



Variability patterns differ between standing stock and process rates

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Standing stocks are typically easier to measure than process rates such as production. Hence, stocks are often used as indicators of ecosystem functions although the latter are generally more strongly related to rates than to stocks. The regulation of stocks and rates and thus their variability over time may differ, as stocks constitute the net result of production and losses. Based on long-term high frequency measurements in a large, deep lake we explore the variability patterns in primary and bacterial production and relate them to those of the corresponding standing stocks, i.e. chlorophyll concentration, phytoplankton and bacterial biomass. We employ different methods (coefficient of variation, spline fitting and spectral analysis) which complement each other for assessing the variability present in the plankton data, at different temporal scales. In phytoplankton, we found that the overall variability of primary production is dominated by fluctuations at low frequencies, such as the annual, whereas in stocks and chlorophyll in particular, higher frequencies contribute substantially to the overall variance. This suggests that using standing stocks instead of rate measures leads to an under- or overestimation of food shortage for consumers during distinct periods of the year. The range of annual variation in bacterial production is 8 times greater than biomass, showing that the variability of bacterial activity (e.g. oxygen consumption, remineralisation) would be underestimated if biomass is used. The P/B ratios were variable and although clear trends are present in both bacteria and phytoplankton, no systematic relationship between stock and rate measures were found for the two groups. Hence, standing stock and process rate measures exhibit different variability patterns and care is needed when interpreting the mechanisms and implications of the variability encountered.

The variability of ecosystem functions and the processes which influence them are currently of focal interest, for example in the context of the diversity–variability debate (Loreau 2000, Hooper et al. 2005) and for predicting the consequences of land use and climate change (Fay et al. 2009, Felzer et al. 2009). The quantity and temporal variability of ecosystem functions are frequently inferred from measurements of standing stocks, such as biomass and chlorophyll concentration (Tilman et al. 1996, 1997, van der Heijden et al. 1998, Hector 1999, Huston et al. 2000, Lu 2006) since they are often easier to measure than process rates. However, standing stocks constitute the net result of production and losses and may exhibit variability patterns which differ from those of the process rates. In fact, some previous studies acknowledged the necessity of distinguishing standing stocks from ecosystem functions (Petchey 2003) and suggested that standing stocks may be less able to capture trophic level effects than process rate measures (Srivastava et al. 2009).

Standing stocks are linked to process rates as the latter are influenced by the amount of biomass available at a particular time. However, process rates are also governed by mass specific rates, that is, how much the available biomass is actually processing given the biotic and abiotic factors

influencing it. Using standing stocks as surrogates for process rates assumes the mass specific rates to be constant, which is known to be equivocal (Begon et al. 2006). Process rates are influenced by abiotic factors such as temperature and light availability, and biotic mechanisms such as the life history strategy of the dominant species and the extent of predation pressure. Hence, production, which is here of focal interest as it sustains the biomass of the higher trophic levels and is linked to numerous ecosystem functions, may be strongly influenced by density dependent factors at a multitude of time scales. For autotrophs, self-shading is well known to reduce the mass specific production (P/B ratio) when high plant biomass is attained; primary production levels off at high abundance (Häse et al. 1998) resulting in a negative density dependence. The opposite pattern has been observed for bacteria which show increasing P/B ratios with biomass when resources are abundant. Under these conditions, the mean growth rate of the bacterial community also increases because a higher portion of the previously metabolically inert cells becomes active (Simon and Wunsch 1998).

The present study investigates the variability in production and stock values and in P/B ratios in two contrasting models – negatively density-dependent phytoplankton and

positively density-dependent bacteria – in order to test the relationship between standing stocks and production. Long term high-frequency measurements of both standing stocks and production of bacteria and phytoplankton were conducted in Lake Constance, making it an excellent case to explore the potential relationships between the two. Phytoplankton biomass, chlorophyll concentration and bacterial biomass constitute our standing stocks measurements and their variability patterns will be compared to direct simultaneous measures of primary and bacterial production in the same water body. Both stocks and production levels are strongly driven by physical factors in this system but variability also arises from endogenous food-web interactions during the growing season (Vasseur et al. 2005).

The variability of natural populations and communities is scale-dependent (Vasseur et al. 2005, Keitt and Fischer 2006, Vasseur and Gaedke 2007) and their quantification is subject to numerous potential sources of error (McArdle et al. 1990, Gaston and McArdle 1994). There is not one single measure which accounts for all aspects of variability and as a consequence, different complementary techniques were used and compared. In particular, we analyze the total amount of variability using the coefficient of variation, the main annual patterns using a spline approach and the frequency-resolved variability pattern of the long time series using spectral analysis, since differences in variability patterns at one frequency may be obscured by coherence at others (Micheli et al. 1999, Vasseur et al. 2005, Downing et al. 2008).

Stocks are often used as surrogates to infer the variability patterns of process rates and ecosystem functions due to the lack of process rate estimates (Cardinale et al. 2006). Overall, our objective is to evaluate the predictive power of stocks for process rates given that standing stocks and process rates depend on numerous different factors acting at different temporal scales. In particular, we examine the deviations between stock and rates, notably in respect to density dependence factors. A better understanding of the differences in their variability patterns is of outstanding importance for ecosystem and food web research.

Study site, material and methods

Data acquisition

Upper Lake Constance (Bodensee) is a large (472 km²), deep (depth = 101 m) temperate lake located at approximately 47°40'N, 9°20'E and bordered by Germany, Switzerland and Austria. Warm-monomictic Lake Constance underwent a re-oligotrophication process with a decline of total phosphorus concentrations (the most limiting nutrient for phytoplankton) from > 80 in 1979 to 17 µg TP l⁻¹ in 2000, resulting in a pronounced phosphorus depletion in the epilimnion during summer (Güde and Gries 1998). Mean annual phytoplankton biomass declined by a factor of 2 with phosphorous decline and mean chlorophyll concentration and primary production showed no significant decrease between 1980 and 1997 (Gaedke 1998, Häse et al. 1998), indicating that the long-term changes are very small compared to the seasonal dynamics

(Vasseur and Gaedke 2007). Plankton sampling and production measurements were conducted weekly during the growing season and approximately fortnightly in winter by a large team of scientists, culminating in extended time series' for phytoplankton biomass (1979–1999), chlorophyll concentration (1980–2000), primary production (1980–1998) and bacterial biomass and production (1990–1997). Abundances and production of both phytoplankton and bacteria were assessed as described in Gaedke 1998, Simon et al. 1998 and Häse et al. 1998. Production estimates were obtained independently of biomass using 4 h in situ incubation with ¹⁴C (primary production) and with ³H-thymidine and ¹⁴C-leucine using the dual label approach (bacterial production). All measurements are provided per unit area and comprise the biomass and production within the uppermost water layer from 0–20 m depth, which roughly corresponds to the epilimnion and the euphotic zone. Prior to the spline and spectral analyses we log-transformed the biomass and production measurements to account for their long-tailed residual distribution, given that the seasonal variation covered approximately two orders of magnitude (Gaedke 1998). We then applied each of the following measures to phytoplankton biomass, chlorophyll concentration, primary production, bacterial biomass and production and the P/B ratios (primary production/phytoplankton biomass, primary production/chlorophyll concentration and bacterial production/bacterial biomass).

Coefficient of variation

The overall variability was estimated using the coefficient of variation (CV), which is the ratio of the standard deviation to the mean. The CV allows comparison of measures with different units or different means. In order to statistically compare the CVs among the different variables, we calculated the CV per year for each time series and applied a non parametric Wilcoxon-test. The CVs of the P/B ratios were not computed as we do not expect a mean-variance scaling relationship.

Spline fitting

Splines were used to separate the general seasonal signal of each measure from measurement noise. Therefore, we assumed only seasonal dependency for the measure in question, which is continuous and smooth. In order to find this seasonal pattern, we looked for a periodic function approximating the data; that is an optimal compromise between data fit and smoothness. The function is optimal in the sense that it minimizes

$$\frac{1}{N} \sum_{i=1}^N \{f[x(\tau_i)] - \tau_i\}^2 + \frac{1}{\lambda} \int [f^{(2)}(x)]^2 dx$$

for the data points $(x(\tau_i), \tau_i)$, x being the time lapsed since 1 January of the running year. A function solving this minimization problem is called a spline (for details see Wahba 1990). The measurement y_i is the sum of the signal $f(x_i)$ and the noise. The smoothing parameter λ , controlling the tradeoff between data fit (first term) and smoothness (second

term), is optimal when it minimizes the expected prediction error. It is determined by means of generalized cross validation (Craven and Wahba 1979).

We dealt with this fitting problem using a statistical point of view as described in Craven and Wahba (1979). With this approach, we can fit the curve and, in addition, give a well interpretable confidence interval for the 'true' curve. The spline can then be interpreted as the expectation for the measurement depending on the time of the year. The confidence intervals give the uncertainty for the measured value (Wood 2004).

Spectral analysis

Fourier analysis can be used to represent data measured over time (or space) as the sum of many cosine waves of different frequencies. At each frequency the squared amplitude or 'power' is proportional to the amount of the temporal variance it explains, and together the frequencies and squared amplitudes are known as the periodogram. Periodogram estimates are typically averaged over a number of frequencies to generate the spectrum (Chatfield 2004) which has a well described statistical distribution for a variety of noise models. Traditional methods of spectral analysis use a Fourier transformation to generate the periodogram, which requires data sampled at evenly spaced intervals. We employed an alternative method, the Lomb–Scargle periodogram (Lomb 1976, Scargle 1982) which takes into account an uneven distribution of sampling events. At each frequency the Lomb–Scargle periodogram represents the contribution of this frequency to the sum-of-squares. Normalizing the periodogram by twice the variance of the time series generates a χ^2 distribution against which the significance of peaks can be established (Scargle 1982), given an appropriate null model.

We calculated the Lomb–Scargle periodogram using the algorithm provided by Press et al. (2001) and estimated the significance of peaks in the periodogram using an iterative algorithm adapted from Horne and Baliunas (1986). For each time series we generated ten thousand I.I.D. (independent and identically distributed) random normal datasets, with the same mean, variance and sampling distribution as the observed dataset. We selected the largest values from each of the ten thousand periodograms to construct the background distribution. We set the false detection probability as the 95th percentile of this distribution, which is represented as a horizontal line in the periodograms. Since biological variables typically show power which decreases with frequency according to an inverse power law $1/f^\beta$ (Inchausti and Halley 2002, Vasseur and Yodzis 2004) we estimated β as the slope of a log-log regression of power on frequency and added the trend to our null model in order to consider the same amount of colored noise prior to estimating the significance of the peaks in the periodogram. Given a significant peak, we estimated the amplitude and phase according to the method of Hocke (1998). On top of the periodograms, we obtained for each variable a harmonic model $S(\tau_i)$ representing the data in a period equivalent to the annual frequency as the sum of n cosine waves of the n significant frequencies $f_{1,\dots,n}$ with respective amplitudes $A_{1,\dots,n}$ and phases $\Phi_{1,\dots,n}$:

$$S(\tau_i) = \sum_{j=1}^n A_j [\cos(2\pi\tau_i f_j + \Phi_j)]$$

Furthermore, the area under the curve of each periodogram corresponds to the total variance present in the data. The relative contribution of each significant frequency to the total variance was calculated as the percentage of the total area under each peak. All analyses were performed using R ver. 2.6.0 for Windows (2007).

Results

Amount of total variability

The CV reveals a similar amount of total variability for the phytoplankton stock and production measures. Primary production exhibits a CV of 80%, followed by chlorophyll concentration with 91% and phytoplankton biomass with 93% (no significant differences). The CV of bacterial biomass and production are very different, and in contrast to phytoplankton, the CV of production (CV = 90%) significantly exceeds that of biomass (CV = 41%) (p-value < 0.001, $W = 49$).

Splines and harmonic $S(\tau_i)$ models

The splines indicate that the annual patterns for phytoplankton biomass, chlorophyll concentration and primary production are governed by similar processes and are generally characterized by low winter values followed by a spring bloom, a clear-water phase, a summer bloom, and a descent towards low winter values (Fig. 1). Beyond this overall bimodal pattern, differences are found among the different measures. First, in chlorophyll, the spring bloom is more pronounced than the summer bloom; this pattern is weaker in primary production and non-existent in biomass. Secondly, the clear-water phase is less pronounced in primary production than in both measures of stocks. Third, primary production exhibits a larger annual amplitude than the standing stocks measures by reaching relatively higher values during the growing season and lower ones during winter. Fourth, the splines suggest minor deviations in the timing between stock and process rate measures (Fig. 1f). The harmonic $S(\tau_i)$ models are in agreement with the splines, except for primary production, for which only the annual frequency is captured (Fig. 1c). The splines of bacterial biomass and bacterial production show a less complex seasonal pattern than the phytoplankton measures (Fig. 2a–b). Both splines follow the same pattern of low winter and high summer values, with little intra-seasonal fluctuations, but the range of annual variation of the bacterial production spline is 8 times greater than biomass (Fig. 2d). The corresponding harmonic $S(\tau_i)$ models capture only the annual cycle for both measures, with very different amplitudes between bacterial biomass and production.

The differences in the seasonal patterns between standing stocks and production are reflected in the seasonal patterns of the mass-specific rates which are not constant in time but vary up to a factor of 4 for phytoplankton (Fig. 1d–e) and 8 for bacteria (Fig. 2c) throughout the season. An annual cycle remains in the P/B ratios with low winter and high summer

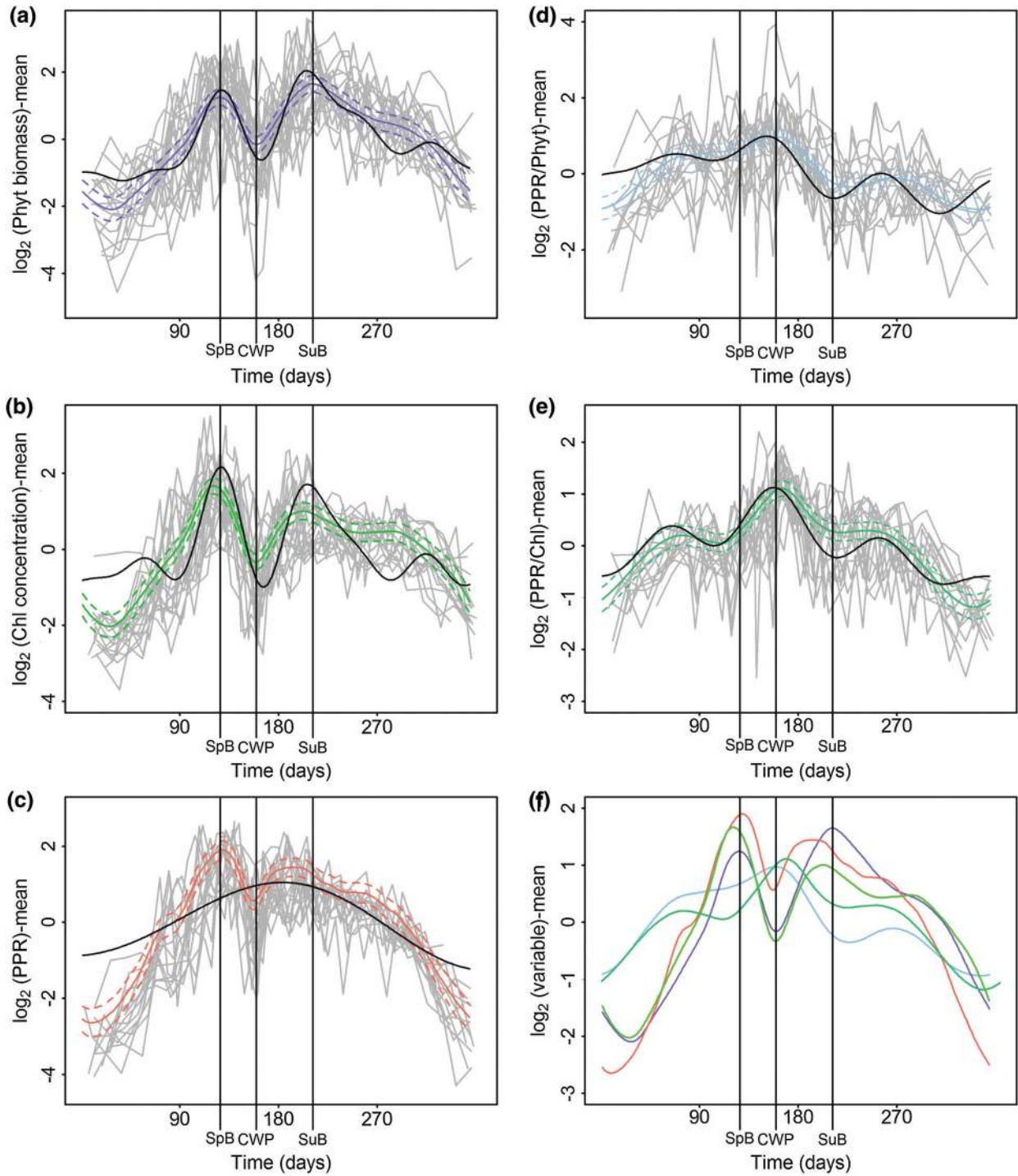


Figure 1. Splines (colored lines), their 95% confidence interval (dashed colored lines), raw time series (grey lines) and harmonic models (black curves) of: (a) phytoplankton biomass (Phyt biomass) (dark blue), (b) chlorophyll concentration (Chl concentration) (dark green), (c) primary production (PPR) (salmon), (d) ratio between primary production and phytoplankton biomass (PPR/Phyt) (light blue), and (e) ratio between primary production and chlorophyll concentration (PPR/Chl) (light green). (f) Splines of Phyt biomass, Chl concentration, PPR, PPR/Phyt and PPR/Chl with the same colors as described above. The three solid vertical lines correspond in order of time to spring bloom (SpB), clear water phase (CWP) and summer bloom (SuB) in phytoplankton biomass. Units: Phytoplankton biomass (g C m^{-2}), Chlorophyll concentration (mg Chl m^{-2}), primary production ($\text{g C m}^{-2} \text{d}^{-1}$). Note the \log_2 scale on the y-axis.

values for all measures, and in particular for the bacterial P/B. In phytoplankton, the clear-water phase is inverted in the P/B ratios as the primary production shows a less pronounced clear-water phase than phytoplankton biomass and chlorophyll concentration.

Periodograms and phase, amplitude and contribution to the overall variance of independent peaks

The periodograms of phytoplankton biomass, chlorophyll concentration and primary production are represented in

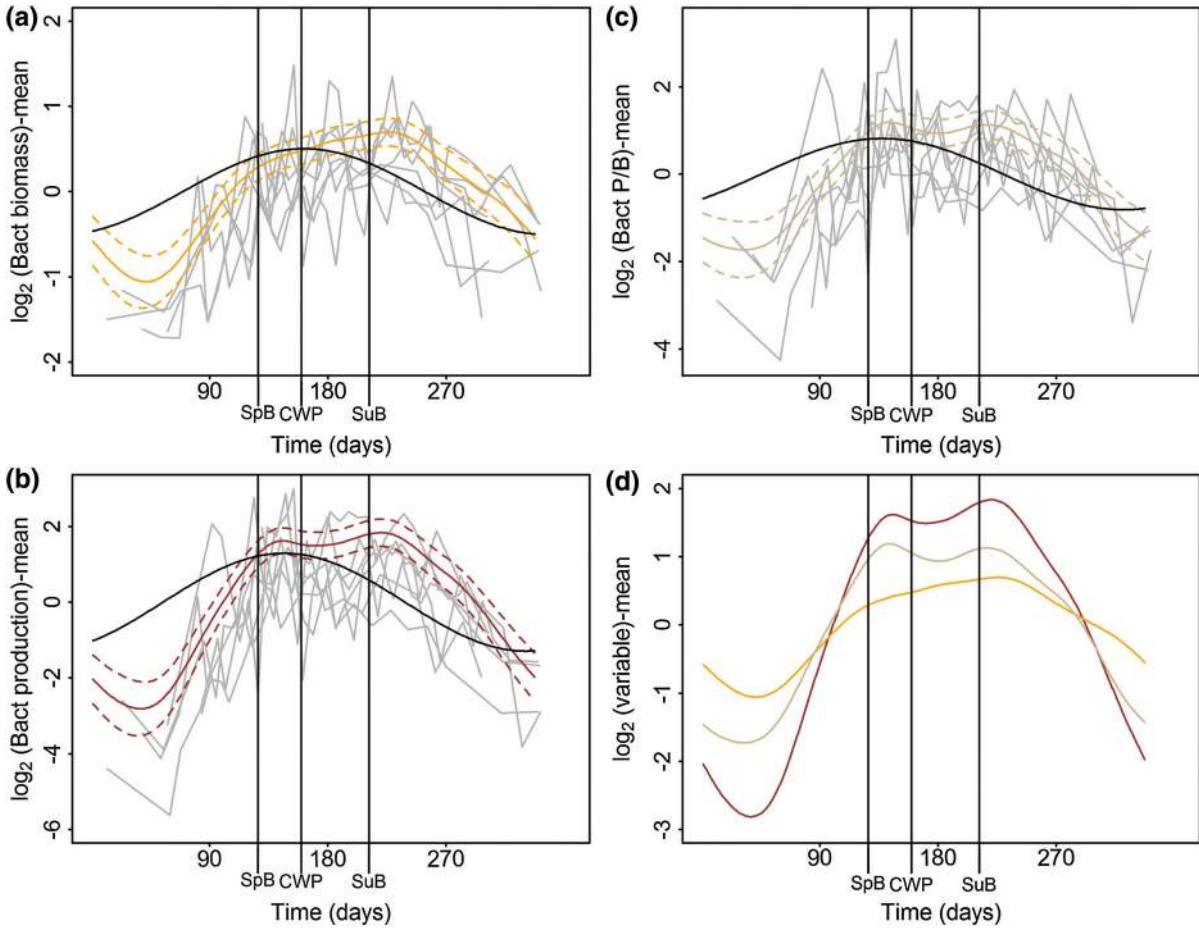


Figure 2. Splines (colored lines), their 95% confidence interval (dashed colored lines), raw time series (grey lines) and harmonic models (black curves) of: (a) bacterial biomass (Bact biomass) (orange), (b) bacterial production (Bact production) (dark brown), and (c) the ratio between bacterial production and bacterial biomass (Bact P/B) (light brown). (d) Splines of Bact biomass (orange), Bact production (dark brown) and Bact P/B (light brown). The three solid vertical lines correspond in order of time to spring bloom (SpB), clear water phase (CWP) and summer bloom (SuB) in phytoplankton biomass. Units: bacteria biomass (mg C m^{-2}) and bacteria production ($\text{mg C m}^{-2} \text{d}^{-1}$). Note the \log_2 scale on the y-axis.

Fig. 3 and phase and amplitude information are synthesized in Fig. 4. The presence of different significant frequencies in the periodograms indicates that the measures vary at different temporal scales. The phytoplankton biomass periodogram has significant frequencies of 1-, 3-, 4-, 5- and 6- cycles per year and the amplitude of the annual is clearly larger than those of the other cycles (Fig. 3a). Chlorophyll concentration is driven by the same frequencies as in phytoplankton biomass and, in addition, by the frequencies of 2- and a new frequency of approximately 4-cycles per year (precisely an 88-day cycle) (Fig. 3b). Here, the annual frequency is also the largest frequency but higher frequencies play an important role as well. The primary production differs greatly from the other measures; the annual amplitude is relatively larger here than in other measures (Fig. 3b) and is accompanied by a second frequency close to the annual (corresponding precisely to a 321-day cycle) which has a much lower amplitude than the annual. Regarding the P/B ratios, significant frequencies remain throughout the year (Fig. 3d-e), as already indicated by the splines. For bacterial biomass and production, only the annual frequency is significant revealing that the largely different amount of variability in bacteria is very similarly

distributed across time for both stock and rate measures (Fig. 3f-g). The amplitude of this frequency is considerably higher in production than in biomass, confirming the results of the splines. As a consequence, the amplitude of the P/B ratio at the annual frequency is still high and even higher than that of the biomass (Fig. 3h).

Synchrony is reflected in the phase relationship between variables at each frequency. Small phase differences in the polar plots result in synchrony, however as phase differences increase, dynamics become more compensatory with maximum compensation at a phase difference of π . The different cycles are rather synchronous for most of the variables and frequencies. In phytoplankton, chlorophyll usually lags behind biomass, and primary production lags behind chlorophyll (Fig. 4). The P/B ratios are in phase with each other but not with the measures of standing stocks and production. Notably for the frequencies of 3- and 4-cycles per year, the ratios are positioned diametrically opposed to the other two standing stocks variables, which can be explained by the inverted clear-water phase. In bacteria, production lags behind biomass as well.

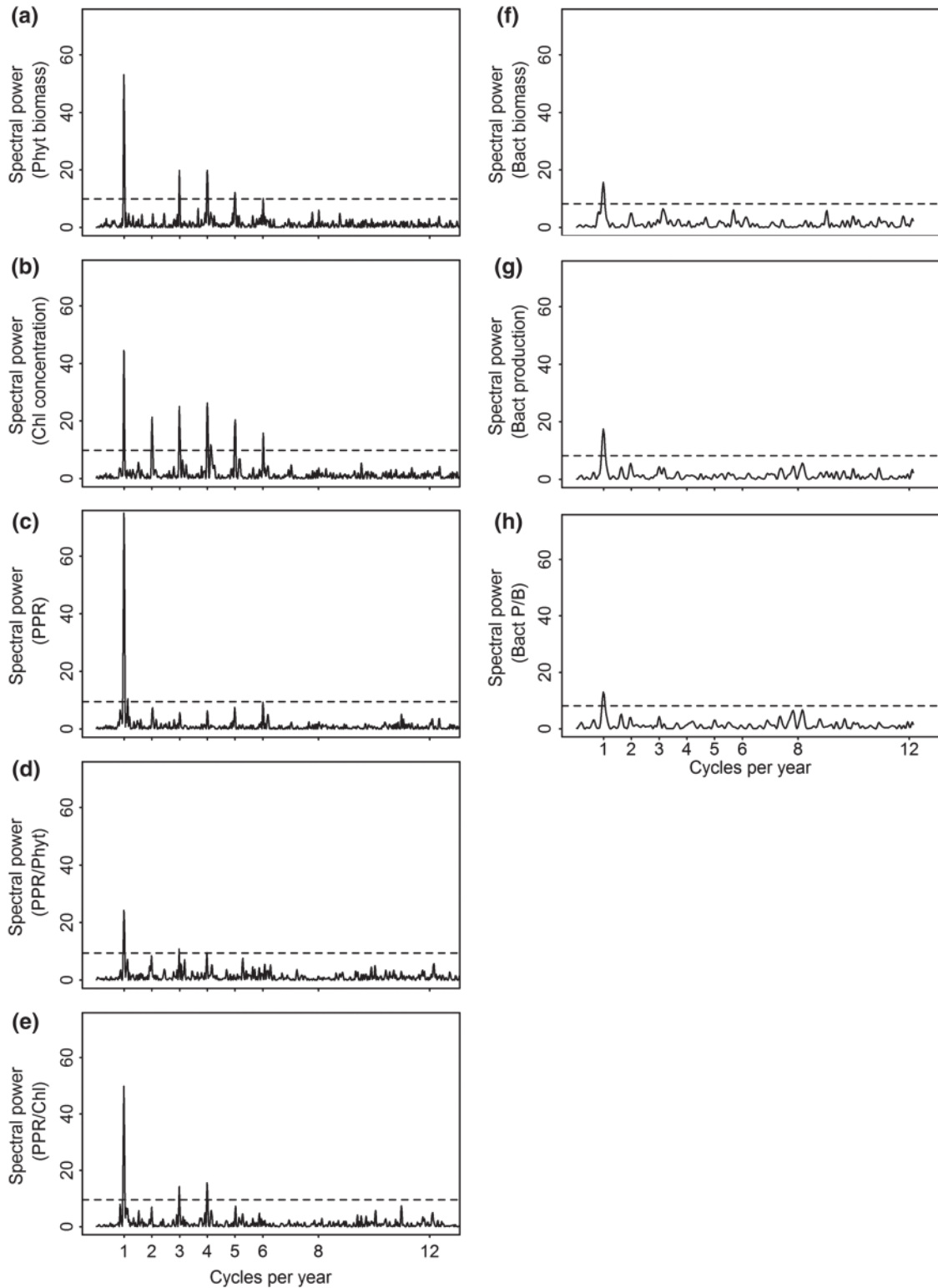


Figure 3. The periodograms show the amount of temporal variance of the log-transformed time-series explained by each frequency. The solid black line is the periodogram of the variables indicated on the y-axis of the graph: phytoplankton biomass (Phyt biomass), chlorophyll concentration (Chl concentration), primary production (PPR), primary production/phytoplankton biomass (PPR/Phyt), primary production/chlorophyll concentration (PPR/Chl), bacteria biomass (Bact biomass), bacteria production (Bact production), bacterial production/bacterial biomass (Bact P/B). The dashed horizontal line indicates the significance level of 5%. Note that in primary production (c), the frequency corresponding to 6-cycles per year does not surpass the significance line. Due to the higher number of sampling dates in the phytoplankton time series, the spectral power is calculated for a higher number of frequencies than those of bacteria. As specified in our methods section, no smoothing was applied. Frequency is shown in cycles per year to ease interpretation.

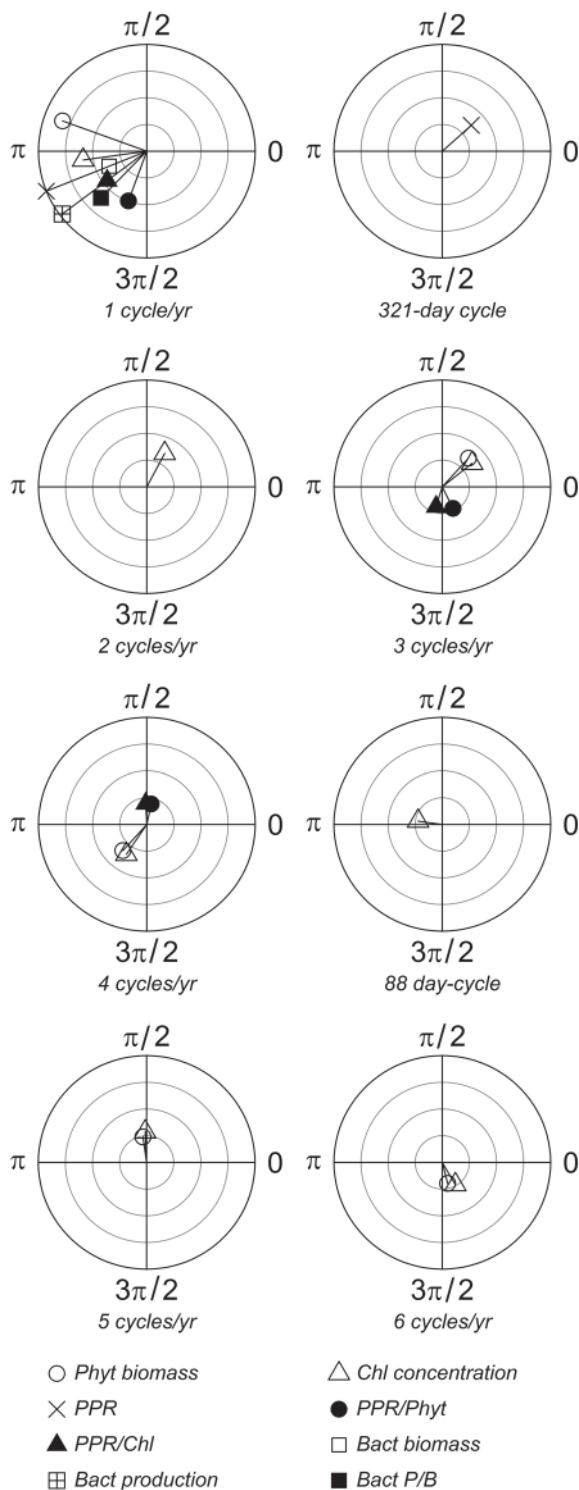


Figure 4. Polar plots of the amplitude (radius) and phase (angle) of each variable reflect the synchrony or asynchrony at each significant frequency. The phase (in radians) measures the shift of the origin of the cosine wave (relative to day 0, in our case 1 January), scaled to the frequency of the wave in question. Small phase differences in the polar plots correspond to synchrony and as phase differences increase, dynamics become more compensatory and maximum compensation is reached at a phase difference of π . The radius of all circles is 1.4, corresponding to the annual amplitude of primary production, the highest amplitude found amongst all variables: phytoplankton biomass (Phyt biomass), chlorophyll

The area under each significant frequency indicates its contribution to the total variance present in the data. Regarding phytoplankton, we found a striking difference between rate and stock measures for the contribution of the annual frequency to the total variance: it explains 34% of the total variance in primary production, 20% in phytoplankton biomass and 13% in chlorophyll. In addition to the annual, significant higher frequencies explain another 4% of the variance in primary production, 11% in phytoplankton biomass and 25% in chlorophyll. The annuals explain 15% of the total variance in the ratio of primary production to phytoplankton biomass and 20% in the ratio of primary production to chlorophyll concentration. Contrary to what we observe in phytoplankton, the annuals of bacterial biomass and production explain similar amounts of the overall variance present in the data (25% and 30%, respectively) despite the strong difference between the annual amplitudes (Fig. 4). The annual explains 22% of the overall variance in bacterial P/B.

Discussion

Our analysis shows that differences are found in the variability patterns of stock and process rate measures, although the qualitative congruency of many of the measures is at the same time quite high. For both bacteria and phytoplankton, stocks are efficient for determining the timing of peaks and troughs present in process rate measures but they are less suitable for indicating the magnitude of the peaks and troughs. In phytoplankton, the overall variability of primary production was strongly dominated by lower frequencies, whereas in stocks, and chlorophyll in particular, higher frequencies substantially contributed to the overall variance. Moreover, our analysis shows that the P/B ratios were variable. In phytoplankton, the P/B ratios were low during blooms and at their maximum when the biomass was low during the clear-water phase. This buffers the variability in food supply for higher trophic levels during the growing season. In contrast, in bacteria, the P/B ratio increased with biomass, implying a much higher variability in bacterial activity than expected from biomass measurements.

The deviations between the variability patterns of the different measures could be quantified by the different methods and they are in agreement with qualitative expectations derived from previous limnological research. The methods complemented each other by assessing different aspects of the variability and pointed out some unexpected features. The CV allowed us to compare the different amounts of total variability and it highlighted the difference between bacterial stock and rate measures. It is important to note that the CV is potentially influenced by the lower number of measurements during winter, leading us to explore other ways to assess the variability in our data.

concentration (Chl concentration), primary production (PPR), primary production/phytoplankton biomass (PPR/Phyt), primary production/chlorophyll concentration (PPR/Chl), bacteria biomass (Bact biomass), bacteria production (Bact production), bacterial production/bacterial biomass (Bact P/B). Each circle represents a different frequency and the length 2π matches the equivalent period.

In contrast to the CV (and spectral analysis, see below), splines are not influenced by the lower number of measurements in winter. They equally represent all parts of the annual patterns for each variable demonstrating important intra-annual patterns. The general seasonal patterns of stock and production measures resembled each other qualitatively due to the similar timing of peaks and troughs, but presented some quantitative differences. For example, the spring bloom was more pronounced in chlorophyll concentration than in phytoplankton biomass whereas the opposite held for the summer bloom. The spring bloom consisted of fast growing, very productive species which are rich in chlorophyll at the still rather low underwater light climate, whereas slow growing larger K-strategists with a lower chlorophyll content dominate during the summer bloom (Sommer et al. 1986). Furthermore, the clear-water phase is less pronounced in primary production than in both measures of stocks due to the presence of very fast growing species and the optimal light availability. We obtained very interesting features for the P/B ratios, with higher values during the clear water phase than during the spring and summer bloom, characterizing self-shading during the blooms, which may have strong implications for the relationship between standing stocks and process rates.

Spectral analysis reveals the distribution of the variance in the frequency domain and how much individual frequencies contribute to the overall variance, as well as their phase and amplitude information. It is important to note that not every frequency can be independently related to a biological process but that it is the result of the sum of frequencies which can properly reflect the general patterns present in the data. The extent to which the harmonic $S(\tau_i)$ models reflected the seasonal pattern shown by the splines depended on the number of significant frequencies. Further differences less visible by the splines were revealed. Only the annual frequency, and a neighbor frequency very close to the annual, were significant in primary production. Higher frequencies are mainly related to the biotic driven processes taking place during the growing season. Even though these processes are present in primary production (as shown by the splines) spectral analysis did not find them significant. This shows how less important their magnitude is compared to the annual for this rate measure. Even though the annual is a clear feature in all variables, winter values were in general overestimated by spectral analysis due to less frequent measurements during winter. The absence of the 2 cycles per year frequency in phytoplankton biomass is another interesting feature and is due to compensatory dynamics within different functional types. Individual species present the two cycles per year frequency but with such different phases that it is no longer apparent in the total biomass (Vasseur and Gaedke 2007). This pattern was not observed in chlorophyll which may partly be attributed to species-specific differences in the chlorophyll content and changes in phytoplankton composition.

The annual frequency was still preserved in the P/B ratios with low winter and high summer values. In phytoplankton, this is due to the fact that during winter, at low light, the phytoplankton is not as productive as in summer. In bacteria, this can be explained by a highly variable fraction of active cells depending on the amount and quality of degradable organic matter and the strong temperature dependence of bacterial

growth (Simon and Wünsch 1998). Furthermore, the phytoplankton P/B ratios were perfectly out of phase with their corresponding stock measures during the growing season, due to the already mentioned processes taking place during blooms and the clear water phase. This suggests that using standing stocks instead of rate measures leads to an underestimation of food shortage for consumers during winter and to a lesser extent during blooms, and an overestimation during the clear-water phase. Hence, P/B ratios vary and there is no simple relationship between standing stocks and process rates. This is particularly important when considering that standing stocks and production both play a crucial yet different role for understanding food web dynamics: the grazing pressure depends on the biomass of the predator whereas how much predator biomass may be sustained depends on prey production rather than on biomass in the long-run. Phytoplankton standing stocks and production are related to different kinds of ecosystem functions: stocks variability gives us information about the variability of stored carbon whereas variability in production addresses rates of carbon fixation which may or may not be stored in the phytoplankton biomass but pass quickly into other components of the ecosystem. In analogy, bacterial biomass indicates the food concentration for bacterivores and the amount of nutrients stored in this food web compartment whereas bacterial production relates to the turn-over rate of organic matter. Hence, these measures provide different information about the system.

The reasons why P/B ratios vary and the differences between them (e.g. self-shading, metabolically inert bacteria, light or temperature dependent rates) are by no means specific to our system but they also apply to most other pelagic and terrestrial systems. Generally, variability of stocks will exceed that of production when a negative density-dependence prevails among production and biomass. For example, dense stands of autotrophs lead to self-shading which will prevent a further increase in production at high biomasses as will a lack of other resources in different contexts as well. In contrast, production will be more variable than stocks when the individual weight specific metabolic rates track strongly the fluctuations in resource supply (e.g. bacteria) and when biomass is bounded e.g. by density dependent loss rates. Both types of density dependence may subsequently occur within one community. For example, a coherent decline of production and biomass at adverse growth conditions in winter and a dampening of production at high biomasses built up under favorable growth conditions were found in phytoplankton.

This underlines the importance of considering time-scale when relating standing stocks and process rates. Although primary production varied slightly less than biomass during the growing season, the highly variable process rates resulted in general in comparatively constant biomasses. Thus, the variability in all ecosystem functions more closely related to process rates (e.g. food supply, rates of carbon fixation, respiration, oxygen consumption and remineralisation) are underestimated if biomass is used as a surrogate for process rates. In the context of the diversity–stability debate, the stability of ecosystem functions is used as a key indicator of the ecosystem's performance. Investigations which look into the stability of ecosystems through measures of stocks disregard a considerable amount of variability in numerous ecosystem

functions and this may have important implications. In general, the mechanisms leading to the variability patterns in stocks and process rates are different showing us that caution is needed when interpreting the consequences of the variability patterns in analyses which incorporate stocks with no information on process rates.

Acknowledgements – We thank J. Freund, A. Rossberg and F. de Castro for comments on the manuscript. MR was partly funded by the Univ. of Potsdam Graduate initiative on Ecological Modelling UPGradE. Data acquisition was performed by a large team of scientists within the Special Collaborative Program (SFB) 248 “Cycling of Matter in Lake Constance” supported by Deutsche Forschungsgemeinschaft (DFG).

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