OIKOS 114: 265–276, 2006

The role of predation for seasonal variability patterns among phytoplankton and ciliates

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Huber, V. and Gaedke, U. 2006. The role of predation for seasonal variability patterns among phytoplankton and ciliates. – Oikos 114: 265–276.

Investigating the mechanisms which underlie the biomass fluctuations of populations and communities is important to better understand the processes which buffer community biomass in a variable environment. Based on long-term data of plankton biomass in Lake Constance (Bodensee), this study aims at explaining the different degree of synchrony among populations observed within two freshwater plankton groups, phytoplankton and ciliates. Established measures of temporal variability such as the variance ratio and cross-correlation coefficients were combined with first-order autoregressive models that allow estimating species interactions from time-series data. We found that predation was an important driver of the observed seasonal variability patterns in phytoplankton and ciliates, and that competitive interactions only played a subordinate role. In Lake Constance copepods and cladocerans, two major invertebrate predator groups, focus their grazing pressure at different times of the season. Model results suggested that compensatory dynamics detected in phytoplankton originate from the differential vulnerability of species to either one of these two predator groups. For ciliates model results advocated that synchrony among species occurs because ciliates tend to be vulnerable to both predator groups. Our findings underline the necessity of extending studies of community variability to multiple trophic levels because accounting for predator–prey interactions may often be more important than accounting for competitive interactions at one trophic level.

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The temporal variability patterns encountered in natural communities can be a source of information on the processes which buffer communities in a fluctuating environment (Micheli et al. 1999). A better understanding of these processes is important to anticipate the impact of increasing anthropogenic disturbances on ecosystems. Many theoretical studies have analysed the biological and stochastic processes which influence the variability of aggregate community biomass when investigating the relationship between biodiversity and stability (reviewed by Loreau et al. 2002). At the same time, only few observational studies exist which link ecological mechanisms to temporal variability patterns of biomass fluctuations encountered in natural communities (Hooper et al. 2005).

The temporal variability of the aggregate community biomass is strongly dependent on the degree of synchrony in the biomass fluctuations of the component species (Doak et al. 1998, Yachi and Loreau 1999). Negative covariances in species biomass fluctuations lead to compensation: the decrease in biomass of one species is at least partly compensated for by the increase in biomass of another species, dampening the variability of the aggregate community biomass. When positive

Accepted 9 January 2006
Subject Editor: Veijo Kaitala

ISSN 0030-1299

covariances in species biomass fluctuations dominate, compensation is weak keeping the variability of the aggregate community biomass at about the same level as the average variability of the individual species biomass.

Many different mechanisms are involved in determining the degree of synchrony in species biomass fluctuations (reviewed by Cottingham et al. 2001). Besides stochastic processes deterministic processes, such as the reaction to the abiotic environment or species interactions, most strongly influence the degree of synchrony in biomass fluctuations (Tilman et al. 1998). In temperate regions abiotic factors determine plankton growth during winter and early spring, whereas plankton dynamics are dominated by biological processes such as competition and predation during the growing season (Sommer et al. 1986). Our study period is limited to the growing season, and we focus on the role of species interactions for temporal variability patterns. Competition between species has been discussed so far as the most important biological process which creates negative covariances in species biomass fluctuations lowering community variability (Lehman and Tilman 2000). However, most studies have focused on one trophic level and have neglected predator–prey interactions (Ives et al. 2005). Here, we consider two trophic levels and assess the relative importance of competitive interactions as opposed to trophic interactions for influencing community variability in a plankton food web.

A promising method to estimate species interactions from time-series data are multivariate autoregressive models of first order, MAR(1) models (Ives et al. 2003). MAR(1) models allow separating environmental noise from the biological processes such as species interactions. There are several studies that have already successfully applied MAR(1) models when investigating ecological mechanisms underlying population dynamics in plankton food webs (Frost et al. 1995, Ives et al. 1999, Klug et al. 2000, Fischer et al. 2001).

Phytoplankton and ciliates constitute two major plankton groups, each consisting of ecologically similar species that share certain resources and predation risks. Both have relatively short generation times with up to several generations per week (Lampert and Sommer 1993). Phytoplankton species are primary producers, which are dependent on dissolved nutrients and light. Ciliates are protozoans that obtain most of their energy from phytoplankton in the examined lake (Müller et al. 1991, Gaedke et al. 2002). The two plankton groups provide a good opportunity to assess the relative importance of competitive as opposed to trophic interactions for influencing community variability because strong grazing effects exerted by invertebrate zooplankton have been found for both phytoplankton (Sommer et al. 1986) and ciliates (Burns and Schallenberg 1998, Adrian and Schneider-Olt 1999). Our analysis considers two functionally different predator groups, the raptorial-feeding copepods and the filter-feeding cladocerans, which dominate the grazing pressure on phytoplankton and protozoans in most freshwater lakes (Lampert and Sommer 1993). Cladocerans can affect ciliates indirectly through exploitative competition in addition to predation because both plankton groups graze the same nanoplanktonic algae (Wickham and Gilbert 1993).

Based on time-series data of plankton biomass in Lake Constance we quantify seasonal variability patterns for phytoplankton and ciliates applying the variance ratio (Schluter 1984) and calculating cross-correlation coefficients among species. We investigate species interactions that may underlie the observed variability patterns using results from MAR(1) models. The models allow us to simulate the seasonal variability patterns of biomass fluctuations and to explore the importance of competition and grazing effects by copepods and cladocerans in creating the characteristic variability patterns.

Material and methods

Study site and data preparation

Lake Constance is a large (476 km^2), deep (mean depth = 101 m), warm-monomictic lake north of the Alps (47°40′N, 9°20′E), bordered by Switzerland, Germany and Austria. Plankton samples were collected at a central sampling site in the north-western part of Upper Lake Constance (Überlinger See) at a range of different depths within the upper 20 metres. The abundance and cell sizes of plankton organisms were assessed using advanced microscopy techniques. Conversion to units of carbon was based upon empirical relationships. For details on the counting and conversion methods see Müller et al. (1991), Gaedke (1998), Straile and Geller (1998) and Gaedke et al. (2002). Organisms were grouped into morphotypes which represent either individual species or higher taxonomic units.

The time-series used in this analysis last from 1987–1998 when data on phytoplankton, ciliates and crustaceans was available. We limited the time scale of the study to the period April–October (week 13 to week 42) when weekly samplings were taken and biological interactions, on which we focused in this study, are known to be most important (Sommer et al. 1986). For simplicity, analyses at the population level were restricted to the ten most important morphotypes (Table 1), which comprised on average 78% of total community biomass for phytoplankton and 80% for ciliates. Morphotypes were ranked by the number of days on which they constituted more than 2.5% of total biomass and the ten first ranked morphotypes were selected. Phytoplankton and ciliates will be termed communities in the following in order to facilitate the

Table 1. Taxonomy, cell volume of individual cells and edibility classification for the most important phytoplankton and ciliate morphotypes, which were included in the analysis. Colony forming phytoplankton species are marked with an asterisk.

Phytoplankton			
Species code	Taxonomic units	Cell volume (μm^3)	Edibility
Rho	*Rhodomonas minuta*	130	edible
Sth	*Stephanodiscus hantzschii*	50	edible
Stn	*Stephanodiscus neoastraea*	8 000	less edible
Chl	*Chlorella* spp.	33	edible
Cry	*Cryptomonas ovata*	2 000	edible
Cer	*Ceratium hirundinella*	50 000	less edible
Ana	*Anabaena planctonica*	400*	less edible
Ast	*Asterionella formosa*	450*	less edible
Fra	*Fragilaria crotonensis*	700*	less edible
Mel	*Melosira varians*	750*	less edible
Ciliates			
Species code	Taxonomic units	Cell volume (μm^3)	
Urf	*Urotricha furcata*	1700	
Bal	*Balanion planctonicum*	1300	
Ask	*Askenasia* sp.	20 000	
Oli	Oligotrichs $<35\mu m$	4000	
Ped	Peritrichs on diatoms	22 000	
Tin	Tintinnids	24 000	
LiP	*Limno-/Pelagostrombidium*	50 000	
His	*Histiobalantium bodamicum*	50 000	
Ur3	*Urotricha* sp.	50 000	
Rim	*Rimostrombidium lacustris*	119 000	

comparison with theoretical concepts of community variability. They form communities in the sense that they consist of trophically similar, sympatric species which can compete with each other.

For phytoplankton morphotypes we took into account a classification of edibility. This classification scheme has been previously established based on the feeding demands of cladocerans (Knisely and Geller 1986), which dominate crustacean zooplankton during summer in Lake Constance (Straile and Geller 1998). We aggregated data on all phytoplankton morphotypes classified as edible to construct a time-series of edible phytoplankton, which is also considered important prey for ciliates (Gaedke et al. 2002). Cladocerans in Lake Constance comprise *Daphnia hyalina*, *D. galeata* and *Bosmina* sp. and copepods include the calanoid copepod *Eudiaptomus* sp. and three cyclopoid species (Straile and Geller 1998). Data on water temperature (measured at 8 m depth), global radiation and vertical mixing intensity within the upper water column (inferred from a hydrodynamic k-ε simulation model, Bäuerle et al. 1998) was available for the period 1987–1995.

Variability metrics

To characterize the temporal variability of phytoplankton and ciliate at the population and community level, we used the coefficient of variation (CV) defined as the ratio of the standard deviation to the mean. As an aggregate measure for the degree of synchrony among morphotypes of each community we applied the variance ratio (Schluter 1984). The variance of an aggregated group of species G can be calculated from the sum of the variance of individual species S_i and the covariance among species (Box et al. 1978):

$$\mathrm{var}(G) = \mathrm{var}\left(\sum_{i=1}^{n} S_i\right) = \sum_{i=1}^{n} \mathrm{var}(S_i) + 2\sum_{i=1}^{n}\sum_{j=1}^{i-1} \mathrm{cov}(S_i, S_j) \quad (1)$$

The variance ratio (VR) relates the variance of the aggregated group of species to the variance of the individual species:

$$VR = \frac{\mathrm{var}(G)}{\sum_{i=1}^{n} \mathrm{var}(S_i)} \quad (2)$$

If the sum of covariances among species is positive (corresponding to synchronous dynamics), the variance ratio is >1. If species fluctuate independently, the sum of covariances equals zero resulting in a variance ratio of 1. If the sum of covariances among species is negative (corresponding to compensatory dynamics), the variance ratio is <1. We determined whether the extent of compensation or synchrony within the phytoplankton and ciliate community was significantly greater than in a community of independently fluctuating morphotypes by using the bootstrap method suggested in Fisher et al. (2001): the variance ratio calculated from the real data was compared to the distribution of variance ratios

calculated from 10 000 scrambled data sets. The proportion of variance ratios in the distribution which were greater (smaller) than the value calculated from the real data gave statistical confidence for concluding on synchronous (compensatory) dynamics.

Detecting compensatory dynamics within a subgroup of species strongly depends on the level of aggregation because negative and positive covariances can cancel each other out (Vinebrooke et al. 2003). Therefore, we additionally computed cross-correlation coefficients of ln-transformed biomasses for all pairs of the ten most important morphotypes within each plankton group to detect individual pairs of morphotypes that showed positive or negative covariance. Spearman correlation coefficients were used because data for most morphotypes deviated from the normal distribution.

Autoregressive models

Multivariate autoregressive models of first order (MAR(1) models) predict the biomass of species at each sampling date from the biomass of species and possible environmental covariates at the preceding sampling date. Data of the plankton time-series were fitted to MAR(1) models of the general form:

$$x_i(t) = a_i + \sum_{j=1}^{n} b_{ij} x_j(t-1) + \sum_{k=1}^{m} c_{ik} u_k(t-1) + \varepsilon_i(t) \qquad (3)$$

where $i = 1 \ldots n$ is the number of species, $x_i(t)$ and $x_i(t-1)$ are the ln(x)-transformed biomass of species i at time t and $t-1$ respectively, a_i is a constant, b_{ij} are coefficients for the interactions between species (b_{ij} describes the effect of the biomass of species j on the per capita population growth rate of species i), $u_k(t)$ are the environmental covariates, c_{ik} gives the effects of these covariates on per capita population growth rates of species i, m is the number of environmental covariates and $\varepsilon_i(t)$ contains variability in species growth rates not explained by the model including variability due to environmental noise. Separated models were constructed for phytoplankton and ciliates, each including the ln-transformed biomass of the ten dominant morphotypes listed in Table 1 as variates $x_i(t)$. The covariates $u_k(t)$ were ln-transformed biomass of copepods and cladocerans in both models. Zero values, which occurred when densities dropped below detection limit, were replaced by 0.5 times the minimum value measured during time span considered (Ives et al. 1999). Because MAR (1) models require evenly spaced data, the model was coded so that it ignored data that did not correspond to consecutive weeks.

Methods for parameter estimation and model selection were used according to Ives et al. (2003). For model fitting we made the assumption that observation error was negligible in comparison to the error resulting from the stochastic nature of processes that determine plankton growth. The parameter estimation was then carried out by the method of conditional least squares (CLS). Model selection translates to deciding which of the coefficients of the model can be set to zero on statistical grounds because their non-zero estimates do not improve the fit between the model and the data. To evaluate the model fit, we used the Akaike information criterion (Akaike 1974):

$$AIC = -2L + 2p$$

where L is the log-likelihood (calculated with the CLS estimates) and p is the number of parameters. The AIC criterion includes the number of parameters as a penalty factor and leads to the selection of those parameters that contribute a certain amount of additional information to the system. To find the best-fitting model based on the AIC criterion, we constructed a search algorithm that started from 500 initial random models and tested each coefficient in turn by either including (setting it non-zero) or excluding it (setting it zero). The combination of non-zero coefficients which produced the lowest AIC was then chosen as the AIC best-fitting model. During this model selection process, the models were restricted based on consideration of ecological plausibility: all coefficients estimated were assumed to predominantly reflect direct effects such as negative interactions between competitors, positive effects of prey on predators and negative effects of predators on prey. If estimated coefficients violated the sign restrictions in a fitted model, they were set to zero. To confirm that each coefficient included in the final AIC best-fitting model contributed significantly to the predictive power of the model, we performed a log-likelihood ratio test as suggested in Ives et al. (2003) and outlined in Dennis and Taper (1994) creating 10 000 bootstrapped data sets for each test. Computation was done using Matlab 6.5 and parts of the programs were taken from or inspired by the supplement of Ives et al. (2003, ESA's Electronic Data Archive).

We used the AIC best-fitting models to investigate the importance of accounting for interactions between morphotypes (competitive interactions) and the effect of copepods and cladocerans (trophic interactions) as opposed to accounting for competitive or trophic interactions only. For both phytoplankton and ciliates we fitted two null-models each. In the first null-model (called competition null-model) coefficients for trophic interactions (c_{ik}) were set to zero; in the second null-model (called predation null-model) coefficients for the interactions between morphotypes (b_{ij}, $i \neq j$) were set to zero and only coefficients for the effect of morphotypes on themselves (b_{ij}, $i = j$) and trophic interactions (c_{ik}) were kept (inspired by Beisner et al. 2003). The likelihood ratio test was applied in the same manner as when testing the significance of individual coefficients, using

the null-models to create bootstrapped data sets. This allowed us to determine for phytoplankton and ciliates whether the full AIC best-fitting model predicted the data significantly better than each of the two null-models.

Results

Temporal variability patterns

During the time period considered (April–October) the biomasses of phytoplankton and ciliates showed very different seasonal variability patterns (Fig. 1A). At the level of morphotypes coefficients of variation were higher for phytoplankton than for ciliates ($p < 0.05$, Wilcoxon rank test, Fig. 2). However, at the aggregate community level phytoplankton and ciliates showed a very similar temporal variability (both phytoplankton and ciliate community $CV = 0.8$). In phytoplankton there was a larger reduction in variability when aggregated from the morphotype to the community level. This means that there was a stronger extent of compensation among phytoplankton morphotypes than among ciliate morphotypes.

Variance ratios (VR) were $VR = 1.2$ for the phytoplankton community and $VR = 1.7$ for the ciliate community. For both phytoplankton and ciliates the variance ratio was significantly >1 (with $p < 0.01$ for phytoplankton and $p < 0.001$ for ciliates), indicating synchronous dynamics for both groups. However, the higher variance ratio of the ciliate community pointed to stronger synchrony than in the phytoplankton community, corresponding to less compensation between ciliate morphotypes as indicated by the CVs.

Accordingly, most pairs of ciliate morphotypes exhibited low to intermediate positive correlations (Fig. 3). For phytoplankton there was a pattern of two groups (morphotypes Rho, Sth, Stn, Chl versus Cry, Cer, Ana, Ast, Fra, Mel) containing morphotypes that tended to correlate positively with each other, but lacked, or exhibited negative correlations with morphotypes of the other group. Overall, while phytoplankton morphotype biomass showed relatively strong variability and compensation between two subgroups, ciliate morphotype biomass depicted relatively low variability and strong synchronization (Fig. 1A).

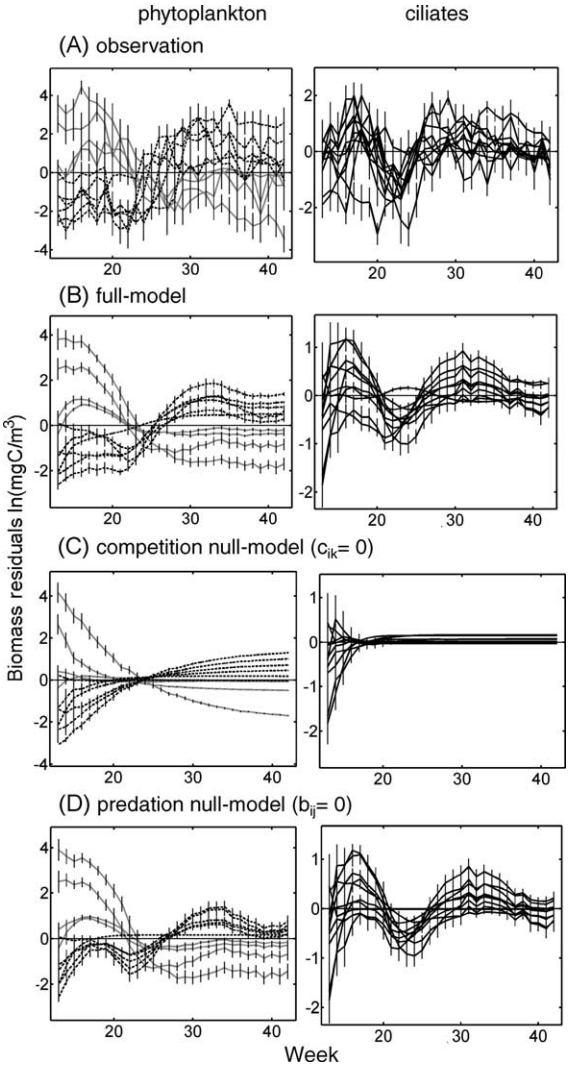

Fig. 1. Mean seasonal variability patterns for phytoplankton (left) and ciliates (right) in Lake Constance. Biomass at weekly sampling dates was averaged across years (1987–1998), vertical bars indicating ± 1 SE, and residuals from overall mean calculated. (A) observed biomass, (B) one-step ahead predictions based on the full-model (as presented in Table 2), (C) one-step ahead predictions based on the competition null-model where coefficients for the effect of copepods and cladocerans were forced to be zero, and (D) one-step ahead predictions based on the predation null-model where coefficients for interactions between morphotypes were forced to be zero. (Note the different scales on the y-axes).

Autoregressive models for phytoplankton and ciliate morphotypes

We fitted multivariate autoregressive models to the data in order to estimate strengths of biological interactions that may underlie the seasonal variability patterns observed in the phytoplankton and ciliate community (Table 2). The AIC best-fitting model for phytoplankton (Table 2A) explained on average $\sim 52\%$ and for ciliates (Table 2B) on average $\sim 36\%$ of the observed variation in morphotype biomass. Comparing the two models for phytoplankton and ciliates revealed differences between the two plankton groups regarding, first, the importance of interactions between morphotypes and, second, the effect of copepods and cladocerans. While the phytoplankton model contained 18 coefficients for the interactions between morphotypes (out of which 11

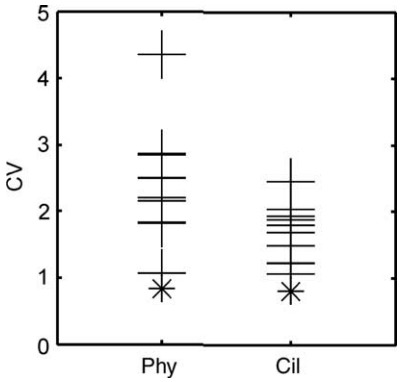

Fig. 2. Coefficients of variation (CV) for temporal biomass fluctuations (April–October). Crosses correspond to the biomass of individual morphotypes; asterisks correspond to the aggregate community biomass (sum of morphotype biomasses). Abbreviations: phy – phytoplankton, cil –ciliates.

were significant according the log-likelihood ratio test), the ciliate model contained only 13 (7 significant) coefficients for the interactions between morphotypes. The models included coefficients indicating an effect of cladocerans and/or copepods for all phytoplankton and ciliate morphotypes with the exception of *Cryptomonas ovata* (Cry, Table 2A) and *Rimostrombidium lacustris* (Rim, Table 2B). In the phytoplankton model, these coefficients divided the phytoplankton morphotypes clearly into two groups, which comprised morphotypes that were either affected by cladocerans (Rho, Sth, Stn, Chl) or copepods (Cer, Ana, Ast, Fra, Mel). In opposition, for six ciliate morphotypes (Urf, Bal, Ask, Oli, Ped, Tin) the model revealed negative effects by both copepods and cladocerans which is not the case for any of the phytoplankton morphotypes (compare Table 2A and 2B). This finding suggests that while phytoplankton morphotypes are vulnerable to grazing by either copepods or cladocerans, many ciliate morphotypes are negatively affected by both copepods and cladocerans.

Can the differences in biological interactions suggested by the models explain the differences in biomass variability patterns observed in the phytoplankton and ciliate community? The AIC best-fitting models reproduced the main characteristics of the seasonal biomass variability patterns observed for phytoplankton and ciliates (compare Fig. 1A and 1B): compensation occurred between two subgroups of phytoplankton while ciliate morphotypes showed relatively synchronous dynamics. The bootstrapped log-likelihood ratio test indicated that the full AIC best-fitting models predicted the data significantly better than each type of null-models, the competition null-models, which accounted for interactions between morphotypes only, and the predation null-models, which accounted for the effect of copepods and cladocerans only (all tests $p < 0.001$). The competition null-models failed to reproduce the main characteristics of seasonal variability patterns observed (Fig. 1C). In contrast, despite the statistically significant higher predictive power of the full models, the predation null-models were sufficient to mirror the main characteristics of the seasonal variability patterns observed in phytoplankton and ciliates (Fig. 1D). Differences in vulnerability to copepods and cladocerans, as suggested for phytoplankton and ciliates in the AIC best-fitting models, may therefore be sufficient to explain the major differences in seasonal variability patterns observed.

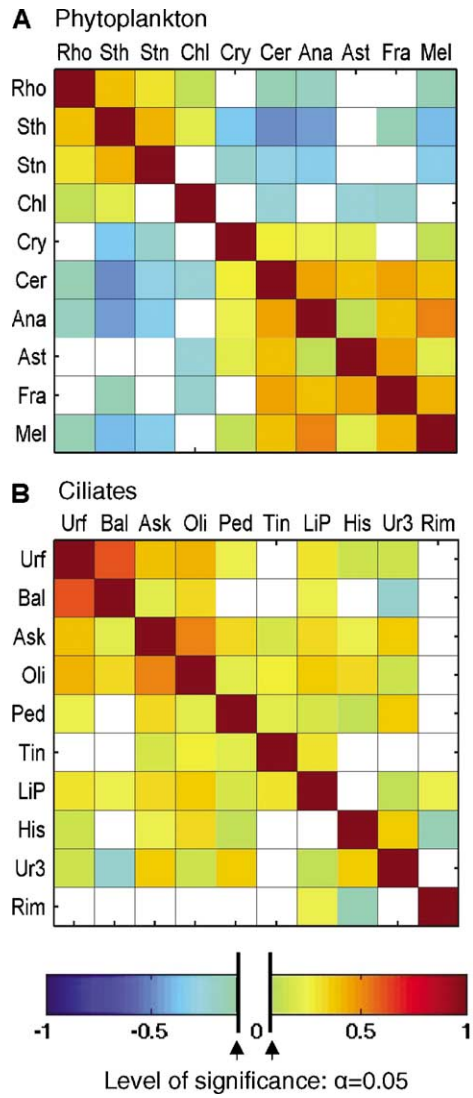

Fig. 3. Pair-wise Spearman correlation coefficients for the ln-transformed biomass of (A) phytoplankton and (B) ciliate morphotypes. The colour of each square indicates the correlation coefficient as specified in the colour bar for morphotypes which are named in the corresponding row and column. For abbreviations see Table 1.

Table 2. Parameter estimates for the AIC best-fitting autoregressive models describing dynamics of phytoplankton and ciliate morphotypes. Coefficients represent effects of morphotype and predator group biomass (columns) on per capita growth rates of focal morphotypes (rows). As an example, the negative coefficient for covariates in row one (−0.14) translates to a negative effect of the biomass of cladocerans (clado) on the growth rate of *Rhodomonas minuta* (Rho). Asterisks* mark significance ($p < 0.05$) as determined with bootstrapping method. Cope-copepods, for further abbreviations see Table 1.

A: Phytoplankton morphotypes (T = 295)

	Coefficients for morphotypes										Coefficients for covariates		Model fit
	Rho	Sth	Stn	Chl	Cry	Cer	Ana	Ast	Fra	Mel	cope	clado	R^2
Rho	0.44			−0.02*	−0.05			−0.03				−0.14*	0.40
Sth	−0.15	0.74			−0.15*	−0.03				−0.07*		−0.22*	0.77
Stn			0.48							−0.12*		−0.34*	0.50
Chl	−0.26*			0.68				−0.13				−0.16*	0.49
Cry		−0.09*			0.47								0.33
Cer		−0.16*				0.57					−0.32*		0.50
Ana		−0.15*	−0.12*				0.61				−0.51*		0.62
Ast				−0.10*				0.60			−0.39*		0.44
Fra				−0.04					0.67		−0.62*		0.59
Mel		−0.06	−0.15*							0.62	−0.28*		0.57
										average model fit			0.52

B: Ciliate morphotypes (T = 276)

	Coefficients for morphotypes										Coefficients for covariates		Model fit
	Urf	Bal	Ask	Oli	Ped	Tin	LiP	His	Ur3	Rim	cope	clado	R^2
Urf	0.42					−0.04*					−0.17*	−0.13*	0.35
Bal		0.44				−0.10*			−0.06	−0.17*	−0.17*	−0.19*	0.45
Ask			0.46								−0.16*	−0.03*	0.29
Oli			−0.09	0.61							−0.21*	−0.02*	0.40
Ped					0.42						−0.37*	−0.10*	0.29
Tin		−0.15*				0.59					−0.30*	−0.19*	0.46
LiP		−0.08					0.33			−0.06		−0.11*	0.16
His	−0.13*					−0.08*		0.75			−0.21*		0.64
Ur3		−0.12*							0.55		−0.42*		0.43
Rim			−0.18	−0.15						0.33			0.15
										average model fit			0.36

How may grazing of copepods and cladocerans determine compensatory and synchronous dynamics among phytoplankton and ciliate morphotypes? In Lake Constance copepods reach their maximum biomass earlier in the year than cladocerans indicating that copepod grazing pressure peaks earlier than cladoceran grazing pressure (Fig. 4A). We compared the seasonal variability patterns observed in the phytoplankton and ciliate community with model results for the effect of copepods and cladocerans (Fig. 4B). For most pairs of synchronously fluctuating morphotypes in the phytoplankton community, such as *Ceratium hirundinella* vs *Melosira varians* and *Stephanodiscus hantzschii* vs *Stephanodiscus neoastraea* (Fig. 4B, panel 1 and 2), the model suggested vulnerability to the same predator group, either copepods or cladocerans. In the ciliate community, on the other hand, the model revealed an effect of both copepods and cladocerans for most pairs of the many synchronously fluctuating morphotypes, such as *Urotricha furcata* vs *Balanion planctonicum* (Fig. 4B, panel 3). Where compensation between morphotype pairs occurred as observed frequently within the phytoplankton community, such as for *Fragilaria crotonensis* vs *Chlorella* spp. (Fig. 4B, panel 4), and rarely within the ciliate community, such as for *Histobalantium bodanicum* vs *Limno-/Pelagostrombidium* (Fig. 4B, panel 5), the model suggested that one morphotype is vulnerable to grazing by copepods while the other one is vulnerable to grazing by cladocerans. Thus, grazing effects by copepods and cladocerans, which dominate at different times during the season, could explain both compensation and synchrony within the phytoplankton and ciliate communities.

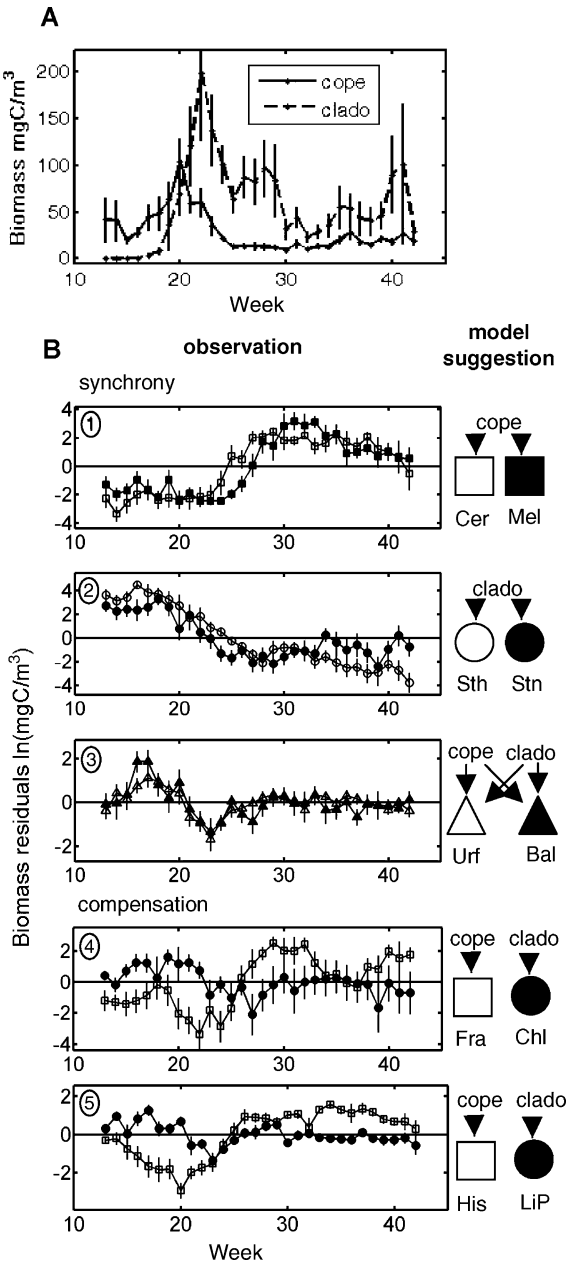

Fig. 4. Mean seasonal dynamics of (A) predator groups and (B) selected pairs of phytoplankton and ciliates morphotypes. Biomass respectively ln-transformed biomass at weekly sampling dates was averaged across years, vertical bars indicating ± 1 SE. In (B) residuals from overall mean were calculated. Organigrams in (B) depict vulnerability by morphotypes to copepod (cope) and cladoceran (clado) predators as suggested in the AIC best-fitting models (Table 2). For morphotype abbreviations see Table 1.

Discussion

We characterized two functionally different plankton groups in Lake Constance, phytoplankton and ciliates, in terms of their temporal variability patterns in seasonal biomass fluctuations. Estimating interaction strengths from time-series suggested relatively weak differences between phytoplankton and ciliates concerning competitive interactions within the community, but revealed clearly different patterns concerning the effect of grazing by copepods and cladocerans. Trophic interactions as advocated by model results were sufficient to explain the major characteristics of biomass variability patterns of phytoplankton and ciliates.

Variability patterns

Coefficients of variation indicated that phytoplankton and ciliates exhibited similar temporal variability at the community level while at the morphotype level temporal variability was higher in phytoplankton than in ciliates. It is important to point out that comparing different species on the basis of simple variability measures does not only reveal true differences in the species dynamics, but is complicated by a number of possible bias such as different mean-variance rescaling factors, differences in

measurement error and zero values in the data (McArdle et al. 1990, Gaston and McArdle 1994). This problem is addressed in a more detailed study on the variability patterns found in the plankton food web of Lake Constance (U. Gaedke, unpubl.). Overall, our main results on the seasonal variability patterns of phytoplankton and ciliates in Lake Constance are in agreement with the results of this study.

Biological plausibility of interactions suggested in the models

It is important to note that autoregressive models are based on correlations and are therefore primarily descriptive. Clearly, interactions suggested by the models do not necessarily point to direct biological interactions between species, but can reflect correlations in observed biomasses that result from indirect relationships. We investigated whether model coefficients for the effect of grazers really reflected predator–prey interactions or whether they could also result from indirect relationships. First, we compared our model results to other studies on copepod and cladoceran ecology. Second, we fitted supplementary models (results shown in the Appendix) that included additional biotic covariates (edible phytoplankton as potential prey for ciliates and ciliates as potential grazers of phytoplankton) and abiotic covariates (mean weekly values of water temperature, global radiation and vertical mixing intensity).

Mesocosm experiments (Sommer et al. 2001, 2003), manipulating copepod and cladoceran biomass experimentally, found a complementary impact of cladocerans and copepods on phytoplankton, similarly to what is suggested in our model: Small phytoplankton is suppressed by cladocerans while large phytoplankton is suppressed by copepods. Here, the AIC best-fitting model advocated a negative effect of cladocerans on phytoplankton morphotypes which are relatively small and a negative effect of copepods on phytoplankton morphotypes which are relatively large (compare Table 2A with details on cell sizes in Table 1). In particular, these mesocosm experiments and our model both suggested a negative impact of copepods on *Ceratium hirundinella* (Cer) and *Anabaena planctonica* (Ana), which are usually not considered preferred food for copepods (Lampert and Sommer 1993). In the short-term experiments by Sommer et al. (2001) seasonal effects can be excluded and the only conceivable indirect effects could result from competition with small phytoplankton species that are less grazed by copepods. Interestingly, it has been demonstrated that copepods are able to predate on *Ceratium furcoides* (Santer 1996). In addition, a previous classification in edible or less edible with regard to the feeding of cladocerans (Table 1) corresponded with only one exception (*Stephanodiscus neoastraea*) to model results on specific vulnerability to either of the two predator groups. For ciliates no edibility classification is readily available, but several experimental studies have reported that ciliates are affected by both cladocerans and copepods (Wickham and Gilbert 1993, Burns and Schallenberg 1998, Adrian and Schneider-Olt 1999).

The large diatom species *Stephanodiscus neoastraea*, which is known to have high sinking rates (Lampert and Sommer 1993), was classified less edible (Table 1) but the model suggested a strong predation effect by cladocerans (Table 2). Since high cladoceran biomass and low mixing intensity approximately coincide in Lake Constance, we investigated whether the model coefficient for the effect of cladocerans on *S. neoastraea* represented a negative effect of sedimentation rather than of grazing. However, even if vertical mixing intensity was explicitly accounted for, the coefficient for the effect of cladocerans kept its explanatory force. Overall, supplementary analysis showed that coefficients indicating the effect of copepods and cladocerans did not simply reflect other environmental factors that might covary with copepod and cladoceran biomass in Lake Constance. The supplementary models contained all coefficients for the effect of copepods and cladocerans that appeared in the models presented in Table 2, with the exception of missing coefficients for only one phytoplankton morphotypes and two ciliate morphotypes (see Appendix for details).

Ciliates and cladocerans both prey on small, edible phytoplankton (Wickham and Gilbert 1993). Thus, while most of the model coefficients for the effect of grazers on phytoplankton morphotypes should reflect direct predation, coefficients for the effect of cladocerans on ciliate morphotypes might mirror exploitative competition rather than direct grazing effects. In fact, negative coefficients for the effect of cladocerans were replaced by positive coefficients for the effect of edible phytoplankton for two morphotypes in the supplementary model. For completeness, we also considered the potential grazing effects of ciliates on small phytoplankton (Gaedke et al. 2002). We were not surprised to find only one significant model coefficient indicating the effect of ciliates on the growth rates of phytoplankton morphotypes because ciliates are known to exert a substantial grazing on phytoplankton but do not influence its dynamics as strongly as cladocerans (Tirok and U. Gaedke, unpubl.).

Mechanisms for compensatory and synchronous dynamics in phytoplankton and ciliates

The AIC best-fitting models included more negative coefficients for interactions between phytoplankton than ciliate morphotypes. Stronger competition between phytoplankton species possibly explains why negative covar-

iances in biomass fluctuations are more frequent within phytoplankton. This is in agreement with Vasseur et al. (2005) who proposed that compensatory dynamics of edible and less edible phytoplankton in Lake Constance evolve because edible algae are the superior competitor in the absence of cladoceran grazing and less edible algae are relieved from competition when edible algae are under severe grazing pressure. However, this study ignored the role of copepod grazing on less edible algae, and therefore did not take into consideration that compensatory dynamics could potentially evolve in the absence of competitive interactions between phytoplankton morphotypes.

In fact, we achieved to simulate the main characteristics of seasonal variability patterns for phytoplankton and ciliates based on the predation null-model, which accounted for trophic interactions of copepods and cladocerans only and excluded competitive interactions between morphotypes. This is particularly interesting in the case of the phytoplankton community because negative covariances among species are most commonly associated with competitive interactions (Fig. 5A, Cottingham et al. 2001). In contrast, our results implied a mechanism of negative covariances in the biomass of specialised consumer species that are transmitted down to the lower trophic level of the resource species (Fig. 5B). In our study compensation among resource species potentially occurs although competition between resource species is weak or entirely absent. This is different from other mechanisms of consumer-driven negative covariances between resource species where apparent competition evolves from a generalised consumer (Holt 1977).

Our models suggested vulnerability to the same predator group for morphotypes which exhibited synchrony in their biomass fluctuations. For some morphotypes indirect relationships certainly contribute to the effect of copepods and cladocerans. Yet, our results allow us to conclude that trophic interactions involving copepods and cladocerans were more important than direct competitive interactions between morphotypes to explain observed differences in seasonal variability patterns. Raimondo et al. (2004) have demonstrated how generalist predators can act as synchronizing agents and have used the proposed mechanism to explain the synchrony among forest Lepidoptera species belonging to the same feeding guild. This evidence from both aquatic and terrestrial systems and the general importance of top-down control across ecosystems (Shurin et al. 2002) suggest that predation influences patterns of community variability in a wide range of different ecosystems. Up to date only very few theoretical studies on the relationship between diversity and temporal variability have investigated the impact of trophic interactions, but they have instead focused on competitive communities at one trophic level (Hooper et al. 2005, Ives et al. 2005). Our findings suggest that, in order to realistically reflect the processes that drive temporal variability patterns in natural communities, it could often be more important to account for specific predator–prey interactions than competition between species at one trophic level.

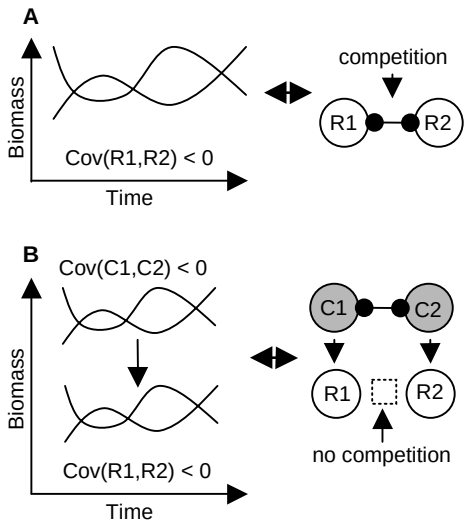

Fig. 5. Sketch of two possible mechanisms leading to negative covariance in biomass of two resource species (R1 and R2) involving (A) competitive interactions and (B) top-down control of two specialized consumers (C1 and C2).

Acknowledgements – Data acquisition was mostly performed within the Special Collaborative Program (SFB) 248 'Cycling of Matter in Lake Constance', supported by Deutsche Forschungsgemeinschaft. We are especially grateful to Thomas Kumke who gave advice on statistical and other methodical questions. Guntram Weithoff and David Vasseur provided valuable comments on earlier versions of the manuscript. VH was funded by a scholarship from Ecole normale supérieure in Paris, France.

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Appendix 1.

Table A1. Parameter estimates for AIC best −fitting autoregressive models with an extended number of environmental covariates $u_k(t)$ (cf. Eq. 3) for (A) phytoplankton and (B) ciliate morphotypes. The additionally tested covariates were mean weekly values of global radiation (light), vertical mixing intensity (mix) and water temperature (temp), as well as ln-transformed aggregated ciliate biomass (cil) and ln-transformed biomass of phytoplankton classified as edible (ed). Soluble reative phosphorous (SRP) was tested as a further covariate in the phytoplankton model, however, none of the coefficients was different from zero in the AIC best-fitting model. For further abbreviations see Table 1 and 2. Asterisks* mark significance ($p < 0.05$) as determined with bootstrapping method. Note that the number of data points is smaller here than for the models presented in Table 2.

A: Phytoplankton morphotypes (T = 191)

	Coefficients for morphotypes										for covariates					
	Rho	Sth	Stn	Chl	Cry	Cer	Ana	Ast	Fra	Mel	cope	clado	cil	light	mix	temp
Rho	0.45				−0.07							−0.15*	−0.11			
Sth		0.72			−0.19*					−0.07*		−0.30*			−2.24*	
Stn			0.40							−0.12		−0.26*			2.78	
Chl	−0.21			0.81								−0.21*				
Cry		−0.10*			0.53							−0.09	−0.27*	0.004*		
Cer				−0.06		0.36									3.13*	0.34*
Ana							0.55				−0.37*				5.39*	0.27*
Ast				−0.11*				0.58			−0.46*					
Fra									0.69		−0.75*					
Mel			−0.14*		−0.14					0.57	−0.43*					0.08
Model fit											average model fit					
R^2	0.38	0.78	0.46	0.70	0.36	0.57	0.71	0.44	0.60	0.54		0.56				

B: Ciliate morphotypes (T = 260)

	Coefficients for morphotypes										for covariates			
	Urf	Bal	Ask	Oli	Ped	Tin	LiP	His	Ur3	Rim	cope	clado	ed	temp
Urf	0.42	−0.07				−0.05*					−0.23*	−0.13*	0.29*	
Bal	−0.09	0.45				−0.12*				−0.19*	−0.17	−0.21*	0.28*	
Ask			0.44								−0.21*		0.17*	
Oli			−0.12*	0.54							−0.17*	−0.07*	0.22*	0.04*
Ped					0.41						−0.53*		0.53*	
Tin		−0.16*				0.56					−0.27*	−0.21*		
LiP		−0.08					0.32			−0.06		−0.12*		
His	−0.10					−0.06*		0.67			−0.14			0.09*
Ur3		−0.11*							0.50		−0.39*			0.06*
Rim			−0.25*	−0.18*						0.34	−0.14		0.36*	
Model fit											average model fit			
R^2	0.39	0.48	0.31	0.42	0.35	0.45	0.17	0.67	0.45	0.20		0.39		