The role of copepods in the Baikal ecosystem

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Abstract

This describes a study of the pelagic zone of Lake Baikal with particular reference to copepods. In addition the cycling of matter and energy in lacustrine basins is described. © 1998 Elsevier Science B.V. All rights reserved.

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1. Introduction

This paper reports on a study of the pelagic zone of Lake Baikal with particular reference to copepods. On a broader limnological base, the cycling of matter and energy in lacustrine basins was studied within the scope of the International Biological Programme using Lake Baikal as an example.

The biological component of this cycle—the "minor cycle"—includes the autotrophic production of organic matter by photosynthesis and its transformation through heterotrophic food chains to usable bioproducts.

While the biont of Lake Baikal is diverse and the lake itself has a wide range of biomes, the biocenosis of the open water is relatively simple, comprising only a few species and trophic groups living in a comparatively homogeneous environment (which represents the greater part of the lake). The pelagic zone plays the major role in the biotic cycle by determining nature and extent of the primary production and thus largely the whole character of the lake. The basis of the final production is generated in the water column where all the remaining commercially valuable species also live. The importance of the pelagic zone in Lake Baikal is not surprising because each square meter of the bottom is overlain on average by a water column 730 m high.

2. Results and discussion

The phytoplankton (with 10 species the most typical and numerous) are the autotrophs: bacteria, protozoa, rotifers, two species of copepods, and one species of amphipod are the heterotrophs of the first and second level; the top heterotrophs are tinted fishes, zooplankton and the seal. Only a few species are involved. Such a simple structure in the pelagic zone is not specific to Baikal since Dumont (1994) has shown that other ancient lakes have a simple structure too.

The first heterotrophic level in such lakes is usually represented by one endemic species of calanoid copepod: in Lake Baikal this is Epischura baikalensis Sars. As in other ancient lakes copepods predominate over cladocerans which in Baikal are not a
constant component of the plankton. At the end of summer, a few species of Palaearctic derivation temporarily penetrate the open water from the coastal zone and shallow bays (even without being able to complete life cycles.

The second heterotrophic level in ancient lakes is represented by a small and large predator. In the case of Baikal, these are a copepod, *Calanus kolenos Lill.*, and an endemic amphipod, *Macrothecopus brunickii*, respectively. Zooplankton feeding fishes are mainly enemies; these are two species of *Cosmopelidah* (golomjanka), the sculpin (*Cotossomus gravimanus*) and the omul (*Coregonus autumnalis migratorius*). The cyclopid and the omul are rather late invaders of the lake and occupy a subordinate position in the Baikalian ecosystem.

The first data on the composition and functioning of the pelagic community of the lake were obtained in the 1930s and 1940s (e.g. Janitskii, 1930). The observations were made in the Brsion of Irkutsk University in the village Bolshoye Koty (South Baikal) and in other places. In 1947, a quantitative view of feeding interactions in the pelagic zone became apparent (Koshekh, 1947). Finally, Koshekh (1962, 1963, 1972) summarised all the information available on the zooplankton in two monographs. At the end of the fifties and sixties, the Limnological Station gave the Limnological Institute of the Siberian Division of the Russian Academy of Sciences made a systematic survey of the whole complex of biotic turnover in the pelagic zone, first along a transect in Southern Baikal, and then in the lake as a whole.

The seasonal and long-term dynamics of abundance and biomass of phyto- and zooplankton as well as of fishes and the seal were studied, together with their distribution, productivity and the biology of the most important species. Those data laid the foundation for a quantitative scheme of the biotic balance in the pelagic zone (Fig. 1). The flow of matter (C, C, O, and energy (k. cal) under 1 m² of the surface per year for the pelagic zone is a whole have been estimated on the base of the amount of organic C in the organisms (Vorontsov et al., 1969; Vorontsov, 1971, 1978, 1985, 19910 (Fig. 1). Phytoplankton in Lake Baikal, as in other large water basins, is the main source of organic matter and serves as food for heterotrophic organisms such as bacteriaria and crustaceans of the first and in part of the second trophic levels.

According to this scheme, the energy contribution of the phytoplankton amounts to 972 kcal m⁻² yr⁻¹, the net production, minus 10% expenditure for respiration, that is, to 875 kcal m⁻² yr⁻¹. At the first heterotrophic level, in the copped *Epischura baikalensis*, the expenditure of energy for production is 80.5 kcal. This is only one third of the energy expenditure, for metabolism (245.2 kcal) and one tenth of net primary production. The same proportions apply to the second heterotrophic level. The production of *Calanus kolensis* and amphipods is 8.1 kcal, viz. 0.9% of the net primary production and expenditure for metabolism amounts to 22.5 kcal. The regularity observed by Oskam (1964) for other water basins, viz. a 10-fold dispersion of energy in the process of basal metabolism in every subsequent link of the food web, can thus also be confirmed for Lake Baikal. Only in the links between zooplankton and fishes and between fish and the seal are the proportions different. The production of all pelagic fishes amounts to 0.4% (3.5 kcal) of the net primary production 99% of it being due to *Cosmopelidah* that of the seal to 0.024% (0.22 kcal/m²).

Bacteria are also heterotrophic, but do not depend directly on the primary production (decaying phytoplankton) but rather on the dead bodies of other heterotrophic organisms. They use 60% of the organic matter of the primary production. Their own production amounts to about 35-5 (14.8 kcal). Bacteria in turn are used by other heterotrophs, in particular by *Epischura baikalensis* (but also by protists, rotifers, and to some extent by nematodes of *Calanus kolensis*).

These estimates of energy turnover in the pelagic zone have revealed that on the basis of the intensity of primary production (due to the great transparency of the water, the large euphotic layer, and extensive water exchange), and the estimated high productivity of subsequent heterotrophic levels, the lake is near to mesotrophic (Vorontsov, 1971) yet on the basis of physical-chemical characteristics it is sills-oligotrophic. The usable production of the pelagic fishes is rather small because 90% of them are non-commercial *Cosmopelidah* which are widely dispersed. The trophic 'dead end' is partly overcome by the seal.
Fig. 1. Scheme of energy flow (kcal m\(^{-2}\) yr\(^{-1}\)) in the main trophic chains of the pelagic system of Lake Baikal. Updated from Voronin (1971). The amounts of energy are represented graphically by the spheres of corresponding volume: the outer sphere—assimilation (A); the inner sphere—net production (P); W = expenditure for respiration.

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<thead>
<tr>
<th></th>
<th>A</th>
<th>P</th>
<th>W</th>
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<tr>
<td>PH</td>
<td>Phystoplankton</td>
<td>72.0</td>
<td>14.8</td>
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<tr>
<td>B</td>
<td>Bacteria</td>
<td>605.5</td>
<td>354.8</td>
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<tr>
<td>E</td>
<td>Epischoen</td>
<td>505.8</td>
<td>85.8</td>
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<tr>
<td>M</td>
<td>Macrobenstos</td>
<td>18.8</td>
<td>47.7</td>
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<tr>
<td>C</td>
<td>Cintomycetan</td>
<td>0.9</td>
<td>0.9</td>
</tr>
<tr>
<td>C</td>
<td>Cyclops</td>
<td>12.6</td>
<td>3.4</td>
</tr>
<tr>
<td>S</td>
<td>Sculpin</td>
<td>1.1</td>
<td>0.2</td>
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<tr>
<td>O</td>
<td>Ovaal</td>
<td>0.4</td>
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<td>Seal</td>
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Not only is the flow of energy important, ecological features too are of great importance. Uniformity of the pelagic zone does not mean lack of dynamics. The severe Siberian climate, the immense size and great depth of the lake, the wind and thermal differences in the water resulting in translocations of water masses which are highly heterogeneous during the ice-free period, as well as the currents and influences of rivers discharging into the lake, make the pelagic zone and its internal processes highly dynamic. This becomes apparent in the seasonal, spatial and long-term fluctuations in the life of different organisms which are affected in different ways.

The most obvious variations take place in the phytoplankton because the algae occur in the upper, most mobile, layer of the water (Figs. 2 and 3). Algal abundance is not the same every year and not the same in different parts of the lake. The composition of species also changes in different years. The biomass of the main species may differ 10-fold in different years (the abundance of the diatom Melosira biculminata, for example, varied 50-fold during a period of 5 years, and that of the phytoplankton as a whole, 20-fold) (Vorontsev et al., 1975).

Seasonal changes are also considerable. In favourable years, the amplitude of biomass at the different stations varies between 10 and 200 times.
(in 1964 for example). The spatial changes in biomass are greatest in spring and summer where they vary between 10 and 150 times (Vostinsev et al., 1975).

At the first heterotrophic level, viz. in *Epischura*, the variation is less pronounced than in the algae (Fig. 4). Yet there are highly productive and unproductive years. In productive years, maximal biomass reaches 19–41 g/m³ in September in the 50 m water column, in unproductive years it is between 4 and 8 g/m³, but most of the time only hundreds of a gram.

Spatial differences are greatest in June. In the long term, changes in biomass in the entire lake showed a 6-fold variation in June, in September, the variation was only 4-fold. In the southern basin, variations in biomass in June were as much as 23-fold, in mid-Baikal about 9.5-fold, and in the northern basin, only 4-fold. In September, these variations were dampened—3.0, 3.7- and 4.5-fold, respectively (Fig. 5). In some years, spatial differences in amplitude of the biomass in June reached 5, 10 or even 20 times, in other years only values of 1.1 and 2.6. The biology of *Epischura bicaulentis* is described by Afanasyeva (1977).

![Fig. 5. Distribution of biomass of *Epischura bicaulentis* over Lake Baikal in the layer 0–50 m in 1963 (productive year) and in 1968 (unproductive year). Redrawn after Afanasyeva (1977).](image)

![Fig. 4. Seasonal and long-term changes in the numbers of copepods of *Epischura bicaulentis* and its total biomass (1944–1964 in average for V-XII, in 1965–1968 for IX) in the layer 0–200 m of the northern Lake Baikal. After Kozlova (1962) for 1944–1957, Kozlova (1972) for 1961–1964 and Afanasyeva, 1977 (for the biomass).](image)
Cyclops kolensis generally belongs to the second heterotrophic level because as copepods and adults it feeds mainly on larvae of Epischura. Nauplii of Cyclops are micro-feeders and in times of abundant phytoplankton copepods and adults can also consume algae.

The abundance of Cyclops kolensis is different in different years (Fig. 6). It is never completely absent from the plankton, but in the period 1945–1964 only 5 years of high abundance were observed. In the abundant years (1946 and 1950), Cyclops reached 80–90% of the total biomass of the zooplankton. Its biomass in these years was even higher than that of Epischura. It reached 57.69 g/m² in the water column between 0 and 250 m in 1946, and 46.99 g/m² in 1950, that is, 12–28 times its biomass in unproductive years (1948, 1949). The biomass of Epischura in years of high Cyclops abundance is low due to predation by Cyclops (Mazepova, 1963, 1978).

Between 1965 and 1974, the biomass of Cyclops was very low, its annual mean ranging between hundreds of a gram (1973) and 3–4 g/m² (1965 and 1968) (Afanajeva, 1977). Seasonal fluctuations in biomass of C. kolensis are more noticeable in productive years when biomass is smaller in winter and with a maximum in summer (August). The maximum may be 55 times the value of the minimum (in 1943) or even 126 times (in 1950). At one station, the biomass may fluctuate 10-fold within a single month. In unproductive years, seasonal differences in abundance (minimum–maximum) are also great, ranging from 24 to several hundred times (Mazepova, 1963).

Distribution of Cyclops in the lake is very uneven. There are regional differences in biomass, so that in unproductive years at the time when biomass is highest this can be 10 times higher in one region than in another, and even 40–50 times higher in unproductive years. In different basins, numbers may differ or be nearly the same.

With regard to the biology of Cyclops kolensis and Epischura baicalensis and their role in the Baikalian ecosystem, a number of points can be made. Adult C. kolensis from Lake Baikal do not differ morphologically from populations elsewhere. Seasonal and local variability is expressed only in

Fig. 6. Seasonal and long-term changes in the number of Cyclops kolensis in southern Lake Baikal in 1945–1957 and in 1961–1964 (ind./m² in the layer 0–250 m). After Koshov (1962, 1977).
size and not in body form. Maximum size is reached in June, and minimum size in December. Local and seasonal variability are similar in extent.

*C. koleniis* is a constant element of the plankton and is present every year, throughout the lake, but not always in great numbers. On the whole, it plays a subordinate role in the zooplankton except in years of large crops when, however, it may exceed *Epis
cucha* in abundance. During one year, three generations may develop in the open water. There is first a peak of adults (three of the first generation) in May/June. The second peak lasts from May almost to October and comprises the adults of the second and third generation which reach maturity in August and the end September/beginning of October, re-
spectively, and also the adults—which are later off-
spring of the first generation. During that time, num-
bers of 70–15 thousand/0.001 m³ may be reached in
some layers. Young hirne in winter grow up to form the first generation of the next year. This clear seasonal trend in the life cycle of *C. koleniis* is not observed in unproductive years.

In the shallow waters of the Selenga region, *Cy-
clops* behaves somewhat the same as in open waters. In the sors, abundance decreases towards summer. As in other water bodies, it disappears here from the plankton and enters diapause when the water is warmest. It reappears in September. In the open wa-
ters, reproduction takes place all year with partic-
ular intensity from May until August.

In the laboratory, the longest period of reproduc-
tive activity in *Cyeclops* (at temperatures between 9
and 17°C) is 2 months. The total life span is 4–7 months. The mean number of eggs per two egg sacs is 29. Greatest numbers are observed from May until August. During that time one female may produce 12–14 pairs of egg sacs. In winter, fecundity de-
creases to 60–240 eggs. In the laboratory, egg develop-
ment takes 3–4 days at temperatures between 13
and 19°C and 6–8 days at 5–7°C. The mean period
necessary for the development of nauplii and cope-
pods is 250 degrees days. In the wild, development time is shortest in summer (50 days) and longest in winter (250 days).

Nauplii of *Cyeclops koleniis* feed on inorganic and aggregations of bacteria though their mouthparts are less well adapted to deal with small particles than those of *Epis
cucha baikalensis*. Third copepodids and older stages feed on nauplii and first copepodids of *Epis
cucha* and partly also on diatoms. In years of high abundance, *Cyeclops* markedly reduces the *Epis
cucha* population. In such years, there is no maxi-
mum of nauplii of *Epis
cucha* in summer.

*C. koleniis* inhabits the upper layers of Lake Baikal, up to 80% of all individuals occurring in the upper 50 m. Only in spring and autumns, when water circulation takes place, does it disperse down to 150–250 m. At even greater depths, only occasional individuals are found. Diurnal vertical migration takes individuals to a depth not exceeding 25 m. In winter, its intensity is reduced. Upward migration occurs at twilight, in summer in the morning and evening, but in winter individuals remain in the upper layers under the ice in both the day and night.

Under snow-covered ice some of them aggregate in
the top 10 cm of water.

Life in the open water of Lake Baikal has changed the natural history of *C. koleniis*; the number of generations has increased, summer diapause has dis-
appeared, and the time of maximum abundance has shifted to a later date when the water is warmest. Despite these changes, the species can still be called cold stenothermic because temperature conditions in Lake Baikal are more severe than in other water bodies where it occurs. In the warm sors, it also disappears from the plankton in summer when the temperature reaches 18°–20°C.

There are some indications that *Cyeclops* is less well adapted to the Baikal environment than *Epis
cucha*. This is supported by the great fluctua-
tions in abundance, by the structure of the mouth-
parts and by the fact that *C. koleniis* remains in the upper water levels. Temperature is not the only reason because *C. koleniis* is a winter species else-
where. Food conditions may be unfavourable be-
cause outside Baikal it seems to thrive better in eu
crophic water bodies.

The high abundances of *Cyeclops* coincide with algal blooms, especially those of *Melosira*. It has been suggested that in such years better food condi-
tions (bacteria, protozoans) are created in spring under the ice for the nauplii of the first generation of *C. koleniis* so that the foundations are laid for a successful development of subsequent generations.

These features of the ecology of *C. koleniis* suggest that unlike *Epis
cucha baikalensis* it may be
a fairly recent invader of the pelagic zone of Lake Bukal. It belongs to the Siberian-Bukalinean complex of species (Wetter and Jorgensen, 1955) which consists of

Palaearctic species actively entering the lake and adapting to life in this new environment.

Epishare biocenosis is an old endemic and a typical representative of the Bukalinean complex of species. It predominate in the plankton, plays a significant role in the biontic cycle and, as a filter feeder, adds to the improvement of water quality. At the same time, through its metabolism it produces so much CO₂ (25 g m⁻² yr⁻¹) that it may influence the gas regime of the lake, but this is not dangerous because of active gas exchange between the lake and the atmosphere (Vorontzev et al., 1953). It has been shown that on average the Epishare population filters a water layer of 15 m (63.8 ml) all over the lake. This contributes to the self-nutrition of one third of the whole volume of the upper, biologically most active layer of the lake and, together with the activity of microorganisms, helps about the high transparency of the lake water. This in turn creates the necessary conditions for the formation of an extensive impregnation layer enabling a high phytoplankton productivity (Vorontzev, 1990).

3. Conclusions

It is obvious that Cyclops, with a production reaching only 4% of Epishare (on the average 3.92 million tons of organic matter), and with a different feeding strategy, could not substitute for the latter in Lake Bukal. In the surrounding fauna also there is no species to replace E. biocenosis. This particular trophic and the structure of the pelagic community of Lake Bukal call for urgent measures of protection. Shifting Epishare disappear one day from the lake the functioning of the ecosystem of the pelagic zone would be spoilt with negative consequences for the whole lake and water quality. The intention systematically to control the condition of the pelagic ecosystem is therefore of great importance. The most sensitive indicators need to be determined to be used in a special monitoring programme to assess the status of the lake.

Apart from E. biocenosis and C. kolomica, there are other copepods in Lake Bukal, in particular a great number of brine species belonging to the Cyclopoida and Harpacticoida. Their contribution to the biontic turnover of the lake is negligible, but they are an integral part of the endemic fauna and add to its overall diversity. An understanding of the history of the brine of the lake is possible only by taking into account the particular features of all its inhabitants.

References


