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A seasonal alternation of coherent and compensatory dynamics occurs in phytoplankton

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Functional groups with diverse responses to environmental factors sum to produce communities with less temporal variability in their biomass than those lacking this diversity. The detection of these compensatory dynamics can be complicated by a spatio-temporal alternation in the environmental factors limiting growth (both abiotic and biotic), which restricts the occurrence of compensatory dynamics to certain periods or locations. Hence, resolving the spatio-temporal scale may uncover important spatial and/or temporal components in community variability. Using long-term data from Lake Constance (Bodensee), we find that a reduction in grazing pressure and relaxed competition for nutrients during winter and spring generates coherent dynamics among edible and less edible phytoplankton. During summer and fall, when both grazing pressure and nutrient limitation are present, edible and less edible phytoplankton exhibit compensatory dynamics. This study supports recent work suggesting that both abiotic and biotic interactions promote compensatory dynamics and to our knowledge, this is the first example of a system where compensatory and coherent dynamics seasonally alternate.

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The temporal variability of populations and communities, and the relationship between population and community variability, has received much attention over the past half-century. Odum (1953) and Elton (1958) both suggested that communities made up of diverse assemblages of species have less temporal variability in biomass than their species-poor counterparts. Later theoretical results were not supportive (May 1973); however, recent advances have shown that this relationship can depend on the response of the individual populations to environmental fluctuations; where individual populations negatively co-vary, they sum to produce less variable communities due to compensatory dynamics (Tilman 1996, 1998), and where individual populations vary independently they sum to produce less variable communities due to simple statistical averaging (Doak et al. 1998). Despite these not mutually exclusive relationships, empirical evidence for a general relationship between population and community variability has not been unequivocal (reviewed by Cottingham et al. 2001).

In an experimental study of planktonic algae, Gonzalez and Descamps-Julien (2004) showed that communities experiencing periodic temperature fluctuations were less variable than those experiencing a constant temperature; thus compensatory dynamics can occur with periodic regularity in response to periodic environmental fluctuation. However, this introduces an additional issue in natural systems; negative co-variance between functional groups at short temporal scales

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may be obscured by positive co-variance between functional groups in response to long term changes in the physical environment (e.g. annual variability, el Niño/la Niña events) or they may only be evident during periods when certain limiting factors operate (e.g. during drought, food scarcity). Resolving the temporal dependence of compensatory dynamics may provide new insight into the way functional diversity influences the variability of aggregate metrics such as community biomass.

In temperate lakes and marine systems, plankton communities experience a seasonal succession of population dominance that is driven to a large extent by exogenous abiotic factors in winter/spring and endogenous food-web processes in summer (Sommer et al. 1986). Late winter and early spring phytoplankton populations are typically limited by low light availability; grazing pressure from predators is low and nutrient concentrations are at maximum (non-limiting) values. In deep waters, wind-driven mixing continuously forces photosynthesising organisms into depths beyond which adequate light penetrates. Following this period, a decrease in deep-mixing triggers the onset of the spring phytoplankton bloom (Gaedke et al. 1998), which in turn leads to a depletion of available nutrients and an increase in herbivore biomass (and thus grazing pressure). Phytoplankton remains under mixed control by nutrients and herbivore grazing for the remainder of the summer and fall (Sommer et al. 1986).

Due to the seasonal succession of growth determining factors in temperate waters, phytoplankton functional groups may elicit differential responses to environmental factors only during a fraction of the year. It is well established that various functional groups of phytoplankton recurrently occur in temperate waters whereas their species compositions are more variable across time and systems (Reynolds 1993). In Lake Constance, a clear pattern of positive covariance exists between species within a functional group (Huber and U. Gaedke, unpubl.), and hence, there is no principal difference if the dynamics of the entire functional group, or of representative members, are considered. Hulot et al. (2000) showed that a community model of functional groups, rather than individual species, provided a better mechanistic understanding of a lake ecosystem to nutrient enrichment. We search for such temporal patterns at the level of functional groups rather than at the species level to achieve a higher level of generality and predictability.

We aggregated phytoplankton into groups classified by their degree of edibility, which captures aspects of size, shape, colonialism, and additional factors such as growth rate, nutrient demands, sedimentation, etc. Edible phytoplankton morphotypes are heavily grazed by ciliates and herbivorous cladocerans during the growing season, while less edible morphotypes are predominantly consumed by other zooplankton, such as copepods or specialized microzooplankton. This raises the expectation that edible and less edible phytoplankton will vary coherently during periods of light limitation, due to a synchronous response of both groups to changes in light intensity. During periods of mixed control by nutrients and grazing we expect edible and less edible groups to show compensatory dynamics, due to their differential susceptibility to grazing and competition for nutrients (Fig. 1). Theoretical studies have shown that differential susceptibility to predators generates negative covariance, and thus compensatory dynamics among prey functional groups (McCann 2000). In our example fast-growing edible morphotypes reach their peak biomass when grazing pressure is low, but during periods of heavy grazing they decline and less edible morphotypes are released from competition (Fig. 1 bottom-right). Combinations of abiotic and biotic interactions driving a competitive release have been observed to generate compensatory dynamics in previous studies (Pollock et al. 1995, Fischer et al. 2001). Here we provide an example where temporal resolution of functional group dynamics shows a seasonal alternation of coherent and compensatory dynamics, enhancing our understanding of the relationship between functional diversity and variability.

Methods

Data collection

Plankton samples were collected from the north-western arm of large (473 km^2), deep ($\bar{z}$ =101 m), mesotrophic Lake Constance (Bodensee, located north of the European Alps) from 1979–1998. A total of N = 836 samples were unevenly distributed over the sampling duration; sampling generally occurred weekly during the growing season and every 2–3 weeks in winter ($\Delta f_{avg} = 1/9.07\ day^{-1}$). Organisms were taxonomically resolved to species or to a higher taxonomic level at the time of counting. To account for the large differences in cell size among species, cell densities were converted to units of carbon based upon regular measurements of species-specific cell volumes and assuming a carbon:freshweight ratio of 0.14 (Gaedke 1998, Gaedke et al. 2002). Phytoplankton morphotypes were functionally grouped into "edible" and "less edible" categories based upon their shape, size, defence tactics, and susceptibility to grazing – mainly by ciliates and rather small cladocerans such as *Daphnia hyalina* and *D. galeata* (Gaedke 1998). Edible phytoplankton are typically fast-growing small unicellular nanoplankters and small centric diatoms, whereas large unicells, colony forming species, filamentous algae and pennate diatoms are typically less edible for the above mentioned grazers (Knisely and Geller 1986, Müller and Schlegel 1999). Calanoid and cyclo-

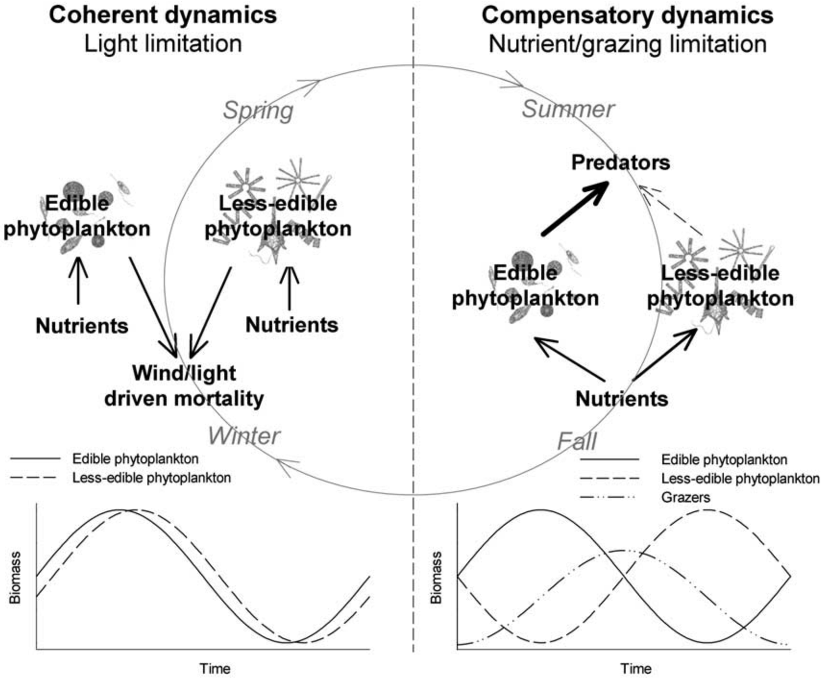


Fig. 1. A seasonal alternation of coherent and compensatory dynamics among edible and less edible phytoplankton is expected from changes in the factors limiting phytoplankton growth. In winter/spring, grazing pressure from predators is low, nutrients are non-limiting and both edible and less edible phytoplankton are similarly affected by wind-driven changes in the underwater light climate. In summer/fall, edible and less edible phytoplankton compete for nutrients but experience different levels of grazing pressure from predators. The temporal dynamics shown in the bottom panels are examples of the expected dynamical relationship, but do not reflect normal temporal trends during those seasons.

poid copepods often graze upon these larger particles but contribute less to overall herbivory. In Lake Constance there are few truly inedible species such as cyanobacteria (Gaedke 1998) and most primary production is consumed (Gaedke et al. 2002).

Within each functional group, and for the aggregate phytoplankton, we summed the biomasses of individual morphotypes at each sampling event. We log-transformed these data to account for the long-tailed residual distribution of biomasses common to phytoplankton; seasonal variation in the biomass of individual morphotypes commonly covers three to four orders of magnitude.

Data analysis

Detection of temporal trends in the co-variance of functional groups is complicated by the year-to-year variability in the timing and intensity of limiting factors and by the natural variability and measurement error incorporated in phytoplankton biomass measurements. In addition, long term data with high temporal resolution is required to find recurrent annual trends. Here we use a novel methodological approach incorporating spectral analysis and phase estimation to test our hypothesis using data from Lake Constance.

Addressing the problem we have specified here requires the identification of temporal changes in the variance and co-variance of functional groups, which is complicated by our use of unevenly sampled data. This limitation is often overcome by interpolating missing observations or ‘‘re-binning’’ data into equally spaced intervals of time. However, the former can introduce artefactual autocorrelation in the interpolated points (Schulz and Stattegger 1997) and the latter comes at the cost of reducing the temporal resolution of the results. Alternatively, one can compute the frequency spectrum from the data and use these results to formulate a continuous-time proxy of the discretely sampled time-series. We adopt this approach to identify the temporal scales and periods at which edible and less edible functional groups co-vary. We focus on temporal scales from approximately one month to one year to capture recurrent dynamical patterns and to ignore variance generated from long term changes in the eutrophication status of Lake Constance (Güde and Gries 1998).

The utility of spectral analysis in ecological research was first described by Platt and Denman (1975) and has since been used to seek periodicities in data (Van Voris et al. 1980) and to examine the underlying structure of biomass variability (Inchausti and Halley 2001) and environmental variability (Vasseur and Yodzis 2004). Traditional spectral analysis computes a smoothed periodogram, where the periodogram, which represents the ‘‘fit’’ of each harmonic frequency in the temporal data, is first calculated from the discrete Fourier transform of the data (Chatfield 2004). However, this transform requires the data to be evenly spaced in time. We employ a smoothed Lomb-Scargle periodogram (Lomb 1976, Scargle 1982), which has seen only limited use in ecological research (Kirchner and Weil 2000), to estimate the spectrum and to overcome the requirement of evenly spaced data. We use the algorithm provided by Press et al. (2001) which defines the periodogram P as a function of angular frequency ω:

$$P(\omega) = \left\{ \frac{\left(\sum_j (X(t_j) - \bar{X}) \cos\omega(t_j - \tau) \right)^2}{\sum_j \cos^2\omega(t_j - \tau)} + \frac{\left(\sum_j (X(t_j) - \bar{X}) \sin\omega(t_j - \tau) \right)^2}{\sum_j \sin^2\omega(t_j - \tau)} \right\}$$

where $X(t_j)$ is the log-transformed biomass taken on day t_j, $j = 1 \ldots N$ (for our dataset t_1 is 01 Jan 1979), $\bar{X}$ is the mean of $X(t_j)$, and τ is defined by the relation:

$$\tan(2\omega\tau) = \frac{\sum_j \sin 2\omega t_j}{\sum_j \cos 2\omega t_j}$$

Defining τ in this manner makes estimates of P(ω) invariant to any differences in the phases of harmonic components in the data (Scargle 1982). At each frequency (ω) the periodogram P(ω) is the reduction in the sum-of-squares of $X(t_j)$ achieved by removing a periodic component with frequency ω from the time-series $X(t_j)$. Thus, frequencies with larger amplitudes in the periodogram explain a larger proportion of the temporal variance (σ_X^2) than those frequencies with smaller amplitudes. To estimate the spectrum $\hat{S}(\omega)$, we smoothed the periodogram using a Bartlett window:

$$\hat{S}(\omega) = \frac{1}{2M + 1} \sum_{j=-M}^{M} P(\omega_j) \left(1 - \frac{|j|}{M} \right)$$

where j varies across $M = 6$ consecutive integers so that the ω_j are symmetric about ω (Chatfield 2004).

The Lomb-Scargle approach to spectrum estimation has the additional advantage that the spectrum, normalised by twice the variance of the time-series $X(t_j)$ – $\hat{S}_N(\omega) = \hat{S}(\omega)/2\sigma_X^2$, follows an exponential probability distribution (Scargle 1982). We use this distribution to determine the probability that the value of $\overline{S}_N(\omega)$ at each frequency ω was significantly different from white noise (all frequencies contributing equally to the temporal variance). Before significance estimation we first removed any log-linear trend in the spectrum using least-squares regression. This transformation was performed since the critical distribution of $\hat{S}_N(\omega)$ assumes no trend (white noise), and our data have spectra that scale according to the inverse power law $1/\omega^\beta$, $\beta > 0$ (red noise – low frequencies contribute relatively more to the temporal variance). This scaling property is common to a large variety biological data (Inchausti and Halley 2001) and the adjustment used here makes our significance estimates more conservative than had we left the spectrum untransformed.

To account for the effects of spectral leakage, whereby a dominant peak at some frequency generates additional, albeit lesser, peaks at harmonic frequencies, we used a recursive approach to determine the significance of subsequent components. After estimating the significance of the largest component in the spectrum, and provided that $p < 0.05$, we detrended the time-series at the frequency of this component using least-squares harmonic regression. Following this we re-generated the spectrum, and estimated the significance of the largest remaining component in the spectrum. We continued this process of spectrum-generation, significance estimation and detrending until the largest spectral component was not significant ($p > 0.05$). For ease of comparison to the data we converted angular frequency ω to temporal frequency f ($f \equiv \omega/2\pi$) which has the more amenable units of 1/day.

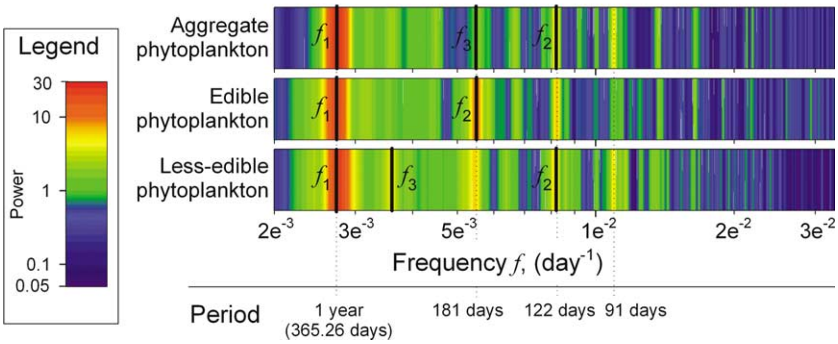
Results and discussion

Figure 2 shows the estimated spectra for aggregate phytoplankton, edible phytoplankton, and less edible phytoplankton in Lake Constance. In this figure, we use a gradient of colour to represent the spectrum $\hat{S}_N(\omega)$; violet bands represent frequencies with the weakest contributions to the time-series whilst red bands represent frequencies with the strongest contributions. Frequencies with significant periodic components are labelled f_i where i denotes their order of dominance. Significant frequencies, their associated p-values, and the fraction of temporal variance explained by each are shown in Table 1.

Not surprisingly, the periodic component at $f \approx 1/365.25$ days (1/year) dominates each of the three spectra. This component represents the variability explained by the annual environmental cycle, which is the strongest periodic force in this and most other temperate systems. The strength of this frequency in the "aggregate phytoplankton" spectrum indicates coherence among the annual cycles of edible and less edible phytoplankton. For example, if edible and less edible phytoplankton negatively co-varied at the yearly scale, their summed biomass would show little remaining periodicity, provided that the mean and amplitude of the seasonal variability are approximately even among groups (which is true here). The actual phase difference between these groups is approximately 1/6 year with edible phytoplankton peaking earlier than less edible phytoplankton.

In addition to the seasonal cycle, each of the spectra have one or two subsidiary periodic components. It is interesting to note that these components are also common to herbivorous cladocerans, which graze heavily on edible phytoplankton, and to copepods, which consume the majority of less edible phytoplankton (D. A. Vasseur and U. Gaedke, unpubl.). Particularly

Fig. 2. Power spectra for the aggregate phytoplankton, edible, and less edible phytoplankton. The colour intensity describes the relative amount of temporal variance that is explained by each frequency (Methods); both the colour intensity and frequency are shown using logarithmic scales. Significant periodic components f_i are labelled in their order of dominance (Table 1). Spectra show the frequency interval from 1/500 days to 1/30 days and they are smoother at low frequencies due to the linear distribution frequencies shown on a log scale.



interesting is the partitioning of the 1/181 and 1/122 day^{-1} components in the aggregate phytoplankton to the edible and less edible phytoplankton, respectively. The ratio of the frequencies of these two components (2:3) creates an annually repeating dynamic; over one year edible phytoplankton complete two cycles in their biomass while less edible phytoplankton complete three complete cycles. We detail this pattern of oscillation below and show how it describes the seasonal alternation of compensatory and coherent dynamics shown in Fig. 1.

Figure 3a and 3b show the secondary periodic components of edible and less edible phytoplankton superimposed over two years of data that are typical of the entire 20-year dataset. These data have the seasonal trend and mean removed and the phase and amplitude of the periodic components were estimated using harmonic regression. Overlaying the two components from panels in Fig. 3a and 3b shows a smooth transition from coherent dynamics in winter and spring to compensatory dynamics in summer and fall (Fig. 3c). Plotting the relative phase difference (Fig. 3e) confirms this transition and shows that the two groups reach absolute coherence near Julian day 63 (approximately March 4) and absolute compensation near Julian day 245 (approximately September 2). These results are supported by the cross-correlation coefficients of the two functional groups segregated into winter/spring and summer/fall periods: during winter/spring $r = 0.28 \pm 0.06$ (SE) and summer/fall $r = 0.06 \pm 0.06$ (SE). This alternation suggests that the variability of aggregate phytoplankton biomass should be reduced by negative co-variance among edible/less edible phytoplankton during the summer/fall, yet increased by positive co-variance during winter/spring. This is easily seen in Fig. 3d, where the sum of edible and less edible phytoplankton biomass from Fig. 3c shows that extreme biomass values occur during winter and spring whilst in summer and fall, biomass is less variable. We find that the temporal variance of aggregate phytoplankton, segregated into winter/spring and summer/fall periods, corroborates this suggestion: winter/spring $\sigma^2 = 0.16$; summer/fall $\sigma^2 = 0.09$. Resolving the extent to which this alternation in the variance of aggregate phytoplankton biomass influences the grazing community may provide insight into their temporal biomass patterns and ultimately into food-web stability.

Table 1. Significant periodic components in the aggregate phytoplankton and in the edible and less edible phytoplankton functional groups.

f_i	Frequency (day^{-1})	Period (day)	p-value	$\%\sigma^2_X$ explained†
Aggregate phytoplankton community				
f_1	0.0027	365.7	<0.0001	31.4
f_2	0.0082	122.2	<0.0005	5.6
f_3	0.0055	181.4	<0.01	4.2
Edible phytoplankton				
f_1	0.0027	365.7	<0.0001	22.8
f_2	0.0055	181.4	<0.0001	13.8
Less edible phytoplankton				
f_1	0.0028	365.3	<0.0001	22.9
f_2	0.0082	122.0	<0.0001	9.5
f_3	0.0036	277.4	<0.001	4.3

†$\%\sigma^2_X$ explained is the percentage reduction in the temporal variance of $X(t_j)$ following detrending at f_i. These estimates are slightly larger than those produced by integration of the spectrum, since they also account for the variance explained at harmonic frequencies.

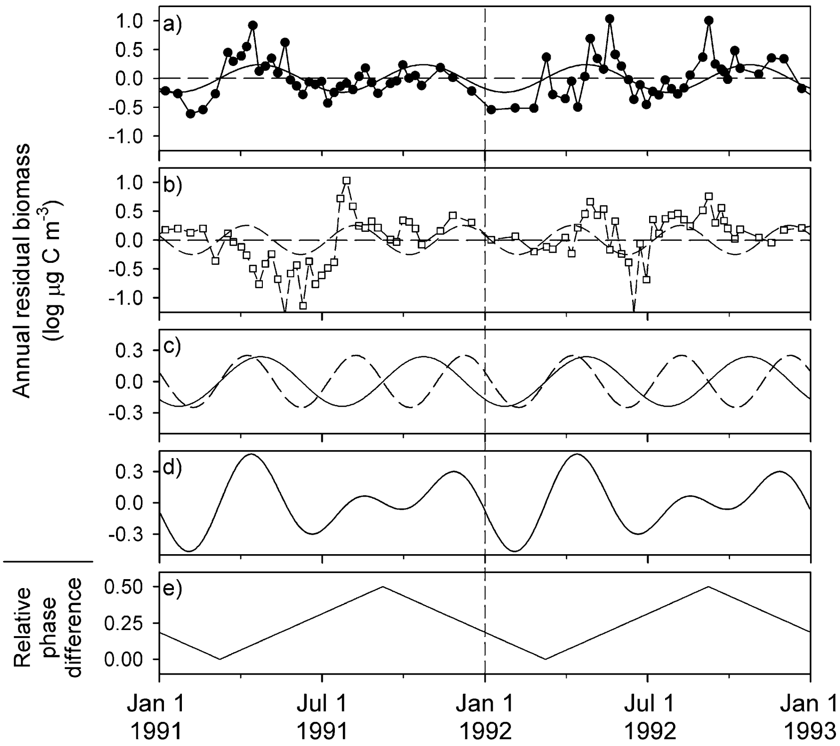


Fig. 3. Annual residual biomass of (a) edible phytoplankton and (b) less edible phytoplankton and their secondary periodic components (1/181 day^{-1} and 1/122 day^{-1} respectively) for two years that are typical of the entire dataset (1991–92). Annual residual biomass was obtained by subtracting the annual mean biomass from each data point. Panel (c) shows the two secondary periodic components from panels (a) and (b) overlaid, and panel (d) shows their sum. In panel (e) the relative phase difference of the secondary periodic components is shown; when the phase difference is zero the dynamics are perfectly coherent while a phase difference of 0.5 produces perfectly compensatory dynamics. Intermediate values are either more coherent (<0.25) or more compensatory (>0.25).

Our suggestion from Fig. 1, that the change in dynamics from coherent to compensatory is driven by a seasonal alternation in the factors limiting phytoplankton growth, is upheld by correlative data. Figure 4 shows the relative phase difference of edible and less edible phytoplankton from Fig. 3e, plotted against the annual residuals of soluble reactive phosphorous concentrations (SRP) and cladoceran biomass. Phosphorous is the limiting nutrient in Lake Constance (Gaedke 1998) and cladoceran biomass provides a useful measure of the grazing pressure experienced by edible phytoplankton during summer (Sterner 1989, Gaedke et al. 2002). In summer and fall, competition among edible and less edible phytoplankton is elevated due to low nutrient availability. Higher growth rates of edible morphotypes allow them to grow quickly but grazers respond – lowering the biomass of edible morphotypes and releasing the less edible morphotypes from competition. Thus, the two functional groups display compensatory variability during this period. These results corroborate the majority of studies cited by Micheli et al. (1999) which emphasised that compensatory dynamics are stimulated by both abiotic and biotic interactions. To our knowledge this study provides the

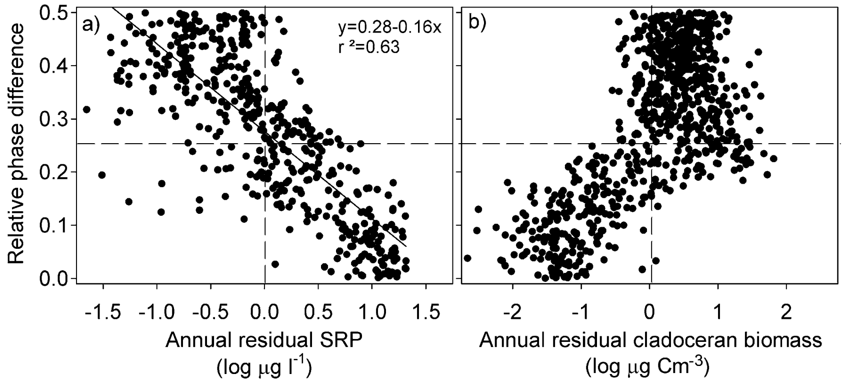


Fig. 4. The relationship between the relative phase difference (Fig. 3e) and (a) annual residual soluble reactive phosphorus (SRP) concentration (mean value 0–20 m depth) and (b) annual residual cladoceran biomass (providing a measure of grazing pressure). We show annual residual values in both panels to remove inter-annual variability caused by a shift in the trophic status of Lake Constance over the study period (Güde and Gries 1998). Both low phosphorus concentration and high grazing pressure are needed to generate compensatory dynamics (relative phase difference >0.25).

first example of a system displaying both compensatory and coherent dynamics, where the temporal pattern is explained by a seasonal alternation in the intensity of competition for nutrients, grazing pressure and light limitation.

The advantage of using the spectrum to analyse dynamics is evident in our study, since the found alternation in coherent and compensatory dynamics is not detectable in a simple analysis of co-variance. In our example coherent dynamics during winter and spring would counteract summer and fall compensatory dynamics leading to an overall much weaker expression of any co-variance between functional groups. The method used here to separate periodic components from background noise is warranted only when periodic components explain a significant portion of the variance. This requirement is likely satisfied in the majority of systems given that environmental variables often cycle at the annual scale and that biotic interactions can themselves generate cycles (e.g. predator–prey cycles). Micheli et al. (1999) highlighted the potential for the spatial and temporal scale of measurement to obscure patterns in the variability and here we show that temporal patterns can be revealed given the proper methodology. Application of this method to spatial data may reveal a similar obscurity of small-scale patterns in the spatial distribution of organisms.

Although the taxonomic composition of the edible and less edible functional groups can be highly variable across systems, the existence and role of these functional groups in aquatic systems is consistent. Similarly consistent across systems is the seasonal succession of events described in the introduction (Sommer et al. 1986). This suggests that the seasonal alternation in coherent and compensatory dynamics between edible and less edible phytoplankton found here may be a general phenomenon for temperate plankton systems. Further research is warranted to determine the extent to which these results influence the dynamics of the entire food-web, the generality of these results for other systems and the importance of other temporally-variable limiting factors.

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