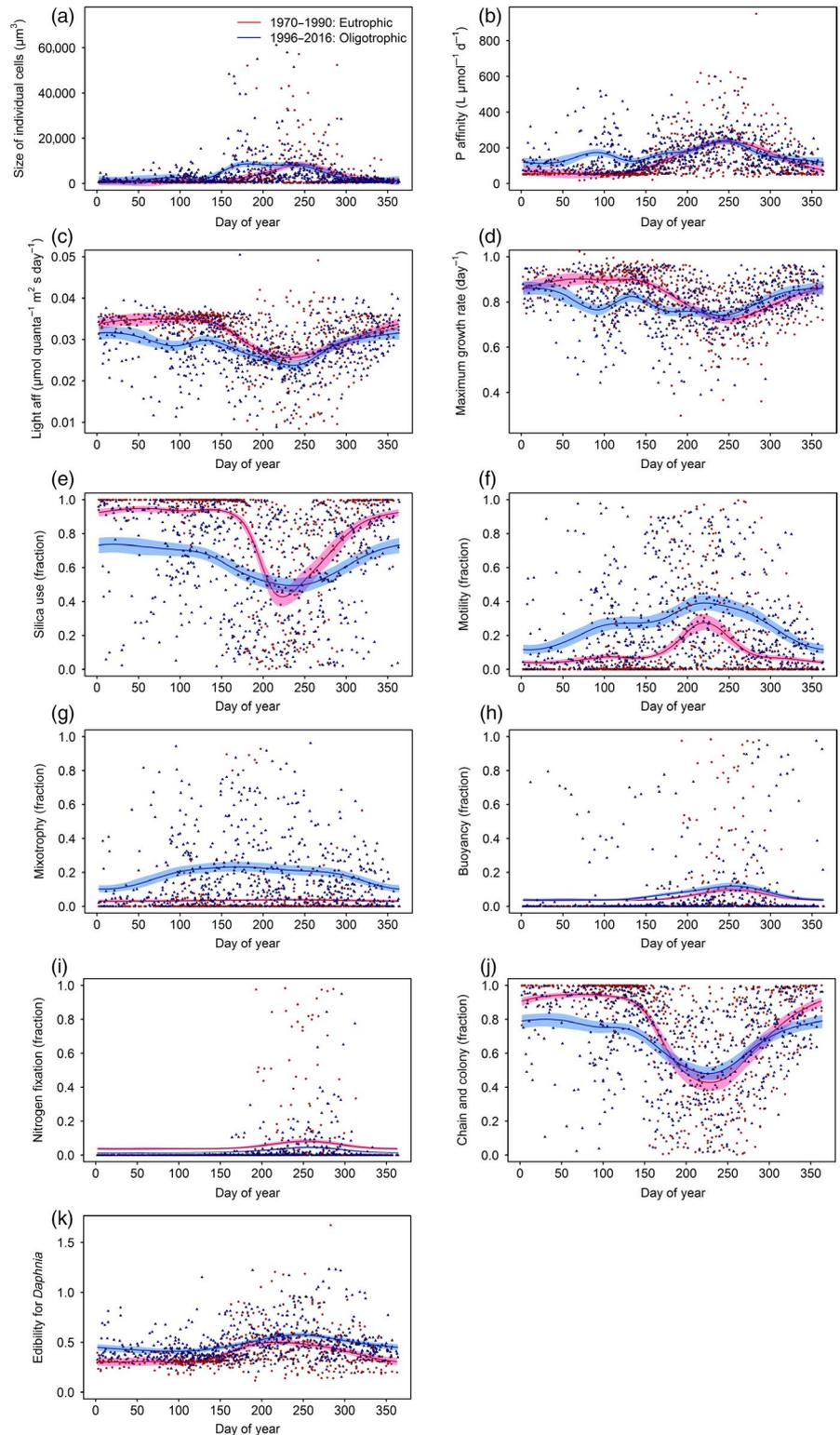
For comparison of the seasonal development of environmental parameters and individual trait values between the eutrophic and oligotrophic period, generalized additive models (GAM) were fitted to the intra-annual development of environmental variables and community-weighted mean trait values, using the method `gam()` from the R-package `MGCV` (Wood, 2017). In a GAM, relationships between predictors and dependent variables follow smooth patterns and can be nonlinear. Due to their flexible predictor functions and their easy interpretation, GAMs can uncover hidden patterns in the data, particularly in case of nonlinearities and abrupt changes, and are hence an attractive tool for analysing environmental time series. Most variables were modelled using a Gaussian normal

distribution. Only for binary traits a beta-probability distribution with a logit transformation was used, since this family can better represent proportion data, which are bounded between the interval $[0, 1]$. The GAM fits are visualized together with the actual data points in Figures 2 and 3. The GAM fits are also displayed without the data points in Figures 1 and 2 in Supporting Information S2.

2.3.3 | Synthesis of seasonal differences in trait composition

As a graphical method to synthesize the information obtained from the individual traits and to evaluate the importance of selected traits for the eutrophic and oligotrophic period, radar charts were created for each season, using the `'radarchart'` function from the R-package `FMSB` (Nakazawa & Nakazawa, 2019). In radar charts, multiple variables, here traits, can be represented on axes starting from the centre. The axes have equal distances between each other and are arranged radially around the centre. For the charts, the average of the community-weighted mean trait values was calculated for each

FIGURE 3 Seasonal development of different phytoplankton traits, including (a) size of individual cells, (b) phosphate affinity, (c) light affinity, (d) maximum growth rate, (e) need to use silica for cell walls, (f) motility, (g) mixotrophy, (h) buoyancy, (i) ability to fix nitrogen, (j) ability to form chains or colonies and (k) edibility for *Daphnia*, during the eutrophic (red) and oligotrophic (blue) period in the Rappbode Reservoir. The points are the measured data. The solid lines are the smooth terms from the generalized additive models fitted to the data; the shades indicate the confidence intervals of these fits



period (eutroph vs. oligotroph) and each phase (spring, clearwater, summer and winter). These trait mean values were drawn into the radar chart, where the data length of a spoke is proportional to the magnitude of the trait value relative to the maximum magnitude across all sampling points. For binary traits the axes are scaled from zero to maximum, instead of minimum to maximum value. Minima and maxima of the axes are the same for all plots.

3 | RESULTS

3.1 | Ecological trait space spanned by the species

Separating the phytoplankton species according to their functional traits in a PCA (Figure 1a) yielded 27% and 20% of explained variation in the first two principal components. The traits buoyancy and

nitrogen fixation were closely related because both only occurred in cyanobacteria. The silica use trait was located opposite of the traits nitrogen fixation and buoyancy, indicating a good separation between diatoms (mostly in the upper half of Figure 1a) and cyanobacteria (lower half of Figure 1a). Larger cell size was associated with motile and mixotrophic species. In contrast, species with smaller cell size occurred together with higher maximum growth rate, edibility for *Daphnia*, light affinity and chain- and colony-forming ability. The traits mixotrophy and motility were ordinated in far distance to high maximum growth rate indicating a trade-off between mixotrophy and fast growth, or in other words, characterize mixotrophs as *K*-strategists. Species from the taxonomic groups diatoms and chlorophytes, dinoflagellates, desmids, chrysophytes and cryptophytes showed different degrees of overlap in trait space. While most of the groups were well separated and obviously occupy specialized areas in the trait space, e.g. diatoms, dinoflagellates and cyanobacteria, the chlorophytes apparently cover a wider trait space and constitute the most trait-diverse phylogenetic group in our analysis. This implies that species from different phylogenetic groups can share similar functional traits. Among the well-separated groups, diatoms and cyanobacteria stand out in terms of the large area they occupied in the trait space while dinoflagellates, chrysophytes and euglenophytes remain relatively constrained to a narrower trait space. This observation has a sampling bias because far more diatom and cyanobacterial species are in the dataset than species from the other groups; but nevertheless it is worth mentioning that trait diversity in our 46-year-long record of phytoplankton communities are higher for diatoms and cyanobacteria compared with the other groups. Phylogenetic relatedness was therefore a poor predictor for functional characterization, particularly for chlorophyte and diatom species.

As depicted by the PCA (Figure 1a) as well as by the correlation matrix (Figure 1b), some traits co-vary. For instance, positive correlations among traits occurred between P-affinity and edibility, buoyancy and nitrogen fixation as well as between mixotrophy and motility. Examples for negative correlations are mixotrophy and maximum growth rate, mobility and maximum growth rate, cell size and light affinity as well as cell size and maximum growth rate. These correlations show that some traits often occur together in the same species and traits are not freely combinable in nature. As different traits are not completely independent from each other and driven by the same species, some of the pattern found in one trait might actually be caused by another, ecologically more relevant trait.

3.2 | Seasonal development of environmental variables and phytoplankton biomass

The phytoplankton biomass and environmental parameters, including water temperature, soluble reactive phosphorus, nitrate, silica, oxygen, pH and secchi depth showed clear seasonal patterns (Figure 2; Figure 1 in Supporting Information S2) and seasonality explained between 3.6% (Secchi depth) and 94.6% (water temperature) of variability in the data (Table 2 in Supporting Information S2). As

indicated by the GAMs, the seasonal development of biomass during the eutrophic period differed substantially from that of the oligotrophic period (Figure 2a). While eutrophic years showed a clear biomass maximum during spring between days 100 and 150, followed by a biomass minimum, representing the clearwater phase, seasonal fluctuations were less pronounced during oligotrophic years and biomass was more equally distributed over the season. Water temperature was very well explained by seasonality (>90% explained deviance, Table 2 in Supporting Information S2). Temperatures were higher during the oligotrophic period, especially in summer (Figure 2b). This point towards increased summer stratification due to climate warming during recent years. SRP concentrations in the epilimnion were high during winter and early spring, decreased after the spring bloom from day 150 onwards, and then increased again in autumn after the offset of stratification when nutrients got re-mixed into upper water layers (Figure 2c). Besides higher SRP concentrations during the whole year in eutrophic years, the seasonal differences in SRP concentrations were also far more pronounced than during oligotrophic years. Nitrate concentrations peaked around day 100 and decreased from then on until late summer (Figure 2d), but never reached limiting concentrations for algae. The seasonality for both periods showed synchronous dynamics, with higher NO₃ concentrations during eutrophic years. Silica concentrations during the eutrophic period were higher in spring and lower in summer compared with the oligotrophic period (Figure 2e). The lower Si concentrations in eutrophic summers were associated with higher shares of silica using phytoplankton in spring, which removed Si from the epilimnion due to sedimentation. Oxygen concentrations in the epilimnion were higher during eutrophic years (Figure 2f). Also a more pronounced oxygen peak was visible in spring from day 100 to 150, which indicated higher photosynthetic activity during eutrophic years. This corresponds to a stronger seasonality of pH during high nutrient years, the highest pH values were found in eutrophic summers (Figure 2g). The seasonality in secchi depth, especially for the eutrophic period, was not as clear as for other environmental parameters, as displayed by wide confidence intervals and low explanatory power of the annual GAM. However, at least for the oligotrophic period, some patterns become visible: Secchi depth was lowest around day 140 (Figure 2h). After day 140 secchi depth continuously increased and peaked in late summer during the time of maximum stratification. In summary, phytoplankton biovolume and most of the abiotic environmental variables (except NO₃ and secchi depth) showed a stronger seasonal development in eutrophic years while dynamics during the oligotrophic years remained lower, and in some variables no clear seasonal patterns could be identified under nutrient-poor conditions.

3.3 | Seasonal development of phytoplankton functional traits

Many individual functional traits exhibited a recurrent seasonal pattern during the eutrophic as well as during the oligotrophic

period, depicted by the GAMs of the annual time series (Figure 3; Figure 2 in Supporting Information S2). The variation in trait data explained by seasonality, varied between 10.1% and 63.4% (Table 2 in Supporting Information S2). Similar to the seasonal variations in abiotic variables, for most traits a more pronounced seasonality was found during eutrophic years. This was indicated by the larger differences in trait composition between spring and summer, shown by the radar plots (Figure 4), as well as by the higher explanatory power of the GAMs during nutrient-rich compared with nutrient-poor years (Table 2 in Supporting Information S2). For many traits, the values for the eutrophic and oligotrophic time series were very different during spring, while they became more similar in summer. This higher overlap in summer was also visible in the GAMs (Figure 3, e.g. for the traits maximum growth rate, P-affinity, light affinity, chain and colony formation and silica use) and in the radar plots (Figure 4). This converging trait composition towards summer indicates that nutrient limitation is a dominant driver of phytoplankton community composition irrespective of the trophic state. In contrast to this, the diverging trait composition between oligotrophic and eutrophic states during spring clearly reflects the difference in nutrient availability. While oligotrophic spring communities were already under the influence of nutrient limitation, eutrophic spring communities showed no sign of nutrient limitation and were selected for *r*-strategists having high maximum growth rates and high light utilization.

At the same time, the general succession patterns of plankton traits along the season also displayed some similarities between nutrient-rich and nutrient-poor years (Figures 3 and 4; Figure 2 in Supporting Information S2). Independent of nutrient status, the spring community was characterized by algae with small size of individual cells, higher maximum growth rates, higher light affinities, the need to use silica and the ability to form chains and colonies. Towards summer these traits became less important and the abundance in large, phosphate affine, motile, mixotrophic, nitrogen fixing and buoyant species increased. For example, from spring to summer the average size of individual cells increased from around 1,500 to 8,000 μm^3 and phosphate affinity from around 100 to 240 $\text{L } \mu\text{mol}^{-1} \text{day}^{-1}$, while maximum growth rate decreased from around 0.86 to 0.73 per day and the share of silica users from almost 100% to 40%. In winter, the community developed back

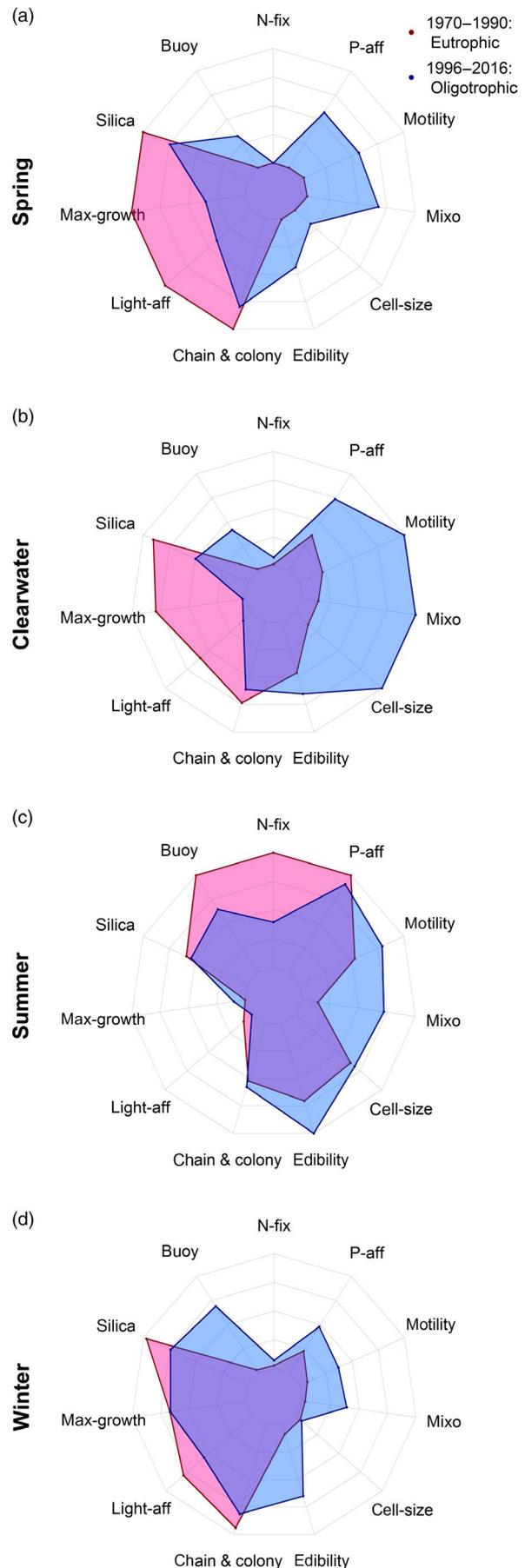


FIGURE 4 The radar charts represent the importance of selected phytoplankton traits (each spoke represents one trait) for the eutrophic (red) versus the oligotrophic period (blue) during (a) spring (March, April and May), (b) clearwater phase (June), (c) summer (July, August, September and October) and (d) winter (November, December, January and February). The data length of a spoke is proportional to the magnitude of the trait value relative to the maximum magnitude across all data points. For binary traits the axes are scaled from zero to maximum value, instead of minimum to maximum value. The axis minima and maxima are the same for all plots. Note that for the oligotrophic period winter samples were only available from 1996 to 2008 (d)

towards higher maximum growth rate and light affinity and a higher share of silica users and colonial algae—a community composition similar to spring. Noteworthy, the seasonal trends in coloniality were mainly shaped by diatoms, as the community changed from a dominance of chain-forming diatoms in spring (e.g. *Asterionella formosa* and *Tabellaria fenestrata*) towards a more diverse community in summer with lower shares of colonial diatoms, but higher shares of single-celled organisms such as *Cryptomonas*, *Ceratium hirundinella* or *Peridinium*. Throughout the year, mobile and mixotrophic species as well as algae edible for *Daphnia* were more abundant during the oligotrophic period (Figure 3f,g,k). Especially the increase in mixotrophy with oligotrophication was very prominent, which have gone up from less than 5% throughout the year in eutrophic years to almost 25% in nutrient-poor summers. In summary, the calculation of community-averaged traits (Figures 3 and 4) allowed for a quantitative assessment of changes in functional characteristics of the plankton community over seasonal and nutrient gradients.

4 | DISCUSSION

The trait space spanned by the phytoplankton species (Figure 1a) showed that phosphate affinity, mixotrophy and motility increased with increasing cell size, while maximum growth rate and light affinity decreased (Banse, 1976; Edwards, Thomas, Klausmeier, & Litchman, 2015; Finkel, 2001; Tang, 1995). This basically indicates a trade-off between *r*-strategists (small cell size, high maximum growth rate and light affinity, low efficiency of resource use) and larger celled *k*-strategists with slower growth rates, but more complex mechanisms for survival (high mixotrophy, motility and N-fixation) and high efficiency to use mineral nutrients (high P affinity; Grover, 1991; Huisman & Weissing, 1995; Leibold, 1997; Litchman & Klausmeier, 2001; Sommer, 1986b). These trade-offs among functional traits drive species replacements along environmental gradients and are therefore the basis for the seasonal succession patterns observed in Rappbode Reservoir.

4.1 | Functional traits quantitatively show a change from *r*- to *k*-strategists from spring to summer

The development of phytoplankton traits showed distinct reoccurring patterns over the season, which are conceptualized in Figure 5. These successional trait patterns were largely retained with trophic status, which is considerable given the large differences in nutrient concentrations between the two trophic periods (average TP concentrations: 0.13 mg/L for eutrophic and 0.02 mg/L for oligotrophic years). All traits, except the edibility for *Daphnia* trait (which is discussed separately below), clearly mirrored the environmental pressures over the year, e.g. high P affinity during P limitation in summer and high light affinity during light limitation in spring. Major differences in functional trait composition exist between the summer period, when the reservoir was strongly stratified and times when a large mixing layer was present. In spring, when turbulence and nutrient input was high, species with small cell sizes and high growth rates (*r*-strategists) dominated (Gaedke, 1992; Reynolds, 1984b; Sommer et al., 1986). Silica users were also most abundant under well-mixed conditions such as in spring. This was probably because silica users have high sedimentation velocities due to their siliceous cell wall and were therefore favoured by turbulence preventing them from sinking out of the photic zone (Sommer, 1984; Trimbee & Harris, 1984). The mixing of the water column and the poor light conditions in spring gave a competitive advantage to species with high light affinities (Edwards et al., 2013a; Yoshiyama, Mellard, Litchman, & Klausmeier, 2009), i.e. the ability for more efficient utilization of low light, since they are better adapted to fluctuating light conditions. Phosphate affinity and alternative strategies for mineral nutrient acquisition, such as the traits nitrogen fixation and mixotrophy were less relevant in spring, since nutrient availability was high. Also the proportion of motile and buoyant species was lower in spring since cells were moved upwards towards the light by turbulence and hence investing in motility was not necessary (Jäger, Diehl, & Schmidt, 2008; Visser, Massaut, Huisman, & Mur, 1996).

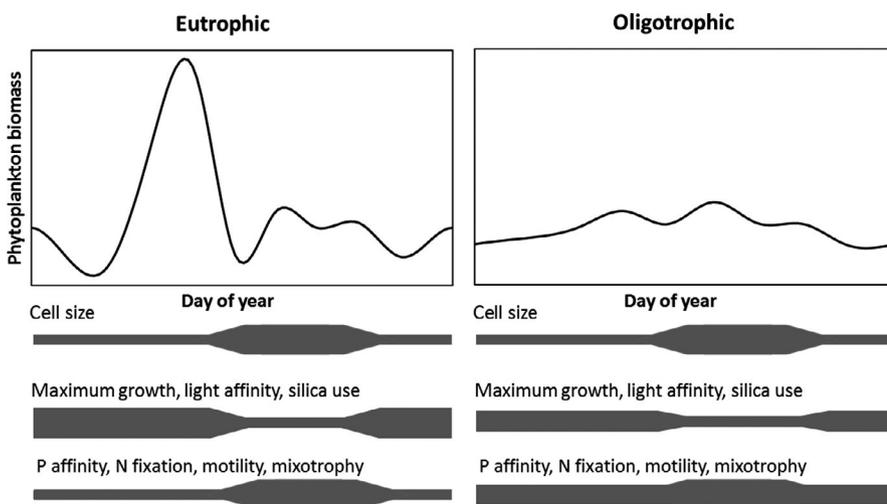


FIGURE 5 Seasonal patterns of phytoplankton biomass and the importance of different phytoplankton traits during eutrophic (left) and oligotrophic (right) years. The thickness of the horizontal bars indicates the seasonal change in relative importance of the phytoplankton traits cell size, maximum growth rate, light affinity, silica use, phosphate affinity, nitrogen fixation, motility and mixotrophy

In contrast, turbulence and nutrients were low in summer and light penetrated deeper into the water column. In response to the changed environmental conditions phytoplankton developed different functional strategies to survive. In agreement with predictions from ecological theory (Litchman & Klausmeier, 2001; Margalef, 1978; Wirtz & Eckhardt, 1996), the summer community shifted towards slower growing species with larger cell sizes and higher tolerances towards periods of nutrient stress (*k*-strategists). The nutrient limitation in summer provided opportunities for phosphate affine phytoplankton and the development of more complex nutrient acquisition strategies such as mixotrophy and nitrogen fixation. Organisms also invested in motility, which was either realized by the possession of flagella or by the regulation of buoyancy to overcome sedimentation losses and nutrient deficiency by migrating to deeper waters, which are important stressors during stratification in summer. This agrees with experiments, which observed a replacement of sinking taxa with buoyant and flagellated taxa with decreasing mixing depth (Jäger et al., 2008; Reynolds, Wiseman, Godfrey, & Butterwick, 1983).

In summary, our results quantitatively show a shift from *r*-strategists (small cell size, high maximum growth rate and low efficiency of nutrient use) in spring to *k*-strategists (large cell size, slow growth rate and complex mechanisms of resource acquisition) in summer, which is in line with verbal descriptions of the typical successional sequence observed in temperate lakes (Margalef, 1978; Reynolds, 1984a; Sommer et al., 1986). The major advancement of our analysis is to put these findings into a quantitative framework using functional traits. This allows not only to provide a quantitatively characterized functional template for trait-based succession patterns (Figure 5) but moreover also provides a testable framework that is prone to advanced statistical and experimental analysis.

4.2 | Edibility trait shows unexpected seasonal pattern

The seasonal development of the edibility trait, i.e. the susceptibility towards grazing by *Daphnia*, as well as the ability of algae to form chains and colonies was surprising as it was contrary to expectations and widespread belief. Theories about plankton succession, observations from lakes as well as modelling studies predict that the edibility of phytoplankton decreases after the clearwater phase towards summer and the algae composition responds to the increased grazing pressure by changing to less-edible, grazing-resistant species (Gaedke, 1998; Lampert, Fleckner, Rai, & Taylor, 1986; Sommer et al., 1986; Vanni & Temte, 1990; Wirtz & Eckhardt, 1996), which is, e.g. attained by the ability to form chains, colonies or filaments (Gliwicz, 1977). We observed the opposite pattern with low edibility and high coloniality during spring and an increase in algae edible for *Daphnia* and low coloniality later in the year, when grazing pressure is expected to be high (Sommer et al., 1986), both in nutrient-rich and -deficient years. In line with our observation, also studies from other lakes reported an increase in inedible algae in the absence of

severe grazing and higher shares of edible algae when grazing pressure was high (Agrawal, 1998; Carpenter, Morrice, Elser, Amand, & MacKay, 1993), which contradicts predictions of defence theory (Coley, Bryant, & Chapin, 1985; Fagerstrom, Larsson, & Tenow, 1987; Porter, 1973). Agrawal (1998) hypothesizes that this paradox outcome might be explained by selective and size-specific grazing by zooplankton. As herbivores vary in their ability to consume the same phytoplankton species (Lundstedt & Brett, 1991), taxa that are edible to one grazer may be inedible to another. Hence edibility and resistance are specific to the particular grazer species, which can have opposing impacts on the phytoplankton composition (Knisely & Geller, 1986; Sommer et al., 2001). In this study edibility by *Daphnia* herbivores was considered. Possibly grazing pressure by other grazers, such as protozoans and calanoid or cyclopoid copepods, had a higher impact, resulting in algae being more edible towards *Daphnia* in summer. For example, *Rhodomonas* spp. (130 μm^3 cell volume) and *Cryptomonas* spp. (1,500 μm^3 cell volume) were characterized as rather edible to *Daphnia*, but have been shown to be spared by copepod grazing (Sommer et al., 2001). Hence, high grazing pressure by copepods in summer might have triggered an increase in those algae species, which were inedible to copepods, but edible to *Daphnia*.

This shows that the edibility of algae is predator specific and thus difficult to define, making generalizations about the edibility of algae as proposed by the PEG model (Sommer et al., 1986) difficult. Moreover, it is possible that the unexpected trends in the colony formation and edibility for *Daphnia* trait were due to reasons other than grazing pressure. For example, the low abundance of colonial and filamentous organisms during summer stratification might be related to higher sinking velocities of colonies (Reynolds, 2006) rather than to grazing pressure. Since different traits are not completely independent from each other and therefore not freely combinable, the unexpected trends in coloniality and edibility might have been shaped by trends in other more important traits. This would indicate that losses by grazing were not as important in shaping the phytoplankton communities (top-down) and that the seasonal phytoplankton dynamics in the Rappbode system were primarily regulated by resource availability (bottom-up).

4.3 | Nutrient reductions affect biomass and functional traits mainly during spring

While the general succession patterns of functional traits were independent of nutrient regime, the extent of the seasonal changes in functional traits from spring to summer clearly differed with trophic status. Phytoplankton biomass and functional traits exhibited lower fluctuations along the season during oligotrophic years, as the differences between the traits in spring and summer were relatively small. In contrast, in eutrophic years seasonality of biomass and traits was more pronounced and the differences between spring and summer conditions were large. The increase in seasonal changes in traits with nutrient concentration was expected, as eutrophic systems usually show larger seasonal fluctuations in biomass and phytoplankton

cell size spectra and more successional stages (Gaedke, Seifried, & Adrian, 2004; Kalff, 2002; Sommer, 1986a; Sommer et al., 1986).

Comparing the seasonal biomass development between the two trophic states, it became also evident that the strong phytoplankton spring bloom found in eutrophic years vanished with oligotrophication, while summer biomass changed little (or even became higher). This contradicts the PEG model which expects the disappearance of summer blooms with oligotrophication, while the magnitude of the spring bloom is less affected (Sommer et al., 1986). Water residence time and internal lake processes might be a reason for the differences in biomass patterns between Rappbode Reservoir and, e.g. Lake Constance, which was a major study site for the development of the PEG model. The Rappbode system has a shorter residence time (approximately 1 year) and external nutrient loads are more important than in Lake Constance given its much longer residence time (4.3 years). However, the relative importance of external nutrient inputs versus internal nutrient processing changed during the oligotrophication process in Rappbode Reservoir. While in the eutrophic phase high external inputs restored high nutrient conditions during the cold season and induced a massive spring bloom followed by high downward nutrient export by sedimentation (Wentzky et al., 2018), this pulsed regime got largely replaced by internal processing in the oligotrophic phase. High shares of motile and mixotrophic species during the oligotrophic period reduced sedimentative losses and speeded up internal nutrient recycling and finally lead to a more dampened succession with less pronounced spring blooms and a higher persistence of algal communities throughout the growing season. These observations comply with findings from the re-oligotrophication in Lake Constance, where significant internal processing and nutrient regeneration have been documented (Gaedke & Straile, 1994; Tilzer, Gaedke, Schweizer, Beese, & Wieser, 1991).

A study from Lake Constance also showed that differences in the functional composition after nutrient reduction were most apparent during nutrient limitation in summer (Weithoff & Gaedke, 2016). In contrast, in the Rappbode Reservoir the largest changes with changing trophic status occurred in the spring community, while the traits in summer largely overlapped in the eutrophic and oligotrophic period. Hence, in oligotrophic years the functional composition of spring communities resembled summer communities, while in eutrophic years spring and summer communities were functionally very different. Intense nutrient limitation, which already occurred in spring during oligotrophic years, forced the community to adapt to low nutrient levels earlier in the year. This observation may provide an explanation for the relatively high summer biomasses observed in oligotrophic years in the Rappbode Reservoir (Wentzky et al., 2018). Since species adapted to low nutrient availabilities were already present in significant amounts in spring, they had longer time to develop high abundances during summer. In summary, our study shows that trophic status strongly affected biomass and functional composition during spring, contradicting previous theories and observations that expect the largest changes in summer (Sommer et al., 1986; Weithoff & Gaedke, 2016).

5 | CONCLUSIONS

The study provides a quantitatively supported functional template for phytoplankton succession in temperate lakes under different nutrient regimes (Figure 5). In line with conceptual models (Margalef, 1978; Sommer et al., 1986), we quantitatively showed that succession patterns of plankton communities were mainly driven by a trade-off between small-celled, fast-growing species that are able to incorporate existing resources at a reasonable short time (*r*-strategists) and large-celled species with more complex and efficient mechanisms to exploit scarce mineral nutrients or acquire previously unexploited nutrient pools (*k*-strategists). Moreover, the seasonal development of functional traits mirrored environmental pressures over the year. For example, phosphate affinity and mixotrophy peaked during phosphorous limitation in summer, while maximum growth rate and light affinity were high during the mixing season when light was limiting but nutrients were highly available. Noteworthy, the main features of functional trait succession were independent of nutrient regime and the seasonal development of functional properties of the community was similar during oligotrophic and eutrophic conditions. Distinct changes in functional composition occurred, however, and seasonal differences during oligotrophic years were generally less pronounced over the year. Spring communities in the oligotrophic state moreover showed clear sign of nutrient limitation and therefore showed more functional resemblance with summer communities than under eutrophic conditions.

The study shows that translating species into functional traits by assigning trait values compiled from the literature provides a powerful method towards a more predictive community ecology. Functional traits can be applied to translate information about taxonomic composition into ecologically interpretable functions and eco-physiological processes that can be linked to resource competition, succession and ecosystem dynamics. It enables ecological interpretation of observed phytoplankton community dynamics by quantification of functional characteristics and improves the predictability of community shifts in response to changing environmental conditions. This should open new perspectives for predictive limnology using lake ecosystem models.

Our method of assigning static trait values to each algal species does not take intraspecific trait variability into account, which can sometimes be significant (Boliu, Wiedner, & Weithoff, 2017; Malerba, Heimann, Connolly, & Leroux, 2016; Morabito, Oggioni, Caravati, & Panzani, 2007). However, in contrast to measuring traits directly on the natural community and thus including intraspecific trait plasticity, our method has the advantage that it can be applied to historic taxonomic data. This allows to follow long-term trends of the community from a functional perspective, e.g. to study the response to eutrophication or climate change. Moreover, our method can also explore patterns in traits, which are not directly measurable on the natural community (e.g. physiological traits such as maximum growth rate).

In summary, the reduction in taxonomic complexity to the common currency of functional traits allows assessing community

structure in historic datasets, but the method can also be used to make comparisons across different environments and habitats. As trait-based approaches can serve as a unifying concept in ecology, we strongly encourage researchers to take advantage of them.

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AUTHORS' CONTRIBUTIONS

V.C.W., J.T., C.G.J. and K.R. conceived the ideas and developed the research questions; J.B. extended and improved the PhyloPars model and provided the resulting trait values; V.C.W. analysed the data, made the figures and tables and led the writing of the manuscript. All authors interpreted the results, contributed critically to the drafts and gave their final approval for publication.

DATA AVAILABILITY STATEMENT

Data are available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.fbg79cnrs> (Wentzky, Tittel, Jäger, Bruggeman, & Rinke, 2020).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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