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Size structure of aquatic communities: Lake Kinneret case

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Abstract

A size spectra model of Lake Kinneret biota is presented. Mean-annual data on all major groups of aquatic organisms, collected over some 25 years at the Kinneret Limnological Laboratory, were used with corrections reflecting changes observed in 1996. The resulting spectrum is similar to the typical pattern known from previous comparative studies. Comparison of size spectra and quantitative descriptors of complete communities reveals consistent patterns. Highly important are the size spectra extremities, i.e. the smallest and largest organisms. Recent changes in the large organism (fish) part of the spectrum have been documented through application of dual-beam echosounder.

Introduction

Lake Kinneret is one of the most thoroughly studied and unusual aquatic ecosystems. Changes of the lake ecosystem which took place in recent decades are of high theoretical and practical interest due to the great importance of the lake for people of the region. In recent years ecosystem was analyzed with the help of many modern methods (Stone et al., 1993; Walline et al., 1993).

As a result of years of study there is now available a large and valuable data base on long-term dynamics of most groups of organisms, including zooplankton (Gophen, 1978a,b; Gophen, 1997 in Annual Report of YKLL), phytoplankton (Zohary & Pollinger, 1997, Annual Report; Shteinman et al., 1996a), phototrophic bacteria and eucaryotic picoplankton (Bergstein et al., 1979; Malinsky-Rushansky et al., 1995), fish (Walline et al., 1993), bacteria (Cavary & Bergstein, 1984) and Kinneret watershed organisms (Degani, 1996). Although the data base is comprehensive, the problem of analyzing long-term changes remains difficult, not only because of high taxonomic diversity, spatial heterogeneity and dynamism of parameters, but also due to the high flexibility of many characteristics of living organisms, and the fuzziness and ambiguity of many biological definitions. Ecosystem models based on formal quantitative parameters, suitable for application of strictly defined measurement procedures and automated or remote means of data acquisition are especially useful in such situation.

The minimal ecosystem model (IMES; Kamenir, 1986) that we use (Figure 1) describes the ecosystem as a dissipative structure, a ‘living vortex’, i.e. an hierarchy of closed recycling fluxes resembling objects studied for many years by hydro- and aerodynamics. The most effective methods for dealing with such objects are those based on rather sophisticated mathematics, mainly statistical methods and spectral analysis (Shteinman & Gutman, 1993; Shteinman et al., 1993, 1996a,b). A method of this type, Size Spectra (SS), has been in use for several decades in aquatic sciences.

Recently size spectra have been used more and more frequently for description of marine particles (Sheldon et al., 1972; Jonasz & Fournier, 1996), lake plankton (Sprules & Munawar, 1986; Sprules & Goyke, 1994) and benthos (Schwinghamer, 1981). A natural development of such an approach is the description of the complete ensemble of living organisms of an ecosystem or its ‘Living Matter’ (Vernadsky, 1978). The suitability of such a formal scheme (SS) for graphic description and comparative analysis resulted in the discovery of typical patterns (Schwinghamer, 1981) of size structure of plankton (Sprules & Munawar, 1986), benthos (Schwinghamer, 1981), terrestrial and the world ocean flora and fauna (Chislenko, 1981), and living matter of aquatic ecosystems of various types (Kamenir & Khailov, 1987; Kamenir, 1993).

Analysis based on typical patterns has gained wider acceptance in recent years due to use of a comparative approach; study of spatial, seasonal and interannual variability; and statistical analysis of SS variability (Schwinghamer, 1981; Sprules & Munawar, 1986; Boudreau & Dickie, 1992; Gaedke, 1992). To compress community structure description, several types of approximating SS formulae have been applied, i.e. several spectrum producing mechanisms or ecosystem functioning models (Kerr, 1974; Chislenko, 1981; Boudreau & Dickie, 1992; Sprules & Goyke, 1994; Jonasz & Fournier, 1996).

Analysis of IMES-model properties led to hypotheses concerning the character of the size spectrum of stable communities and of SS changes to be expected during ecosystem succession and degradation (Kamenir, 1986). In such a model, the SS as a whole can be described as an hierarchy of log-normal distributions. The most informative parts of the SS are its extremities, i.e. the smallest and largest organisms (Kamenir, 1986). The proposed scheme of SS evolution agrees well with the natural community succession changes described in the (Odum, 1971). As Kerr and Dickie (1984) write, since 1970 there have been a number of investigations showing as a general tendency the change in the average body size in communities subjected to contamination and other exogenous factors. Change of sizes of organisms influences many important parameters of their life history and metabolic activity (Schwinghamer, 1981; Peters, 1983). So, changes in the mixing conditions, input of hydrocarbons or other contaminants could be expected to cause characteristic changes in the trophic organization, hence size-spectra, of aquatic systems. Ubiquitous sensitivity of size-spectra to environmental changes may provide a sensitive, early-warning criterion for monitoring and assessing the health of ecological communities (Kerr & Dickie, 1984; Sprules & Goyke, 1994).

The effectiveness of the SS method and its usefulness for ecosystem analysis depend upon the quality and integrity of the data describing the community. Long-term investigations of the Lake Kinneret ecosystem have created the information store necessary for such analysis. In this study, for the first time, an analysis of the SS of the Lake Kinneret community has been made.

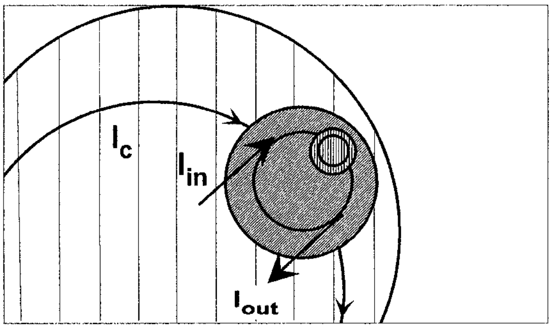

Figure 1. Ideal Minimal Ecosystem (IMES) model.

Materials and methods

The model used, Ideal Minimum Ecosystem, is an hierarchical structure of cyclic fluxes and processes implemented through huge numbers of ‘flow-through’ (having birth or division, development, growth, posteriors production, death and resources-regeneration) elements. Their stores, inertia and nonlinear characteristics produce the medium bufferness and equilibrium of the main parameters. Viewed as a whole, this structure, or Living Vortex (Figure 1), seems to be far too complicated for analysis of dynamics of the parts, but quite suitable for application of formal quantitative decomposition, i.e. spectrum, spectral analysis and a statistical description of its steady state form (Kamenir, 1986).

In such a model, annual averaged biomass data for all groups of organisms of the ecosystem (g protein per m^2) should be used for construction of the size spectrum. The averaged mean-annual data from long-term investigation of the main groups of the Lake Kinneret biota biomass (B) and abundance (N) were used, as described by L. Stone et al. (1993). For the most variable part of the community (small organisms), more recent data for 1996 (Gophen M. Zooplankton. In: Kinneret Limnological Laboratory Annual Report; Zohary & Pollinger, 1997. Phytoplankton. In: Kinneret Limnological Laboratory Annual Report) was used.

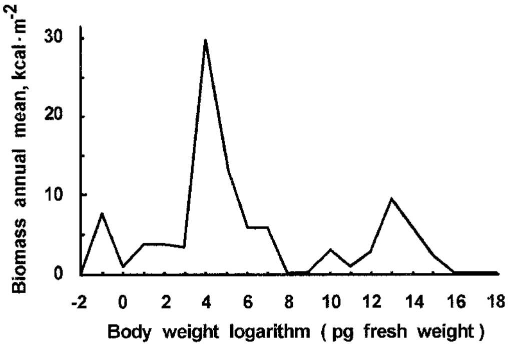

Figure 2. Size Spectrum of Lake Kinneret biomass. Mean of 1996 data. Size Class: $\Delta \log W = 1$.

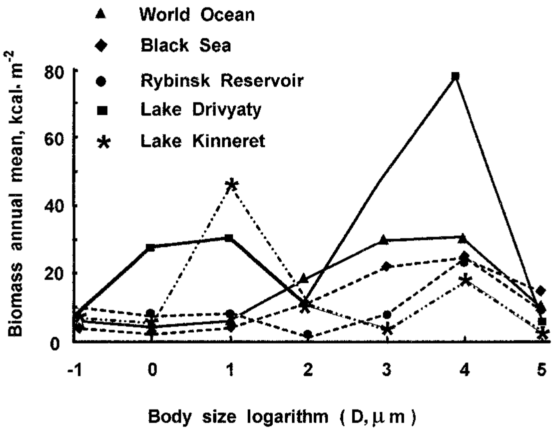

Figure 3. Comparison of biomass size spectra of aquatic communities. Mean annual data. From (Kamenir, 1993) with correction. Size Class: $\Delta \log D = 1$.

The formal quantitative parameter, Size Fraction (SF), was added to the collected data to develop size spectra. The size spectra calculation and plotting were done as described by Sheldon et al. (1972), Chislenko (1981), Schwinghamer (1981). All organisms were divided into size fractions or classes (Sieburth et al., 1978) according to their size (*D*) as given by the authors or calculated from the cell volume (*V*) or body weight (*W*): $\log D \sim 0.33 \log V$, where $V = W/\rho$, $W = B/N$, $\rho \sim 1$ g cm^{-3} (Schwinghamer, 1981). Size fractions are standard increments of the logarithm of the organisms size D or W ($\Delta \log D = \text{const}$). Size fraction number i corresponds to its left border, i.e. its minimum size D_i ($i = \log D_i$, μm) or body weight value.

Caloric content estimates from all groups of organisms, summed up, give the total for the living matter. For some groups of organisms (e.g., *Copepoda, Cladocera*) specific caloric coefficients were used (Gophen, 1978a; Gophen & Landau, 1977). Groups of organisms, which belong to several SF, were subdivided among the SF in equal parts. Per unit area parameters were calculated as averaged over the ecosystem surface (168 km^2).

Fish size spectra were calculated from acoustic data using dual beam techniques (Traynor & Ehrenberg, 1979; Beurkle, 1987; MacLennan & Simmonds, 1992). The equipment used was a BioSonics Model 105 dual-beam echosounder operating at 105 kHz. Individual targets from 6 representative transects were combined into a single data set. Data were collected at night, when a high percentage of targets can be resolved because the fish do not school then. The biomass of each SF was expressed as a percentage of the total so the shape of the curves can be compared.

Results and discussion

The biomass Size Spectrum (SS) of the Lake Kinneret biota shows three peaks (Figure 2) corresponding to bacteria and pico-phytoplankton (0.5–3 μm), large phytoplankton (*Peridinium*) and meso-zooplankton (30–300 μm), and fish (3–30 cm). The estimate of integral biomass was about 89 kcal per m^2, i.e. very close to the typical value of 10 g protein, 100 kcal or 100–200 g wet weight per m^2, discussed by Schwinghamer (1981) and Kamenir (1993). Nevertheless, large changes of biomass of some groups of organisms, especially phytoplankton, registered during last decades, demand additional, more detailed analysis of this coincidence. The shape of the biomass size spectrum (Figure 2, 3) also is very close to those known from the literature (Sprules & Munawar, 1986; Sprules & Goyke, 1994) and our previous studies (Kamenir, 1993). There are some definite differences in the middle-size part of the spectrum (Figure 3), which can be attributed to the presence of small quantities of phyto- and zoobenthos due to the bottom configuration, large anoxic zone of Lake Kinneret and strong daily winds. These characteristics have a long history and should be subjected to additional, more detailed analysis.

The most difficult problems are associated with small organisms (< 100 μm, the left side of the size spectra). Showing extremely high specific activity and SV (surface-to-volume ratio), they can produce substantial changes of community metabolic activity through very small variation in biomass. Hence, a more thorough account of the integral biomass and

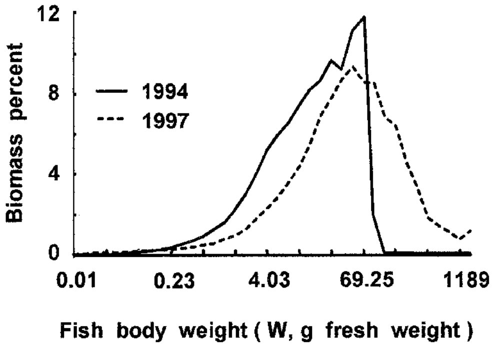

Figure 4. High resolution size spectra. Large size classes of Lake Kinneret biomass. Size Class: $\Delta \log W \sim 0.14$.

size spectrum of microorganisms in the water column and bottom sediments is necessary. In particular, ATP and protein measurements based on highly sensitive biochemical methods (Bergstein et al., 1979; Cavary & Bergstein, 1984) should be repeated.

The size spectra of the right part of the SS (mostly fish), changed between June 1994 and June 1997 (Figure 4). The distribution of acoustic targets from June 1994 appears truncated, with larger sizes of fish completely absent. This is consistent with fact that the lavnun (*Acanthobrama terrasanctae terrasanctae*) fishery collapsed in 1993 because of the lack of large individuals. In 1994–97, the lavnun fishery was subsidized by the State of Israel, with the objective of improving water quality by top-down food chain effects. Up to 1000 tons of lavnun (maybe 30% of the total stock) were removed in each year using nets with a smaller than usual mesh size. The plan was to remove small lavnun during the winter, to reduce predation pressure on zooplankton during the spring bloom period, and to allow the remaining lavnun to reach larger sizes. The fish biomasss size spectra show that biomass of larger fish comprise a much larger fraction of the total in 1997 than in 1994, before the lavnun removal program.

Equations relating TS (obtained from the dual-beam echosounder) to length and then to weight are available for lavnun, the most abundant fish. The application of these equations to larger targets (probably all those to the right of the mode) is only an approximation. The large targets are probably mainly tilapias, and the largest targets are probably silver carp, hence, separate approximation formulae and data collection schemes should be used for the largest fish to obtain more precise approximation of this part of the spectrum.

Analysis of the shape of the fish biomass SS shows considerable shift to the right. The same trend is evidenced for mesozooplankton. In the terms of the approach we use, this means positive succession of the community and its large-body part. However, change in one part of the community can be misleading, if not related to changes of other parts. A more detailed analysis of the SS as a whole is needed. Overall distinctions between ecosystems size structures are quite small, and Lake Kinneret does not appear to be especial, different from other ecosystems.

Conclusions

The model used (Figure 1), based on hierarchy of cyclic fluxes and processes, Living Vortex, helped to select the spectral approach as appropriate for analysis of the natural community of Lake Kinneret.

The biomass size spectrum of the Lake Kinneret community shows three peaks corresponding to 1) bacteria and pico-phytoplankton (0.5–3 μm), 2) larger phytoplankton (*Peridinium*) and mesozooplankton (30–300 μm), and 3) fish (3–30 cm) (Figure 2).

Comparison of biomass size spectra of different aquatic ecosystems (Figure 3) shows their high resilience (stability), existence of typical patterns in their structure. The peaks and gaps between them, distinctive for the ecosystem selected, should be subjected to more detailed analysis.

Evidence of changes in a community (including the system succession or degradation) emerges through analysis of the size spectrum fine structure. The fine structure of an SS can be obtained via upgrading of the spectrum description and measurement precision. According to theoretical model used and empirical data, the most important for diagnostics purposes part of the SS is its right extremity, i.e. large organisms.

Application of modern automated tools (hydroacoustics) showed changes in the fine structure of the SS right extremity (i.e. fish community), including a shift of median size from about 20 to 50 g during last three years (Figure 4).

We conclude that size spectra analysis is a useful tool for making comparative investigations of the Lake Kinneret ecosystem and for analyzing trends. Because the apparent sensitivity of SS to environmental changes, the approach may provide a useful tool for monitoring the Lake Kinneret ecosystem and detecting its changes.

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References

Bergstein, T., Y. Henis & B. Z. Cavary, 1979. Investigations on the photosynthetic sulfur bacterium *Chlorobium phaeobacteroides* causing seasonal blooms in Lake Kinneret. Can. J. Microbiol. 25: 999–1007.

Beurkle, U., 1987. Estimation of fish length from acoustic target strengths. Can. J. Fish. aquat. Sci. 44: 1782–1785.

Boudreau, P. R. & L. M. Dickie, 1992. Biomass spectra of aquatic systems in relation to fisheries yield. Can. J. Fish. aquat. Sci. 49: 1528–1538.

Cavary, B. Z. & T. Bergstein, 1984. Fluctuations of bacterial activity in Lake Kinneret sediments. Verh. int. Ver. Limnol. 22: 1161–1166.

Chislenko, L. L., 1981. Structura fauny i flory v svyazi s razmerami organizmov. Moscow Univ. Press, Moscow, 208 pp. [Structure of fauna and flora as related to the sizes of organisms.] (In Russian.)

Degani, G., 1996. The Salamander at the Southern Limit of its Distribution. Laser Pages Publ., Jerusalem, 154 pp.

Gaedke, U., 1992. The size distribution of plankton biomass in a large lake and its seasonal variability. Limnol. Oceanogr. 37: 1202–1220.

Gophen, M., 1978a. The Productivity of *Mesocyclops leuckarti (claus)* in Lake Kinneret (Israel). Hydrobiologia 60: 17–22.

Gophen, M., 1978b. Zooplankton. In C. Serruya (ed.), Lake Kinneret. Monographiae Biologicae. Dr W. Junk Publishers, The Hague: 297–309.

Gophen, M. & R. Landau, 1977. Trophic interactions between zooplankton and sardine *Mirogrex terraesanctae* populations in Lake Kinneret, Israel. Oikos 29: 166–174.

Jonasz, M. & G. Fournier, 1996. Approximation of the size distribution of marine particles by a sum of log-normal functions. Limnol. Oceanogr. 41: 744–754.

Kamenir, Y., 1986. Razmernaya structura ciklicheskih sistem: Vzaimosvyaz parametrov. Ecologiya Morya, 24: 42–51. [Dimensional structure of cyclic systems: Interrelation of parameters.] (In Russian.)

Kamenir, Y., 1993. Interdisciplinary investigation of aquatic communities using size spectra. In H. Sterr et al. (eds), Interdisciplinary Discussion of Coastal Research and Coastal Management Issues and Problems: Proc. Intern. Coastal Congress, ICC-Kiel ’92. Lang, Frankfurt-am-Main: 468–476.

Kamenir, Y. G. & K. M. Khailov, 1987. Metabolic characteristics and total surface area of the living matter of the ocean: A comparison of size spectra. Oceanology 27: 492–496.

Kerr, S. R., 1974. Theory of size distribution in ecological communities. J. Fish. Res. Bd Can. 31: 1859–1862.

Kerr, S. R. & L. M. Dickie, 1984. Measuring the Health of Aquatic Ecosystems. In V. W. Cairns et al. (eds), Contaminant Effects on Fisheries. Wiley & Sons, New York: 279–284.

MacLennan, D. N. & E. J. Simmonds, 1992. Fisheries Acoustics. Chapman & Hall, London, 324 pp.

Malinsky-Rushansky, N., T. Berman & Z. Dubinsky, 1995. Seasonal dynamics of picophytoplankton in Lake Kinneret, Israel. Freshwat. Biol. 34: 241–254.

Odum, E. P., 1971. Fundamentals of Ecology. Saunders, Philadelphia, 574 pp.

Peters, R. H., 1983. The Ecological Implications of Body Size. Cambridge Univ. Press, Cambridge, 329 pp.

Schwinghamer, P., 1981. Characteristic size distribution of integral benthic communities. Can. J. Fish. aquat. Sci. 38: 1255–1263.

Sheldon, R. W., A. Prakash & W. H. Sutcliffe, 1972. The size distribution of particles in the ocean. Limnol. Oceanogr. 17: 327–340.

Sieburth, J. M., V. Smetacek & J. Lenz, 1978. Pelagic ecosystem structure: Heterotrophic compartments and their relationship to plankton size fractions. Limnol. Oceanogr. 23: 1256–1263.

Sprules, W. G. & M. Munawar, 1986. Plankton size spectra in relation to ecosystem productivity, size, and perturbation. Can. J. Fish. aquat. Sci. 43: 1789–1794.

Sprules, W. G. & A. P. Goyke, 1994. Size-based structure and production in the pelagia of Lakes Ontario and Michigan. Can. J. Fish. aquat. Sci. 51: 2603–2611.

Shteinman, B. & A. Gutman, 1993. Flow dynamics study for the river mouth in a freshwater lake (on example of River Jordan-Lake Kinneret). In S. S. Y. Wang (ed.), Advances in Hydro-Science and Engineering. Univ. Mississippi: 1154–1159.

Shteinman, B., E. Mechrez & A. Gutman, 1993. Spatial structure of a jet flow at a river mouth. Boundary-Level Meteorology 62: 379–383.

Shteinman, B., A. Gitelson, Y. Yacobi, A. Parparov, S. Plotnitsky & S. Kaganovsky, 1996a. New approaches to determination of temporal and spatial variation of phytoplankton distribution in aquatic ecosystems. Lake Kinneret case study. In Y. Steinberger (ed.), Preservation of our World in the Wake of Change, 6B. ISEEQS Publ., Jerusalem: 565–568.

Shteinman, B., V. Nikora, M. Ekhnich & A. Sukhodolov, 1996b. An experimental validation of the ‘frozen’ turbulence hypothesis for river flows. In S. Gavrilakis et al. (eds), Advances in Turbulence, 6. Kluwer Academic Publishers, Dordrecht: 531–535.

Stone, L., T. Berman, R. Bonner, S. Barry & S. W. Weeks, 1993. Lake Kinneret: A seasonal model for carbon flux through planktonic biota. Limnol. Oceanogr. 38: 1680–1695.

Traynor, J. J. & J. E. Ehrenberg, 1979. Evaluation of the dual-beam acoustic fish target strength measurement method. J. Fish. Res. Bd Can. 36: 1065–1071.

Vernadsky, V. I., 1978. Zhivoye Veshchestvo. Nauka, Moscow, 358 pp. [Living Matter.] (In Russian.)

Walline, P. D., S. Pisanty, M. Gophen & T. Berman, 1993. The ecosystem of Lake Kinneret, Israel. In V. Christensen & D. Pauly (eds), Trophic Models of Aquatic Systems. ICLARM Conf. Proc. 26: 103–109.