

The Living Whirl Self-Maintenance of Stable Size Structure Patterns of Aquatic Communities

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Abstract—Our aim was to analyse size structure typical patterns of phytoplankton and mechanisms explaining such pattern generation and persistence. Long-time study of the size structure of integral phytoplankton and their main phyla was carried out in considerably different aquatic ecosystems. Several types of statistical distributions and quantitative indices of the pattern similarity were applied to find reliable patterns suitable for ecological forecast. Even with apparently unsystematic shifts in the taxonomic composition, the emergence and long-time restoration of extremely analogous spreading patterns of the integral phytoplankton and their main taxonomic parts were ascertained. The biodiversity histogram (FTSS) pattern steadiness was found for integral phytoplankton assemblages. Specific changes in the FTSS fine structure of some phytoplankton phyla were evident. Several phyla were remarkably susceptible to environmental changes. Such phyla can serve for diagnostics. Long-tailed asymmetric histograms were established as enduring traits elucidated by a multi-stressor mechanism of aquatic assemblage self-maintenance. Consistent patterns and quantitative similarity indices can characterize integral assemblage stability. Such patterns can be applied to develop mathematical models elucidating multi-stress proliferation in hierarchical structures of aquatic assemblages. Consistent structural patterns of large-scale aquatic assemblages can help in ecological modelling, aquatic management, and forecast.

Keywords— *Aquatic Communities; Biodiversity Distribution; Ecosystem Restoration; Monitoring; Multidisciplinary Studies; Multi-stress System; Phytoplankton; Similarity; Size Spectra; Typical Pattern*

I. INTRODUCTION

Study of stable structural patterns of living communities is among central problems of aquatic ecology. The conceptual (theoretical) and formalized mathematical models are among the most powerful tools to analyse the structure and functioning of aquatic assemblages. Numerous tools and methods were developed supporting modelling of living systems, e.g., the general theory of systems, various mathematical approaches and quantitative generalizations. A special field of science, i.e., the art of modelling has been developed. Very powerful optimization principles were formulated, first of all, the Ockham's law of economy of thought. Due to this law, the number of parts, links, and traits described should be a minimum. Such models called minimal (e.g., the minimal cell, the minimal genome, and the minimal ecosystem models) take ever growing application in all biological sciences [1]. Statistical models, built with the help of very few parameters, describing the structure of living assemblages, also are among the most frequently applied tools. Such statistical models are capable to find very general patterns of the community structure, further leading to explanations of mechanisms generating such common patterns. Especially important are the repeating (typical) patterns [2] and self-maintenance mechanisms generating the typical distribution patterns.

Numerous structural patterns, resulting from interaction of organisms, have been found by modern ecology. A number of factors, influencing the structure of a given aquatic community, were studied. Field and literature-based analyses of several traits of integral living communities were performed by us to look for typical patterns and constant estimates describing integral aquatic communities. Several criteria were used to develop sets of notable (widely cited) scientific publications: 1) analysis of systems in a maximally broad ecosystem size interval; 2) comparison of natural and artificial systems; 3) comparisons of marine and freshwater communities; 4) comparisons of laboratory and field studies [1].

Attempts to describe a complex natural community by a single attribute (e.g., biomass, species richness, equitability, etc.), seem to be unrealistic and went further to more detailed and complicated pictures. Analyses of several attributes of the assemblage (e.g., the biomass, cell volume, taxonomic variability of a plankton assemblage) can provide much more powerful comparisons. One of the most important tendencies is the application of statistical distributions of both 'ataxonomic' (based on the living being body mass) size spectra and taxonomic (the biodiversity) size distributions.

Application of formal quantitative indices and mathematical models support the ability of histograms to cover the whole aquatic assemblage and to demonstrate some reliable typical patterns suitable for monitoring and ecological forecast [1]. We went to comparative studies based on general patterns describing the structure and self-maintenance of natural aquatic assemblages, as well as concepts attempting to explain the observed patterns.

The study was devoted to analysis of phytoplankton assemblage size structure, its typical patterns and mechanisms explaining such pattern generation and persistence.

II. MATERIALS AND METHODS

A. Monitoring Sites

Long-term analysis of the size structure of integral phytoplankton and their main phyla was carried out in considerably different aquatic ecosystems. Several types of statistical distributions and quantitative indices of the distribution pattern similarity were applied to find reliable patterns suitable for ecological forecast. The comparisons were based on the whole phytoplankton assemblage monitoring performed during long-time intervals. Several aquatic ecosystems provided the phytoplankton long-time monitoring data.

Lake Kinneret (LK), monomictic, with winter homothermal temperatures of 14-16°C, 210 m below mean sea level. The lake, some 170 km², maximum depth of 44 m, is located in the Eastern Mediterranean, northern part of the Afro-Syrian Rift System. The lake is classified as mesotrophic to eutrophic. In summer the lake is stratified; the thermocline depth is about 15 m. The summer maxima of the epilimnion temperature exceed 30°C. The lake is highly productive.

For 25 years and until the mid-1990s the most prominent feature of the lake was a spring bloom of the dinoflagellate *Peridinium gatunense* accounting for more 95 % of the spring phytoplankton biomass. The remainder of the phytoplankton biomass was mostly nanoplankton. Some man-induced and natural changes (first of all, the water misbalance leading to higher water temperatures and diminishing water level) led to the drastically change of the annual succession patterns since 1994 [3].

Lago Maggiore (LM), one of largest subalpine lakes of Italy, 213 km², the maximum depth of 370 m. The lake is situated at 193 m above mean sea level. LM is oligotrophic by nature. The eutrophication began in the 1960s. In the eighties, the phosphorus loads have been gradually reduced by various means, the TP values have gradually decreased. The long-term oligotrophication of Lago Maggiore is described in many papers [4].

Lake Tahoe (LT) is a mountain deep, large, oligotrophic lake. The lake is located at an altitude of 1898 m in the Sierra Nevada, USA. The lake has 501 km², maximum depth is 501 m. LT has been studied by numerous authors, monitored continuously almost 50 years [5].

The Plymouth marine site at station L4 (PML) is situated in the western English Channel. That is a long-term time-series station (<http://www.westernchannelobservatory.org.uk/l4/>), near Plymouth (UK), 50°15' N, 4°13' W. The station environment can be called coastal temperate. Temperatures are 8°C-16°C. The physical and chemical environment has been monitored during several decades [6].

B. Phytoplankton Data Acquisition and Processing

The plankton samples at Lake Kinneret were collected bi-weekly from several depths from the surface to thermocline. Lugol-preserved samples were brought to the lab for microscopic counting using the sedimentation chamber, and a Zeiss M24 Axiovert inverted microscope. All phytoplankton species with individual cells greater than 2 µm diameter were identified and counted. Also, the relatively common colony-forming cyanophyta ($V \sim 1 \mu\text{m}^3$), were counted. For nanoplanktonic species (< 20 µm diameter), 10 ml subsamples were sedimented for 24 h; then cells were counted at x 320. For larger species (> 20 µm diameter), 1 ml samples were sedimented and counted on the following day. Phytoplankton were identified to species, and counted according to species and size categories. Phytoplankton biovolume values were calculated from specific biovolumes (V_i) approximated to simple geometrical shapes.

The data processing at all other ecosystems (LT, LM, PML) was rather similar. Small details can be seen in [1].

C. Size Spectrum Analyses

Methods of biomass size spectra (BSS) calculation and plotting were used as described by Sheldon et al. [7] and Kamenir et al. [8]. All organisms counted and measured in a sample of water were classified according to size classes. Size classes were standard augmentations of the cell volume logarithm ($\Delta \log V = \log 2$), i.e., doubling of the cell volume. The V_{xx} notation is used, where xx is the class right border. The wet weight biomass of each size class 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. The depth integrated BSS per unit area, or BSS-B2, was calculated using data from all layers within the euphotic zone and conducting a linear interpolation between the depths. Finally, the biomasses of each size class were summed up and the depth-integrated phytoplankton biomass (B2) was shown in each size class (Fig. 1A).

Twenty five BSS-B2 distributions (mgww per m² per binary size class) were calculated each year. The mean estimates and SD of each size class were computed (Fig. 1B), for each of four seasons (CV1-CV4).

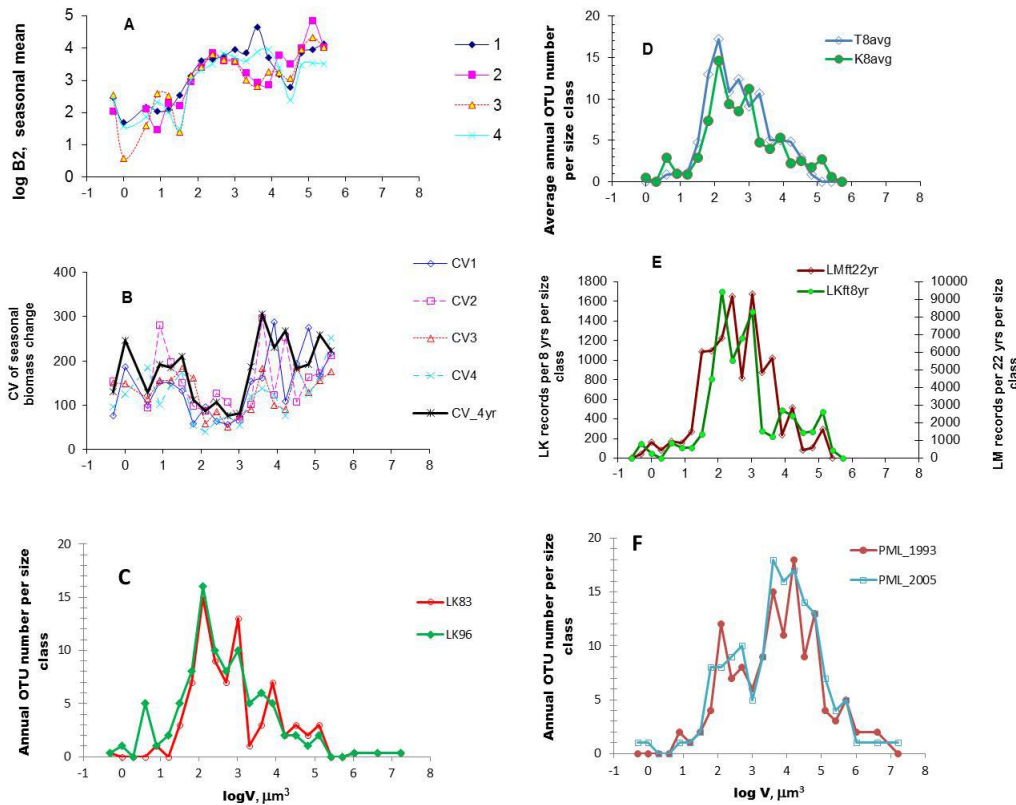


Fig. 1 Comparisons of several types of size spectra describing freshwater and marine phytoplankton. A) Biomass size spectra (BSS) of the 4-year mean average (B2, mgww per square meter), for each of the seasons 1- 4 (winter to autumn) of Lake Kinneret. B) BSS-B2 seasonal variability as Coefficients of Variance (CV, i.e., SD in percent of the respective class average value) for the 4-year (1996-1999) period; n=25 spectra for each season. The central region (logV=2 to 3) (the nanoplankton plateau) demonstrates a low CV. C) Annual traditional taxonomic size spectrum (TTSS) representing the ecosystem (LK) stability (1983) and highly disturbed (1996) years. D) Average TTSS for 8 years of two lacustrine ecosystems, lakes Kinneret and Tahoe (LK, LT, respectively). E) Frequency-weighted taxonomic size spectra (FTSS) for 8 years of Lake Kinneret (LK) and 22 years of Lago Maggiore (LM). F) Annual TTSS for a marine ecosystem, the Plymouth Marine Laboratory (PML) station for two distant years (1993 and 2005).

The development of taxonomic size spectra included two types of spectra, i.e., traditional and frequency-weighted taxonomic size spectra (TTSS and FTSS, respectively). The cell volume (V) was the parameter used for allocating a taxonomic unit to a size class. Since our individual taxonomic component is not strictly a species, but can represent a size category within a species, we refer to them as operational taxonomic units (OTU_j-s) [9]. Each TTSS was built as a histogram depicting the distribution of the phytoplankton-biodiversity (total number of OTUs) to size classes (Fig. 1C). The same methods were applied to Lake Tahoe (LT), Lago Maggiore (LM), and the Plymouth Marine Station (PML), see Figs. 1 D, E, and F.

The frequency-weighted taxonomic size spectrum (FTSS) was simultaneously applied to study the SS dynamics [1]. While TTSS ignores the time-spatial structure of the assemblage, the FTSS applies to each OTU_j a 'weight' – its frequency rate (FR_j) – that is the number of water samples where such OTU_j was registered. Not cell abundance is considered here but only OTU_j incidence, i.e., whether an OTU_j occurred in the annual database (TTSS) or in a specific sample (FTSS). Frequency rate values were plotted along the Y axis of the FTSS histogram (Fig. 1E). These values are the total numbers of times all OTUs which belong to a specific size class (i) were registered during the year. The 'team score' of each size class (FRR_i) integrates the FR_j-weights of all OTUs falling into size class i (FR_{ji}), according to:

$$FRR_i = \sum FR_{ji} [1].$$

Using the histogram and crosstab procedures, we calculated FTSS as the size-frequency distribution of all database records. Analogous spectra (FTSS) were prepared for several years. The SS_{yy} notation was applied to refer to the spectrum of a particular year (yy), for example, FTSS₉₂ was the FTSS for 1992. A pair of annual spectra (TTSS and FTSS) were developed in the current study, each year, for each of eight major taxonomic groups (phyla) of Lake Kinneret phytoplankton, which are Cyanophyta, Diatomea, Chlorophyta, Dinoflagellata, Cryptophyta, Prasynophyta, Euglenophyta, and Haptophyta (cya2, dia3, chl4, din5, cry6, pras7, eug8, and hap9). The 15-year interval (1985 to 1999) was divided into three 5-year periods and proximity matrices of 15x15 cells were calculated from the TTSS and FTSS sets [10].

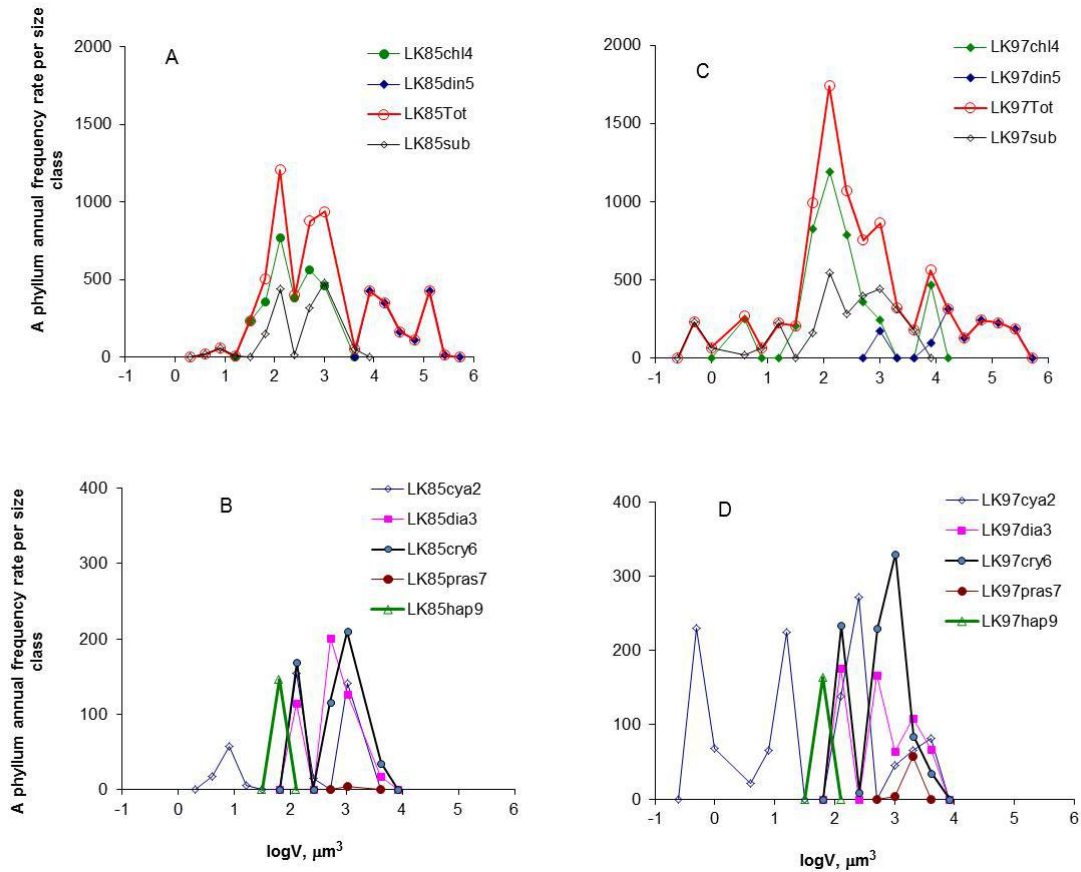


Fig. 2 Frequency-weighted taxonomic size spectrum (FTSS) comparison for the major taxonomic groups (phyla) of Lake Kinneret phytoplankton: Cyanophyta, Diatomea, Chlorophyta, Dinoflagellata, Cryptophyta, Prasynophyta, Euglenophyta, and Haptophyta (cya2, dia3, ch14, din5, cry6, pras7, eug8, and hap9, respectively). LK_XX_Y means Lake Kinneret FTSS of year XX (1985 and 1997) for phylum Y. "Tot" describes the whole phytoplankton assemblage, while "sub" stands for the sum of all subdominant phyla represented in the respective lower plate. Some phyla exhibit pronounced differences between the two years. Note the Y-axes scale difference between the upper and lower plates.

D. Similarity Estimation

Treating a histogram (TTSS, or FTSS; discontinuous distribution functions) as numerical vectors, we can estimate the similarity level in sets of spectra, using hierarchical cluster analysis [11]. The Pearson correlation (r) was applied [11] as the spectrum similarity measure. The estimates were based on between-group linkage. Then a separate dataset was produced from each proximity matrix describing a phylum or the whole assemblage for 15 years. Fourteen elements of the respective matrix 1st column, excluding its 1st trivial diagonal element, were used to describe the similarity dynamics [10].

III. RESULTS

A. The Pattern Similarity

A long-term analysis of taxonomic and ataxonomic size structure patterns of integral phytoplankton assemblages and main phyla of lacustrine phytoplankton was carried at considerably different aquatic ecosystems. Then we looked for typical patterns of statistical distributions suitable for ecological forecast. The subsequent quantitative assessment of the pattern similarity was performed with the help of linear regression, correlation and cluster analyses [10].

The BSS, TTSS, and FTSS comparison (Figs. 1 to 3) showed the general pattern high similarity (e.g., Fig. 1C) and some differences in fine structure: compare several years of each ecosystem (Figs. 1C and F); compare LK and LT (Fig. 1D); much higher difference was observed between very different systems (LK and PML, Figs. 1D-F). The similarity of TTSS in Lago Maggiore strongly resembled the Kinneret results [4].

The proximity of size spectrum patterns was measured by the Pearson correlation coefficient (r). For Lake Kinneret (1982-1985), the similarity measures for any pair of TTSS were very close to 1, ranging from 0.927-0.985. For the highly disturbed years 1996-1999, the similarity between TTSS pairs was still close to the ideal estimate of 1 (r = 0.896-0.980). Thus, lower r values were indicative of lower levels of the assemblage stability (i.e., during the disturbed period after 1995) [8]. Likewise, for LM, for all pairs of years (1984-2005), the TTSS similarity estimates were (r > 0.861). Such similarity levels resemble the Pearson r estimates obtained at LK, LT, and PML. The comparisons between ecosystems (LK vs. LM, LK vs. PML, etc.)

produced much lower results ($r = 0.317-0.578$) for considerably different ecosystems (freshwater LK and marine L4) [4-6].

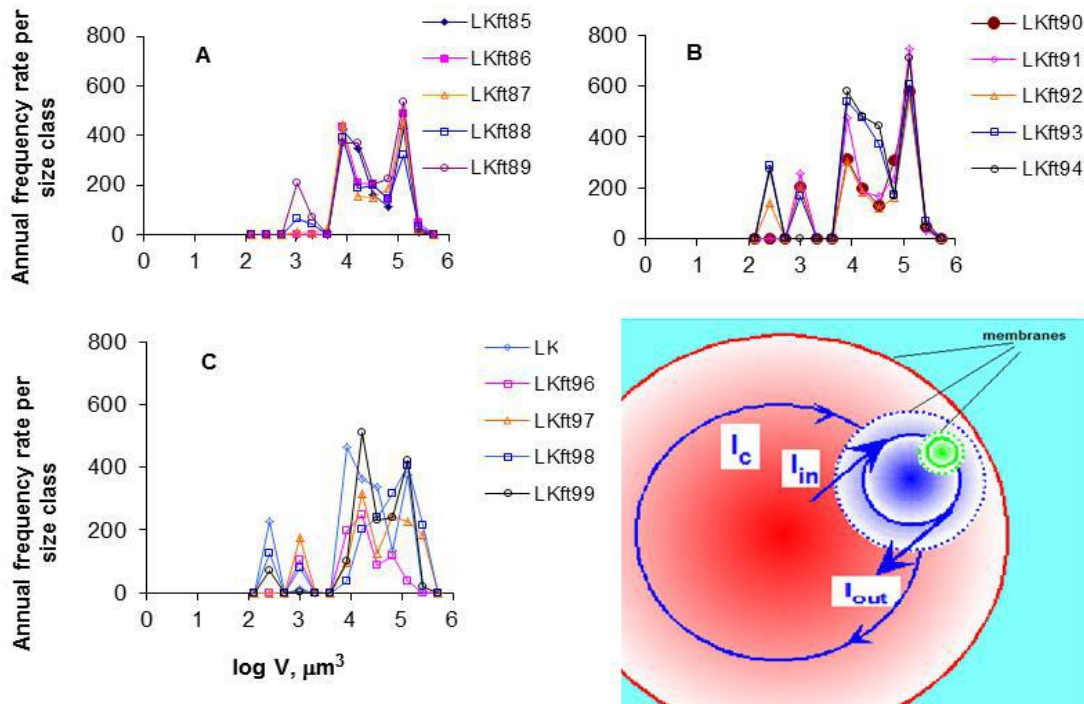


Fig. 3. Comparison of frequency-weighted size spectra (FTSS) annual patterns for one phytoplankton phylum (Dinophyta, din5) of Lake Kinneret (LK). A, B, C) 3 consecutive periods of 5 years each (1985-1989, 1994, 1999, respectively). After 1990, ever growing disturbances were evident for Dinophyta algae. Two main and two smaller peaks are distinguishable. Changes of the peak height, breadth, and even side shifts are seen. D) Ideal Minimal Ecosystem (IMES). I_{in}, I_{out}, I_c - in-, out-, recycling flow, respective. Note the hierarchy of membranes producing the hierarchy of spaces and recycling flows.

B. The Assemblage and its Main Phyla

The FTSS curves for two of the 15 years, specifically 1985 and 1997, are shown in Figs. 2A-D, comparing all phytoplankton phyla found in the Kinneret. These two years represent the long-time ‘typical’ and the more recent disturbed periods, respectively. The biodiversity distribution (FTSS) general-pattern consistency was found for the whole phytoplankton. Comparisons of the species richness (FTSS) patterns of specific phyla have shown the general pattern consistency; the similarity coefficients were high. This similarity drastically diminished during the ‘disturbed’ years, after 1995 (Figs. 3A-C). While specific taxa demonstrated rather high pattern similarity (Figs. 2 and 3), this similarity was much lower than the whole phytoplankton similarity, e.g., compare Fig. 1C and Fig. 3. Specific phyla often indicated rather low similarities ($r < 0.5$), which never took place for the whole assemblage. The whole phytoplankton and all phyla demonstrated much lower similarities when the water body state drastically changed [3], proceeding from 1985 to 1997 (Fig. 2). Specific changes in the FTSS fine structure of some phytoplankton phyla were evident. Some phyla, e.g. cya2 (Fig. 2) were notably sensitive to environmental changes. Their similarity (Pearson r) can drop down up to 0.346 during stable years, and even $r < 0$ (cya2) during extreme disturbances of LK [10].

We distinguished two stages of the spectrum pattern description: the general pattern (ignoring slight variations of specific peak heights and side shifts) and the spectrum fine structure (quantitative analysis of each peak and trough). Both FTSSs of the whole assemblage (index ‘Tot’ at the curve-symbol end) are similar in their general shape (Figs. 2A and C). The shape of specific peaks drastically changed from 1985 to 1997, for some peaks and some phyla (Figs. 2 and 3).

IV. DISCUSSION

Long-term monitoring revealed the emergence and reestablishment of rather similar (typical) patterns of several taxa and of the whole assemblage of aquatic algae, in spite of seemingly random changes in the species list. Even with pronounced shifts of the taxonomic composition of LK, the emergence and multi-annual reinstatement of very similar distributions (i.e., typical patterns) of the whole assemblage and main phyla of phytoplankton were found during so called ‘stable’ period (before 1995). The FTSS general-pattern consistency was found both for the whole phytoplankton assemblage spectrum and for major phytoplankton phyla; however, the similarity of specific phyla was lower than similarities of whole phytoplankton assemblage. Some phyla of phytoplankton (e.g., Cyanophyta) were notably sensitive to climate change. Specific changes in the fine structure of FTSS distributions were evident and may be applicable for diagnostics. Such pattern diagnostics can be helpful for

monitoring and modelling of the living assemblage dynamics.

Long-tailed, considerably asymmetric patterns were found by many authors as a permanent peculiarity; however, the distribution bells become almost symmetric if a logarithmic transformation of cell volume (V_j) estimates was performed providing $\log V$ -scales (Figs. 1-3). The log-normal and Pareto distributions are very often found in numerous fields of science including aquatic ecology. Such distributions seem to be suitable for explanation as multi-stressor mechanisms of generation and persistence of specific patterns. Some authors have suggested very simple and general models explaining the generation of highly asymmetric (lognormal, Pareto, and $1/f$) distributions. It is shown [12] that, for an assemblage engaged in multi-stage tasks dependent on the successful completion of many independent stages, the distribution function for the final results is lognormal. For example, distributions of the scientific paper publication by researchers in very productive physical laboratories have such patterns [12]. Large-scale studies in national economics show that the annual income distributions of wage-earners follow such patterns [13].

A mechanism of such type may exist in aquatic communities producing organic matter, i.e., phytoplankton (living cells) subjected to multi-stress environmental conditions. Look, for example, at a set of environmental factors regulating the aquatic algae metabolism: nutrient concentrations within drops of water, solar radiation fluctuations under changing atmospheric conditions, waves created by the wind fluctuations, local water body temperatures, grazer concentrations, etc. The general situation resembles dynamics of numerous water droplets within a turbulent water body, i.e. a hydrodynamic dissipative structure with log-normal energy dissipation spectra [1]. For many biological sciences this model – the ideal minimal ecosystem (IMES) [1] - can resemble a whirl (Fig. 3D) or tourbillon vital (i.e., the living whirl) described by G. Cuvier [14] and V. Vernadsky [15]. For many ecosystem scales, from microlitosphere [16] to the world ocean, it looks as the recycling web with numerous feedback loops of metabolic links, producing the self-stabilized lognormal distributions. Such biodiversity distribution patterns strongly resemble the lognormal one if the number of OTUs is high, and less consistent when the respective numbers of OTUs are small; e.g., in some small phyla (Figs. 1-3).

V. CONCLUSIONS

Long-term monitoring revealed the emergence and reestablishment of very similar size distribution patterns of the whole phytoplankton assemblage. The biodiversity distribution (TTSS and FTSS) general-patterns showed the emergence and multi-annual reinstatement of very similar distributions. Such repeating patterns can be applied to establish quantitative indices characterizing the stability-variability of the integral assemblage dynamics. The living whirl (i.e., the recycling web of aquatic communities) supports the multiannual reinstatement of self-maintaining plankton assemblages. Mechanisms explaining such pattern generation and persistence are multi-stress sets (i.e., sets of disturbing environmental factors) that destroy and re-establish again almost the same pattern during repeating annual cycles of biotic and abiotic limitation factors. Reliable structural patterns of natural aquatic assemblages can serve as helpful means of modelling, ecological management, and forecast.

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