Application of Spectral Methods for Ecological Modeling: Lake Kinneret Example

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ABSTRACT: Aim of the study is interdisciplinary integration of models of biotic and abiotic components of natural aquatic ecological systems, based on application of spectral analysis. The study presents size spectra analysis based on long-term data collected on one of the most thoroughly studied freshwater ecosystems of the world, Lake Kinneret. The Lake Kinneret biomass spectrum shows three peaks corresponding to bacteria and pico-phytoplankton, larger phytoplankton and zooplankton, and fish. The right extremity of the spectrum deserves closer attention. Due to the model applied (Ideal Minimum Ecosystem), it can be used as an important diagnostic parameter describing the ecosystem state. Resemblance of this model to structures studied by hydrodynamics seems to reflect very profound and important properties of the natural ecosystem taken as a whole. Spectral analysis can be a useful tool for comparative investigations of aquatic ecosystems, for analyzing trends, development of methods of ecological forecasting and interdisciplinary cooperation.

1 INTRODUCTION

1.1 *Ecological modeling*

Quality of information systems, describing natural aquatic reservoirs, depends on interdisciplinary co-operation of specialists that use sufficiently different points of view and methods for the study of the same object. Though positive experience has accumulated in this field (Odum 1971, 1993; Patten 1974; Holling 1978), the problem is still rather large. Especially complicated problems emerge in zones of interaction of biological and formal (physics-mathematical) sciences, e.g. in aquatic ecosystems monitoring and management.

The problem is so difficult that some specialists suggest that formal means or mathematical language may be in principle unacceptable for description of ecological systems (Uhmanski 1980). This report is devoted to results of a possible approach to the problem. That is interdisciplinary integration of models of biological and abiotic components of natural aquatic ecosystems with the help of spectral analysis.

A key solution of these problems is development of simple and formal, but realistic models. Formal parameters and schemes of ecosystem description can help develop operational approaches to these problems. Creating a frame for interdisciplinary communication, they provide means of integration of sophisticated mathematical apparatus, High-Technology products (computers, electronics, lasers, optics, molecular biology reagents) and quantitative biology information stores (Kamenir 1987, 1993).

The problem of ecological analysis and forecast is very difficult not only due to high number of species of organisms, time-and-space heterogeneity of physical, chemical, biological parameters, large size of natural ecosystems, but many other factors, such as links between the ecosystem elements, cannot be neglected. Results obtained in controlled conditions of mesocosms demonstrate important interactions that often do not have sufficient attention (Sullivan & Banzon 1990). Complex, multi-component character of the aquatic medium and web of links, that stabilize its properties, are very important and must be dealt with. However, study of interactions of many parts is very difficult, even if they are very generalized.

On the other hand, there are parameters suitable for measurements and distinctive of high uniformity. This is the case with the whole community description in terms of energy flow per unit area (Odum 1971). The General Systems Theory (Holling 1978; Jones 1972) recommends to apply in such situations the top-down analysis starting from the model of the object as a whole.

1.2 Minimal model of the object (aquatic ecosystem)

The model that we use, Ideal Minimal Ecosystem (IMES; Fig. 1), 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 resource-regeneration) elements.

Their stores, inertia and nonlinear characteristics produce the buffering properties of the medium and equilibrium of the main parameters. Viewed as a whole, this structure (Fig. 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 statistical description of its steady state form (Kamenir 1986). It takes hierarchy of closed metabolic recycling fluxes and their corresponding quasi-cyclic processes as the central point of analysis.

The model helps integrate the biotic components into a general scheme of intertwined and interacting whirlwinds. Resemblance of this structure to structures studied by hydrodynamics seems to reflect very profound and important properties of the natural ecosystem taken as a whole. IMES describes the ecosystem as a dissipative structure, created and existing only due to the constant flux of energy dissipated as heat (Kamenir 1993). The most effective methods for dealing with such objects are those based on rather sophisticated mathematics, mainly on statistics and spectral analysis (Shteinman & Gutman 1993; Shteinman et al. 1993).

Energy dissipation, indispensable property of every biological structure, takes central place in the aquatic community analysis (Odum 1971). This energy flow can be presented through decomposition to spectrum of size fractions (Kamenir & Khailov 1987), integrating organisms of different taxonomy but similar body weight or size. Statistical analysis of the object static, applied instead of dynamics simulations, produces a very compact and graphic scheme suitable for application of mathematical methods developed by hydrodynamics and for use in automated data acquisition and processing means.

1.3 Size Spectra method

A method of this type, Size Spectra (SS), is in use in aquatic sciences for several decades. Studies of the last century gave evidence to existence of regularities of very general nature, concerned with probability distributions of living and dead organisms (Sheldon et al. 1973) and inorganic particles (Wentworth 1931), i.e. solid discontinuous phase of natural aquatic systems. Integration of all these

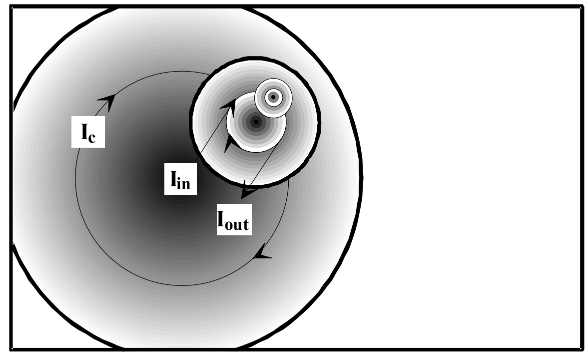

Figure 1. Ideal Minimal Ecosystem (IMES) model.

components with the help of unified models could provide information links between hydrodynamics and biological science via application of schemes and methods of hydrodynamics of two-phase flows.

Such an approach describes multitudes of living and non-living particles as an integral particle ensemble, a specific matter suitable for description with the help of standard physical and chemical parameters (Vernadsky 1978).

Size spectra (nontaxonomic formal quantitative description schemes) are among the most interesting methods that have been used for studies of various marine and freshwater basins (Sheldon et al. 1973; Schwinghamer 1981; Sprules & Munawar 1991; Witek 1995). Their combination with traditional taxonomic descriptions may be very effective, taking into account the real complication of the taxonomic structure of the ecosystem considered, from one hand, and the time and finance limits, from the other.

Size spectra are used more and more frequently for description of suspended marine particles (Sheldon et al. 1973; Jonasz & Fournier 1996), lake plankton and fish (Sprules & Goyke 1994) and benthos (Schwinghamer 1981). A natural development of such an approach is description of the complete ensemble of living organisms of an ecosystem.

2. LAKE KINNERET SIZE SPECTRA ANALYSIS

2.1 Lake Kinneret

Lake Kinneret size spectra can serve as an illustration of the methods discussed. The lake is located in the north-eastern part of Israel. This is a warm, monomictic lake with surface area of 170 km^2, maximum and average depths of 42 and 24 m, respectively. The water level altitude varies between 208.9 and 213.0 m below mean sea level, within the limits legislated by the water administration (Serruya 1978; Gophen 1993). Kinneret is the largest natural freshwater lake in Israel. Therefore, it is utilized for recreation, tourism, commercial fishery, water supply. As a national water reservoir it supplies annually some 25% of the country's freshwater consumption, including 50% of the drinking water demand. The water quality is of prime national importance (Berman 1985; Gophen 1993).

Therefore, that is one of the most thoroughly studied freshwater ecosystems of the world. There are long-term data on all main groups of organisms (C.Serruya 1978; Gophen 1985; Pollinger 1986; Yakobi & Pollinger 1993; Malinsky-Rushansky et al. 1995; Berman et al. 1995; Berman 1997).

Several hydrodynamics models were developed for Lake Kinneret, starting with works of S. Serruya (1975). These numerical models range from simple two-dimensional and steady state models to a few more sophisticated time-dependent three-dimensional models (Serruya & Hollan 1981; Serruya et al. 1984; Volohonsky et al. 1983; Herman 1996). The models were used for studies of the surface and internal oscillations, wind-driven circulation, dissolved and suspended matter concentrations and fluxes.

A series of interdisciplinary studies (cooperation of specialists in hydrodynamics and biological science) was done for analysis of links between the annual pattern of phytoplankton bloom and water mass turbulence. The mean rate of turbulent kinetic energy (TKE) per unit mass ε was obtained on the basis of the analysis of frequency spectra, as described by Yokosi (1968), Monin and Yaglom (1971), Nikora and Shteinman (1996). The existence of the inertial intervals in the frequency spectra allows to calculate the dissipation energy on the basis of the famous Kolmogorov (1941) law.

Significant correlation was found between the turbulence parameters (rate of TKE dissipation ε and intensity of the eddies spinning in vertical plane Duv). In the periods of high ε and Duv, the algal biomass and chlorophyll concentration were sufficiently diminished, i.e. significant negative correlation took place. These studies show that turbulence might be a selective factor favorable for some species of the Kinneret plankton and unfavorable for others, depending on other conditions. It can be the inhibitor or a switch that triggers the change of the dominating species and the phytoplankton bloom parameters.

Changes of the lake ecosystem, that were evidenced during recent years (Yacobi & Pollinger 1993; Berman 1997) demonstrated the necessity of additional studies and importance of interdisciplinary analysis of ecosystem level processes. Several models of the ecosystem were developed recently (Stone et al. 1993; Walline et al. 1993).

2.2 Size spectra

The first size spectra of the lake community were developed in 1996 by the authors in collaboration with M.Gophen, T.Bergstein-Ben Dan and P.Walline. 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 Stone et al. (1993) and Walline et al. (1993) for previous models. For the most important parts of the community (small organisms and fish) corrections were made here on the basis of more recently (partially unpublished) collected data (1994-1997).

The size spectra calculation and plotting were done as described by Sheldon et al. (1973), Chislenko (1981), Scwinghamer (1981). All organisms were divided into size fractions or classes 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 community. Groups of organisms, that belong to several size fractions, were subdivided among them in equal parts. Per unit area parameters were calculated as averaged over the ecosystem surface. Fish size spectra were calculated from acoustic data using dual beam techniques (MacLennan & Simmonds 1992). Dual-beam echo-sounder (BioSonics Model 105 operating at 105 kHz) was used. The biomass of size fractions was expressed as a percentage of the total biomass.

3 RESULTS

The biomass Size Spectrum (SS) of the Lake Kinneret biota shows three peaks (Fig. 2A) corresponding to bacteria and pico-phytoplankton (0.5-3 μm), large phytoplankton and meso-zooplankton (30-300 μm), fish (3-30 cm). The shape of the biomass size spectrum (Fig. 2A) is very close to typical patterns (Fig. 2B) known from the literature (Sprules & Munawar 1991; Sprules & Goyke 1994) and our previous studies (Kamenir 1993). Nevertheless, changes of many groups of organisms, especially phytoplankton, registered during last years (Berman 1997) demand additional, more detailed analysis. There are gaps in the middle-size part of the spectrum (Fig. 2A), which can be attributed to small quantities of macrophytes and zoobenthos. The main reasons are specific bottom configuration, large anoxic zone at the bottom and strong daily winds (Serruya 1978; Shteinman et al. 1997).

The size spectra of the right part of the SS (fish), changed in 1994 - 1997 (Fig. 2C). The distribution of acoustic targets from June 1994 appears truncated. This is consistent with the collapse in 1993 of fishery of lavnun (the most important commercial fish of the lake), caused by the lack of large individuals (Hambright & Shapiro 1997). In 1994-1997 important regulations were introduced, with financial support of the State of Israel. Analysis of the fish biomass SS shows considerable shift to the right. The same trend is evidenced for mesozooplankton.

Overall distinctions between ecosystems size structures are quite small, and Lake Kinneret does not appear to be different from the typical patterns evidenced for other ecosystems. The estimate of integral biomass was about 89 kcal per m^2. This estimate also is very close to typical values discussed in the world literature: 100-200 g wet weight per m^2 (Schwinghamer 1981); 10 g protein or 100 kcal (Kamenir 1993).

4 DISCUSSION

The model used (IMES), based on an hierarchy of cyclic fluxes and processes (Fig. 1) helped to select the spectral approach as appropriate for analysis of aquatic ecosystems, for integrating descriptions of the water mass and the organisms inhabiting them. Comparative analysis shows high stability of size spectra of different aquatic ecosystems (Fig. 2B) and existence of typical patterns of their structure.

Simple mathematical expressions were used for approximation of experimentally-based SS patterns (Kerr 1974; Silvert & Platt 1978; Kamenir 1986; Jonasz & Fournier 1996). The form of these expressions is similar to those applied in hydrodynamics for turbulent spectra analysis and can be satisfactorily approximated by power-law and log-normal distribution. Similarity of patterns of SS of pelagic and benthic communities (inhabiting the surface and the bottom layer of the water reservoir) was demonstrated. Significant differences were seen in parameters' estimates necessary for the approximating formulae. This fact may be connected with differences in the hydrodynamic temporal and spatial structure of corresponding water masses.

Changes in hydrodynamic factors affect the conditions to which aquatic organisms are exposed: fluxes of nutrients and pollutants, sedimentation, turbidity; temporal and spatial scales of temperature, oxygen concentrations and other hydrological parameters of

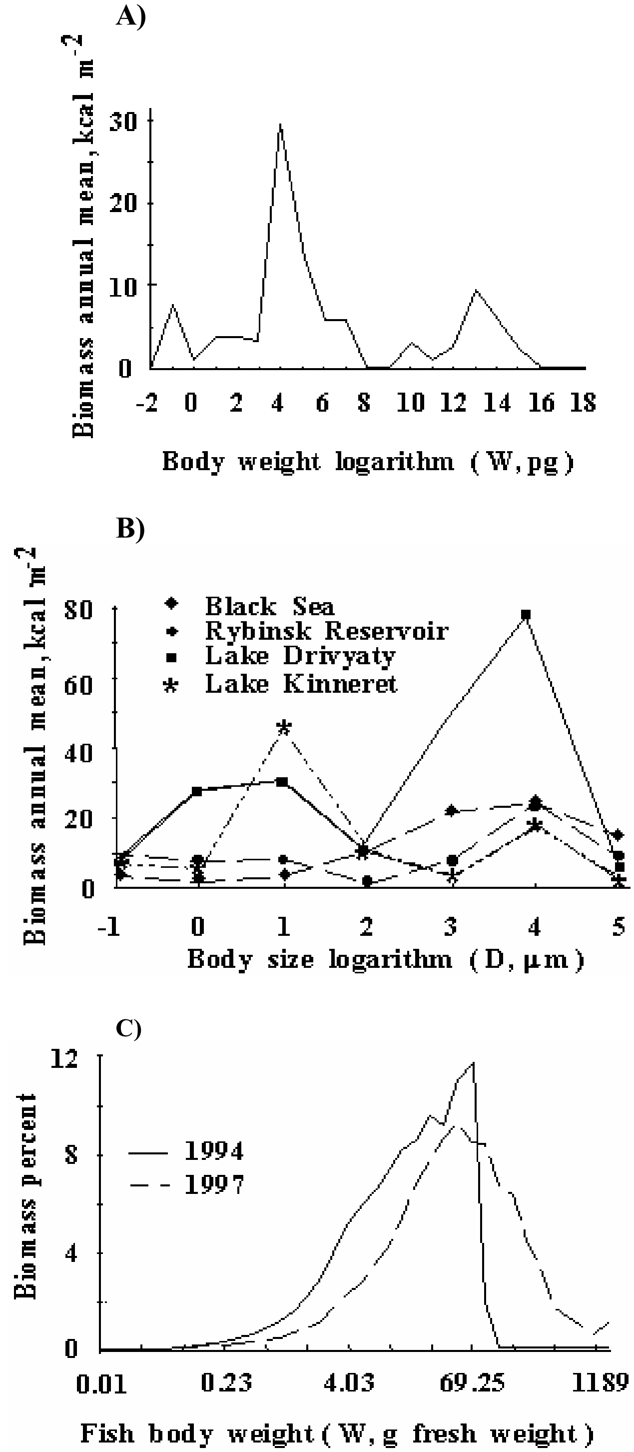

Figure 2. Size Spectra:
A) Lake Kinneret community. Mean of 1996 biomass data. Size Class: Δ log W = 1.
B) Comparison of biomass size spectra of aquatic communities. Mean annual data. From (Kamenir 1993) with correction. Size Class: Δ log D = 1.
C) High resolution size spectra. Large size classes of Lake Kinneret biomass. Size Class: Δ log W ~ 0.14.

major importance for the phyto-, zoo- and bacterio-plankton, resulting in different community structures. Influence of hydrodynamic factors on the phytoplankton in lakes and oceans has been described by Reynolds (1994). The size of the smallest eddies is much larger than the plankton cell size, however, these organisms live in a viscous medium and are strongly influenced by the temporal and spatial parameters and by some secondary effects of turbulence (Reynolds 1984, 1994). Vertical mixing and currents can seriously influence plankton sinking, resuspension and upward movement, light and nutrient supply conditions, and eco-physiological processes, including photosynthesis.

Temporal and spatial parameters of vertical mixing can influence photosynthesis through change in light intensity and spectral composition (Viner & Kemp 1983; Gargett 1991). Turbulent mixing and bottom shear velocity can change the sinking-resuspension regime, influence the concentration and size composition of the suspended matter, which, in turn, can change the water mass turbidity and euphotic layer depth. Turbulent mixing is a limiting factor comparable to other abiotic environmental parameters that influence the spatial distribution of phytoplankton cells, as well as their growth rates (Kreiman et al. 1992).

Selective effect of the temporal and spatial patterns of turbulent fluctuations on development of algal cell types is described by Denman & Gargett (1983) and Thomas & Gibson (1990). Interaction between planktonic populations and physical processes plays a major role in determining the distribution and abundance of planktonic organisms. The distribution of large organisms often is reflecting the location of physical processes that influence production, vertical distribution, and aggregation of their prey (Hunt 1997).

Analysis of the hydrodynamic structure of the water mass and its influence on metabolic activity and life history patterns of all groups of organisms has been for many years an important part of the study of the Kinneret ecosystem structure and functioning. Intensive study of the hydrodynamic factors have been carried out in KLL since 1990 (Shteinman et al. 1993; Shteinman & Gutman 1993).

Effect of small-scale turbulence on microalgae depends on several characteristics. Many of these effects are known qualitatively but have not been quantified. Various phytoplankton groups have different sensitivities to turbulence. The most sensitive to turbulence are dinoflagellates (Thomas & Gibson 1990), i.e. the group of algae that dominated the Kinneret phytoplankton before the above mentioned change of hydrodynamic conditions).

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). Changes in the mixing conditions and input of contaminants could be expected to cause characteristic changes in the size-spectra of aquatic systems. 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 sizes in communities subjected to contamination and other exogenous factors. Sprules & Munawar (1991), having studied spatial and seasonal patterns in phytoplankton and zooplankton communities in lake St.Clair (southern Canada), write that biomass size spectra are typical in structure for mesotrophic lakes, but low explained variance of the annual spectrum is indicative of a perturbed system.

Spectrum decomposition using the temporal and spatial scales of "quanta" of self-organizing matter can be an effective means of analysis of its structure and changes of its state. In ecology, SS can help integrate descriptions of the biotic and abiotic components and organize interdisciplinary communication. The peaks and gaps between them, distinctive for the ecosystem selected, should be used for a more detailed analysis. Evidence of changes in a community (including the system succession or degradation) emerges through changes of the spectrum fine structure. The fine structure of an SS can be obtained via upgrading the precision of the spectrum measurement and description.

Mathematical analysis of this model (IMES) produced a scheme of evolution of size spectrum of integral self-sustainable community in the course of succession and regression. Due to such a scheme, succession of the ecosystem manifests itself in broadening of the integral community size spectrum. Degradation under environmental stress or anthropogenic influence leads to the opposite trend. They can be seen through movement of the spectrum extreme right point, describing the largest organisms (Wm) of the community (Kamenir 1986). Such a scheme of SS evolution agrees well with natural community succession changes described by Odum (1971).

It seems strongly evidenced that organisms with large body and life-durability are essential parts and evident signs of the health of any aquatic ecosystem (Agusti at al. 1992). Shifts of the size spectrum (size composition) of the community to the left (i.e. degradation of the biomass and the individual body weight composition of the fish and zooplankton) is described as an important character of many aquatic systems in recent years (Sprules & Munawar 1991; Stone et al. 1993; Kamenir 1993). Sprules & Munawar (1991) hypothesize that high flushing rate with high seasonal variability and contaminant loading have led to the above-mentioned shift of the size spectra of plankton community of the lake studied, i.e., have resulted in dominance of small-bodied species. The most important part of the SS for diagnostics purposes is its right extremity, i.e. large organisms (Kamenir 1986, 1993). Application of modern automated tools (hydro-acoustics) demonstrates changes in the fine structure of the right extremity of Lake Kinneret SS, including a shift of median size of the fish from about 20 to 50 g during last three years (Fig. 2C).

Empirical (regression) and theoretical models can be effective means of analysis of the regularities described. Most of them deal with nonlinear (allometric) change of geometrical, spatial, temporal and physiological parameters of organisms due to change of the organisms' sizes (Hemmingsen 1960; Peters 1983, etc.). Change of sizes of organisms influences many important parameters of their life history and metabolic activity (Schwinghamer 1981; Peters 1983). Similar correlations connect some community characters with size parameters of particles of non-living matter that they use (Hargrave 1972). There are several models aimed at explanation of the regularities of community Size Spectra and of their stability (Kerr 1974; Silvert & Platt 1978; Kamenir 1986, 1993).

Analysis of typical patterns has gained wider acceptance in recent years; there are studies of spatial, seasonal and inter-annual variability of SS and statistical analysis of this variability (Schwinghamer 1981; Sprules & Munawar 1991; Boudreau & Dickie 1992; Gaedke 1992). Several types of approximating SS formulae have been applied, i.e. several spectrum producing mechanisms or ecosystem functioning models (Kerr 1974; Chislenko 1981; Kamenir 1986; Boudreau & Dickie 1992; Sprules & Goyke 1994; Jonasz & Fournier 1996). Methods of this type have long been applied in hydrodynamics for a very broad range of problems and have proven to be highly efficient. The hydrodynamics experience shows that spectral analysis can give very informative results. The models' scaling can provide ways of using results from studies made on objects of one suitable scale to obtain forecasts of future dynamics for other objects of sufficiently different scales.

It seems that "ataxonomic" (Schwinghamer 1981; Boudreau & Dickie 1992; Sprules & Goyke 1994) approaches to analysis and modeling of the aquatic community structure and dynamics can be a good alternative to traditional taxonomic models, especially when a large number of environmental parameters is involved or the community taxonomic composition is dynamic. Application of spectral analysis, spectral distributions and mathematical apparatus of their analysis can produce very informative results (Silvert & Platt 1978), and the hydrodynamical impact on these typical patterns of spectra can be very significant (Margalef 1997).

Through operational definition of the object and its components, such an approach can help to integrate the above-mentioned typical patterns, allometric regressions (Peters 1983), mathematical methods and Hi-Tech means of information support of such models (Kamenir 1987). A new operational approach to analysis of the ecosystem temporal and spatial structure may emerge, capable of overcoming many difficulties arising during development of the most commonly used taxonomic simulations (Odum 1971; Holing 1978) and food webs (Patten 1985; Cohen et al. 1993). Through use of formal mathematical schemes and operational definitions it can work as a specific language and provide effective means of interdisciplinary communication necessary in studies of large-scale aquatic systems.

Because of the sensitivity of SS to environmental changes, the approach may provide tools for ecosystem monitoring. Description schemes, based on formalized quantitative parameters well adapted for use of computerized instruments, provide opportunities for application of highly automated technical means of measurement and monitoring, like image analysis, flow cytometry, cell selectors and microcalorimetry. Thereby they can help save resources and time by concentrating on most important points (Kamenir 1987, 1993). Hence, spectral analysis can be an effective means for empirical data collection and processing, for development of theoretical models and for ecological forecast.

5. CONCLUSION

We conclude that size spectra analysis is a useful tool for comparative investigations of aquatic ecosystems, for analyzing trends, development of methods of ecological forecasting and interdisciplinary cooperation.

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