First publ. in: Ecology Letters ; 16 (2013), 1. - S. 81-89

Compensatory dynamics and the stability of phytoplankton biomass during four decades of eutrophication and oligotrophication

Marc C. Jochimsen,[1] Reiner Kümmerlin,[2] and Dietmar Straile[1]*

[1]Limnological Institute, University of Konstanz, Konstanz, 78464, Germany
[2]Institut für Seenforschung, Langenargen, 88085, Germany

**Correspondence: E mail: dietmar. Straile@uni konstanz.de*

Abstract

The link between compensatory dynamics and regime shifts is not well understood. We analyse a regime shift in phytoplankton in a large lake with respect to: (1) environmental forcing and (2) the type of dynamics (compensatory or synchronous) between phytoplankton groups. The regime shift in phytoplankton was related to gradual changes in nutrient levels, but unrelated to an almost concurrent shift in climatic conditions. The relationship between total phytoplankton biomass and phosphorus concentrations was sigmoid. Trajectories of phytoplankton biomass and community dynamics suggest that eutrophication effects can successfully be reversed when management efforts decrease nutrient loading to a level sufficiently low to overcome community resilience. The regime shift was associated with a loss of biomass compensation and compensatory dynamics among the phytoplankton groups. This suggests that the type of interactions is important for a better understanding of the existence and shape of nonlinear responses of phytoplankton biomass to environmental change.

Keywords

Biomass compensation, climate warming, community dynamics, functional diversity, nonlinear response, regime shift, resilience, reversibility of anthropogenic change, trophic state.

INTRODUCTION

Human activity during the past century has put increasing stress on natural ecosystems in almost all habitats on the earth (Vitousek *et al.* 1997; Jackson *et al.* 2001; Smith & Schindler 2009). During the last decade, it has become increasingly clear that ecosystem responses to stress are often nonlinear and may involve abrupt changes or even catastrophic shifts after critical environmental conditions have been surpassed (Scheffer *et al.* 2001). The specific response trajectories to environmental change, i.e. smooth, abrupt or catastrophic, also have major implications for the system's ability to recover from stress or disturbance (Duarte *et al.* 2009).

The response of food webs and communities to environmental change is mediated by their properties, including their taxonomic and functional diversity and types of species interactions. For example, important factors and processes contributing to the stability of ecosystem functioning are biodiversity via, e.g. portfolio effects (Schindler *et al.* 2010) and response diversity (Elmqvist *et al.* 2003) and the existence of compensatory dynamics between different populations (Gonzalez & Loreau 2009). In a changing environment, abundance decreases of species susceptible to a specific environmental driver may be compensated by increased growth of less sensitive taxa. An abrupt shift in ecosystem response to environmental change therefore may be the consequence of the decline of the compensatory capacity of the community. While there are studies showing that compensatory dynamics in response to environmental change or variability exist in natural communities (Fischer *et al.* 2001; Bai *et al.* 2004; Gonzalez & Loreau 2009), there is hardly any study in which fast shifts in ecosystem states are linked to the existence, decrease and final collapse of compensatory dynamics.

Lake communities provide classical examples for abrupt shifts in ecosystem status and multiple attractors caused by changes in nutrient influx (Scheffer *et al.* 2001; Scheffer & Carpenter 2003; Carpenter 2005). Resilience of phytoplankton communities to respond to management efforts reducing nutrient inflow into lakes has been observed in many studies (e.g. Jeppesen *et al.* 2005). Typically, responses of phytoplankton biomass to nutrient reductions lagged behind several years and presumably occurred only once nutrient loading or concentration fell below a critical level. The total phytoplankton biomass and its dynamics are aggregate, respectively, emergent properties of the dynamics of individual phytoplankton taxa. Hence, analysing the dynamics of different phytoplankton groups is crucial for understanding the dynamics and responses of total phytoplankton biomass. Phytoplankton communities are known to be rich in both species and functional types, and many laboratory experiments have shown that they are strongly structured by competition and can show a high response diversity (e.g. Sommer 1989 and references therein). A resilience of phytoplankton biomass to directly track decreasing nutrient levels might suggest that declines of sensitive species are compensated by opposing responses of more tolerant taxa, thereby buffering the effects of environmental change. A time delayed response of total biomass might then indicate that the remaining capacity of the community to compensate for biomass declines of some taxa is not strong enough any more to maintain community stability. Here, we test this hypothesis with the analysis of an exceptional long term data set of phytoplankton sampled in Lake Constance over 43 study years. Lake Constance is of outstanding importance as a recreational site and as one of the most important drinking water reservoirs in Europe, providing water for about 4 million people. Severe eutrophication of the lake during post war industrialisation was stopped at the end of the 1970s, and finally reversed with a comprehensive sewage purification programme for the whole catchment area at a cost of more than 4 billion US $. The 43 years considered in this study cover the last 15 years of the eutrophication period of Lake Constance, its peak and 28 year period of subsequent oligotrophication. Hence, these data provide a unique possibility to examine: (1) the potential resilience of phytoplankton response to nutrient changes, (2) the role of phytoplankton interactions in this response and (3) whether this response was characterised by hysteresis, i.e. differing biomass and community trajectories during eutrophication and oligotrophication.

MATERIAL AND METHODS

Study site and sampling

Lake Constance is a deep (z_{mean} = 101 m) warm monomictic lake in central Europe. As a proxy of the lake's trophic status in each specific sampling year, we used the total phosphorus concentration measured during the February/March mixing period (TP_{MIX}, Fig. 1a). In total, 1040 phytoplankton samples were taken from 1965 to 2007 at the centre of Upper Lake Constance. For details on phytoplankton sampling procedures and measurements of TP and water temperature (WT), see Appendix S1. Phytoplankton species were grouped into eight major taxonomic groups: Cyanobacteria, Chrysophyta, Cryptophyta, Dinophyta, Chlorophyta, Conjugales and two orders of Bacillariophyceae, Centrales and Pennales. All statistical analyses were done at this taxonomic level. This phylogenetic grouping is a close analogue to a functional grouping, as these groups differ in important functional features like size, motility, nutrient requirements and uptake kinetics and importance of different nutrition modes (photoautotrophy or mixotrophy) (Litchman *et al.* 2007).

Statistical methods

We tested for the occurrence of a regime shift in our time series using Rodionov's regime shift detection method (RRSD, Rodionov 2004). As this test indicated a regime shift for WT and phytoplankton biomass, we fitted these long term developments with a modified logistic function, which connects two stable periods by a transitional period. The relationship of annual mean phytoplankton biomasses (and biomass lagged by 2 years) to TP_{MIX} and WT was analysed with generalised additive models (GAMs) (Wood 2006). To analyse whether phytoplankton groups displayed compensatory, independent or synchronous dynamics during distinct time periods, we calculated two related metrics, the variance ratio (VR) (Schluter 1984) and ϕ_P (Loreau & Mazancourt 2008). Both metrics relate the variance of the community biomass to the variances of the biomasses of individual taxa within the community. A VR of 1 occurs when taxa fluctuate independently or when positive and negative covariances between species neutralise each other exactly (Gonzalez & Loreau 2009). A VR > 1 indicates that the sum of covariances among taxa is positive (synchronous dynamics), whereas a VR < 1 (compensatory dynamics) occurs when the sum of covariances is negative. In contrast, ϕ_P is standardised between 0 and 1, denoting perfect compensatory and

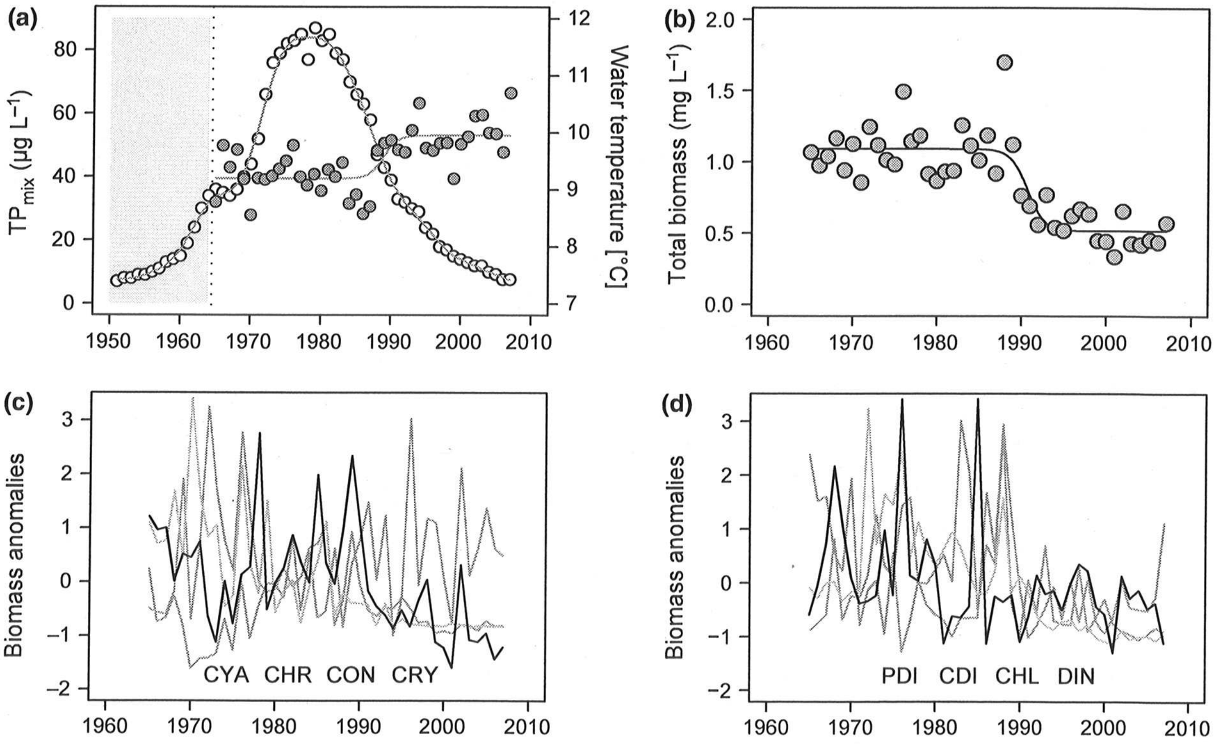

Figure 1 Temporal development of (a) total phosphorous concentrations during winter mixis (open symbols) and annual average water temperatures (blue line and dots), (b) total phytoplankton biomass, (c) anomalies of the biomasses of cyanophytes (CYA), chrysophytes (CHR), Conjugales (CON) and cryptophytes (CRY) and (d) biomasses of pennate diatoms (PDI), centric diatoms (CDI), chlorophytes (CHL) and dinophytes (DIN). No phytoplankton data were available for the time period shaded in panel 1a. The temporal development of water temperature and phytoplankton biomass was fitted with a modified logistic function: $Y_t \quad a + b\frac{e^{T \quad t}}{1+e^{T \quad t}}$ with parameter estimates of a 9.95 ± 0.09 SE, b 0.76 ± 0.12 SE and T 1989 ± 1 SE for water temperature and a 0.51 ± 0.05 SE, b 0.58 ± 0.06 SE and T 1991 ± 1 SE for phytoplankton biomass.

perfect synchronous dynamics respectively. We calculated VR and ϕ_P for the total time series and for subperiods. To analyse to which extent these metrics are scale dependent, i.e. sensitive to the length of the analysis period, and the range of environmental conditions encountered, we performed an 'expanding window' analysis: we first calculated both community metrics for the time period from 1965 to 1975. Then the calculation window was continuously expanded by one additional study year until the full time series was included. The temporal dynamics of the type of community interactions during the study period were investigated via performing an 11 year 'moving window' analyses of VR and ϕ_P. Bray Curtis dissimilarities between the study years were used as a basis for non metric multidimensional scaling (NMDS) ordination and to test for relationships between community dissimilarity and differences in TP_{MIX} between years (Mantel test). For details on the calculation of community metrics and statistical analyses, see Appendix S1.

RESULTS

During the first 15 years of the study period, phosphorus concentrations during the winter mixing period (TP_{MIX}) increased twofold to a maximum of 87 μg TP L^{-1}, followed by a subsequent approximately tenfold decrease towards the most recent years (Fig. 1a). Epilimnetic WT increased during the study period ($\tau = 0.32$, $P < 0.005$). However, this increase was not gradual, but included a rather steep change in 1988 (Fig. 1a, RRSD, $P < 0.0001$). The annual average of phytoplankton biomass was remarkably stable during the first two decades of the study period (Fig. 1b). Thereafter, biomass declined within a few years approaching a new phase of stable, but lower biomass since the mid 1990s. RRSD suggests the existence of one regime shift in the time series occurring in 1990 ($P < 0.0001$), i.e. 2 years after the shift of WT. The timing of the biomass shift was also supported when fitting a modified logistic function, which indicated an inflection point in 1991 (Fig. 1b) and stable biomasses until approximately 1986, and again from approximately 1996 onwards. These two periods of relative biomass stability will be referred to in the following as 'high biomass period' (HBP) and 'low biomass period' (LBP) respectively. Taxonomic groups differed strongly in their temporal dynamics showing biomass decreases (cyanophytes, chlorophytes, conjugatophytes and centric diatoms), biomass increases (chrysophytes) as well as complex dynamics (pennate diatoms, cryptophytes and dinophytes) (Fig. 1c,d). However, with the exception of pennate diatoms, biomasses of all groups differed significantly between HBP and LBP (*t* tests, all $P < 0.05$)

Biomasses of all phytoplankton taxa with the exception of dinophytes were significantly related to TP_{MIX} (Table 1, Appendix S2), but not to WT in the full model (Table 1). Removing TP_{MIX} from the models strongly reduced deviances and changed the e.d.f.'s, i.e. the form of the biomass WT relationships (Table 1). In contrast, removing WT from the full models did neither significantly reduce deviances nor changed the e.d.f.'s of the biomass TP_{MIX} relationships (Table 1). This suggests that the significance of WT biomass models for some taxa is spurious and most likely results from the negative correlation between TP_{MIX} and WT ($r = -0.6$, $P < 0.001$).

The type of biomass relationships with TP_{MIX} varied strongly between the different algal groups, i.e. from a linear biomass increase with increasing TP_{MIX}, saturating or sigmoid relationships,

Table 1 Summary of GAMs relating phytoplankton biomasses of total phytoplankton (TOTAL) and of the different phytoplankton groups to TP_{MIX} and WT (full model) and to TP_{MIX} and WT separately

		TP_{MIX}		WT		
Taxon	model	e.d.f.	*F*	e.d.f.	*F*	dev. expl.
TOTAL	full	2.89	33.3 ***	2.8 e 05	3e 06 ns	75.8%
	TP_{MIX}	2.89	33.3 ***			75.8%
	WT			0.94	16.45 ***	29.8%
CYA	full	2.54	21.9 ***	0.69	2.26 ns	69.9%
	TP_{MIX}	2.43	26.2 ***			67.2%
	WT			1.8	4.28 *	23.7%
CHR	full	0.91	10.2 **	7.1 e 06	3 e 06 ns	21.3%
	TP_{MIX}	1.60	5.2 **			23.5%
	WT			1.39	2.7 ns	14.4%
CDI	full	0.98	46.8 ***	1.8 e 06	2 e 07 ns	53.8%
	TP_{MIX}	0.98	46.8 ***			53.8%
	WT			1.81	4.70 *	24.4%
PDI	full	2.97	2.8 *	1.51	2.02 ns	36.1%
	TP_{MIX}	3.37	3.1 *			30.2%
	WT			1.64	1.7 ns	12.7%
DIN	full	0.65	1.9 ns	1.5 e 06	8 e 08 ns	5.83%
	TP_{MIX}	0.65	1.9 ns			5.83%
	WT			4.40	2 e 05 ns	0.00%
CRY	full	2.38	11.8 ***	2.6 e 05	2 e 06 ns	49.0%
	TP_{MIX}	2.38	11.8 ***			49.0%
	WT			0.89	8.14 **	18.1%
CHL	full	3.12	45.5***	0.98	0.51 ns	86.8%
	TP_{MIX}	3.07	60.0 ***			85.7%
	WT			2.23	7.91***	39.0%
CON	full	2.77	14.8***	0.67	2.04 ns	71.4%
	TP_{MIX}	2.84	24.7 ***			69.7%
	WT			0.96	25.86 ***	39.5%

Abbreviations used for phytoplankton groups are: cyanophytes (CYA), chrysophytes (CHR), centric diatoms (CDI), pennate diatoms (PDI), dinophytes (DIN), cryptophytes (CRY), chlorophytes (CHL) and Conjugales (CON). For all variables in the models, the estimated degrees of freedom (e.d.f.) and F values with corresponding significance levels (***$P < 0.001$, **$P < 0.01$, *$P < 0.05$, n.s. $P > 0.05$) are shown. Model performance is indicated by the deviance explained (dev. expl.) of the respective models.

decreases with increasing TP_{MIX}, to a complex relationship with a biomass maximum at intermediate TP_{MIX} values (Appendix S2). Total phytoplankton biomass (Fig. 2), i.e. the aggregated property of the biomass responses of the individual taxa, was sigmoidally related to TP_{MIX} (Fig. 2, GAM, e.d.f. = 2.89, $P < 0.0001$), but no relationship with WT was evident (e.d.f. = 2.8×10^{-6}). We also found no convincing evidence for an influence of WT on annual average phytoplankton biomasses when we considered a time lag of biomass of 2 years to account for the shift in WT 2 years before the total phytoplankton biomass shift (Appendix S3).

High biomass period and LBP differed with respect to: (1) the existence of compensatory dynamics and (2) the importance of TP_{MIX} for structuring the phytoplankton community. During HBP, the phytoplankton community showed compensatory dynamics (Fig. 3a) and community change was significantly related to changes in TP_{MIX} (Fig. 3b), whereas during LBP, phytoplankton group biomasses varied independently based on VR, but synchronously based on ϕ_P (Fig. 3a) and their changes were not significantly related to changes in TP_{MIX} (Fig. 3b). Considering the total time series, phytoplankton groups showed significant synchronous dynamics (Fig. 3a) and community dynamics were strongly related to TP_{MIX}

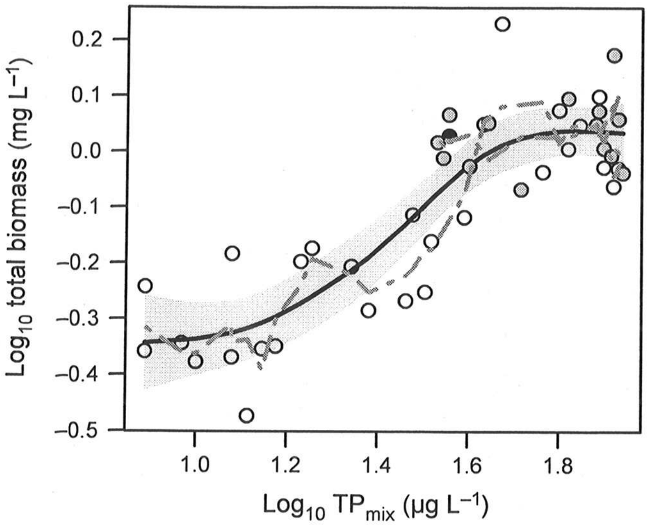

Figure 2 Relationship between $\log_{10}$ transformed total phosphorus concentrations and total phytoplankton biomass. The solid line represents the fit of the generalised additive model (see Table 1). The grey areas represent ± 2 SE of the fit. The dashed grey line indicates the temporal trajectories based on a 3-year moving average. The black dot represents the start of the study period (1965), the grey dots the years of eutrophication and the white dots the subsequent years of oligotrophication.

dynamics (Fig. 3b). Differences in ϕ_P between periods paralleled those observed for VR.

The 'expanding window' analysis shows VRs around 0.5 up to a window, which encompasses the first half of the study period until 1987 (Fig. 3c). The further inclusion of study years afterwards resulted into continuously increasing VRs shifting the dynamics from compensatory towards independent dynamics. Note that compensatory dynamics started to cease in importance prior to the phytoplankton regime shift. After 1997, overall dynamics among the phytoplankton community components became significantly synchronous. The 11 year 'moving window' analysis supports this overall trend towards higher VR values (Fig. 3d). However, this analysis suggests more complex dynamics also within the HBP and LBP and strongest synchronous dynamics during the early 1990s, i.e. during the transition between HBP and LBP. The dynamics of ϕ_P paralleled those of VR, both in the moving window and expanding window analyses (data not shown). Note that both the 'expanding window' and 'moving window' analyses show a rather large increase of VR in 1988 (Fig. 3c, d), which is caused by the peak of total biomass occurring in this year (Fig. 1b). Overall VR dynamics were, however, not strongly influenced by this specific year, which can be demonstrated by substituting the biomass values of 1988 with average values from 1987 and 1989 (see Appendix S4).

Biomass trajectories, shown as 3 year running means (Fig. 2, Appendix S2), suggest that biomass responses to TP$_{MIX}$ of all taxonomic groups at TP$_{MIX}$ values > 40 μg L^{-1} did not depend on whether TP$_{MIX}$ was increasing or decreasing. This is supported by the residuals of the GAM smooths, which did not exhibit a significant temporal trend (all $P > 0.05$, except for Conjugales and Cryptophytes). Likewise, analyses at the community level do not suggest

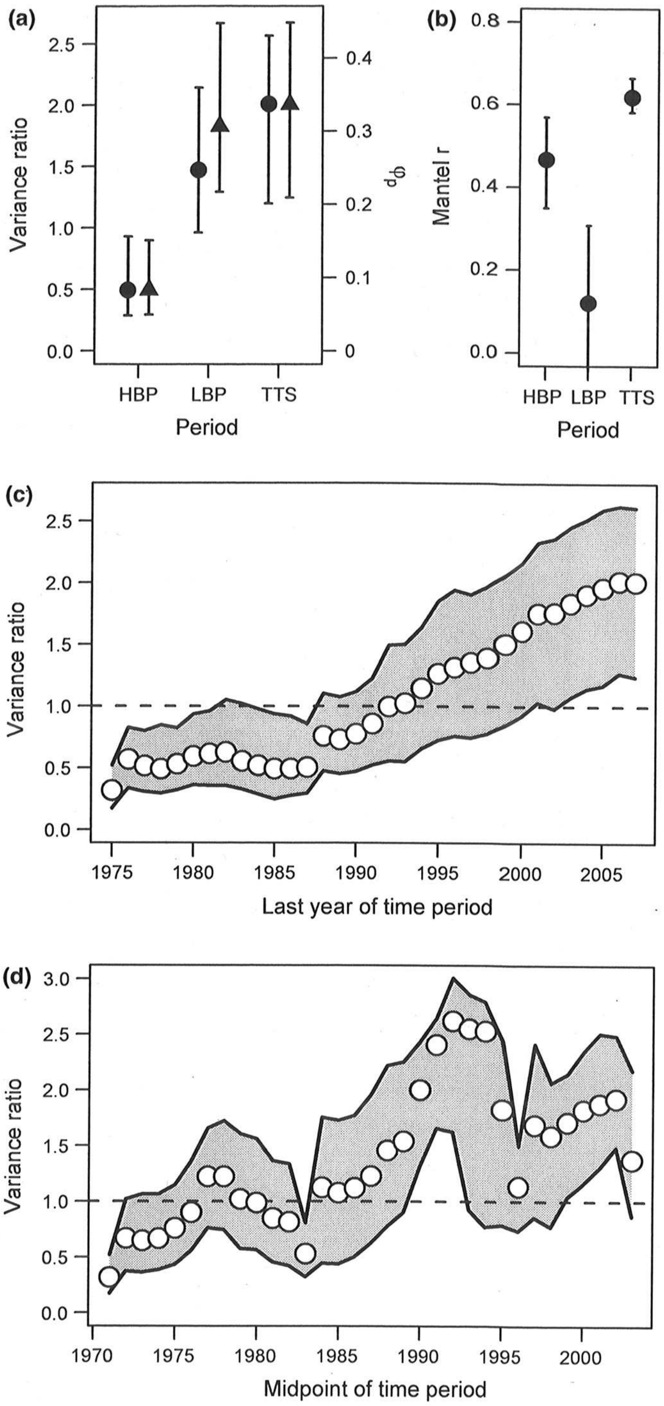

Figure 3 (a) Variance ratio (circles) and ϕ_P (triangles) during the high (HBP) and low biomass periods (LBP) and for the total time series (TTS), (b) Mantel r (± 1SE) relating changes in phytoplankton community composition to changes in TP$_{MIX}$ during the HBP, LBP and TTS, (c) 'expanding window' analysis of variance ratios and (d) 11-year 'moving window' analysis of variance ratios. In (c), the last year of the expanding window (first year always 1965) is shown on the x-axis. In (d), the midpoint of the moving window is shown on the x-axis. Vertical lines and shaded areas represent 95% bootstrap confidence intervals. The vertical dashed line at VR = 1 indicates independent dynamics.

different community states during eutrophication and oligotrophication at TP_{MIX} levels above 40 μg TP L^{-1}. The NMDS ordination clearly separated the most eutrophic from the most oligotrophic study periods, but suggests a similar community composition in both periods with mesotrophic conditions, i.e. the years 1965 1972 during eutrophication and the years 1984 1996 during oligotrophication (Fig. 4a). The reversal of community composition is also evident in the development of Bray Curtis dissimilarities of the first 3 years with the following years until 1990 (Fig. 4b). Dissimilarities to these first years strongly increased until peak eutrophication and then started to decrease again, resulting in a highly significant quadratic relationship with time (all three adjusted $R^2 \geq 0.3$, $P < 0.01$). As a consequence, dissimilarities of the years 1965 1967 with the year 1968 were very similar to those with the year 1990, as were TP_{MIX} values (1968: 36 μg/L, 1990: 39 μg/L).

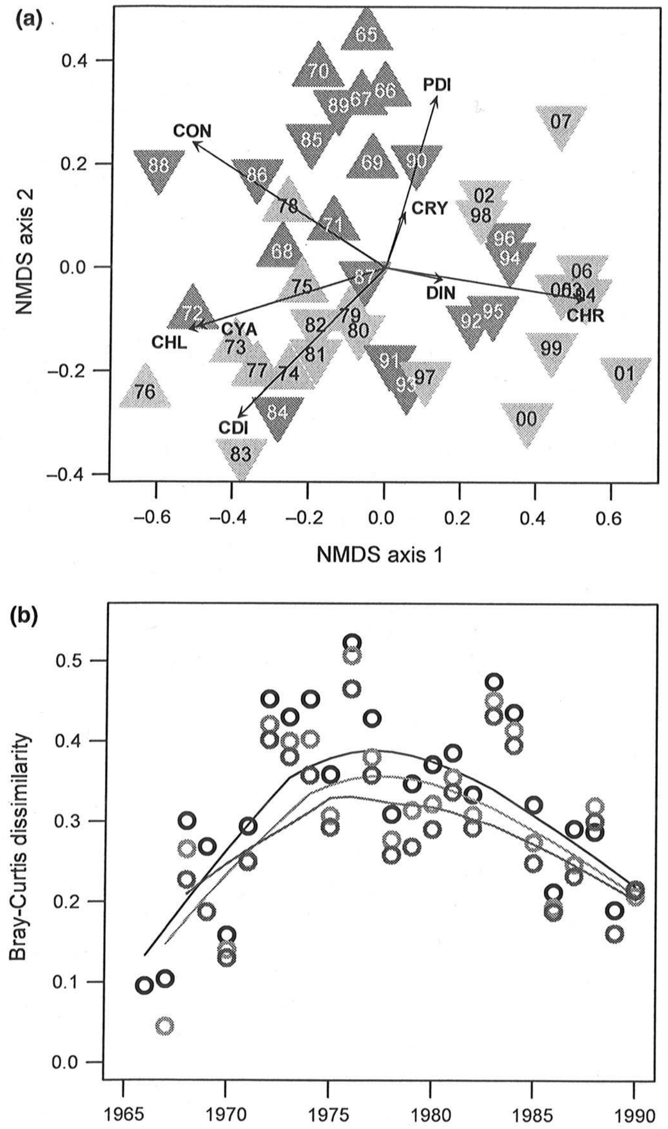

Figure 4 (a) NMDS ordination of study years based on Bray Curtis dissimilarities of phytoplankton groups (stress 0.135). Eutrophic years are shown as green, mesotrophic years as dark blue and oligotrophic years as light blue triangles. The years from 1965 to 1979 are shown as upward triangles (eutrophication years), the year from 1980 to 2007 as downward triangles (oligotrophication years). The arrows show the ordination of the different phytoplankton groups: for abbreviations see Fig. 1. (b) Bray Curtis dissimilarities of phytoplankton composition in the year shown on the x axis with the phytoplankton composition in 1965 (black), 1966 (red) and 1967 (blue). Lines represent loess fits.

DISCUSSION

Using a four decade data set on phytoplankton dynamics, we show that a gradual change in nutrient availability of over one order of magnitude during eutrophication and subsequent oligotrophication was associated with a strong and fast decline of biomass within a few years. Such a rapid decline is a regime shift *sensu* Scheffer & Carpenter (2003) and Andersen *et al.* (2009). To demonstrate bistability, i.e. the existence of two locally stable stationary states in a dynamical system, a data set with several shifts between two different states would be necessary (Scheffer & Carpenter 2003; Andersen *et al.* 2009). The sudden shift in phytoplankton biomass, i.e. the regime shift observed in Lake Constance separated two stable periods of annual average phytoplankton biomass, but is not sufficient evidence for bistability.

The regime shift occurred concurrently with the disappearance of both, biomass compensation, i.e. the adjustment of total biomass to environmental change, and compensatory dynamics between different phytoplankton groups. This might suggest that: (1) the maintenance of the community's capacity for biomass compensation and compensatory dynamics and (2) after a critical nutrient level was surpassed, the lack of compensation, and loss of compensatory dynamics, were key mechanisms leading to the phytoplankton biomass regime shift in Lake Constance. During the high biomass state, TP_{MIX} encompassed a range between 35 and 87 μg L^{-1} and shifted from mesotrophic to eutrophic conditions and back. During this time period, community change was strongly related to changes in TP_{MIX}, i.e. increases of some taxa with increasing nutrients were offset by decreases of other taxa resulting in a remarkable resilience of phytoplankton biomass. After the end of the period with significant compensatory dynamics, biomass dropped to 47% within a few study years, although during this time TP_{MIX} decrease did not accelerate. The magnitude of this regime shift is large compared to regime shifts observed in other large aquatic ecosystems. For example, recent, presumably climate related, regime shifts in the equatorial Pacific and the North Sea were associated with a 36% decline in phytoplankton biomass in the former case (Chavez *et al.* 2003), and a 13 21% increase in the latter case (McQuatters Gollop *et al.* 2007). Likewise, the invasion of Flathead Lake by opposum shrimp was suggested to have shifted primary productivity upward by 21% (Ellis *et al.* 2011). More data are needed to see whether there is a relationship between a community's capacity for compensation and the magnitude of the regime shift after an environmental threshold has been surpassed.

The shift in water temperatures observed in Lake Constance is also found in other aquatic habitats, e.g. lakes (Anneville *et al.* 2005), rivers (Hari *et al.* 2006), marine sites (Alheit *et al.* 2005) and even groundwater (Figura *et al.* 2011), and triggered by variability of the Arctic Oscillation (Figura *et al.* 2011). In Lake Constance, the regime shift of total phytoplankton biomass was statistically unre lated to this shift of water temperatures, but instead related to gradual changes in TP_{MIX}. Furthermore, the observed patterns of phytoplankton biomass and composition are largely opposite to those expected from warming, as it is generally believed that warming will resemble and intensify effects of eutrophication on food webs (Moss *et al.* 2011) and result in e.g. higher biomasses of cyanobacteria (Paerl & Huisman 2008). More importantly, there is no convincing mechanistic explanation on why fast growing phytoplankton should decrease only with a delay of 2 years in response to increased water temperatures: (1) surface temperatures of Lake Constance never exceeded 24 °C, which suggests that the step wise increase of 0.7 °C was unlikely to result in temperatures exceeding algal physiological optima, thereby reducing their growth rates, (2) Likewise, this increase will have only a small effect on zooplankton feeding rates and cannot overcompensate for the decline of herbivores with oligotrophication (Appendix S5), (3) Warming did not result in a reduced length of the stratification period and (4) We also found no evidence for a role of enhanced stratification and subsequently reduced nutrient transport to the epilimnion for the phytoplankton decrease, e.g. substituting a measure of water column stability, the Schmidt stability, for WT in GAMs did not improve model performance related to models only considering TP_{MIX} as an independent variable (statistical analyses not shown). Note that our results do not imply that warming has no influence on the plankton succession and the pelagic food web of Lake Constance, which is clearly not the case (e.g. Straile *et al.* 2010). However, this influence seems not to be detectable on the scale of interest in this study, i.e. annual averages of phytoplankton biomass within the upper 20 m of the water column. At this scale, biomass dynamics seem to be driven strongly by changes in the trophic status of the lake. This result, derived from the GAM models, is furthermore strongly consistent with longitudinal and cross sectional field data (e.g. Watson *et al.* 1997; Jeppesen *et al.* 2005), as well as laboratory experiments (Sommer 1989) with respect to relative phytoplankton occurrence and performance patterns. To summarise, the decrease of phytoplankton biomass in Lake Constance is statistically unrelated to and although we cannot fully exclude a role of temperature in, e.g. triggering the timing of the regime shift unlikely caused by the step wise increase of water temperatures in 1988 in this lake. Hence, our results support Scheffer & Carpenter (2003) suggesting that factors slowly undermining resilience such as steady nutrient influx may be as important causes for regime shifts as more stochastic events like climate anomalies and/or species invasions. Similarly, regime shifts in other ecosystems should not be uncritically attributed to changes in climate even when there is an almost concurrent climatic shift, as in the case of Lake Constance.

Phytoplankton community dynamics clearly differed during both stable states. The HBP was characterised by compensatory dynamics among the phytoplankton taxa and year to year community dissimilarities were related to TP_{MIX} differences. During the LBP, neither compensatory dynamics nor a relationship of community dynamics to TP_{MIX} was observed (Fig. 3a,b).This is in accordance with recent results from grassland experiments where stronger compensatory dynamics were observed in fertilised communities (Grman *et al.* 2010). In contrast, in a microcosm experiment, phytoplankton species showed higher compensatory capacity at low nutrient availability (Zhang & Zhang 2006). However, these results might be less relevant for functionally diverse natural phytoplankton communities, because only six chlorophyte species were used as a model community. That said, our data and these experiments clearly show that the occurrence of compensatory dynamics is context dependent and that nutrient availability is an important factor regulating the type of interactions in algae and plant communities.

Our study also highlights the scale dependency of the relationship between compensatory dynamics and biomass compensation and also of the occurrence of compensatory dynamics. Compensatory dynamics and biomass compensation are tightly related concepts, but their occurrence within a community is not necessarily linked, i.e. compensation can occur in the presence or absence of compensatory dynamics, and vice versa (Gonzalez & Loreau 2009). In our case, this relationship changes depending on the length of the time series considered: During the HBP, compensation was associated with compensatory dynamics, during the LBP, compensation was associated with independent or even synchronous dynamics of phytoplankton groups, whereas when considering the whole time series, synchronous dynamics were associated with the lack of compensation, i.e. a regime shift. Thus, considering the complete study period, our results seem to support a recent review suggesting that compensatory dynamics are rare in nature (Houlahan *et al.* 2007). However, this conclusion based on the prevalence of positive covariances in community time series has been suggested to be premature (Gonzalez & Loreau 2009) because positive covariances can be consistent with compensatory dynamics (Loreau & Mazancourt 2008) and because scale resolving methods, i.e. methods that allow the simultaneous consideration of different time scales, may be necessary to detect compensatory dynamics (Vasseur *et al.* 2005). Our study demonstrates that the occurrence of compensatory dynamics depends also on the scale of environmental change. Changes in the type of community dynamics, i.e. a shift towards synchronous dynamics within a zooplankton community were also observed in response to acidification (Keitt 2008). In our study, only during a specific range of phosphorus concentrations, some phytoplankton taxa were able to compensate for the decline of less tolerant taxa, whereas after a critical phosphorus threshold was passed, community dynamics became synchronous. Hence, during the high biomass state, strong compensatory dynamics of phytoplankton in response to gradual environmental change existed. Indeed, strong 'out break' compensatory dynamics are predicted to occur when there are high levels of autocorrelation in the environment (Gonzalez & Loreau 2009). Under these circumstances, the detection of compensatory dynamics seems to be possible even without the use of scale resolving methods.

The loss of compensatory dynamics with oligotrophication may be caused by a change in the dominance pattern of factors limiting phytoplankton growth occurring during the transition from the high biomass towards the low biomass state. Large phytoplankton blooms in the HBP led to strong depletion of silicate and CO_2 and increased light attenuation within the water column (Appendix S5). In the LBP, phosphorus concentrations were strongly limiting throughout most of the season (Anneville *et al.* 2005), and low phytoplankton abundances were less able to reduce the availability of silicate, carbon and light (Appendix S5). Simultaneously, daphnids declined during oligotrophication in Lake Constance (Stich & Brinker 2010) indicating that also grazing losses decreased (Appendix S5). Consequently, the system shifted from a multifactorial control during the HBP (Sommer 1987), in which the controlling factor probably differed between phytoplankton groups (see below), to a strong bottom up control dominated by phosphorus limitation for most phytoplankton groups.

Despite the loss of compensatory dynamics, total phytoplankton biomass was also rather stable in the low biomass period. The resilience of phytoplankton to further track the threefold decline of TP_{MIX} after the mid 1990s might possibly be the result of reduced daphnid grazing, which declined threefold from the early 1990s towards 2007 (Stich & Brinker 2010), i.e. a decline exceeding that of phytoplankton biomass. As a consequence, the *Daphnia* abundance/phytoplankton biomass ratio decreased (Appendix S5). This might suggest that the main factor contributing to overall phytoplankton biomass resilience shifted from algal algal interactions during the high biomass state to algal zooplankton interactions in the low biomass state. This pattern is partially consistent with food chain theory, which predicts a shift in the importance of bottom up to top down control in structuring communities with changing ecosystem productivity (Oksanen *et al.* 1981).

Our results also have important implications for the management of lake ecosystems. When considering the range from ultra oligotrophic to hypereutrophic trophic states, the relationship between phosphorus concentrations and phytoplankton biomass (Watson *et al.* 1992), or phosphorus concentrations and chlorophyll (McCauley *et al.* 1989) among lakes has been shown to follow a sigmoid form with nitrogen limitation resulting in a plateau of the phosphorous biomass relationship at TP levels exceeding approximately 1000 $\mu g\ L^{-1}$. Our study is the first demonstrating such a sigmoid relationship for an individual lake. However, in Lake Constance, the plateau, or carrying capacity with respect to phosphorus is not due to nitrogen limitation (Sommer 1987), but rather due to a multitude of limiting factors (see above, Appendix S5, Sommer 1987), which most likely affect the various phytoplankton groups differently and thereby induce a variety of individual responses of the algal taxa leading to the observed compensatory dynamics. For example, high phytoplankton biomasses during periods of high phosphorus loading can result in silicate limitation for diatoms (Huber *et al.* 2008), CO_2 limitation especially for chrysophytes (Maberly *et al.* 2009), or light limitation, which might first affect chlorophytes, cryptophytes and dinophytes (Schwaderer *et al.* 2011). Clearly, detailed analyses of the relationships between phytoplankton groups and other potential drivers are logical next steps to pursue; such detailed analyses are, however, beyond the scope of this study. Nevertheless, our results indicate that the observed sigmoid phosphorus phytoplankton relationship across lakes (McCauley *et al.* 1989) covering several orders of magnitude of phosphorus and biomass values might be actually composed by a multitude of lake specific sigmoid phosphorus phytoplankton relationships each covering a smaller individual range of phosphorus and biomass values.

Total phytoplankton biomass, the biomass of most taxonomic groups as well as community composition showed a similar response to TP_{MIX} variability independently, whether TP_{MIX} was increasing or decreasing (see trajectories in Figs 2 and 4b, Appendix S2), i.e. there was no strong evidence for hysteresis (Scheffer & Carpenter 2003). Currently, it is unclear to what extent the reversibility of phytoplankton trajectories in Lake Constance is also present at a) a higher taxonomic resolution, e.g. at species level and b) for an extended range of TP_{MIX} values. Diatom species lists from sedimentary records which extend also to time periods prior to the 1960s, i.e. to the pre eutrophication period, show that at least some species (e.g. *Achnanthes minutissima*, *Cyclotella cyclopuncta*, *Tabellaria fenestrata*) which disappeared during eutrophication eventually reappeared in the course of oligotrophication (Kümmerlin 1998). Reversibility of trajectories after a fast recovery from high levels of diffusive nutrient inflow has also been shown for a diatom community in an Irish lake (Donohue *et al.* 2010). Likewise, zooplankton response to fish additions revealed reversibility and smooth transitions between community states (Mittelbach *et al.* 2006). This suggests that community changes that were caused by environmental change might at least partly be reversible also at the species level. On the other hand, microevolutionary adaptation might result into irreversible changes in populations as has been suggested for the cladoceran *Daphnia* in Lake Constance (Brede *et al.* 2009). However, for a diatom species in a Danish fjord, no changes in genetic structure with eutrophication were found (Härnström *et al.* 2011). Hence, it is presently not clear whether and to which extent microevolutionary changes will prevent the reversibility of phytoplankton trajectories. Nevertheless, the results presented in our study seem to be in contrast to the results of Duarte *et al.* (2009), which suggest that phytoplankton trajectories in coastal seas should be characterised as non reversible due to regime shifts and shifting baselines. Rather, the Lake Constance phytoplankton data suggest reversibility despite the occurrence of a regime shift and a shift in baseline temperatures. However, the conclusion of Duarte *et al.* (2009) was not based on statistical analyses but primarily on visual examination of phytoplankton trajectories in four case studies. In deep lakes, the lagged response of phytoplankton biomass during phosphorus decline has also been regarded as evidence for hysteresis (Dokulil & Teubner 2005). However, in almost all deep lakes, high quality data cover mostly the period of oligotrophication, whereas only sparse data document the process of eutrophication. Hence, in most other studies, analyses whether and to which extent the biomass response to oligotrophication really differed from that to eutrophication in deep lakes was not possible. Clearly, there is a need for more data to allow for a robust evaluation regarding the reversibility of phytoplankton trajectories as a consequence of nutrient reduction efforts in these lakes and in other aquatic systems. Likewise, it should be acknowledged that our conclusions should be viewed keeping in mind the general limitations of observational studies. Hence, there is an urgent need to test experimentally whether specific types of community interactions or changes in the type of community interactions may prevent, delay or cause regime shifts.

CONCLUSIONS

Using a unique data set of phytoplankton dynamics covering four decades, we show that compensatory dynamics maintained stable phytoplankton biomasses over a large gradient of phosphorus concentrations. Presumably, only after phosphorus concentrations fell below a critical threshold, compensatory dynamics within the phytoplankton community ceased and consequently biomass dropped to a lower level within a few years. The Lake Constance case study shows that the trajectories of eutrophication can be reversed successfully in deep lakes. However, to reduce phytoplankton biomass, restoration measures needed to overcome the compensatory capacity of the phytoplankton community. Long term changes in the phytoplankton community of Lake Constance hence provide an example showing that continuous environmental change can affect the compensatory capacity of a natural community.

ACKNOWLEDGEMENTS

We thank the Internationale Gewässerschutzkommission für den Bodensee (IGKB) for providing the long term data, and Karl Otto Rothhaupt, Ursula Gaedke, Robert Ptacnik and Ulrich Sommer for discussions and comments on a previous version of the manuscript. We thank Roxana Halbleib for statistical advice and three anonymous referees for insightful comments. Funding was provided by the LUBW, Landesanstalt für Umwelt, Messungen und Naturschutz Baden Württemberg.

AUTHORSHIP

MCJ analysed the data. MCJ and DS wrote the first draft of the manuscript. RK provided the long term data and contributed substantially to revisions of the manuscript.

REFERENCES

Alheit, J., Mollmann, C., Dutz, J., Kornilovs, G., Loewe, P., Mohrholz, V. *et al.* (2005). Synchronous ecological regime shifts in the central Baltic and the North Sea in the late 1980s. *ICES J. Mar. Sci.*, 62, 1205 1215.

Andersen, T., Carstensen, J., Hernandez-Garcia, E. & Duarte, C.M. (2009). Ecological thresholds and regime shifts: approaches to identification. *Trends Ecol. Evol.*, 24, 49 57.

Anneville, O., Gammeter, S. & Straile, D. (2005). Phosphorus decrease and climate variability: mediators of synchrony in phytoplankton changes among European peri-alpine lakes. *Freshw. Biol.*, 50, 1731 1745.

Bai, Y.F., Han, X.G., Wu, J.G., Chen, Z.Z. & Li, L.H. (2004). Ecosystem stability and compensatory effects in the Inner Mongolia grassland. *Nature*, 431, 181 184.

Brede, N., Sandrock, C., Straile, D., Spaak, P., Jankowski, T., Streit, B. *et al.* (2009). The impact of human-made ecological changes on the genetic architecture of *Daphnia* species. *Proc. Natl Acad. Sci. USA*, 106, 4758 4763.

Carpenter, S.R. (2005). Eutrophication of aquatic ecosystems: Bistability and soil phosphorus. *Proc. Natl Acad. Sci. USA*, 102, 10002 10005.

Chavez, F.P., Ryan, J., Lluch-Cota, S.E. & Niquen, M. (2003). From anchovies to sardines and back: Multidecadal change in the Pacific Ocean. *Science*, 299, 217 221.

Dokulil, M.T. & Teubner, K. (2005). Do phytoplankton communities correctly track trophic changes? An assessment using directly measured and palaeolimnological data. *Freshw. Biol.*, 50, 1594 1604.

Donohue, I., Leira, M., Hobbs, W., Leon-Vintro, L., O'Reilly, J. & Irvine, K. (2010). Rapid ecosystem recovery from diffuse pollution after the Great Irish Famine. *Ecol. Appl.*, 20, 1733 1743.

Duarte, C.M., Conley, D.J., Carstensen, J. & Sanchez-Camacho, M. (2009). Return to Neverland: Shifting Baselines Affect Eutrophication Restoration Targets. *Estuaries Coasts*, 32, 29 36.

Ellis, B.K., Stanford, J.A., Goodman, D., Stafford, C.P., Gustafson, D.L., Beauchamp, D.A. *et al.* (2011). Long-term effects of a trophic cascade in a large lake ecosystem. *Proc. Natl Acad. Sci. USA*, 108, 1070 1075.

Elmqvist, T., Folke, C., Nystrom, M., Peterson, G., Bengtsson, J., Walker, B. *et al.* (2003). Response diversity, ecosystem change, and resilience. *Front. Ecol. Environ.*, 1, 488 494.

Figura, S., Livingstone, D.M., Hoehn, E. & Kipfer, R. (2011). Regime shift in groundwater temperature triggered by the Arctic Oscillation. *Geophys. Res. Lett.*, 38, L23401. DOI:10.1029/2011GL049749.

Fischer, J.M., Frost, T.M. & Ives, A.R. (2001). Compensatory dynamics in zooplankton community responses to acidification: Measurement and mechanisms. *Ecol. Appl.*, 11, 1060 1072.

Gonzalez, A. & Loreau, M. (2009). The Causes and Consequences of Compensatory Dynamics in Ecological Communities. *Annu. Rev. Ecol. Evol. Syst.*, 40, 393 414.

Grman, E., Lau, J.A., Schoolmaster, D.R. & Gross, K.L. (2010). Mechanisms contributing to stability in ecosystem function depend on the environmental context. *Ecol. Lett.*, 13, 1400 1410.

Hari, R.E., Livingstone, D.M., Siber, R., Burkhardt-Holm, P. & Güttinger, H. (2006). Consequences of climatic change for water temperature and brown trout populations in Alpine rivers and streams. *Glob. Change Biol.*, 12, 10 26.

Härnström, K., Ellegaard, M., Andersen, T.J. & Godhe, A. (2011). Hundred years of genetic structure in a sediment revived diatom population. *Proc. Natl Acad. Sci. USA*, 108, 4252 4257.

Houlahan, J.E., Currie, D.J., Cottenie, K., Cumming, G.S., Ernest, S.K.M., Findlay, C.S. *et al.* (2007). Compensatory dynamics are rare in natural ecological communities. *Proc. Natl Acad. Sci. USA*, 104, 3273 3277.

Huber, V., Adrian, R. & Gerten, D. (2008). Phytoplankton response to climate warming modified by trophic state. *Limnol. Oceanogr.*, 53, 1 13.

Jackson, J.B.C., Kirby, M.X., Berger, W.H., Bjorndal, K.A., Botsford, L.W., Bourque, B.J. *et al.* (2001). Historical overfishing and the recent collapse of coastal ecosystems. *Science*, 293, 629 638.

Jeppesen, E., Sondergaard, M., Jensen, J.P., Havens, K.E., Anneville, O., Carvalho, L. *et al.* (2005). Lake responses to reduced nutrient loading - an analysis of contemporary data from 35 European and North American long term studies. *Freshw. Biol.*, 50, 1747 1771.

Keitt, T.H. (2008). Coherent ecological dynamics induced by large-scale disturbance. *Nature*, 454, 331 U39.

Kümmerlin, R.E. (1998). Taxonomical response of the phytoplankton community to Upper Lake Constance (Bodensee-Obersee) to eutrohication and re-oligotrophication. *Arch. Hydrobiol. Spec. Issues Advanc. Limnol.*, 53, 109 117.

Litchman, E., Klausmeier, C.A., Schofield, O.M. & Falkowski, P.G. (2007). The role of functional traits and trade-offs in structuring phytoplankton communities: scaling from cellular to ecosystem level. *Ecol. Lett.*, 10, 1170 1181.

Loreau, M. & de Mazancourt, C. (2008). Species synchrony and its drivers: Neutral and nonneutral community dynamics in fluctuating environments. *Am. Nat.*, 172, E48 E66.

Maberly, S.C., Ball, L.A., Raven, J.A. & Sultemeyer, D. (2009). Inorganic Carbon Acquisition by Chrysophytes. *J. Phycol.*, 45, 1052 1061.

McCauley, E., Downing, J.A. & Watson, S. (1989). Sigmoid Relationships Between Nutrients and Chlorophyll Among Lakes. *Can. J. Fish. Aquat. Sci.*, 46, 1171 1175.

McQuatters-Gollop, A., Raitsos, D.E., Edwards, M., Pradhan, Y., Mee, L.D., Lavender, S.J. *et al.* (2007). A long-term chlorophyll data set reveals regime shift in North Sea phytoplankton biomass unconnected to nutrient trends. *Limnol. Oceanogr.*, 52, 635 648.

Mittelbach, G.G., Garcia, E.A. & Taniguchi, Y. (2006). Fish reintroductions reveal smooth transitions between lake community states. *Ecology*, 87, 312 318.

Moss, B., Kosten, S., Meerhoff, M., Battarbee, R.W., Jeppesen, E., Mazzeo, N. *et al.* (2011). Allied attack: climate change and eutrophication. *Inland waters*, 1, 101 105.

Oksanen, L., Fretwell, S.D., Arruda, J. & Niemelä, P. (1981). Exploitation ecosystems in gradients of primary productivity. *Am. Nat.*, 118, 240 261.

Paerl, H.W. & Huisman, J. (2008). Climate - Blooms like it hot. *Science*, 320, 57 58.

Rodionov, S.N. (2004). A sequential algorithm for testing climate regime shifts. *Geophys. Res. Lett.*, 31, Art. No. L09204. DOI: 10.1029/2004 GL019448.

Scheffer, M. & Carpenter, S.R. (2003). Catastrophic regime shifts in ecosystems: linking theory to observation. *Trends Ecol. Evol.*, 18, 648 656.

Scheffer, M., Carpenter, S., Foley, C. & Walker, B. (2001). Catastrophic shifts in ecosystems. *Nature*, 413, 591 596.

Schindler, D.E., Hilborn, R., Chasco, B., Boatright, C.P., Quinn, T.P., Rogers, L. A. *et al.* (2010). Population diversity and the portfolio effect in an exploited species. *Nature*, 465, 609 U102.

Schluter, D. (1984). A Variance Test for Detecting Species Associations, with Some Example Applications. *Ecology*, 65, 998 1005.

Schwaderer, A.S., Yoshiyama, K., De Tezanos Pinto, P., Swenson, N.G., Klausmeier, C.A. & Litchman, E. (2011). Eco-evolutionary differences in light utilization traits and distributions of freshwater phytoplankton. *Limnol. Oceanogr.*, 56, 589 598.

Smith, V.H. & Schindler, D.W. (2009). Eutrophication science: where do we go from here? *Trends Ecol. Evol.*, 24, 201 207.

Sommer, U. (1987). Factors controlling the seasonal variation in phytoplankton species composition - A case study for a deep, nutrient rich lake. *Prog. Phycol. Res.*, 5, 123 179.

Sommer, U. (1989). The role of competition for resources in phytoplankton succession. In *Plankton Ecology: Succession in Plankton Communities*. (ed Sommer, U.). Springer, Berlin, pp. 57 106.

Stich, H.B. & Brinker, A. (2010). Oligotrophication outweighs effects of global warming in a large, deep, stratified lake ecosystem. *Glob. Change Biol.*, 16, 877 888.

Straile, D., Kerimoglu, O., Peeters, F., Jochimsen, M.C., Kümmmerlin, R., Rinke, K. *et al.* (2010). Effects of a half a millennium winter on a deep lake - a shape of things to come? *Glob. Change Biol.*, 16, 2844 2856.

Vasseur, D.A., Gaedke, U. & McCann, K.S. (2005). A seasonal alternation of coherent and compensatory dynamics occurs in phytoplankton. *Oikos*, 110, 507 514.

Vitousek, P.M., Aber, J.D., Howarth, R.W., Likens, G.E., Matson, P.A., Schindler, D.W. *et al.* (1997). Human alternation of the global nitrogen cycle: sources and consequences. *Ecol. Appl.*, 7, 737 750.

Watson, S., McCauley, E. & Downing, J.A. (1992). Sigmoid Relationships Between Phosphorus, Algal Biomass, and Algal Community Structure. *Can. J. Fish. Aquat. Sci.*, 49, 2605 2610.

Watson, S.B., McCauley, E. & Downing, J.A. (1997). Patterns in phytoplankton taxonomic composition across temperate lakes of differing nutrient status. *Limnol. Oceanogr.*, 42, 487 495.

Wood, S.N. (2006). *Generalized Additive Models: An Introduction with R.* Chapman & Hall/CRC, Boca Raton.

Zhang, Q.G. & Zhang, D.Y. (2006). Resource availability and biodiversity effects on the productivity, temporal variability and resistance of experimental algal communities. *Oikos*, 114, 385 396.

SUPPORTING INFORMATION

Additional Supporting Information may be downloaded via the online version of this article at Wiley Online Library (www.ecologyletters.com).

Compensatory dynamics and the stability of phytoplankton biomass during 4 decades of eutrophication and oligotrophication

Marc Jochimsen[1], Reiner Kümmerlin[2] & Dietmar Straile[1]

1 Limnological Institute, University of Konstanz, 78464 Konstanz, , Germany
2 Institut für Seenforschung, 88085 Langenargen, Germany

Appendix A1 Detailed description of material and methods

Sampling of phytoplankton and abiotic parameters - Phytoplankton was sampled from 1965 to 2007 at the centre of Upper Lake Constance. During these 43 years a total number of 1040 phytoplankton samples was taken, which corresponds on average to an approximately half-monthly sampling regime. The seasonal resolution of sampling was higher in the first 4 study years (30-48 samplings per year) and lower in 1972, 1974 and 1975 (13-15 samplings per year). From 1965 – 1975 the phytoplankton sampling procedure comprised discrete depths sampling of the 0-50 m water column with a Ruttner sampler, thereafter the 0-20 m water column was sampled with an integrated Schröder sampler. A depth of 20 m is considered as the maximal vertical extent of the euphotic zone in Lake Constance during eutrophic and mesotrophic years (Tilzer & Beese 1988). To achieve comparability between both sampling methods, biomass estimates until 1975 were adjusted by assuming that phytoplankton was evenly distributed throughout the water column when the water column was fully mixed, but concentrated in the upper mixed layer during the stratified season. We assume that the water column within the upper 50 m is fully mixed if gradients along water temperature profiles did not exceed 1 °C m^{-1}. The extension of the upper mixed layer was estimated from water temperature profiles as the minimum depth (z_{min}) at which a gradient exceeding 1°C m^{-1} occurs. If $z_{min} < 20$m all phytoplankton is assumed to be concentrated in the upper 20 m of the water column, i.e. the water column sampled after 1975. Hence, phytoplankton biomass estimates prior to 1976 were adjusted according to $B_{adj} = B_{0-50} * 50/z_{min}$, with z_{min} varying between 20 and 50.

After fixation in Lugol's iodine solution phytoplankton cells were enumerated using inverted microscopy (Utermöhl 1958) and taxonomically resolved mostly to species or, where not possible, to a higher taxonomic level. For the most part of the study period (1984-2007), one of us (RK) was responsible for counting and identification of the species which ensured the comparability of the data. Abundance estimates were converted to fresh mass based on measurements of species-specific cell volumes, using a specific weight factor of 1.03 g/cm^3 (Hillebrand *et al.* 1999). The response of phytoplankton to changing nutrient concentrations varies seasonally and is expected to be stronger in e.g., summer as compared to spring (Anneville *et al.* 2005;Gaedke 1998). Oligotrophication results in an increase of the seasonal window of limiting phosphorus concentrations from only a short period during summer in eutrophic years towards a longer period encompassing summer and spring during oligotrophic years (Anneville *et al.* 2005). In order to adequately consider also this seasonal increase of the phosphorus limitation window on phytoplankton biomass, we focus our analyses on annual averages of biomasses and not on e.g. summer averages. In order to achieve a homogenous and seasonally balanced data set for the calculation of annual biomass averages, the latter were calculated from a data set linearly interpolated to a evenly spaced matrix of 26 data points per year.

Chemical variables and water temperatures were measured monthly or biweekly (since 1995) at water column depths of 0, 5, 10, 15, 20, 30, 50, 100, 200, and 250 m using standard methods (Rossknecht 1998). Zooplankton samples were collected with net hauls (mesh size 100 μm) from 100m depth (Seebens *et al.* 2007).

Statistical methods – Significance of the water temperature trend was assessed using the trend-free pre-whitening procedure (Yue *et al.* 2002). As a test for the occurrence of a phytoplankton biomass regime shift we used Rodionov's regimes shift detection method (RRSD, Rodionov 2004). Results of the test were robust against reasonable choices of the model parameters, i.e., the minimum regime length (5 - 25 years) and the Huber weight parameter (0.5 - 1). In addition, we fitted the long-term development of total phytoplankton biomass and water temperatures with a modified logistic function,

$$Y_t = a + b\frac{e^{T-t}}{1+e^{T-t}},$$

which connects two periods of stable state variables by a transitional period: Y_t is total phytoplankton biomass, respectively WT in year t, a and b determine the biomasses, respectively WT at the two stable periods, and T denotes the inflection year, i.e., the year with the largest change in Y_t.

The relationship between phytoplankton groups and potential environmental drivers (TP_{MIX} and WT) was analysed using generalized additive models (GAMs) with Gaussian errors and restricted maximum likelihood (REML) as smoothness selection method using the mgcv package within R (Wood 2006). Phytoplankton biomasses and TP_{MIX} were log-transformed to achieve normality and variance homogeneity and to allow for a better comparison with published phytoplankton biomass – phosphorus relationships (Watson *et al.* 1992). GAMs fit smoothing functions of the independent variables and hence permit nonlinear relationship between dependent and independent parameters. The estimated degrees of freedom (e.d.f.) indicate the degree of non-linearity of the GAMs, e.d.f. close to 1 imply linear relationships and e.d.f. > 1 progressively higher-order relationships. e.d.f. close to zero indicate that the estimated smooths for a specific independent variable have been virtually removed from the model. In such cases (when e.d.f. < 0.5) no p – values are reported by the mgcv package because distributional approximations of p – values break down (Wood 2006). When smooths of an independent variable were non-significant or their e.d.f. were close to 0, we refitted the model without them in order to verify that the smooths of the parameters remaining in the models have not changed and model deviances have not strongly increased.

To analyse whether phytoplankton groups displayed compensatory, independent or synchronous dynamics, we calculated two related community metrics, VR (Schluter 1984) and φ_P (Loreau & de Mazancourt 2008). Both metrics relate the variance of the community biomass (C) to the variances of the biomasses of individual taxa (P_i) within the community:

$$VR = \frac{\mathrm{var}(C)}{\sum \mathrm{var}(P_i)}$$

$$\varphi_P = \frac{\mathrm{var}(C)}{\left(\sum \sqrt{\mathrm{var}(P_i)}\right)^2}$$

As $\mathrm{var}(C) = \sum \mathrm{var}(P_i) + 2\sum\sum \mathrm{cov}(P_i, P_j)$, a VR of 1 occurs when taxa fluctuate

independently or when positive and negative covariances between species neutralise each other exactly (Gonzalez & Loreau 2009). A VR > 1 indicates that the sum of co-variances among taxa is positive (synchronous dynamics), whereas a VR < 1 (compensatory dynamics) occurs when the sum of covariances is negative. In contrast, φ_P is standardized between 0 and 1 denoting perfect compensatory and perfect synchronous dynamics, respectively. Using φ_P it is possible to directly compare communities differing in the number of taxa considered. It additionally makes no specific assumption about the magnitude and distribution of biomasses and variances (Loreau & de Mazancourt 2008). Both community metrics were calculated for distinct periods within the time series (HBP, LBP, TTS). In addition, we performed an 11-year 'moving window' analysis and an 'expanding window' analysis. For the latter, we first calculated both community metrics for the time period from 1965-1975. Then the calculation window was continuously expanded by one additional study year until the full time series was included. 95 % confidence intervals of VR and φ_P were calculated with time series bootstrapping using the R package boot (Canty & Riley 2010). To account for the autocorrelation structure of the time series we used bootstrapping through block resampling (Davison & Hinkley 1997) with a mean geometric block length of 5 years. Estimated confidence intervals were robust in respect to changes in block length.

In order to study the overall community trajectories, we calculated Bray-Curtis community composition dissimilarities between the study years, which were used as a basis for NMDS ordination and to test for relationships between community dissimilarity and the ratio of TP_{MIX} values between years (Mantel test). Data analysis was performed using the software packages SAS for Windows 9.12 (SAS Institute 1988) and R for Windows 2.9.1 (R Development Core Team 2005).

References

Anneville O., Gammeter S. & Straile D. (2005) Phosphorus decrease and climate variability: mediators of synchrony in phytoplankton changes among European peri-alpine lakes. *Freshwater Biology* 50, 1731-1745

Canty A. & Ripley B. (2010) boot: Bootstrap R (S-Plus) functions. R package 1.2-43.

Davison A.C. & Hinkley D.V. (1997) Bootstrap methods and their applications. Cambridge University Press, Cambridge.

Gaedke U. (1998) Functional and taxonomical properties of the phytoplankton community of large and deep Lake Constance: interannual variability and response to re-oligotrophication (1979-1993). *Arch.Hydrobiol.Spec.Issues Advanc.Limnol.* 53, 119-141

Gonzalez A. & Loreau M. (2009) The Causes and Consequences of Compensatory Dynamics in Ecological Communities. *Annual Review of Ecology Evolution and Systematics* 40, 393-414

Hillebrand H., Durselen C.D., Kirschtel D., Pollingher U. & Zohary T. (1999) Biovolume calculation for pelagic and benthic microalgae. *Journal of Phycology* 35, 403-424

Loreau M. & de Mazancourt C. (2008) Species synchrony and its drivers: Neutral and nonneutral community dynamics in fluctuating environments. *American Naturalist* 172, E48-E66

R Development Core Team (2005) R: A language and environment for statistical computing. *R Foundation for Statistical Computing, Vienna, Austria.ISBN 3-900051-07-0* URL: http://www.R-project.org.

Rodionov S.N. (2004) A sequential algorithm for testing climate regime shifts. *Geophysical Research Letters* 31, Art. No. L09204, DOI: 10.1029/2004GL019448

Rossknecht H. (1998) Langjährige Entwicklung chemischer Parameter im Bodensee-Obersee. *Ber.Int.Gewässerschutzkomm.Bodensee* 48, 1-137

SAS Institute (1988) *SAS/STAT user's guide, release 6.03 edition.* SAS Institute, Cary, North Carolina, USA.

Schluter D. (1984) A Variance Test for Detecting Species Associations, with Some Example Applications. *Ecology* 65, 998-1005

Seebens H., Straile D., Hoegg R., Stich H.B. & Einsle U. (2007) Population dynamics of a freshwater calanoid copepod: complex responses to changes in trophic status and climate variability. *Limnology and Oceanography* 52, 2364-2372

Tilzer M.M. & Beese B. (1988) The seasonal productivity cycle of phytoplankton and controlling factors in Lake Constance. *Schweiz.Z.Hydrol.* 50, 1-39

Utermöhl H. (1958) Zur Vervollkommnung der quantitativen Phytoplankton-Methodik. *Mitt.Internat.Verein.Limnol.* 9, 1-38

Watson S., McCauley E. & Downing J.A. (1992) Sigmoid Relationships Between Phosphorus, Algal Biomass, and Algal Community Structure. *Canadian Journal of Fisheries and Aquatic Sciences* 49, 2605-2610

Wood S.N. (2006) *Generalized Additive Models: An Introduction with R.* Chapman & Hall/CRC, Boca Raton.

Yue S., Pilon P., Phinney B. & Cavadias G. (2002) The influence of autocorrelation on the ability to detect trend in hydrological series. *Hydrological Processes* 16, 1807-1829

Compensatory dynamics and the stability of phytoplankton biomass during 4 decades of eutrophication and oligotrophication

Marc Jochimsen[1], Reiner Kümmerlin[2] & Dietmar Straile[1]

1 Limnological Institute, University of Konstanz, 78464 Konstanz, , Germany
2 Institut für Seenforschung, 88085 Langenargen, Germany

Appendix S2 The relationship between annual average biomasses of phytoplankton groups and TP$_{MIX}$

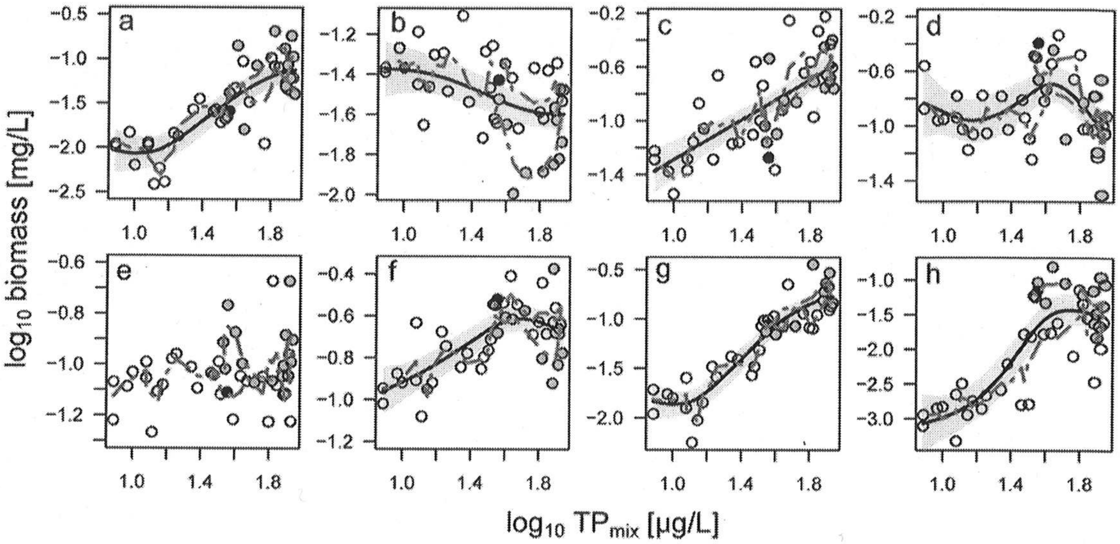

Fig. S2-1 Relationships between $\log_{10}$ transformed total phosphorus concentrations and log-transformed biomasses of a) cyanophytes (CYA), b) chrysophytes (CHR), c) centric diatoms (CDI), d) pennate diatoms (PDI), e) dinophytes (DIN), f) cryptophytes (CRY), g) chlorophytes (CHL) and h) Conjugales (CON). The solid lines present the significant smooths (± 2 SE, grey areas) of the generalized additive models with TP$_{MIX}$ as independent variable (see Table 1). The dashed grey lines indicate the temporal trajectories based on a three year moving average. The black dots represent the start of the study period (1965), the grey dots the years of eutrophication, and the white dots the subsequent years of oligotrophication.

Compensatory dynamics and the stability of phytoplankton biomass during 4 decades of eutrophication and oligotrophication

Marc Jochimsen[1], Reiner Kümmerlin[2] & Dietmar Straile[1]

1 Limnological Institute, University of Konstanz, 78464 Konstanz, , Germany
2 Institut für Seenforschung, 88085 Langenargen, Germany

Appendix S3 Results of statistical analyses relating phytoplankton biomasses lagged by two years with TP_{MIX} (lagged by two years) and WT

Table 1. Summary of GAMs relating phytoplankton biomasses of total phytoplankton lagged by two years (TOTAL) and of the different phytoplankton groups to TP_{MIX} (lagged by 2 years) and WT (full model) and to TP_{MIX} and WT separately. Abbreviations used for phytoplankton groups are: cyanophytes (CYA), chrysophytes (CHR), centric diatoms (CDI), pennate diatoms (PDI), dinophytes (DIN), cryptophytes (CRY), chlorophytes (CHL) and Conjugales (CON). For all variables in the models the estimated degree of freedom (e.d.f) and F values with corresponding significance levels (*** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$, ns $P > 0.05$) are shown. Model performance is indicated by the deviance explained (dev. expl.) of the respective models.

Variables		**TP_{Mix}**		**WT**		
taxon	**model**	**e.d.f.**	***F***	**e.d.f.**	***F***	**dev. expl.**
TOTAL	full	2.70	17.19 ***	3.96	2.87 *	84.4 %
	TP_{Mix}	2.79	33.26 ***	-	-	76.1 %
	WT	-	-	3.04	9.71 ***	52.1 %
CYA	full	2.41	25.6 ***	1.4 e-05	2.8 e-05 ns	67.7 %
	TP_{Mix}	2.41	25.6 ***	-	-	67.7 %
	WT	-	-	2.12	5.79 **	33.2 %
CHR	full	0.71	2.42 ns	0.78	3.54 ns	26.8 %
	TP_{Mix}	2.04	5.06 *	-	-	23.8 %
	WT	-	-	1.44	7.19 **	25.8 %
CDI	Full	0.97	38.19 ***	0.29	0.43 ns	57.4 %
	TP_{Mix}	0.98	50.13 ***	-	-	56.7 %
	WT	-	-	2.12	8.44 ***	40.0 %
PDI	full	1.0 e-05	7.8 e-05	2.36	2.95 *	25.5%
	TP_{Mix}	4.54	ns	-	-	24.5 %
	WT	-	1.45 ns	2.36	2.95 *	0.0 %
DIN	full	0.64	0.87 ns	4.7 e-05	3.3 e-05	5.84 %
	TP_{Mix}	0.64	1.8 ns	-	-	5.84 %
	WT	-	-	2.5 e-05	2.3 e-05 ns	0.0 %
CRY	full	2.25	11.21 ***	3.1 e-05	1.09 e-07	47.7 %
	TP_{Mix}	2.25	11.21 ***	-	-	47.7 %
	WT	-	-	1.62	3.44 *	19.4 %
CHL	full	2.99	39.48 ***	2.07	3.07 *	88.7 %
	TP_{Mix}	2.99	58.57 ***	-	-	85.7 %
	WT	-	-	0.96	22.47 ***	37.6 %
CON	full	2.67	25.51	3.4 e-05	1.3 e-05 ns	70.0 %
	TP_{Mix}	2.67	25.51	-	-	70.0 %
	WT	-	-	2.18	8.99 ***	42.1 %

Compensatory dynamics and the stability of phytoplankton biomass during 4 decades of eutrophication and oligotrophication

Marc Jochimsen[1], Reiner Kümmerlin[2] & Dietmar Straile[1]

1 Limnological Institute, University of Konstanz, 78464 Konstanz, , Germany
2 Institut für Seenforschung, 88085 Langenargen, Germany

Appendix S4 Results of 'expanding window' and 'moving window' analyses with biomasses of the year 1988 replaced by average biomasses of the years 1987 and 1989.

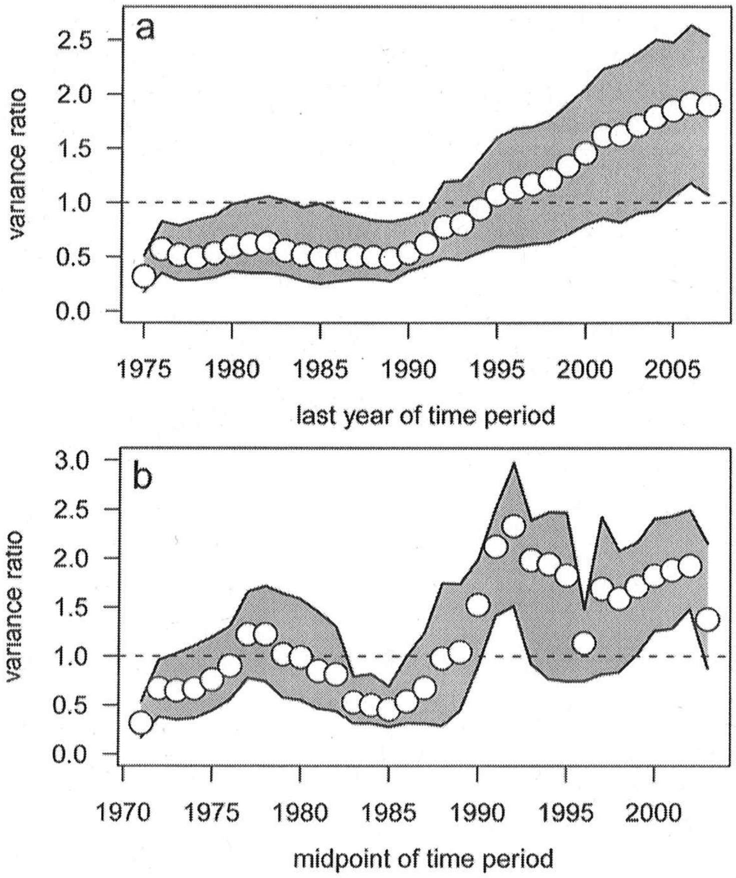

Fig S4-1 a) 'expanding window' analysis of variance ratios, and b) 11-year 'moving window' analysis of variance ratios. In the 'expanding window' analysis the first data point presents the respective value for the period 1965-1975, subsequent ones time periods starting in 1965 and lasting until the year shown on the x – axis. In the 'moving window' analysis the midpoint of the moving window is shown on the x-axis. Vertical lines and shaded areas represent 95% bootstrap confidence intervals with block resampling (see Appendix S1). The vertical dashed line at VR = 1 indicates independent dynamics. Biomasses of the year 1988 were replaced by average biomasses of the years 1987 and 1989 in order to demonstrate that the overall VR dynamics is not strongly influenced by the high biomass values of the specific year 1988.

Compensatory dynamics and the stability of phytoplankton biomass during 4 decades of eutrophication and oligotrophication

Marc Jochimsen[1], Reiner Kümmerlin[2] & Dietmar Straile[1]

1 Limnological Institute, University of Konstanz, 78464 Konstanz, , Germany
2 Institut für Seenforschung, 88085 Langenargen, Germany

Appendix S5 Factors limiting phytoplankton during the high biomass and low biomass periods

Lake Constance has traditionally been considered as a predominantly phosphorus limited system (Sommer 1987). Extensive studies by Sommer (Sommer 1983;Sommer & Stabel 1983;Sommer 1984b;Sommer 1984a;Sommer 1985;Sommer 1986;Sommer 1987) during the eutrophic period revealed that besides phosphorus also silicate, light and grazing limited phytoplankton growth in Lake Constance. Limitation by silicate, light and grazing during the vegetation period is an indirect consequence of high phosphorous input and consequently increased algal biomass. High algal (diatom) biomasses caused increased silicate depletion during the growing season, strong light absorption due to the photosynthetic pigments of algae especially in upper water layers (Tilzer 1983), and high abundances of zooplankton, especially of *Daphnia* (Straile & Geller 1998). CO_2 has not been considered as a potential limiting factor in the studies undertaken by Sommer (Sommer 1983;Sommer & Stabel 1983;Sommer 1984b;Sommer 1984a;Sommer 1985;Sommer 1986;Sommer 1987) and unfortunately no measurements on dissolved CO_2 concentrations are available. However, as CO_2 consumption by algae will increase the pH of the water column (Wetzel 2001), pH maxima may be used to infer the severeness of CO_2 limitation. Laboratory experiments have shown that especially growth of chrysophyte species is restricted at low CO_2, respectively high pH levels, apparently due to a lack of carbon-concentrating mechanisms used by most other algae and therefore missing access to inorganic carbon sources (Maberly *et al.* 2009).

Limnetic enclosure experiments suggest termination of population growth of several chrysophyte species when pH exceeded 8.8 (Reynolds 1986). The reduction of phytoplankton biomass with oligotrophication hence should have resulted into an increased light availability in deeper water layers, increased silicate concentrations due to reduced demand by diatoms, decreased pH maxima and reduced zooplankton, especially *Daphnia* abundances.

Fig. S5-1 compares the high versus low biomass periods in respect to chl *a* profiles of the water column, relative occurrences of limiting concentrations of soluble reactive phosphorus and silicate, annual pH maxima and zooplankton abundance – algal biomass ratios.

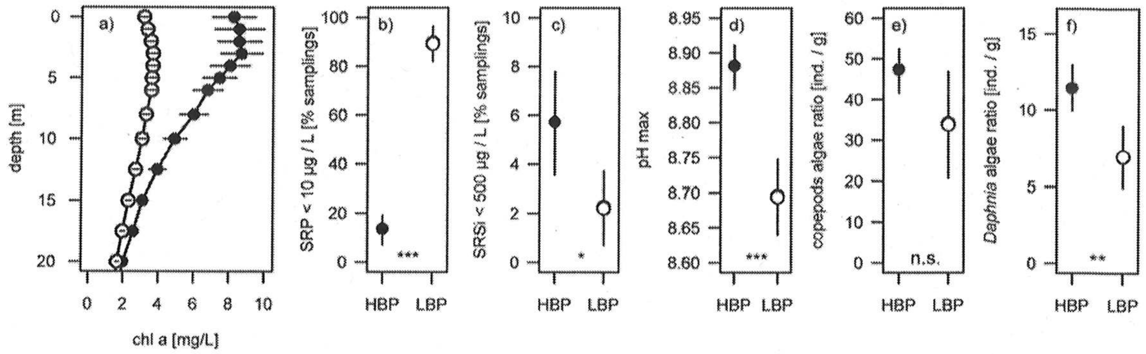

Fig. S5-1 **Factors limiting phytoplankton during the high biomass and low biomass periods.** a) Mean chlorophyll *a* profiles during HBP (full symbols) and LBP (open symbols). Horizontal lines indicate ± 2 standard errors (SE). b) relative frequency of soluble reactive phosphorus measurements below 10 µg/L within the upper 20 of the water column during HBP and LBP, c) relative frequency of silicate measurements below 500 µg/L within the upper 20 of the water column during HBP and LBP, d) Mean annual pH maxima during HBP and LBP within the upper 20 m of the water column. e) *Daphnia* and f) copepod abundance to algae biomass ratios during HBP and LBP. Vertical bars indicate ± 2 SE, significance levels are classified as * $p<0.05$, ** $p<0.01$, *** $p<0.001$, n.s. $p>0.05$

Chl *a* concentrations have strongly decreased from the HBP to the LBP in the upper water layers suggesting higher light availability below a water depth of e.g. 5 m. However, note that chl *a* concentrations in the two periods approach each other with increasing depth, i.e., there is no indication that the decline of phytoplankton biomass was due to a vertical displacement of phytoplankton biomass beyond the 0-20m sampling depth. HBP and LBP differed strongly in respect to the mean relative frequency of limiting soluble reactive phosphorus (SRP) and silicate concentrations in a study year, maximum pH values in each study year and average *Daphnia* abundance – phytoplankton biomass ratios, but not in copepod abundance – phytoplankton biomass ratios. While SRP concentrations during the HBP were below a threshold indicating phosphorus limitation (Sommer *et al.* 1993) on average during 15 % of measurements within a year, this value rose to an average of 90 % during the LBP indicating that phosphorus was at concentrations limiting phytoplankton growth almost during all measurements within the upper 20m of the water column during this period. In contrast, relative frequencies of silicate measurements below a threshold indicating silicate limitation (Thackeray *et al.* 2008) decreased approximately 3-fold from the HBP to the LBP. Likewise yearly pH maxima declined and daphnids declined disproportionately as compared to phytoplankton biomass from the HBP to the LBP. Note that daphnids are considered to have a much stronger impact on phytoplankton than copepods due to their larger size and higher filtrations rates.

Overall, the results presented here suggest that phytoplankton during the HBP was limited by a multitude of factors including phosphorus, light, herbivory, silicate and possibly CO_2; whereas in the LBP phosphorus limitation increased strongly and the importance of other limiting factors has decreased.

References

Maberly S.C., Ball L.A., Raven J.A. & Sultemeyer D. (2009) Inorganic Carbon Acquisition by Chrysophytes. *Journal of Phycology* 45, 1052-1061

Reynolds C.S. (1986) Experimental Manipulations of the Phytoplankton Periodicity in Large Limnetic Enclosures in Blelham Tarn, English Lake District. *Hydrobiologia* 138, 43-64

Sommer U. (1983) Light, stratification and zooplankton as controlling factors for the spring development of phytoplankton in Lake Constance. *Schweiz.Z.Hydrobiol.* 45, 394-404

Sommer U. (1984a) Population dynamics of three planktonic diatoms in Lake Constance. *Hol.Ecol.* 7, 257-261

Sommer U. (1984b) Sedimentation of principal phytoplankton species in Lake Constance. *J.Plankt.Res.* 6, 1-14

Sommer U. (1985) Seasonal succession of phytoplankton in Lake Constance. *Bioscience* 5, 351-357

Sommer U. (1986) The periodicity of phytoplankton in Lake Constance (Bodensee) in comparison to other deep lakes of Central Europe. *Hydrobiol.* 138, 1-7

Sommer U. (1987) Factors controlling the seasonal variation in phytoplankton species composition - A case study for a deep, nutrient rich lake. *Progress in Phycological Research* 5, 123-179

Sommer U., Gaedke U. & Schweizer A. (1993) The first decade of oligotrophication of lake Constance. II. The response of phytoplankton taxonomic composition. *Oecologia* 93, 276-284

Sommer U. & Stabel H.H. (1983) Silicon Consumption and Population-Density Changes of Dominant Planktonic Diatoms in Lake Constance. *Journal of Ecology* 71, 119-130

Straile D. & Geller W. (1998) Crustacean zooplankton in Lake Constance from 1920 to 1995: response to eutrophication and reoligotrophication. *Arch.Hydrobiol.Spec.Issues Advanc.Limnol.* 53, 255-274

Thackeray S.J., Jones I.D. & Maberly S.C. (2008) Long-term change in the phenology of spring phytoplankton: species-specific responses to nutrient enrichment and climatic change. *Journal of Ecology* 96, 523-535

Tilzer M.M. (1983) The Importance of Fractional Light-Absorption by Photosynthetic Pigments for Phytoplankton Productivity in Lake Constance. *Limnology and Oceanography* 28, 833-846

Wetzel R.G. (2001) *Limnology - Lake and River Ecosystems*, 3rd edn. Academic Press, San Diego.