

Ecological Peculiarities of the Sympatric Species of Mayflies, *Cloeon dipterum* L. and *C. inscriptum* Btss. (Ephemeroptera, Baetidae)*

A. E. SILINA

Voronozh State University

Abstract. The coexistence of two closely related species of mayflies in a small flooded lake is achieved by reducing the level of isostasy of their ecomiches. The species prefer different zones of the lake. The difference in the periods of mass emergence of second-generation subimagines is in the range of 1.5 months. There is no restriction on the abundance of species by trophic conditions.

Key words: Ephemeroptera; Baetidae; *Cloeon*; ecology.

The species *Cloeon dipterum* L. and *C. inscriptum* Btss., which are similar morphologically and biologically, were formerly confused under one name. The absence of distinct morphological differences does not permit separation of these species at the larval stage. Therefore, for example, in the *Limnofauna of Europe* (Putz, 1978), *C. inscriptum* is cited as a synonym of *C. dipterum*. However, Mikulski (1936), Machel (1969), Chernova (1963), and others consider *C. inscriptum* a valid species on the basis of some morphologic differences in imagines (shape and color of eyes in ♂s and length and color of legs).

Investigation of relationships between *C. dipterum* and close species and forms (Sowa, 1975) and their life cycles are discussed in papers of several researchers (Brown, 1961; Macan, 1961; Brestschko, 1965; Kjellberg, 1973; Brittain, 1974). According to their data *C. dipterum* is predominantly a univoltine species with imagines emerging mainly in the first half of summer, although in some years the species may have a second rapidly growing generation. In southern Norway emergence of subimagines takes place in July. Growth of the next generation in the univoltine cycle is most intensive in August and September and decelerates in the period when water is covered with ice (Brittain, 1974). Larvae expand their wings while on the surface of water, and emergence of subimagines takes place chiefly about noon and in evening hours; molting into imagines takes place after 26-38 hours. The lifespan of adult ♂s reaches up to 48 days, the flight period in different years may fluctuate from 36 to 50 days, from June to late August (Machel, 1969). In distribution *C. dipterum* is a Transpalearctic species.

Data on the ecology and biology of *C. inscriptum* are extremely few. It is known that larvae of this species, as well as larvae of *C. dipterum*, live among vegetation of water bodies with slow running or stagnant water and are poor swimmers. According to Machel (1969), in vicinity of Głogów, western Poland, imagines occur in late August. In distribution, *C. inscriptum* is a West Palearctic species known from Europe, Caucasus, and West Siberia.

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Table 1

Distribution of population density and biomass of *Cloeon inscriptum* Bgtss. and *C. dipterum* L. emerging at different depths in the floodplain lake

Zone of Lake	Depth, m	<i>C. dipterum</i>		<i>C. inscriptum</i>	
		Number of spms./m ² /day		Number of spms./m ² /day	
Littoral	0.5	1.56±0.35	11.23±3.60	0.71±0.29	6.72±2.94
Sublittoral	1.5	1.29±0.31	9.07±2.36	0.44±0.15	4.44±1.46
	2.5	0.68±0.19	3.65±1.25	0.29±0.10	2.97±1.09
Deep	3.5	0.91±0.22	3.37±0.68	0.58±0.16	4.38±1.18
	4.5	1.53±0.41	5.51±1.24	0.56±0.15	3.39±1.09
Total lake		1.19±0.14	6.58±0.95	0.51±0.08	4.38±0.76

Table 2

Distribution and relative association of *C. inscriptum* and *C. dipterum* with habitats in the lake

Species of mayflies	Littoral	Sublittoral		Deep Profound	
	0.5 m	1.5 m	2.5 m	3.1 m	4.5 m
<i>C. dipterum</i>	<u>27.4</u>	<u>17.1</u>	<u>11.5</u>	<u>22.3</u>	<u>21.7</u>
	-0.06	-0.08	+0.03	+0.18	-0.05
<i>C. inscriptum</i>	<u>26.1</u>	<u>21.7</u>	<u>11.3</u>	<u>15.3</u>	<u>25.6</u>
	-0.09	+0.68	+0.02	-0.05	+0.06

Note. Above the line, percent of abundance of species below the line, F_{ij} - value of coefficients of relative association.

Table 3

Average individual mass of imagines of *Cloeon inscriptum* Bgtss. and *C. dipterum* L. of 1st- (spring) and 2nd- (summer) generation emerging from the floodplain lake (mg)

Generation	<i>C. inscriptum</i>		<i>C. dipterum</i>	
	♂	♀	♂	♀
I	6.47±0.31	11.38±0.42	8.21±0.53	14.43±0.58
II	2.26±0.11	3.58±0.21	3.15±0.29	4.45±0.29

Data on these species living together are available in Machel (1969). He notes the *C. dipterum* isolated swarming of *C. inscriptum* and also of joint swarming with *C. dipterum* with numerical predominance of the latter.

In Voronezh Prov. *C. dipterum* is cited in all hydrobiological investigations beginning from 1992 (Sent-Iler, 1925), and was recorded in the Don, Voronezh, and Bityg rivers, floodplain lakes and fish-hatchery ponds (Sent-Iler, 1935; Sent-Iler and Bukhalova, 1937; Sklyarova, Shcherbakova, and Bortnikova, 1960; Shillo and Bobrova, 1965; Sklyarova, 1971; Skuf'in, 1978). However, because the authors determined this species by larva, it is not excluded that in some cases they were dealing also with *C. inscriptum* or a mixture of these two species.

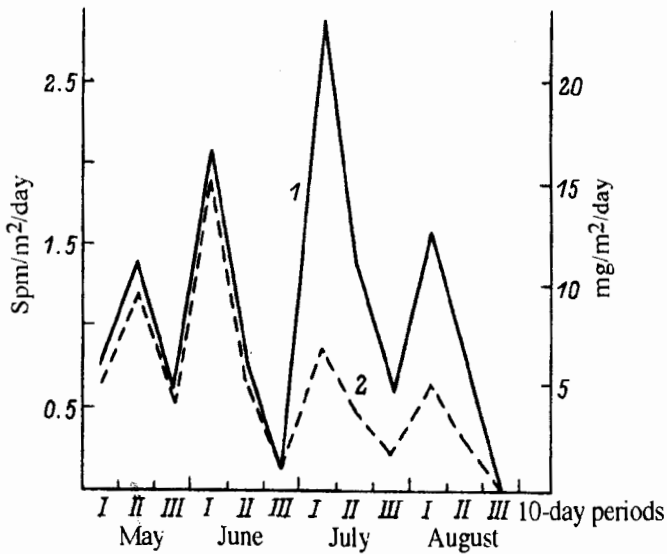


Fig. 1. Seasonal changes of population density and biomass of *Cloeon inscriptum* emerging from floodplain lake: 1) density, 2) biomass.

Data on records of *C. inscriptum* in the Upper Don River basin in the literature are lacking.

Because identification of these species at the larval stage cannot be accomplished using morphological characters, it is necessary in taxonomic and faunistic investigations to use other criteria, ecological, genetic, and geographic, which have been used successfully for the separation of close species.

The lack of data on the ecology and biology of these species of mayflies, which in the central zone are often background species, determined the goal of my investigations.

To study certain aspects of the ecology and biology of *C. dipterum* and *C. inscriptum* I investigated the emergence of the winged phases of mayflies in Voronezh Prov., 9 km north of Somovo. The lake used is submerged in time of high water, situated 100 m from the river bed, maximal depth 4.5 m, black slit on the bottom, with hydrogen sulfide, transparent according to the Sekka disc to 2.5 m. The background plant species is *Phragmites communis*; in the near-shore area continuous thickets of *Stratiotes aloides* and *Nuphar luteum* occurred; from mid-June to the end of the growing season the lake surface was entirely covered with *Lemna trisulca*.

For quantitative survey of winged mayflies emerging out of the water I used floating-net insect catchers (Savitskiy et al., 1986), which were checked no less than 3 times every 10 days. The total number of trap/days surveyed was 340, and more than 600 specimens of insects of the two species were collected. Investigations were conducted from 7.V to 23.IX.1990, at 5 constant stations with gradation of depth of 1 m: 1 in the littoral (depth 0.5 m), 2 in sublittoral (1.5 and 2.5 m), 2 in the deep part of the lake (3.5 and 4.5 m). Distances between traps were from 7 to 15 m.

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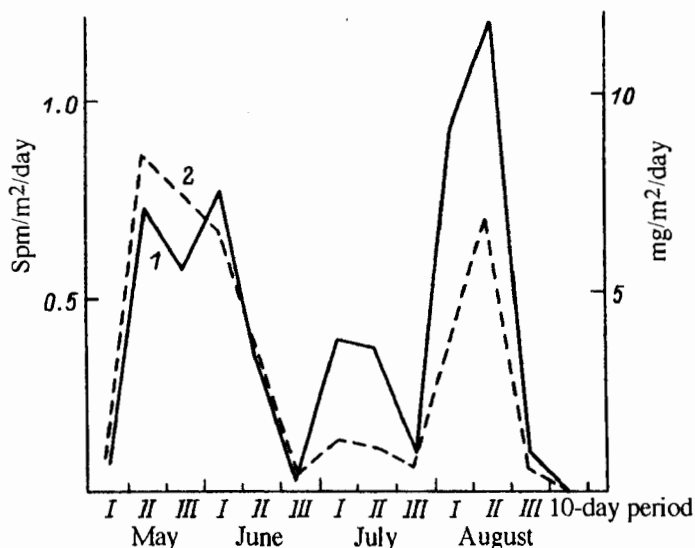


Fig. 2. Seasonal changes of population density of *C. dipterum* emerging from floodplain lake: 1) density, 2) biomass.

C. dipterum and *C. inscriptum* were dominant species in the mayfly community of the lake. *C. inscriptum* constituted 65.8%, and *C. dipterum* 28.4% of the total number of collected mayflies, biomass was 49.8% and 33.1%, and frequency of occurrence in traps was 35.3% and 21.8%, respectively. Average daily emergence of *C. inscriptum* was 1.19 spms./m²/day. Ratio of population density of species was 2.3:1, ratio of biomass was 1.5:1.

Dominance of these species was observed in all 5 depths of the lake. The proportion of *C. inscriptum* fluctuated from 57.6% in the littoral to 73.4% in the sublittoral, *C. dipterum* from 25% in the sublittoral to 38.2% in the deep part of the lake. Average daily values of emergence density and biomass at localities with different depth are shown in Table 1.

Both species had their maximal density in the littoral. The population density of *C. inscriptum* was also high in the deep lake, at a depth of 4.5 m. However, these characteristics were not enough for a complete picture of the spatial distribution of species in a small water body. According to the coefficient of relative association of species with water depth (Pesenko, 1982), *C. inscriptum* apparently prefers the sublittoral (depth 1.5 m), and *C. dipterum* prefers the deep part (3.5 m) (Table 2).

It should be noted that for larvae of *Cloeon* the depth is not likely a critical factor in the distribution of population. Apparently the presence of food among duckweed and relatively high water temperature in the upper water layer where larvae swim are more important. Probably here we deal with spatial division of ecological niches, which is displayed in distinct difference in the preferred parts of the water body.

Judging by the shared habitat of two close species, with numerical predominance of one of them and association of species with different parts of the lake, competition between them must exist. Relief from competition takes place at the expense of divergence of their ecological niches. This may be displayed in morphologic changes such as body size (Hutchinson, 1959). Many researchers accept differences between species by size 1.3 as constant, and by weight 2.

The studied species differ by individual weight in both generations (Table 3). In 1st generation ♂s and ♀s of *C. inscriptum* weighed 0.79 that of *C. dipterum*, and in 2nd generation, ♂s of *C. inscriptum* weighed 0.72 and ♀s 0.81 that of *C. dipterum* (differences are significant, $p < 0.05$).

According to results of investigation of two sympatric species of *Unio* (Kuznetsova and Danilin, 1991) without restrictions caused by the food, the overlapping of ecological niches could exceed the theoretically expected value, and Hutchinson's constant appeared to be lower than its low limit. This is confirmed by my data. The body weight of two coexisting species of mayflies on the average differed only by 30%.

Both species under the conditions of northern Voronezh Prov. are bivoltine, with emergence of the 1st generation in May-June, and the 2nd generation in July-August. The generations do not overlap, which may be confirmed by the difference of individual body weight (Table 3). Individuals of the spring generation in terms of size and weight are considerably larger than individuals of the rapidly growing summer generation, because the 1st generation developed over about 8 months, and the 2nd generation in 1 to 3 months. Thus, ♀s of the 1st (spring) generation of both species have body weight 3.2 times that of ♀s of the 2nd (summer) generation. The average individual body weight of 1st-generation ♂s of *C. inscriptum* was 2.8 times, and in *C. dipterum* 2.6 times, the body weight of 2nd-generation ♂s (differences were significant, $p < 0.05$).

Population density of the summer generation of *C. inscriptum* is 1.5 times the density of the spring generation. In *C. dipterum* density of emerging subimagines of both generations is approximately equal. The emergence of the 1st generation of *C. inscriptum* takes place from early May to mid-June (Fig. 1), with maximum in early June (2.8 spms./m²/day), emergence of the 2nd generation takes place from early July to mid-August, with a maximum in early July (2.90 spms./m²/day). If it is assumed that the period between these two density peaks reflects the average time of development of the summer generation, then in *C. inscriptum* it would be as long as 1 month; including extreme cases of emergence this period would increase to 2.5 months.

In *C. dipterum* the major period of emergence of the 1st generation is shorter, with maximum in early June (0.78 spms./m²/day), although occasional individuals occurred in early May (Fig. 2). The emergence of the 2nd generation was observed from early July to the end of August, with maximum by middle of August (1.20 spms./m²/day). It is possible to tell by the pattern of the emergence that the development of the summer generation is longer, on average, 1.5-2.5 months. Including extreme cases the time of the emergence fluctuates from 1 to 3 months.

Therefore, differences in the life cycles in these two species are in the more rapid development of the summer generation of the smaller species, *C. inscriptum*. A delay in development of *C. dipterum* may be determined by its preference for life in the less heated deep zone of the lake, which is associated with a larger body weight. As a result, the time of the maximal emergence of subadults of the 2nd generation of the species studied are separated by a period of 1.5 months, which probably should prevent a mixed swarming.

In both species the numerical predominance of ♀s in the 1st generation and ♂s in the 2nd generation is observed. In the 1st generation this phenomenon is more obvious in *C. dipterum* (1:2), and in the 2nd generation in *C. inscriptum* (2:1). In *C. dipterum* the number of ♂s and ♀s in the 2nd generation is almost equal, 1.2:1.

Seasonally the fact of asynchronous emergence of ♂s and ♀s of both species is remarkable. In some periods (10-day periods) multiple cases with predominance of one sex in samples was observed.

Thus, in *C. dipterum* of the 1st generation peak of emergence of ♀s (0.56 spms./m²/day) took place in mid-May, and ♂s in early June; in the 2nd generation the mass emergence of ♀s was observed in the beginning of the emergence (0.30 spms./m²/day), ♂s in mid-August, before the end of the emergence of the 2nd generation (2.35/m²/day). Therefore in both 1st and 2nd generations of *C. dipterum* mass emergence of ♀s in general preceded the mass emergence of ♂s.

In *C. inscriptum* only sharp predominance of ♀s is noted (1.33 spms./m²/day) at the end of the emergence of the 1st generation, and ♂s in early period of the 2nd generation (2.35 spms./m²/day).

Probably the observed phenomenon of unequal sex ratio in different generations, as well as phenomenon of asynchronous emergence of ♂s and ♀s in the season, has an adaptive meaning and is a part of the mechanism of regulation of density of populations.

Therefore, the possibility of the coexistence of two very close species in the same habitats is achieved by the decrease of overlapping of their ecological niches. Partial spatial isolation is expressed in the preference of different zones in the floodplain lake, *C. dipterum* prefers the deep zone, and *C. inscriptum* prefers the sublittoral. The individual body weight of *C. dipterum* on the average is 30% greater than the body weight of *C. inscriptum*.

The isolation of these species in time is displayed in the lack of coincidence of periods of the mass emergence of their subimagines. The difference between summer generations is as great as 1.5 months. This is achieved by longer time of development of the summer generation of *C. dipterum* and probably should help to prevent a mixed swarming.

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