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# LONG-TERM CHANGES IN THE COMPOSITION, PRODUCTIVITY AND TROPHIC EFFICIENCY IN THE ZOOPLANKTON COMMUNITY OF HEATED LAKES NEAR KONIN (POLAND)

ABSTRACT: In three lakes, intensively mixed and heated (due to a long-term discharging of heated waters), the following tendencies were found: a dominance of small forms (particularly rotifers), an increase in their relative production, and analogous changes in their predators (carnivorous cyclopoids), retreating and production decrease of filter-feeding cladocerans, reduction in individual body size of all crustaceans and an increase in fecundity of most zooplankton species. The possible causes of these changes (turbulence, entrainment mortality, fish pressure and detritus abundance) were discussed.

KEY WORDS: Heated lakes, zooplankton, productivity, *P* : *B* coefficient.

## 1. INTRODUCTION, STUDY AREA

The studies the aim of which is to assess the primary and secondary productivity of the pelagic plankton and changes in it caused by the inclusion of the lakes near Konin in the power-plant cooling system there, have been continued for nearly 20 years (P a t a l a s 1970). They have covered three of the five lakes found there (Fig. 1), constituting the cooling system of the power plants of Pątnów and Konin (H i l l b r i c h t - I l k o w s k a and Z d a n o w s k i 1978), i.e., L. Licheńskie ($A = 153.6$ ha, $z_{max.} = 13.3$ m, $\bar{z} = 4.9$ m), L. Wąsosko-Mikorzyńskie [1] ($A = 245.3$ ha, $z_{max.} = 38.0$ m, $\bar{z} = 11.9$ m) and L. Ślesińskie ($A = 141.1$ ha, $z_{max.} = 25.7$ m $\bar{z} = 7.5$ m) (other morphometric data on the lakes can be found in H i l l b r i c h t - I l k o w s k a and Z d a n o w s k i 1988b).

In 1966 when the studies were begun only L. Licheńskie was during the whole year affected by hot waters discharged into it in point mode by a canal (so-called 1st stage of

[1] Hereafter referred to as L. Mikorzyńskie.

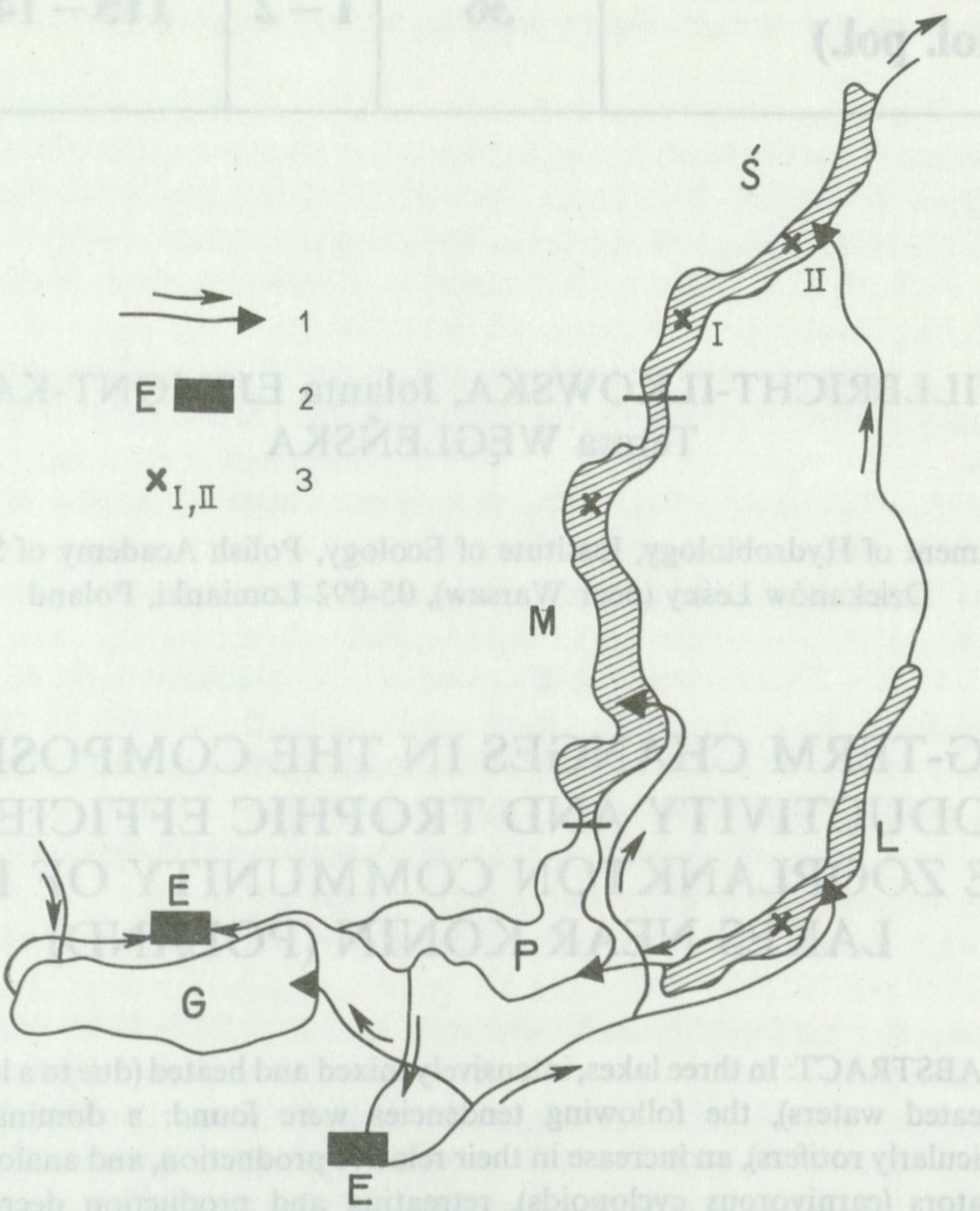


Fig. 1. A sketch-map of the Konin lakes (lakes under study are shaded)
Lakes: G(osławskie), P(ątnowskie), M(ikorzyńskie), L(icheńskie), Ś(lesińskie), 1 – heated-water discharge and water flow direction in canals, 2 – power plant, 3 – study stations

the operation of the cooling system), whereas L. Mikorzyńskie represented a control system (Hillbricht-Ilkowska and Zdanowski 1988b). Since 1970, as a result of a further growth of the energy-producing industry in the region (2nd stage of operation), L. Ślesińskie has been temporarily linked up with the cooling system functioning in the summer (so-called great cooling cycle). The latter lake is fed with water drained from L. Licheńskie by a canal and discharged into it in waterfall ("spring-board") mode. The warm waters from this lake flow on into the northern part of L. Mikorzyńskie. Thus, there are two heating zones in L. Mikorzyńskie – one of them functions throughout the year (the canal extending from L. Pątnowskie) and affects the southern part of this lake, and the other, temporary (summer), affects the northern part via L. Ślesińskie (cf. Figs. 2 and 3 in Hillbricht-Ilkowska and Zdanowski 1988b, and Hillbricht-Ilkowska and Zdanowski 1978). In 2nd stage of the operation of the cooling system there have occurred significant changes in the circulation of water masses, this applying to the intensity of vertical movement (lack of thermal stratification, or deepening of the epilimnion) and directions and velocity of horizontal movement (Hillbricht-Ilkowska and Zdanowski 1988b).

Table 1. Study scheme, data on the zooplankton and general information about water heating and retention time (summer) of the Konin lakes

| Year – study period | L. Licheńskie (A = 153.6 ha, $\bar{z}$ = 4.9 m) | L. Mikorzyńskie (A = 245.3 ha, $\bar{z}$ = 11.9 m) | L. Ślesińskie (A = 141.1 ha, $\bar{z}$ = 7.5 m) | Kind of data and source |
|---|---|---|---|---|
| 1966 August | 7th year of heating (from 1958 on). Time of water retention in lake ~ 5 days[1] | not heated[2] | not heated | Numbers and biomass of rotifer and crustacean species. Joint production and $P:B$ of rotifers and crustaceans and trophic groups for L. Licheńskie and Mikorzyńskie acc. to Patalas (1970) per $m^2$ lake surface area |
| 1973 30 July – 10 August | 14th year of heating. Time of water retention in lake and epilimnion ~ 3.5 days[3] | 4th year of heating[2]. Lake water retention ~ 42 days[4]. Epilimnion water retention ~ 4 days[4] | 4th year of heating. Lake water retention ~ 8 days[5] Epilimnion water retention ~ 3 days[5] | Numbers, biomass, fecundity, production and $P:B$ for rotifer and crustacean species and trophic groups for all three lakes, acc. to Hillbricht-Ilkowska et al. (1976) per $m^2$ lake surface area |
| 1978 1 – 12 August | 19th year of heating. Retention time unchanged (as above) | 9th year of heating. Retention time unchanged (as above) | 9th year of heating. Retention time unchanged (as above) | as above – data from the present study |
| 1983 30 July – 10 August | 24th year of heating. Retention time as above | 14th year of heating. Retention time as above | 14th year o heating. Retention time as above | as above – data from the present study |

[1] Relates to retention time in summer when L. Licheńskie receives half of the total discharge = 33 $m^3 \cdot s^{-1}$. Retention time has been calculated as the ratio of lake volume to the 24-hour water amount discharged (acc. to Zdanowski and Korycka 1976). [2] Applies to the northern lake part (cf. Hillbricht-Ilkowska and Zdanowski 1988b). [3] Acc. to Zdanowski and Korycka (1976). [4] As the ratio of the maximum discharge of heated water (summer) and water from L. Ślesińskie (Hillbricht-Ilkowska and Zdanowski 1988b) to the total lake volume. Data on epilimnion water retention. [5] As the ratio of maximum discharge (summer) of heated waters to the total lake volume or epilimnion volume acc. to Hillbricht-Ilkowska and Zdanowski (1988b).

Research on the productivity of the pelagic zone (primary production and zooplankton production and biomass) was carried out every several years from 1966 on, i.e., in 1973, 1978, 1983 (Table 1), in summer (usually in the period: end of July-beginning of August), that is, when the cooling system was in full operation, including the great cycle. In this period all the lakes take part in the cycling of the cooling-system water (Fig. 1), and as a result, the water retention time varies between the lakes, from about 3.5 days in L. Licheńskie to about 42 days in L. Mikorzyńskie [2] (Table 1). Then the highest annual surface-water temperatures (about 24 – 27°C) are recorded, always the highest in L. Licheńskie. In this period also the greatest temperature differences are found between the station near the discharge site (station II) and that far from it (control station I) in L. Ślesińskie (Table 2), and also between the deeper waters of the shallow lakes (the hypolimnion of L. Licheńskie is always warm, its temperature being higher than or equal to 10°C) and those of the deep ones (the hypolimnion of L. Mikorzyńskie and the control part in L. Ślesińskie are always cold, their temperature being lower than or equal to 10°C) (Table 2).

Table 2. Mean temperatures (summer) in the epi- (E) and hypolimnion (H) of the Konin lakes in different study years (acc. to Patalas 1970, Zdanowski 1976, 1988)

| Lake | | | 1966 | 1973 | 1978 | 1983 |
|---|---|---|---|---|---|---|
| Licheńskie | | E | 27.1 | 27.9 | 27.4 | 25.6 |
| | | H | – | 16.0 | 13.0 | 13.6 |
| Mikorzyńskie | | E | 21.6 | 24.7 | 23.9 | 23.4 |
| | | H | – | 12.3 | 7.0 | 7.02 |
| Ślesińskie | I (control) | E | – | 25.5 | 24.0 | 23.5 |
| | | H | – | 7.5 | 5.6 | 6.4 |
| | II (discharge) | E | – | 25.7 | 24.5 | 24.3 |
| | | H | – | 25.0 | 24.0 | 23.9 |

## 2. METHODS

In all the study periods (Table 1) the same sampling, sample-analysing, measuring and data-presenting methods were used, and similar methodological principles were adopted to make the results fully comparable to the data obtained in the years 1966 – 1970 (Patalas 1970).

Zooplankton samples were taken every 2 – 3 days for about two weeks (Table 1). As recommended by the Plankton Ecology Group (in Botrell et al. 1976), subsamples

[2] For a rough estimate of the water retention time the maximum (recorded in summer) hot water quantities discharged, according to Hillbricht-Ilkowska and Zdanowski (1988b), were adopted. However, these quantities vary widely during the year, and consequently the longest retention time (lowest discharge) only of the epilimnion waters comes up to 12, 25 and 11 days, respectively, for lakes: Licheńskie, Mikorzyńskie and Ślesińskie, these high retention values occurring in winter and/or spring.

taken within particular thermal layers (i.e. every 1 m in the epi- and metalimnion, and every 2 or 3 m in the hypolimnion) of each of the lakes were pooled. A subsample was the contents of a 5-litre Bernatowicz type sampler, filtered through a nylon net, 50 – 60 $\mu$m in mesh size. The samples were fixed at first with Lugol solution and next with formalin. Adult and larval forms of crustaceans (nauplii, copepodid stages of copepods, and juvenile stages of cladocerans), their eggs (in sacs and brood chambers), as well as a plankton rotifers and their eggs were counted and identified. The body length of crustaceans and rotifers was measured (at least 20 – 30 measurements per sample), and the biomass of crustaceans was estimated according to the corresponding ratios (weight to length), and that of rotifers according to the formulae for the volume of the appropriate solids (acc. to the methods recommended in Botrell et al. 1976). Biomass production of crustaceans and rotifers was assessed according to the methods recommended by Edmondson and Winberg (1971) and Hillbricht-Ilkowska and Patalas (1967), applying the appropriate corrections for the temperature (Table 2). Data relating to numbers, fecundity, biomass, production and daily $P:B$ coefficient were calculated in average values for the study period (i.e. two weeks) and for the whole water column, that is, per $m^2$ lake surface area at a particular station. In the above study periods (Zdanowski 1976, 1988) the thickness (in m) of the epi-, meta- and hypolimnion at the sampling stations was, respectively, in: L. Licheńskie – 6.5 and 2 m, L. Mikorzyńskie – 11.6 and 12 m, L. Ślesińskie station I – 6.5 and 13 m, Ślesińskie station II – 6.5 and 9 m.

For the evaluation of the inter-level trophic efficiency (acc. to Hillbricht-Ilkowska 1977) in the planktonic trophic chain, that is, the ratio between the production of biomass by non-predatory zooplankton and the primary production ($EP_{herb.}$), and the analogous ratio of the production of predatory to non-predatory zooplankton ($EP_{pred.}$), Zdanowski's (1976, 1988) data on the average daily gross production of the phytoplankton (measuring by the oxygen method, using light and dark bottles) were used, as well as the appropriate calculation factors applied by Patalas (1970). The relative production was also estimated of the phytoplankton, that is, the $P:B$ coefficient as the ratio of the daily gross production to the biomass (in carbon units), using Zdanowski's (1976, 1988) data on production and data on phytoplankton biomass in the surface layer acc. to Simm (1988a).

The aim of the frequent (every 2 – 3 days) measurements and sampling, carried on for two weeks in summer, was to obtain more reliable estimates that could be accepted as characterizing the whole summer period, i.e., when the cooling system is in full operation.

## 3. RESULTS

### 3.1. AVERAGE ZOOPLANKTON NUMBERS AND BIOMASS, AND THE MAIN TRENDS OF CHANGES IN THE ABUNDANCE OF GROUPS AND SPECIES

In their studies Hillbricht-Ilkowska et al. (1976) and Hillbricht-Ilkowska and Zdanowski (1978) have analysed the differences in zooplankton abundance and biomass found in the study year 1973, as compared with the year 1966 (acc. to the data of P a t a l a s 1970), in two lakes: Licheńskie and Mikorzyńskie, and, for comparison, at two stations in L. Ślesińskie.

A summary of all the comparable data on the numbers and biomass of rotifers and crustaceans in the zooplankton has been presented in Figure 2 to demonstrate to what extent the trend of changes seen in the particular lakes in the 1st study period, i.e., until 1973, was maintained in the next decade, that is, after the long-term heating of the waters of the whole system and changed retention time in individual lakes (Table 1).

In L. Licheńskie a period during which there occurred almost a twofold increase in

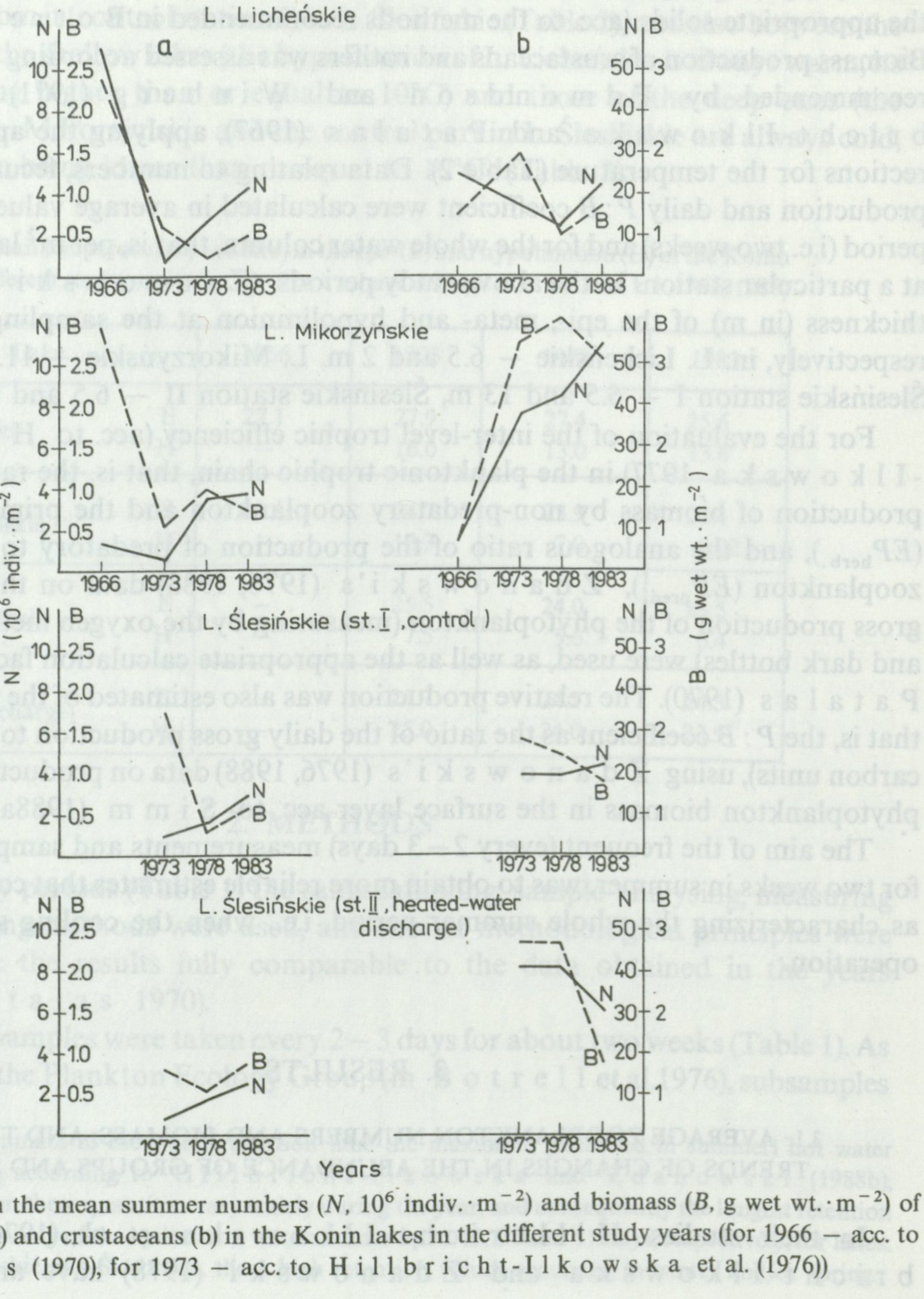


Fig. 2. Variation in the mean summer numbers ($N$, $10^6$ indiv.$\cdot$m$^{-2}$) and biomass ($B$, g wet wt.$\cdot$m$^{-2}$) of plankton rotifers (a) and crustaceans (b) in the Konin lakes in the different study years (for 1966 – acc. to P a t a l a s (1970), for 1973 – acc. to H i l l b r i c h t - I l k o w s k a et al. (1976))

crustacean biomass (1966 vs. 1973) was followed by a rapid decrease in 1978 and persistence of this level also in 1983, that is, after the accordingly longer period (Table 1) of the existence of "riverine" conditions in this lake, the warmest of all the lakes (Table 2). Along with the above changes there have occurred: at first a considerable drop in abundance and biomass of the pelagic rotifers followed by a smaller decrease and stabilization of the level of their biomass, yet with a very high rate of their increase in numbers.

A different picture of changes is seen in L. Mikorzyńskie (Fig. 2). In the first period, that is, before 1973, when the lake began to receive heated waters from L. Ślesińskie, the biomass of planktonic crustaceans increased almost 7-fold and their numbers about 3-fold. A high level of biomass and numbers persisted until 1983, in which year the biomass decreased slightly. Likewise, for planktonic rotifers, whose numbers and biomass appeared to be in 1973 much lower than they were in 1966, the values of these parameters in later years were twice or three times as high as in 1973. Generally, since its inclusion in the great cooling cycle this deep lake has shown the highest biomass, whereas the numbers of both of the zooplankton groups were among the highest ones, higher than in L. Ślesińskie, equally deep, heated, but with a shorter water retention time (Table 1).

In the period from 1973 to 1983, in L. Ślesińskie the heated-water discharge station, where hot water is constantly mixed down to the bottom, always differs from the control station I which is stratified (Fig. 2). Zooplankton numbers and/or biomass are always higher, often nearly twofold, at the warm and mixed station. No such clear directional long-term changes were seen in planktonic crustaceans: an exception was only the last study year (1983), in which the estimated biomass was definitely lower than during the preceding years, although the level of numbers was only slightly lower. Plankton rotifers continued to grow in numbers and biomass in individual study periods at both of the stations.

Generally, it must be stated that as a result of the starting of the full cycle of the heated waters, L. Mikorzyńskie, with a very deep and warm epilimnion, and the hot and constantly mixed discharge station in L. Ślesińskie show the highest zooplankton biomass per $m^2$ water column, the lowest biomass quantity being found in shallow L. Licheńskie, the warmest of all and with a high-rate through-flow.

The overall changes in zooplankton biomass are determined by the crustaceans, since the rotifers (despite being equally abundant and even more abundant) contribute only 1 – 3 per cent of the total biomass due to their small body size. However, this group, as can be seen from Figure 2, has continued to grow in numbers in all the lakes from 1973 on, i.e., since the inclusion of all the lakes in the cooling cycle, although the increase in numbers is not always accompanied by an increase in biomass. Their numbers and biomass are lower than those found by Patalas (1970) in 1966 in L. Licheńskie (heated) and L. Mikorzyńskie (not heated then). The cause of this difference, as indicated by Hillbricht-Ilkowska et al. (1976), is no doubt, the difference in the sample-taking technique (in 1966 the sedimentation method was used). However, in the light of what is known about the selectivity of the net used in later studies (in Botrell et al. 1976), this difference cannot be attributed to the techniques alone. It seems that as the new pattern of water-mass mixis become established in summer throughout the lake system, this zooplankton group – though insignificant from the viewpoint of biomass quantities in the pelagic zone, find suitable conditions for their growth.

From the above follows, among other things, that the nature of the long-term changes in numbers differs from that of biomass changes – this is true of both of the zooplankton groups, especially of the plankton rotifers. The cause of this is the changed dominance structure in both communities, generally towards the dominance of species and groups of smaller body size and weight.

The growth in biomass and numbers of the plankton crustaceans that took place in all the study lakes during the 1st study period (1966 – 1973) was brought about by the development (see Hillbricht-Ilkowska et al. 1976, and Hillbricht-Ilkowska and Zdanowski 1978) of several cladoceran species: *Daphnia cucullata* G. O. Sars (most numerous), *Bosmina coregoni thersites* Poppe, *Diaphanosoma brachyurum* (Lièven) and *Daphnia longispina* O.F. Müller (least numerous, sporadic). The community of these cladocerans – typical filter-feeders (the average body size of an adult individual of these species ranges from 630 $\mu$m to 1400 $\mu$m) is characterized by a high thermal tolerance (warm water species) and a high fecundity, found at all the stations and lakes studied in 1973. These species also were the cause of a high trophic inter-level efficiency in the plankton, that is a very high degree of primary production utilization (the $EP_{herb.}$ coefficient recorded in 1973 ranged from 0.22 to 0.18) (Hillbricht-Ilkowska et al. 1976).

The comparison (Fig. 3) of the numbers of these species in the summer periods of the 2nd study decade indicates, however, that the above trend has not only failed to persist, but it has also been followed by a numerical decline of these zooplankton components. This decrease is most conspicuous in L. Licheńskie, where in 1978 the numbers of *D. cucullata, D. longispina* and *B. coregoni thersites* were already several times lower than in 1973, whereas in the next period (1983) they were even lower than or equal to those recorded by Patalas (1970) in 1966. In L. Licheńskie a less conspicuous decline in this cladoceran group was recorded for *D. brachyurum*. In L. Mikorzyńskie, where the initial increase of this community in 1966 – 1973 was the strongest, as early as 1978 and/or 1983 a clear drop was seen, although in 1983 their numbers were still comparatively high, almost 10 times as high as in the control year (1966) (Fig. 3). A similar tendency, i.e., retreat of these cladocerans, could be seen in the whole of L. Ślesińskie, as the numbers were there in 1983 and/or 1978 at both stations generally lower than in 1973. It may, therefore, be presumed that in the 2nd period of the operation of the cooling system (1973 – 1983) the filter-feeding cladocerans tended to reduce their numbers as compared to the initial increase that took place in the lakes in the years 1966 – 1973. This tendency has been most marked in the warmest and most "rivérine" (the shortest retention time) of the lakes, i.e., L. Licheńskie.

Predatory Cyclopidae (the total number of predatory forms, that is, adult stages, copepodids and herbivorous forms – nauplii) represent a taxonomic group whose changes are opposite to those described above. The average body size of the nauplius, copepodid and adult are 0.190, 0.560 and 0.850 mm, respectively. This group always

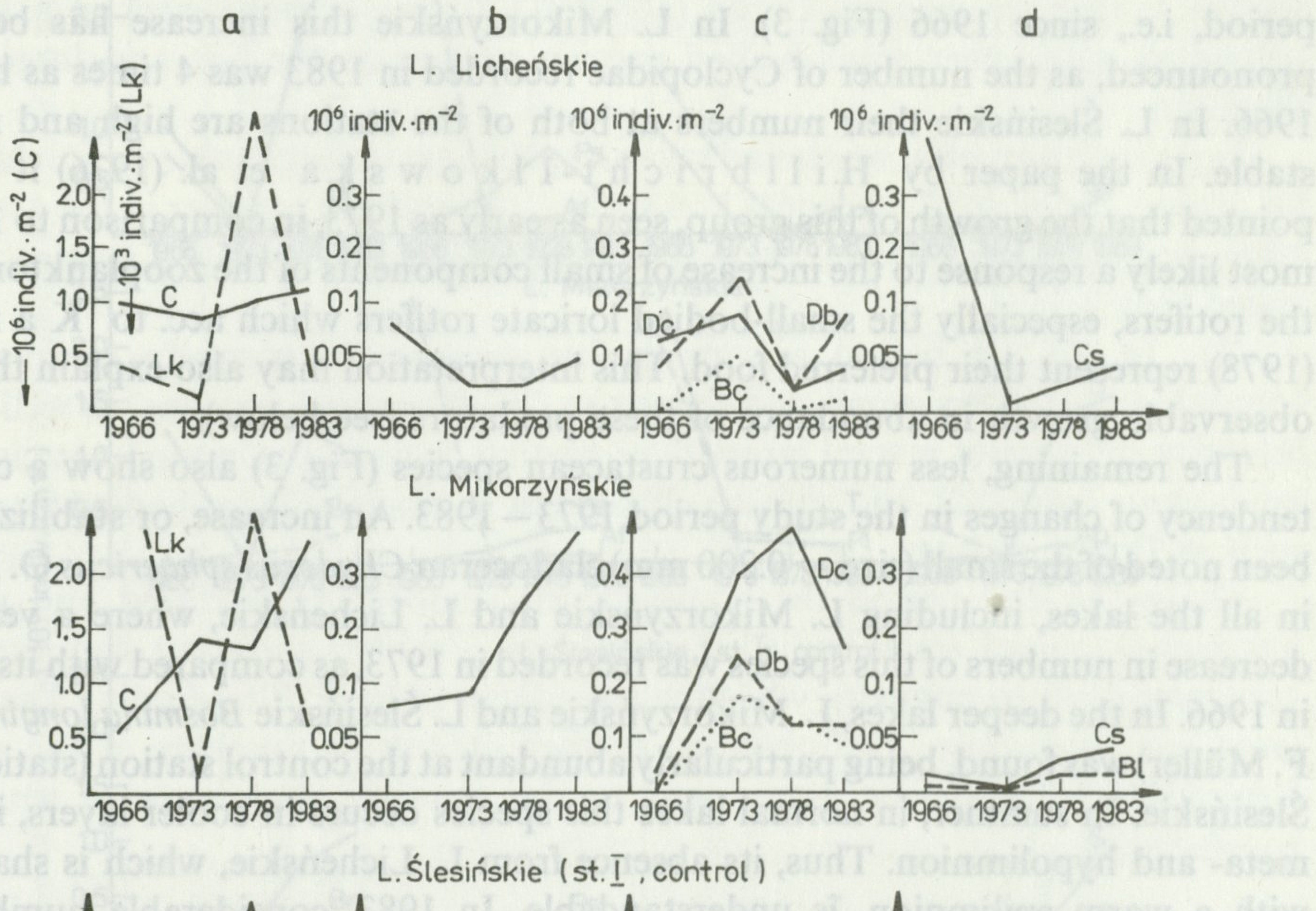


Fig. 3. Variation in the mean summer numbers ($N$, $10^6$ indiv. $\cdot$ m$^{-2}$) [1] of plankton crustaceans in the Konin lakes in different study years [2]

a — predators (Cyclopidae, all stages, Lk — *Leptodora kindtii* Focke), b — large filter-feeders, that is, Diaptomidae (all stages), c — medium-size and small filter-feeder cladocerans (Dc — *Daphnia cucullata* + *D. longispina*, Db — *Diaphanosoma brachyurum*, Bc — *Bosmina coregoni theresites*, Bl — *B. longirostris*), d — Cs — *Chydorus sphaericus*

[1] For *L. kindtii* — $10^3$ indiv. $\cdot$ m$^{-2}$ (note — the scale in the figure varies). [2] For 1966 — acc. to P a t a l a s (1970), for 1973 — acc. to H i l l b r i c h t - I l k o w s k a et al. (1976)

dominates in numbers of the whole crustacean community (from 60 to 85% of numbers), and their abundance in all the lakes has increased throughout the study period, i.e., since 1966 (Fig. 3). In L. Mikorzyńskie this increase has been most pronounced, as the number of Cyclopidae recorded in 1983 was 4 times as high as in 1966. In L. Ślesińskie their numbers at both of the stations are high and relatively stable. In the paper by Hillbricht-Ilkowska et al. (1976) it has been pointed that the growth of this group, seen as early as 1973, in comparison to 1966, was most likely a response to the increase of small components of the zooplankton, such as the rotifers, especially the small-bodied loricate rotifers which acc. to Karabin (1978) represent their preferred food. This interpretation may also explain the further observable growth in abundance of these predators (see below).

The remaining, less numerous crustacean species (Fig. 3) also show a consistent tendency of changes in the study period 1973 – 1983. An increase, or stabilization has been noted of the small (size ~ 0.200 mm) cladoceran *Chydorus sphaericus* O. F. Müller in all the lakes, including L. Mikorzyńskie and L. Licheńskie, where a very strong decrease in numbers of this species was recorded in 1973, as compared with its numbers in 1966. In the deeper lakes, L. Mikorzyńskie and L. Ślesińskie *Bosmina longirostris* (O. F. Müller) was found, being particularly abundant at the control station (station I) in L. Ślesińskie. In summer, in normal lakes this species occurs in cooler layers, i.e., in the meta- and hypolimnion. Thus, its absence from L. Licheńskie, which is shallow and with a warm epilimnion, is understandable. In 1983, considerable numbers were recorded of *Daphnia cristata* G. O. Sars, a species previously found only sporadically.

A different situation is found as regards changes in total numbers (nauplii, copepodids and adult forms) of the filter-feeding copepods Diaptomidae represented by: *Eudiaptomus graciloides* (Lilljeborg) (dominant) and *E. gracilis* (G.O. Sars) (less numerous) (of an average body size of 0.31 mm – nauplius, 0.850 mm – copepodid, 1.23 mm – adult forms). In their study Hillbricht-Ilkowska et al. (1976) have found that the observed low numbers and their decrease in L. Licheńskie and Mikorzyńskie in 1973 vs. 1966 may be the result of a higher sensitivity of these species to high temperatures, as their fecundity recorded in warmer lakes or sites was lower than at colder stations. Data obtained from later studies (1978 – 1983) indicate, however, an increase in numbers of the Diaptomidae, particularly significant in L. Mikorzyńskie and L. Ślesińskie, and less so in L. Licheńskie (Fig. 3). Similarly different is the occurrence of the predaceous, large-bodied cladoceran *Leptodora kindtii*. Its absence or low abundance recorded in the period 1966 – 1973 was interpreted, following Patalas's (1970) view, as resulting from a high "mechanical" mortality brought about by the water turbulence and entrainment in the cooling system. In 1978, definitely large numbers of the species were recorded in all the lakes considered (Fig. 3).

The zooplankton group of the most conspicuous numerical growth in 2nd period of the functioning of the cooling system (1973 – 1983) generally included rotifers (Fig. 4), and particularly a few small species (0.100 – 0.160 mm in size), feeding by filtration or sedimentation, preferring fine nannophytoplankton and small-particle suspensions containing bacteria and detritus (Gliwicz 1974, Hillbricht-Ilkowska 1977). They include primarily *Keratella cochlearis* (Gosse) (most intensive

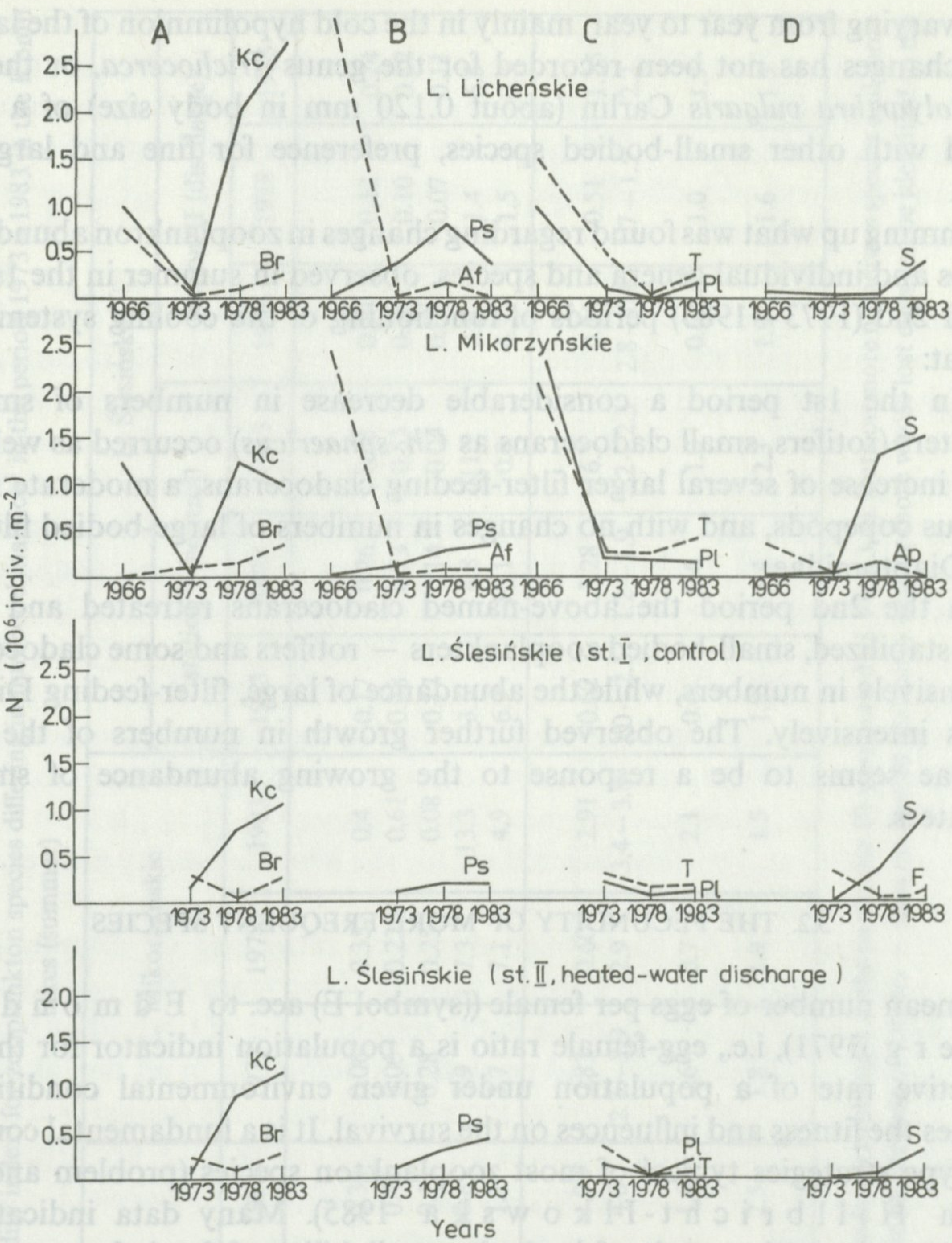


Fig. 4. Variation in the mean summer numbers ($N$, $10^6$ indiv. $\cdot$ m$^{-2}$) of plankton rotifers in the Konin lakes in different study years [1]

A, B — small bacteria- and detritus-feeders (Kc — *Keratella cochlearis*, Br — *Brachionus* sp. div., Ps — *Pompholyx sulcata*, Af — *Anuraeopsis fissa* Gosse), C — actively catching nannoplankton cells or sucking bigger phytoplankton (Pl — *Polyarthra vulgaris*, T — *Trichocerca* sp. div.), D — catching or filtering, typical of circulation periods, such as *Synchaeta* sp. div. (S), predatory, such as *Asplanchna priodonta* Gosse (As), or cold-liking such as *Filinia terminalis* + *Keratella hiemalis* (F) [2]

[1] For 1966 — acc. to Patalas (1970), for 1973 — acc. to Hillbricht-Ilkowska et al. (1976).
[2] Mainly in the hypolimnion

growth, seen throughout the system and at all stations), *Pompholyx sulcata* Hudson and *Brachionus* sp. div. (mainly *B. angularis* Gosse). Since 1978 the increase in numbers has been recorded of the genus *Synchaeta* (especially the small species *S. kitina* Rousselet), a genus and species found particularly during the spring and autumn circulation in "normal" lakes. At station I (control) in L. Ślesińskie the cold water species, *Filinia terminalis* (Plate) and *Keratella hiemalis* Carlin have occurred in numbers varying from year to year, mainly in the cold hypolimnion of the lake. Such a trend of changes has not been recorded for the genus *Trichocerca,* or the common species *Polyarthra vulgaris* Carlin (about 0.120 mm in body size) of a higher, as compared with other small-bodied species, preference for fine and larger nanno-plankton.

In summing up what was found regarding changes in zooplankton abundance, total for groups and individual genera and species, observed in summer in the 1st (1973 vs. 1966) and 2nd (1973 – 1983) periods of functioning of the cooling system, it can be stated that:

(1) In the 1st period a considerable decrease in numbers of small-bodied zooplankters (rotifers, small cladocerans as *Ch. sphaericus*) occurred as well as a very intensive increase of several larger filter-feeding cladocerans, a moderate increase of predaceous copepods, and with no changes in numbers of large-bodied filter-feeders, such as Diaptomidae.

(2) In the 2nd period the above-named cladocerans retreated and next their numbers stabilized, small-bodied zooplankters – rotifers and some cladocerans, grew very intensively in numbers, while the abundance of large, filter-feeding Diaptomidae grew less intensively. The observed further growth in numbers of the predatory Cyclopidae seems to be a response to the growing abundance of small-bodied zooplankters.

### 3.2. THE FECUNDITY OF MORE FREQUENT SPECIES

The mean number of eggs per female ((symbol E) acc. to Edmondson and Winberg 1971), i.e., egg-female ratio is a population indicator for the potential reproductive rate of a population under given environmental conditions which determines the fitness and influences on the survival. It is a fundamental component of the "*r*" type strategies typical of most zooplankton species (problem and literature survey in Hillbricht-Ilkowska 1985). Many data indicate that the egg-female ratio is the result of both the availability of food, factors accelerating individual growth (e.g. temperature) and egg production (e.g. effect of the varying pressure of fish and other predators). If the changes of egg-female ratio values are consistent with the direction of changes in numbers, it may indicate that the rate of population growth realized in a habitat is primarily the result of an increased reproduction of individuals, or that the latter is greater than the losses of individuals; if not consistent with the direction of abundance changes, they may indicate a high-rate elimination of individuals from the population.

Presented in Table 3 are the mean values, for a 2-week summer period, of the fecundity of the more abundant rotifer and crustacean species, particularly those responsible for the changes observed during the 10-year period (1973 – 1983). In fact, in the period 1973 – 1983 in each of the lakes the fecundity of most species increased, independently of the changes in abundance discussed in the preceding section.

Generally, crustacean fecundity is of the same magnitude as in "normal" lakes, or even higher.

Table 3. Mean number of eggs per female (*E*, fecundity index) for zooplankton species differing in number dynamics[1] in the period 1973 – 1983 in the Konin lakes (summer)

| Group, species | L. Licheńskie | | | L. Mikorzyńskie | | | L. Ślesińskie | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | | | station I (control) | | | station II (discharge) | | |
| | 1973 | 1978 | 1983 | 1973 | 1978 | 1983 | 1973 | 1978 | 1983 | 1973 | 1978 | 1983 |
| Increasing numbers: | | | | | | | | | | | | |
| *Keratella cochlearis* | 0.20 | 0.36 | 0.34 | 0.06 | 0.35 | 0.4 | 0.17 | 0.26 | 0.35 | 0.28 | 0.12 | 0.24 |
| *Brachionus angularis* | 0.30 | 0.22 | 0.41 | 0.05 | 0.22 | 0.61 | 0.38 | 0.13 | 0.53 | 0.36 | 0.10 | 0.17 |
| *Pompholyx sulcata* | 0.10 | 0.22 | 0.11 | 0.28 | 0.25 | 0.08 | 0.17 | 0.14 | 0.04 | 0.08 | 0.07 | 0.11 |
| Cyclopidae | 2.2 | 4.3 | 10.8 | 3.9 | 7.3 | 13.3 | 3.5 | 4.8 | 11.2 | 2.3 | 1.4 | 6.5 |
| Diaptomidae | 2.0 | 2.1 | 1.1 | 5.7 | 7.1 | 4.9 | 6.9 | 10.1 | 0.9 | 4.3 | 1.5 | 0.3 |
| Decreasing numbers: | | | | | | | | | | | | |
| *Polyarthra vulgaris* | 1.07 | 1.40 | 1.94 | 0.83 | 0.60 | 2.91 | 0.62 | 3.28 | 6.7 | 0.26 | 0.51 | 1.25 |
| *Daphnia cucullata + longispina* | 2.4 – 1.9 | 3.1 – 2.0 | 4.0 | 2.7 – 2.9 | 2.9 | 3.4 – 3.8 | 3.0 – 2.5 | 1.2 – 1.9 | 2.2 – 2.3 | 2.8 – 0.8 | 1.7 – 1.5 | 2.2 |
| *Diaphanosoma brachyurum* | 0.6 | 0.9 | 1.6 | 0.6 | 0.7 | 2.1 | 0.6 | 0.6 | 1.0 | 0.6 | 1.0 | 1.9 |
| *Bosmina coregoni thersites* | 1.5 | 1.7 | 2.5 | 1.8 | 1.9 | 1.5 | 1.9 | 1.4 | 2.3 | 1.9 | 1.6 | 1.5 |

[1] Taken into account were species with a clear tendency to changes in the particular 10-year period (cf. Figs. 3, 4). Data on more numerous species and those for which egg numbers determination is more reliable (in the case of rotifers – data on species that carry eggs or those whose lost eggs can be identified to the species).

In the case of three cladoceran species for which at first (1966 – 1973) a growth in numbers and then (1973 – 1983) a decline were recorded, fecundity increased in the latter period (*D. cucullata* in lakes Licheńskie and Mikorzyńskie, *B. coregoni thersites* in L. Licheńskie, *D. cucullata* and *B. coregoni* in L. Ślesińskie, *D. brachyurum* in all the lakes) or showed small non-directional changes (Table 3).

In predatory Cyclopidae a continuous growth in fecundity was observed from year to year – the highest fecundity level in 1983 attaining 13 eggs per female (L. Mikorzyńskie). This level is several times higher than that found in "normal" lakes. A similarly steady fecundity change trend, i.e., growth (often severalfold in each successive study year) has been recorded for planktonic rotifers: *K. cochlearis* (a species which has continued to increase its numbers throughout the system), *Brachionus angularis* and *Polyarthra vulgaris* (a species whose numbers varied slightly during the study period). In the latter species the number of eggs comes up to 6 per female, this being a very high value, rarely encountered. Fecundity decrease or a lack of directional changes has been recorded for the rotifer *Pompholyx sulcata* and Diaptomidae (Table 3).

The fecundity of the rotifers and copepods (Diaptomidae and Cyclopidae) at the control station in L. Ślesińskie was as a rule higher than at the heated-water discharge station, which can be attributed not only to a higher sensitivity to temperature (this is particularly true of the copepods), but also to a strong water turbulence which increases egg losses. The latter factor was not raised in the paper by Hillbricht-Ilkowska et al. (1976) as, possibly, accounting for the lower fecundity indices at warmer and intensively mixed stations.

Generally, regardless of changes in numbers, retreating or dominating of the various groups and species in the summer periods of the years 1973 – 1983, a tendency has been observed towards an increase in the reproduction of both small (rotifers) and larger (cladocerans) filter-feeders, and predatory Cyclopidae in all the lakes and at all the study stations, with generally lower increase values at the heated-water discharge site in L. Ślesińskie. Particularly intensive and steady changes (i.e. growth) in fecundity have been recorded for three rotifer species (*K. cochlearis, B. angularis, P. vulgaris*) and predatory Cyclopidae.

### 3.3. AVERAGE INDIVIDUAL BODY SIZE OF MORE FREQUENT CRUSTACEAN SPECIES

The average body size of an adult individual in a planktonic crustacean population is a particularly plastic individual feature indicating the growth rate and time of attainment of the mean final body size in a population under specific temperature and food conditions (on the whole the faster the growth, the smaller the final size), and (above all) the rate of selective elimination by predators, as well as by other elimination factors, e.g., mechanical (a survey of problem and literature in Hillbricht-Ilkowska 1985, Pijanowska 1985). This is particularly true of the crustaceans preferred by fish, i.e., planktonic cladocerans.

In the conditions prevailing in the Konin lakes the effect of all these factors must be expected, that is, a varying mortality due to the entrainment in the cooling system,

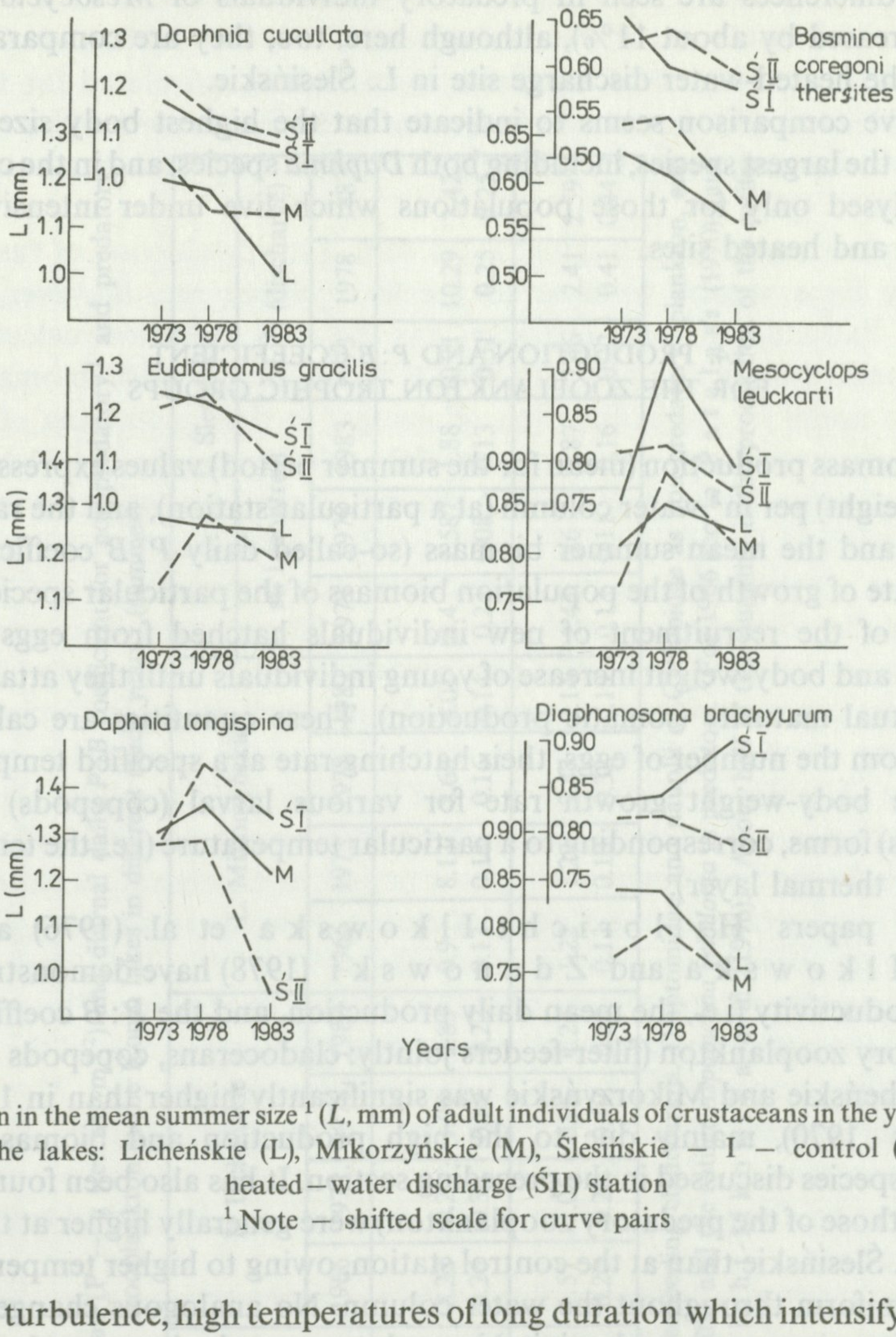


Fig. 5. Variation in the mean summer size [1] (*L*, mm) of adult individuals of crustaceans in the years 1973, 1978 and 1983 in the lakes: Licheńskie (L), Mikorzyńskie (M), Ślesińskie — I — control (ŚI) and II — heated-water discharge (ŚII) station

[1] Note — shifted scale for curve pairs

higher water turbulence, high temperatures of long duration which intensify crustacean growth-rate, and an intensified selective elimination by fish as a result of their increased food requirements at high temperatures. The general effect of all these factors should lead towards a decrease in body size of an adult crustacean individual as the lakes continue to function as cooling-system water source and recipient reservoirs.

This tendency is confirmed by the data set out in Figure 5, although the absolute differences between successive years are sometimes small. They are most conspicuous in the case of the three largest species (food items most preferred by the fish and fish fry), i.e., the genus *Daphnia* and species *Eudiaptomus gracilis* in the most affected lakes (i.e. heated and mixed), that is, L. Licheńskie and L. Ślesińskie (both stations or only the mixed one). In 1983, the mean individual body size was smaller by about 17% than it was in 1973. In smaller cladoceran species (*Bosmina coregoni thersites* and *Diaphanosoma brachyurum*) the differences are on the whole smaller ranged from 6 to11%.

Smaller differences are seen in predatory individuals of *Mesocyclops leuckarti* (Claus) (decreased by about 11%), although here, too, they are comparatively most marked at the heated-water discharge site in L. Ślesińskie.

The above comparison seems to indicate that the highest body size decrease is recorded for the largest species, including both *Daphnia* species, and in the case of all the species analysed only for those populations which live under intensively mixing (turbulence) and heated sites.

### 3.4. PRODUCTION AND *P*:*B* COEFFICIENT FOR THE ZOOPLANKTON TROPHIC GROUPS

Daily biomass production (mean for the summer period) values expressed in weight units (wet weight) per $m^2$ water column (at a particular station), and the ratio between production and the mean summer biomass (so-called daily *P*:*B* coefficient) inform about the rate of growth of the population biomass of the particular species or groups as a result of the recruitment of new individuals hatched from eggs (generative production) and body-weight increase of young individuals until they attain their final size and sexual maturity (somatic production). These quantities are calculated (see Methods) from the number of eggs, their hatching rate at a specified temperature and the average body-weight growth rate for various larval (copepods) or juvenile (cladocerans) forms, corresponding to a particular temperature (i.e., the temperature of a particular thermal layer).

In their papers Hillbricht-Ilkowska et al. (1976) and Hillbricht-Ilkowska and Zdanowski (1978) have demonstrated that in 1973 the productivity (i.e., the mean daily production, and the *P*:*B* coefficient) of the non-predatory zooplankton (filter-feeders jointly: cladocerans, copepods and rotifers) in lakes Licheńskie and Mikorzyńskie was significantly higher than in 1966 (data in Patalas 1970), mainly due to the high production and biomass of several cladoceran species discussed in the preceding section. It has also been found that these values (like those of the predatory zooplankton) were generally higher at the discharge station in L. Ślesińskie than at the control station, owing to higher temperatures there and more uniform throughout the water column. No analogous changes have been found (that is an increased productivity) in predatory zooplankton (predatory stages of Cyclopoida and rotifer *Asplanchna priodonta*), in 1973 in comparison with 1966 in either of the above-mentioned lakes.

The production and *P*:*B* coefficient values (Table 4) for the non-predatory and predatory zooplankton for all the study years indicate that despite wide variation in the production of these trophic groups (in general, consistent with the tendency of changes in their abundance discussed in the preceding sections), the *P*:*B* coefficient for these groups generally remained at a similar level from 1973 on, that is in the 2nd period of the functioning of the cooling system. The rate of daily production of the non-predatory zooplankton in L. Licheńskie and at the discharge station of L. Ślesińskie, that is, two sites with permanently warm and most turbulent water, has been of the range of 0.2 – 0.3, whereas of the range 0.1 – 0.2 in L. Mikorzyńskie and at the control station in

Table 4. Diurnal production (P – g wet wt. · $m^{-2}$) and diurnal daily $P:B$ coefficient for non-predatory[1] and predatory[1] zooplankton in the Konin lakes in different study years[2] (summer)

| Zooplankton group | L. Licheńskie | | | | L. Mikorzyńskie | | | | L. Ślesińskie | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | | | | | st. I (control) | | | st. II (discharge) | | |
| | 1966 | 1973 | 1978 | 1983 | 1966 | 1973 | 1978 | 1983 | 1973 | 1978 | 1983 | 1973 | 1978 | 1983 |
| Non-predatory | | | | | | | | | | | | | | |
| $P$ | 3.22 | 9.2 | 1.99 | 2.83 | 0.9 | 8.13 | 8.66 | 6.01 | 4.4 | 1.587 | 1.88 | 10.71 | 10.29 | 3.42 |
| $P:B$ | 0.26 | 0.36 | 0.30 | 0.22 | 0.13 | 0.18 | 0.16 | 0.14 | 0.23 | 0.08 | 0.13 | 0.31 | 0.25 | 0.25 |
| Predatory | | | | | | | | | | | | | | |
| $P$ | 1.57 | 1.05 | 0.96 | 1.24 | 1.22 | 1.27 | 2.47 | 2.14 | 1.43 | 0.6 | 0.87 | 2.46 | 2.41 | 2.59[3] |
| $P:B$ | 0.20 | 0.20 | 0.19 | 0.23 | 0.13 | 0.10 | 0.32 | 0.19 | 0.13 | 0.11 | 0.16 | 0.22 | 0.41 | 0.44 |

[1] Total of: rotifers, filter-feeding cladocerans, Diaptomidae and nauplii of Cyclopidae as non-predatory plankton, and predatory forms of Cyclopidae and the rotifer *Asplanchna priodonta* as predators. [2] For 1966 acc. to Patalas's (1970) data, 1973 – acc. to Hillbricht-Ilkowska et al. (1976). [3] About half of this quantity is the production of the rotifer *Asplanchna priodonta*.

L. Ślesińskie. The predatory zooplankton increases its biomass at a daily rate of 0.2 – 0.4 in L. Licheńskie and at the discharge site in L. Ślesińskie, and of 0.1 – 0.2 in other lakes. The very high $P:B$ coefficients (up to 0.4), calculated for the summer periods of 1978 and 1983 at the discharge site in L. Ślesińskie are the result of the significant contribution of the predatory rotifer *A. priodonta* which has a very high $P:B$ coefficient (Table 4).

Daily production values calculated as the sum of the production of various species (related only by a similar location in the food chain) are, however, the rough assessments. Particularly rough character has the $P:B$ coefficient calculated as the ratio of the total production of many species to the sum of their biomass. For this reason, more useful for the illustration of changes in the functioning of trophically different zooplankton groups is an analysis of the relative and the absolute production of smaller and more homogenic trophic groups. In the non-predatory zooplankton these are: rotifers as the small filter-feeders preferring the finest ($\leqslant 10$ $\mu$m), bacteria-detritus food suspension and the cladocerans and copepods as the filter-feeders preferring small and medium particle size (up to $\leqslant 20$ $\mu$m), including nannoplankton. In the predatory zooplankton these are: predatory rotifers (primarily *A. priodonta*, which in effect is an omnivorous species) and predatory stages of Cyclopidae.

As has been mentioned in section 3.1, rotifers, especially non-predatory rotifers, do not represent a significant contribution to the biomass of the zooplankton as a whole. Their production rate ($P:B$ coefficient) in summer increased steadily in all the lakes and at all stations (Table 5) throughout the study period, attaining values close to 1, which means that their average biomass doubles during 24 hours in summer. This increase results both from the increase in biomass seen since 1973 and/or 1978 (depending on the lake and site) and the increase (more intensive) in daily production. The cause of this is the increased fecundity, discussed in the preceding sections, of most of the species, and particularly the increased fecundity of dominanting species, e.g., *K. cochlearis*. A similar, steady increase of the $P:B$ coefficient has been recorded for *A. priodonta*, a low-abundance species of relatively high biomass which is omnivorous. The $P:B$ ratios come up to about 2 – 5 owing to the very high production of embryos in this viviparous species.

An analysis of the productivity values of the rotifers in different years and lakes does not reveal any significant differences between lakes – the above long-term change trend is similar in all the study lakes and sites.

For the filter-feeding crustaceans no steady production rate increase is found, similar to that of the rotifers, but conversely – a tendency towards its decrease (Table 5). This is particularly true of large cladocerans, such as both of the *Daphnia* species and *Eudiaptomus graciloides, Bosmina coregoni,* and to a lesser extent – *Diaphanosoma brachyurum.* A generally high, or even increasing production rate is seen in the non-predatory nauplial stages of Cyclopidae and the small cladoceran *Chydorus sphaericus.* Values of the daily $P:B$ coefficient of the predatory stages of Cyclopidae are relatively stable within the lakes, in different years, or variable in random manner (Table 5).

Table 5. Mean summer daily $P:B$ coefficient (daily production to biomass in units of wet weight) for different trophic groups and zooplankton species of the Konin lakes in different years of study [1]

| Species | L. Licheńskie | | | | L. Mikorzyńskie | | | | L. Ślesińskie | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | | | | | st. I (control) | | | st. II (discharge) | | |
| | 1966 | 1973 | 1978 | 1983 | 1966 | 1973 | 1978 | 1983 | 1973 | 1978 | 1983 | 1973 | 1978 | 1983 |
| Rotifers: | | | | | | | | | | | | | | |
| non-predatory | 0.29 | 0.39 | 0.54 | 0.89 | 0.11 | 0.20 | 0.31 | 1.26 | 0.41 | 0.36 | 0.87 | 0.47 | 0.14 | 0.63 |
| predatory [2] | 0.15 | – [3] | – | 1.92 | 0.13 | 0.16 | 2.04 | 5.01 | 0.63 | 1.07 | 1.75 | 1.4 | 1.3 | 2.42 |
| Crustacean filter-feeders: | | | | | | | | | | | | | | |
| *Daphnia cucullata* + *Daphnia longispina* | 0.28 | 0.45 | 0.25 | 0.15 | 0.13 | 0.17 | 0.15 | 0.11 | 0.17 | 0.05 | 0.07 | 0.30 | 0.24 | 0.17 |
| *Bosmina coregoni thersites* | 0.37 | 0.22 | 0.11 | 0.02 | 0.25 | 0.19 | 0.19 | 0.16 | 0.23 | 0.09 | 0.11 | 0.25 | 0.22 | 0.28 |
| *Diaphanosoma brachyurum* | 0.34 | 0.32 | 0.30 | 0.24 | 0.11 | 0.18 | 0.17 | 0.16 | 0.32 | 0.09 | 0.15 | 0.29 | 0.29 | 0.25 |
| *Eudiaptomus graciloides* | 0.14 | 0.20 | 0.05 | 0.05 | 0.13 | 0.12 | 0.11 | 0.08 | 0.32 | 0.12 | 0.06 | 0.17 | 0.21 | 0.07 |
| *Chydorus sphaericus* | – [1] | – | 0.20 | 0.35 | – | – | 0.09 | 0.17 | – | 0.07 | 0.08 | – | 0.10 | 0.08 |
| Nauplii of Cyclopoida | – [3] | 1.2 | 1.75 | 1.13 | – | 0.3 | 1.0 | 1.0 | 0.64 | 0.39 | 0.68 | 1.09 | 1.72 | 1.65 |
| Predatory crustaceans Cyclopidae (copepodids and adult forms) | 0.20 | 0.19 | 0.19 | 0.19 | 0.14 | 0.10 | 0.19 | 0.14 | 0.11 | 0.07 | 0.09 | 0.18 | 0.29 | 0.21 |

[1] For 1966 acc. to Patalas (1970), for 1973 – acc. to Hillbricht-Ilkowska et al. (1976). [2] Only the genus *Asplanchna* (mainly *A. priodonta*). [3] No data, or occurring only sporadically, which makes $P:B$ assessment impossible.

The above phenomenon of a decreasing or relatively stable production rate of non-predatory and predatory crustaceans is the result of variable absolute values of the production and biomass of individual species, sometimes of an opposite tendency. Generally these are: a decrease (from 1973 on) in the production and biomass (and the $P:B$ ratio) of the several cladoceran species discussed above, a lack of directional changes in production, but with a biomass growth in Diaptomidae (hence also a lower $P:B$), and a growth in the biomass and production of small and less abundant cladocerans and of nauplial and predatory forms of Cyclopidae, which generally results in a stabilized or increasing rate of their production measured by the $P:B$ ratio.

However, almost all the $P:B$ values recorded for particular species of predatory and non-predatory crustaceans at the discharge site in L. Ślesińskie and L. Licheńskie are as a rule higher than those recorded for stratified systems. This is the result of a higher temperature, and uniform throughout the water column (Table 5).

Compared with the above relative stabilization of the biomass and production of the predatory (adult and copepodid) forms, the clear increase in the fecundity and total numbers of Cyclopidae (discussed in section 3.1 ) (together with the non-predatory nauplial stages) indicates that in the period 1973 – 1983 the expansion of this group in the whole lake system dependent primarily on the youngest, herbivorous larval forms, that is, nauplii. This is confirmed by the assessment of the production and biomass of these forms for the years 1973, 1978 and 1983, which shows that in this period their productivity (both the production and biomass) increased 2 – 3-fold in each lake and at each station. For instance, in L. Licheńskie the daily production of these forms was in 1983 found to have increased in comparison to that recorded for 1973 from 0.17 to 0.36, in L. Mikorzyńskie from 0.20 to 0.63, in L. Ślesińskie (at the discharge station) from 0.35 to 0.58 $g \cdot m^{-2}$. The parallel growth of their biomass resulted in the stable, high values (shown in Table 5) of the $P:B$ coefficient of the range of 1.0.

This indicates that the main changes in the structure of the zooplankton of the whole lake system tend towards the dominance of its small-bodied components.

### 3.5. TROPHIC EFFICIENCY IN THE PLANKTON – RELATIVE RATE OF PRIMARY PRODUCTION AND THE EFFICIENCY OF ITS UTILIZATION BY THE NON-PREDATORY AND PREDATORY ZOOPLANKTON

The ratio between the production of herbivorous (non-predatory zooplankton) and primary production of the phytoplankton ($EP_{\text{herb.}}$), and the analogous ratio of the production of predators to that of non-predators ($EP_{\text{pred.}}$) indicate the degree of the so-called inter-level efficiencies, i.e., utilization of the energy contained in one trophic level by the next trophic level. They are used for comparing the functioning and rate of energy flow in different ecological systems (H i l l b r i c h t - I l k o w s k a 1977). When estimated for the groups consisting of many species and calculated on the basis of the sum of their production (including the primary production of the phytoplankton), with many assumptions and simplifications made, the values of these indices are in reality very diverse and variable. Hence their possible usefulness depends not on their absolute value, but rather on the possibility to recognize the trend of changes in the trophic efficiency of a particular system if a sufficiently large set of data is available, e.g., for different time periods and/or for different sites.

For lakes Licheńskie and Mikorzyńskie there are available data on the average daily gross production of the phytoplankton for different years (Z d a n o w s k i 1976, 1988), characterizing the summer period (an average value for the summer period from measurements made every 2–3 days during a fortnight), as well as the data on the production of non-predatory and predatory zooplankton discussed in this paper. By using appropriate calculation methods (see Table 6), the same as those used by P a t a l a s (1970), production values were obtained for each trophic link in $kJ \cdot m^{-2} \cdot 24\ hours^{-1}$. The variation of the calculated $EP_{herb.}$ and $EP_{pred.}$ indices is considerable (Table 6). It results from the long-term variability of the production of the phytoplankton (Z d a n o w s k i 1988) and its consumers (discussed in section 3.4 ).

Table 6. Daily gross production (in $kJ \cdot m^{-2} \cdot 24\ hours^{-1}$) of phytoplankton ($GPP$)[1], non-predatory and predatory zooplankton (summer) and inter-level trophic efficiency coefficients ($EP$)[2] in lakes Licheńskie and Mikorzyńskie in different study years

| Parameters | L. Licheńskie | | | | L. Mikorzyńskie | | | |
|---|---|---|---|---|---|---|---|---|
| | 1966 | 1973 | 1978 | 1983 | 1966 | 1973 | 1978 | 1983 |
| $GPP$[1] | 107.2 | 57.4 | 60.3 | 73.3 | 55.3 | 64.9 | 52.8 | 73.3 |
| zooplankton | | | | | | | | |
| non-predatory | 4.4 | 12.7 | 2.8 | 3.9 | 1.3 | 11.2 | 12.0 | 8.3 |
| predatory | 2.2 | 1.5 | 1.3 | 1.4 | 1.7 | 1.8 | 3.4 | 3.0 |
| $EP_{herb.}$[2] | 0.04 | 0.22 | 0.05 | 0.05 | 0.02 | 0.17 | 0.23 | 0.11 |
| $EP_{pred.}$[2] | 0.49 | 0.11 | 0.48 | 0.35 | 1.33 | 0.16 | 0.29 | 0.36 |

[1] Acc. to Z d a n o w s k i (1988). [2] $EP_{herb.}$ – ratio of the production of non-predators to $GPP$, $EP_{pred.}$ – of non-predators to predators. Adopted acc. to P a t a l a s (1970), 1 mg $O_2$ = 14.69 J, 1 mg wet wt. of zooplankton = 1.38 J

In L. Licheńskie, where the primary production of the phytoplankton was found in 1973 to have dropped in comparison to 1966 (Z d a n o w s k i 1976) and then slightly increased and stabilized at a level of about 54–71 $kJ \cdot m^{-2} \cdot hours^{-1}$, there occurred at first an almost 5-fold growth (described in H i l l b r i c h t - I l k o w s k a et al. 1976) and then (in the years 1978–1983) a decrease in its utilization by non-predatory zooplankton to a level of about 0.05. It is a result of a considerable fall of the production of the primary consumers (see section 3.4 ). The general conclusion from this is that the greater proportion of the gross production of the phytoplankton is not used by the herbivores. It must be remembered, however, that it is not known what proportion of the actually produced phytoplankton biomass is available to the consumers, as the respiration loss of the phytoplankton is not known. High indices of the use of the production of the herbivores by their predators (of the range of 0.3–0.4) may indicate a very efficient energy flow in this trophic link.

In L. Mikorzyńskie, during the first year of the effect of warm waters on its epilimnion, i.e., in 1973, no significant changes (only a slight growth) in primary production could be seen as compared to the control year 1966. In subsequent years the moderate increase was noted, but the value recorded in the summer of 1983 is the highest for the study period, being the same as that found in L. Licheńskie. As a result of at first a very intensive (1973) growth of the production of herbivores and then (1978 – 1983) its relative stabilization, the index of utilization of primary production by this trophic system ($EP_{herb.}$) was found in 1973 to be severalfold higher than in 1966, whereas in the later years it became stabilized at the level of about 0.1 – 0.2, i.e., several times higher than in L. Licheńskie in the same period.

The indices of utilization of the production of herbivores by predators ($EP_{pred.}$) are high and similar in both of these lakes, showing a similar trend of long-term changes – a decrease in 1973, as compared to 1966, and a severalfold growth in the later years.

One may venture an opinion that when both of these lakes function in the cooling system, the values of their primary production become similar, but because of differences in the rate of production of its consumers, this primary production is not fully utilized in the shallower of the lakes (where the water-flow rate is high), and is utilized to a larger extent in the deeper of the lakes (which is more stable hydrologically).

The use of the production of herbivores by the plankton predators is generally high, similar in both the lakes.

The above general conclusion agrees with the direction of changes in numbers and production of the herbivores of both the lakes. The lowest values of non-predatory zooplankton production are recorded in L. Licheńskie, where they are severalfold lower than in L. Mikorzyńskie, and generally lower than in L. Ślesińskie (Table 4).

As there were data on the primary production in both the above lakes for the summer periods of the four study years as well as estimation of the mean phytoplankton biomass (acc. to Spodniewska 1984, Simm 1988a, and Sosnowska's data acc. to Hillbricht-Ilkowska and Zdanowski 1978), the daily $P:B$ coefficient was estimated for the phytoplankton, i.e., the relative rate of its production. Appropriate conversion factors were used to express both the final values in units of carbon (Table 7).

As can be seen from Table 7, the phytoplankton biomass of both the lakes is generally low – especially if compared with the quantities for the summer period in other eutrophic lakes (Spodniewska 1983), lower than the values characteristic of water blooms (about 10 mg·l$^{-1}$). In shallow L. Licheńskie, after its inclusion in the so-called great cooling cycle (i.e., from 1973 on), there occurred a rapid fall in algal biomass (about tenfold), and the lowest values were recorded in the last study year, i.e., in 1983. In L. Mikorzyńskie there was a temporary increase in phytoplankton biomass in 1973 and 1978, as compared with 1966, and also a twofold decrease in biomass in the last study year, i.e., 1983. With a relatively stable and/or slightly variable gross photosynthetic production in both the lakes, the above changes in algal biomass result in a very high production rate, i.e., the daily $P:B$ ratio, its value often is 1, and sometimes as high as 4, being always higher in L. Licheńskie (Table 7). The actual division rate of algal cells must of course be lower (the calculated values concern gross production), but even so, the above indices are very high, compared with,

Table 7. Phytoplankton composition, production, and assessment of the $P:B$ coefficient for the phytoplankton (summer, epilimnion) in lakes Licheńskie and Mikorzyńskie in different years

| Lake and year | Biomass mg wet wt. $\cdot l^{-1}$ | Composition, dominant | Gross primary production[4] g $O_2 \cdot m^{-2} \cdot 24$ hours$^{-1}$ | $P:B$[5] |
|---|---|---|---|---|
| Licheńskie | | | | |
| 1966[1] | 30 | diatoms, blue-green algae | 7.3 | 0.3 |
| 1973[1] | 3.1 | diatoms | 3.9 | 1.57 |
| 1978[2] | 3.7 | green algae, diatoms | 4.1 | 1.38 |
| 1983[3] | 1.5 | green algae, blue-green algae | 4.98 | 4.15 |
| Mikorzyńskie | | | | |
| 1966[1] | 2.7 | blue-green algae, green algae | 3.7 | 0.93 |
| 1973[1] | 5.1 | diatoms | 4.7 | 0.62 |
| 1978[2] | 7.1 | diatoms, green algae | 3.6 | 0.35 |
| 1983[3] | 1.8 | green algae, dinoflagellates, diatoms, blue green algae | 4.98 | 1.88 |

[1] Acc. to Hillbricht-Ilkowska and Zdanowski (1978), Simm (1988a). [2] Acc. to Spodniewska (1984). [3] Acc. to Simm (1988a, 1988b). [4] Acc. to Patalas (1970), Zdanowski (1976, 1988). [5] In units of carbon. Assumption: C = 5% in phytoplankton wet wt., 1 mg $0_2$ = 0.375 mg C. In the calculation the epilimnion (trophogenic layer) was assumed to be 6 and 11 m thick, respectively, in lakes Licheńskie and Mikorzyńskie.

e.g., the Masurian lakes of normal temperature and mictic cycles (Hillbricht-Ilkowska and Spodniewska 1969, Hillbricht-Ilkowska et al. 1972). The cause of this may be the dominance in the phytoplankton of small-cell species (acc. to Simm 1988a – 40–60%), mainly green algae and diatoms. The relative production rate of these groups is high on account of the high ratio of cell surface area to its weight.

## 4. DISCUSSION

In the 2nd decade (1973–1983) of the functioning of the lakes near Konin as permanent or temporary recipients of heated waters, when the intensity (depth of the mixed layer) and duration of water mixing increased in all the lakes, higher temperatures prevailed, the permanent thermal zones occurred, the chemical compositon of the water became uniform and so did other environmental conditions in the lakes in comparison to the 1st period of the functioning of the lakes (when the above changes were less marked or spatially limited), the following changes in the structure and productivity of the plankton were noted:

(1) A tendency towards the dominance of small-bodied zooplankton species feeding on fine-particle suspension (rotifers, small cladocerans, the youngest stages of

predatory species), whose biomass, numbers and daily production rate (*P* : *B* coefficient) continually increased. This was accompanied by a tendency to retreat (among other things also production rate decrease) of bigger filter-feeders, particularly the genus *Daphnia* or *Eudiaptomus*. During the 1st decade of the functioning of the lakes as the cooling system these consumers responded by a very intensive growth of production and biomass (Hillbricht-Ilkowska et al. 1976, Hillbricht-Ilkowska and Zdanowski 1978).

(2) Related to the above structural changes in the non-predatory zooplankton community an increase or a relative stabilization of productivity of invertebrate predators, was recorded that is predatory rotifers and copepods. In this "prey--predator" system an increase in trophic efficiency occurs. Consequently, the structure type of the zooplankton can be defined as a "rotifer-copepod" system.

(3) The above tendency was realized in spite of the fact that in summer the fecundity, expressed as the average number of eggs per individual, of the successful and "non-successful" species was higher in the study years than in the previous period, and that the average size of an adult individual in crustacean populations (predatory and non-predatory cladocerans or copepods) tended to decrease.

(4) The above tendency of structural changes in the zooplankton community towards the dominance of forms feeding on fine-particle suspension (mainly detritus and bacteria) was, however, accompanied by a very high production rate of the phytoplankton dominated by small forms, that is, nannophytoplankton, green algae, small diatoms, for which a very high *P* : *B* is found despite very low values of biomass (decreased during the study period) and a relatively stable production rate (Simm 1988b, Zdanowski 1988).

Searching for factors to explain the above tendency of changes in the plankton of lakes which are permanently heated and intensively mixed, one must take into account the possibility of a synergetic effect of many factors. The intensive mixing of the lakes at higher temperatures (but not attaining the lethal levels, Hillbricht-Ilkowska and Zdanowski 1988b) is accompanied by a reduction in their trophic state, like nutrient content (Zdanowski et al. 1988), by a considerable inorganic pollution, including suspensions stimulate that water turbidity (Zdanowski et al. 1988), water alkalization and salinity (ibidem). Finally structural changes in the ichthyofauna occurred which may change the pressure on the zooplankton. Despite the observed steady decline in the fish catches of the Konin lakes (Hillbricht-Ilkowska and Zdanowski 1988b, Wilkońska 1988) the dominating of the small species and forms of a relatively higher demand for food was noted.

It seems that the observed changes in the zooplankton may be the result of differences in the resistance and/or selective mortality, of the species to (primarily) two factors: a high water turbulence and fish pressure which both operate in the relatively good food conditions for all consumers as it is manifested by their high fecundity.

High temperatures do not seem to be the main factor diversifying the chance of the zooplankton to survive and grow in numbers (except a few species inhabiting the cold layers of the control station in L. Ślesińskie or occurring in spring (Ejsmont-Kar a b i n and W ę g l e ń s k a 1988)), for, as has been pointed out in H i l l-b r i c h t - I l k o w s k a and Z d a n o w s k i (1988a), Z d a n o w s k i et al. (1988), high temperatures do not attain a level lethal for these mostly eurythermic species.

Rotifers in general, and particularly the genera of small-bodied forms (e.g., *Keratella, Polyarthra, Synchaeta*) have a higher resistance to a permanent and high water turbulence than the bigger cladocerans. This was indicated by the studies carried out by J. Ejsmont-Karabin and T. Węgleńska (unpublished data) on a dam-reservoir with a water-exchange rate of about 5 – 10 days (thus comparable to the 7-day cycle of surface waters in the lake system near Konin) and by a comparison of the in-stream parts of this system with the off-stream parts which revealed higher rotifer numbers and productivity in the former. According to the hypothesis put forward by the persons mentioned, this resistance consists in a very fast replenishing of a continually "thinned" population through an intensive egg production and at 25 – 28°C individual growth. For small species of rotifers this growth rate can last from several to over a dozen hours, at least several times shorter than in the crustaceans. Moreover, the size of an adult cladoceran female is as a rule smaller when the growth is fast, which in turn has a limiting effect on the number of eggs laid, in accordance with the relationship between the size of an individual and the number of eggs in a clutch (e.g. W ę g l e ń s k a 1971). In the lakes near Konin a tendency has been found towards a reduction in average body size of an individual, especially in bigger cladoceran species (*Daphnia, Diaphanosoma*).

J. Ejsmont-Karabin (unpublished data) estimated the elimination of rotifer individuals for each study station in the Konin lakes by comparing their production for successive 2 – 3-day periods (summer) with their respective abundance values. She has found that losses of individuals at particular stations usually amount to 60 – 100%. This is proof that the above hypothesis explaining the dominance of small rotifers in high-rate through-flow or turbulent aquatic environments can be applied to the situation observed in heated lakes.

It follows that the rate of replenishment of the steadily "thinned" rotifer population would be a feature of their life strategy ensuring their predominance over the cladocerans which are bigger, grow more slowly and are relatively less fecund in the Konin lakes where there is a long-term continuous, high-rate warm-water flow. One other factor which intensifies the above success of rotifers would be the almost twice lower entrainment mortality (about 50%) in comparison with the crustaceans, as it was estimated by T u n o w s k i (1988).

A factor that favours a high fecundity of the rotifers and the remainder of the zooplankter species, irrespective of the tendency of changes in their numbers, is both the high-rate multiplication of the fine-particle (thus available to the filter-feeding cladocerans) nannoplankton and – as suggested by E j s m o n t - K a r a b i n and W ę g l e ń s k a (1988) – the continual input of detritus and bacterial suspension dispersed by water motion and decomposed by the bacterioplankton at high temperatures and oxic conditions. This seems to be confirmed by the high turbidity of the waters of the Konin lakes (particularly the shallow ones) (Zdanowski et al. 1988).

However, the increase in fecundity of the cladocerans, observed in the lakes (this increase is smaller, relatively, than that of the rotifers) in the last decade, does not seem to be sufficient to compensate for their losses, due to "entrainment mortality" and continual population "thinning" brought about by the flow of the water.

Another agent, whose eliminating selective pressure must not be overlooked when the Konin lakes are considered, is the predation of fish, particularly of small forms of relatively high food requirements at high temperatures. Their greater proportion in the catches during the last decade (Hillbricht-Ilkowska and Zdanowski 1988b) generally coincides with the above-described structure changes of the zooplankton, i.e., elimination of bigger cladocerans which dominated in the zooplankton of the 1st period of the functioning of the system. As has been known (for literature survey see Hillbricht-Ilkowska 1985), this component of the zooplankton is preferred by eye-orientated fish, and they respond to a selective elimination by a reduction in both numbers and individual body size of ovigerous females. Continuous water mixing may make it impossible for these animals to escape or migrate into deeper "dark" waters. Small members of the zooplankton (especially rotifers) are on account of their size more successful, hence, as it has been known, under the strong fish pressure, rotifers and predatory copepods become dominating in the zooplankton (Hillbricht-Ilkowska 1985).

In heated lakes it is difficult to separate these two principal factors, i.e., the selective effect of a higher turbulence (as described above) and fish pressure. Anyway, the effects of both these factors coincides, and it seems to intensify the changes in zooplankton productivity and structure, found in the lakes near Konin in the 2nd decade of their constant operation as receivers of warm waters.

Generally, the mode of functioning and the plankton productivity of the lakes which are constantly heated and mixed can be described as follows: a relatively high rate of phytoplankton production but with a very low level of its biomass and abundance (small form domination) does not determine the productivity of the consumers (low inter-level efficiency indices) whose proliferation depends to a larger extent on the content of detritus and bacteria, permanently maintained by water turbulence and water input from outside. The composition and quantitative relations of the zooplankton result from differences in the "resistance" to various eliminating agencies (continual population "thinning", mortality due to mechanical factors, fish pressure) and different rates of population growth in turbulent and warm waters. This system favours the dominance and high productivity of small forms, particularly rotifers and their invertebrate predators (copepods). The efficiency of production in this link is always high, and increasing. The productivity relationship that has arisen in the 2nd decade of the functioning of the lakes differs from that found earlier in which there was a high productivity in the 1st trophic link (owing to the growth in the production of large filter feeding cladocerans) and a lower one in the 2nd link.

## 5. SUMMARY

In the summer periods of 1978 and 1983, zooplankton composition and abundance, and the size-structure and fecundity of about a dozen plankton rotifer and crustacean species were studied in samples taken every 2–3 days for a fortnight at different stations in three of five lakes (Fig. 1): Licheńskie, Mikorzyńskie and Ślesińskie (Table 1, Fig. 1) constituting the cooling system of two power plants.

The biomass, production and daily $P:B$ coefficient were assessed and compared with data for 1966 according to P a t a l a s (1970) and for 1973 according to H i l l b r i c h t - I l k o w s k a et al. (1976).

In the period up to 1970 (1st period) only L. Licheńskie was heated in its whole volume, only the southern part in L. Mikorzyńskie and L. Ślesińskie was not heated. From 1971 to date (2nd period) in the summer periods L. Ślesińskie has been heated and fed with warm waters from L. Licheńskie, discharged in waterfall mode (due to which the waters of the lake are spatially diversified into a part that is intensively mixed and heated to the bottom, and a control part that is stratified) (Fig. 1, Table 1), discharging part of the warm waters into the northern part of L. Mikorzyńskie (for details see H i l l b r i c h t - I l k o w s k a and Z d a n o w s k i 1988b, Z d a n o w s k i et al. 1988). In both the periods the temperature of the surface and near-bottom water (Table 2), and the retention time (Table 1) changed considerably and became diversified among the lakes. In the summer seasons of 2nd period of the operation the average water retention time for the whole lake system has been about several days.

In 1st period of the operation of the system (as compared with the control system, i.e., before the lakes were heated, or when they were slightly heated) there occurred a considerable fall in numbers and biomass of small-bodied species of zooplankton (particularly rotifers, small cladocerans, as *Chydorus sphaericus*) and a very intensive growth of non-predatory cladocerans (*Daphnia cucullata, Diaphanosoma brachyurum, Bosmina coregoni thersites*) with a moderate increase of predatory copepods (*Mesocyclops leuckarti* and *M. oithonoides* (Sars)) and a lack of changes in large filter-feeders, such as *Eudiaptomus gracilis* and *E. graciloides* (Figs. 2–4).

In 2nd period of the operation of the cooling system there occurred a change in the above tendency: a reduction in numbers (or stabilization at a relatively low level) of the above-named cladocerans, a rapid growth in abundance of rotifers (particularly *Keratella cochlearis, Brachionus angularis, Pompholyx sulcata, Synchaeta* sp. div.), some cladocerans (*Ch. sphaericus, Bosmina longirostris, D. cristata*) and of large filter-feeder copepods (Diaptomidae). There also occurred a further increase in numbers of predatory Cyclopidae, probably in response to the growth in abundance of small zooplankters (Figs. 2–4).

Regardless of the kind of changes in numbers, during the whole study period in all the lakes and at all the stations a tendency towards a higher fecundity (mean number of eggs per adult female) has been recorded primarily for small rotifers and predatory Cyclopidae, followed by bigger filter-feeder cladocerans (Table 3). Several crustacean species tended to decrease the average length of an adult individual (Fig. 5). The above changes were as a rule more conspicuous in L. Licheńskie, the warmest of the lakes which is heated for the longest time, and has the lowest retention time.

At the discharge station in L. Ślesińskie higher values of zooplankton numbers and/or biomass and production (with a lower fecundity) were always recorded than at the control station. In the hypolimnion of the latter cold-water species (*Filinia terminalis, K. hiemalis, B. longirostris* (Figs. 2–4, Tables 3–6)) were found.

Long-term changes in the biomass and fecundity of various species and trophic groups of the zooplankton are followed by changes in their absolute production and $P:B$ ratio – the latter being particularly high in small rotifers, and in the nauplii and predatory forms of Cyclopidae (Tables 4, 5).

From data on algal gross primary production (Z d a n o w s k i 1988) and biomass (S i m m 1988a) the $P:B$ coefficient has been evaluated for this community (Table 7). The values of this coefficient have been found to be particularly high, higher than in "normal" lakes, the highest ones having been recorded in L. Licheńskie (Table 7). Despite the high primary production rate (mainly owing to a considerable reduction in algal biomass) during 2nd period of the operation of the system, and dominance of nannoplankton forms of diatoms and green algae (S i m m 1988a) the indicator of its utilization for the production of the non-predatory zooplankton was very low in this period (in the preceding period the utilization rate was high)

while the rate of utilization of the production of the latter for the production of the predators remained at a high level (Table 6).

A general description of the productivity of the plankton of continually heated and intensively mixed lakes in summer is as follows: a relatively high phytoplankton production rate, but with a very low phytoplankton biomass (small forms predominating), does not determine the productivity of the consumers (low indices of inter-level efficiencies (Table 6)), whose fecundity depends to a larger extent on the supplies of detritus and bacteria continually generated by high temperatures and maintained by a high water turbulence. The composition and quantitative relations of the zooplankton result from differences in the resistance to various eliminating factors (continual "thinning" of the population, mortality due to mechanical factors, fish pressure) and varying rates of population growth in turbulent and warm waters. These conditions favour the dominance and high productivity of small forms, especially rotifers, and their invertebrate predators (copepods). The efficiency of this link is always high (Table 6).

# 6. POLISH SUMMARY

W trzech z pięciu jezior (rys. 1: Licheńskie, Mikorzyńskie i Ślesińskie), stanowiących układ chłodzący dla dwóch elektrowni, przeprowadzono w okresach letnich lat 1978 i 1983 badania składu i obfitości zooplanktonu oraz struktury wielkościowej i płodności kilkunastu gatunków wrotków i skorupiaków planktonowych na podstawie prób pobieranych z różnych stanowisk co 2–3 dni przez okres dwu tygodni (tab. 1, rys. 1).

Oceniono biomasę i produkcję oraz dobowy współczynnik $P:B$ i porównano z danymi z roku 1966 według Patalasa (1970) i z roku 1973 według Hillbricht-Ilkowskiej et al. (1976).

W okresie do roku 1970 (I okres) jedynie J. Licheńskie było podgrzane w całej swojej objętości, w J. Mikorzyńskim jedynie ploso południowe, zaś J. Ślesińskie nie było podgrzane. Od roku 1971 do chwili obecnej (II okres) w okresie letnim zostaje podgrzane J. Ślesińskie i przyjmuje wody ciepłe z J. Licheńskiego zrzucane wodospadowo (co różnicuje przestrzennie wody tego jeziora na ploso silnie mieszane i podgrzane do dna oraz kontrolne stratyfikowane) (rys. 1, tab. 1) i oddaje część wód ciepłych do północnego plosa J. Mikorzyńskiego (szczegóły w pracach: Hillbricht-Ilkowska i Zdanowski 1988b, Zdanowski et al. 1988). W obu okresach temperatura wód powierzchniowych i przydennych (tab. 2), jak też okres retencji (tab. 1) silnie się różnicują. Retencja wód całego systemu w okresie letnim II okresu działania wynosi kilka dni.

W I okresie działania układu (w porównaniu z kontrolnym, tzn. przed podgrzaniem jezior lub ich słabym podgrzaniem) wystąpił silny spadek liczebności i biomasy drobnych składników zooplanktonu (szczególnie wrotki, drobne wioślarki jak *Chydorus sphaericus*), zaś bardzo silny wzrost niedrapieżnych wioślarek (*Daphnia cucullata, Diaphanosoma brachyurum, Bosmina coregoni thersites*) przy umiarkowanym wzroście drapieżnych form widłonogów (*Mesocyclops leuckarti* i *M. oithonoides* Sars)) oraz braku zmian dużych filtratorów jak *Eudiaptomus gracilis* i *E. graciloides* (rys. 2–4).

W II okresie działania układu następuje zmiana powyższych tendencji: tzn. zmniejszanie się (lub stabilizacja na względnie niskim poziomie) liczebności wymienionych wyżej wioślarek, natomiast bardzo silny wzrost obfitości wrotków (szczególnie *Keratella cochlearis, Brachionus angularis, Pompholyx sulcata, Syncheata* sp. div.), niektórych wioślarek (*Ch. sphaericus, B. longirostris, D. cristata*) jak też dużych filtrujących widłonogów (*Diaptomidae*). Obserwuje się również dalszy wzrost liczebności drapieżnych Cyclopidae, który wydaje się reakcją na wzrost obfitości drobnego zooplanktonu (rys. 2–4).

Niezależnie od rodzaju zmian liczebności w całym okresie badań we wszystkich jeziorach i stanowiskach obserwuje się tendencję wzrostu rozrodczości (tj. średniej liczby jaj na dojrzałą samicę), szczególnie drobnych wrotków i drapieżnych *Cyclopidae*, ale również większych filtrujących wioślarek (tab. 3). Obserwuje się tendencję spadku średniej długości dojrzałego osobnika (samicy) kilku liczniejszych gatunków skorupiaków (rys. 5). Powyższe zmiany są na ogół silniej wyrażone w jeziorze najcieplejszym, najdłużej podgrzanym i najbardziej przepływowym (J. Licheńskie).

Stwierdza się stale utrzymujące się większe wartości liczebności i (lub) biomasy zooplanktonu oraz produkcji (przy zmniejszonej płodności) niektórych gatunków na stanowisku przyzrzutowym w J.

Ślesińskim w porównaniu z kontrolnym. W hypolimnionie tego ostatniego stwierdzono występowanie gatunków zimnolubnych (*Filinia terminalis, K. hiemalis, B. longirostris*) (rys. 2–4, tab. 3–6).

W konsekwencji wieloletnich zmian biomasy i płodności różnych gatunków i grup troficznych zooplanktonu następują zmiany w ich produkcji bezwzględnej i współczynnika *P*:*B*, który wzrasta szczególnie w przypadku drobnych wrotków, naupliusów oraz drapieżnych form *Cyclopidae* (tab. 4, 5).

Dysponując danymi o produkcji pierwotnej brutto (Z d a n o w s k i 1988) i biomasy glonów (S i m m 1988a) oceniono również współczynnik *P*:*B* dla tego zespołu (tab. 7) – wartości te okazały się szczególnie wysokie, wyższe niż w jeziorach „normalnych", zaś najwyższe w najbardziej podgrzanym i przepływowym J. Licheńskim (tab. 7). Mimo wysokiego tempa produkcji pierwotnej (głównie za przyczyną silnego spadku biomasy glonów w II okresie działania układu i dominowania form nannoplanktonowych okrzemek i zielenic) (S i m m 1988a), wskaźnik wykorzystania jej na produkcję biomasy niedrapieżnego zooplanktonu jest bardzo niski w tym okresie (w przeciwieństwie do wysokiego wykorzystania w okresie wcześniejszym) przy utrzymującym się wysokim wykorzystaniu produkcji tych ostatnich przez produkcję drapieżników (tab. 6).

Ogólnie charakteryzując: sposób funkcjonowania produktywności planktonu jezior stale podgrzanych i intensywnie mieszanych w okresach letnich stwierdza się, że względnie wysokie tempo produkcji fitoplanktónu przy jednakże bardzo niskiej biomasie (dominują drobne formy) nie stanowi o produktywności konsumentów (niskie wskaźniki wydajności międzypoziomowej (tab. 6)), których rozrodczość zależy bardziej od zasobów detrytuso-bakteryjnych stale generowanych przez wysokie temperatury i utrzymywanych przez wysoką turbulencję wód. Skład i stosunki liczebnościowe zooplanktonu są wynikiem zróżnicowanej odporności na różnorodne czynniki eliminacji (stałe rozrzedzanie populacji, mechaniczna śmiertelność, presja ryb) i zróżnicowanej szybkości rozwoju populacji w warunkach turbuletnych i ciepłych wód. Układ ten sprzyja dominowaniu i wysokiej produktywności form drobnych, zwłaszcza wrotków, oraz ich drapieżników bezkręgowych (widłonogów). Efektywność wydajności w tym ogniwie jest stale wysoka (tab. 6).

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