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Temporal Variability of Standing Stocks of Individual Species, Communities, and the Entire Plankton in Two Lakes of Different Trophic State: Empirical Evidence for Hierarchy Theory and Emergent Properties?

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With 2 Text-Figures and 3 Tables

Abstract

[GAEDKE, U. & BARTHELMESS, T. & STRAILE, D. (1996): Temporal variability of standing stocks of individual species, communities, and the entire plankton in two lakes of different trophic state: empirical evidence for hierarchy theory and emergent properties? – Senckenbergiana marit. **27** (3/6): 169–177, 2 figs., 3 tabs.; Frankfurt a. M.]

Hierarchy theory claims that the structure and function of ecosystems can be analyzed by defining different hierarchical levels which exhibit specific dynamic properties, e.g. higher levels vary on larger spatio-temporal scales than lower ones. These properties are attributed to complex asymmetric interactions between the different subunits and levels. In the present study, comprehensive data sets are evaluated in order to test this hypothesis empirically by analyzing the temporal variability of standing stocks at the levels of individual populations, communities, and the entire plankton in mesotrophic Lake Constance and oligotrophic Königssee. In both lakes, temporal fluctuations decrease consistently with increasing hierarchical levels of integration. The average coefficients of variation (CV) of standing stocks of algal, ciliate, rotifer, and crustacean species, respectively, are all higher than the CV of the total biomass of their communities. The entire plankton biomass, in turn, has a lower CV than each community. In oligotrophic Königssee, the overall level of variability at all hierarchical levels is smaller than in mesotrophic Lake Constance. In both lakes, rotifers exhibit the largest fluctuations on the species and community level. These results hold equally well for root-transformed time series. Thus, a striking regularity of decreasing temporal variability at higher levels of integration can be clearly identified using hard data despite the impact of various other factors influencing temporal fluctuations (e.g. trophic state, generation time, life history). The extent up to which variability changes between hierarchical levels depends on the lake and the considered time scale. This suggests that the smaller temporal fluctuations observed at superior levels of integration are not merely stochastic processes but provide empirical evidence for the validity of hierarchy theory and the related issue of emergent properties.

Kurzfassung

[GAEDKE, U. & BARTHELMESS, T. & STRAILE, D. (1996): Zeitliche Variabilität der Biomasse von Einzelarten, Lebensgemeinschaften und des gesamten Planktons in zwei Seen unterschiedlicher Trophiegrade: Empirische Belege für die Hierachietheorie und emergente Eigenschaften. – Senkkenbergiana marit. **27** (3/6): 169–177, 2 Abb., 3 Tab.; Frankfurt a. M.]

Die Hierarchietheorie postuliert, daß Ökosysteme einen hierarchischen Aufbau haben und daß jede Ebene innerhalb dieser Hierarchie spezifische und teilweise "emergente" Eigenschaften hat, die sich aus den komplexen Wechselwirkungen innerhalb und zwischen den einzelnen Ebenen ergeben. Beispielsweise wird vermutet, daß die unteren Ebenen wesentlich hochfrequentere räumliche

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und zeitliche Fluktuationen aufweisen als die höheren, da letztere die Signale der unteren Ebenen dämpfen und filtern können. Diese bisher eher qualitative Vermutung wurde auf der Basis von umfassenden Datensätzen empirisch überprüft, indem die zeitliche Variabilität der Biomasse auf den hierarchischen Ebenen von Einzelpopulationen, Lebensgemeinschaften (Phytoplankton, Ciliaten, Rotatorien, Crustaceen) und des gesamten Planktons durch Berechnung der jeweiligen Variationskoeffizienten (CV) verglichen wurde. Um den Einfluß externer Faktoren zu quantifizieren, wurde dieser Vergleich mit Messungen vom eu-mesotrophen Bodensee und oligotrophen Königssee durchgeführt. In beiden Seen zeigte sich eine stetige Abnahme der zeitlichen Variabilität mit Zunahme der betrachteten hierarchischen Ebene: Der mittlere CV der einzelnen Populationen jeder Lebensgemeinschaft lag immer über den Werten der Lebensgemeinschaften und diese wiesen wiederum stets eine höhere Variabilität auf als die gesamte Planktonbiomasse. Die absoluten Werte der CV lagen im mesotrophen Bodensee immer über den Vergleichswerten aus dem oligotrophen Königssee. Die Rotatorien wiesen in beiden Seen sowohl auf Artebene als auch als Gemeinschaft die größten Fluktuationen auf. Wurzeltransformationen der Zeitreihen veränderten das Gesamt-Ergebnis nicht. Die vermutete Regelmäßigkeit einer Abnahme der zeitlichen Fluktuationen mit zunehmendem Integrationsniveau konnte also trotz verschiedener anderer Einflußgrößen in realen Datensätzen klar identifiziert und quantifiziert werden. Die Variabilität nahm mit zunehmendem Integrationsniveau je nach betrachtetem See und Zeitintervall in unterschiedlichem Maße ab, was darauf schließen läßt, daß diese Abnahme kein rein stochastischer Effekt ist, sondern auch auf die im Rahmen der Hierarchietheorie postulierten Fähigkeiten zur Selbstregulation zurückzuführen ist.

Introduction

Since the first introduction of the term *ecosystem,* suitable perceptions of ecosystems and their potential properties, succession, and evolution have continuously been debated. One central issue within this framework concerns the controversy between "holists" and "reductionists", i.e. the character and degree of interdependencies between species and their integration within an ecosystem. The assumption that the distribution of species is largely determined by (1) autecological requirements of the individual species, and (2) stochastic transport processes represents a purely reductionistic point of view (for details and references see e.g. Sommer 1996). In contrast, the holistic tradition postulates that "the whole is more than the sum of its parts". The "more" is attributed to the highly integrated, complex hierarchical structure of ecosystems which enables self-organization and self-regulation. The latter give rise to so-called emergent properties of the higher levels of integration (e.g. communities or the entire food web) which are e.g. not derivable from the behaviour of the lower levels of integration (for details, examples, and references see e.g. Salt 1979; Müller 1996). The goal of this investigation is to analyze the validity of this concept from an empirical point of view.

A number of testable hypotheses can be derived from hierarchy theory which formulates rules to identify and characterize levels of integration and their interaction schemes (for details and references see e.g. Müller 1992; Müller 1996). One central hypothesis is that the higher levels act on a larger spatio-temporal scale and define the overall envelope in which the ecosystem may (re)act (e.g. the degree of nutrient recycling) while the lower ones (e.g. the level of populations) represent the biological potential and exhibit much faster changes in space and time. Thus, the superior levels are presumed to have the potential for filtering and smoothing signals received from lower units. This is partially attributed to the potential of self-organization of the system and not merely to the law of great numbers. We will test this hypothesis by analyzing the temporal variability of standing stocks at different levels of integration using comprehensive measurements of plankton abundance from Lake Constance and Königssee. We selected three different levels of integration: the level of individual species [i.e., units of reproduction (Sommer 1996)], the level of various communities (algae, ciliates, rotifers, crustaceans), and the system level represented by the entire plankton. Although being primarily taxonomical groups, the different assemblages of algae, ciliates, rotifers, and crustaceans may be regarded as functional units which perform specific tasks within the lakes under consideration (e.g. Gaedke & Straile 1994; Gaedke et al. 1995; Straile 1995; Barthelmess 1995).

The total biomass of a group of species, a community, or an ecosystem is generally not regarded as an emergent property but as a collective attribute since, in this case, the whole is exactly the sum of the parts. In contrast, temporal changes of standing stocks may represent an emergent property as they reflect the dynamic nature of the system and may serve as indicators for e.g. its resilience and buffer capacity against endogenic and exogenic perturbations which, in turn, depend on direct and indirect species interactions and the food web structure.

Empirical and theoretical evidence suggests that the temporal variability of standing stocks is not only influenced by the hierarchical level of the units under consideration but also by abiotic factors. In order to enable a comparison of the relative impact of external abiotic factors and the hierarchical level of integration, a comparison of the temporal variability of biomasses at the same levels of organization (i.e. species, communities, and the entire plankton) in two lakes of different trophic state (Lake Constance and Königssee) was conducted. Both lakes have rather similarly structured food webs and were investigated with similar frequency and techniques. It is to be expected that the overall temporal variability is considerably lower in the oligotrophic Königssee owing to a tough bottom-up control by nutrients which prevents the development of pronounced blooms.

Study Sites, Material and Methods

Lake Constance (in German: Bodensee) is a large (area 500 km^2, volume 47.7 km^3) and deep (mean depth 95 m, $z_{max} = 253$ m), prealpine lake of warm-monomictic character at the northern fringe of the Alps (altitude 395 m). It is presently undergoing reoligotrophication changing from a rather eutrophic state (around 1980) to mesotrophy (around 1990). Total phosphorus concentrations during winter mixing decreased from more than 80 to less than 30 ug l^{-1} (for details see e.g. TILZER et al. 1991; GAEDKE & SCHWEIZER 1993). Königssee is a deep (mean depth 98 m, $z_{max} = 190$ m) oligotrophic fjordlike lake in the Alps sheltered by high mountains (area 5.2 km^2, volume 0.51 km^3, altitude 603 m). Total phosphorus concentrations during winter mixing are 2–4 ug l^{-1} (for details see SIEBECK 1985).

In Lake Constance, sampling has been carried out weekly during the growing season and every fortnight in winter since 1979 (phytoplankton, crustaceans), respectively 1987 (all other plankton) until now at different depths at a 147 m deep sampling site in the north-western part of the lake (Überlinger See). Abundance of all planktonic organisms was assessed by microscopy using advanced sampling and counting techniques appropriate to the size and fragility of the organisms. Individual body sizes were estimated by measuring either size frequency distributions (bacteria, heterotrophic flagellates, autotrophic picoplankton (APP)), or average biovolumes of individual taxa (larger phytoplankton, ciliates, rotifers), or the individual length of the organisms in each sample (crustaceans). Original measurements of body size were converted to units of carbon using measurements from Lake Constance or from the literature. A detailed description and a complete list of references can be found in GAEDKE (1992) with the following exception: the conversion factor of ciliate cell volume to units of carbon was changed from 11 to 15.4% (g C/g FW) to allow for shrinkage during fixation.

In Königssee, abundance of all plankton organisms was assessed by weekly sampling from April to November 1992 using the same counting techniques as for Lake Constance. Individual body masses were obtained from length measurements in each sample (ciliates, rotifers, crustaceans) and size frequency distributions comparable to those used for Lake Constance applying the same biovolume to carbon conversion factors as provided above.

Temporal variation of standing stocks was quantified using the coefficient of variation (CV). The CV is defined as the ratio between the standard deviation and the mean. Therefore it is independent of the mean which allows comparisons of the variability among species with very different biomasses. The CV was determined for the untransformed time series and for root-transformed data $y' = y^b$, with b set to 0.3, 0.5 and 0.7, respectively. Similarly to a log-transformation such a root-transformation accounts for multiplicative processes strongly determining population fluctuations and reduces the strong impact of individual records of exceptionally high standing stocks on the overall CV. A value of b close to zero strongly diminishes all differences between non-zero observations whereas a transformation with a value of b close to 1 has hardly any effect. Unlike the log-transformation, the root-transformation can be performed without the necessity to specify inevitably questionable zero replacement values for samples in which no specimen of a particular species was detected.

The variability at the level of individual populations was estimated by first calculating the CV for each individual species and then taking the unweighed average of all values unless a species was encountered on less than 10% of the sampling dates and therefore disregarded. Additionally, morphotypes which were not determined on the species level but on a higher taxonomical level were omitted as well. This ensured that the hierarchical level of populations was well-defined by comprising only biological species which represent units of reproduction and selection. For Lake Constance, 56 algal species, 7 species of ciliates, 20 species of rotifers and 5 species of crustaceans were included in the analysis. The corresponding numbers of species for Königssee were 52, 16, 18, and 5.

The variability at the community level was determined by calculating the CV of the total biomass of algae, ciliates, rotifers, and crustaceans, respectively. Therefore, the biomasses of the communities exceed the sum of the biomasses of the individual species considered on the population level because all organisms belonging to the respective groups were included independently of whether they were determined to the species level or not.

The variability at the system level was established by computing the CV of the total plankton biomass which included bacteria, autotrophic picoplankton, and heterotrophic flagellates in addition to the communities mentioned above.

The comparability of the data sets of the two lakes was improved by excluding samples taken in January and February in Lake Constance because no sampling was done in Königssee in deep winter. The sampling period from March to December in Lake Constance reflects approximately the seasonal course covered by samples from Königssee which is at a higher altitude. Additionally, the long-term time series from Lake Constance were analyzed 1) by computing the CV for each season (March-December) separately (variability "within seasons"), and 2) by calculating the CV for the entire period of investigation ("long-term" variability, 5 years for algae, ciliates, and rotifers, 14 years for crustaceans).

Results

Variability within Seasons

Lake Constance

The CV on the *population level* vary greatly between species, e.g. between 70 and 500% for algal species and are mostly independent of the mean seasonal biomass of the respective species (i.e. the standard deviation increases roughly proportionally with the mean) (Fig. 1). However in most communities, species with a high average biomass tend to fluctuate less than species with extremely low mean biomasses. The latter are mostly encountered at very short periods of the year only. High CV with intermediate or even high mean biomasses are typical for large species which build up pronounced blooms in restricted time periods. The average CV of all algal, ciliate, and rotifer species, respectively, are in the same order of magnitude, ranging from 200–235% (Tab. 1). The mean variability of crustacean species is lower (142%). This statement holds for the original and root-transformed data. Differences between the average CV of biological species and other morphotypes are unsystematical and negligible (Fig. 1).

Moving up to the *community level of integration,* the CV of the standing stocks of the different communities become considerably and consistently lower than the average values at the population level (Tab. 1). Confirming the expectations the variability of each community is smaller than the average of the variability of the individual species. This statement holds for the original and the transformed data. The community of rotifers exhibits relatively large fluctuations whereas the CV of the crustacean community falls within the range of the CV of the phytoplankton and ciliate communities.

Regarding the *system level of integration* a further decrease in the temporal fluctuations is observed. The CV of the original and transformed time series of the entire plankton biomass are always considerably smaller than the smallest CV at the community level.

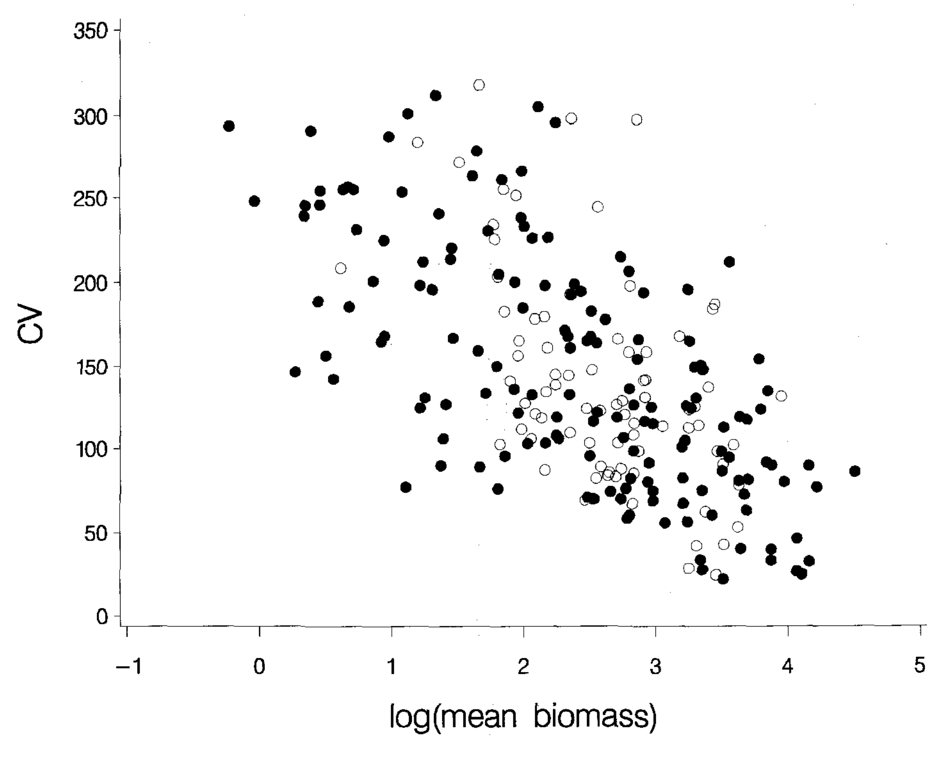

Fig. 1. The coefficients of variation (CV, in percent) of individual algal species (full dots) and other phytoplankton morphotypes not determined to species level (open circles) in relation to their mean biomass [$\log_{10}$ (biomass) (μg C m^{-3})]. – Each season (March-December) is considered separately (original, untransformed data). The average value of the CV of all individual algal species (here 235%) is taken as an indicator of the average variability on the population level.

Table 1. Coefficients of variation (CV) in percent at different levels of integration (populations, communities, entire plankton) for Lake Constance. Each season is considered separately. – The table provides average values for the individual species of each community (for details see text).

	original data			transformed data[1]		
Lake Constance	individual species	community level	system level	individual species	community level	system level
algae	235	83	/	146, 168, 194	24, 40, 57	/
ciliates	201	83	/	96, 121, 151	27, 44, 59	/
rotifers	217	114	/	121, 146, 174	41, 64, 85	/
crustaceans	142	91	/	69, 88, 109	26, 44, 62	/
plankton	/	/	57	/	/	17, 28, 40

[1]) Prior to computations of the CV, the time series were root-transformed $y' = y^b$ with b set to 0.3 (first column), 0.5 (second column), and 0.7 (third column).

Königssee

The CV of standing stocks decrease with increasing levels of integration in accordance with expectations based on hierarchy theory and with the results derived from Lake Constance (Fig. 2). The overall magnitude of the fluctuations is consistently smaller in oligotrophic Königssee than in eu-mesotrophic Lake Constance. On the *population level* the average CV of algal, ciliate, rotifer, and crustacean species range from 100 to 140% (Tab. 2), the CV of individual algal species lie between 32 and 408% (original data). CV of 29–55% indicate that fluctuations at the *community* level are strongly reduced compared to the population level. Again, rotifers represent the most variable community. Temporal variability decreases again if approaching the system level; the CV of the entire plankton biomass in Königssee is as low as 21% (original data) (Tab. 2). All results mentioned hold equally well for root-transformed time series.

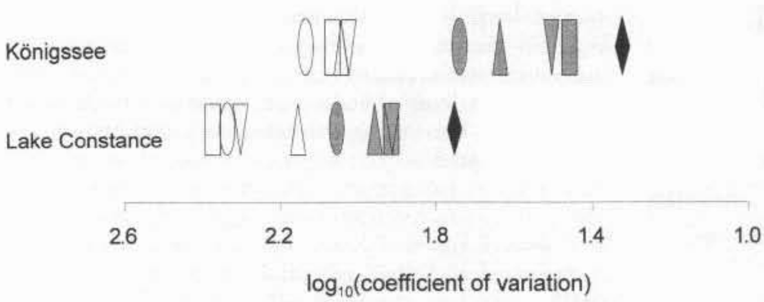

Fig. 2. Comparison of the coefficients of variation (CV, expressed in percent) of standing stocks of individual species (open symbols, averaged over all species belonging to one community), communities (grey symbols), and the entire plankton (black symbols) in eu-mesotrophic Lake Constance (Bodensee, lower panel) and oligotrophic Königssee (upper panel). – Symbol key: rectangles – phytoplankton, inverted triangles – ciliates, ellipses -rotifers and triangles- crustacean zooplankton.

Table 2. Coefficients of variation (CV) in percent at different levels of integration for Königssee. – The table provides average values for the individual species of each community (for details see text).

	original data			transformed data[1]		
Königsee	individual species	community level	system level	individual species	community level	system level
algae	116	29	/	55, 73, 90	9, 15, 20	/
ciliates	105	32	/	48, 62, 78	10, 16, 23	/
rotifers	136	55	/	72, 88, 107	19, 31, 41	/
crustaceans	111	43	/	44, 65, 85	14, 22, 31	/
plankton	/	/	21	/	/	6, 10, 15

[1]) Prior to computations of the CV, the time series were root-transformed $y' = y^b$ with b set to 0.3 (first column), 0.5 (second column), and 0.7 (third column).

Table 3. Coefficients of variation (CV) in percent at different levels of integration for Lake Constance. – *The table provides average values for the individual species of each community for a period of 5 to 14 years (for details see text).*

	original data			transformed data[1]		
Lake Constance	individual species	community level	system level	individual species	community level	system level
algae	343	96	/	163, 198, 247	25, 42, 62	/
ciliates	261	85	/	107, 137, 179	27, 44, 60	/
rotifers	345	155	/	156, 196, 249	47, 76, 106	/
crustaceans	159	99	/	68, 89, 113	26, 44, 64	/
plankton	/	/	61	/	/	17, 29, 41

[1]) Prior to computations of the CV, the time series were root-transformed $y' = y^b$ with b set to 0.3 (first column), 0.5 (second column), and 0.7 (third column).

Long-Term Variability in Lake Constance

The average values of the CV of individual species (i.e. on the *population level*) increase to 160–350% in Lake Constance if the period of investigation is extended from individual seasons to 5 (crustaceans: 14) years (January and February excluded; Tab. 3). Under these assumptions (original data) the CV of algal species vary between 100 and 650%. Mean abundances of numerous species exhibit strong interannual fluctuations which are often in the order of a factor of 5 to 10. Considering each year separately yields remarkably lower values of the CV of individual species (cf. Tabs. 3 and 1). The average CV of crustacean species increases only moderately if extending the time interval from one to 14 years which indicates relatively small interannual variability. The same statement holds for the *community level of integration:* The CV of the individual communities increase slightly (besides rotifers) if including interannual fluctuations (Tabs. 1 *vs.* 3). This implies that the differences in variability between the population and community level within one lake depend on the considered time scale. The same pattern is observed on the *system level* where the CV is largely independent of the period of investigation (cf. Tabs. 1 and 3). Again, root-transformed data deliver the same overall results.

The sampling interval was generally fixed to one week and the different groups of organisms differ greatly in body size and, hence, their internal time constants. However, no systematic impact of body size on the variability of individual species or the communities is found in this kind of analysis (Fig. 2). Generally, rotifers exhibit the largest temporal fluctuations on the population and community level. Individual algal species have on average a high CV whereas the standing stock of the phytoplankton community varies relatively little. In contrast, crustaceans show on the level of individual species relatively small fluctuations, but exhibit intermediate variability on the community level.

Discussion

Quantifying and comparing the variability of ecological time series is not straightforward and the selected measure may influence the overall result (e.g. Wolda & Marek 1994). We accounted for this problem by using the CV as a simple and well-established measure, and by analyzing the robustness of the overall results against root-transformations which allow for the multiplicativity underlying most processes which determine population dynamics.

According to our expectations, temporal fluctuations were smaller on all hierarchical levels in oligotrophic Königssee. Besides the presumably strong impact of the considerably lower concentrations of bioavailable phosphorus in the euphotic zone this might be enhanced by the frequently pronounced impact of internal seiches on the abundance of non-migrating plankton organisms in Lake Constance (Gaedke & Schimmele 1991). Owing to its lower altitude Lake Constance reaches higher maximum temperatures which implies higher seasonal fluctuations of the water temperature. Despite the various external factors influencing the overall level of variability a clear pattern of reduction in variation with increasing levels of integration was identified based upon the original and the transformed data for both lakes.

A point of concern is, however, to what extent this regularity is merely attributable to stochastic processes (i.e., the law of great numbers) rather than the buffering and self-organizing capacity of the system. The CV of a sum (CV_s) of independent variables which have the same expected value and variance is equal to the CV of the individual variables (CV_i) divided by the square root of n, where n denotes the number of independent variables:

$$CV_s = n^{-0.5}\ CV_i$$

In practice expected values and variances of individual species differ by orders of magnitude (Fig. 1) and the species vary not completely independent of each other. For example, all algal species face insufficient light conditions in winter and low nutrient concentrations in high summer which will prevent all of them from developing large blooms during these periods. These two violations of the above mentioned assumptions reduce the difference between CV_s and the average CV_i which is to be expected from the statistical point of view to a value smaller than $n^{0.5}$ (W. Nagl, pers. comm.). For example, CV_s equals the average of CV_i if the individual variables are completely dependent on each other. A comparison of the CV at the population, community, and system level provided in Tabs. 1–3 reveals that the variability at superior levels exceeds frequently the variability which is to be expected if all species vary independently (white noise) and have the same expected value and variance, i.e. mostly $CV_s > n^{-0.5}\ CV_i$ (ignoring the further complication that not all organisms included at the higher levels are considered at the lower ones, see method section). From this kind of analysis the impact of stochastic and self-regulation processes cannot be distinguished.

However, arguments against a merely stochastic process include the observations that the relative and absolute reduction of variability related to a change of the level of integration differed between lakes, time scales, and communities. It was more pronounced in Königssee than in Lake Constance (Tabs. 1 *vs.* 2), and if considering several years rather than individual seasons in Lake Constance (Tabs. 1 *vs.* 3).

The relatively stronger decrease of variability of all communities along the hierarchy in Königssee cannot be explained by a statistical argument (e.g. in both lakes an approximately equal number of species was considered in each community on the population level). The assumption appears more likely that in oligotrophic Königssee the fluctuations of functional units as they are represented by different communities and the entire plankton are more severely restricted by external boundary conditions imposed on the system. The remarkable constancy at the community and system level indicates the fulfilment of basic system functions independently of changes in species composition. In analogy, the communities in Lake Constance show much less interannual variability than the individual populations, and the CV at the system level merely increases if extending the period of investigation from one to five seasons. This suggests a regulation of large functional groups and contradicts expectations derived by statistical arguments because the maximum value of the CV increases with the square root of the number of observations (SACHS 1984), i.e. from the statistical point of view, the maximum value of the CV is higher in long time-series.

The differences in the average variability of algae, ciliates, rotifers, and crustaceans at the population level should not be overstressed and cannot contribute substantially to the distinction between stochastic and self-regulation processes since they may partially be caused by differences in the taxonomic resolution, at least in the data set from Lake Constance. The numerous algal species include rare ones which occur irregularly. Such species in the ciliate and rotifer community were more often not determined to the species level and, thus, were not included in the average value. This might also be one reason why the CV decreased strongest for phytoplankton if moving from population to community level. The relatively low average CV of crustacean species might be related to their relatively long generation times compared to the other plankton organisms. The CV of individual daphnid species was found to depend on life history characteristics like diurnal vertical migration (r- *versus* K-strategists; GELLER 1986). This observation is likely to be representative for other species as well. Our results are in agreement with investigations by KRATZ et al. (1987) who found a higher temporal variability of rotifers than of crustaceans which was attributed to the differences in generation times. However, the smaller variability of ciliates in our study suggests that generation time is only one among several factors which influence variability. Population dynamics of individual species and plankton assemblages have been investigated in great detail in Lake Constance. However, mechanisms of food web regulation are not yet known to such an extent that the final reasons for e.g. the large seasonal and interannual fluctuations of rotifers on the species and community level can be readily identified beyond general statements. A detailed discussion of individual species including e.g. their life history, temperature dependency and predator and prey spectrum is beyond the scope of the present study focusing on ecosystem properties.

To summarize, standing stocks of communities and the entire plankton are kept more constant than those of individual populations and react much less sensitively to seasonal and interannual changes, for example of abiotic parameters. The existence of such a striking regularity of decreasing temporal variability at higher levels of integration has been proposed more often, but systematic and quantitative investigations have been scarce, so far. It could be clearly identified from the actual data sets despite the impact of various other factors influencing temporal fluctuations (e.g. trophic state, generation time, life history). Similar regularities may be assumed to exist in other communities and habitats as well unless they are severely impoverished in respect to e.g. species diversity and self-organization capacity. However, further empirical studies based on comprehensive data sets are required in order to evaluate whether the overall tendency of a reduction of variability at higher levels dominates other factors of influence.

Our findings support the postulate of hierarchy theory that ecosystems may be considered to consist of a hierarchy of levels of integration each of which exhibits specific dynamic properties which emerge from the (asymmetric) relationships acting between the subunits and levels (e.g. MÜLLER 1992 and this volume). Our empirical results are also in agreement with findings derived from dynamic simulation models. The models indicated that an increase in spatio-temporal self-organization reduced the variability at the system level and increased the variability at the population level (PAHL-WOSTL 1993, 1995).

Additional empirical arguments related to the issue of emergent properties of ecosystems can be obtained from other studies which analyze the response to a reduction in nutrient loading or which use ecosystem approaches considering the structure and function of the pelagic food web of Lake Constance in its entirety. These investigations largely support the perception of the ecosystem as a system with a capability of self-organization and filtering at the superior levels. Phosphorus concentrations presenting the most limiting nutrient in Lake Constance have been reduced to about one third of the maximum value within the last 15 years. In the beginning, the plankton community reacted mostly with changes on the species level whereas a response on the community level (e.g. overall reduction of phytoplankton and crustacean standing stocks, primary production) if happening at all, lagged years behind (Tilzer et al. 1991; Gaedke & Schweizer 1993; Sommer et al. 1993; Geller 1994). The first argument based on ecosystem approaches is derived from biomass size distributions: Biomass is approximately regularly distributed along the size gradient in Lake Constance (Gaedke 1992) and other large pelagic systems essentially independent of species compositions. This observation may be traced back to the predominant flow of matter from small to large organisms, and the close relationship between body size and physiological and ecological properties (Gaedke 1993; Pahl-Wostl 1995). Further evidence is obtained from an analysis of the structure of a binary food web model consisting of 22 plankton guilds. Small seasonal and interannual changes of the overall food web structure, e.g. indicated by almost constant linkage densities and connectance (Lang 1993), are contrasted by large fluctuations of the relative importance of individual feeding links which indicate a continuous reorganization at the population level (Lang pers. com.). Finally, analyses of mass-balanced carbon flow diagrams reveal a gradual and regular seasonal development of the trophic structure at the system level independently of the fast and large fluctuations of the relative contribution of the numerous component organisms (Straile 1995). The (relative) ascendency was suggested as a "goal function" emergent at the system level to describe ecosystem maturing (Ulanowicz 1986). In Lake Constance, it exhibits a regular seasonal trend which stands, however, in contradiction to expectations formulated by Ulanowicz (Straile 1995).

To conclude, empirical evidence was provided for the hypothesis that the higher hierarchical levels exhibit a higher "stability" than most individual populations. Often, processes at superior levels were little affected by changes in species compositions and abiotic factors which yields a relatively high degree of predictability of overall system functioning. This implies that factors influencing individual species (e.g. host specific parasites) are of minor importance for ecosystem functions like primary and secondary production, trophic transfer efficiency, remineralization and nutrient regeneration. Such functions will change significantly if the biological potential and the interactions between hierarchical levels represented by e.g. species richness and complex, highly connected food webs are reduced. This relationship can be studied during the seasonal development of the food web structure and biomass size distributions of small sulphurous Lake Cisó (Pedros-Alio & Guerrer 1993), and by comparing the ecosystem of this lake with that of Lake Constance. The "stability" and predictability on the higher levels are no properties of the populations but of the ecosystem, although it is often conferred by interactions at lower hierarchical levels (cp. Pomeroy et al. 1988). Our results underline that the dynamics and regulation of populations and food webs cannot be understood unless one investigates simultaneously the major processes at the level of individual populations in concert with those acting over the domain of the entire community.

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