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Contribution to the Themed Section: Phytoplankton traits, functional groups and community organization

Mean functional traits of lake phytoplankton reflect seasonal and inter-annual changes in nutrients, climate and herbivory

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Trait-based approaches have become increasingly successful in community ecology. They assume that the distribution of functional traits within communities responds in a predictable way to alterations in environmental forcing and that strong forcing may accelerate such trait changes. We used high frequency measurements of phytoplankton to test these assumptions. We analyzed the seasonal and long-term dynamics of the community trait mean within a multi-dimensional trait space under alternating multifactorial environmental conditions. The community trait mean exhibited a distinct recurrent annual pattern that reflected minor changes in climate, herbivory and nutrients. Independent of early spring conditions, the community trait mean was repeatedly driven into a narrow confined area in the trait space under pronounced herbivory during the clear water phase. The speed of movement was highest at the onset and the relaxation of such strong unidirectional forcing. Thus, our data support the conceptual framework of trait-based ecology that alterations in environmental conditions are systematically tracked by adjustments in the dominant functional trait values and that the speed of trait changes depends on the kind and intensity of the selection pressure. Our approach provides a sensitive tool to detect small functional differences in the community related to subtle differences in forcing.

KEYWORDS: phytoplankton; temporal dynamics; climate; trait distribution; Lake Constance; functional traits

INTRODUCTION

Trait-based approaches have become increasingly successful in ecological research, e.g. for the understanding of ecosystem properties and processes (Smith *et al.*, 1997; Diaz and Cabido 2001; Litchman and Klausmeier 2008), ecological assembly rules (Weiher and Keddy 1999; Kraft *et al.*, 2008, 2014; Götzenberger *et al.*, 2012) and patterns in biogeography (Acevedo-Trejos *et al.*, 2013; Barton *et al.*, 2013). Since environmental forces act on specific functional traits or sets of traits, they are expected to lead to directed mean trait changes within a community. However long-term, trait-based studies on community responses to environmental forces are rare, investigating e.g. plant succession in newly established sites (Helsen *et al.*, 2012; Ulrich et al., 2014) or seasonal phytoplankton development (Edwards *et al.*, 2013). Understanding such trait changes is key to better forecasting community responses to global change and other environmental impacts. Under field conditions, many environmental forces are relevant which may act during different periods at various scales on sets of different traits (Verberk *et al.*, 2013), such as susceptibility to predation, resource use and adaptation to a number of abiotic factors. Thus, there is a need for studies investigating long-term changes of the most relevant set of traits under natural, multifactorial conditions for communities subjected to alternations in abiotic and biotic conditions.

Results from population genetics suggest that temporal trait changes are fast when under strong directional selection (Lande 1982). This has also been demonstrated for the community level by trait-based model approaches (Wirtz and Eckhardt 1996; Norberg *et al.*, 2001). It requires that trait changes enable a substantial gain in net growth along with a sufficient standing trait variation. We test in this study whether these model results can be backed-up with data.

Lake phytoplankton is ideal to study the effect of environmental forcing on the direction and speed of trait changes, because many traits can relatively easily be measured and populations can rapidly track environmental changes (e.g. Stewart and Wetzel, 1986; Weithoff *et al.*, 2000) due to the short generation times of algae (up to more than 100 generations per year). Furthermore, the driving forces are well understood. In principal, the seasonal dynamics of phytoplankton in temperate, stratifying lakes follows a distinct pattern with explainable variations related to lake depth, winter conditions and trophic state summarized in the verbal model of the "Plankton Ecology Group" known as the PEG-model (Sommer *et al.*, 1986, 2012). In its basic form, the PEG-model predicts a phytoplankton development in spring, followed by the growth of herbivorous zooplankton such as ciliates and rotifers followed by crustaceans (mainly *Daphnia* spp. and *Bosmina* spp.) imposing a high grazing pressure which leads to the clear water phase. After that, herbivores suffer from food shortage and invertebrate and fish predation. Hence, the grazing pressure on phytoplankton relaxes and diversifies since then different groups contribute to the herbivore community. During summer and early autumn nutrient depletion becomes increasingly important in many stratified lakes.

The functionally and species rich phytoplankton community in large, deep Lake Constance adheres to this general pattern. Accordingly, its functional (ataxonomic) characteristics expressed as the community trait mean exhibited recurrent seasonal changes during a 19-year period (Weithoff *et al.*, 2015). However, year-to-year variability during some periods of the year was substantial. Here, we postulate that this reflects differences in the driving forces. Within this long period, the lake underwent a continuous oligotrophication (Gaedke, 1998) and was subjected to climate variability. Variable environmental drivers such as late winter/early spring temperature, light conditions and mixing regimes varied among years and led to a temporally highly variable onset of the spring bloom (Peeters *et al.*, 2007, Tirok and Gaedke; 2007) that translated into different herbivore species compositions in late spring. These differences manifested in years, when *Daphnia* was responsible for the initiation of the clear water phase ("*Daphnia* years"), and in years when ciliates, rotifers and copepods dominated during its initiation ("non-*Daphnia* years", Tirok and Gaedke, 2006). This allows us to separate the 19 years of data into nutrient rich, i.e. more eutrophic, early years and nutrient poor, i.e. more oligotrophic, late years (nutrient availability) and into years when either *Daphnia* or other herbivorous zooplankter initiated the clear water phase (climate signal). The forcing factors nutrient availability and climate or weather conditions are well defined so that the mechanisms of their impact are well understood. The clear water phase was a decisive seasonal event for the entire plankton community in Lake Constance provoking major changes in most of its characteristics (Boit and Gaedke, 2014). Largely independent of how and when it was initiated, the clear water phase represented for phytoplankton a short recurrent period with coherent forcing factors such as severe grazing, enhanced nutrient remineralization and an improved underwater light climate due to low algal biomass.

We use this phytoplankton data set to analyze the temporal movements or trajectories of the community trait mean in a multi-dimensional trait space in response to different environmental forcing. Following Weithoff *et al.* (2015) we conduct an ordination of each individual sampling date in a multi-dimensional trait space spanned according to five functional traits of the phytoplankton taxa. This allows us to test whether the movements in the trait space are idiosyncratic or can be linked to distinct driving forces. In particular, we test the following hypotheses. (i) During periods of strong and inter-annually recurrent environmental forcing, such as the clear water phase, inter-annual variability in the community trait mean is low. (ii) Rapid changes in the environmental drivers lead to fast responses of the community composition manifested in fast and pronounced changes in its trait mean values. (iii) During the different groups of years (more eutrophic vs. more oligotrophic or *Daphnia* vs. *non-Daphnia* years) the respective community trait mean exhibits different trajectories in the trait space during distinct parts of the season, i.e. inter-annual variation previously found can be explained by the two drivers. More specifically, we hypothesize that differences in the trajectories between *Daphnia* and non-*Daphnia* years are apparent before the clear water phase and differences between the trajectories of the more eutrophic and more oligotrophic years become larger after the clear water phase.

METHOD

Data acquisition

Upper Lake Constance (Bodensee) is a large (472 km^2), deep (101 m) temperate lake located at approximately 47°40′ N, 9°20′ E and bordered by Germany, Switzerland and Austria. Warm-monomictic Lake Constance underwent a re-oligotrophication process with an almost monotonous decline of total phosphorus concentrations from more than 2.81 μM P in 1979 to 0.55 μM P in 1998, resulting in an increasing and pronounced phosphorus depletion in the epilimnion during summer (Tirok and Gaedke, 2006). Plankton sampling was conducted weekly during the growing season and approximately fortnightly in winter by a large team of scientists, culminating in an extended time series for phytoplankton biomass (1979–1998, 1983 excluded because of lacking data). Phytoplankton counts and cell volume estimates were obtained using Utermöhl's inverted microscope technique (Utermöhl, 1958). All measurements are provided per unit area and comprise the biomass within the uppermost water layer from 0 to 20 m depth, which roughly corresponds to the epilimnion and the euphotic zone, except for bloom conditions and increasing self-shading. In the present study, we considered the 36 most abundant morphotypes of phytoplankton (constituting 92% of total phytoplankton biomass) comprising individual species or higher taxonomic units that are functionally identical or very similar under the functional classification employed here (Rocha et al., 2011a, 2012). This guaranteed a consistent resolution of phytoplankton counts across the 19 years of sampling.

Selection of functional traits

A functional trait is a morphological and/or physiological property that affects fitness via its effects on growth, reproduction and survival (Violle *et al.*, 2007; Salmaso *et al.*, 2015). The selection of functional traits is of crucial importance because all subsequent calculations of ecological distance (see below) depend on them (Gitay and Noble, 1997; Petchey and Gaston, 2006). We selected five functional traits in the present study because previous investigations revealed their importance in Lake Constance, at least during parts of the investigation period (Kamjunke *et al.*, 2007; Rocha *et al.*, 2012). They determine the net growth as the sum of intrinsic growth, sedimentation, grazing losses and some other less important loss factors, taking into account that the environment selects typically not for a single trait but for a trait combination (Verberk *et al.*, 2013). We quantified the traits (cell size, longest linear dimension of the cell/filament/colony, motility, phagotrophy, silica demand) for the 36 morphotypes; for details see Supplementary Materials 1 and 2 and Weithoff *et al.* (2015).

Calculation of the community trait mean

We used the same procedure and data as proposed in Weithoff (2003) and used in Weithoff *et al.* (2015) which basically compares to the functional dispersion proposed by Laliberté and Legendre (2010). In summary, as an ordination technique we used a Principal Coordinates Analysis (PCoA) for transforming the trait matrix of the 36 morphotypes into a distance matrix (Villéger *et al.*, 2008) using the Bray Curtis coefficient (CANOCO software, version 4.5, Ter Braak and Smilauer, 2002). A PCoA is an appropriate analysis when dealing with various discrete data and where the original distances remain after the calculations. The first three axes generated explained 57%, 24% and 12% of the variation in the trait data set and this three-dimensional ordination can be viewed as an ecological trait space that is spanned by the morphotypes according to their traits. The eigenvalues of each axis were standardized and used as weights for the coordinates. For further analysis, we used only the first two axes, since a two-dimensional presentation better visualizes the temporal dynamics and the explanatory power was still high. According to its specific trait values, each morphotype has distinct coordinates within this ecological trait space (Weithoff *et al.*, 2015). Subsequently, for each sampling date we calculated a community trait mean representing the center of gravity (Villéger *et al.*, 2008) or centroid (Laliberté and Legendre, 2010) in this two-dimensional trait space based on the coordinates of the individual morphotypes, which were weighted by their relative contribution to the total biovolume. These metrics were coded using R 2.9.0. To estimate the inter-annual variation of the monthly mean, we multiplied the standard error (SE) of the monthly values of all 19 years of Axis 1 with the one of Axis 2. The temporal rate of change was calculated as the Euclidean distance between two consecutive monthly mean values.

Seasonal standardization to the clear water phase

We defined the onset of the clear water phase according to a combination of three measures: Secchi depth, algal biovolume and chlorophyll a concentrations, the species composition itself was not a determinant (Tirok and Gaedke, 2006). To account for the inter-annual variability in the calendaric date of the onset of the clear water phase, data were standardized relative to the onset of the clear water phase (Tirok and Gaedke, 2006). The first week of the clear water phase corresponds to Week 0, weeks before the CWP to values <0 and weeks after the beginning of the CWP to values >0. The mean of 4-week periods was calculated as a substitute of a monthly mean and these periods were named "month" to distinguish them from calendar months. The "month" 0 reflects the clear water phase and sometime thereafter, in case the clear water phase lasted for <4 weeks. The initiation of the clear water phase fell within the "month" −1 and the spring bloom into "month" −2. Before that was the early spring representing the transition from winter to spring. The "months" after the clear water phase (1–4) cover roughly the months from July to October.

The two factors, type of herbivores initiating the clear water phase and trophic state, were assigned to the 19 years as follows: Eight of our study years were classified as *Daphnia* years (1979, 1980, 1985, 1988, 1989, 1992, 1993 and 1994), with a daphnid biomass >1000 mg C m^2 before the clear water phase (Tirok and Gaedke 2006). In contrast, 11 years were non-*Daphnia* years (1981, 1982, 1984, 1986, 1987, 1990, 1991, 1995, 1996, 1997 and 1998), when ciliates, rotifers and copepods predominantly initiated the clear water phase. Nine of these eleven non-*Daphnia* years exhibited a daphnid biomass even below 500 mg C m^2. Note that in all years during the clear water phase, daphnids generally dominated the herbivore community although their biomass remained often lower in non-*Daphnia* years. Furthermore, we separated the years into an early, more eutrophic period from 1979 to 1988, with a mean in the winter total phosphorus concentration of 2.29 µM P, ranging from 2.81 in 1979 to 1.52 µM P in 1988 and a late, mesotrophic period with a mean of 0.94 µM P ranging from 1.39 in 1989 to 0.55 µM P in 1998. Consequently, in the early, more eutrophic phase, soluble reactive phosphorus was less severely depleted during the season than in the later more oligotrophic period.

Statistical analysis

To test for statistical significance of the inter-annual differences in the trajectories we calculated the temporal autocorrelation of the coordinates of the community trait mean using Lag 1 and Lag 2 distances according to the respective years. As a significance level, an autocorrelation coefficient larger than 0.2 was chosen for positive autocorrelation.

Additionally, we calculated the average pairwise distance between the z-transformed "monthly" community trait means of years sorted according to the winter phosphorus concentration and daphnid biomass and compared these with those from randomly shuffled years. Small pairwise distances when sorted according to nutrient level or daphnid biomass relative to randomly shuffled years indicate a nutrient or herbivore effect on the "monthly" community trait mean, respectively.

RESULTS

We found a distinct recurrent pattern in the seasonal movement of the community trait mean through the trait space after the standardization of the time series according to the clear water phases (Fig. 1A). The periods before and after the clear water phase were clearly separated and the clear water phase itself was separated from both of the two periods. The clear water phase occupied a trait area that is not located on the direct trajectory from the spring to the summer situation, but it represented a seasonal event with its own ecological characteristics. Furthermore, compared to the other "monthly" community trait means, the inter-annual variation around the "months" 0 (clear water phase) and 1 was low, underlining the recurrent and pronounced role of the strong grazing pressure as an attractor for the dynamics in the trait space (Fig. 1B). The inter-annual variation of the other "months" was higher, in particular

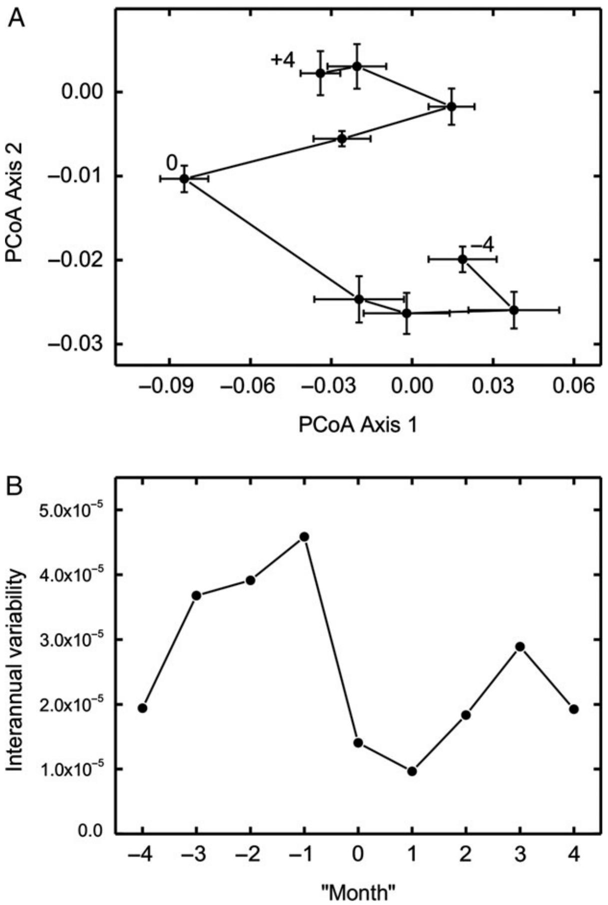

Fig. 1. (**A**) "Monthly" mean of the community trait mean ±SE. 0 denotes the 4-week period from the beginning of the clear water phase. Negative values indicate "months" before and positive values "months" after the clear water phase. (**B**) Inter-annual variability of the community trait mean calculated as the product of the SEs from Axis 1 and Axis 2 from (A).

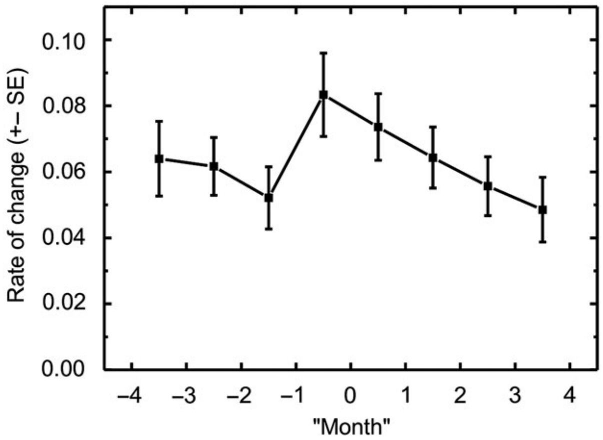

Fig. 2. Rate of change of the community trait mean calculated as the Euclidian distance between two consecutive monthly mean values; error bars represent the SE of the mean across the 19 years of sampling.

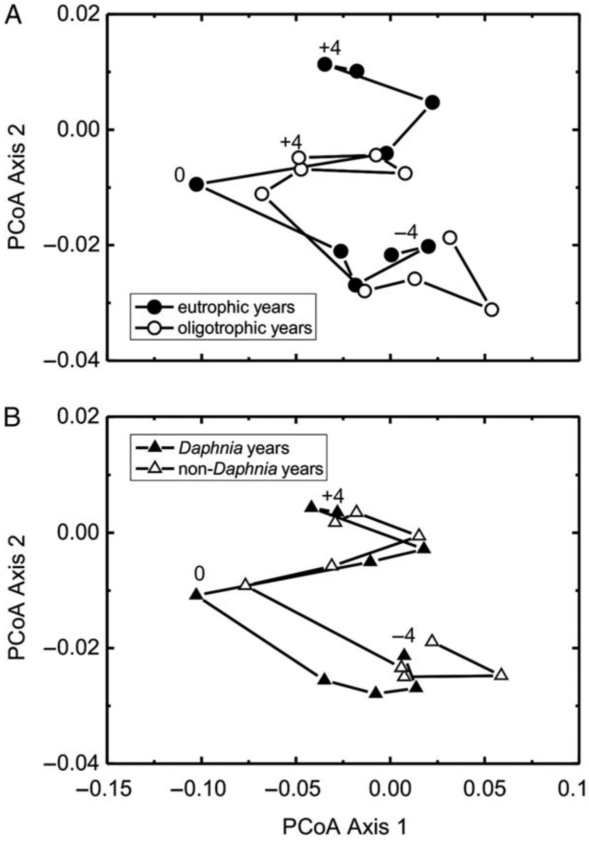

Fig. 3. Trajectories of the four types of years through the trait space. (**A**) More eutrophic and more oligotrophic years. (**B**) *Daphnia* and non-*Daphnia* years. 0 denotes the 4-week time interval ("month") including the clear water phase, −4 and +4 the intervals 4 "months" earlier or later, respectively.

during spring and summer. Besides the low inter-annual variation of the community trait mean during the clear water phase, we found a fast movement through the trait space towards and after the clear water phase (Fig. 2), indicating that strong environmental forcing drove the phytoplankton community rapidly to a different and distinct average trait composition. Later in the season, the rate of change decelerated and became low at the beginning of autumn.

Comparing more eutrophic and more oligotrophic years, the community trait means moved along rather similar trajectories from late winter until the clear water phase (Fig 3A). The most prominent differences occurred later in the year, i.e. when nutrient depletion was most apparent in the more oligotrophic years: The community trait mean during more eutrophic years occupied a separate area in the upper part of the trait space which was not reached later on (Fig. 3A). The analysis of the autocorrelation underlines this view by values mostly above 0.2 from "month" −1 to 4 (Fig. 4). The analysis of the pairwise distances (not shown) confirmed this result. The trait values during the clear water phase were consistently located in a more extreme part of the trait space when daphnid biomass was comparatively high, i.e. during the more eutrophic years and during *Daphnia* years (Fig. 3).

Separating the different years according to the type of spring weather conditions manifested in herbivore type revealed less prominent differences. Comparing *Daphnia* and non-*Daphnia* years, some differences between the trajectories towards the clear water phase occurred, which then diminished later in the year (Fig 3B). However, the autocorrelation of the time series sorted by daphnid biomass prior to the clear water phase was not significant (data not shown). The spring weather conditions and type of herbivores were more important during the more eutrophic years than in the more oligotrophic years (Supplementary Material 3). Thus, climate and different initiators of the clear water phase altered the functional trait mean of the phytoplankton community less pronouncedly than the reduced total phosphorus level. After the clear water phase was reached and *Daphnia* dominated the herbivore community during all years, the phytoplankton community trait mean lay repeatedly in the same sector within the trait space and also later in the year, both groups moved along similar trajectories (Fig. 3B).

DISCUSSION

We found that strong environmental forcing, such as the rapidly developing herbivory in late spring, pushed the phytoplankton community trait mean to a narrow, confined area in the multi-dimensional trait space. This was a recurrent phenomenon during all years independent of the trophic state of the lake and the other environmental conditions during the time before the clear water phase. It supports our first hypothesis that strong forces drive a community recurrently to a defined functional trait mean. Similar results were found for phytoplankton in a long-term study of Lake Arancio, a (hyper-)eutrophic reservoir in Sicily (Italy) (Naselli-Flores, 2013). A recurrent seasonal development of defined ecological strategies was observed in periods of similar environmental conditions such as water level and mixing depth. When these external drivers changed, phytoplankton strategies also recurrently adapted to the altered conditions. Comparisons with non-planktonic systems are hampered by their different characteristics, including the type of forcing, and the lack of long-term data covering many generations. In grassland communities, plant traits were found to converge during succession, i.e. the communities became functionally similar despite a diverging species pool (Fukami *et al.*, 2005; Helsen *et al.*, 2012). These results indicate that environmental forces select for certain traits regardless of the individual species. In Lake Constance, the species composition during the clear water phase was typically dominated by small cryptophytes and diatoms and changed only slightly during the study period, but variations between years occurred (Gaedke, 1998). Nevertheless, the inter-annual variation of the community trait mean was very low during the clear water phase. This holds also for the following "month". The relaxing grazing pressure allowed the phytoplankton community to develop a broader taxonomic diversity (Weithoff *et al.* 2015) but the community trait mean was confined to a very narrow trait area indicating very low inter-annual variation. This holds despite a substantial increase in biomass and change in its functional properties and the change in the trophic state from more eutrophic to mesotrophic conditions.

Considering intra- rather than inter-annual variability, the rate of change of the community trait mean was high prior to and after the clear water phase. Thus, the community trait mean shifted rapidly towards and away from the clear water conditions, supporting our second hypothesis that the phytoplankton community changed rapidly and unidirectionally to pronounced changes in environmental forcing by shifting its community trait mean. In general, shifts in the community trait mean were the result of simultaneous changes in several traits. That is, they cannot be attributed to one individual trait. In addition to changes in environmental forcing the rate of change of the community trait mean may also be influenced by the generation time of the component

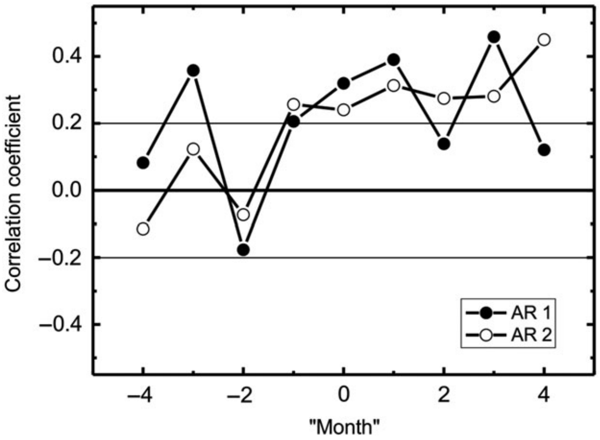

Fig. 4. Autocorrelation coefficient from temporal Lag 1 and Lag 2 distances of the community trait mean in the trait space. Values above 0.2 (thin line) indicate significant positive autocorrelation.

organisms as it originates from species sorting, i.e. the differential growth and decline of species with different trait values. Short generation times facilitate such recurrent fast trait changes, which was fulfilled for Lake Constance as indicated by a high ratio between primary production and phytoplankton biomass (Rocha *et al.* 2011b). It was high during spring, reached its maximum during the clear water phase (mean value 0.6 day^{-1}, Boit and Gaedke, 2014) and declined steadily thereafter. Furthermore, a potential for fast temporal trait changes demands sufficient standing trait variation or immigration. Standing trait variation was high during late spring but it declined strongly during the clear water phase (Weithoff *et al.*, 2015). Nevertheless, trait changes remained fast directly after the clear water phase. This may be due to an increase of functionally divergent phytoplankton types such as large pennate diatoms and dinoflagellates from e.g. cysts or deep waters. Such an increase was sufficient to alter the community trait mean pronouncedly given the small biomass of the resident community during the clear water phase.

The trophic state of Lake Constance had a marked impact on the phytoplankton community trait mean. In the early, more eutrophic years, the area in the trait space occupied during late summer/autumn was quite different from the area occupied in late, nutrient-poor years (See top area in Fig. 3A and Fig. 4). The phytoplankton community in summer/autumn was dominated by cryptophytes and pennate diatoms throughout the investigation period. Thus, smaller changes in relative abundances, e.g. a decline of large chlorophytes and an increase in mixotrophic dinoflagellates and chrysophytes, led to the separation of the community trait mean. This supports our hypothesis that differences in trophic state become apparent during the period when nutrients were depleted. We found weak evidence that the phytoplankton community was already affected by the reduced phosphorus levels during the spring bloom in the later years (Fig 4). The molar phytoplankton C:P ratio during the spring bloom in 1995, i.e. at more oligotrophic conditions, increased to more than 400 but reached a maximum of almost 750 later in the year (Hochstädter, 2000).

The highest inter-annual variation in the community trait mean occurred during the spring bloom towards the clear water phase (Fig. 1B). This is in line with other studies also exhibiting the maximum inter-annual variation in e.g. biomass, chlorophyll a concentration or primary production during this time (Gerten and Adrian, 2000; Rocha *et al.*, 2011b) that is particularly sensitive to altering weather conditions. We could only weakly attribute the high inter-annual variability to our indicator of spring weather conditions, i.e. the type of herbivory. We found no significant differences in the trajectories during spring, potentially because differences diminished under more oligotrophic conditions when the spring bloom was also affected by phosphorus depletion. Furthermore, daphnid biomass did not change gradually in contrast to the total phosphorus concentration. As hypothesized, the trajectories converged towards the clear water phase, when daphnids generally dominated and remained similar later in the year. The different herbivorous groups ciliates, rotifers, calanoid copepods and cladocerans, show a large overlap in their food spectrum. Differences lie e.g. in the degree of selectivity (high in ciliates, e.g. Sanders, 1988; Kivi and Setälä, 1995) or in the capability to use additional resources such as bacteria (e.g. Geller and Müller, 1981). This might explain why the herbivore type has a limited impact on the community trait mean. Furthermore, although daphnid biomass is directly linked to influential factors for spring phytoplankton growth such as light, temperature, mixing intensity, it cannot fully reflect all aspects of spring climate variation.

CONCLUSION

Our data support the conceptual framework of trait-based ecology at the community level that the dominant functional trait values systematically track alterations in environmental conditions. This leads to predictable trajectories in the trait space under recurrently changing conditions. The approach applied here allowed for the detection of differences in the trajectories of the community trait mean according to lake trophic state and resulting nutrient depletion later in the year and to a lesser extent to climate manifested in type of herbivory before the clear water phase. Furthermore, strong environmental forcing during the clear water phase caused a recurrent, directed shift in the community trait mean to a narrow area in the trait space. The community trait mean changed most rapidly during rapidly changing herbivory and similarly fast with the relaxation of the grazing pressure. This confirms that findings derived for population genetics also hold at the community level where changes in trait means originate from species sorting. Thus, our data support trait-based modeling approaches in that strong directional selection leads to fast changes of the mean trait values in a community context.

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SUPPLEMENTARY DATA

Supplementary data are available at *Journal of Plankton Research* online.

DATA ARCHIVING

We are in the process of depositing the data in a collaborative lake data base in the context of a DFG-funded project (GA 401/30-1).

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