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LIFE CYCLES OF *CLOËON DIPTERUM* (L.) IN NATURAL ENVIRONMENT

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ABSTRACT

On the basis of two-year studies (1972 and 1973) on the life cycle of *Cloëon dipterum* (L.) in a small, isolated pond (at Wawer, near Warsaw) a yearly incidence of two generations of this species was observed, namely: a long-lived winter generation and a short-lived summer generation. In the development of the winter generation periods of slow, quick, and stopped growth were differentiated. The individuals from the summer generation were developing quickly, without any changes in the growth rate, but they were of a smaller size than those from the winter generation.

1. INTRODUCTION

The larvae of *Cloëon dipterum* of the swimming type (Bertrand 1954) may be often found among the aquatic plants or at the muddy bottom of rivers, slow-running water channels, old river-beds, littoral zone in the lakes, ponds, and small, seasonal water bodies. The conditions of life in this type of environment may undergo considerable changes; the temperature (Gieysztor 1934, Paschalski 1959, Chodorowski 1961) and oxygen content in water (Lewkowicz, Wróbel 1971) often reach the extreme values. The larvae of *Cloëon dipterum* show a high degree of tolerance for the changes in environmental conditions; they endure wide-range fluctuactions of temperature (Whitney 1939, Pattee 1965), decrease in oxygen content in water (Fox et al. 1937, Wingfield 1939, Chaurin 1956) or even oxygen deficiency in water (Kamler 1971), changes in the pH of the environment (Fox, Simmonds 1933, Brittain 1974), and fairly great speed of the water flow (Dorier, Vaillant 1954). *C. dipterum* as a typically eurybiontic species shows also a wide geographical distribution. In the Paleoarctics — this species is very common in the bentic waters all over Europe (Illies 1967). *C. dipterum* occurs mainly in lowlands and sporadically in the water bodies situated higher than 200 m above sea level (Brittain 1974). In its proper environment *C. dipterum* is quite often more numerous than other species of Ephemeroptera (Harnisch 1957, Macan 1962, Ikonomov 1960). In Poland, this is a predominant species among other mayflies (Kamler 1971, Keffermüller 1972) occurring often in great abundance, in the ponds (Sowa 1959).

C. dipterum as a largely prevalent species, frequently occurring in abundance, may play a very important ecological role. Evaluation of the significance of the examined species in its natural environment is not possible without a thorough knowledge of the biology of its development. The data on the incidence and development of *C. dipterum* in various regions of this country are not yet sufficiently complete. These investigations had in view the observation of the life cycle, seasonal changes in body size, growth rate and dynamics of the biomass of *C. dipterum* in natural environment.

2. MATERIAL AND METHODS

The object of the studies was: *Cloëon dipterum* (Linne) of genus *Cloëon* (Leach 1815) — (Ephemeroptera: Baetidae) identified on the basis of the classification key by: Mikulski (1936), Bogoescu (1958) and Sowa (1975).

Samples were collected in a small, isolated water body (surface area — about 40 m^2, depth — to 2 m deep) lying in the region of Wawer (southeastward from Warsaw). The material was sampled using a sieve 30 cm in diameter with 1mm mesh. In the time between March 1972 and December 1973 altogether 65 samples were collected every 7–10 days. The temperature of water was measured each time. The material used for the analysis of the life cycle of *C. dipterum* was preserved in 4% formalin solution.

On the basis of the size of mesothoracic wing-pads evaluated in relation to the consecutive segments of the thorax and abdomen eight stages: seven larval (L_I–L_{VII}) and one nymphal (N) differentiated (Cianciara, in prep. a) within the period of the postlarvular development of *Cloëon dipterum.* In accordance with the above-mentioned criterion, for evaluation of the degree of development, developmental stages of the collected individuals were determined and the percentage of particular stages in the sample was calculated. On the basis of the changes in the ratio of various age-groups in consecutive samples the course of the life cycle of the examined species in its natural environment was inferred.

The individuals caught in the first 14 samplings (from March 10 till June 18, 1972) underwent biometrical measurements (Cianciara, in prep. b); body length (l, mm), width of head capsule (h, mm), wet and dry body weight (W_{wt}, mg) and (W_{dry}, mg) of altogether 1096 individuals from all stages were measured and correlations between various parameters of biometric characteristics of this species development were calculated (Cianciara, in prep. b). The individuals from the consecutive 51 samplings (n=10,928) were classified into definite stages, then the body length was measured and wet weight was calculated on the basis of the earlier determined correlations.

The body length (l, mm) and wet weight (W_{wt}, mg) of an average individual from each sample was calculated. On the basis of the data from two-year studies curves of the growth rate of *C. dipterum* population in winter and summer generations were calculated and compared as well as the rate of the lengthening of the body and increase in wet weight in various seasons of the year.

Mean body length and wet weight of the average individual in the population were determined as well as the mean percentage of various developmental stages in the total numbers and the biomass of *C. dipterum* population in the samples collected in consecutive months of the year. Taking into account the qualitative (changes in the percentage of the different developmental stages in the natural population of *C. dipterum*) and not quantitative character (dynamics of the increase in numbers of this species in the pond) of the collected samples the biomass of the *C. dipterum* population was calculated in a unified sample of 100 individuals. These measurements and calculations made possible the analysis of seasonal changes in the size of the larvae and nymphs of *C. dipterum* and dynamics of the biomass of this species population in natural environment.

3. RESULTS

3.1. LIFE CYCLES OF *C. DIPTERUM* IN NATURAL ENVIRONMENT

In 1972 and 1973 the annual occurrence of two generations of *C. dipterum* was recorded (Fig. 1). The emergence of the first generation was observed throughout May and the first half of June. Large numbers of the youngest forms (larvulae, L_0, and larvae, L_I), of the new generation appeared at the end of June, 1972 (in a sample collected on June 25) and about two weeks earlier in the following year (in a sample collected on June 12, 1973). In both years, at the beginning of August a second short-lasting and less abundant, the emergence of insects of *C. dipterum* had been observed and shortly after that young larvae appeared again.

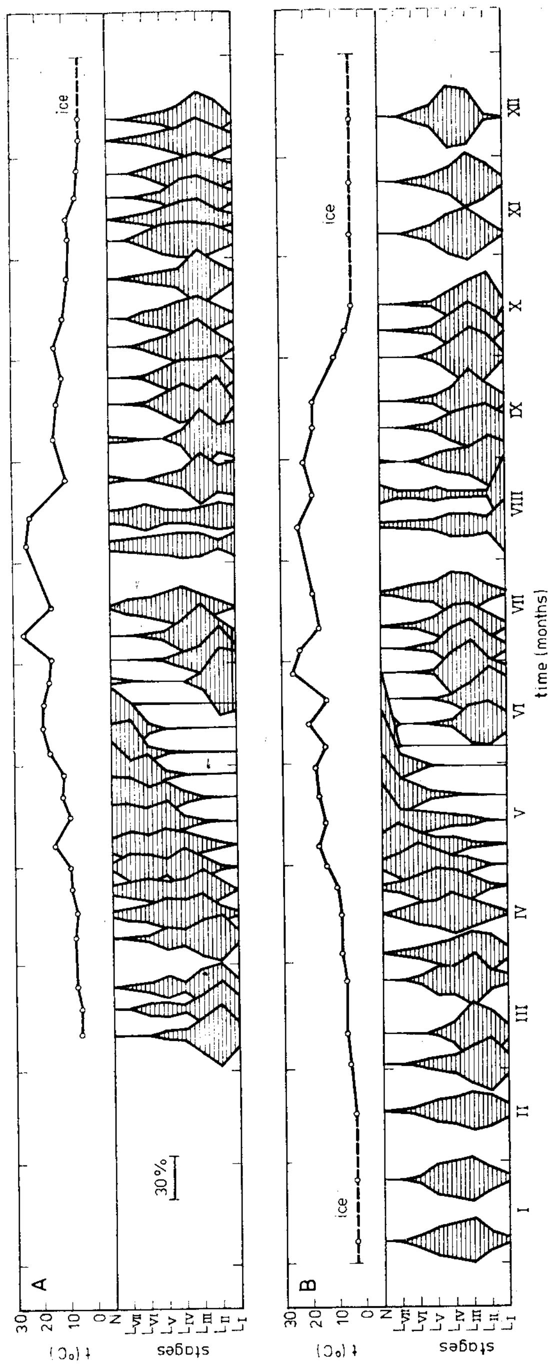

Fig. 1. Water temperature and life cycles of *C. dipterum* in a natural pond (Wawer, near Warsaw) in 1972 (A) and 1973 (B)

In the autumn-spring period (from September till March) young larvae predominated in the samples; at that time L_{II}–L_{IV} stages made up 60–80 % of the collected individuals. The temperature of water in the pond (Fig. 1) was below 10°C and from December 1972 till February 1973 the surface of the pond was covered with ice.

In 65 samples altogether 12,024 individuals of *Cloëon dipterum* (Linne) were recorded. The mean ratio of the different stages of development was as follows: L_I — 9.0%, L_{II} — 18.0%, L_{III} — 23.4%, L_{IV} — 16.2%, L_V — 10.7%, L_{VI} — 7.4%, L_{VII} — 6.2% and N — 6.2%. In the total number (1099) of the collected nymphs females constituted about 53 per cent.

3.2. CHANGES IN THE GROWTH RATE OF *C. DIPTERUM* INDIVIDUALS WITHIN A YEAR

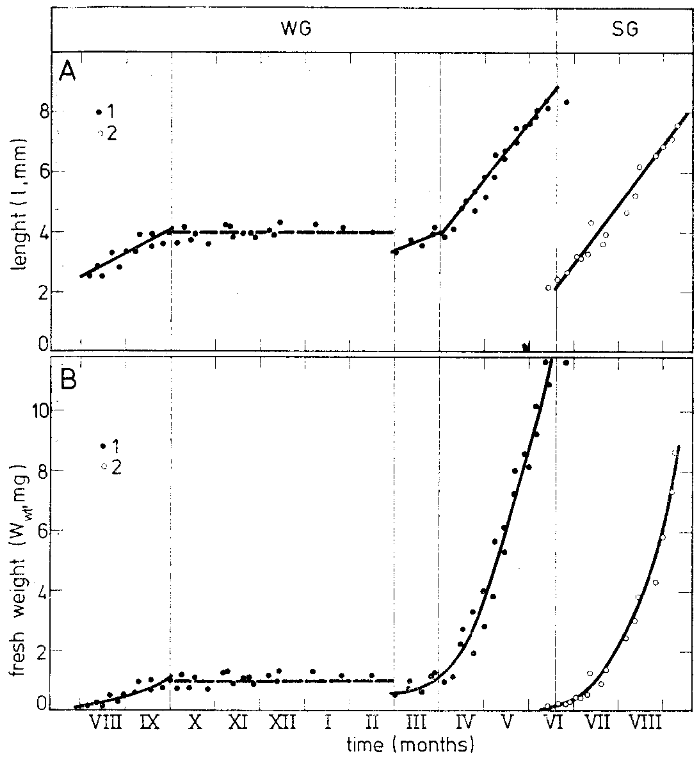

Fig. 2. Growth-rate of individuals from *C. dipterum* natural population. Winter generation (1 — WG), summer generation (2 — SG). A — mean body length (*l*, mm), B — mean wet neight (W_{wt}, mg) of an average individual from the samples collected in 1972 and 1973

In natural environment the changes in the rate of lengthening of the body and the increase in the wet weight of the individuals of *C. dipterum* was irregular, but seasonal (Fig. 2, Tab. I). In the initial period of the development of winter generation (August and September) the growth rate of the individuals in the population is low; 1 mm increase in the body length takes on the average 41.2 days. At the end of that period an average individual in the *C. dipterum* population is about 4 mm long and its wet weight is about 1 mg (Fig. 2). At that time (Fig. 1) young larvae predominate in the samples (L_{II}–L_{IV} larval stages make up 60–80% of the total number of the larvae in the samples). In the autumn-winter period (about 150 days) growth and development are almost stopped; the body length and weight of an average individual remain at the same level (Fig. 2), the age structure of population does not change either (Fig. 1). In spring a large number of smaller individuals of *C. dipterum* appears in the pond and progress in growth is none too

Table I. Comparison of the growth rate (W_{wt} ; mg) body length (l, mm) of *C. dipterum* in the development periods of winter and summer generations. (The specific growth rate (SGR) values were calculated after Winberg (1968)).

Generations	Winter				Summer
Months	May–Sept.	Oct.–Feb.	March	Apr.–June	June–Aug.
Δt_{max} (days)	56	151	31	86	80
$n_{(measurements)}$	12	17	6	21	17
ΔW_{wt} (mg)	0.63	—	0.83	10.06	8.47
SGR* W_{wt} (day^{-1})	0.023	—	0.023	0.026	0.049
$W_\tau = W_0 \cdot e^{q \cdot t}$	$W_\tau = 0.20 \cdot e^{0.024 \cdot t}$				$W_\tau = 0.10 \cdot e^{0.049 \cdot t}$
SGR** $l \left(\frac{\text{day}}{1\text{mm}}\right)$	41.2	—	36.5	15.8	15.3
type of growth	slow	stopped	slow	fast	fast

$$* \; SGR_{W_{wt}} = q = \frac{\log W_\tau - \log W_0}{\tau \cdot 0.4343} = \frac{\Delta W_{wt}}{\tau \cdot W} \; (\text{day}^{-1});$$

$$** \; SGR_l = q^{-1} = \frac{\Delta t}{\Delta l} \left(\frac{\text{day}}{1 \text{ mm}}\right).$$

rapid at the beginning of the season (in March 1 mm lengthening of the body length takes on the average 36.5 days). In the following months (from April till the emergence of insects at the end of June) the growth rate is considerably higher — on the average 1 mm lengthening of the body length within 15.8 days. Thus, in the development of winter generation, lasting over 10 months (T_{max}=324 days), four periods with distinctly varying rate of growth may be differentiated, (Fig. 2 A, Tab. I) as follows: slow (T_{max} =56 days), without growth (T_{max} =151 days), again slow (T_{max} = =about 31 days) and fast (T_{max} =up to 86 days). The curve of the increase in body weight (Fig. 2 B, Tab. I) has the shape of exponential one with an interval in the autumn-spring period. The growth rate of wet weight is defined by an exponential equation:

$$W_\tau = 0.2 \cdot e^{0.02 \cdot t}$$

where t — in the initial period of growth — is equal to the time of the duration of a generation ($t=\tau$), whereas after the period without growth: $t=\tau-180$ days (since within about 180 days following the time of the stopping of growth in the autumn, an average individual in the population of *C. dipterum* weights again about 1 mg (Fig. 2 B).

The growth of summer generation (Fig. 2, Tab. I) is regular and as fast as that of winter generation in the last period of its development; the 1 mm lengthening of the body takes 15.3 days, on the average. The curve of wet weight growth is defined by an exponential equation:

$$W_\tau = 0.2 \cdot e^{0.05 \cdot t}$$

The measurements of the body length showed considerable differences between the body size of *C. dipterum* individuals of winter and summer generations in all the stages of their development (Fig. 3). The individuals from the summer generation occuring in large numbers and developing very rapidly reached in all the stages of their development much smaller sizes than the average individuals from the winter generation in the reciprocal stages of development.

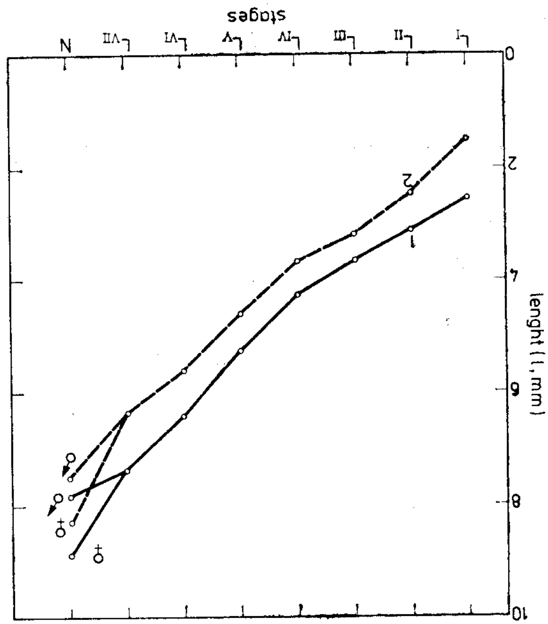

Fig. 3. Mean body length (*l*, mm) in consecutive stages of development of *C. dipterum* from winter (1) and summer (2) generations

3.3. DYNAMICS OF THE CHANGES IN THE BIOMASS OF *C. DIPTERUM* POPULATIONS

Seasonal changes in the biomass of *C. dipterum* population in a unified sample ($n=100$ individuals) are presented in Fig. 4. The minimum value of the biomass was recorded in the autumn-spring (September-March) period of the slower and stopped growth, while the age-structure of *C. dipterum* population remains almost

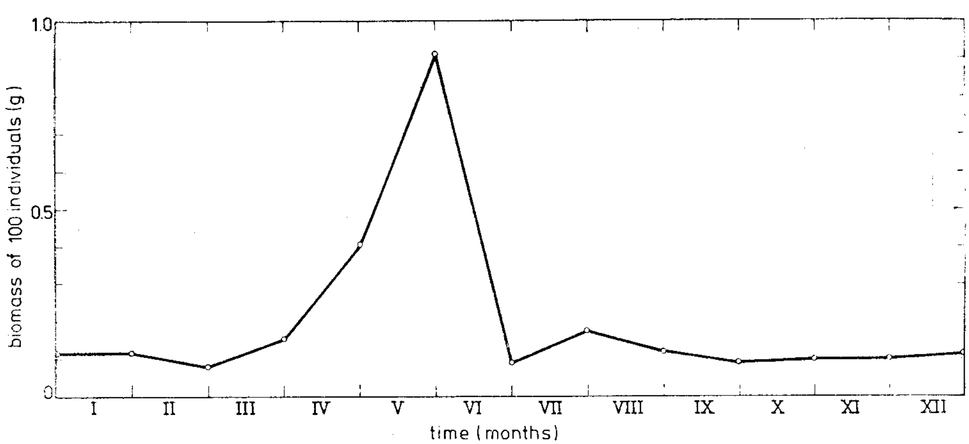

Fig. 4. Dynamics of the changes in the biomass of *C. dipterum* populations; seasonal changes in the biomass values (g) in a unified sample ($n=100$ individuals)

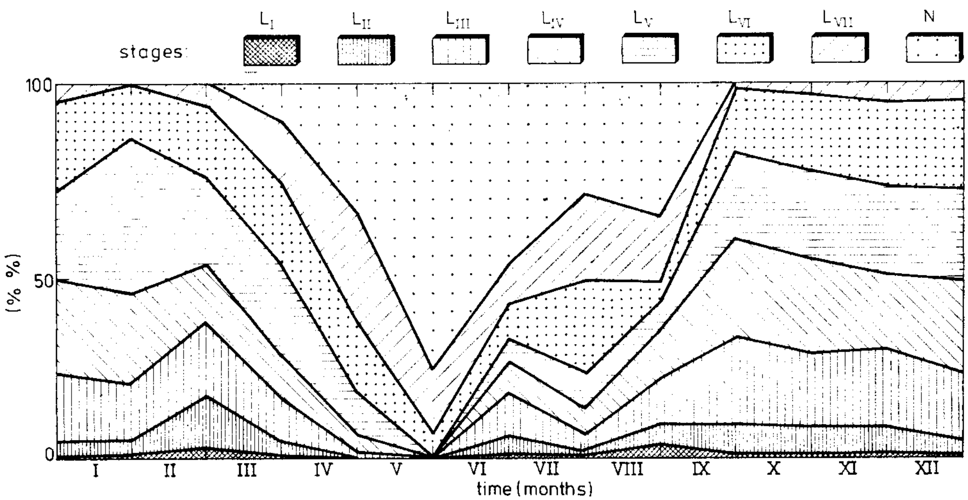

Fig. 5. Seasonal changes in the percentage of developmental stages in the biomass of *C. dipterum* populations in a natural pond

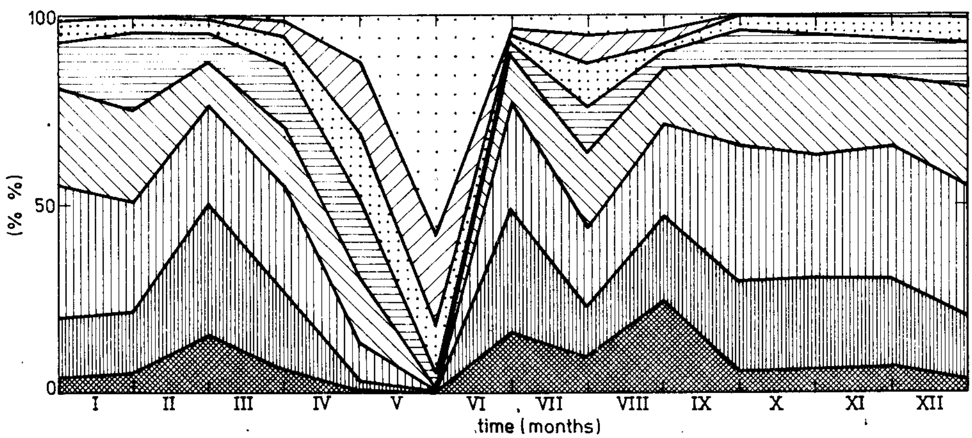

Fig. 6. Seasonal changes in the percentage developmental stages in the number of *C. dipterum* population in a natural pond (as in Fig. 5)

unchanged. At that time about one half of the total biomass is comprised in the bodies of the young larvae (L_I–L_{IV} stages) making up 75–90% of the total number of the individuals of this species (Fig. 6). In the late spring period a rapid development of *C. dipterum* population and an increase in the ratio of older larvae and nymphs in the samples (Fig. 6) is reflected in the quicker growth of the biomass (Fig. 4). The maximum of the biomass values (Fig. 4) at the end of May and begining of June, in both years, corresponds to the end of the winter generation, when the oldest larvae (L_{VII}) and nymphs (N) predominate in the samples (Fig. 6). Another, though much less distinct (in the unified sample) peak of the biomass production occurring in August (Figs. 4 and 5) is connected with the appearance of *C. dipterum* in the latest stages of development of the summer generation (Fig. 7). In the periods

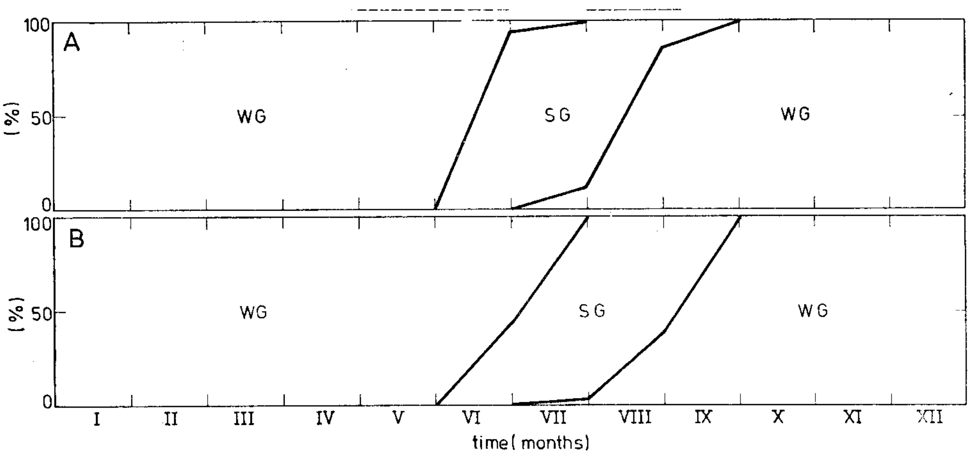

Fig. 7. The percentage of the individuals from winter generation (WG) and summer generation (SG) in the number (A) and the biomass (B) of the natural population of *C. dipterum*; dashed line — emergence of imago

of the emergence (the first and the second) the appearance of young individuals from a new generation has a considerable effect upon their ratio in the total numbers of the population (Fig. 7 A) and a much less important effect upon their ratio in the total biomass (Fig. 7 B).

4. DISCUSSION

On the basis of the analysis of the field samples it has been demonstrated that predominance of the definite stages of the development of *C. dipterum* corresponds to the definite seasons of the year. The emergences are of short duration; each generation emerges in a fairly well defined period of year (Fig. 1). Hynes (1970) presented this type of the development in the models of the seasonal cycles of the development of aquatic insects beside the irregular, non-seasonal cycles. He has differentiated a slow (S) seasonal cycle when the growth occurs after the hatch from non-diapausing eggs and a fast (F) seasonal cycle after the diapausing stages, or when in the development cycle of a species more than one generation appears within a year. The type of development including more than one generation annually is observed in many species of Ephemeroptera and is characteristic for a greater part of aquatic invertebrates living in a temperate climate (Hynes 1970).

In the pond investigated in 1972 and 1973 the appearance of two generations in the life cycle of *C. dipterum* was observed during each year. Landa (1968) classed the development of *C. dipterum* as belonging to type B_1. Species of Ephemeroptera wintering in the form of young, slow-growing larvae and having two generations, one: longliving — winter generation and another: shortliving — summer generation. Also, Schmidt (1951), Bertrand (1954), and Bretschko (1965) report a similar course of *C. dipterum* development. Macan (1962), on the other hand, observed the occurrence of two generations in England only in very warm years, and Brittain (1972) noted in Norway the appearence of only one generation of *C. dipterum* within a year.

In the autumn-spring period, when the temperature of water in the pond was below 10°C, age-structure of the population of *C. dipterum* was almost unchanged and young larvae dominated in the samples. At that time an average individual was about 4 mm long and weighed about 1 mg wet wt.; the L_{II}–L_{IV} stages made up 60–80% of the total number of the larvae in the samples. The stoppage of the development and growth of *C. dipterum* larvae in the autumn is connected not only with a lower temperature of water (Illies 1959, Pleskot 1958, Thorup 1963, Macan, Maudsley 1966) with shorter days (Pleskot 1961, Khoo 1964) and limitation of food resources (Zahar 1951). A longlasting period of abundance of the young larvae in the early stages of development, throughout the restricted growth of the population, resulted in the highest percentage of these stages in the total number of the individuals of *C. dipterum* in the collected samples. Though the use of a net with a mesh not dense enough might have reduced, indeed, the ratio of the youngest, very small larvae (L_I stage) in the samples, but this fact did not have any significant effect upon the evaluation of the life cycle of *C. dipterum*, nor upon any other results from these studies.

The investigations showed that the shortliving summer generation was represented by individuals smaller than those from winter generation. This kind of seasonal variation in the size of larvae and nymphs of *C. dipterum* were observed likewise by Bertrand (1954), Macan (1961), Bretschko (1965), as well as by Harker (1952) and Pleskot (1958) in the species of genus *Baetis*. Macan (1961), Pleskot (1961), Bretschko (1965) and Clifford (1970) found a correlation between the diapause, or the period of stopped growth, and the final size of the nymphs of mayflies and the growth rate of a given generation (Britt 1962). Thus, the fast growing individuals from the summer generation are smaller.

There is, probably, a lack of the resting stages (Illies 1952, Macan 1961, Bretschko 1965, Landa 1968, Hynes 1970) in the development, of *C. dipterum* just as in that of the greater part of Ephemeroptera. However, the appearance of a greater number of young individuals in the spring samples may give evidence to possibility that though for the most part the eggs of this species hatch in autumn, shortly after the time of egglaying, nonetheless a certain number of the eggs winter and hatch but in spring time.

The increment in the body length of *C. dipterum* individuals is not regular under natural conditions. In the course of a year the larvae of this species grow fast, slowly, or they do not grow at all; a 1 mm lengthening of the body takes less than 20 days in late spring and summer, about 40 days — in autumn and early spring, and for about five autumn-winter months, the growth of the larvae is stopped. According to Bretschko (1965) the 1 mm growth of the body of *C. dipterum* takes from 26 up to 67 days throughout the year (except in the about 150-day period of the lack of growth).

Using the model by Hynes (1970), the development of *C. dipterum* may be described by an expression: S+F (S — slow cycle — winter generation, F — fast cycle — summer generation), though maybe, the following expression: $S_1+F_1+F_2$ would be more to the point, where S_1 — the autumn-spring period of the slow and stopped growth of winter generation (1), F_1 — spring period of rapid growth ending the development of that generation, F_2 — fast development of summer generation (2).

In connection with this rhythm of development (periodicity of development, changes in the growth-rate, etc.) the fluctuations in the number of animals in the water bodies were noted. Hynes (1970) gave a hypothetical model of the seasonal changes in the numbers and the biomass of the invertebrate animals in the rivers. Besides smaller fluctuations in the development rate, the summer decrease in the density of population and the biomass, the maximum of the density in autumn and the maximum of the biomass in early spring are very characteristic features. Though, Hynes' models refer to running waters, nonetheless, the fluctuations in the density of population and the biomass occur likewise in lentic waters (Starmach et al. 1976). The following species may be differentiated in the ponds: in early spring (Crustacea, Tubificidae), in early summer (Chironomidae), in summer (Ephemeroptera, Odonata, Trichoptera) and this brings about a change in the composition of the food supply used by fish. Mikulski (1936), Bertrand (1954), Beeton (1956), Straskraba et al. (1966), Levanidova (1968) and other authors emphasize the great importance of the larvae of Ephemeroptera in the feeding of various fishes, e.g. they constitute a high per cent of the total diet of salmon (up to 46% — Maitland 1965), perch, bass, European whitefish, and many other fishes. Periodically, in the summer (when Chironomidae and Tubificidae are absent) mayflies become the basic food also for carps.

In result of a very high density of the population of the shortliving generation of mayflies the maximum of the biomass of these insects corresponds to the end of summer generation. Levanidova (1968) recorded the peak value of the biomass of the larvae of mayflies (17.8 g/m^2), in large rivers (Amur and its tributaries), in July. According to Kamler (unpubl.) the density of the summer generation of *C. dipterum* (in flood waters of the Rivers Bug and Narew) was fivefold higher than the density of winter generation and the peak of the biomass (about 7 g/m^2) of this species was noted also in July.

The samples were collected in a small, isolated pond in which larger predators were absent. The density of the population of *C. dipterum* was considerably higher under these conditions than the density of this species in the typical water bodies in which species composition is much more differentiated usually. In result of the qualitative character of the samples, collected with the sole purpose in view to investigate thoroughly the course of the life cycle of *C. dipterum*, and calculation of the dynamics of the biomass in the unified samples, the actual summer peak of the biomass of *C. dipterum* in the investigated water body was only roughly assessed.

In the natural environment the course of development of *C. dipterum* populations runs in regular, seasonal cycles depending on various environmental conditions the whole duration of the development may range from 2 months (summer generation) up to 10 months (winter generation), or even 12 months (when there is only one generation per year). The rate of the lengthening of the body of *C. dipterum* individuals is variable. During a year periods of fast, slow, and stopped growth are observed. The fast-growing individuals from summer generation are smaller than those from winter generation. A high degree of *C. dipterum* resistance to the changes in the environmental conditions leads to a widespread geographical distribution of this species. The lack of real diapause by a period of slower growth in winter, plasticity of life cycle and a possibility of the appearance (under favourable conditions) of the fast-growing summer generation are indicative of the adaptation of *C. dipterum* to the conditions in small, periodical water bodies (Brown 1961). The larvae and nymphs of *C. dipterum* occurring in super abundant masses may constitute a significant link in the trophic chain and be an important component of the fish diet. The high density of *C. dipterum* populations in the natural environment, often much higher than that of other species of Ephemeroptera, indicates the probability of a great importance of this species in the biocenosis of various water bodies.

5. SUMMARY

Studies on the life cycle of *Cloëon dipterum* (L.) were carried out, in 1972 and 1973, in a small, isolated water body situated in the southeast region of Warsaw (near Wawer). Altogether 65 samples were collected in the pond. On the basis of changes in the percentage of developmental stages in

the consecutive samples the course of the life cycle was determined, while the biometrical measurements supplied information about the growth-rate of the body length and body weight, seasonal changes in the larvae and nymphs size and the dynamics of the biomass of *C. dipterum* population in the natural environment.

During the two-year investigations the annual occurrence of two generations of *C. dipterum* was observed: a longliving (from autumn till spring) generation, wintering in the form of young larvae, the emergence in spring (May-June) and a short-living summer generation the emergence (in August). In the annual life cycle seasonal changes in the growth rate and the body sizes of the larvae and nymphs of *C. dipterum* were noted. In the development of winter generation periods of slow and fast growth were differentiated as well as an about 150-day period of wintering, when growth is stopped. Summer generation grew fast, without any changes in the growth rate, but the specimens of this generation were of a smaller size than those of winter generation. The dynamics of the changes in the biomass of *C. dipterum* population in a unified sample ($n=100$) individuals showed low values of the biomass in the autumn — spring period of the predomination the young larvae of winter generation and the peaks of biomass were recorded at the end of the respective generations, the oldest larvae and nymphs predominated in the samples.

6. STRESZCZENIE

Badania nad cyklem życiowym *Cloëon dipterum* (L.) prowadzono w latach 1972 i 1973 w małym, izolowanym zbiorniku wodnym, zlokalizowanym w południowo-wschodnim rejonie Warszawy (okolice Wawra). Ogólnie pobrano 65 prób terenowych. Na podstawie zmian procentowego udziału stadiów rozwojowych w kolejnych próbach wnioskowano o przebiegu cyklu rozwojowego, a pomiary biometryczne dały informację o tempie wzrostu długości i ciężaru ciała, sezonowej zmienności rozmiarów larw i nimf oraz o dynamice biomasy populacji badanego gatunku w środowisku naturalnym.

W obu latach badań występowały dwie generacje *C. dipterum* rocznie: długa (od jesieni do wiosny), zimująca w postaci młodych larw, z wylotem wiosennym (maj-czerwiec) i krótka, letnia (z wylotem w sierpniu). W cyklu rocznym stwierdzono sezonowe zmiany tempa wzrostu i rozmiarów ciała larw i nimf *C. dipterum*. W rozwoju generacji zimowej wyróżniono okresy wolnego i szybkiego wzrostu, a przez około 150 dni zimowania wzrost był zahamowany. Generacja letnia rozwijała się szybko, bez zmian tempa wzrostu, lecz osobniki tego pokolenia osiągały mniejsze rozmiary, niż w pokoleniu zimowym. Dynamika biomasy populacji *C. dipterum* w zunifikowanej próbie ($n=100$ osobników) wykazała niski stan biomasy w jesienno-wiosennym okresie dominacji młodych larw pokolenia zimowego, a szczyty biomasy odpowiadały końcom poszczególnych pokoleń, gdy w próbach dominowały najstarsze larwy i nimfy.

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