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Influence of basin scale on structure of natural aquatic communities

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Abstract

The aim of the study was to analyze the influence of aquatic ecosystem size on community structure. Analysis is based on quantitative indices, describing integral communities and comparison of their biomass size spectra with standard patterns. Comparative analysis of widely differing aquatic communities shows that certain characteristics of the community structure withstand considerable changes of many important parameters of the abiotic environment and taxonomic composition of the community. At the same time, there are some changes in fine structure of the community size spectra, which can now be documented and measured with relatively high precision due to development of modern automated means of data acquisition. In this study, application of spectral descriptions is discussed as applied to communities of River Jordan-Lake Kinneret aquatic system. It follows from the theoretical scheme developed that, for analysis, the most important part of the community size spectrum is its right extreme, i.e. body size of the largest species of the ecosystem. In the case of Lake Kinneret, that is fish. The fish biomass size spectra were obtained using dual-beam hydro-acoustics techniques. The parameter comparison shows that for riverine systems (i.e. ecological systems with a high role of allochtonous organic matter in the total energy influx of the community), both the water area and the watershed basin (including its terrestrial part) deserve attention as the appropriate scaling parameter.

Introduction

Study of stable patterns of community structure is one of the central problems of ecology. Especially important, from both a theoretical and empirical point of view, are the mechanisms and limits of stability of communities subjected to ever growing anthropogenic impact (Begon et al., 1986). Taxonomic structure of the community is the most often studied, but is highly difficult to analyze. Mathematical modeling pays ever growing attention to analysis of trophic structure (Higashi et al., 1992; Stone & Berman, 1993). A number of structures or patterns, resulting from interaction of organisms with their environment, are also subjects of scientific interest: patterns of stratification, zonation, periodicity (periodical activity), social activity, etc.

There are many factors, such as physical environmental parameters, level of succession and external stresses (including pollution and other anthropogenic impacts), which influence the aquatic community structure (Odum, 1971). Ecosystem size is considered by many scientists as one of the most important parameters which is suitable for quantitative analysis. There are a number of studies describing its impact on taxonomic composition of communities (MacArthur & Wilson, 1967; Begon et al., 1986).

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 stability of a natural community and the factors that influence it.

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Size spectra (SS) analysis can be a valuable instrument in such studies (Sheldon et al., 1972; Sprules & Goyke, 1994). Being very compact, graphic and flexible, SS are also suitable for mathematical analysis. As many important cases of ecosystem dynamics are linked with considerable changes in the community taxonomic structure and composition (Odum, 1971; Begon et al., 1986), SS and other 'ataxonomic' (Schwinghamer, 1981; Steinberg et al., 1996) schemes are especially valuable. Size spectra describe conservative community properties irrespective of species composition changes. As such, they are suitable for description of large-scale natural systems with huge numbers of species, for comparative analysis of systems with different taxonomic composition, and for systems with temporally and spatially changing species composition.

SS are suitable for analysis of natural aquatic ecosystems, water bodies with high time-spatial heterogeneity, ecosystems going through succession or degradation, species invasion or introduction; and for comparative studies necessary for analysis of impact of some external or internal ecosystem parameters on the structure of its community. The method has been applied to a large number of marine and freshwater systems (Sheldon et al., 1972; Schwinghamer, 1981; Thiebaux & Dickie, 1993; Sprules & Goyke, 1994). Size spectra seem to be especially suitable for analysis of the effect of quantitative parameters of ecosystem, such as its size. Nevertheless, little attention has been given to this problem.

In this paper, we make an analysis of the influence of aquatic ecosystem size on community structure, based on size spectra methods. We use original data for Lake Kinneret (Israel) in comparison with a set of examples from the literature.

Materials and methods

Lake Kinneret is situated in north eastern Israel, in the northernmost part of the Syrian–African rift valley. That is a warm, monomictic lake with a 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, the limits established by the water commission (Serruya, 1978; Gophen, 1993). Kinneret is the only natural freshwater lake in Israel. Because of this, it is used for many purposes: recreation, tourism, fishing, agriculture and domestic water supply. The lake is utilized as a national water reservoir supplying annually 25% of the country's freshwater consumption, including 50% of the drinking water demand. Clearly, water quality is of prime national importance (Berman, 1985; Gophen, 1993).

The same methods were applied to process original data from Lake Kinneret and descriptions of several aquatic communities, taken from literature. They produced a set of quantitative indices of integral communities and their biomass size spectra (Kamenir & Shteinman, 1998). The biomass SS of Lake Kinneret was developed on the basis of data collected by the Kinneret Limnological Laboratory of Israel Oceanographic and Limnological Research (KLL-IOLR). The data on main groups of Lake Kinneret organisms (phyto-, zooplankton, benthos, bacteria) were taken from a previously compiled data set (Walline et al., 1993) and transformed to the size spectra form suitable for the aims of this study.

A special attention was given to right extremity of the community size spectrum, as we consider (see 'Discussion') the body weight of the largest species of the ecosystem, as an important parameter helpful to analyze trends of the ecosystem succession and degradation. For Lake Kinneret, the largest organisms are fish. Since 1993, pronounced changes in fish community composition were noted, so more recent and detailed data were used here. 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 120 kHz. Individual targets from six representative transects were combined into a single data set. Data were collected at night, when a high percentage of individual targets can be resolved because the fish do not school then.

The relation was developed by comparing size distribution of the fish caught in purse seine nets with the distribution of target strength obtained simultaneously. Individual targets (as opposed to multiple targets made up of more than one fish) were identified based on criteria specifying the acceptable maximum and minimum pulse widths, and the length for each individual target was calculated from the TS–length relation. The length–weight relation for the dominant pelagic fish (Kinneret sardine, *Acanthobrama terraesanctae*) was then used to convert lengths to weight. Although most of the fish in the lake are sardines, there are other species present. Thus, the sizes calculated constitute an approximation.

Methods of size spectra calculation and plotting are used as described by Sheldon et al. (1972) and Schwinghamer (1981). All organisms are distributed into size fractions (classes) according to their size (D) obtained from the cell volume (V), weight (W) or the biomass (B) and number of organisms (N) given: $\log D \sim 0.33 \log V$, where $V = W / \rho$, $W = B / N$, $\rho \sim 1$ g cm^{-3}, and size fractions (SF) are standard increments of the organism size logarithm ($\Delta \log D = 1$). Size fraction number (i) corresponds to its left border, i.e. its minimum size D_i ($i = \log D_i$, μm). For biota from other natural ecosystems, the data for the individual groups of organisms were assigned to size fractions by means of a Sieburth et al. (1978) classification table. When one group of organisms described belongs to several SF, it is subdivided among them in equal parts.

All contributions from various groups of organisms were summed up inside each size fraction. All SF were summed up to give the total value of biomass. Parameters per unit area were obtained through normalization of integral values of parameters to the ecosystem surface area (S_{es}). To convert the units, the following approximations were used: 1 cm^3 $\sim$ 1 g fresh weight $\sim$ 0.1 gC $\sim$ 1 kcal (Schwinghamer, 1981).

On the base of the biomass size spectra, the integral surface of the community (S_{sum}) was calculated. Sum of body surfaces was counted for each size fraction of organisms from their biomass according to the surface approximation scheme described by Kamenir & Khailov (1987), then integral surface of the community was calculated as sum of the size fractions.

Regression analysis of relationship between the parameters, estimated on the base of published by other authors data, was done using standard software.

Results

Two morphometric parameters of Lake Kinneret and three biotic parameters of its community are shown in comparison with regression equations, calculated for similar parameters, using a set of aquatic communities described in literature (Figure 1). The right extremity of the Lake Kinneret biomass size spectrum is shown in Figure 2, in comparison with a freshwater community of an artificial system (mesocosm), described by Whittaker (1961), in Figure 3. Figure 2 presents some 50 points obtained from echo-sounder data, which makes possible more precise approximation and quantitative comparison.

Discussion

Comparison of a set of aquatic communities shows evidence for a log-linear relationship between the ecosystem area size and several parameters of the community: its biomass and surface of bodies of all organisms; maximal body weight (Figure 1, curves B_{sum} and S_{sum}; W_m, respectively). It seems that relations connecting B_{sum}, S_{sum} to the water body volume (V_e) are more complicated than relations connecting them to the water area (S_{es}), which have the power coefficient estimate very close to 1.0, i.e. describe a linear growth.

Therefore, while normalized to the water area size, these parameters seem to be relatively constant for ecosystems of various size. Total biomass ($B2$) estimates for these systems are near 100 kcal per square meter, total surface of all organisms is about 20–200 m^2 m^{-2}. These values are close to estimates which we described previously for another set of ecosystems (Kamenir, 1991). Size spectrum descriptions of the aquatic communities of Lakes Superior and Michigan, Scotian Shelf, Bay of Fundy, and Brown Banks, including both pelagic and benthic parts (Boudreau & Dickie, 1992), show about the same biomass estimate ($\log B2 \sim 2$) and size distribution. A similar estimate (100 g wet weight) was discussed previously (Schwinghamer, 1981) as typical for natural aquatic systems. Another index characterized with low variability, i.e. integral community destruction per unit area of ecosystem (kcal m^{-2} y^{-1}), was discussed by Odum (1971).

The right extremity of the community size spectrum, i.e. the maximum organism size (W_m) also seems to show a log-linear relation with the water body area size (Figure 1), but the power coefficient sufficiently differs from 1.0.

An additional analysis of the influence of ecosystems size on community size structure was done in this study, based on the Ideal Minimal Ecosystem (IMES) model suggested by Kamenir (1993) and Kamenir & Shteinman (1998). The main logic of IMES describes closed branched recycling flow implemented by large numbers of ‘flow-through elements’ having the same (hierarchical) structure. Each element exists only during a definite time interval; nevertheless, their death or destruction does not lead to the collapse

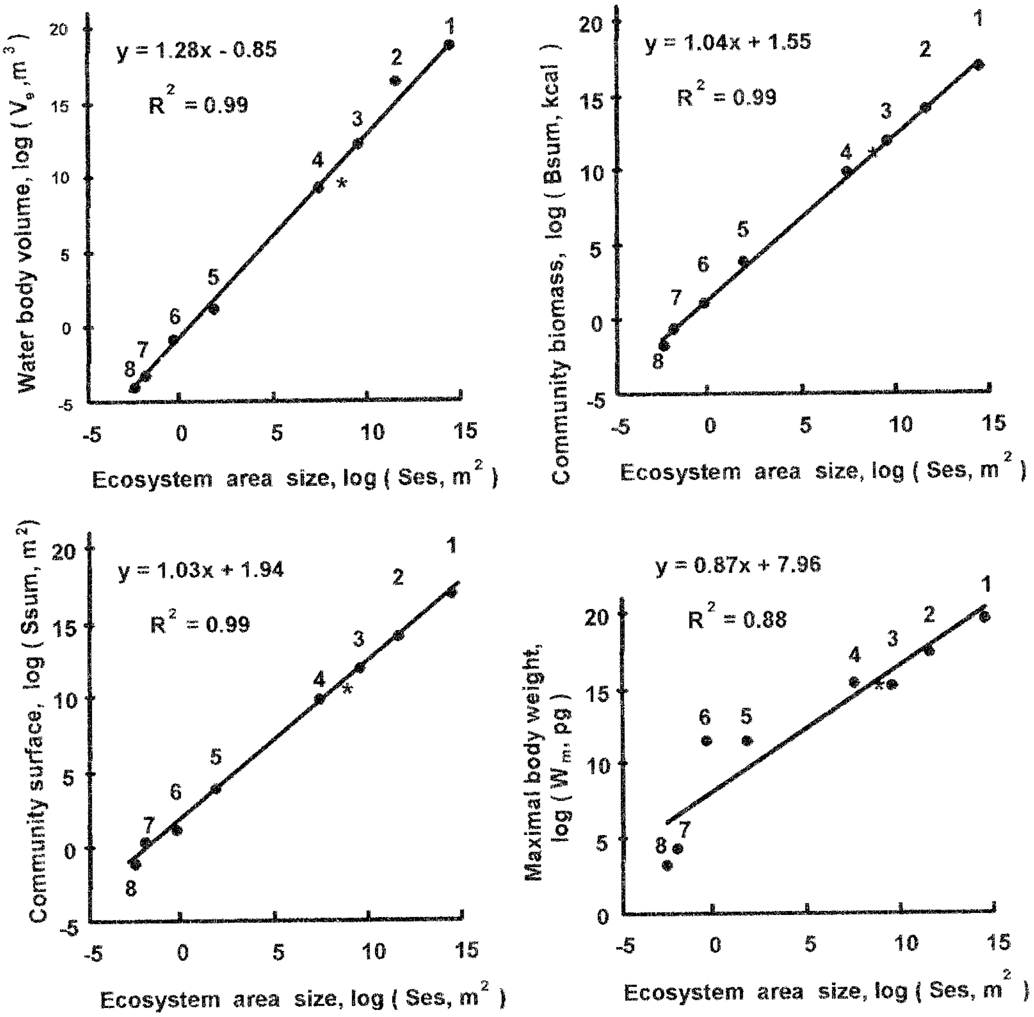

Figure 1. Influence of size (area) of aquatic ecosystem on its morphometric and biologic parameters. Numbers of points: (1) World Ocean (Sorokin, 1978), (2) Black Sea (Sorokin, 1982), (3) Rybinsk Reservoir (Sorokin, 1978), (4) Lake Drivyaty (Vinberg, 1969), asterisk – Lake Kinneret (original data), (5) outdoor pond (Whittaker, 1961), (6) indoor aquarium (Whittaker, 1961), (7) microcosm (Taub, 1969), (8) microbial community in a sealed vial (Fishtein & Kovrov, 1985). S_{es} is the water body area (m^2), V_{e} is its volume (m^3); B_{sum} (kcal), S_{sum} (m^2) – integral biomass of all organisms of the community and external surface of their bodies, respectively; W_{m} (pg fresh weight) is the maximum body weight of the community organisms.

of all system (IMES), as new flow-through elements are produced after regeneration of resources obtained from the elements which collapsed. Therefore, the eternal movement of all resources, stability and close coupling of the recycling loops seem to be intrinsic properties of such a system.

Succession means (in terms of the model) increasing width of SS (mainly, growth of the maximal size of the community organisms) – i.e. growing role of large organisms (in biomass, production, destruction, etc.) and growing estimate of maximal body weight of organisms of the community (Kamenir & Shteinman, 1998). Such trends agree with the “Tabular model of ecosystem development” (Odum, 1971, 1985).

The aim of this study is to establish links between the community structure and size of its ecosystem. Due to the above model, analysis of community size structure with help of size spectra is selected, as an effective means.

The size spectrum of the Kinneret community biomass has a pattern similar to those known from the literature, i.e. several ‘domes’ or ‘bells’, using terms

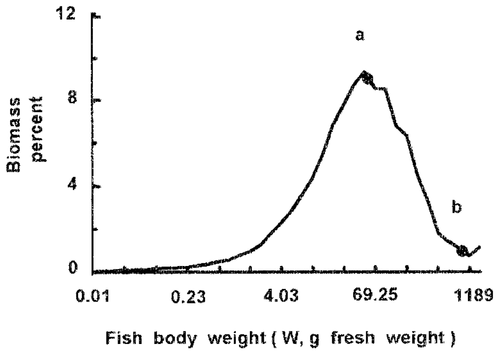

Figure 2. High resolution size spectrum. Large size classes of Lake Kinneret biomass. Size Class: Δ log $W \sim 0.14$. Point *a* is the modal value of spectrum, some 30 g wet weight; *b* is the 'end' of the distribution, near 1000 g fresh weight; fish hydro-acoustic data, June 1997.

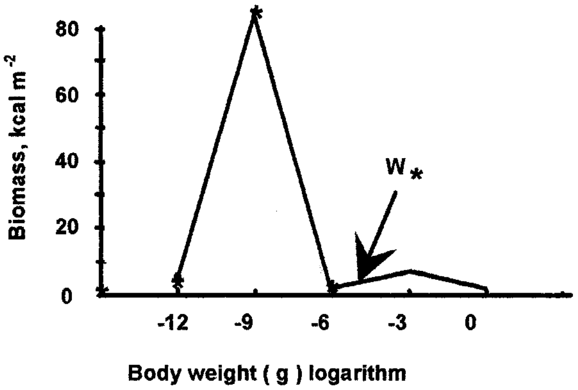

Figure 3. Biomass size spectrum (Kamenir & Shteinman, 1998) of a mesocosm (outdoor pool) aquatic community; built on the base of data of Whittaker (1961).

of Boudreau & Dickie (1992) and Sprules & Goyke (1994). The spectra described are composed of bells of about the same order of magnitude, more or less symmetrical on the logarithmic scale of the X-axis, with gaps between them. Some combinations of periodic (in log *W* scale) and quadratic (Thiebaux & Dickie, 1993) or log-normal (Chislenko, 1981; Kamenir & Shteinman, 1998) functions can be used for approximation of SS. The amplitudes and position of the bells are different for different communities. If all SS can be approximated using a periodically repeating simple function (quadratic or Gaussian), several points are sufficient to obtain the approximation parameters. The extreme point of the SS can be one of such points. Therefore, parameter W_m seems to be especially interesting, as determining an important position in the community size structure.

Here we will try to analyze a hypothesis that power coefficient $b = 1$ can be better (than the above 0.87) estimate for W_m-S_{es} regression. The second (i.e. dashed) line, going from point 1 with power coefficient $b = 1$, is compared with the W_m regression in Figure 4. Point 1 (the Blue whale) is selected as the record, unique for all the Earth estimate. It looks very stable, as close values of W_m were achieved several hundred million years ago. That was Dinosaur, some 80–90 t of Brachiosaurus body weight (Schmidt-Nielsen, 1984). One can note that the dashed line (equation: $\log W_m = \log S_{es} + 5.5$) passes very close to point 8, i.e. connects two ecosystems, the most close to the notion of *ideal* ecosystem described above.

All natural ecosystems are not completely closed, so there are always some in- and out-flows. However, for a balanced system such as the World ocean (the least dependent on anthropogenic impacts), recycling index, describing the measure of the recycling flux closure (Finn, 1980; May, 1981), is about 0.9927 (for organic carbon) for marginal regions and 0.9988 for central zones of the ocean (Romankevich, 1977). Such values imply that the World Ocean is nearly completely closed, and that large water bodies can be considered as such, especially near their central parts. Another example of a closed system is the self-maintained microbial community (autotrophs and heterotrophs) supporting stable biotic parameters and closed recycling of nutrients inside a hermetically sealed ampoule during several years (i.e. very many generations), described by Fishtein & Kovrov (1985). Both systems (World Ocean and sealed microbial community) do not depend on the external world for material substances. Both are dependent on the external energy influx (light energy, in both cases) compensating for heat dissipation, the indispensable property of every living system.

Important from the point of view of generality is that all natural aquatic ecosystems and experimental micro- and mesocosms have sizes between these two extremes. Several points, built on the basis of published data (Kamenir & Shteinman, 1998), fill the range between these two extreme points (Figure 1). The ecosystem set forming a chain of points (with about regular logarithmic size intervals between them) includes: the world ocean, a sea, a lake, a river reservoir, a pond, an indoor mesocosm, a microcosm and a microbial vial. Such a set includes all ecosystem size interval possible for this planet. It allows comparison of natural and artificial, marine and freshwater com-

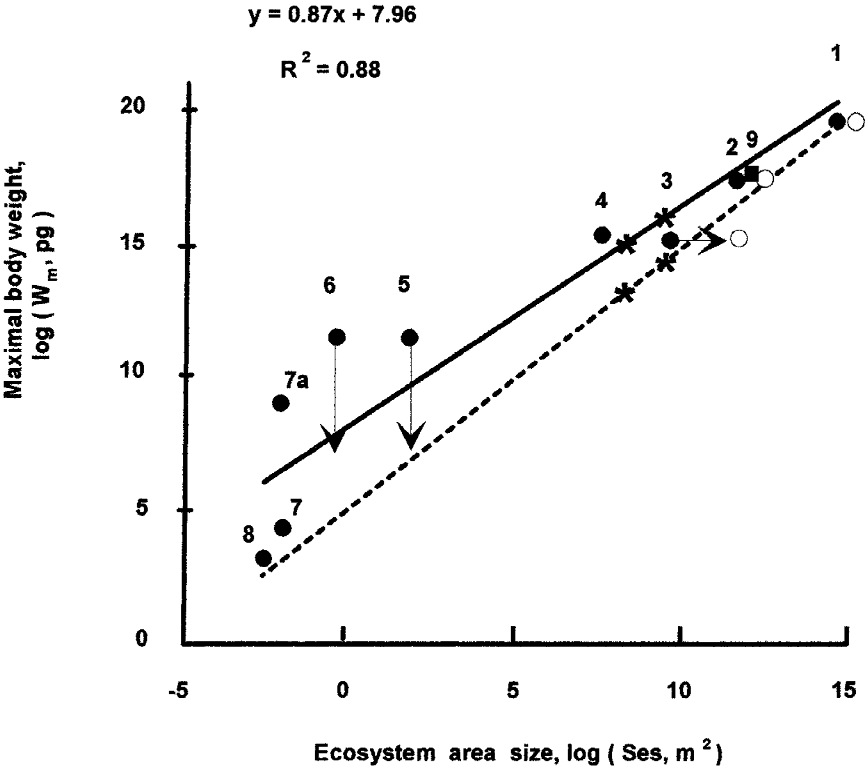

Figure 4. Dependence of the maximum body mass (W_m, pg) of the community organisms on the water body area (S_{es}). According to Figure 1. Arrows and open circles – correction of the point position: (5) (6) supposed limit of W_m (micro-zooplankton) in the experimental ponds, if the insect larvae, fish etc. are only 'strangers' (would die in case of the system sealing); (7a) *Artemia salina*, population of 100 dies in 50 d after sealing of the flask (Nixon 1969); asterisks (Lake Kinneret) – W_m estimates on the base of the lake area and its watershed, using two allometric equations; (9) the Volga River watershed used as S_{es} estimate (square).

munities; and includes both laboratory measurements and field data.

One can see (Figure 4) that almost all points lie rather close to the line connecting points 1 and 8, corresponding to the most closed systems (World ocean and microbial vial). Nearly all the points are above this line.

A possible explanation, consistent with the IMES concept described above, is that not all organisms present in the original data sets (i.e. inside the ecosystem), especially in artificial, experimental systems, are members of a self-sufficient community. Some would die out if the systems are sealed. For example, *Artemia salina Linn* in a Roux flasks dies out (Figure 4, point 7a) in 50 days after sealing of the system (Nixon, 1969); therefore, point 7 corresponding to this system, *Tetrahymena vorax* (Taub, 1969), is closer to the dashed line in Figure 4.

As Whittaker (1961) stated, animal populations can be deliberately introduced into an aquarium, as in his experiment quoted here, but their biomass is likely far to exceed what plant growth in the aquarium would naturally support.

In his study, aquariums with pond or river water generally did not support sufficient for studies numbers of micro-crustaceans. *Daphnia pulex* abundance dropped in 4 d so, that it could not be effectively sampled. Using the dashed line of Figure 4, for the ecosystem size given (point 5, log S_{es} = 1.7), we get a body weight estimate (log $W_m \sim 7.2$), indicating that organisms should not be larger than some 14 μg fresh weight. In size spectrum of system 5 (Figure 3), one can see 2 peaks with a gap between them. In the original data (Whittaker, 1961), 14 μg value is close to 'plankton: micro-crustaceans' (21.6 g dry weight = 2 10^6 individuals, i.e. $W \sim 10.8$ μg dry ~ 54 μg fresh weight). Thus, the micro-crustacean taxonomic composition and size structure are especially interesting. Larger organisms, i.e. nymphs, fish, etc. should be regarded as visitors, and not true members of the community. They should not be included in the W_m-S_{es} regression data, and point 5 in the figure should be adjusted correspondingly. The same is true for Whittaker (1961) point 6.

Now let's consider points 1–4 (Figure 4), describing natural aquatic communities. For these systems a complicated problem is to estimate the area (S_{es}). All these systems have some exchange with the outer world, hence the borders of the systems are not strictly defined. Therefore, we think that the watershed area deserves a thorough analysis as a perspective scaling parameter. This follows from the IMES logic, which states that the energy influx is the key regulator. For natural ecosystems it is the sunlight flux. However, allochtonous organic matter, coming from the watershed, is often very significant. Its leading role in the energy budget of the Rybinsk reservoir (point 3 in Figure 4) is stated by Sorokin (1978). Thus, total energy inflow is determined by the size of the drainage basin.

For many small water bodies and even for some large circum-continental seas this factor can make the ecosystem area estimates several times higher, as illustrated by asterisks (Lake Kinneret) between points 3 and 4 in Figure 4. Such an approach provides also the ecosystem area estimation for rivers. According to their drainage basin areas, great rivers, like the Volga, Nile and Amazon, especially in their lower reaches, are comparable to seas: log $S_{es} \sim 12$. Thus, point 9 of Figure 4, added for the Volga River, where W_m is several hundred kilogram (*Huso huso*, log $W_m \sim 17$–18), falls rather close to the line 1–8. A hypothesis, supported by the results of our analysis (Figure 4), is that both the watershed and the water body area should be considered as the ecosystem scale parameters. Such a correction, almost negligible for point 1 (about 5 billion of square kilometer instead of 3.4, i.e. log S_{es} displacement of ~ 0.2), is considerable for small water bodies like lakes and river reservoirs (open circles on Figure 4).

For the largest organisms body weight (W_m), fish was analyzed at Lake Kinneret, as macrophytes are practically absent in the lake. The largest organisms of zoobenthos (*Uno terminalis*, mollusks) have a body weight of only ~ 10 g (Serruya, 1978).

From two regression lines, estimates of some 50 g (fresh weight), 1 kg, 1 kg and 17 kg can be obtained (Figure 4) on the basis of the lake and the watershed area estimates, 170 and 3000 km^2, respectively. Detailed analysis of the Kinneret SS right extremity (i.e. SS of fish, Figure 2) shows the modal size of fish (point *a*) about 30 g wet weight, while the largest (point *b*) are about 1 kg. The most abundant pelagic fish species, lavnun (*Mirogrex terrasanctae*), has a maximum body weight of about 150 g. Several other important species, Tilapias (*Tilapia zillii*, *Sarotherodon galilaeus* and others) have body weights up to 750 g (Walline et al., 1993), i.e. between points *a* and *b* on the figure.

There are fish species in the lake that have a maximum body weight more than 1000 g corresponding to point *b*. These are (Walline et al., 1993) mullets (*Mugil cephalus*, *Mugil capito*), the piscivorous species *Clarias lazera* and silver carp (up to 16 kg). However, these were introduced and are supported by annual stocking.

So, a more detailed analysis and approximation of the SS and, especially, its right part can be helpful for quantitative analysis of influence of the ecosystem size on parameters of structure of inhabiting aquatic communities.

Conclusion

The drainage basin and water area size (S_{es}) can be viewed as potential scaling parameters of an ecosystem, determining community size structure parameters, such as the largest species body size (W_m).

Often the largest organisms included in an experimental system are the main object of studies. Hence, the Wm-Ses relationship can describe some important properties and deserves detailed analysis.

Analysis of a broad range of aquatic ecosystems, done with the help of the IMES model, shows that for a large range of ecosystem sizes, there are parameters, like the maximum body weight, which change log-linearly with ecosystem size. Integral community biomass and surface, community destruction grow about linearly with ecosystem size, so these parameters, when normalized to the ecosystem size and averaged over the annual cycle period, are nearly constant for various ecosystems size.

Parameters of the right extremity of the Lake Kinneret biomass size spectrum are in good agreement with the relations derived from data published on other aquatic ecosystems.

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