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Henn TIMM

PRODUCTION OF MACROZOOBENTHOS IN LAKE PEIPSI

Lake Peipsi constitutes the northern and largest part of the compound Lake Peipsi-Pihkva (2670 km² out of total 3555 km²). Although the lake is regarded as eutrophic, with mesotrophic features in its northern part, the water quality and biota in Lake Peipsi have lately been quickly worsening (Мяэметс et al., 1985).

Zoobenthos surveys were carried out as early as in the 1930s. The dynamics of the zoobenthos standing stock (Минина, 1982; ТИММ et al., 1982) and production (Антипова, 1982; Асельборн, 1983; ТИММ, 1986; ТИММ, 1987) have been the preferable investigation topics during a number of years.

Material and methods

Macrozoobenthos was collected with grab bottom samplers (225 cm²) at four stationary sampling spots (Fig.) from May 4, 1984 to May 15, 1986. Samples were washed on a sieve N 14, macrobenthic animals were sorted, fixed and kept in 70% ethanole. After the weight stabilization (at least three months) they were weighed on torsion scales. In order to determine weight changes in the fixing fluid, some animals were weighed twice: first alive and after three months as the fixed ones. Altogether 826 samples were collected and examined.

The production (P) is defined as a sum of growth increments of all specimens, including the newborn and the eliminated ones, during the investigation period. The population production consists of different cohort productions (cohort — a group of individuals born simultaneously and developed in similar conditions). The individual cohort production was estimated according to the instantaneous growth rate method

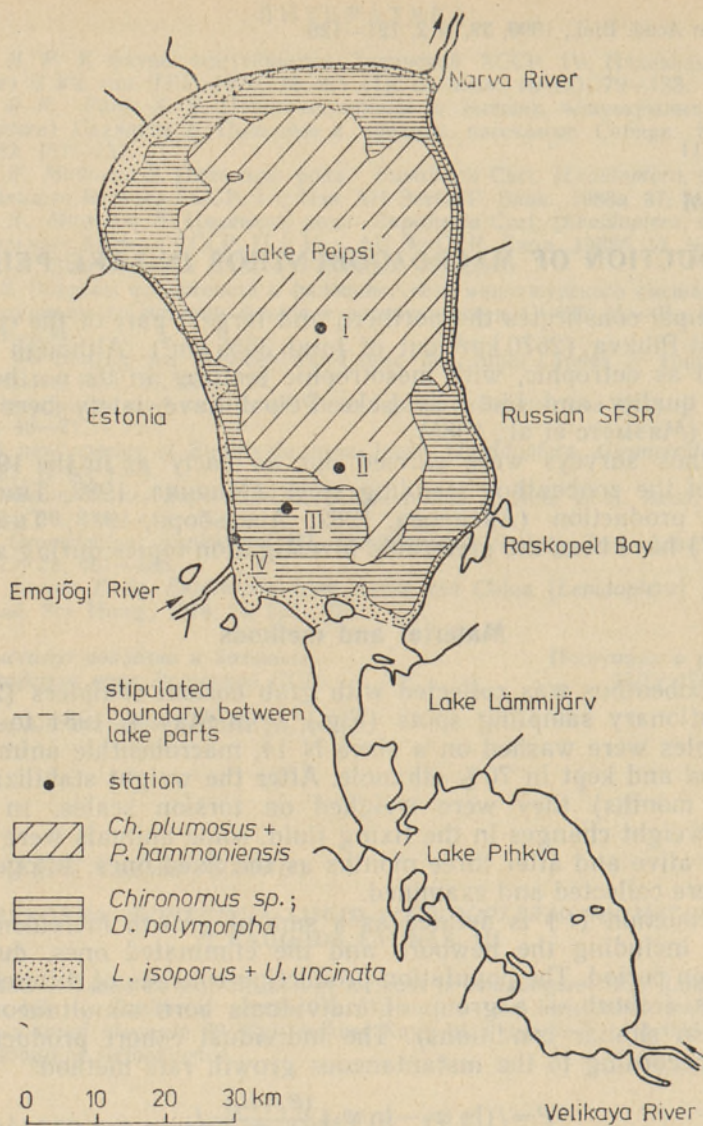
$$P = (\ln \omega_2 - \ln \omega_1) \frac{(B_1 + B_2)}{2} I,$$

where ω_1 and ω_2 — the mean individual weights, B_1 and B_2 — the mean standing stock at two consecutive sampling times (Chapman, 1978; Winberg et al., 1971). Different cohort productions were added up in case the species production for a longer period (e.g. a year) was calculated.

Production/standing stock ratios (P/B) for 12 more abundant species were calculated for two investigation periods (years). When possible, production/maximal standing stock ratios (P/B_{\max}) and cohort P/B ratios were also determined. Literature data on P/B were used for calculating the production of some rare species (Winberg et al., 1972; Алимов et al., 1986) as well as for giving weight in energy units (Waters, 1977; Алимов, Финогенова, 1984).

Results and discussion

According to the production samples in 1984—1986 and the samples gathered by the members of the Institute of Zoology and Botany of the Estonian Academy of Sciences in 1964—1986, four main animal communities inhabit the open benthos of Lake Peipsi (the Figure).



Lake Peipsi-Pihkva * Озеро Псковско-Чудское

1) *Chironomus plumosus* + *Potamothenis hammoniensis* community. In the profundal, 52% of the lake area. Depth 9—11 m, substratum — brownish-grey mud.

2) *Chironomus* sp. (another species of the *plumosus*-group, not exactly determined) community. In the lower sublittoral, forms 41% of the lake area together with the next community. Depth 3—8.5 m, substratum — fine sand.

3) *Dreissena polymorpha* community. In sandy, gravelly and stony areas at a depth of 3—8 m; in the north-eastern part even at 1 to 10 m. Alternates with the former community as separate spots or wide fields.

4) *Lamprodrilus isoporus* + *Uncinaxis uncinata* community. In the higher sublittoral and/or littoral (6% of the lake area). Depth 1—3 m, sandy substratum.

Littoral parts at a depth of less than 1 m, as well as the peculiar Raskopel Bay (about 1% of the lake area) were not taken into consideration in this study.

Sampling spots I and II were situated in the *Ch. plumosus* + *P. hammoniensis* community; III — in *Chironomus* sp. and *D. polymorpha* communities; IV — in the *L. isoporus* + *U. uncinata* community (Fig.).

By means of the mean standing stock and individual weight, the production of 8 chironomid, 3 oligochaete and 1 mollusc species (*Dreissena polymorpha*) was estimated (Table 1).

Table 1
Таблица 1

Production (P , g/m², live weight) and P/B ratios of macrozoobenthos in Lake Peipsi.
 B_{\max} — the maximal standing stock. $(P/B)_k$ — cohort P/B
Продукция (P , г/м², живой вес) и отношения P/B макрозообентоса в Чудском озере.
 B_{\max} — максимальная биомасса. $(P/B)_k$ — P/B когорты

Parts of benthal and species Части бентали и виды	V 1984 — V 1985				V 1985 — V 1986		
	P	P/B	P/B_{\max}	$(P/B)_k$	P	P/B	P/B_{\max}
I Macrozoobenthos without large molluscs							
Кормовой макрозообентос							
Higher sublittoral							
Верхняя сублитораль							
<i>Stictochironomus histrio</i>	0.97	3.3	1.6	3.3	1.29	5.7	1.2
<i>Cryptochironomus redekei</i>	0.85	4.0	0.9	—	0.51	3.6	1.7
<i>Cladotanytarsus mancus</i>	0.37	8.3	1.1	2.4; 5.8	0.26	6.2	0.5
<i>Monodiamesa bathyphila</i>	0.30	3.3	1.3	—	0.04	1.0	0.15
<i>Lamprodrilus isoporus</i>	4.26	2.5	1.6	3.2	17.59	4.8	2.2
<i>Uncinaiis uncinata</i>	0.19	5.4	0.5	—	0.78	4.5	0.2
Others — Остальные	8.08	—	—	—	4.36	—	—
Total — Всего	15.02	—	—	—	24.83	—	—
Lower sublittoral							
Нижняя сублитораль							
<i>Chironomus</i> sp.	43.36	4.3	1.4	4.9	9.57	2.5	0.9
Others — Остальные	9.49	—	—	—	9.27	—	—
Total — Всего	52.85	—	—	—	18.84	—	—
Profundal — Профундаль							
<i>Chironomus plumosus</i>	30.37	1.9	1.35	1.75	9.10	0.4	0.35
<i>Einfeldia carbonaria</i>	0.30	2.5	0.5	2.75	0.91	5.9	1.7
<i>Procladius choreus</i>	0.23	1.1	0.5	—	0.23	1.3	0.65
<i>Potamothrix hammoniensis</i>	3.31	1.2	0.6	—	3.05	0.9	0.3
Others — Остальные	0.86	—	—	—	1.31	—	—
Total — Всего	35.07	—	—	—	14.60	—	—
Total — average for the whole lake							
Всего — средневзвешенное							
g/m ² — г/м ²	40.80	2.4	—	—	18.37	1.5	—
kJ/m ² — кДж/м ²	111.1	—	—	—	53.0	—	—
Tons — Тонны	109000	—	—	—	49000	—	—
II Large molluscs (average for the whole lake)							
Крупные моллюски							
(средневзвешенное значение)							
g/m ² — г/м ²	200	—	—	—	156	0.5	—
kJ/m ² — кДж/м ²	200	—	—	—	156	0.5	—
Tons — Тонны	537000	—	—	—	420000	—	—

Many chironomid species have a one-year life cycle in Lake Peipsi. *Cladotanytarsus mancus* had two generations in 1984 but only one in 1985. *Procladius choreus*, *Cryptochironomus redekei* and *Monodiamesa bathyphila* probably have a two-year life cycle. A relatively small generation number per year causes a low annual production, and especially low P/B of chironomids. Among oligochaetes, *Lamprodrilus isoporus* and *Uncinails uncinata* have mainly an one-year life cycle, whereas the individuals of *Potamothrix hammoniensis* and bivalve mollusc *Dreissena polymorpha* live for several years.

Without considering large molluscs, *Chironomus* larvae formed the main part of macrozoobenthos production. They dominated in the profundal (*Ch. plumosus*) as well as in the lower sublittoral (*Chironomus* sp.). The contribution of the other chironomids and oligochaetes was considerably smaller. In spite of that, the latter constitute an important food chain component, especially for invertebrate predators, but also for fish during the emergence period of *Chironomus*.

In the higher sublittoral where *Chironomus* is lacking *Lamprodrilus isoporus* had the highest annual production.

The most intensive growth rate for most chironomids and oligochaetes was observed during complete water circulations (especially in October–November), but not during highest water temperatures (July–August).

The production of other fine macrozoobenthos is less considerable: while chironomid larvae formed 70% and oligochaetes 20% of the total production, the share of small molluscs and all other animals was only 10% (mean data of two years) (Table 1).

As compared with literature data (about 100 publications not included in the list) on other lakes, reservoirs, rivers, springs and ponds, almost all main species in Lake Peipsi had lower P/B, P/B_{\max} and cohort P/B ratios. The reasons may lie in relatively constant conditions and low near-bottom temperature (on the average +12.5°C from May to November).

Dreissena polymorpha and other scarce large molluscs (*Unionidae*, *Viviparus* sp. etc.) are treated separately in this study because of the inability of fishes to consume them. However, big roaches have been reported to eat *Dreissena* shells as long as 10 mm (Антипова, 1982).

The average standing stock of *Dreissena* for Lake Peipsi (according to the data from sampling spot III) amounted to 200 g/m² in 1984–1985, and 156 g/m² in 1985–1986 (live weight). V. Timm (unpublished data) estimated the same value for the whole Lake Peipsi-Pihkva during 1985–1988 as 583 g/m². In any case, the standing stock and weight production of *Dreissena* considerably exceeds the corresponding values of finer zoobenthos. Because of the low energetic value of molluscs in comparison with chironomids and oligochaetes this difference appears less noticeable in energy units.

Using the non-parametric bootstrap method (Efron, Tibshirani, 1986), 5 more representative cohorts of benthic animals were chosen for estimating the production and P/B standard errors. The computation program was made by T. Oja (Tartu State University). The mean standard error of the cohort production formed 8% of the mean production, the standard error of P/B — 23% of P/B. The estimation accuracy obtained may be regarded satisfactory; however, in the case of rarer animals it will doubtless be lower.

Due to their insignificance predatory invertebrate (*Procladius*, *Cryptochironomus*, leeches) rations were not taken into consideration when calculating the production of communities. The most productive benthic zones (resp. communities) were the profundal and the lower sublittoral in 1984–1985, and the higher sublittoral in 1985–1986 (Table 1). Two observation years (May 1984 — May 1985 and May 1985 — May 1986) gave the

following results: in the first year the mean standing stock for the whole lake was 17.2 and production 40.8 g/m² (live weight), in the second year 12.4 and 18.4 g/m², respectively. In summer 1985 the majority of *Chirono-*

Table 2
Таблица 2

Production (P , kJ/m²) of macrozoobenthos without large molluscs in lakes and reservoirs (from literature data). * — without ration of invertebrate predators, ** — calculated from dry weight data, *** — average of several years, **** — with meiobenthos and large molluscs

Продукция (P , кДж/м²) кормового макрозообентоса в разных озерах и водохранилищах по литературным данным. * — без рациона беспозвоночных хищников, ** — вычислено из сухого веса, *** — многолетнее среднее, **** — вместе с мейобентосом и крупными моллюсками

Water body Водоем	P	Author Автор
Leven (Scotland)	710.6	Charles et al., 1974
Kievskoye	623.7*	Gak et al., 1972
Marion (Canada)	317.7**	Hall, Hyatt, 1974
Biwa (Japan)	7.1	Hiro, Sato, 1975
Tatsu-numa (Japan)	62.3	Inoue et al., 1975
Ontario, Bay of Quinte (Canada)	1060	Johnson, Brinkhurst, 1971
Esrom (Denmark)	431.4	Jónasson, 1972
Mývatn (Iceland)	877.8	Jónasson, 1972
Mikolajskie (Poland)	169.3	Kajak, Dusoge, 1975
Taltowisko (Poland)	424.3	Kajak, Dusoge, 1975
Sniardwy (Poland)	177.2	Kajak, Dusoge, 1976
Kurazhkovskoye	11.8	Pidgaiko et al., 1972
Pääjärvi (Finland)	80.3****	Sarvala, 1978
Mirror (USA)	278.0****	Strayer, Likens, 1986
Manitoba (Canada)	140.4	Tudorancea et al., 1979
Drivyaty	13.0	Winberg, 1970
Narotsh	42.2	Winberg, et al., 1972
Myastro	4.6	Winberg, et al., 1972
Zelenetskoye	7.9*	Алимов, 1975
Krivoye	11.5*	Алимов, 1975
Krugloye	4.2*	Алимов, 1975
Shutshye	94.5*	Алимов et al., 1986
"	71.1*	Алимов et al., 1986
Onezhskoye (Bay of Bolshoye Onego)	81.2*	Алимов et al., 1982
Pihkva	300.7	Антипова, 1982
Peipsi	196.5	Антипова, 1982
Gorkovskoye	66.2	Волков, 1979
Tsherepovetskoye lake part	73.7***	Выголова, 1979
river part	20.9	Выголова, 1979
Narotsh	38.1	Гаврилов, 1985
Myastro	54.0	Гаврилов, 1985
Batorino	12.2	Гаврилов, 1985
Krasnoye	40.5*	Кузьменко, 1976
Ilmen	174.9	Лукьянова, 1974
Tsimlyanskoye	1647*	Мирошниченко, 1984
Vodlozerskoye	68.1*	Новосельцев, 1981
Ivanovskoye	71.5*	Пидгайко, 1978
Uglitshskoye	395.8*	Пидгайко, 1978
Rybinskoye	218.2*	Пидгайко, 1978
Gorkovskoye	303.5*	Пидгайко, 1978
Kuybyshevskoye	1047*	Пидгайко, 1978
Saratovskoye	1283*	Пидгайко, 1978
Volgogradskoye	513.3*	Пидгайко, 1978
Kharbey	10.5*	Попова, 1976
Tshalpan	147.0	Скопцов, 1976
Utshinskoye	52.3**	Соколова, 1980
Latsha	95.0	Фадеева, 1981
Kara-Kul	65.2*	Хусайнова et al., 1973

mus plumosus larvae did not pupate and remained in the lake. Therefore, the production of the next generation failed.

As compared with literature data (Table 2), the macrozoobenthos production (without large molluscs) of Lake Peipsi (111 and 53 kJ/m² in different years) proved on a medium or high level among lakes of similar latitudes. However, the value estimated by L. F. Antipova (Антипова, 1982) for 1979, exceeds the production determined in this study for 1984—1985 almost two times, and the production for 1985—1986 four times. The difference is probably caused by a different estimation of the number of generations of large chironomids per year (1 in this study in contrast to 2 for 1979), and by yearly fluctuations.

The macrozoobenthos production of several northern lakes (Krivoye, Krugloye, Zelenetskoye, Kharbey) is lower than in Lake Peipsi. On the contrary, a number of values from the reservoirs of the USSR and several water-bodies of other countries exceed the latter value (Table 2).

Unlike the production, the standing stock of macrozoobenthos in Lake Peipsi exceeds the corresponding values of most large lakes and/or reservoirs of the Soviet Union and neighbouring countries (Баканов, 1985; Тимм et al., 1982).

A relatively high fish productivity in Lake Peipsi is due to the combination of the high trophic level and favourable oxygen conditions. The yield of industrial fish for the whole Lake Peipsi-Pihkva formed 9850 tons (27.6 kg/ha) in 1984 and 7860 tons (22.0 kg/ha) in 1985. The share of benthophagous fishes (bream, whitefish, large roach; ruff and other fine fishes) formed 30% of the whole catch in 1984 and 40% in 1985. However, the macrozoobenthos production (without large molluscs) in Lake Peipsi exceeded the corresponding fish catch values in 1984—1985 49 times and in 1985—1986 21 times. This difference is more noticeable when we take into consideration that the group of fine fishes includes, besides benthivores, also planktivores (young perch and roach) which are not distinguished in official statistics.

The author's data support Antipova's supposition that the increment of the bream population in Lake Peipsi-Pihkva is not limited by macrozoobenthos but by zooplankton for young individuals (Антипова, 1986). Moreover, the whole population of benthophagous fishes cannot essentially affect the macrozoobenthos production.

If eutrophication continues, worsening oxygen conditions in the sublittoral and the disappearance of oxygen from the profundal are predicted (particularly in winter). As a result, macrobenthic species will also disappear, except for the most resistant ones (*Tubificidae*, *Chironomus plumosus*, *Procladius* sp.). The total macrozoobenthos production will, in all likelihood, not decrease, but benthic food will become less attainable for fish predators.

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MAKROZOOBENTOSE PRODUKTSIOON PEIPSI JÄRVES

Peipsi järve põhjaloomad kuuluvad nelja suuremasse kooslusse. Makrozoobentose produktsiooni on hinnatud kasvu hetkkiiruse meetodil aastail 1984—1986 võetud proovide põhjal. Kirjanduse andmetega võrreldes osutus produktsiooni ja keskmise biomassi suhe (kasvukiirus massiühiku kohta) enamikul uuritud liikidest madalaks. Produktsiooni absoluutväärtuse poolest on Peipsi võrreldav muude samal laiusel asuvate järvedega.

Peipsi kõige suurema biomassi ja produktsiooniga põhjaloom on rändkarp, keda kalad peaaegu ei söö. Ka teiste loomade produktsiooni ei suuda nad märgatavalt amendada.

Henn TIMM

ПРОДУКЦИЯ МАКРОЗООБЕНТОСА В ЧУДСКОМ ОЗЕРЕ

Методом суммы прироста особей изучена продукция макрозообентоса в 4 сообществах. Отношение продукции к средней биомассе у животных в Чудском озере относительно низкое, а продукция всего озера, по сравнению с другими водоемами — средняя. Продукция кормового макрозообентоса и крупных моллюсков явно недоиспользуется бентосоядными рыбами.