

## Phenology of Four *Chaoborus* Species<sup>1,2</sup>

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### ABSTRACT

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The phenology of four *Chaoborus* species in four bog lakes in the upper peninsula of Michigan was documented. The sequence and timing of pupation was: *Chaoborus americanus*, early May; *C. flavicans*, end of May; *C. punctipennis*, early July; *C. trivittatus*, end of August and early September. *C. americanus*, *C. punctipennis*, and *C. trivittatus* each occurred in two of the lakes. Differences in the timing of pupation for each of these species between lakes were not always correlated with environmental differences between lakes. *C. punctipennis*, *C. flavicans*, and one of the *C. americanus* populations was univoltine. The other *C. americanus* population may have been bivoltine. One *C. trivittatus* population appeared to be univoltine, whereas the other may have had a 2-year generation time. The significance of the sequence and timing of pupation of these species is discussed in relation to seasonality, interspecific competition, and predation.

In stream systems, closely related insect species often differ in their periods of abundance and their timing of adult emergence (Grant and Mackay 1969). It has been argued that staggering the periods of emergence promotes coexistence by minimizing the time at which each species has a maximum impact on the resources (Grant and Mackay 1969). Reproductive isolation also is reinforced by the staggering of periods of reproduction. Although less well documented, similar patterns occur for aquatic insects in lake systems (Cannings and Scudder 1978). Species of *Chaoborus*, the phantom midge, are a common component of the benthic and planktonic communities of lakes. This is a report of the phenology of four regionally co-occurring *Chaoborus* species—*Chaoborus americanus* (Johannsen), *C. flavicans* (Meigen), *C. punctipennis* (Say), and *C. trivittatus* (Loew)—in four bog lakes in the upper peninsula of Michigan. Because the species occur in the lakes in different combinations, it was possible to compare the life cycles of the species alone versus those of a species combined with another species (*C. americanus* and *C. punctipennis*), or with different species (*C. trivittatus*). The majority of the *Chaoborus* life cycle is spent in the larval stage (four larval instars). The pupal stage lasts from several days to several weeks, depending on water temperatures. Adults can live up to 6 days in the laboratory, so probably they live about a week in natural systems.

### Materials and Methods

Four bog lakes at the University of Notre Dame Environmental Research Center (UNDERC) in Gogebic County, Mich., were sampled in 1972 and 1973 (Forest Service Bog, Hummingbird Bog, North Gate Bog, and Tender Bog). The four species occurred in the lakes in various combinations (Table 1). Hummingbird and North Gate bogs contained fish, whereas Forest Service and Tender bogs did not. Other characteristics of the lakes and the com-

positions of the zooplankton communities are presented in Table 1.

In 1972 I collected samples monthly from September through November. In 1973 I sampled the lakes approximately biweekly from mid-May until early September and in October. A large plankton net (55 cm in diameter, 153- $\mu$ m mesh size) was used for vertical tows from specific depths to the surface. In Hummingbird, North Gate, and Tender bogs, 1.5-m tows (356 liters) gave sufficiently large samples for all instars of the different species. Tows of 1.5 m also were used for *C. americanus* larvae in Forest Service Bog. Because *C. trivittatus* larvae, especially 4th instars, rarely were concentrated in the surface waters in Forest Service Bog, 2.5-m (593 liters) tows were taken from mid-May until mid-August, and 3.5-m (832 liter) tows were taken from mid-August until mid-October to collect *C. trivittatus*. Deeper tows were taken in the late summer and fall because the later-instar larvae remained deeper. All samples were collected between 2400 and 0130 h, when larvae of all species, except for *C. trivittatus* in Forest Service Bog, were in the upper waters.

All 4th-instar larvae and pupae were identified to species by using the keys of Cook (1956), Roth (1967), and Saether (1972). The 1st instars cannot be identified to the species level. The identification of 2nd, 3rd, and 4th instars of *C. americanus* and *C. trivittatus* was based on characters used by Fedorenko and Swift (1972). Head capsule size data from LaRow and Marzolf (1970) were used to distinguish the instars of *C. punctipennis*. For all species, head capsule length (at  $45\times$ ,  $n = 30$ ) was measured for 2nd-, 3rd-, and 4th-instar larvae. The larval instars of *C. flavicans* were identified based on the larval characters suggested by Parma (1971). The life history data are presented as percent frequency for each instar of each species throughout the sampling period. Except for *C. trivittatus*, only the 1973 data are presented. Results for 1st instars are presented only for *C. americanus* and *C. punctipennis* for the lakes where they occurred alone. Temperature profiles

<sup>1</sup> Diptera: Chaoboridae.

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Table 1.—*Chaoborus* and zooplankton species, and characteristics of the four bog lakes

Species	Fish present		Fish absent	
	North Gate	Hummingbird	Tender	Forest Service
<i>Chaoborus americanus</i>			X	X
<i>Chaoborus flavicans</i>		X		
<i>Chaoborus punctipennis</i>	X	X		
<i>Chaoborus trivittatus</i>		X		X
<i>Bosmina longirostris</i>	X	X		
<i>Cyclops bicuspidatus thomasi</i>	X			
<i>Daphnia catawba</i>		X		
<i>Daphnia parvula</i>		X		
<i>Daphnia pulex</i>	X		X	X
<i>Diaphanosoma leuchtenbergianum</i>				X
<i>Diaptomus leptopus</i>			X	X
<i>Holopedium gibberum</i>		X		X
<i>Tropocyclops prasinus</i>		X		
Lake characteristics				
Maximum depth (m)	8.0	7.5	10.0	4.5
Secchi disk (m)	1.1	.7	1.5	2.2
Stained	Yes	Yes	Yes	No
pH	4.9	5.4	4.2	4.8

were taken in each lake in September and October in 1972, and at about 1-month intervals from the end of May until September in 1973. These results are presented as mean differences for the surface to 4 m, the strata occupied by the earlier-instar larvae.

### Results and Discussion

There was a definite sequence of pupation for the four species. *C. americanus* was the first to pupate during the first half of May, soon after the ice left the lakes (Fig. 1). It was followed in several weeks by *C. flavicans*, near the end of May (Fig. 2). Pupation by *C. punctipennis* was greatest in the early part of July (Fig. 3). *C. trivittatus* was the last, with pupation occurring at the end of August and in early September (Fig. 4). In general, this order of pupation is comparable to that found in other northern parts of North America for these species, the only exception being variation in the timing by *C. trivittatus*. In Quebec, Carter and Kwik (1977) found the order of pupation was *C. trivittatus*, *C. americanus*, *C. flavicans*, and *C. punctipennis*. In these Matamek lakes, *C. trivittatus* preceded *C. americanus* in the early summer. *C. trivittatus* also preceded *C. americanus* by several weeks in the spring in Eunice Lake, British Columbia (Fedorenko and Swift 1972). In lowland western Washington (Lake MacDonald), *C. trivittatus* was bivoltine (Pastorok 1978). Pupation occurred in the early spring and late summer. In southern Michigan, *C. americanus* pupated early in the spring (Bradshaw 1973). *C. flavicans* pupated in June in Lake MacDonald (Pastorok 1978). Stahl (1966) found *C. flavicans* pupation preceded *C. punctipennis* in Myers Lake, Ind. *C. punctipennis* emerged near the end of June in a small northern Wisconsin lake (Malueg 1966). Thus, with the exception of *C. trivittatus*, the timing of pupation of the *Chaoborus* species at UNDERC is in agreement

with reports in the literature. The *C. trivittatus* populations in Forest Service and Hummingbird bogs are the only *C. trivittatus* populations with generation times of 1 year or greater that have been reported to pupate in the fall. All other reported *C. trivittatus* populations pupate in the spring.

A major goal of ecological studies is to understand the patterns we observe in natural systems. One explanation for the sequence of pupation of these four species is that the timing of pupation represents adaptation both to the seasonal environmental conditions and to the presence of other *Chaoborus* species. The early pupation of *C. americanus* is plausible because it is found most frequently in shallow ponds that lack fish (Bradshaw 1973, von Ende 1979). Shallow ponds are subject to more unpredictable conditions later in the summer, so there is a premium on getting to the hardier 4th instar by the time these conditions occur. In part this can be accomplished by having emergence occur as soon as possible in the spring. Although such conditions do not exist in the fishless lakes at UNDERC, these populations must have been founded by immigrants from the numerous woodland ponds nearby, where presumably selection for the timing of pupation has occurred. *C. flavicans* occurs both in shallow or temporary ponds (Cook 1956) and in permanent lakes (von Ende 1979). The earlier pupation period for this species also may reflect selection for exploiting shallow or temporary ponds as well as suggest the recent adaptation of the species to more permanent bodies.

*C. punctipennis* occurs widely in lakes and ponds that contain fish (von Ende 1979). The selective value of a widely spread species such as this pupating in the middle of the summer is not obvious, although it may be correlated with increased zooplankton production. Also, because *C. punctipennis* co-occurs

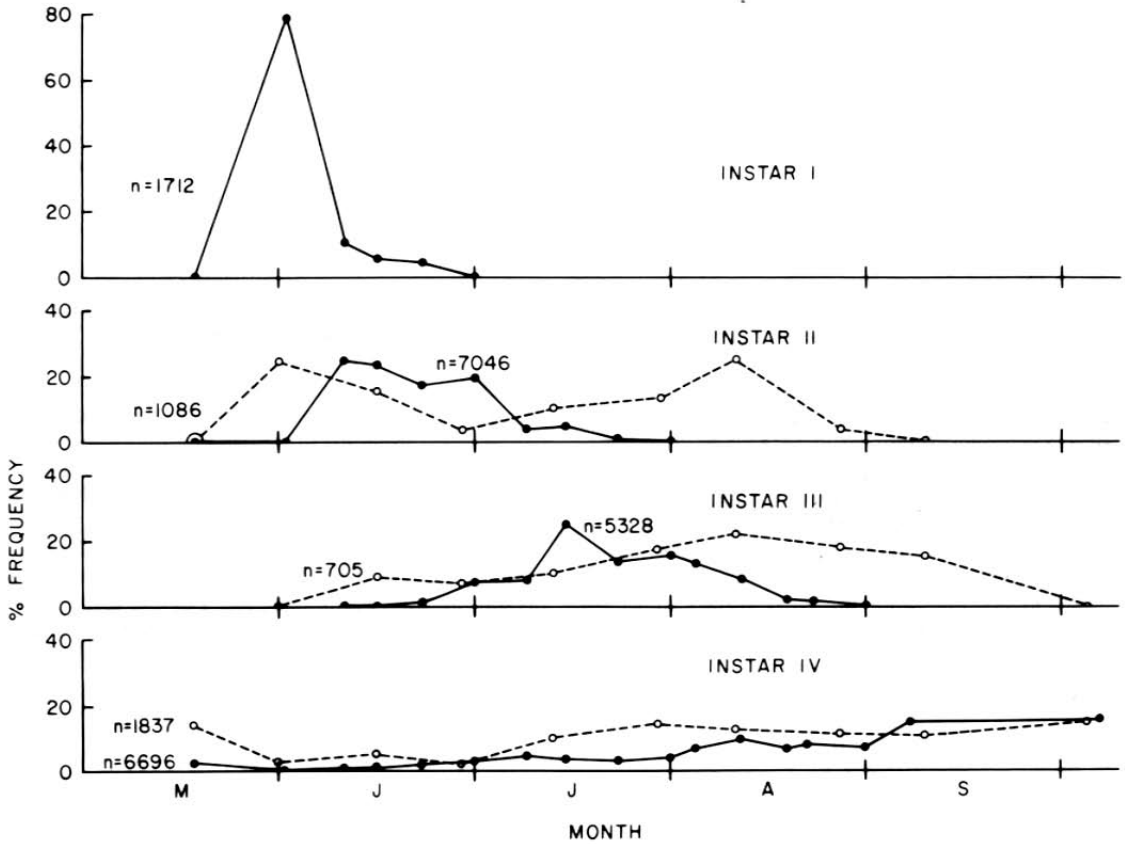


FIG. 1.—Percent frequency distribution of *C. americanus* larval instars in Tender Bog (—) and Forest Service Bog (----) during summer and fall 1973.

frequently with *C. flavicans* (von Ende 1979), the later pupation may reduce competition between larvae of these species in the next generation. Equivalent instars of the two species have different mean head capsule lengths (Table 2). However, because head capsule length is correlated with the maximum size of prey eaten (Fedorenko 1975), there is probably considerable overlap in prey taken by these species. Therefore, the staggering of the occurrence of equivalent instars may further reduce competition for prey. Alternatively, the timing of pupation may reduce competition by reducing spatial overlap of the early instar larvae. For those species whose 3rd- and 4th-instar larvae undergo extensive diurnal vertical migration (e.g., *C. flavicans*, *C. punctipennis*), the extent of vertical migration increases with older instars. 1st instars exhibit minimal vertical migration, 2nd instars exhibit a bit more, etc. For example, 3rd-instar *C. flavicans* would be deeper during the day than 2nd-instar *C. punctipennis*. Consequently, they may encounter different prey during the daylight hours. Finally, the staggering of pupation may reinforce reproductive isolation between these species.

The variation in the timing of pupation of *C. trivittatus* in different parts of North America is intriguing. The UNDERC population appears to be unique in having late summer pupation. The seasonal tem-

perature regimes of Eunice Lake in British Columbia (Fedorenko and Swift 1972) and the Matamek River lakes in Quebec (Carter and Kwik 1977) are generally the same as those in Wisconsin and Michigan (frozen from November–December until April–May). Eunice Lake and Forest Service Bog have similar zooplankton communities (Fedorenko 1975). Therefore, Forest Service and Hummingbird bogs do not have obviously unique features that might explain the late summer pupation of this species in these lakes. In spite of this, one can develop a scenario to suggest why it might be advantageous for a *C. trivittatus* population coexisting with *C. americanus* to pupate in the late summer, or in the spring before *C. americanus*.

The timing of pupation of *C. trivittatus* may serve to minimize interspecific predation by *C. americanus*. *C. americanus* excludes *C. punctipennis* and perhaps the other two species from stained, fishless bog lakes such as Tender Bog, because the older instars of *C. americanus* prey on the early instars of *C. punctipennis* (von Ende 1979). This occurs because of the early recruitment of *C. americanus* and the lack of vertical migration by the older instars of this species. Therefore, coexistence of a congener with *C. americanus* would be most likely if the larvae of the congener were the same size or larger than

Table 2.—Larval head capsule lengths (mm) of the four *Chaoborus* species<sup>a</sup>

Species	Instar		
	2nd	3rd	4th
<i>C. punctipennis</i>	0.344 ± 0.003	0.607 ± 0.003	1.039 ± 0.007
<i>C. flavicans</i>	0.457 ± 0.003	0.824 ± 0.004	1.343 ± 0.006
<i>C. americanus</i>	0.492 ± 0.005	0.934 ± 0.006	1.559 ± 0.019
<i>C. trivittatus</i>	0.626 ± 0.003	1.140 ± 0.009	1.841 ± 0.001

<sup>a</sup> Mean ± SE; n = 30.

the *C. americanus* larvae throughout the summer. Then predation by *C. americanus* should be minimal. The timing of pupation by *C. trivittatus* in Forest Service Bog could represent such a strategy. In Forest Service Bog *C. trivittatus* overwinters as 2nd- and 3rd-instar larvae. When 1st-instar *C. americanus* larvae hatch out in May, they are smaller than the *C. trivittatus* larvae. *C. americanus* does not have a chance to get a head start on *C. trivittatus*. This explanation does requires a sufficiently low predation rate over the winter so that the *C. americanus* larvae do not eliminate the early instars of *C. trivittatus*. The combination of low temperatures and

the presence of alternate prey (calanoid copepods overwinter in Forest Service Bog but not in Tender Bog) may produce such a situation. This scenario for the timing of pupation by *C. trivittatus* and *C. americanus* also accommodates the springtime pupation of *C. trivittatus* in British Columbia and Quebec in which these co-occur in lakes, because *C. trivittatus* still is larger than *C. americanus* throughout the year (Table 2).

The examples of *C. punctipennis* and *C. flavicans* as compared with *C. americanus* and *C. trivittatus* present an interesting contrast. For the former two species I am suggesting that maximizing size differ-

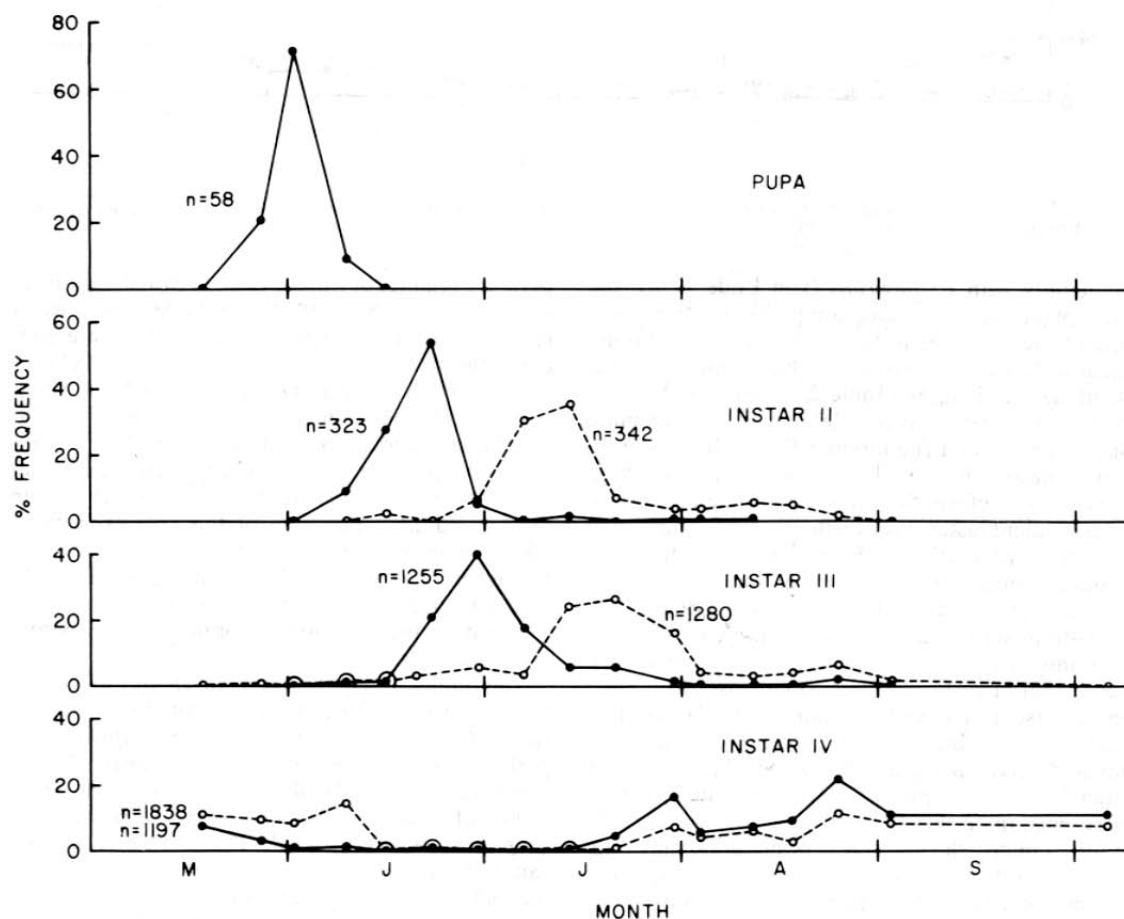


FIG. 2.—Percent frequency distribution of *C. flavicans* (—) and *C. punctipennis* (----) larval instars and pupae in Hummingbird Bog during summer and fall 1973.

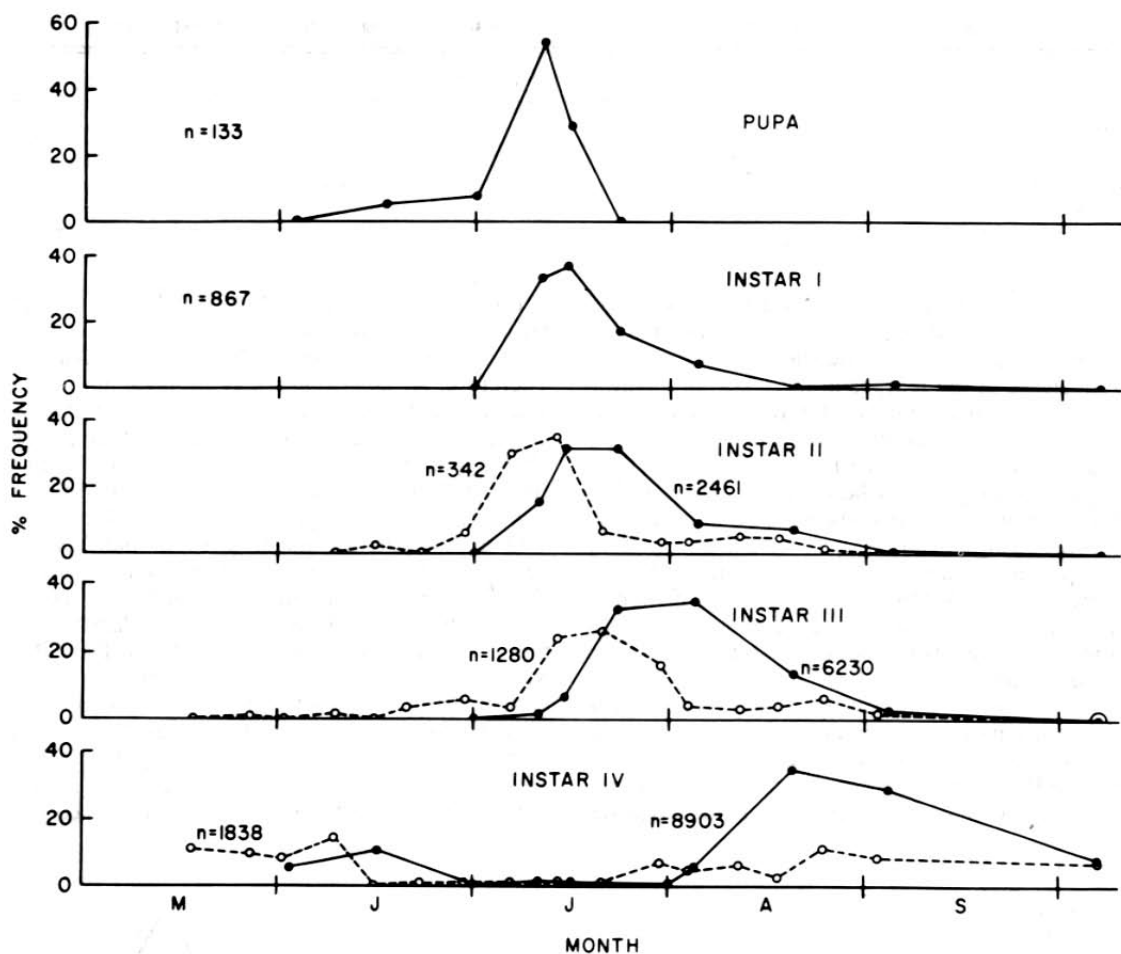


FIG. 3.—Percent frequency distribution of *C. punctipennis* larval instars and pupae in North Gate (—) and Hummingbird (----) bogs during summer and fall 1973.

ences of larvae by temporal separation and morphological differences promotes coexistence. For the latter two species, the optimum situation for coexistence appears to be to have a size difference between larvae (by temporal scheduling and morphological differences) that minimizes interspecific predation but that still allows for coexistence by minimizing exploitation competition. Thus, for *C. trivittatus* and *C. americanus* larvae I suggest that it pays to be different sizes when co-occurring, but not so different that one species has a predatory advantage (Fig. 1 and 4, Table 2).

*C. trivittatus* is unique among these four congeners in that it co-occurs with all the species. Because it lives in two different kinds of lakes, it may be exposed to conflicting selection pressures. If the timing of the larval instars of *C. punctipennis* and *C. flavicans* is compared with *C. trivittatus* in Hummingbird Bog (Fig. 2, 4), generally larvae of different head capsule size co-occur (Table 2), again suggesting a minimization of competition through resource partitioning. The exception occurs in the spring (and possibly the winter), when 3rd-instar *C. trivittatus*

and 4th-instar *C. punctipennis* are present at the same time. This may be an example of a situation in which a species is unable to adapt to all contingencies, but in which the consequences are not severe enough to drive it to extinction locally. Alternatively, this may be an indication that morphological size differences are less important than I have suggested above.

Within the general pattern described above for the four species, there was variation in the timing of pupation between lakes for three of the species. The *C. americanus* population in Forest Service Bog was ca. 2 weeks ahead of the population in Tender Bog. In the former lake, pupation begins in the spring as soon as ice leaves the lake, whereas it begins several weeks later in Tender Bog (unpublished data). If one assumes similar adult survivorship and oviposition rates in the two lakes, this later pupation was reflected in the appearance of 2nd instars earlier in Forest Service than in Tender Bog (Fig. 1). Bradshaw (1973) described developmental polymorphism in *C. americanus*. He found a continuum in pupation time for this species when 4th instars were exposed

Table 3.—Mean temperature differences (°C) between lakes (0 to 4 m), using Tender Bog as the standard<sup>a</sup>

Lake	Date (mo/day)						
	9/9	10/14	5/21	6/14	7/2	8/14	7/6
Forest Service	+3.9	+2.0	+2.4	+4.5	+4.8	+5.8	+4.3
Hummingbird	+0.5	-0.3	+1.0	+1.2	+1.1	+0.8	+0.8
North Gate	-0.2	-0.4	-1.6	0	-0.2	+0.8	+0.3

<sup>a</sup> First two dates are in 1972; the others are in 1973.

to the cues of long day and food to break winter diapause. The difference between the populations in these two lakes could be the result of different frequencies of the morphs in the lakes, or environmental (e.g., temperature) differences between the lakes, or a combination of the two. Forest Service Bog is warmer than Tender Bog throughout the summer (Table 3), probably because it is shallower than Tender Bog and because its water is not stained as is Tender Bog's (Table 1).

Typically, *C. americanus* is univoltine, although Carter and Kwik (1977) reported a population in Quebec with a 2-year generation time. The population in Tender Bog fits the univoltine pattern in terms of the sequence of the four instars (Fig. 1). In Forest Service, however, there was a second peak of 2nd instars near the middle of August, and the decline of 3rd instars was considerably later in Forest Service Bog. Although I cannot be sure of the species, there was a large increase in 1st-instar larvae

in Forest Service at the end of July (26% of the 528 1st-instar larvae collected during the summer). This correlates with the pulse of 2nd instars in August. Therefore, *C. americanus* may be bivoltine in this lake, although this is not supported by a second pulse of 4th instars. Alternatively, these could have been offspring of immigrants from nearby ponds that had completed development earlier, or offspring of "slow developing morphs" in Forest Service Bog.

In addition to the pupation of *C. punctipennis* being later than *C. flavicans* in Hummingbird Bog (Fig. 2), there was a difference for the former species between lakes (Fig. 3). Based on instar distribution, the *C. punctipennis* population in North Gate Bog was about 2 weeks behind the Hummingbird population. If the timing of pupation reflects an effort to minimize competition with *C. flavicans*, and if there is limited gene flow between populations, we might expect "ecological release" to produce an earlier pupation time for *C. punctipennis* in lakes in

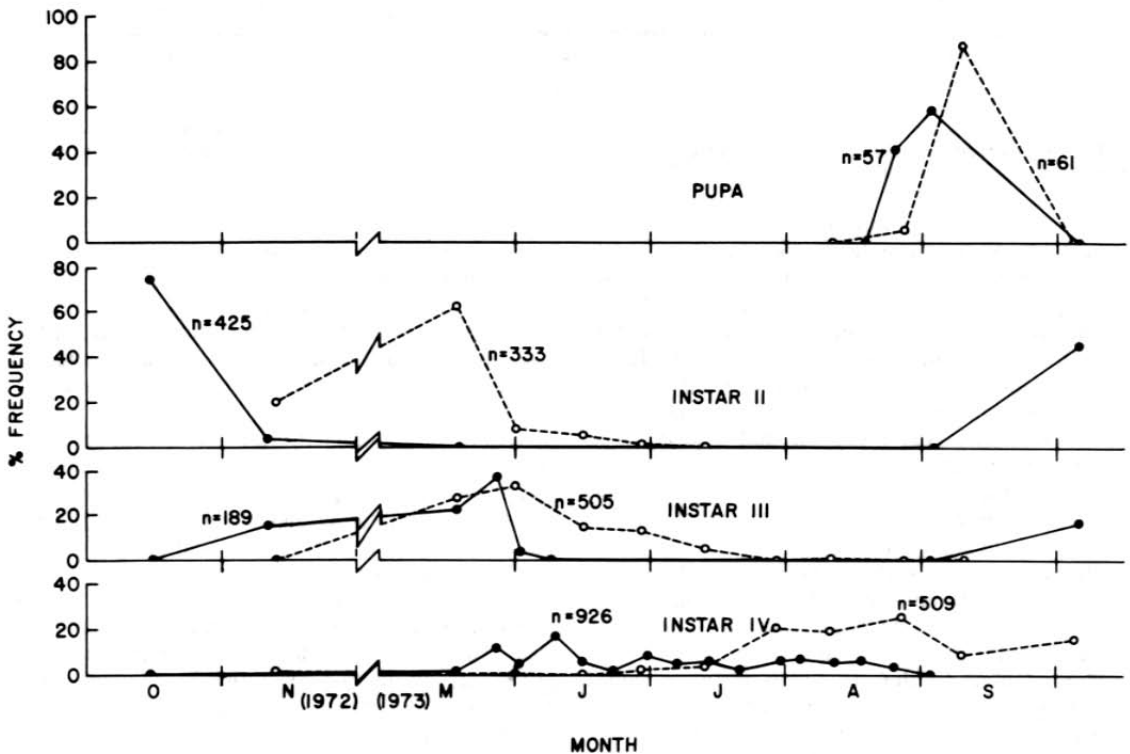


FIG. 4.—Percent frequency distribution of *C. trivittatus* larval instars and pupae in Hummingbird (—) and Forest Service (-----) bogs during fall 1972 and summer and fall 1973.

which it is the only *Chaoborus* species present. That just the opposite occurred suggests that the exact timing of pupation depends on local environmental conditions or that there is limited gene flow between populations and the genetic differences between the populations are unrelated to the presence or absence of a congener. *C. punctipennis* was univoltine in these lakes (Fig. 2 and 3), which is typical in deep north temperate lakes (Carter and Kwik 1977, Stahl 1966). Welch (1968), however, found *C. punctipennis* to be bivoltine in a Georgia farm pond. Lindeman (1942) reported several overlapping generations for *C. punctipennis* in Minnesota in shallow Cedar Bog Lake.

*C. flavicans* also was univoltine in Hummingbird Bog. However, I observed emergence of large numbers of adult *C. flavicans* at the end of July from productive Tenderfoot Lake on the UNDERC property (collection of adults only, not sampling throughout summer), which suggests this species is bivoltine in that lake. Berg (1937) reported that *C. flavicans* was univoltine in large Esrom Lake but bivoltine in the shallower Frederiksborg Castle Lake. Carter and Kwik (1977), Pastorok (1978) and Stahl (1966) reported a univoltine life cycle for *C. flavicans*.

There was only a slight difference between lakes for the *C. trivittatus* populations. Pupation and subsequent development occurred slightly earlier in Hummingbird Bog (Fig. 4). Because Hummingbird was cooler throughout the summer (Table 3), I would have predicted just the opposite. The zooplankton community in Hummingbird was dominated by smaller species because of fish predation. Because the smaller species are more suitable prey for *Chaoborus* larvae, this condition may have produced faster growth rates. In Quebec, Carter and Kwik (1977) found that this species had a 1-year generation time, whereas in British Columbia Fedorenko and Swift (1972) reported a 2-year generation time. In the latter population the second year was spent in the 4th instar. First- and second-year 4th instars were differentiated by the size of the tracheal bladders and the color of the larvae. Because of small sample sizes, I cannot be sure of the generation time of *C. trivittatus* in the UNDERC lakes. It appears to be 1 year; however, the presence of 4th instars in October in Forest Service Bog shows that not all the population pupated in August. These larvae may have pupated in the spring of 1974. Again, the fishless situation in Forest Service Bog may have contributed to the slower growth rate. *C. trivittatus* further demonstrated flexibility in its life cycle by being bivoltine in Lake MacDonald in Washington, although *C. flavicans* was univoltine in the same lake (Pastorok 1978). Finally, *C. trivittatus* differed from the other species in the UNDERC lakes by overwintering as 2nd or 3rd instars, whereas the other species overwintered as 4th instars.

In conclusion, there was a definite sequence of pupation for these four species in the upper peninsula of Michigan. This may promote regional coexistence by minimizing interaction between the lar-

vae of some of the species. However, within this pattern there was variation within species between lakes in the exact timing of pupation and perhaps in generation time. To understand the significance of phenological differences between these species, further experimental studies are required to determine the extent to which the larvae interact (von Ende 1979) and to elucidate the relative importance of local environmental conditions and genetic differences between populations in producing intraspecific variation in the timing of pupation and emergence.

#### Acknowledgment

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positions of the zooplankton communities are presented in Table 1.

In 1972 I collected samples monthly from September through November. In 1973 I sampled the lakes approximately biweekly from mid-May until early September and in October. A large plankton net (55 cm in diameter, 153- $\mu$ m mesh size) was used for vertical tows from specific depths to the surface. In Hummingbird, North Gate, and Tender bogs, 1.5-m tows (356 liters) gave sufficiently large samples for all instars of the different species. Tows of 1.5 m also were used for *C. americanus* larvae in Forest Service Bog. Because *C. trivittatus* larvae, especially 4th instars, rarely were concentrated in the surface waters in Forest Service Bog, 2.5-m (593 liters) tows were taken from mid-May until mid-August, and 3.5-m (832 liter) tows were taken from mid-August until mid-October to collect *C. trivittatus*. Deeper tows were taken in the late summer and fall because the later-instar larvae remained deeper. All samples were collected between 2400 and 0130 h, when larvae of all species, except for *C. trivittatus* in Forest Service Bog, were in the upper waters.

All 4th-instar larvae and pupae were identified to species by using the keys of Cook (1956), Roth (1967), and Saether (1972). The 1st instars cannot be identified to the species level. The identification of 2nd, 3rd, and 4th instars of *C. americanus* and *C. trivittatus* was based on characters used by Fedorenko and Swift (1972). Head capsule size data from LaRow and Marzolf (1970) were used to distinguish the instars of *C. punctipennis*. For all species, head capsule length (at  $45\times$ ,  $n = 30$ ) was measured for 2nd-, 3rd-, and 4th-instar larvae. The larval instars of *C. flavicans* were identified based on the larval characters suggested by Parma (1971). The life history data are presented as percent frequency for each instar of each species throughout the sampling period. Except for *C. trivittatus*, only the 1973 data are presented. Results for 1st instars are presented only for *C. americanus* and *C. punctipennis* for the lakes where they occurred alone. Temperature profiles

<sup>1</sup> Diptera: Chaoboridae.  
<sup>2</sup> Received for publication 28 May 1980.