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THE EFFECT OF SAMPLING FREQUENCY AND THE METHOD OF ASSESSMENT ON THE PRODUCTION VALUES OBTAINED FOR SEVERAL ZOOPLANKTON SPECIES

(Ekol. Pol. 18: 539–557). Together with a decreasing sampling frequency the variability of calculated values of production and biomass of three species (*Eudiaptomus graciloides, Daphnia cucullata, Keratella cochlearis*) increase in comparise to the value obtained on the basis of very frequently taken samples, i.e. everyday. Especially great deviations are noticed, when the sampling interval is longer than 6 days. Assessments of production and biomass on the basis of the mean parameters for the given sampling interval give less variable values as compared with the values calculated on the basis of initial parameters. An effect of the character of population dynamics on the relation „calculated production values - sampling frequency" was noticed. The production values of rotifers calculated according to the three different methods were compared.

The chief problem in production assessment is the reliability of basic parameters such as number of individuals, their fecundity, age and size distribution in population estimated from the samples taken in the habitat, and the life span usually estimated experimentally. The great seasonal variation of these parameters in natural conditions, which is typical for zooplankton species, allows to suspect that calculating the production on the basis of optionally frequently taken samples and for optionally long intervals may result in errors regardless to the accepted method of assessment.

The subject investigated here is the effect of sampling frequency on the calculated values of production and its indicators. The values obtained for increasing sampling intervals are compared to the value obtained on the basis of everyday sampling, that is with the sum of the production values calculated for each successive day. It is assumed that the latter value is the closest one – in conditions of applied sampling technique and method of assessment – to the real value of production of the examined species in the study period, as it is the most faithful recording of their natural variation in time in the habitat.

Furthermore, the values of rotifer production calculated by different methods and the production values of all analysed species calculated by two different modifications of the applied methods were compared.

Three common and abundant species from three zooplankton groups were chosen for the investigations: a copepod *Eudiaptomus graciloides* Lilljeborg, a cladoceran *Daphnia cucullata* Sars and a rotifer *Keratella cochlearis* (Gosse), which differ as to the development rate and life span.

I. METHODS OF ASSESSMENT AND THE PARAMETERS APPLIED FOR PRODUCTION CALCULATIONS

The crustacean production was estimated by a method of Vinberg, Pečen, Šuškina (1965) and Vinberg (1968), in which the calculation is based on the growth rate, daily weight increments of respective stages of the species and on the numbers of these stages in the habitat[1].

According to this method the population production (P_{WT_I}) of the investigated species for the interval between the successive samples (T_I) is expressed by the formula:

$$P_{WT_I} = \left[\frac{N_e \cdot W_e}{t_e} + \frac{N_I \cdot \Delta W_I}{t_I} + \frac{N_{II} \cdot \Delta W_{II}}{t_{II}} \right] \cdot T_I, \tag{1}$$

where:

P_{WT_I} – production in units of weight per volume unit of the habitat (e.g. in mg/m^3) and for a period equal T_I, in days;

N_e, N_I, N_{II} ... number of eggs (N_e) and individuals in successive distinguished developmental stages (N_I, N_{II}), i.e. nauplii and copepodits in the case of *Copepoda* or juvenile and adult individuals in *Cladocera*, expressed by the number of individuals/m^3;

W_e, ΔW_I, ΔW_{II} – total weight increment of individuals in respective stages in mg. This is the difference between the initial weight of the given stage and the initial weight of the following stage. It was assumed that

[1] A detail explanation and discussion of the premises involved in this method, as well as more precise explanation of the symbols used here, is in a survey made by Hillbricht-Ilkowska and Patalas (1967).

the „total weight increment" of an egg (W_e), equals to the weight of the youngest nauplius or the youngest juvenile cladoceran;

t_e, t_I, t_{II} – time (in days) of egg development (t_e) and development of successive stages (t_I, t_{II}) in given habitat conditions;

$\frac{\Delta W_I}{t_I}$ – designates the weight increment of the given stage for 24 hours, i.e. the weight increment per one day of its life span.

Production ($P_{W\,T}$) for the whole study period (T) (in our studies equal to 40 days) is a sum of partial production values determined for successive sampling intervals, i.e. successive days:

$$P_{W\,T(40)} = P_{W\,T_I} + P_{W\,T_{II}} + P_{W\,T_{III}} \ldots \text{ and so on} \tag{2}$$

Series of quantitative samples of crustaceans (40 samples) were taken everyday for period of 40 days from July 22 to August 30 of 1964, out from the epilimnion of Mikołajskie Lake (0–10 m). Every metre, 5 litres of water were taken (this was the capacity of sampler), filtrated and poured into one container. In each sample, 1/5 of its volume was taken for determination of the number of individuals of respective stages of *E. graciloides* (nauplii, copepodits, adults) and *D. cucullata* (juvenile forms, adults), and the number of eggs. Also measurements were made of the body length of at least fifty individuals from all stages.

The time of egg development and of the development of the stages of *D. cucullata* and *E. graciloides* were estimated according to the data obtained by Pečen (1965) and Šuškina (1964 acc. to Hillbricht-Ilkowska and Patalas 1967) where the dependence of development on temperature were taken under consideration. The temperature of epilimnion, during the period of investigations, was 18–21°C, showing a regular decrease. As the cladocerans also grow after attaining the maturity, therefore an information on the average life span of the adults is indispensable to assess correctly their production. Average life span of an adult cladoceran was calculated on the basis of measurements of the body length of young and adult individuals, assuming, that after the maturity is attained, the linear growth rate is about three times slower than the linear growth rate of the juvenile form (Węgleńska 1968 and in press, Edmondson 1971).

Thus the average life span of an adult cladoceran ($\tilde{t}_a$) is:

$$\tilde{t}_a = \frac{3\, t_j\, (\bar{L}_a - L_{o\,a})}{L_{o\bar{a}} - L_{oj}}, \tag{3}$$

where:

t_j – development time of the juvenile form;

L_{oj} – body length of the new born juvenile form (neonata);
L_{oa} – body length of the juvenile form at the moment of reaching maturity (primipara), i.e. body length of the youngest adult individual;
$\overline{L}_a$ – average body length of an adult individual.

All measurements of length were made on the individuals sampled from the habitat. Average life span of adult cladoceran was separately assessed for each successive sample. Values from 3 to 8 days were obtained.

The weights of individuals of different stages were calculated out of formulas of the relation: length – weight (Pečen 1965, Klekowski and Šuškina 1966, Hillbricht-Ilkowska and Patalas 1967), on the basis of length measurements made separately for each sample. The total weight increment of each stage was taken as a difference between the weight of an average individual in the smallest class of size of the given stage and the one in the smallest class of size of the following stage. As the total weight increment of an adult cladoceran during its life the difference between the average weight of all adult individuals in the population and the average weight of the youngest adult individuals – primiparae was taken.

The production of the rotifer *Keratella cochlearis* was assessed using three methods: Edmondson's methods (1960, 1965) of the estimation of the theoretical population size, assuming its exponential and linear growth, and Galkovskaja's method (Galkovskaja 1965, Vinberg 1968).

Both Edmondson's methods of estimating the theoretical population size base on the birth rate calculated out of the number of eggs in the habitat and the time of their development, while in Galkovskaja's method the so-called „generation time" is used, i.e. the period from the hatching of the individual till the hatching of its offspring[2], which covers the development time of an egg and the postembrional development of the individual.

Hillbricht-Ilkowska (1967) made an attempt to assess the production of this rotifer on the basis of the „exponential" method of Edmondson.

According to the above methods production, P_{NT_I}, for a sampling interval, T_I, is:

assuming an exponential growth of population

$$P_{NT_I} = (N \cdot e^{bT_I}) - N, \tag{4}$$

assuming the linear growth of population

$$P_{NT_I} = N \cdot B \cdot T_I, \tag{5}$$

according to Galkovskaja's method

[2]Detail explanation of these three methods is in the survev made by Hillbricht-Ilkowska and Patalas (1967).

$$P_{NT_I} = N \cdot \frac{1}{t_{(e+p)}} \cdot T_I, \quad (6)$$

where:

P_{NT_I} – production for the interval T_I (in days) expressed as the number of new–born individuals per volume unit (ind./l);

N – number of individuals in the habitat (ind./l);

B – birth rate; it is the quotient of the egg–female ratio in population and the time of egg development (t_e) in days, in the given thermic conditions of habitat $\left(\frac{E}{t_e}\right)$;

b = $ln(B+1)$;

e – the basis of natural logarithm;

$t_{(e+p)}$ – "generation time", i.e. the period "from egg to egg", which covers the time of egg development (t_e) and the period of postembrionic development (t_p); a value depending on temperature and obtained in the experiment| (Galkovskaja 1965).

The production for the whole study period (T), equals to 18 days in this paper, is a sum of production values calculated for each successive sampling interval:

$$P_{NT}(18) = P_{NT_I} + P_{NT_{II}} + P_{NT_{III}} \ldots \text{ and so on}$$

Differently than in a case of crustaceans, the production of rotifer population, for the purposes of this paper, is expressed by the number of individuals (P_N) and not in weight units of produced mass (P_W). This is, because in the case of this small species (about 200 μ long) as well as in the case of a majority of rotifer species the weight increments of the individual are not available as it is in the case of crustaceans. Therefore a similar method of production assessment as has been used for crustaceans is impossible. So the only methods left are those of Edmondson and Galkovskaja, described above, which give only the population increase, i.e. its production expressed in the number of individuals born in a given period.

An approximate production values expressed in the weight of produced biomass can be obtained by multiplying the population increase by the average weight of an individual in the population, thus obtaining a value, which can be compared with the production of crustaceans. However, in this paper, which compares the methods and the effect of sampling frequency, such value is not needed, and therefore it has been decided to assess the increase of the number of individuals as a population production of this species.

Quantitative samples of rotifers (18 samples) were taken everyday from June 14 to July 1, 1966 in the epilimnion of Mikołajskie Lake, in the same way as those for crustaceans. The number of individuals and eggs was counted in the 1/5–1/10 volume of whole sample, depending on the abundance of organisms.

In the study period the temperature was 18.5–21.5°C, displaying a regular decrease. For each temperature the time of egg development and „generation time" were estimated according to the dependence „development time – temperature" found by Edmondson (1965) and Galkovskaja (1965).

The results obtained for this short period of intensive investigations were compared with data on the production of *K. cochlearis* for the whole period of its occurrence in the epilimnion of Mikołajskie Lake, which was about 10 times longer, i.e. about 200 days (in 1964). These data were obtained from a series of 32 samples taken in 6–7 day intervals.

In order to find the effect of sampling frequency on the calculated production value, production (P) for the whole study period, i.e. 40 days in the case of crustaceans and 18 days in the case of rotifers, was independently calculated by summing up the „everyday" production values and the values for longer intervals obtained by appropriate eliminating of successive samples. And so, in the case of crustaceans the total production for 40 days was estimated on the basis of 3, 6 and 14 day intervals, eliminating an appropriate number of samples from a series of 40 samples; for the rotifer – for 2, 3, 6 and 9 day periods, also eliminating an appropriate number of samples from a series of 18 samples. In case of a series of samples from the whole period of occurrence of this rotifer a lower frequency was obtained by successive elimination of every second sample, or two successive ones, thus obtaining a frequency two and three times smaller than the applied one. Apart from that, both in the case of crustaceans and rotifers, the production was also assessed on the basis of one sample, which was either chosen at random or was characterized by the smallest or greatest biomass, fecundity or daily production. In each sampling frequency the production was calculated for all possible (i.e. within the investigated period) combinations of successive samples in order to be independent from a possible random result. And so, for example, when assessing the production for 3–day intervals it was calculated on the basis of the first, fourth, seventh etc. successive sample (I combination), the second, fifth, eighth etc. sample (II combination) and the third, sixth, ninth etc. sample (III combination), thus obtaining three parallel production values for the 3–day intervals sampling frequency. In each sampling frequency and in each combination of samples, apart from the production, the average biomass (crustaceans) or average numbers (rotifers) were calculated in order to find out to what extent the average biomass depends on the sampling frequency. The latter value is included in some indicators of production rate.

In all production assessments a following modification of the above calculations was also applied: in the method of assessment, which has been used up till now, the production for the given period is calculated usually on the basis of the parameters initial for this period, such as the daily weight increment, fecundity or numbers. The modification introduced in this paper is as following:

The production (P_{T_I}) for the interval between samples (T_I) may be calculated as the product of the arithmetic mean of daily production for the initial moment for this interval (T_1), and for the final moment (T_2), and the length of this interval in days, that is:

$$P_{T_I} = \left[\frac{P_{T_1} + P_{T_2}}{2}\right] \cdot T_I, \qquad (7)$$

where:

P_{T_1} – daily population production in the moment T_1;
P_{T_2} – daily population production in the moment T_2;
T_I – the length of sampling interval in days;
P_{T_I} – production for the whole sampling interval.

The above modification is based on an assumption that relatively smaller variations of the final result of the production calculations should be expected, when interpolating the production values, that is the daily production values of the whole population and not the parameters involved in this calculation. Further, in this paper the modification of production calculation acc. to initial parameters will be called "variant *a*", and the already discussed modification (formula No. 7) – "variant *b*".

Therefore summing up, the subject under consideration in this paper are the changes of production values, average biomass or numbers depending on: 1) sampling frequency (i.e. the length of the interval between samplings) and 2) combinations of samples in each sampling frequency variant. The changes in production are being analysed parallel, while applying the variants *a* and *b* of production calculations. The basis for comparison is the production and biomass values obtained from the most frequently taken samples. Additionally in case of rotifers three methods of production assessment were compared.

II. RESULTS

The study period (40 days, from mid–July to the end of August) is 1/4 for the cladoceran and 1/5 for the copepod of their whole period of occurrence in the investigated lake. The period of 18 days (second fortnight of June) is 1/10 of the period of occurrence of the investigated rotifer species.

In the chosen periods the character of population dynamics of the three investigated species is different (Fig. 1–3). The copepod's biomass, however greatly variable[3], does not display a steady increase or decrease in the study period, and the daily production of its population has relatively constant values

[3]Relatively high variation of the copepod's biomass during the study period is connected with a great differentiation in the age composition of population; the numbers of nauplii and copepodits are very variable.

(Fig. 1) as opposed to the cladoceran, the changes of which in biomass and daily production are characterized by a directional decrease (Fig. 2). Numbers and fecundity of the rotifer population also display a variable course in the period chosen for intensive investigations (Fig. 3).

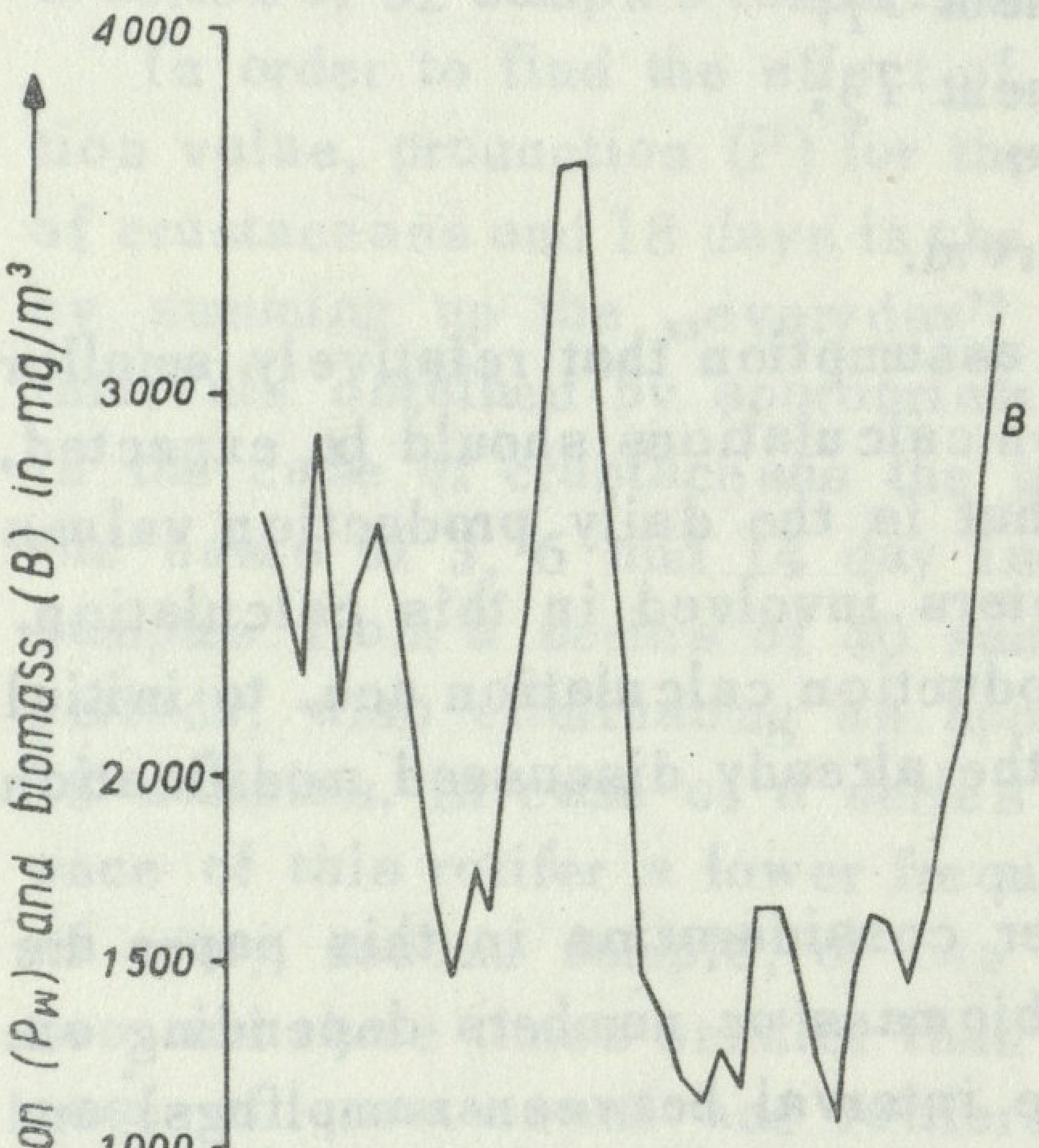

Fig. 1. Daily production (P_W) and biomass (B) of the copepod *Eudiaptomus graciloides* in the epilimnion of Mikołajskie Lake on the basis of everyday samples (July 22 – August 30, 1966)

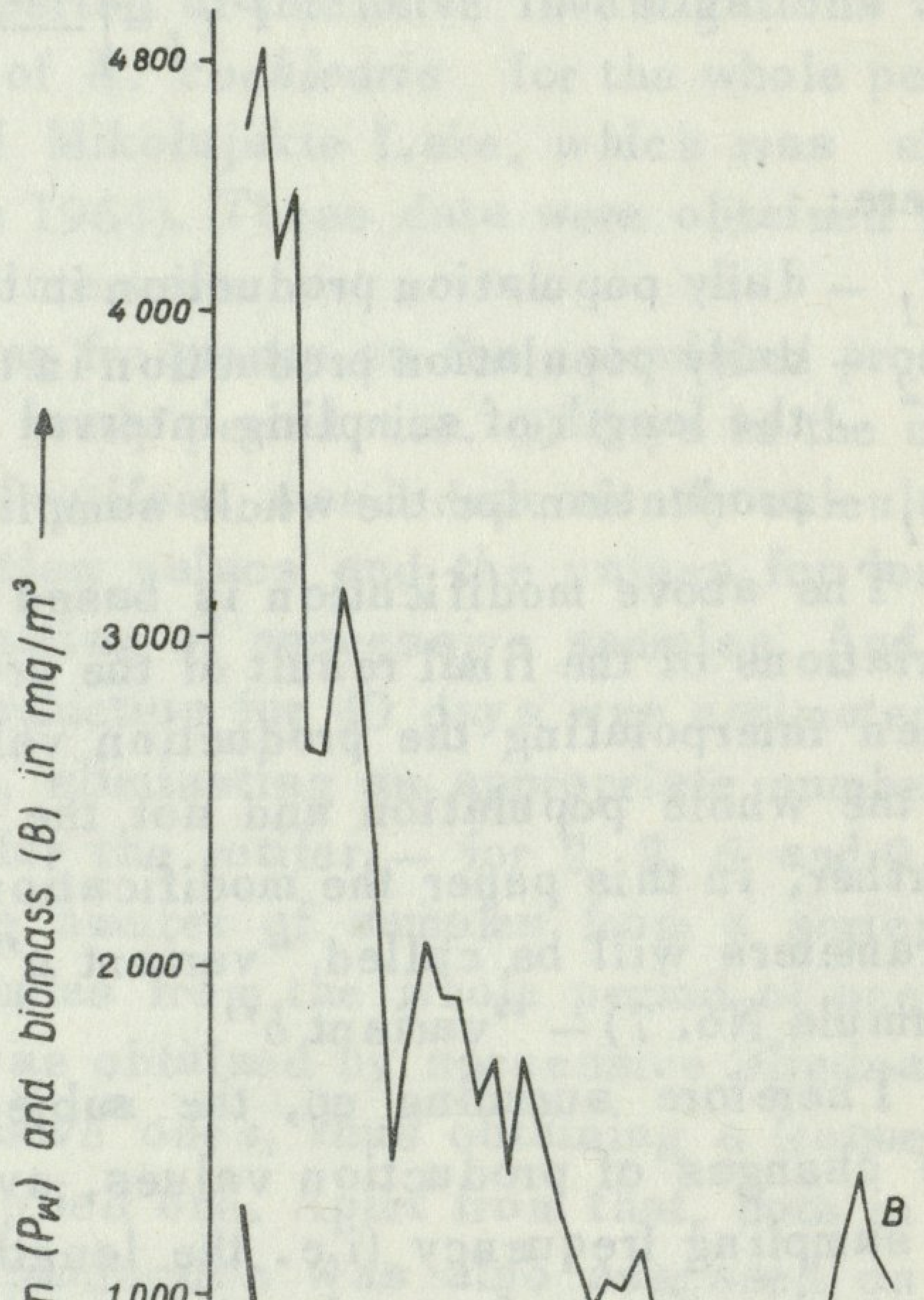

Fig. 2. Daily production (P_W) and biomass (B) of the cladoceran *Daphnia cucullata* in the epilimnion of Mikołajskie Lake on the basis of everyday samples (July 22 – August 30, 1966)

The production values (P_{WT}) of two crustacean species for the study period (equal to 40 days), calculated as the sum of daily productions (formula No. 2), were accordingly: for the cladoceran – 13.47 g/m³, for the copepod – 8.65 g/m³. The production values (P_{NT}) of the rotifer obtained by three different methods (formulas No. 3–5) were: for the short-time series – 762 ind./l (formulas No. 3 and 4 – Edmondson's methods) and 1,205 ind./l (formula No. 5 – Galkovskaja's method), and for the long-time series accordingly – 7,400, 4,300 and 5,000 ind./l. The identity of the result obtained when

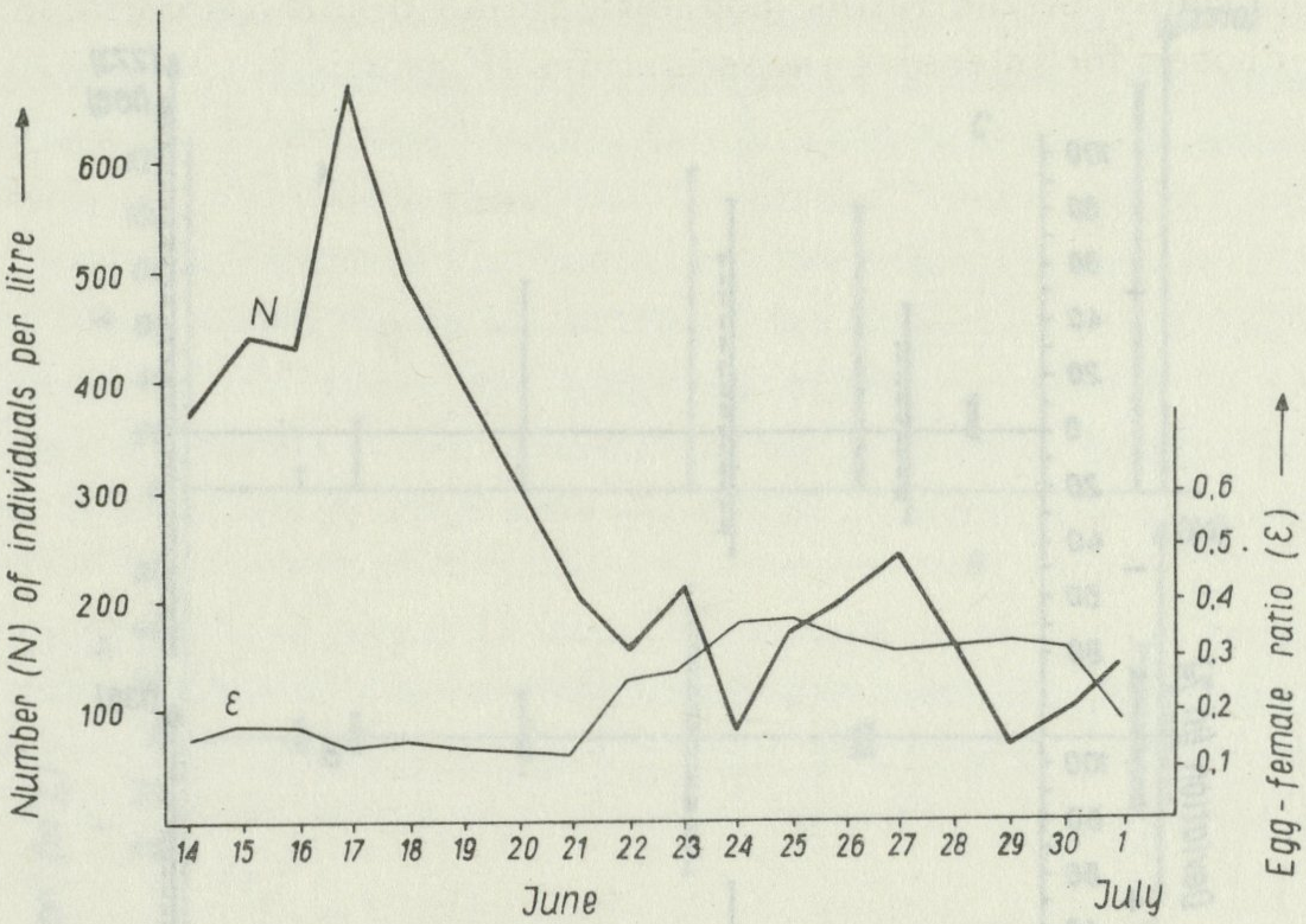

Fig. 3. Numbers (*N*) and fecundity (ε – egg-female ratio) of the rotifer *Keratella cochlearis* in the epilimnion of Mikołajskie Lake on the basis of everyday samples (June 14 – July 1, 1966)

summing up the successive daily production values calculated with the "linear" and "exponential" methods of Edmondson is obvious as the daily population increase calculated with the formulas No. 3 and 4 is identical.

The above production values obtained on the basis of the everyday taken samples display the gradual changes with the decrease of sampling frequency: the longer time interval between sampling – the greater deviation from the "everyday" value (Fig. 4 and 5). It concerns the all three analysed species, and the results obtained by all methods and modifications.

In the case of crustaceans the relatively smallest deviations from the production value calculated on the basis of everyday samples is observed for 3-day sampling intervals (cladoceran – 14%, copepod – 7%) (Fig. 4). While at further decreasing of sampling frequency from 6 to 14 days the deviations from the "everyday" value increased for the cladoceran to 80%, and for the copepod – to 60%, and on the basis of one sample taken during the study period they reached accordingly even 270% and 160% (Fig. 4).

The application of variant *b* in production calculation (formula No. 7) gives a definitely smaller range of variation, i.e. smaller deviation in successive sampling frequency (Fig. 4); the variations in production values calculated on the basis of one sample chosen at random during the study period were two times smaller than in the variant *a*.

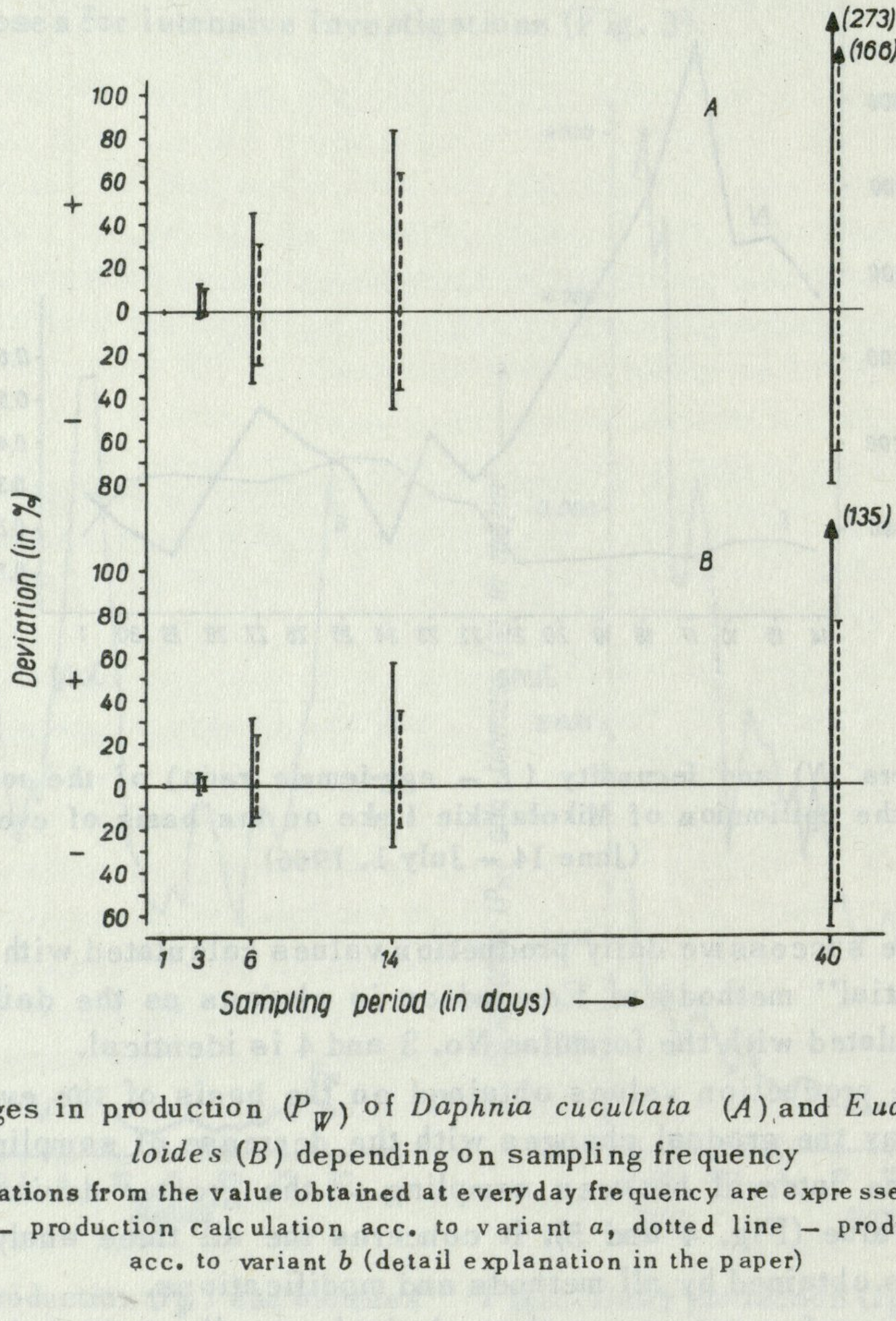

Fig. 4. Changes in production (P_W) of *Daphnia cucullata* (*A*) and *Eudiaptomus graciloides* (*B*) depending on sampling frequency

The deviations from the value obtained at everyday frequency are expressed in per cent

Constant line – production calculation acc. to variant *a*, dotted line – production calculation acc. to variant *b* (detail explanation in the paper)

In the case of rotifer, where besides the introduced modification (variant *b*) three different methods of production calculation were applied, the greatest deviations, that means – the steady increase of the production values together with the increase of the sampling interval, takes place when using the "exponential" method of Edmondson. For example, when the sampling interval is 18 days, the production value calculated by this method is about 231 times greater than the value obtained by summing up the everyday values. This has also been confirmed in the long-time series data (Fig. 5)[4]. It is obvious because

[4] In this method only variant *a* was applied, because at an identical daily production estimated by this method and the "linear" one, calculations of production for several day time intervals acc. to variant *b* give identical results.

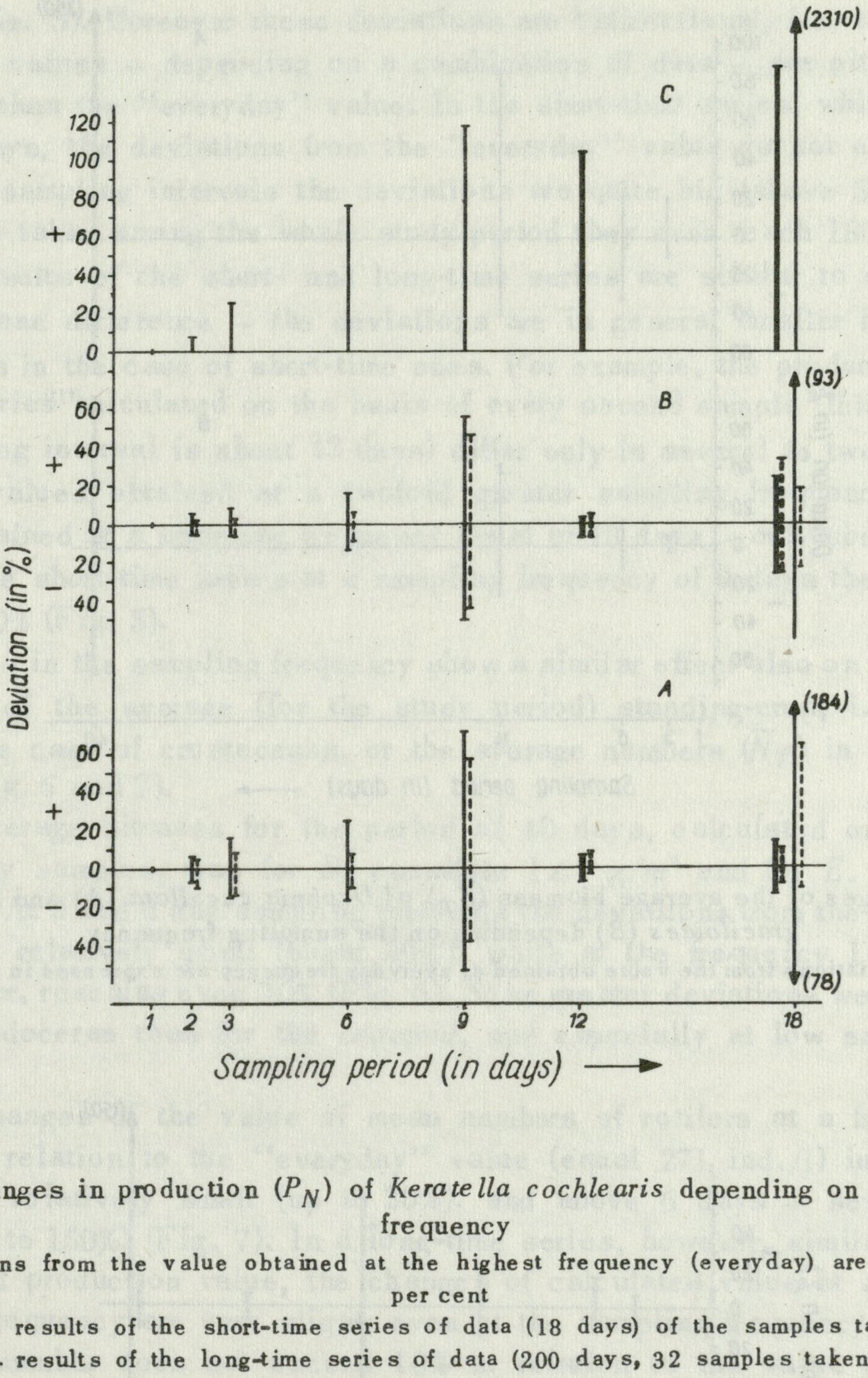

Fig. 5. Changes in production (P_N) of *Keratella cochlearis* depending on the sampling frequency

The deviations from the value obtained at the highest frequency (everyday) are expressed in per cent

Thin lines – results of the short-time series of data (18 days) of the samples taken everyday, thick lines – results of the long-time series of data (200 days, 32 samples taken every 6 days)
Constant line – production calculation acc. to variant *a*, dotted line – production calculation acc. to variant *b* (detail explanation in the paper)

A – production assessment acc. to Galkovskaja's method, *B* – production assessment acc. to Edmondson's "linear" method, *C* – production assessment acc. to Edmondson's "exponential" method

according to this method (formula No. 4) both the birth rate of the population (b) and the sampling interval (T_I) are in the exponent. Opposite to this method the two remaining ones ("linear" method and Galkovskaja's method) give

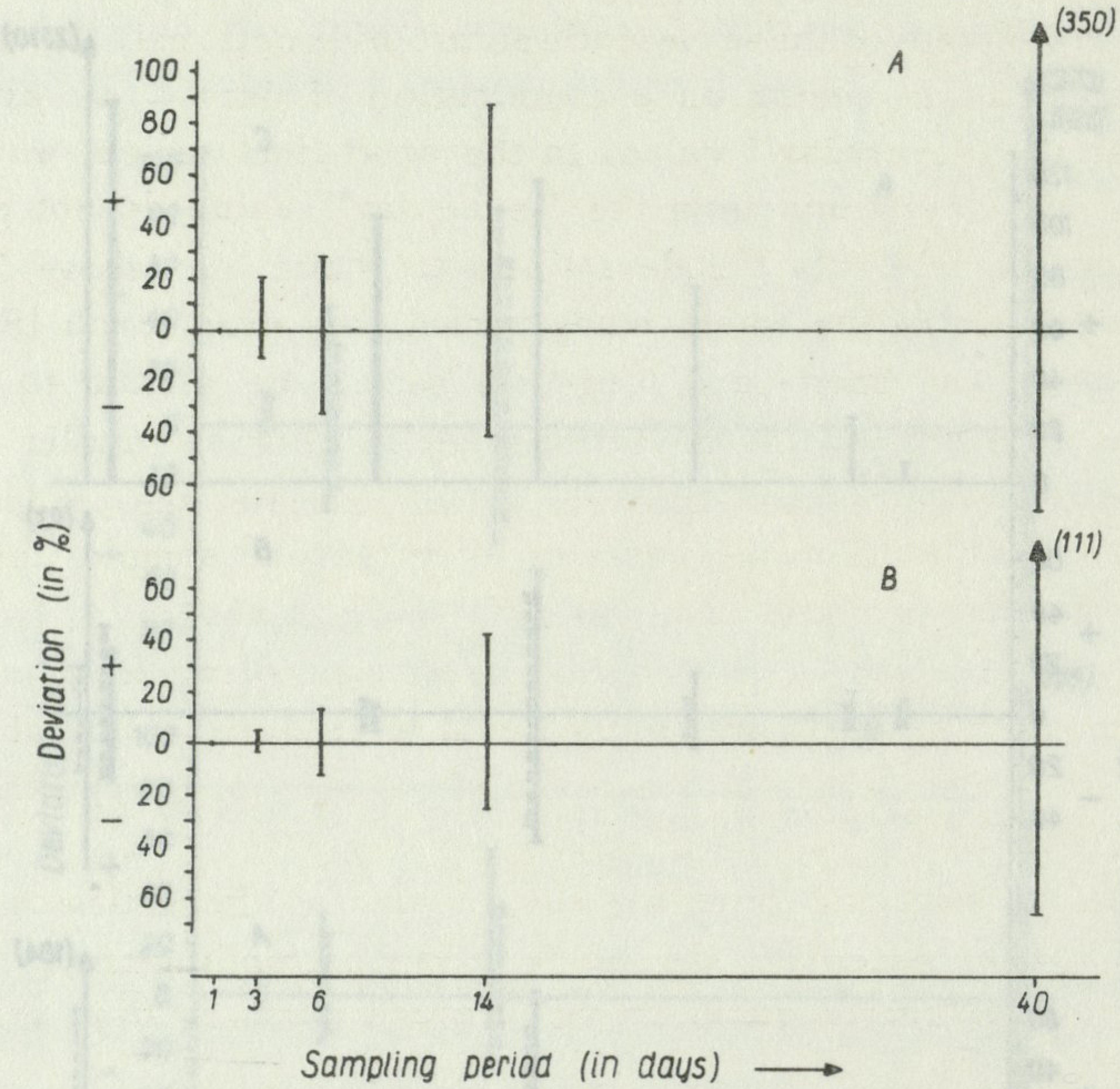

Fig. 6. Changes of the average biomass ($\overline{B}_T$) of *Daphnia cucullata* (*A*) and *Eudiaptomus graciloides* (*B*) depending on the sampling frequency

The deviations from the value obtained at everyday frequency are expressed in per cent

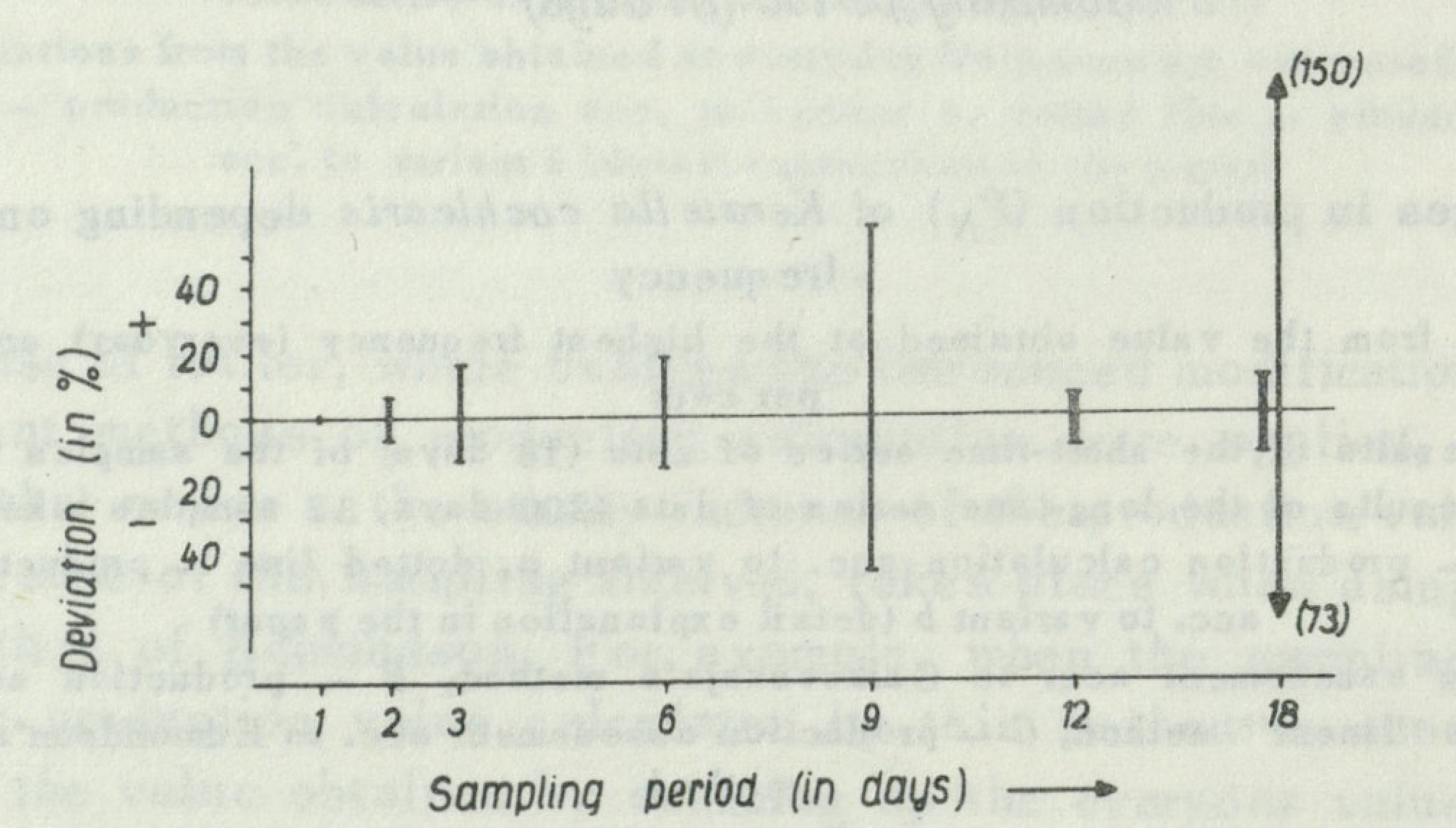

Fig. 7. Changes of the average biomass ($\overline{N}_T$) of *Keratella cochlearis* depending on the sampling frequency

The deviations from the value obtained at everyday frequency are expressed in per cent

Thin lines – results of the short-time series of data (18 days) of the samples taken everyday, thick lines – results of the long-time series of data (200 days, 32 samples taken every 6 days) production values, the deviations of which from the "everyday" value – however increasing while the sampling frequency decreases – are several times smaller (Fig. 5). Moreover these deviations are bidirectional, i.e. the obtained production values – depending on a combination of data – are either smaller or greater than the "everyday" value. In the short-time series, while sampling every 6 days, the deviations from the "everyday" value do not exceed 20%, at greater sampling intervals the deviations are quite big (above 50%), and at one sample taken during the whole study period they even reach 180% (Fig. 5).

The results of the short- and long-time series are similar to each other with only one difference – the deviations are in general smaller in long-time series than in the case of short-time ones. For example, the production values for this series calculated on the basis of every second sample (this means that the sampling interval is about 12 days) differ only in several to twenty per cent from the values obtained at a twofold greater sampling frequency, and the values obtained at a sampling frequency equal to 18 days – only obout 20–30 %. While in the short-time series at a sampling frequency of 9 days the deviations were 50–70% (Fig. 5).

Changes in the sampling frequency show a similar effect also on the calculated value of the average (for the study period) standing-crop, i.e. biomass ($\bar{B}_T$) in the case of crustaceans, or the average numbers ($\bar{N}_T$) in the case of rotifers (Fig. 6 and 7).

The average biomass for the period of 40 days, calculated on the basis of everyday samples, was for *D. cucullata* 1.69 g/m^3 and for *E. graciloides* 2.01 g/m^3. At 3 and 6 day sampling intervals the deviations from the "everyday" value were relatively small (about 30%), while at the frequency 14 days they were greater, reaching even 90% (Fig. 6). Some greater deviations were observed for the cladoceran than for the copepod, and especially at low sampling frequency.

The changes of the value of mean numbers of rotifers at a frequency of 6 days in relation to the "everyday" value (equal 271 ind./l) in short-time series are relatively small (up to 20%), and above 6 days – several times greater (up to 150%) (Fig. 7). In a long-time series, however, similarily as in the case of production value, the changes of calculated value at a decreased sampling frequency are very slight; even at the sampling frequency of 18 days the mean number does not exceed 10% in relation to the value obtained on the basis of three times more frequently taken samples (155 ind./l) (Fig. 7).

As it can be seen the effect of sampling frequency on the value of production and average biomass is smaller in the case of copepod than in the case of the cladoceran, and for *K. cochlearis* – is smaller in the long-time series than in the short-time one.

The reasons for the above differences between species and series of investigations regarding the dependences of production and biomass calculated values on the sampling frequency seem to be as following:

In the case of crustaceans the changes of the calculated production value may be connected with the difference in the length of life span of both species. The development time of *D. cucullata* within the temperature range 18–21°C is three times shorter than that of *E. graciloides*, and it seems likely that the production of a population with a shorter development time depends more on the sampling frequency. However, it cannot be excluded that the above mentioned differences between both crustacean species depend also on the character of the population dynamics in the study period. Namely, in the chosen 40-day study period the dynamics of copepod's biomass, however displaying quite big fluctuations, does not undergo any directional changes in contrast with the biomass of cladoceran, which has the great values at the beginning and a steady decrease towards the end of the study period. Thus, in this latter situation the decrease of sampling frequency may have a greater effect on the result of the calculation. In the similar way one can also explain the differences between the production and mean number values of the rotifer in a short-time series (18 days) and in the long-time series (200 days). During the sampling period in the short-time series directional changes in number and fecundity of this species (great number at the beginning and steady decrease to the end of the period), and in the long-time series the whole period of the variable occurrence of this species has been investigated, i.e. all its increases and decreases in numbers. Thus in such situation decreasing of the sampling frequency has a less deforming effect on the final production values calculated for the whole period of investigations. Furthermore, it seems that the different number of samples in the short-time series (18 samples) and in the long-time series (32 samples) is of no special importance here as for to what extent the given series of successive samples represents the variable character of occurrence, is of greater importance.

In order to compare the production of organisms varying as to their size and life span the indicators informing about their production rate are often used. One of them is the period of the turnover time of biomass ($\bar{T}_B$) or individuals ($\bar{T}_N$) understood as the time in which the production equals the mean biomass, and in the case of individuals – it is the mean life span of the individual (Petrusewicz 1966, 1967, Hillbricht-Ilkowska and Patalas 1967). The basis for calculation of these indicators acc. to the formulas below are the values of production and mean biomass or numbers:

$$\bar{T}_B = T \cdot \frac{B_T}{P_{WT}}, \tag{8}$$

$$\bar{T}_N = T \cdot \frac{N_T}{P_{NT}}, \tag{9}$$

The variation range of the turnover time of biomass of *Daphnia cucullata* and *Eudiaptomus graciloides* depending on the sampling frequency and the variant of production calculation

The turnover time of biomass was calculated acc. to the formula No. 8

Tab. I

Frequency (in days)	Variant*	Turnover time of biomass (in days)	
		Daphnia cucullata	*Eudiaptomus graciloides*
1	*a***	5.0	9.3
3	*a* *b*	4.5–5.5 4.5–5.6	8.5–9.8 8.9–9.5
6	*a* b	4.0–6.0 4.2–6.7	7.4–11.4 7.6–10.5
14	*a* *b*	3.8–6.4 3.1–7.5	6.3–14.8 6.6–12.5
40	*a* *b*	3.0–8.5 2.5–9.0	4.8–16.0 2.9–16.6

*Explanation in the paper.

**At 1-day sampling frequency variant *b* gives the same results as variant *a*.

The absolute values of production and biomass, as it has been already shown, undergo a directional variation depending on the sampling frequency during the period of investigations. Therefore a question should be answer to what extent the sampling frequency affects the values of production rate as the above mentioned production and biomass values are involved in the calculation of the production rate.

The turnover time of biomass ($\bar{T}_B$) calculated on the basis of everyday samples is 5.0 days for *D. cucullata*, and 9.3 days for *E. graciloides* (Tab. I). As the time interval between samplings increases, the values of turnover times of biomass become more variable in comparison with the "everyday" value. At a frequency higher than 14 days the value of the turnover time of biomass essentially differs from the "everyday" value (1.5–3 times).

The turnover time of *K. cochlearis* individuals calculated on the basis of production values obtained by the "exponential" method of Edmondson shows a decreasing value as the interval between samplings increases (Tab. II). At a frequency about 18 days in both series of investigations it may obtain values even smaller than one day. This is the consequence of artificially increased production values obtained by this method at longer sampling intervals (Fig. 4). As the frequency of investigations decreases the turnover times calculated on the basis of the two remaining methods becomes more variable (greater or smaller) as compared with the "everyday" value (Tab.

The variation range of the turnover of individuals *Keratella cochlearis* for the short-time (18 days, 18 samples) and long-time (200 days, 32 samples) series of investigations depending on the methods of production assessment, sampling frequency and the variant of production calculation

The turnover time of individuals was calculated acc. to the formula No. 9

Tab. II

Series	Frequency (in days) and calculation variants*		Turnover time of individuals (in days) at a production assessment acc. to methods: Galkovskaja's	Edmondson's "linear"	Edmondson's "exponential"***
Short-time 18 samples)	1	*a***	4.0	6.4	6.4
	2	*a*	4.0–4.1	6.1–6.4	5.0–5.9
		b	4.1–4.3	6.5–6.6	
	3	*a*	4.0–4.1	6.0–6.8	5.0–5.8
		b	4.1–4.3	5.9–7.1	
	6	*a*	3.8–4.2	5.9–7.0	3.2–4.5
		b	3.4–4.9	5.6–7.8	
	9	*a*	3.7–4.5	5.5–8.3	4.0–9.1
		b	3.1–5.6	5.3–7.9	
	18	*a*	2.9–5.2	3.3–10.2	0.2–4.2
		b	3.7–4.4	5.3–8.0	
Long-time (32 samples)	6	*a*	6.1	7.6	4.1
		b	5.9	6.9	
	12	*a*	5.9–6.0	7.2–7.8	1.9–2.3
		b	5.7–5.8	6.4–7.9	
	18	*a*	5.6–6.3	5.7–10.3	0.7–2.3
		b	5.5–6.0	5.3–9.7	

*Explanation in the paper.

**At 1–day sampling frequency variant *b* gives the same results as variant *a*.

***Variant *b* applied in the "exponential" method gives identical results with those from the "linear" method.

II). In the short-time series the values of the turnover time estimated on the basis of the sampling intervals longer than 6 days and in the long-time series – intervals longer than 12 days, differ essentially as compared with the "every-day" value (1.5–2 times).

III. SUMMING UP THE RESULTS

1. As the sampling frequency decreases (i.e. the interval between samplings increase) the values of production and average biomass (or average numbers)

and also the indicator of production rate (turnover time) differ more and more from the value obtained on the basis of frequently taken samples (everyday). This regularity is valid for the calculations obtained for *D. cucullata* and *E. graciloides* (on the basis of the method of production assessment of Vinberg) and also for the rotifer *K. cochlearis* (on the basis of three different methods), and also, when both calculation variants (*a* and *b*) are applied.

2. The values of production and biomass of crustaceans, of production and numbers of rotifers, and the turnover times obtained at a frequency greater than 6 days differed essentially from the "everyday" values (in the extreme 2–3 times). At a frequency smaller or equal 6 days the deviations from the "everyday" value did not exceed 20–30%.

3. Introduction of the variant *b* of production calculations (formula 7) results in smaller deviations from the "everyday" value in each range of sampling frequency as compared with variant *a*.

4. The values of production and biomass (or mean numbers) calculated for relatively short periods of time (in proportion to the whole period of occurrence of the given species), in which the directional changes in numbers are observed show a well-marked dependence on the sampling frequency. This was also found, when comparing the production values of the cladoceran and copepod and when comparing the production and numbers of the rotifer for a short (18 days) and long (200 days) period of time. Thus, it can be said that when the investigations are limited to short periods of time or to periods characterized by directional changes of the investigated population, the sampling frequency should be greater (i.e. the sampling intervals – shorter) than in the case, when the whole period of variable occurrence of the investigated species or community can be examined.

5. Comparing the results on rotifer production obtained by three different methods, it can be said that Edmondson's "exponential" method (formula 4) provides results with the greatest variations. One obtains a steady increase of production value as the time interval between samplings increa s, which in turn causes a steady decrease of the turnover time. At a frequency equal 2–3 weeks, the values calculated on the basis of this method are not much reliable. The results obtained with the other methods (Edmondson's "linear" method – formula 5, and Galkovskaja's method – formula 6) show similar deviations as the sampling frequency decreases. But the values calculated with the use of Galkovskaja's method, in the case of this species are usually greater than the values obtained by the "linear" method of Edmondson. This is the result of different parameters, on which the both methods are based: the actual number of eggs and their development rate in the habitat – in the first case, and in the second case – the "generation time" determined in the experiment.

The need of the methodical studies as above described was pointed out on the symposium on the methods of assessment of biomass and zooplankton production organized by the Section of Productivity of Freshwater Ecosystems, Polish Committee of the International Biological Programme, in Olsztyn, May 1965.

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WPŁYW CZĘSTOTLIWOŚCI POBIERANIA PRÓB ORAZ METODY KALKULACJI NA WYNIK OCENY PRODUKCJI NA PRZYKŁADZIE KILKU GATUNKÓW ZOOPLANKTONOWYCH

Streszczenie

Prześledzono wpływ częstotliwości pobierania prób na zmiany wartości produkcji i jej wskaźników (okres rotacji biomasy, $\overline{T}_B$ – wzór nr 8 lub osobników, T_N – wzór nr 9), średniej biomasy lub liczebności trzech gatunków zooplanktonu: wioślarki *Daphnia cucullata*, widłonoga *Eudiaptomus graciloides* i wrotka *Keratella cochlearis* w pelagialu

Jeziora Mikołajskiego. Porównywano wartości uzyskane przy różnych, wzrastających odcinkach czasu między pobieranymi ze środowiska próbami z wartością, uzyskaną na podstawie prób pobranych codziennie i stanowiącą sumę oddzielnie dla każdego dnia obliczonej produkcji i biomasy. Ponadto analizowano wartości produkcji, uzyskane w oparciu o parametry wyjściowe (ocena produkcji jako iloczynu długości okresu i produkcji dobowej, stwierdzonej na jego początku) oraz modyfykację tej metody, polegającą na ocenie produkcji jako iloczynu długości okresu i średniej produkcji dobowej stwierdzonej na początku i na końcu tego okresu (wzór nr 7). W przypadku wrotków porównano 3 metody oceny produkcji: metodę „eksponencjalną" (wzór nr 4) i „liniową" (wzór nr 5), Edmondsona (1960, 1965) oraz metodę Galkovskiej (1965) (wzór nr 6).

W wybranych do badań okresach (40 dni dla wioślarki i widłonoga, 18 dni – seria krótkotrwała i 200 dni – seria długotrwała dla wrotka) charakter zmian populacji wszystkich trzech gatunków jest różny (fig. 1–3). Biomasa widłonoga, aczkolwiek zmienna, nie wykazuje stałego wzrostu bądź spadku w okresie badawczym, a dobowa produkcja wykazuje wartości stosunkowo stałe (fig. 1). U wioślarki natomiast zmiany biomasy oraz produkcji charakteryzują się kierunkowym spadkiem (fig. 2). Liczebność i płodność populacji wrotka wykazuje również kierunkowy spadek w wybranym do badań 18–dniowym okresie (fig. 3).

Wartości produkcji i biomasy skorupiaków, produkcji i liczebności wrotka oraz okresy rotacji uzyskane przy częstotliwości większej od 6 dni różniły się istotnie od wartości „codziennych", w skrajnych przypadkach do 2–3 razy. Przy częstotliwości mniejszej lub równej 6 dniom odchylenia od wartości „codziennej" nie przekraczały 20–30% (fig. 4–7, tab. I–II). Prawidłowość ta dotyczy ocen uzyskanych dla wszystkich badanych gatunków i wszystkich stosowanych metod.

Wprowadzenie wspomnianej modyfikacji wyliczenia produkcji (wzór nr 7) daje mniejsze odchylenia od wartości „codziennej" w każdym zakresie częstotliwości pobierania prób w porównaniu do wyliczeń produkcji w oparciu o parametry wyjściowe (fig. 4–5).

Oceny produkcji i biomasy (względnie liczebności) wyliczane dla krótkich okresów (w stosunku do całego okresu występowania danego gatunku), w których obserwuje się kierunkowe zmiany liczebności badanego gatunku, wykazują wyraźną zależność od częstotliwości pobierania prób (fig. 1–7).

Porównując wyniki produkcji wrotka otrzymane trzema różnymi metodami stwierdzono, że metoda „eksponencjalna" Edmondsona daje wyniki wykazujące największą zmienność, polegającą na stałym zwiększaniu wartości produkcji w miarę wydłużania odcinka czasu między pobraniem prób, a w konsekwencji – stałe zmniejszanie okresu rotacji (fig. 5, tab. II). Wyniki otrzymane pozostałymi metodami (metodą „liniową" Edmondsona i metodą Galkovskiej) wykazują podobną zmienność w miarę zmniejszania częstotliwości pobierania prób (fig. 5, tab. II).

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