

Juta HABERMAN

## SEASONAL DYNAMICS OF PELAGIC COPEPODS OF LAKES PEIPSI-PIHKVA AND VÖRTSJÄRV

The area of Lake Võrtsjärv is 270 sq. km, the area of Lake Peipsi-Pihkva 3.550 sq. km. The latter consists of three different parts: the northern part Lake Peipsi (2.670 sq. km in area), the southern part Lake Pihkva (710 sq. km) and narrow Lake Lämmijärv (170 sq. km) connecting the two larger parts.

Hydrobiologically, the investigated lakes belong to moderately eutrophic water bodies. The most eutrophic one is L. Võrtsjärv, being followed by L. Pihkva, L. Lämmijärv and L. Peipsi in this sense. L. Peipsi has preserved some characteristics of mesotrophic lakes.

The article is based on 1,003 quantitative samples of zooplankton taken from the pelagic part of L. Peipsi-Pihkva and L. Võrtsjärv in 1965 and 1966, the whole year round.

The number of pelagic copepods is rather small, their total number in all the four lakes being 12. In L. Peipsi-Pihkva there are 12 and in L. Võrtsjärv 7 species (Table 1). In L. Peipsi, L. Lämmijärv and L. Pihkva there are 10 species in each. The number of species was highest in May, June and July (9), and smallest in February (4).

The frequency of occurrence reveals that *Eudiaptomus gracilis* can be found in all the lakes every month (frequency of occurrence 100%). Very frequent are *Cyclops kolensis*, *Mesocyclops leuckarti* and *M. oithonoides*. Very frequent, but only in L. Võrtsjärv, is *Acanthocyclops viridis*. However, it is never a dominating species.

List of species

Table 1

| Species                                | L. Peipsi | L. Lämmijärv | L. Pihkva | L. Võrtsjärv |
|--|-----------|--------------|-----------|--------------|
| <i>Copepoda</i>                        |           |              |           |              |
| <i>Acanthocyclops viridis</i> (Jurine) | ×         | ×            | ×         | ×            |
| <i>Cyclops abyssorum</i> Sars          | ×         | ×            | ×         | ×            |
| <i>Cyclops kolensis</i> Lilljeborg     | ×         | ×            | ×         | ×            |
| <i>Cyclops vicinus</i> Uljanin         | ×         | ×            | ×         | ×            |
| <i>Eucyclops serrulatus</i> (Fisch)    | ×         | ×            | ×         | ×            |
| <i>Eudiaptomus gracilis</i> (Sars)     | ×         | ×            | ×         | ×            |
| <i>Heterocope appendiculata</i> (Sars) | ×         | ×            | ×         | ×            |
| <i>Mesocyclops crassus</i> (Fisch)     | ×         | ×            | ×         | ×            |
| <i>Mesocyclops leuckarti</i> Claus     | ×         | ×            | ×         | ×            |
| <i>Mesocyclops oithonoides</i> Sars    | ×         | ×            | ×         | ×            |
| <i>Nitocrella hibernica</i> (Brady)    | ×         | ×            | ×         | ×            |
| <i>Paracyclops fimbriatus</i> (Fisch)  | ×         | ×            | ×         | ×            |

The maximum number of species found in a lake during one month forms 80 per cent of the total number of species found in L. Peipsi, 80 of that in L. Lämmijärv, 90 in L. Pihkva and 85.7 in L. Võrtsjärv, thus ranging from 80 to 90 per cent. As regards the fluctuation during a year, copepods form the stablest group of zooplankton. This is well proved by the average ratio of the minimum and maximum number of their species (1:2). For different lakes the ratio is different: 1:4 for L. Peipsi, 1:8 for L. Lämmijärv, 1:9 for L. Pihkva and 1:6 for L. Võrtsjärv,

A. Mäemets (1966) has found 15 species of copepods in the pelagic and littoral region of L. Peipsi-Pihkva, R. Levander 8 species in L. Võrtsjärv (Mühlen, Schneider, 1920). In L. Chervonnoye 9 species of copepods were found in 1953, 8 species in 1954 (Черемисова, 1958). Of other Estonian lakes 19 species have been identified in both L. Saadjärv and L. Veisjärv, and 18 in L. Aheru (Eesti järved, 1968). 27 taxons of copepods were found in L. Ladoga (Деньгина, Соколова, 1968), 19 in L. Onega (Смирнова, 1972).

The maximum of the number of copepods, as a rule, occurs in the warmest month, July or August (Table 2), and the minimum, as in the case of other groups, in winter months. The maxima and minima of biomass are mostly synchronous with the corresponding figures of the number (Table 3). In general, the seasonal dynamics of the number and biomass of copepods is rather regular. After ice-drift the number and biomass of copepods begin to rise (in May in L. Peipsi-Pihkva, in April in L. Võrtsjärv) and reach their maximum in midsummer. Thereupon they continuously decrease as low as the winter minimum.

The highest maximum is reached by copepods in L. Pihkva, followed by L. Peipsi, L. Võrtsjärv and L. Lämmijärv. The highest biomass also occurs in L. Pihkva. The order of the other lakes is as follows: L. Peipsi, L. Lämmijärv and L. Võrtsjärv.

In lakes located to the south from Estonia copepods reach their maximum somewhat earlier. In L. Iلسas-Geranimovas, Latvia, it happens at the end of May or at the beginning of June (Лине, 1966). Approximately at the same time the maximum also occurs in L. Reznas, Latvia, in L. Drivyat, Byelorussia, in the Tsimlyansk Water Reservoir, etc. However, unlike in the lakes investigated by us, copepods in the above-mentioned water bodies have two or even three (L. Drivyat) maxima

Table 2

Number of copepods, ind./m<sup>3</sup>

| Month | L. Peipsi |        | L. Lämmijärv |        | L. Pihkva |         | L. Võrtsjärv |        |
|-------|-----------|--------|--------------|--------|-----------|---------|--------------|--------|
|       | 1965      | 1966   | 1965         | 1966   | 1965      | 1966    | 1965         | 1966   |
| I     | —         | 500    | —            | 2 800  | —         | 1 700   | 2 900        | 2 200  |
| II    | 1 000     | 400    | 5 400        | 4 000  | 900       | 1 200   | 3 900        | 3 100  |
| III   | 700       | 600    | 4 500        | 2 800  | 600       | 1 700   | 5 000        | 1 900  |
| IV    | 1 300     | 1 000  | 4 300        | —      | 0         | —       | 20 900       | 31 600 |
| V     | 6 500     | 1 300  | 9 700        | 15 900 | 22 700    | 21 200  | 42 300       | 56 200 |
| VI    | 21 000    | 26 100 | 36 100       | 54 500 | 58 200    | 80 700  | 53 100       | 82 900 |
| VII   | 136 500   | 66 100 | 69 300       | 92 100 | 134 900   | 200 400 | 89 800       | 98 500 |
| VIII  | —         | —      | —            | —      | —         | —       | 96 200       | 74 000 |
| IX    | 58 100    | —      | 27 300       | —      | 108 200   | —       | 31 300       | 34 000 |
| X     | 12 900    | 14 100 | 19 700       | 9 600  | 29 800    | 23 300  | 22 500       | 13 900 |
| XI    | —         | —      | —            | —      | —         | —       | 19 300       | 15 400 |
| XII   | —         | —      | —            | —      | —         | —       | 5 000        | 4 900  |

Table 3

Biomass of copepods, g/m<sup>3</sup>

| Month | L. Peipsi |       | L. Lämmijärv |       | L. Pihkva |       | L. Võrtsjärv |       |
|-------|-----------|-------|--------------|-------|-----------|-------|--------------|-------|
|       | 1965      | 1966  | 1965         | 1966  | 1965      | 1966  | 1965         | 1966  |
| I     | —         | 0.004 | —            | 0.017 | —         | 0.029 | 0.012        | 0.018 |
| II    | 0.012     | 0.005 | 0.025        | 0.022 | 0.008     | 0.011 | 0.033        | 0.038 |
| III   | 0.009     | 0.006 | 0.048        | 0.014 | 0.004     | 0.014 | 0.055        | 0.021 |
| IV    | 0.011     | 0.006 | 0.039        | —     | 0         | —     | 0.132        | 0.168 |
| V     | 0.049     | 0.010 | 0.055        | 0.142 | 0.130     | 0.134 | 0.410        | 0.436 |
| VI    | 0.149     | 0.133 | 0.350        | 0.446 | 1.169     | 1.282 | 0.395        | 0.459 |
| VII   | 1.007     | 0.479 | 0.608        | 0.793 | 1.052     | 1.709 | 0.479        | 0.579 |
| VIII  | —         | —     | —            | —     | —         | —     | 0.518        | 0.459 |
| IX    | 0.504     | —     | 0.249        | —     | 1.049     | —     | 0.260        | 0.331 |
| X     | 0.147     | 0.212 | 0.240        | 0.118 | 0.495     | 0.455 | 0.334        | 0.225 |
| XI    | —         | —     | —            | —     | —         | —     | 0.280        | 0.254 |
| XII   | —         | —     | —            | —     | —         | —     | 0.029        | 0.066 |

(Кумсаре, Гайле, 1960; Печень и др., 1970), the last of them occurring in September. The fact that copepods in Estonia have one maximum only may be caused by several factors. One of them is probably the monocyclic character of several dominating copepods — analogical to the thoroughly described cycle of *Eudiaptomus gracilis* in a Scottish lake (Chapman, 1969) where but few males born in summer become sexually mature before winter. In the south the beginning of reproduction coincides with an earlier period — in Georgia, for instance, the mass reproduction of copepods begins in early April (Гогиберидзе, 1963). In Siberia a mass appearance of nauplii in late winter has also been observed (Юхнева, 1969). As the development of copepods from an egg to an adult is much slower than that of cladocerans (not to speak of rotifers) (Pejler, 1962), second generations are obviously absent in Estonia. K. Elgmork's (1965) data are interesting: in a lake near Oslo *Cyclops scutifer* becomes sexually mature only at the age of three years, although the water body is not an Extreme Arctic one. Another reason why the curves for Estonian lakes have only one vertex is obviously the small role of two-seasonal species, such as *Cyclops kolensis* and *C. vicinus*. The third reason may be the absence of stratification in the lakes. Its presence is obviously a factor favouring the development of copepods in deeper lakes (Черемисова, 1964; Петрович, 1964). The elimination of nauplii often reaches over 95 per cent as the last copepodite stages as well as sexually mature females feed in a predatory way. In case of the stratification of temperature, the elimination is much lower as different species and copepods of different age stages live in different water layers (Einsle, 1969). Of course, it is problematical whether the few copepods reproducing in late summer could cause the second maximum even under ideal condition. Even in favourable conditions of tropical Africa copepods seem to have only two maxima (Burgis, 1969). It is possible that, unlike rotifers, copepods are simply an evolutionally stable group with established norms of reaction.

In 1966 the minima of the number and biomass of copepods were lower and maxima higher than those in 1965. The only exception was L. Peipsi where a cool summer (1965) seems to favour the development of copepods. Consequently, the amplitudes of the fluctuation in the number and biomass were mostly bigger in 1966 than in 1965 which is

not surprising if to take into account the warmer summer of 1966. In L. Peipsi the number of copepods fluctuates more than the biomass, and in L. Lämmijärv vice versa. In L. Võrtsjärv in 1965 the fluctuation of the biomass was larger, in 1966 that of the number (Table 4). A larger fluctuation of the number (in the case of more or less equal minima) is, as a rule, a proof of better reproduction conditions.

The number of copepods usually increases most quickly in June—July, less often in May—June (Tables 5, 6, 7). The rate of the increase of the number is highest in L. Pihkva. L. Peipsi, L. Lämmijärv and L. Võrtsjärv follow. The order according to the rate of the decrease is almost the same: only L. Võrtsjärv and L. Lämmijärv change places. In L. Pihkva and L. Võrtsjärv the rate of the decrease of the number may be higher than that of the increase. The biomass also increases most intensively either in June—July or in May—June. The only exception is L. Võrtsjärv which warms up most quickly and where the increase of the biomass is highest already in April—May. Both according to the rate of the increase and decrease the order of the lakes is as follows: L. Pihkva, L. Peipsi, L. Lämmijärv, L. Võrtsjärv. Unlike the number, the decrease of the biomass of copepods is never quicker than the increase (Tables 8, 9, 10). Differences in the rate of the increase in the number and biomass of copepods probably occur due to the fact that the increase or decrease of the number is most of all dependent on the appearance and elimination of nauplii, and juveniles in general, while the increase of the biomass depends on the changes in the number of adults and the last copepodite stages. In the first half of summer the maturation of copepods is relatively quick and occurs on a mass-scale, while in the second half of summer and in autumn the elimination of juveniles increases especially (Chapman, 1969). Therefore the increase of the biomass is always higher than the decrease, while in the number the decrease may also be quicker.

The increase rate of groups reflects the relative suitability of a lake for this or that group. The dynamics of zooplankton as a whole reveals that the most favourable lake for the development of zooplankton is L. Pihkva. The same is true of cladocerans. The most suitable place for rotifers is L. Võrtsjärv. As for copepods, their increase is fastest in L. Pihkva in a warm summer, in L. Peipsi in the case of a cool summer. In the zooplankton of L. Peipsi copepods play an especially important role (since, due to the low trophy, the general productivity is also low). The greatest stability is an indirect proof of it. The fluctuation of the number and biomass of copepods is also rather stable in L. Pihkva. Its instability is higher in L. Lämmijärv and highest in L. Võrtsjärv. Obviously due to the comparatively slow reproduction of copepods, differences in the indices of instability of copepods between lakes are most distinct and stablest as compared with other groups (Table 11).

The ratio of the average biomass of copepods during the ice-free and ice-cover periods is biggest in L. Pihkva, followed by L. Peipsi, L. Lämmijärv and L. Võrtsjärv (Table 12).

The average weight of copepods in L. Peipsi, L. Pihkva and L. Võrtsjärv is very similar, while in L. Lämmijärv it is much lower (Table 13). The average weight in the warm year of 1966 was higher everywhere, the spring-summer weight, however, was higher in 1965. Water temperatures in the spring-summer of 1966 were much higher than those in 1965. Copepods are obviously more thermophobe than the other groups.

The average weight of copepods is highest in the autumn — October, in L. Pihkva also in June. An important species, *Eudiaptomus gracilis*,

Table 4

## Maximal and minimal numbers and biomasses of copepods

| Data                        | Year | L. Peipsi        |          | L. Lämmijärv.    |          | L. Pihkva        |          | L. Võrtsjärv     |          |
|-----------------------------|------|------------------|----------|------------------|----------|------------------|----------|------------------|----------|
|                             |      | Absolute numbers | Max./Min | Absolute numbers | Max./Min | Absolute numbers | Max./Min | Absolute numbers | Max./Min |
| Number, ind./m <sup>3</sup> | 1965 | 700—136 500      | 195,0    | 4 300—69 300     | 16,1     | 0—134 900        | —        | 2 900—96 200     | 33,2     |
|                             | 1966 | 400—66 100       | 165,2    | 2 800—92 100     | 32,9     | 1 200—200 400    | 166,8    | 1 900—98 500     | 51,8     |
| Biomass, g/m <sup>3</sup>   | 1965 | 0,009—1,007      | 111,9    | 0,025—0,608      | 24,3     | 0—1,169          | —        | 0,012—0,518      | 43,1     |
|                             | 1966 | 0,004—0,479      | 119,8    | 0,014—0,793      | 56,6     | 0,011—1,709      | 155,7    | 0,018—0,579      | 32,2     |

Ratio of maximum and minimum — Max./Min.

Table 5

## Rate of variability of the number of copepods ind./day

| Lake      | Year | I    | II  | III  | IV   | V     | VI    | VII   | IX    | X     |
|-----------|------|------|-----|------|------|-------|-------|-------|-------|-------|
|           |      | 1965 | —   | -10  | +20  | +12   | +173  | +483  | +3850 | -1307 |
| 1966      | -3   | +7   | +20 | +12  | +173 | +827  | +1333 | -1307 | -578  |       |
| Lämmijärv | 1965 | —    | -30 | -7   | +180 | +880  | +1107 | -700  | -917  | -253  |
|           | 1966 | +40  | -40 | -7   | +218 | +1287 | +1253 | -700  | -917  |       |
| Pihkva    | 1965 | —    | -10 | -20  | +325 | +757  | +2557 | -445  | -1968 | -2613 |
|           | 1966 | -17  | +17 | -20  | +325 | +1983 | +3990 | -445  | -1968 |       |
| Võrtsjärv | 1965 | —    | +37 | +530 | +380 | +360  | +1223 | -975  | -940  | -293  |
|           | 1966 | +30  | -40 | +530 | +905 | +890  | +320  | -975  | -940  |       |

Table 6

Rate of variability of number of copepods, % of biggest growth

| Lake      | Year | I    | II   | III   | IV    | V      | VI     | VII    | IX     | X      |
|-----------|------|------|------|-------|-------|--------|--------|--------|--------|--------|
| Peipsi    | 1965 | -    | -0.3 | +0.5  | +0.9  | +4.5   | +12.5  | +100.0 | -33.9  | -39.1  |
|           | 1966 | -0.2 | +0.5 | -     | -     | -      | +62.0  | +100.0 | -43.4  | -      |
| Lämmijärv | 1965 | -    | -0.3 | -0.1  | +16.2 | +79.5  | +100.0 | +100.0 | -63.3  | -22.8  |
|           | 1966 | +3.1 | -3.1 | -     | +16.9 | +100.0 | +97.3  | -      | -71.2  | -      |
| Pihkva    | 1965 | -    | -0.4 | -0.8  | +28.9 | +45.3  | +97.9  | +100.0 | -17.0  | -100.0 |
|           | 1966 | -0.4 | +0.4 | -     | +8.1  | +49.7  | +100.0 | -      | -49.3  | -      |
| Võrtsjärv | 1965 | -    | +3.0 | +43.3 | +31.0 | +29.4  | +100.0 | +100.0 | -79.7  | -23.9  |
|           | 1966 | +3.2 | -4.3 | -     | +96.2 | +94.7  | +34.0  | -      | -100.0 | -      |

Table 7

Degree of fluctuation of number of copepods, % of biggest growth in comparison with previous month

| Lake      | Year | II  | III  | IV    | V    | VI   | VII  | IX    | X     |
|-----------|------|-----|------|-------|------|------|------|-------|-------|
| Peipsi    | 1965 | -   | 0.8  | 0.4   | 4.0  | 8.0  | 87.5 | 133.9 | 5.2   |
|           | 1966 | 0.7 | -    | -     | -    | 61.1 | 38.0 | -     | 143.4 |
| Lämmijärv | 1965 | -   | 0.2  | 20.4  | 16.3 | 63.3 | 20.5 | 163.3 | 40.5  |
|           | 1966 | 6.2 | -    | -     | -    | 83.1 | 2.7  | -     | 168.5 |
| Pihkva    | 1965 | -   | 0.4  | 7.7   | 29.7 | 16.4 | 52.6 | 114.9 | 83.0  |
|           | 1966 | 0.8 | -    | -     | -    | 41.6 | 50.3 | -     | 149.3 |
| Võrtsjärv | 1965 | -   | 40.3 | 100.5 | 12.3 | 1.6  | 70.6 | 179.7 | 55.8  |
|           | 1966 | 7.5 | -    | -     | -    | 1.5  | 60.7 | -     | 134.0 |

Table 8

## Rate of variability of the biomass of copepods, mg/day

| Lake      | Year | I    | II   | III  | IV   | V     | VI    | VII   | IX    | X     |
|-----------|------|------|------|------|------|-------|-------|-------|-------|-------|
| Peipsi    | 1965 | -    | -0.1 | +0.1 | +0.1 | +1.3  | +3.3  | +28.6 | -8.4  | -11.9 |
|           | 1966 | 0    | 0    |      | +0.1 | +4.1  | +11.5 |       | -3.0  |       |
| Lämmijärv | 1965 | -    | +0.8 | -0.3 | +4.3 | +0.5  | +9.8  | +8.6  | -6.0  | -0.3  |
|           | 1966 | +0.2 | -0.3 |      |      | +10.1 | +11.6 |       | -7.5  |       |
| Pihkva    | 1965 | -    | -0.1 | -0.1 | +2.0 | +4.3  | +34.6 | +3.9  | 0     | -18.5 |
|           | 1966 | -0.6 | +0.1 |      |      | +38.3 | +14.2 |       | -13.9 |       |
| Võrtsjärv | 1965 | -    | +0.7 | +2.6 | +6.9 | +9.3  | -0.2  | +2.8  | -3.6  | +2.5  |
|           | 1966 | +0.7 | -0.6 |      |      | +0.8  | +4.0  |       | -3.9  |       |

Table 9

## Rate of variability of the biomass of copepods, % of biggest growth

| Lake      | Year | I     | II   | III   | IV     | V      | VI     | VII    | IX    | X     |
|-----------|------|-------|------|-------|--------|--------|--------|--------|-------|-------|
| Peipsi    | 1965 | -     | -0.4 | +0.4  | +0.9   | +4.5   | +11.5  | +100.0 | -29.4 | -41.6 |
|           | 1966 | 0     | 0    |       |        | +35.7  | +100.0 |        | -26.1 |       |
| Lämmijärv | 1965 | -     | +8.2 | -0.1  | +3.7   | +5.1   | +100.0 | +87.7  | -61.2 | -3.1  |
|           | 1966 | +1.7  | -2.6 |       |        | +87.0  | +100.0 |        | -64.6 |       |
| Pihkva    | 1965 | -     | -0.3 | -0.3  | +5.2   | +12.4  | +100.0 | +11.3  | 0     | -53.4 |
|           | 1966 | -1.6  | +0.3 |       |        | +100.0 | +37.1  |        | -36.3 |       |
| Võrtsjärv | 1965 | -     | +7.5 | +27.9 | +100.0 | +100.0 | -2.1   | +30.1  | -38.7 | +26.9 |
|           | 1966 | +10.1 | -8.7 |       |        | +11.6  | +58.0  |        | -56.5 |       |

Table 10

Degree of fluctuation of the biomass of copepods,  
% of biggest growth in comparison with previous month

| Lake      | Year | II   | III  | IV    | V    | VI    | VII  | IX    | X    |
|-----------|------|------|------|-------|------|-------|------|-------|------|
| Peipsi    | 1965 | —    | 0.8  |       | 4.1  | 7.1   | 88.5 | 129.4 | 12.2 |
|           | 1966 | 0    |      | 0.9   |      | 34.8  | 64.3 | 126.1 |      |
| Lämmijärv | 1965 | —    | 8.3  |       | 5.2  | 94.9  | 12.3 | 148.9 | 58.1 |
|           | 1966 | 4.3  |      | 6.3   |      | 83.3  | 13.0 | 164.6 |      |
| Pihkva    | 1965 | —    | 0    |       | 12.7 | 87.6  | 88.7 | 11.3  | 53.4 |
|           | 1966 | 1.9  |      | 4.9   |      | 94.8  | 62.9 | 73.4  |      |
| Vörtsjärv | 1965 | —    | 20.4 |       | 72.1 | 102.1 | 32.1 | 68.8  | 65.6 |
|           | 1966 | 18.8 |      | 108.7 |      | 88.4  | 46.4 | 114.5 |      |

Table 11

Indices of the instability of copepods

| Lake      | Number |      |         | Biomass |      |         |
|-----------|--------|------|---------|---------|------|---------|
|           | 1965   | 1966 | Average | 1965    | 1966 | Average |
| Peipsi    | 39.8   | 48.7 | 44.2    | 40.4    | 45.2 | 42.8    |
| Lämmijärv | 50.6   | 56.0 | 53.3    | 54.6    | 54.3 | 54.4    |
| Pihkva    | 49.5   | 50.0 | 49.8    | 42.3    | 47.5 | 44.9    |
| Vörtsjärv | 60.0   | 60.8 | 60.4    | 60.1    | 75.3 | 67.7    |

is of biggest size in several lakes in June (Chapman, 1969), which is one of the reasons for the high average weight at that period.

In L. Peipsi-Pihkva the role of copepods in the number of the whole zooplankton is biggest in the summer and autumn, with the maximum in September, and smallest in winter months. In L. Vörtsjärv, on the other hand, the role of copepods is biggest in winter months when they may form more than a half of the total number of zooplankton, and smallest in May—June (Table 14). The role of copepods in the biomass of zooplankton is similar to that in the number of zooplankton (Table 15). In the cooler year of 1965, especially in early summer, the role of copepods in the biomass was always higher than in 1966. Their role in the number was bigger in the warmer summer of 1966 (except for L. Peipsi). This allows us to conclude that a warm summer creates favourable conditions for the reproduction of small copepods, while optimum conditions for the development of bigger forms (*Eudiaptomus gracilis*, *Heterocope appendiculata*) occur in cool water. In addition, the fauna of zooplankters of L. Peipsi, especially that of copepods, is more thermophobe, a fact that causes differences in the dynamics of groups. The main difference between the investigated lakes as for the role of copepods is the great role of the group in the winter zooplankton of L. Vörtsjärv, while in L. Peipsi-Pihkva this cannot be observed. It can probably be explained by the slight role of the genus *Synchaeta* and the considerable role of *Cyclops kolensis* and *Eudiaptomus gracilis* in the winter plankton of the eutrophic L. Vörtsjärv. Differences between the winter temperatures of water of L. Peipsi-Pihkva and L. Vörtsjärv may possibly be another explanation for it.



Table 12

Ratio of the average biomasses ( $\text{g}/\text{m}^3$ ) of copepods during the ice-free and ice-cover periods

| Lake      | 1965            |       |                  |       | 1966            |       |                  |       | Average         |                  |      |
|-----------|-----------------|-------|------------------|-------|-----------------|-------|------------------|-------|-----------------|------------------|------|
|           | ice-free period |       | ice-cover period |       | ice-free period |       | ice-cover period |       | ice-free period | ice-cover period |      |
|           |                 | Ratio |                  | Ratio |                 | Ratio |                  | Ratio |                 |                  |      |
| Peipsi    | 371.2           | 10.7  | 34.7             | 34.7  | 208.5           | 5.2   | 40.1             | 40.1  | 289.8           | 15.9             | 36.2 |
| Lämmijärv | 300.4           | 37.3  | 8.0              | 8.0   | 374.8           | 17.7  | 21.2             | 21.2  | 337.6           | 27.5             | 12.3 |
| Pihkva    | 779.0           | 4.0   | 194.8            | 194.8 | 895.0           | 18.0  | 49.7             | 49.7  | 837.0           | 11.0             | 76.1 |
| Võrtsjärv | 351.0           | 32.2  | 10.9             | 10.9  | 363.9           | 35.8  | 10.2             | 10.2  | 357.4           | 34.0             | 10.5 |

Table 13

Average weight of copepods, mg

| Lake      | Year | I      | II     | III    | IV     | V      | VI     | VII    | IX     | X      |
|-----------|------|--------|--------|--------|--------|--------|--------|--------|--------|--------|
| Peipsi    | 1965 | —      | 0.0120 | 0.0129 | 0.0085 | 0.0075 | 0.0071 | 0.0074 | 0.0087 | 0.0114 |
|           | 1966 | 0.0080 | 0.0125 | 0.0100 | 0.0060 | 0.0077 | 0.0051 | 0.0072 | —      | 0.0150 |
| Lämmijärv | 1965 | —      | 0.0046 | 0.0107 | 0.0091 | 0.0057 | 0.0097 | 0.0088 | 0.0091 | 0.0122 |
|           | 1966 | 0.0061 | 0.0055 | 0.0050 | —      | 0.0089 | 0.0082 | 0.0086 | —      | 0.0123 |
| Pihkva    | 1965 | —      | 0.0089 | 0.0067 | —      | 0.0057 | 0.0202 | 0.0078 | 0.0097 | 0.0166 |
|           | 1966 | 0.0171 | 0.0092 | 0.0082 | —      | 0.0063 | 0.0159 | 0.0085 | —      | 0.0195 |
| Võrtsjärv | 1965 | 0.0041 | 0.0085 | 0.0110 | 0.0063 | 0.0097 | 0.0074 | 0.0053 | 0.0083 | 0.0148 |
|           | 1966 | 0.0082 | 0.0122 | 0.0110 | 0.0053 | 0.0078 | 0.0055 | 0.0059 | 0.0097 | 0.0162 |

Table 14

The role of copepods (%) in the total number of zooplankton

| Lake      | Year | I    | II   | III  | IV   | V    | VI   | VII  | VIII | IX   | X    | XI   | XII  |
|-----------|------|------|------|------|------|------|------|------|------|------|------|------|------|
| Peipsi    | 1965 | —    | 9.0  | 9.8  | 15.7 | 30.3 | 29.5 | 39.0 | —    | 45.2 | 37.6 | —    | —    |
|           | 1966 | 19.1 | 9.2  | 7.8  | 9.6  | 4.4  | 26.0 | 22.0 | —    | —    | 27.3 | —    | —    |
| Lämmijärv | 1965 | —    | 13.1 | 33.8 | 17.1 | 18.1 | 20.8 | 23.7 | —    | 32.8 | 22.8 | —    | —    |
|           | 1966 | 16.0 | 18.6 | 19.1 | —    | 18.4 | 36.9 | 39.9 | —    | —    | 12.3 | —    | —    |
| Pihkva    | 1965 | —    | 2.4  | 7.4  | 0    | 33.4 | 16.1 | 23.9 | —    | 43.6 | 20.4 | —    | —    |
|           | 1966 | 5.8  | 3.6  | 14.8 | —    | 21.6 | 21.2 | 39.8 | —    | —    | 16.6 | —    | —    |
| Yörtsjärv | 1965 | 14.5 | 24.4 | 39.5 | 42.7 | 21.1 | 13.8 | 30.8 | 26.9 | 33.0 | 21.6 | 34.6 | 31.9 |
|           | 1966 | 26.4 | 57.4 | 52.6 | 21.8 | 8.9  | 25.9 | 36.5 | 34.5 | 34.8 | 22.7 | 37.6 | 45.7 |

Table 15

The role of copepods (%) in the total biomass of zooplankton

| Lake      | Year | I    | II   | III  | IV   | V    | VI   | VII  | VIII | IX   | X    | XI   | XII  |
|-----------|------|------|------|------|------|------|------|------|------|------|------|------|------|
| Peipsi    | 1965 | —    | 21.8 | 25.0 | 36.7 | 50.0 | 58.8 | 35.6 | —    | 53.5 | 51.0 | —    | —    |
|           | 1966 | 28.6 | 20.8 | 15.8 | 16.7 | 11.0 | 48.9 | 29.2 | —    | —    | 36.8 | —    | —    |
| Lämmijärv | 1965 | —    | 14.3 | 64.0 | 40.3 | 44.0 | 45.8 | 33.1 | —    | 40.7 | 33.3 | —    | —    |
|           | 1966 | 19.6 | 21.1 | 40.8 | —    | 30.1 | 50.6 | 28.6 | —    | —    | 15.2 | —    | —    |
| Pihkva    | 1965 | —    | 6.2  | 16.0 | 0    | 38.7 | 39.1 | 41.1 | —    | 57.7 | 25.3 | —    | —    |
|           | 1966 | 17.2 | 7.5  | 28.0 | —    | 27.9 | 27.9 | 46.6 | —    | —    | 27.0 | —    | —    |
| Yörtsjärv | 1965 | 14.6 | 42.3 | 77.5 | 64.4 | 64.7 | 33.0 | 32.5 | 38.2 | 40.5 | 48.8 | 50.8 | 25.2 |
|           | 1966 | 29.5 | 73.1 | 84.0 | 17.5 | 17.1 | 39.7 | 50.4 | 47.9 | 42.3 | 41.6 | 66.8 | 79.5 |

A generally accepted view seems to be: the higher the trophy, the bigger the role of cladocerans and the smaller the role of copepods (Кумсаре, Гайле, 1960; Деньгина, 1964; Петрович, 1970). It has also been mentioned, although not so unanimously, that the role of copepods in deep lakes is greater than in the shallow ones (Петрович, 1964). L. Gordeyeva (1969) considers the winter domination of copepods, *Eud. gracilis* in particular, a characteristic feature of shallow lakes. According to K. Cheremissova (1964) *Eud. gracilis* is less abundant in shallow eutrophic lakes than in deep ones. According to the same author, in winter copepods are mostly to be found in the bottom layers in deep eutrophic lakes, and rotifers in surface layers — a fact which makes the obtaining of an objective picture of the relations between groups difficult, especially in the case of the plankton-net haul. In the overgrown shallow eutrophic L. Zhuvintas copepods form 92 per cent of the biomass in winter, while rotifers are totally absent (Печюлене, 1968). In general, the Latvian zooplanktonologists' opinion is: in deep lakes the role of copepods is biggest, in lakes of average depth the biomasses of cladocerans and copepods are more or less equal, while in shallow lakes cladocerans predominate (Лине, 1966). In Lithuania, in the basin of the River Žeimjane, 14 lakes were investigated and divided (on the basis of the summer biomass only) into 3 types: I — copepods predominate, II — copepods and cladocerans occur more or less equally, III — cladocerans predominate (Киселите, Найнайте, 1969). The total biomass in two first-mentioned types is 0.6—2.2 g/m<sup>3</sup> and 2.0—6.3 g/m<sup>3</sup> in the third one. In Karelia copepods predominate in oligotrophic lakes and pelagic regions of mesotrophic lakes, cladocerans in the littoral of mesotrophic lakes and everywhere in eutrophic ones (Филимонова, 1965). As regards L. Ilmen, rotifers predominate when the water warms up quickly in spring, and copepods when the spring is cold (Эррерт, 1961). In investigated lakes the role of copepods was also much bigger in the cold spring of 1965 as compared with the spring of 1966 when the water became warm relatively quickly (Tables 14 and 15).

The big role of copepods in the zooplankton is positive as regards the nutrition of fishes; copepods contain 20 per cent of fat and 60 of protein (of dry matter). They are especially important as feed for fishes in cold seasons when no cladocerans can be found (Филимонова, 1965). In L. Peipsi-Pihkva and L. Võrtsjärv the whitefish and smelt feed on zooplankton in the winter. Obviously these fish species belong to ecosystems whose peculiarity is the big role of copepods in the zooplankton. In the course of the eutrophication of a water body the role of copepods decreases while the whitefish and smelt disappear. It is possible that such a process is taking place in L. Võrtsjärv where copepods formed 60—70 per cent of the biomass in 1953 (Шенберг, 1958), and only 48—50 at the present time, and where the whitefish is of no significance as a game fish any longer. Therefore we should consider copepods which find suitable living conditions in lakes with low trophy a more archaic group evolutionally, than the cladocerans and rotifers. Some authors consider copepods the most resistant group to unfavourable environmental conditions (Полищук, 1968). Geographical changes in the role of copepods support the idea of their evolutionary plasticity. Predominating in northern water bodies (Деньгина, 1964; Филимонова, 1965), often in the polar circle, like in the lakes of Norilsk (Гордеева, 1962), copepods simultaneously predominate in the Kemashinsk Water Reservoir, Uzbekistan (Афанасьева, 1969), on the middle course and in the flood-plains of the Paraná (Bonetto et al., 1969), in L. George, Uganda, and other rather

southern water bodies. In L. George, where the temperature of water equals 25—35°, copepods form 72 per cent of the number (Dunn, 1969), while during the maxima in September and February the number of nauplii reaches as much as 1.0 and 1.4 million ind./m<sup>3</sup>, respectively (Burgis, 1969). The abundant occurrence of copepods both in the polar and equatorial region is undoubtedly an interesting phenomenon.

In comparison with other water bodies, the investigated lakes are not rich in the biomass of copepods. In the mesotrophic L. Naroch, Byelorussia, the average biomass of copepods during 10 years was 0.827 and in the eutrophic L. Myastro even 3.745 g/m<sup>3</sup> (Петрович, 1969). The average biomass of copepods in L. Peipsi is 0.170, in L. Lämmijärv 0.212, in L. Võrtsjärv 0.250 and in L. Pihkva 0.504 g/m<sup>3</sup>. The average biomass in the warm summer of 1966 was in all the lakes somewhat higher than in 1965, with the exception of L. Peipsi where, vice versa, it was twice lower. In the eutrophic L. Drivyat, Byelorussia, the maximum of copepods in the summer reaches 2.4 g/m<sup>3</sup> (Печень и др., 1970), while in L. Pihkva it is 1.7 g/m<sup>3</sup> as a maximum.

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*Academy of Sciences of the Estonian SSR,  
Institute of Zoology and Botany*

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Juta HABERMAN

## PEIPSI-PIHKVA JÄRVE JA VÖRTSJÄRVE PELAGIAALI KOPEPOODIDE SESOONNE DÜNAAMIKA

### Resüme

Artikkel põhineb 1003 zooplanktoniproovil, mis on kogutud Peipsi-Pihkva järve ja Vörtsjärve pelagiaalist 1965. ja 1966. aastal. Antakse ülevaade kopepoodide liigilisest koostisest (tab. 1), kopepoodide arvukusest (tab. 2), biomassist (tab. 3), miinimumidest ja maksimumidest (tab. 4), arvukuse (tab. 5, 6, 7) ja biomassi (tab. 8, 9, 10) muutlikkuse tempost, määrast ja labiilsuse indeksitest (tab. 11), vegetatsiooniperioodi ja talvise biomassi suhtest (tab. 12), kopepoodide keskmisest kaalust (tab. 13) ja osatähtsusest planktonis (tab. 14, 15).

*Eesti NSV Teaduste Akadeemia  
Zooloogia ja Botaanika Instituut*

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Юта ХАБЕРМАН

## СЕЗОННАЯ ДИНАМИКА ВЕСЛОНОГИХ ПЕЛАГИАЛИ ЧУДСКО-ПСКОВСКОГО ОЗЕРА И ОЗЕРА ВЪРТСЪЯРВ

### Резюме

Материалом статьи являются 1003 количественные пробы зоопланктона, собранные из пелагиали Чудско-Псковского озера и озера Вуртсъярв в 1965 и 1966 гг.

Приводится обзор видового состава (табл. 1), численности (табл. 2) и биомассы (табл. 3), минимумов и максимумов численности и биомассы (табл. 4), темпа изменчивости и степени изменчивости численности (табл. 5, 6, 7) и биомассы (табл. 8, 9, 10) и индексов лабильности (табл. 11), соотношения биомассы в вегетационный и зимний периоды (табл. 12), среднего веса веслоногих (табл. 13), удельного веса веслоногих в зоопланктоне (табл. 14, 15).

*Институт зоологии и ботаники  
Академии наук Эстонской ССР*

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