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Phytoplankton size structure stability in a meso-eutrophic subtropical lake

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Abstract

The aim of the present study was to analyze seasonal and inter-annual variability, and examine the stability of several parameters describing the size structure of the phytoplankton assemblage of Lake Kinneret (Israel). Phytoplankton biomass size spectrum (BSS) patterns were analyzed using cell-volume data based on microscopic counts of samples collected biweekly over 4 years (1996–1999). A typical pattern of Lake Kinneret phytoplankton BSS emerged, as being quasi-stable in spite of unprecedented man-induced lowering of the lake's water levels during those years, atypical phytoplankton biomass dynamics, and extreme inter-annual variations in phytoplankton species composition. The present study included all phytoplankton greater than ca. 2 μm diameter, which comprise most of the lake's autotrophic biomass, and phytoplankton alone. Statistical descriptors of separate size classes elucidate two zones of pronounced variability within Kinneret BSS and a zone of stability near its center. The phytoplankton biomass variability is produced mainly by two bloom zones, at relatively large cell size classes ($V = 2048$–4096 and $V = 65\,500$–$131\,000$ μm^3), corresponding with proliferation of the bloom-forming species *Aulacoseira granulata* and *Peridinium gatunense*, respectively, while the stability zone at the center of the BSS, essentially a 'nanoplankton plateau', corresponds with a diverse assemblage of nanoplanktonic species, of different taxonomic composition at different times. Statistical parameters of BSS approximation provide a tool for the quantitative estimation of the stability/variability of whole phytoplankton assemblages. According to these parameters, Kinneret BSS is comparable to BSS of eutrophic lakes of Canada and Spain but differs from the more stable BSS typical of oligotrophic systems.

Introduction

The study of structure and stability of aquatic communities is one of the central challenges of ecology, since these have always been of great importance for mankind as sources of water and food from fisheries. Especially important from both the theoretical and empirical points of view, are the patterns of the community structure, their underlying control mechanisms and their resilience when subjected to ever-growing external climatic and anthropogenic impacts (Odum, 1971; Begon et al., 1996).

Natural aquatic communities tend to have inherent patterns in size frequency distribution, or size spectra (SS), of organisms comprising them (Sheldon et al., 1972; Kerr, 1974; Chislenko, 1981). Based on simple and general properties of living beings (geometrical dimensions, weight, volume), SS open a wide way to application of modern automated means of data acquisition. Being compact, graphic, and flexible, they are also well adapted for mathematical transformations, comparative analysis, and generalization. Hence, SS offer a specific way to 'predictive limnology' and theoretical ecology for those who agree 'to sacrifice descriptive precision and detail for generality and application in prediction' (Peters, 1986: p. 1144). The goal of predictive ecology is forecasting trends in some salient properties of natural aquatic systems. The

properties should be simple, quantitative and widely studied (Peters, 1986). Organism size is one of variables of high value for the predictive science. The importance of the organism size (body mass, volume) as a major predictor of many temporal, spatial and metabolic characteristics of organisms and communities is strongly established now by numerous scientific papers and monographs, including a huge set of allometric equations (Peters, 1983) and theoretical models of general nature, aimed at explanation of the origin of biological allometry (West et al., 1997). Relevant here is the existence of numerous allometric relationships and hypotheses aimed to explain them, based on phytoplankton cell size (e.g., Banse, 1976; Peters, 1983; Chisholm, 1992).

The identification and description of 'typical patterns' (Schwinghamer, 1981; Sprules & Goyke, 1994) of size structure of natural aquatic communities provide new ways to approach the phenomenon of their stability and quantify the impact of external factors on their structure/state. The term 'stability' is of high importance here, but its use in ecology is not straight forward. Numerous authors are rather skeptical in their assessment of the search for the stability phenomena of natural phytoplankton (Naselli-Flores et al., 2003; Rojo & Alvarez-Cobelas, 2003; Scheffer et al., 2003). Real plankton communities can never be at a steady state due to environmental fluctuations and the species interactions. Their dynamics can be intrinsically chaotic, just because of coupled oscillators which produce the food web. The plankton dynamics seen in the nature, models and experiments are often highly erratic on the species level. Additional controversy is caused by the vagueness of ecological concepts and by the domination of a qualitative language instead of a more formal or mathematical one (Rojo & Alvarez-Cobelas, 2003; Scheffer et al., 2003).

The 'demographic' stability (Begon et al., 1996), describing algal species or lumping them, is most frequently studied and is discussed by the above authors. In spite of chaotic behavior, though plankton dynamics are intrinsically unpredictable in the long run when viewed in detail, some indicators look more suitable for analysis. Unlike the species composition, at a more aggregated level, indices like total algal biomass may show quite regular patterns (Rojo & Alvarez-Cobelas, 2003; Scheffer et al., 2003). Additional optimism can be born also from consideration of this term (stability) done in cybernetics and theoretical ecology (Holling, 1978; Begon et al., 1996). Ecological concepts often are 'translated' from physics or chemistry but 'translations' almost always lack scientific corroboration (Naselli-Flores et al., 2003). It looks that the ecosystem stability means not a fixed point (state) but such kind of dynamics, when estimates of several variables do vary within known and small ranges. Selection of the variables and 'small ranges' is done by the scientist, and they serve as key means of the ecological assessment and management (Holling, 1978).

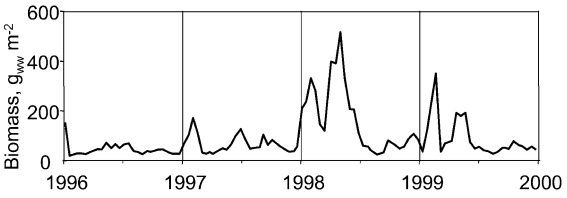

Figure 1. Temporal variations of depth-integrated phytoplankton wet weight biomass in Lake Kinneret, 1996–1999.

Many definitions of stability are known in limnology. A central feature of stability is the ability of a property of an ecosystem to return toward a steady-state equilibrium following a disturbance (Wetzel, 2001). Stable systems tend to resist change and once changed return to initial conditions. Stability of a community is linked with its food-web structure and has a number of related characteristics, such as resilience (the rate at which an ecosystem returns to its previous steady state following a disturbance) and resistance to change (the ability of a population or community to withstand perturbations without marked changes in composition).

One should also see and describe at least stability: demographic and non-demographic, global and local, dynamic robustness and fragility (Begon et al., 1996). Each of these terms is very complicated and requires additional clarification which is too long to put in this manuscript; our results can serve as an illustration (see Discussion). A very important character of the SS stability, seen from the works mentioned above, looks as a 'stable cycle' (Holling, 1978), a dynamic equilibrium, rather than a 'nonmovable' fixed point (Naselli-Flores et al., 2003). All aquatic communities considered above do feel seasonal changes of their environment and react via seasonal adaptation. Nevertheless, this annual cycle is stable. Such cyclic stability was pronounced in L. Kinneret (see below) but seems to be broken recently (Fig. 1; Zohary, 2002). On the other hand, even Fig. 1 reveals some periodicity (annual cycle), but so non-ideal that a number of quantitative descriptors are necessary to describe and compare these year-to-year deformations of the annual pattern.

One could seriously accept only predictions that have been confirmed in repeated trials around the world (Peters, 1986). Size spectra, based on the organism body mass (i.e., an attribute very important and quantitative), are also widely studied recently. One can note large-scale comparative studies of oceanic plankton (Sheldon et al., 1972; Rodriguez & Mullin, 1986; Gin et al., 1999; Li & Harrison, 2001; Li, 2002; Yamaguchi et al., 2002). Comparative analyses of BSS from large groups of lakes were carried out in Canada (Sprules & Munawar, 1986), Denmark and New Zealand (Jeppesen et al., 1997), USA (Cottingham, 1999; Havens et al., 2001), Argentine (Cozar et al., 2003), Spain (Gasol et al., 1991; Alvarez-Cobelas & Rojo, 2000), Germany (Gaedke, 1992; Tittel et al., 1998) and Finland (Turkia & Lepisto, 1999). Cyr & Peters (1996) performed a comprehensive comparison of lake communities (phyto-, zooplankton and benthos, fish) using the extensive datasets of the International Biological Program (IBP).

While the above plankton BSS consider mainly autotroph-heterotroph assemblages, a number of studies focus on phytoplankton. Phytoplankton size structure variability was analyzed under hydrodynamic impacts and water level changes (Sin et al., 2000), trophic level (Chisholm, 1992; Kiorboe, 1993; Cottingham, 1999; Bell & Kalff, 2001; Cavender-Bares et al., 2001), lake seasonal dynamics (Bailey-Watts, 1986; Rojo & Rodriguez, 1994). A very unusual nonparametric technique applied by Bailey-Watts (1986) produced results rather similar to those obtained from more common now SS methods. In spite of irregular shifts in species composition and abundance, phytoplankton assemblage size spectra exhibit distinct seasonal patterns (Bailey-Watts, 1986).

Huge bulk of information on size structure of phytoplankton was obtained via size fractionation of chlorophyll, though such SS are very coarse (generally, 3–4 points), e.g., see review in Bell & Kalff (2001), Chisholm (1992), Cozar et al. (2003) and references therein. Due to the methods involved, usually the volumetric concentration (mg/ml, cell/ml) is used for the SS analysis. Nevertheless, many authors also considered depth-integrated values (Kamenir & Khailov, 1987; Cyr & Peters, 1996; Yamaguchi et al., 2002) as 'more meaningful for the depth stratified communities' (Gasol et al., 1991).

While the language of demographic stability is vague and qualitative (Rojo & Alvares-Cobelas, 2003), the SS approximations and quantitative descriptors are well adapted for mathematical transformations and comparisons. Simple and effective scales begin to emerge for comparative analyses of 'integral community structure' (Kerr, 1974; Sprules & Munawar, 1986) and its shape estimation (Thiebaux & Dickie, 1993; Sprules & Goyke, 1994).

From 1998, BSS analysis for the Lake Kinneret ecosystem has been conducted (Kamenir et al., 1998, 1999). This aquatic community has been intensively studied and monitored for more than 30 years due to the great importance of the lake as the main water source in the region. From the beginning of routine monitoring of water quality parameters in Lake Kinneret in 1969 and until ca. 1993, its phytoplankton community was characterized by distinct stability, and was used in the limnological literature (e.g. Reynolds, 2002) as being one of the best known and attested examples of year-to-year similarity in abundance, distribution and composition of lake phytoplankton. However, since the mid 1990's very pronounced changes to this pattern took place (see below).

Important characteristics of Lake Kinneret are the nearly absolute lack of macrophytic vegetation and low importance of its phytobenthos. As phytoplankton produces more than 90% of the primary production in Lake Kinneret (Serruya, 1978), analysis of the complete phytoplankton assemblage provides a means to study an integral autotrophic part of a natural community. The Period of 1996–1999 was characterized by exceptionally low water levels and irregular phytoplankton dynamics, and thus provided an opportunity to study phytoplankton BSS under conditions of extreme stress and fluctuations.

The specific aim of the study was to analyze the stability and variability of several parameters describing the size structure of the Kinneret phytoplankton assemblage during a period of pronounced deviations from the typical annual patterns. A more general aim was to contribute to the development of quantitative tools for the analysis of the phytoplankton assemblage responses to natural and anthropogenic perturbations.

Materials and methods

Site description

Lake Kinneret is situated ca. 210 m below mean sea level in the northern part of the Afro-Syrian Rift System. At full capacity the lake is some 168 km^2 in surface area, with mean and maximum depths of 26 and 44 m, respectively. Lake Kinneret is monomictic,

winter homothermal temperatures are typically 14–16 °C, while summer maxima of the epilimnion exceed 30 °C. The lake is highly productive, with annual primary production of some 600 g C m^{-2} y^{-1}, mostly produced during the spring bloom of *Peridinium gatunense* (Hambright et al., 1997). The lake is classified as mesotrophic to eutrophic, with mean annual concentrations (1969–2001) of total P and total N in the upper 10 m layer of 20 and 660 μg l^{-1}, respectively. In summer, when the lake is stratified, the thermocline depth is about 15 m, below which anoxic conditions prevail, and the epilimnion becomes nutrient-depleted. Following the autumnal overturn and mixing, the entire water column is oxygenated and nutrients are redistributed throughout the water column.

For 25 years and until the mid 1990's the most salient feature of the Kinneret phytoplankton was a spring bloom of the dinoflagellate *P. gatunense,* which typically accounted for >95% of the spring phytoplankton biomass (Pollingher, 1986). During years with intensive water turbulence in January–February, the filamentous diatom *Aulacoseira granulata* proliferated. The remainder of the phytoplankton biomass was mostly nanoplankton, including many minute chlorophytes, diatoms, cyanobacteria, cryptophytes and some small dinoflagellate species. These dominated the phytoplankton during summer and fall, and were readily consumed by zooplankton. The huge stock of *P. gatunense*, characterized by a high C:N:P ratio of 412:49:1, went mainly to sedimentation (6–68%) and microbial decomposition (Zohary et al., 1998, 2000).

Man-induced changes including the artificial lowering of the Kinneret water level and fisheries practices ultimately led to the drastically changed phytoplankton patterns since 1994 (Zohary, 2002). During the study years of 1996–1999 these changes were expressed in the large annual and interannual variability in phytoplankton biomass (Fig. 1). Changes to this pattern included the absence of the prevailing spring *Peridinium* blooms in some years, intensification of winter *Aulacoseira granulata* blooms, replacement of the summer species assemblage of mostly nanoplanktonic palatable forms with less palatable forms, and proliferation in summer-fall of N_2-fixing, toxic cyanobacteria, previously nearly non-existent in Lake Kinneret. In 1994, the biomass attained during the spring bloom of *P. gatunense* was a record high until that time (Zohary et al., 1998). In late summer that year, the potentially toxic cyanobacterium *Aphanizomenon ovalisporum* bloomed for the first time (Pollingher et al., 1998) while in the following winter of 1995, an unusual bloom of the cyanobacterium *Microcystis aeruginosa* was recorded, followed by a second record *P. gatunense* bloom (Berman et al., 1998). In 1996 and 1997, for the first time in 35 years, *P. gatunense* did not bloom. Instead, a succession of short blooms of nanoplanktonic species was observed (Nishri et al., 1998). These deviations from the typical annual pattern took place over a period of a continuous reduction of the lake's water level beyond its natural level, due to shortage of water in Israel. Between 1993 and 2002 the lake's mean annual water level was lowered by ca. 0.7 m each year.

Phytoplankton data acquisition and processing

As part of the routine monitoring program for Lake Kinneret, phytoplankton samples were collected biweekly from a fixed pelagic station at the deepest part of the lake from 10–12 discrete depths throughout the water column. Lugol-preserved samples were brought to the lab for microscopic counting using the sedimentation chamber and inverted microscope technique (Lund et al., 1958), and a Zeiss M24 Axiovert inverted microscope. All phytoplankton species with individual cells greater than 2 μm diameter (cell volume, V, of 4 μm^3) were identified and counted. From the smaller cell range (picoplankton), only the relatively common colony-forming cyanobacteria *Cyanodictyon* (cell volume 0.5 μm^3) and *Merismopedia minima*, ($V = 1$ μm^3), were counted (Utermöhl, 1958; Lund et al., 1958). For nanoplanktonic species (<20 μm diameter), 10 ml subsamples were sedimented for 24 h after which all phytoplankton cells in 5 arbitrary strips (area: 2 mm^2), making up 2% of the total sample, were counted at ×320. For larger species (>20 μm diameter), 1 ml samples were sedimented in smaller, 1 ml chambers and all netplanktonic cells were counted on the following day. Using this method, we usually counted at least 100 'natural units' (cells, colonies or filaments) of all the abundant species, giving a precision of ±20% for those species.

Cells that were dead at the time of preservation were not counted. Phytoplankton were identified and counted according to species, and for species of highly variable cell size (like *Peridinium gatunense*), also according to size categories (e.g., small, medium, large). Phytoplankton biovolume values were calculated from specific recorded abundances (density, N_i, cells ml^{-1}) and specific biovolumes (V_i) approximated to simple geometrical shapes (Hillebrand et al.,

1999). Biovolumes were based on linear measurements made microscopically. Specific biomass (B_i, mg m^{-3}) calculations were carried out assuming that all phytoplankton have a specific density of one.

Size spectrum analyses

Methods of size spectra calculation and plotting were used as described by Sheldon et al. (1972). All organisms counted and measured in a sample of water were distributed into size classes according to their cell volume (V_i). Size classes were standard increments of the organism size logarithm ($\Delta \log V = \log 2$), i.e., doubling of the cell volume. The Vxx notation is used throughout this paper for size classes, where xx is the class right border (e.g., V32 means cells with volume from 16 to 32 μm^3). The wet weight biomass of each size class (mg_{ww} m^{-3}) was calculated using the biomass (B_i, mg m^{-3}) for each taxon and summing up the contributions from the various taxa inside each size class.

After data compressing, i.e., transformation of vast taxonomic lists into more compact frequency distributions, a second step of data compression was carried out. The depth integrated BSS per unit area or BSS2, was calculated using data from all sampling depths and conducting a linear interpolation between the depths. During stratification, depth integration was only to the mid-thermocline depth, usually between 15 and 20 m, excluding data from deeper depths. Finally, the biomasses of all size classes were summed up to give the depth-integrated total phytoplankton biomass shown in Fig. 1.

Twenty five BSS2 distributions (mg_{ww} per m^2 per binary size class) were calculated each year, each based on biomass data from 8–10 microscopically counted samples, giving a total $n = 100$ size spectra. The mean estimates and SD were computed for each size class (Figs 2–4), using all sampling dates of the studied period, but split according to year, season, or all data set (see Table 1). Formal division of the year into 4 seasons (3 months each) was used. As winter holomixis typically begins in December, the first part (season 1) includes months 1 and 2, and month 12 of the previous year. This way, the BSS change corresponds to the four seasons identified in earlier Kinneret studies: winter holomixis (season 1), spring stratification (season 2), summer stratified water column (season 3) and fall destratification (season 4). The above-mentioned periods are characterized with different composition of the lake plankton (see Pollingher, 1986).

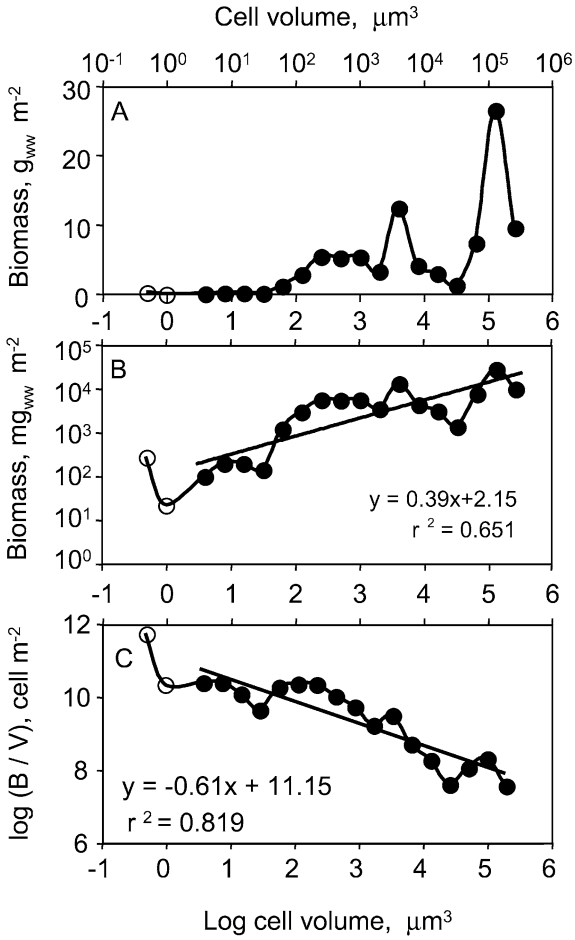

Figure 2. (A) The general pattern of Kinneret phytoplankton depth-integrated biomass size spectrum (BSS2), showing the biomass distribution into classes of progressively increasing cell volumes. Data shown are 4-year (1996–1999) averages ($n = 100$) plotted on a semi-logarithmic scale. (B) same data as above only plotted on a log-log scale and showing the best fit regression line characteristic for Lake Kinneret (the 4-year mean data). (C) Normalized Biomass Size Spectrum (NBS, in which the vertical axis is the total fresh biomass (mg_{ww} m^{-2}) of organisms in a particular cell volume category divided by the change in cell volume across the category. Thus, NBS describes the approximated (averaged) cell density estimate and is marked by us here as 'log (B/V), cell m^{-2}'.

The size spectra were also analyzed as normalized BSS (NBS, Fig. 2C), which were calculated via normalization of the total biomass in the i-th volume size class to the class width ($\Delta V_i \sim V_i$): $\beta_i = B_i/V_i$ (Platt & Denman, 1978).

Table 1. Estimates of linear fit: log Y = $a + b$ log V. Note. BSS and NBS are the Biomass (Sheldon et al., 1972) and Normalized Size Spectrum; a, b, r^2 are the Y-intercept, the regression slope, and the determination coefficient, respectively, of the linear fit line; n is the number of spectra used to compute the average estimates. Unnormalized biomass expressed in $mg_{ww}\ m^{-2}$.

SS type	Season/year	a	b	r^2	n
NBS	Season 1: winter holomixis	11.30	−0.65	0.753	25
NBS	Season 2: spring stratification	10.87	−0.55	0.733	25
NBS	Season 3: summer stratified	11.02	−0.63	0.747	25
NBS	Season 4: autumnal mixing	11.16	−0.68	0.742	25
NBS	Overall avg	11.15	−0.61	0.819	100
BSS	1996	2.24	0.31	0.479	25
BSS	1997	2.31	0.32	0.528	25
BSS	1998	1.35	0.61	0.601	25
BSS	1999	1.80	0.49	0.523	25
BSS	Avg, 1996–1999	2.15	0.39	0.651	100

Statistical analyses

Correlation analysis was done to find the size classes of phytoplankton most closely related to the phytoplankton assemblage biomass. Linear regression was used to estimate parameters of the SS shape. Parameters of those BSS2 linear approximations were used for comparison of intra- and inter-annual variability of the phytoplankton assemblage structure. Coefficient of variance (CV) was calculated for each size class as a measure of its seasonal variability. SPSS program, version 11.0 (Norussis, 1998) was used for all statistical analyses.

Results

During 1996–1999, Lake Kinneret phytoplankton biomass (Fig. 1) showed strong seasonal patterns, high peak values (up to 512 $g_{ww}\ m^{-2}$), and pronounced inter-annual variability. Mean BSS for these four years ($n = 100$) indicates the existence of two distinct peaks, or 'bells' (Fig. 2A), which provide the main part of variability in community biomass. These peaks have a specific taxonomic interpretation for Lake Kinneret: the highest peak, associated with size classes V32 000 to V128 000 and with average biomass for 1996–1999 of about 27 $g_{ww}\ m^{-2}$, was due to *Peridinium gatunense* (cell volume 32 000–160 000 μm^3 with dominance of the intermediate cell sizes). The second peak, associated with the size class V4000 and with average biomass of about 12 $g_{ww}\ m^{-2}$ was due to *Aulacoseira granulata* (cell volume: 1100–6000 μm^3). Correlation analysis between total phytoplankton biomass and the various size classes shows that the most high and significant correlations are with the *Peridinium*-dominated size classes V128 000 ($r = 0.668$, $p < 0.001$, $n = 100$) and V64 000 ($r = 0.551$, $p < 0.001$, $n = 100$), confirming that *Peridinium* is the major biomass contributor in Lake Kinneret. Less strong but significant was the correlation of the community biomass with size class V4000 μm^3 ($r = 0.434$, $p < 0.001$), corresponding to *Aulacoseira*, and its negative correlation ($r = -0.190$ to -0.273, $p < 0.05$) with small algae (V32, V128). A probable explanation of the latter negative correlation may be the shading of the small species during blooms of the large species.

Besides the peaks, characteristic troughs, or 'gaps' were also evident in the BSS, these were more evident in the logarithmic representation of the BSS (Fig. 2B). One can distinguish here four zones ($V < 1$, V4–V64, V100–V10 000 μm^3, and V64 000–V256 000) separated by gaps of an order magnitude or more. Due to the aforesaid incomprehensive quantification of picoplankton abundance, the first bell (and the following gap) may be an artifact and needs a more thorough analysis based on additional data. The third bell (V100–V10 000) seems to be composed of two considerably different parts, which are V4,000 bell of *Aulacoseira* mentioned above, and a broad, much less vulnerable dome (V100–V1000), which we call 'nanoplankton plateau' (see below). The rightmost

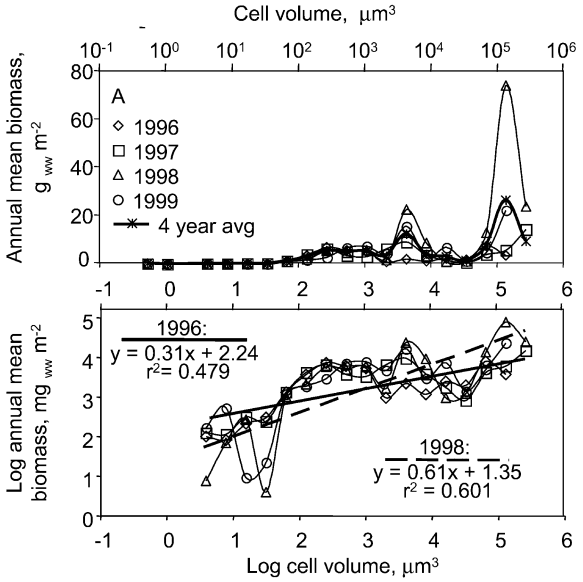

Figure 3. A comparison of 4 annual mean BSS2 (1996, 1997, 1998, 1999) and the 4-year mean spectrum. (A) Semi-logarithmic; (B) Logarithmic scale; $n = 25$ for each year. The regression lines for the most contrasting pair of years, i.e. 1996 (continuous line) and 1998 (dashed line) are shown.

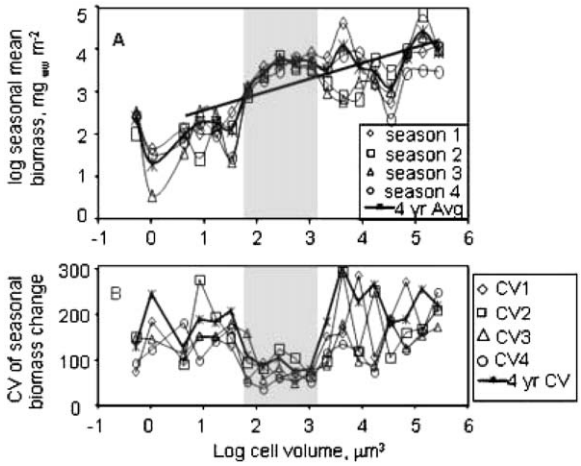

Figure 4. (A) A Comparison of the 4-year mean average BSS2, for each of the seasons 1–4 (winter to autumn). (B) BSS2 seasonal variability as Coefficients of Variance (CV, i.e., SD in percent of the respective class average value) for 1996–1999; $n = 25$ for each season. Hatched areas highlight the region of low CV corresponding to the 'nanoplankton plateau'.

and the highest bell (V64 000–V256 000) is noted on Figure 2A as being due to *P. Gatunense*.

Due to the flawed enumeration and volume estimation of small cells we excluded fractions with cell diameter < 2 µm from all regression line estimations (Fig. 2, Fig. 3, Table 1). A linear regression approximates well such form of SS ($r^2 = 0.651$) and produces the power coefficient estimate $b = 0.39$ (Fig. 2B), rather different from values close to zero, described most often in oceanographic literature (e.g., Sheldon et al., 1972; Gin et al., 1999).

Normalized Biomass Spectrum (NBS, Fig. 2C) facilitates quantification of variation in coarse patterns of SS, and following ideas of Kerr (1974) and Platt & Denman (1978) seems to be the more often used SS form in plankton research. The vertical axis represents here the total depth-integrated wet weight biomass ($mg_{ww}\ m^{-2}$) of organisms in a particular cell volume class divided by the change in cell volume across the same category. Due to the doubling cell volume scale of the X-axis, this change is equal to the left border cell volume of that class. The resulting estimator is close, but not identical, to the real numerical density of organisms in the size class (Platt & Denman, 1978). Thus it describes the approximated (averaged) cell density and is marked by us here as 'log B–log V', i.e., log (B/V) = log N, cells m^{-2}. The linear form is a little more pronounced in the NBS presentations ($r^2 = 0.819$ for the average spectrum, 0.733–0.753 for seasonal ones).

The variability of the BSS2 pattern highlights the annual cycle of phytoplankton succession (Fig. 4A). The plankton composition differences are evident in the shape of the curve for each year or season (Figs 3 and 4; Table 1). For example, the various bells (composed of specific taxonomic groups) vary between years and seasons in their relative height. Linear approximations of the phytoplankton BSS, log B = $a + b$ log V, give relatively high correlation coefficients ($r^2 \sim 0.479$–0.601) for average estimates of individual years and seasons and even slightly higher values for seasonal NBS. Nevertheless, all these estimates are considerably lower than $r^2 > 0.9$ typical of the oligotrophic oceans (Rodriguez & Mullin, 1986; Gin et al., 1999). A 'non-ideal' form of our BSS was caused by several zones of comparably high deviation from a straight line, in the form of the gaps and taxonomic bells described above, e.g., V1, V64, and V64 000 μm^3.

Parameters of the regression line differed for the four years (Table 1): $a = 1.35$–2.31, $b = 0.31$–0.61. Though parameter a describes the approximated biomass level at point log $V = 0$, its high variability is caused mainly by changes in two zones (V4–V64 and V4000–V256 000) and stability of the middle (V100–V1000) zone. This conclusion can be made

from analysis of inter-annual (Fig. 3A) changes. Intra-annual variability (Fig. 4B, coefficient of variation CV) supports this explanation. Due to the pronounced temporal dynamics of phytoplankton (Fig. 1), standard deviation (SD) was high in comparison with the mean biomass estimates, for many size classes. Therefore, instead of the commonly used Y-error bars, we present a special comparison of these estimates expressed as Coefficient of Variance (CV, i.e., SD normalized to the respective class mean value), using a special plot. The obtained result (Fig. 4B) splits the studied cell size region into several sections, differing from each other in their biomass variability (CV). By comparing Figures 2–4, we can conclude that BSS of integral phytoplankton community was composed of several peak zones (bells) separated by rather deep valleys (gaps). Three zones (V4–V64, V4000, and V64 000–V256 000) were much more vulnerable to biomass variability than a 'nanoplankton plateau' (V100–V1000 μm^3), highlighted in Figure 4B.

Comparison of seasonal estimates averaged for 4 years (Fig. 4) helps us see the size effects of temporal changes in phytoplankton biomass (Fig. 1). The right extreme part of BSS shows a large difference between winter and summer *Peridinium* and *Aulacoseira* (V4000) biomass at the beginning and end of the winter season (4 and 1 on Fig. 4). Pronounced seasonal changes are also seen for small nanoplankton (V4–V32), while larger cells (V64–V1000) show almost no seasonal differences. Based on the shape of BSS, the most contrasting pair of years is 1998/1996. Indeed, in 1996 *Peridinium* did not bloom and the spring season was characterized by a succession of dominant chlorophytes, whereas in 1998 the most massive *Peridinium* bloom ever was recorded.

Discussion

Phytoplankton size spectra: General pattern and fine structure

The most striking feature of the presented analysis of L. Kinneret phytoplankton is the existence of some form of stability of its structure; the phytoplankton size structure looks rather stable (Fig. 3; Table 1) despite strong variations of environmental parameters, phytoplankton taxonomic composition and biomass dynamics (Fig. 1). Not only the general BSS and NBS patterns of the phytoplankton assemblage look 'almost the same' from year to year and from season to season, but several descriptors of these patterns (the slope, the intercept and the determination coefficient; Table 1) also seem to be more or less stable. As those descriptors are quantitative, they open a way to proceed from a verbal description 'more-or-less' to some quantitative comparisons and measures of variability. Among such descriptors one can note also the position of the two highest peaks (Fig. 3) and the 'nanoplankton plateau' stability (Fig. 4).

Numerous studies of natural aquatic communities, especially, of plankton, consider very similar patterns of their size structure. Two major types of such studies may be noted: (a) those focusing on the general form of the whole SS (mainly NBS), its linear approximations, and variability of the regression coefficients (e.g., Rodriguez & Mullin, 1986; Rojo & Rodriguez, 1994; Vidondo et al., 1997; Cavender-Bares et al., 2001); and (b) studies of the 'fine structure' of SS, i.e., SS discontinuity, the number and position of separate peaks and troughs (Schwinghamer, 1981; Holling, 1992; Havelicek & Carpenter, 2001), the shape of separate peaks (Chislenko, 1981; Thiebaux & Dickie, 1993; Sprules & Goyke, 1994; Cozar et al., 2003), their hierarchic structure and taxonomic composition (Sheldon et al., 1972; Chislenko, 1981; Rojo & Rodriguez, 1994; Havelicek & Carpenter, 2001). Of course, additional variants are possible between the two extreme approaches mentioned here. They do not contradict each other, but are complementary and can provide additional valuable results when used together. Formal SS representations can also complement more traditional taxonomical analyses. In our study, we applied such a simultaneous approach. It helps better understand changes of SS and its approximation parameters, via analysis of shifts in position and amplitude of the separate 'dome' and 'bell' shaped features which compose the integral community SS.

Typical pattern and quantitative descriptors of non-ideality

In the data presented (Figs 2–4), known typical patterns emerge. While BSS of the integral community is composed of several bells, it still forms a coherent system, which can be approximated by a linear regression, i.e., a simple model. The linear regression parameters seem to be very effective to develop quantitative scales for comparative analyses of the stability/variability of aquatic communities (Sprules & Munawar, 1986) and 'non-ideality' of a real SS, while compared with a theoretically derived pattern (Kerr, 1974; Platt & Denman, 1978). There are ways to

upgrade the analysis efficiency, as a number of specific mathematical procedures should and can be improved, leading to more precise parameter estimation (Vidondo et al., 1997).

Oligotrophic systems such as the Pacific Ocean Central Gyre or Lakes Superior and Huron tend to have more negative slopes of NBS than eutrophic lakes (Sprules & Munawar, 1986). This trend is associated with higher variability in the large zooplankton abundance of eutrophic lakes, while the small algae abundance is almost uniform across all trophy levels. SS from oligotrophic regions also have a higher determination coefficient (r^2) of the approximating linear regression (Sprules & Munawar, 1986). Gin et al. (1999) found a similar trend in microbial communities of the Sargasso Sea: size spectra in oligotrophic waters were characterized by steeper slopes and less seasonal variability than spectra in coastal waters. A comprehensive study of oceanic plankton carried out in the northern Atlantic and equatorial Pacific Oceans (Cavender-Bares et al., 2001) also found clear power-law behavior, but no clear relationship between nutrient concentrations and spectral slopes over the entire data set obtained in oceanic waters. Similar results were obtained from a broad scale comparison of pelagic communities (plankton and fish) of North American lakes. Lakes that differed widely in the area, nutrient status, trophic structure, and species diversity, still had similar species size distributions (Havelicek & Carpenter, 2001).

Individual spectra within large oceanic regions under similar ecological conditions show remarkable consistency (Cavender-Bares et al., 2001). Size distribution characteristics in lakes seem to be conservative properties shaped by common regional ecosystem processes and organism patterns and not by lake-specific factors (Havelicek & Carpenter, 2001). These universal trends of plankton and pelagic community NBS agree well with the seasonal dynamics of Kinneret phytoplankton. Its NBS pattern is almost the same, but the linear regression parameters have some variability (Table 1).

The slope of the regression line for the NBS is steepest ($b = -0.68$) during season 4 (i.e., the most oligotrophic state), and the least steep ($b = -0.55$) during season 2 (i.e., large algae, *Peridinium* bloom). The same is true for r^2, which varies between 0.753 (season 1) and 0.733 (season 2). According to these two criteria, Lake Kinneret is close to Lake Erie and Saginaw Bay of Lake Huron, i.e., the most eutrophic waters on the Sprules & Munawar (1986) scale. The most 'eutrophic' values of these estimators describe season 2 of Kinneret, when the plankton community goes through its annual bloom. A very high slope ($b = 0.59$) was obtained for the phytoplankton BSS in a small hypertrophic lake in Spain, when large cells comprised the main bulk of the assemblage biomass (Rojo & Rodriguez, 1994). The above slope is very close to the unusually high 0.61 estimate of L. Kinneret annual mean BSS of 1998 (Table 1), notable with the most pronounced ever bloom (Zohary, 2002) of *P. gatunense*, the largest phytoplankton species of Kinneret.

Size scale: Cell volume and particle size

A distinctive feature of our study is the use of cell volume as the size variable of SS, rather than the more commonly used particle size, which in the case of phytoplankton would be 'algal units' such as colonies or filaments for multicellular species (e.g., Rojo & Rodriguez, 1994). While numerous allometries are based on the organism size and use cell size for phytoplankton (e.g., Peters, 1986; Chisholm, 1992), the automated measurement units (particle counters, flow cytometers) really work with particles, which not always contain only a single algal cell. In some cases, especially for colony-forming organisms common in warm waters, this distinction is important (Rojo & Rodriguez, 1994). Using particle size rather than cell size would have, for instance, pushed the location of the bell formed by the filamentous *Aulacoseira* (Fig. 3, V4000) to the right, possibly merging into the *Peridinium* bell as a typical *Aulacoseira* filament with 15 cells has a biovolume of 60 000 μm^3. It also may have modified the nanoplankton plateau region, where some but not all of the species are colonial forms. The most right-hand side *Peridinium* bell would not have changed as *Peridinium* is unicellular. Certainly, due to the importance of colonial forms, additional analysis is necessary comparing cell-based SS with spectra obtained via use of particle counters and flow cytometry (e.g., Sheldon et al., 1972; Cavender-Bares et al., 2001).

Bell/gap structure

While statistical parameters of BSS and NBS approximation provide a scale for a quantitative estimation of the size structure stability (Table 1), a comparison of CV of specific size classes (Fig. 4B) also seems to be promising in this respect: It breaks up the full cell

volume range into subranges of high vs. low variability. The large algae bell ($V > 64\,000\ \mu m^3$) is highly variable in time, while the central plateau (V100–V1000 μm^3) is much more consistent and stable. The left part of the curves composed of pico- and small nanoplankton, had a variable right side (V4–V16 μm^3) (Figs 3–4). For the extreme left part of BSS, one should keep in mind that the traditional phytoplankton counting methodology used in the present work excluded most of the small cells ($V < 4\ \mu m^3$), and the presented results require additional field data for the smaller size classes in order to produce a more complete analysis.

An important aspect of stability emerges as the stable position of the two main peaks (Figs 2 and 3), reflecting the lake phytoplankton taxonomic composition, i.e. domination (in terms of biomass) of the same taxonomic components, which safeguard almost the same (in comparison with the integral community size range) mean cell volume. The phytoplankton biomass variability is produced mainly by zones V4000 and V128 000, consisting of *Aulacoseira* and *Peridinium*, respectively (Figs 2–4). These algae differ considerably in their optimal requirements for many abiotic factors. Therefore, such taxonomic composition of the lake phytoplankton can produce SS variations due to changes in the abiotic environment.

The SS non-linearity measure (r^2 of the NBS linear approximation), proposed by Sprules & Munawar (1986) as a quantitative criterion, works well for the analysis of the Kinneret phytoplankton changes and is connected with the bell/gap sharpening during periods of high total biomass (Figs 1 and 3, years 1998–1999). The bell/gap structure, which can cause a strong decline in the NBS regression coefficient of determination, can be better seen on a semi-logarithmic, and especially, BSS plots (compare Figs 2 and 3). A biomass anomaly size spectrum (BASS) (Cozar et al., 2003) can serve as an effective addition to both BSS and NBS with pronounced bell/gap structure.

Phytoplankton vs. plankton studies

It is noteworthy that our study focused only on phytoplankton. Nevertheless, many characters seen in the Kinneret phytoplankton spectra resemble features known from study of freshwater and marine plankton, fish, pelagic and even benthic communities. Such comparisons can be helpful, as they can provide us with ideas and solutions found from large-scale, expensive and more comprehensive studies.

Numerous works (Sheldon et al., 1972; Sprules & Munawar, 1986; Gin et al., 1999; Cavender-Bares et al., 2001) show coexisting of a linear pico-nanoplankton part of the plankton BSS, with several bell/valley zones comprised of larger organisms. This latter feature becomes more evident under eutrophic conditions and is noticeable for Kinneret phytoplankton BSS. Here, relatively constant (over time) biomasses of some of the phytoplankton size groups do not prevent high variability of the integral biomass (Fig. 1) and parameters of the SS linear approximation, caused by high variability of some other size classes (Figs 2–4).

According to interannual (Fig. 3) and seasonal comparison (Fig. 4), the most variable are zones V4–V64 and V4000–V256 000. As the slopes (b) and intercepts (a) may strongly depend on the size range applied, inclusion (or not) of the smaller (bacteria-picoplankton) and larger (nanoplankton – zooplankton – nekton) size classes is important. By design, our study was limited to phytoplankton and therefore excludes the smallest (bacteria) and the largest (zooplankton to nekton) size classes of the pelagic community. Our data are limited to nano- and net-size phytoplankton, as our methods of data collection eliminated picoplankton.

We did calculate the regression equations with and without the limited pico-size data available to us and found that including the picoplankton had a negligible effect on the values of a and b coefficients. We chose to exclude from regression analysis the two picoplankton points (Fig. 3) because our data for the small size classes is inconsistent – two colonial species (*Merismopedia* and *Cyanodictyon*) were counted but many other species that contributed to the picoplankton were not. These two species that were counted were not a fixed proportion of the total picoplankton biomass.

If the spectrum has several bells and gaps (Schwinghamer, 1981; Sprules & Munawar, 1986; Havelicek & Carpenter, 2001), the linear approximation slope can depend on the considered body mass interval. The slope change can be acute when the end point of SS excludes a high bell (e.g., the right extreme part in Figs 2–4). As parameters of linear approximations and variability estimates depend strongly on the size range studied, selection of the whole self-regulating object (a natural community or a phytoplankton assemblage here) seems to be a serious reason that justifies the size limits applied.

Right extremity of SS: Large cells

The correlation of L. Kinneret phytoplankton total biomass with specific size fractions is the strongest for the largest cells. Dominance of large cells (*Peridinium, Aulacoseira*) in the Kinneret phytoplankton biomass is known from many years of monitoring. This feature is well seen from the mean BSS (Fig. 2) and its annual and seasonal means (Figs 3 and 4A). Importance of large organisms in community biomass is well established in aquatic and terrestrial ecology (Odum, 1971) and should be taken into account when using BSS approximation data for comparison. However, in many cases, just these largest members of the studied assemblage are excluded due to methodology and instrumentation limitations. For instance, many flow cytometer systems exclude large phytoplankton cells.

Cavender-Bares et al. (2001) found no clear relationship between nutrient concentrations and spectral slopes in oceanic waters (northern Atlantic and equatorial Pacific) for plankton size spectra 'from bacteria through nanophytoplankton' (a good example of this cell size limitation). Nevertheless, species succession in nutrient-enriched bottles caused spectra to evolve from relatively smooth power laws to distributions showing preferred sizes (i.e., bell/gap structure). Spectral shapes, smooth and log-linear during the spring bloom in the Sargasso Sea, changed to distinctly non–log linear in coastal waters. The authors noted that their experimental design was somewhat flawed as they did not measure the large end of the phytoplankton spectrum, which is "likely to be the most responsive in terms of biomass increase to nutrient enrichment" (Cavender-Bares et al., 2001: 786). The dominant role of the largest cells in the total phytoplankton biomass was described for a small hypertrophic lake by Rojo & Rodriguez (1994).

Quintana et al. (2002) found that the coefficient of determination (r^2) and b-slope of the phytoplankton BSS changed with trophic level in a shallow marsh. Increasing eutrophication caused biomass to accumulate at the large cell regions, including mixotrophic algae, grazing on smaller phytoplankton. Morin et al. (2001) found that biomass of organisms (algae, protozoa, and invertebrates) increased with nutrients concentrations in the water, but the response of invertebrates was stronger than that of algae and protozoans. The authors concluded that increases in nutrient inputs to oligo- and mesotrophic streams might benefit consumers more than primary producers.

According to our interpretation, the above studies show that a large change in nutrient availability in aquatic systems (e.g. from Sargasso Sea to the near shore, shallow marsh, small lake or freshwater streams) leads to an accumulation of the community biomass, mainly at the right end of its SS. As the large organisms accumulate a high biomass, the linearity of the SS becomes less pronounced, while the bell/gap pattern is more evident. This is important in our case, in comparing a lake (i.e., a relatively small and shallow water body) with oceanographic studies.

Whereas small size is a major competitive advantage when diffusive processes control uptake at low nutrient concentrations, larger cells tend to outcompete small cells in nutrient-rich environments (Chisholm, 1992; Kiorboe, 1993). This scheme explains why the SS from the oligotrophic BATS station and from stratified, nutrient-poor waters in Massachusetts Bay are skewed towards smaller cells (Gin et al., 1999). Once small phytoplankton reach their maximal growth rate during nutrient enrichment, the free nutrient concentration can increase rapidly to a point where large phytoplankton can get established (Thingstad & Sakshaug, 1990). So, as the total chlorophyll increases, additions are contributed from progressively larger cells (Chisholm, 1992). Thus, the phytoplankton biomass growth can be channeled to larger size classes once smaller classes receive their quota. Resuspension of cells from the near-bottom (i.e., nutrient-rich zone), also can move upward the large cell bells and amplify the large cell domination.

Left extremity: Picoplankton

Less regular, but even deeper gaps are seen in the left part of the Kinneret BSS. Rather big distances (more than one order of magnitude) from the regression line can be noted for V4–V32 points, in 1998 and 1999 (Fig. 3B). Point V8 is notable with a high CV of close to 300% for season 2 (Fig. 4B). The downward displacements of small cell biomass agree well with the noted above negative correlation between small size classes and the total phytoplankton biomass. Less pronounced anomalies can be seen for picoplankton range ($V < 4$), but they require additional analysis, as our picoplankton data was incomplete. Nevertheless they do not contradict the trends known from the literature on the picoplankton role under different trophic conditions. An extensive review by Bell & Kalff (2001) of the importance of small phytoplankton in marine and freshwater systems showed that the picophyto-

plankton biomass (in terms of chlorophyll a) increases with trophic status, but its relative contribution to total biomass and primary production declines with increasing trophic status in both marine and freshwater systems. Comparable results were evident in vertical profiles of phytoplankton in the oligotrophic Sargasso Sea by means of flow cytometry. The relative role of picoplankton increases at a greater depth, where the total biomass is lower. Most of the seasonal variability in biomass occurs in nanoplankton, while picoplankton mass remains relatively constant (Gin et al., 1999). Increased phosphorus loading of lakes had positive effects on the absolute abundance of small phytoplankton, large phytoplankton, slope of size spectra, and mean phytoplankton size, but negative effects on the relative abundance of small phytoplankton. Although small phytoplankton dominate under low nutrient conditions, large phytoplankton become dominant as lakes become more eutrophic (Cottingham, 1999 and references therein).

In shallow eutrophic lakes, where resuspension and sediment recruitment are important processes, the relatively small contribution of picophytoplankton biomass appears affected by a high but variable contribution of resuspended microplankton (Bell & Kalff, 2001), i.e., large cells. As phytoplankton resuspension plays an important role in Lake Kinneret (e.g. Pollingher & Serruya, 1976) it is interesting to note that the BSS shape of the Kinneret phytoplankton (Fig. 4; $b > 0$) is closer to benthic BSS (Schwinghamer, 1981) than to marine pelagic communities. The typical pattern evidenced for plankton (Gin et al., 1999), pelagic communities (Kerr, 1974; Sprules & Goyke, 1994), and benthos (Shwinghamer, 1981) is almost the same. However, while in pelagic communities biomass spectral density diminishes with the growth of the body mass, in benthic and integral aquatic communities (i.e., pelagic and benthic organisms together; Kamenir & Khailov, 1987; Cyr & Peters, 1996), the opposite trend is evident.

Central part (nanoplankton plateau) vs. the ends

An interesting stable feature of L. Kinneret phytoplankton is seen in the center of BSS as a low variability zone of 'nanoplankton plateau' fractions in the size range V100–V1000 (Figs 3–4) corresponding to the 'nanoplankton plateau'. It is widely held that marine phytoplankton communities are assembled by adding larger cells to a relatively uniform background of smaller cells (Ciotti et al., 2002; Li, 2002). This uniform background comprises of pico and small nanoplankton. As phytoplankton communities grade from low to high biomass, there is a reduction in picoplankton, an increment in large nanoplankton, with no apparent net change in small nanoplankton (Li, 2002). This uniform background of oceanic water nanoplankton bears a resemblance to the Lake Kinneret stable 'nanoplankton plateau'.

Accumulation of the high biomass at the right extremity of SS has already been described for several types of aquatic communities in nutrient-rich environments – benthos (Schwinghamer, 1991), oceanic phytoplankton (Li & Harrison, 2001; Li, 2002), lake plankton (Sprules & Munawar, 1986), and springs or rivers (Morin et al., 2001; Sin et al., 2000). This high right-hand accumulation is typical for Lake Kinneret during some seasons. While for the 'stable zone' (V100–V1000 μm^3), b is close to 0 (compare to results of Sheldon et al., 1972; Gin et al., 1999; Cavender-Bares et al., 2001), a variable angular coefficient $b > 1$ is calculated for the complete phytoplankton assemblage (Figs 3–4), resulting from the huge and variable abundance of large cells, especially *Peridinium*. This distinction holds true for both seasonal and inter-annual variability (Fig. 4). As the central part of SS (nanoplankton) is almost constant (Figs 3 and 4), the angular coefficient of the approximating line (b) changes due to the movement of the end parts of the BSS.

Results interpretation: Stability or variability?

As the general pattern and mean sizes of the dominant groups are almost the same during the four year period, one can say that the object (phytoplankton) is rather stable, while described via 'non-demographic' methods (here biomass size spectra instead of taxonomic groups). At the same time, this stability does not mean something constant or fixed, but rather a quasi-cyclic process, oscillating around a central point, with a known periodicity of one year (i.e. seasonal cycles). This cyclic process is 'quasi'-stable, as some 'noise' components exist, however, the annual descriptors (Table 1) are almost the same each year and seasonal trends seem to agree with widely known trends such as the impact of the trophic level on the slope and non-ideality of the linear regression. The changes in the SS shape (the regression slope, r^2, the peaks' position, height and CV) can be quantitatively compared as displacements from a known (theoretically derived) ideal pattern. A system that retains these

properties over a long time is not fragile (broken), but rather 'resilient'. The mean annual slope returns to its known position (compare 1997–1998 and 1999 slopes and r^2; Table 1), but the rates of such return can be discussed in the future only on the basis of data from several annual cycles. Taken together, these quantitative measures demonstrate the stable features of the L. Kinneret phytoplankton as is evident in its biomass size structure.

The descriptors are quantitative, and the 'stable' (or, rather, typical) values are revealed via statistics, as the mean values. SD or CV can replace the less rigorous term 'variability'. Internal mechanisms and external impacts often cause appreciable changes in the taxonomic composition of a community (Odum, 1971; Begon et al., 1996), highly pronounced in phytoplankton assemblages (Naselli-Flores et al., 2003; Rojo & Alvarez-Cobelas, 2003). Therefore, SS and other 'ataxonomic' (Schwinghamer, 1981) schemes are especially valuable in cases of taxonomic dissimilarity, providing means to develop quantitative indices of structural changes. Size spectra describe community properties irrespective of species composition change. As such, they are suitable for description of natural systems with a large number of species, for comparative analysis of systems with different taxonomic composition, and for systems with temporally- and spatially-changing species composition. At the same time, SS provide effective means of taxonomic interpretation (Sieburth et al., 1978; Chislenko, 1981), which are very valuable for monitoring of a specific aquatic community.

Some speculations on the application of size spectra: Broad range comparisons

Our own results and studies by other authors of different types of aquatic systems point to the existence of specific forms of stability of aquatic communities. These are the community size structure patterns formed as small modifications of the known 'typical patterns' (Schwinghamer, 1981) of BSS or NBS, consisting of several bells separated by gaps. This typical pattern can be approximated by a simple (linear, Pareto, lognormal, polynomial) model. Several parameters of the regression are suitable to build quantitative scales (Sprules & Munawar, 1986) measuring the distance of a given SS from a theoretically derived (Kerr, 1974; Platt & Denman, 1978) 'ideal' pattern.

These patterns seem to be so stable (Rodriguez & Mullin, 1986; Cavender-Bares et al., 2001; Havelicek & Carpenter, 2001) that only comparisons of widely differing systems allow to obtain non-ambiguous interpretation of the effect analyzed. Some tendencies of the pattern modifications seem to be rather similar for the open ocean, lakes, marshes and streams; for phytoplankton, microplankton, pelagic communities and benthos. Many differences exist, but some of them can be treated as known effects of a large-scale impact (e.g., slope difference between the lake plankton and its benthos). Several trends discussed above seem to be co-dependent and could be interpreted together. Then we see the main effect of the increasing trophic level as a growing 'non-ideality' of the pattern, caused by enhanced bell/gap structure. Such a structure produces a lower coefficient of determination of the linear regression of NBS, e.g., $r^2 \sim 0.7$ in a mesotrophic (present study) and $r^2 \sim 0.5$ in hypertrophic lake phytoplankton (Rojo & Rodriguez, 1994) as opposed to $r^2 > 0.99$ in the oligotrophic ocean plankton (Rodrizuez & Mullin, 1986). These quantitative differences (of the slope, r^2, peak amplitudes) can be used for diagnostics of the 'abnormality' of a specific aquatic community. The established trends can be valuable for ecological forecast (Peters, 1986).

The phytoplankton assemblage is an extreme example in such comparisons. Analysis of only autotrophic organisms minimizes the importance of energy flow across trophic levels, usually considered as being the main 'organizing mechanism' producing the 'ideal pattern' of SS (Kerr, 1974; Platt & Denman, 1978). The nutrient enrichment in lakes had opposite effect on small and large phytoplankton. This effect had a strong correlation with the food web structure (quantity of planktivores and large zooplankton) (Cottingham, 1999). The parallels between SS of phytoplankton and entire pelagic community are important as phytoplankton is the most suitable for monitoring part of the pelagic community. An overall conclusion of Cottingham (1999) is that size structure is an excellent descriptor of shifts in phytoplankton communities, following manipulation of nutrient inputs and food-web structure. The slope of the phytoplankton NBS resembles those of the entire plankton community, however, the fit to a straight line is poor and strongly influenced by extremely small and large cells which have low abundance (Gaedke, 1992). So, it seems that phytoplankton has almost the same trends of SS change as the whole aquatic community, but is more vulnerable to some environmental impacts. Due to their photosynthetic pigments, active in 400–700 nm wavelengths, phytoplankton are suitable for

optical methods of monitoring. These pigment assemblages are diagnostic of the major phytoplankton taxa and covary with the dominant size fractions. Therefore, remote sensing may be used to obtain synoptic information on size structure of phytoplankton from large aquatic regions (Ciotti et al., 2002). Hence, if a strong correlation exists between SS of the entire aquatic community and that of its autotrophic component, analysis of phytoplankton size structure pattern and trends of its change under environmental impacts can produce an efficient means for the monitoring and diagnosis of the trophic status in aquatic environments.

Conclusion

A typical pattern of BSS of Lake Kinneret complete phytoplankton assemblage was evident and remained quasi-stable over 4 annual cycles during which the Lake's water level was reduced beyond its natural levels and phytoplankton biomass dynamics and taxonomic composition deviated from its typical patterns.

Statistical parameters of BSS approximation of the autotrophic assemblage allow us to produce quantitative estimates of its size structure stability/variability. According to these parameters, phytoplankton size distribution patterns in Lake Kinneret are similar to those found in most of the eutrophic lakes described (Canada, Spain), and somewhat differ from stable oligotrophic systems.

The above properties of the phytoplankton SS demonstrate a specific form of stability, that of its size structure patterns. Further analysis requires complete accounting of the phytoplankton assemblage, first of all, by the inclusion of the picophytoplankton.

High values of phytoplankton biomass during nutrient inflow periods are produced mainly by large cells. Statistical descriptors of separate size classes identify a zone of stability (nanoplankton plateau) and two zones of pronounced variability within Kinneret BSS. The plankton biomass variability is produced mainly by these two 'bloom zones' of large cells (cell volume 2048–4096 μm^3 corresponding to *Aulacoseira* and 65 500–131 000 μm^3 corresponding to *Peridinium*).

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