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Relative frequency, seasonal pattern and possible role of species rare in phytoplankton in a large shallow lake (Lake Balaton, Hungary)

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Introduction

Numerous studies have been carried out on the seasonal succession of phytoplankton on both *in situ* (seasonal phases and their environmental background) and experimental (models, chemostats) bases. These studies concentrate on the "important" species, i.e. those that are dominant in some way or contribute >5–10% to the total crop density. Other studies – by the same phytoplankton ecologists in many cases – describe the unexpected occurrence, establishment, etc of different, "only" floristically, but not quantitatively interesting phytoplankton species. These two seemingly contradictory attitudes reflect the basic difference between the deterministic and stochastic approaches to the process, which was originally expressed in the plankton paradox. While deterministic terms often describe the events on the dominants' level adequately, they are of little value for treating the "whole community", for which information (e.g. diversity and similarity) are more appropriate.

The present study is formulated on the basis of two considerations. First, succession, generally like all biological processes operating at the supra-individual level, is a stochastic phenomenon, in which the transitions can be expressed by their probabilities (e.g. Drury & Nisbet 1973). Second, the classical, almost dogmatic Clementsian series is more an exception (taking even terrestrial plant communities into consideration e.g. Fekete 1985) than not. Bearing these in mind this study which analyses the quantities of both frequent and scarce species on the same numerical basis attempts

1) to establish the number of species minimally necessary to produce a given particular sequence of seasonal succession;

2) to relate their number to that of others present in the phytoplankton throughout the year; and

3) to estimate the proportion of species having different origins (always present with or without specialized survival strategy, allochthonous/adventive, periphytic) and which can be found together in phytoplankton samples. In addition to discussing the possible mechanisms in different frequency ranges, this paper introduces a yet unrecognized kind of perennation (propagulum populations) and a new hypothesis (the ecological memory of the community).

Sampling and methods

Lake Balaton is the largest shallow lake in Central Europe (e.g. Padisák et al. 1988). The originally mesotrophic lake began to eutrophicate rapidly during the 1970's. Series of vertical samples were collected at the end of the pier in the port of Keszthely (the western, most eutrophic part of the lake) early morning every day between 1 April and 28 October 1980. Water depth at the sampling site was 2 m. Algae were counted in an inverted microscope; diatoms were identified in additional LM, TEM and SEM studies. 101,280 specimens were counted in the 211 consecutive daily samples, which corresponds to an average of 480 in each of the samples. To estimate the quantity of rare species, the *a*verage *r*elative *f*requency (*arf*) was used. This refers to the total number (101,280, roughly 100,000) of enumerated specimens. If a species has an *arf* value of $100{,}000^{-1}$ it means that it was represented by a single specimen in all the samples; in general $100{,}000^{-1}$ *arf* = the number of specimens found among the total of 100,000. Temporal aggregativity was measured in terms of *m*aximal *r*elative *f*requency (*mrf*). To calculate it, data from every consecutive 10 day period (sometimes 11, namely in the end of May, July and August) were accumulated and the *r*elative *f*requency (*rf*) of each species that occurred in the given 10-day period was referred to the whole number of specimens (about 5,000) enumerated in the same period. The highest value was chosen as *mrf*. If *arf* $> 5{,}000^{-1}$, the theoretical maximum of stable temporal distribution is the case when *arf* = *mrf*. In all other cases *arf* < *mrf*, and the difference between them is a measure of the temporary aggregative occurrence (seasonal behaviour) of each species.

Results and discussion

The total number of taxa found in the 211 quantitative samples and in additional diatom studies was 417. Two hundred and eighteen species were extremely rare (*arf* $< 30{,}000^{-1}$). Seventy-eight species had an *arf* between $30{,}000^{-1}$ and 4.000^{-1}, 59 between $4{,}000^{-1}$ and 800^{-1} and 46 between 800^{-1} and 100^{-1}. Only 14 species had an *arf* of $> 100^{-1}$.

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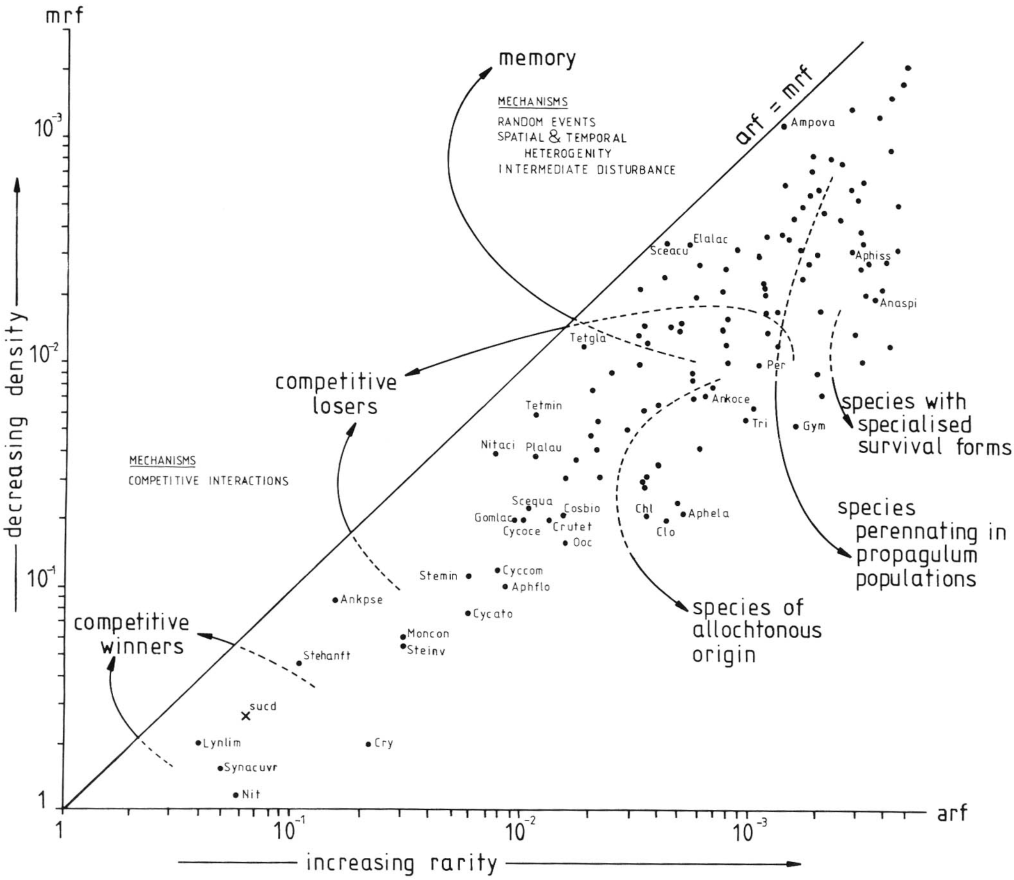

Fig. 1. *M*aximal- (*mrf*) and *a*verage (*arf*) *r*elative *f*requencys of phytoplankton species (see text for more details). Species names are abbreviated.

Approximately 300 of the 417 species were clearly planktonic forms: the other (many diatoms, some filamentous blue-greens and greens) had some different, mostly periphytic origins.

In Fig. 1 *arf* (increasing rarity) is plotted against *mrf* (decreasing density) for all species having an *arf* of $>5{,}000^{-1}$. If the data of *s*mall *u*nicellular *c*entric *d*iatoms (*sucd* = *Stephanodiscus hantzschii* f. *tenuis* (HUST.) HAKAN & STOERM. + *S. invisitatus* HOHN & HELLER. + *S. minutulus* (KÜTZ.) CLEVE & MÖLL. + *Cyclotella atomus* HUST. + *C. ocellata* PANT.) are nor treated separately, three different regions on the plot can be distinguished:

1) Relatively many species (or groups of co-dominating closely related species) can be found in the *mrf* range of $>3^{-1}$. In agreement with competitive exclusion models and studies (e.g. SOMMER 1983) no more than two species dominated in the same period: *Synedra acus* var. *radians* (KÜTZ.) HUST. and *Lyngbya limnetica* LEMM. during the spring bloom (their persistent coexistence even suggests competitive equilibrium state), small or medium size *Cryptomonas* spp. in the "clear water" phase, and small *Nitzschia* spp. and small centrics afterwards (Fig. 2).

2) The relative emptiness of the *mrf* range of $3^{-1}-20^{-1}$ indicates that is the density area, in which the outcome of competition is decided (to win or to fail) in nature (e.g. SOMMER 1988). Population dynamics (Fig. 2) of species in or close to this region resemble very much those identified as competitive losers in chemostat experiments (SOMMER 1983). Note the basically opposite asymmetry (slower increase than decrease) of the graphs as compared to chemostats' results. The slower increase might be explained by the fact that

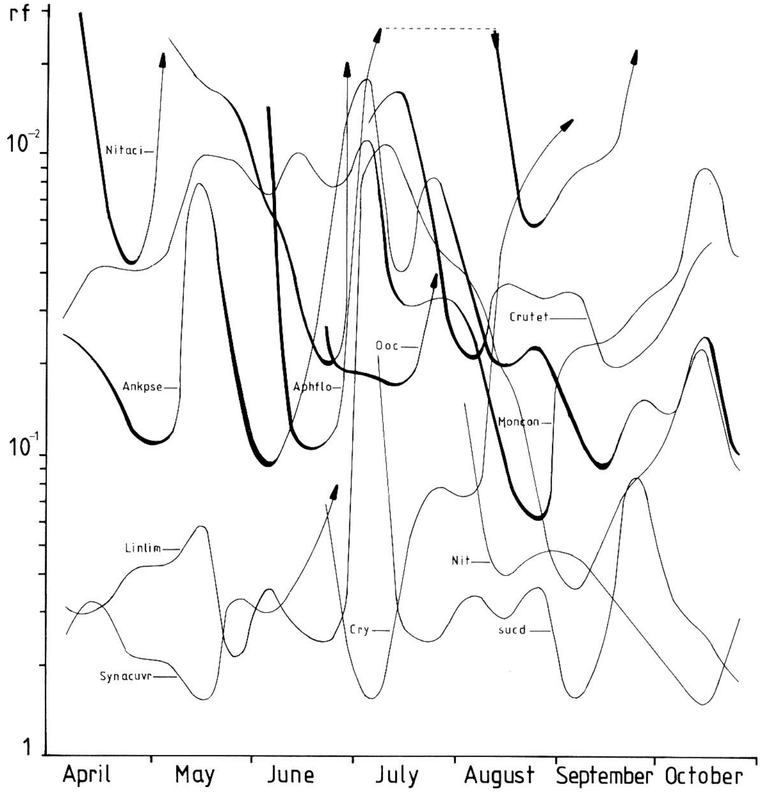

Fig. 2. Changes in relative frequency (*rf*) of some species in the Keszthely-bay of Lake Balaton between 1 April and 28 October, 1980. The thick sections indicate the increasing phases of subdominants.

it takes place within an at least more nutrient limited environment, while the greater diversity and natural specificity of loss processes can explain the rapid decrease. Almost all the species that exhibited at least a slight seasonal peak had a *rf* greater than about $2{,}000^{-1}$ in other periods. On this basis, approximately 100 of the 300 planktonic species played major of minor roles in the matter-energy processes during the vegetation period. The same proportion (1:2) can be established in another natural, but very much different (small, meromictic) lake in Austria (Rott 1983).

3) Coexistence or rather co-occurrence of many species is allowed below the *mrf* level of 20^{-1}. Some of these species (*mrf* ≫ *arf*) showed definite seasonal aggregativity for different reasons. In lower *arf* regions germination and cyst (spore) formation (see dinoflagellates and heterocystic blue-greens on Fig. 1) are characteristic, while species in higher *arf-mrf* regions have other strategies. These species (approx. 15) appeared suddenly in great numbers in the phytoplankton without lag- and log phases, than at various rates completely disappeared. This type of population dynamics leads one to suggest that they are of allochthonous origin. The populations might have been carried by horizontal water currents, but they might have had some truly allochthonous (for example riverine) origin e.g. *Ankyra ocellata* (Korsh) Fott, which is an alien in the flora. Many, even very scarce, species (*mrf* > *arf*) did not exhibit seasonal peaks at all, and they maintained constantly scarce populations. This observation suggests that perennation can be achieved without specialized survival forms (like cysts and spores), and that these constant, scarce populations themselves can be considered as propagules able to begin a rapid increase in favourable environmental conditions. According to chemostat experiments (Sommer 1983) extreme rarity does not prevent a species in "winning" within a few weeks.

Mechanisms that make it possible to exist in quantitatively minor populations include spatial and temporal random processes such as fluctuation in resource rates the intermediate disturbance (REYNOLDS 1988) which is very characteristic of Lake Balaton phytoplankton (e.g. PADISÁK et al. 1988), vertical heterogeneity in the water column, or passage through a zooplankton gut (a good deal of coccal blue-greens and greens are indigestible!). The aforementioned reasons can explain the mechanisms of co-occurrence at first sight, but they reveal nothing about the role of these populations in nature. Although generalized historical aspects are rarely mentioned in phytoplankton ecology (an exception is given in SOMMER 1983 for high densities), this author's view is that the large number of persistent minor populations in natural lakes provides the ecological memory of the community. To support this hypothesis, detailed analyses of many long-term phytoplankton sets would be necessary. As such data are not available in large numbers (and the problem of eutrophication is superimposed on natural changes in most cases), only planktonic "events" in phytoplankton history can be analysed at present. The phytoplankton in Lake Balaton has been studied since the early decades of this century. The blue-green alga *Aphanizomenon issatschenkoi* (USSACZ.) PROSCH.-LAV. was first recorded in the lake in the summer of 1973 (BARTHA 1974), and immediately in large amounts (162,200 ind $\cdot$ l^{-1}, 9^{-1} *rf* in the sample). Since 1973 the species has always been present in the samples mostly in small amounts (as in this study, see Fig. 1), but sometimes – as in 1978 – in considerable quantity (NÉMETH & VÖRÖS 1986). The same pattern was found with *Raphidiopsis mediterranea* SKUJA and *Anabaenopsis* (*Cylindrospermopsis*) *raciborskii* WOLOSZ. (TAMÁS 1974, NÉMETH & VÖRÖS 1986, G.-TÓTH & PADISÁK 1986) in Lake Balaton, but other examples (as *Gyrosigma macrum* both in Balaton and Neusiedlersee in the 70's, KUSEL-FETZMANN 1973, PADISÁK 1980 s.n. *G. prolongatum*) are also available. These historical events outline a pattern: a new species appears in the flora and either quickly becomes completely extinct or rapidly multiples (to bloom proportions as in the case of *Anabaenopsis raciborskii*), then incorporates and maintaines a "callable" minor population. In this respect the large number of minor populations represent the deposit of ecological stability which is widely observed in natural lakes. As this study was carried out on a large, natural lake, the above analysis may be relevant only to similar water bodies; in other lakes, such as small ponds, fishponds and reservoirs, basically different ecological phenomena might be characteristic.

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