Frequencies of Developmental Morphs of Chaoborus americanus in Four Fishless Bog Lakes

ABSTRACT: Samples of fourth instar larvae of the phantom midge *Chaoborus americanus* from four fishless lakes were analyzed for frequencies of different developmental morphs. The percentages of fast-developing morphs found were 92.9, 98.3, 19.6 and 39.2. These values did not correlate with lake temperature regimes. Lake temperature was correlated with the rate of pupation of fast-developing morphs.

Polymorphism may be advantageous for a species under many circumstances. The trend has been to search for singular mechanisms that will explain patterns of polymorphism. In most cases, however, a suite of evolutionary forces probably determines the frequencies of morphs, with only several of these factors operating at a particular location (Jones *et al.*, 1977). To gain a better understanding of the ecological significance of polymorphism, the same characters should be monitored in populations existing under different circumstances.

Bradshaw (1973) described developmental polymorphism in the phantom midge larva *Chaoborus americanus,* a species that typically occurs in shallow woodland ponds. When samples of overwintering populations of fourth instar larvae were exposed to the cues of long day and food, only a portion of the populations pupated immediately; the remaining individuals took longer to pupate. Pupation time was correlated with the size and color of the larvae. At the extremes of this spectrum of variation in size and color were the large yellow larvae that pupated first, and the small pale larvae that pupated last. Bradshaw (1973) concluded the polymorphism was maintained by the unpredictable year-to-year weather patterns of vernal climates of temperate regions. A warm continuous spring would select for the fast-responding morph, whereas a spring in which an initial thaw was followed by refreezing of a pond would favor the slower pupating morph.

Chaoborus americanus also occurs in fishless lakes (Northcote *et al.*, 1978; Pope *et al.*, 1973; von Ende, 1979). If the polymorphism is maintained primarily by the patterns of spring weather, populations from different lakes in a local area should have similar patterns of pupation. This report compares the pupation patterns of *C. americanus* from four fishless bog lakes in the Upper Peninsula of Michigan, as part of a larger study of the population dynamics of *C. americanus* in fishless lakes.

METHODS

The four bog lakes (Ed's Bog, Forest Service Bog, Marathon Bog and Tender Bog) are located at the University of Notre Dame Environmental Research Center (UNDERC) in

TABLE 1.—*Chaoborus* and zooplankton species, physical characteristics and pupation results for the four lakes. Lakes are ordered according to temperature regimes between June and September, with Forest Service being the warmest

	Forest Service	Marathon	Ed's	Tender
Chaoborus americanus	X	X	X	X
C. trivittatus	X	X		
Daphnia pulex	X	X	X	X
Diaphanosoma leuchtenbergianum	X	X		
Diaptomus leptopus	X	X	X	X
Holopedium gibberum	X	X		
Lake characteristics				
Max. depth (m)	5.0	12.0	8.0	10.0
Degree staining[1]	0	0	X	XX
Mean temp. diff. — May[2]	+6.4	+7.0	−7.0	0
Mean temp. diff. — Summer[3]	+6.6	+4.0	+0.7	0
Pupation results				
% FDM[4]	92.9	19.8	39.2	98.3
% FDM pupated by day 0	99.4	75.6	29.8	52.9
Day 95% FDM had pupated	0	2	5	2

[1]0 = unstained, X = lightly stained, XX = darkly stained
[2]Mean temperature difference compared to Tender for 20, 21 May
[3]Mean temperature difference compared to Tender for June-September
[4]FDM = fast-developing morphs

Gogebic Co., Michigan (von Ende, 1979). They are all within several kilometers of each other. The lakes can be classified into two types according to their zooplankton communities, the *Chaoborus* species present and the degree of staining of the lakes' water (Table 1). Forest Service and Marathon differ from Ed's and Tender by having—besides *C. americanus*—a second *Chaoborus* species, *C. trivittatus,* and by having more diverse zooplankton communities and unstained water.

Fourth instar larvae of *Chaoborus americanus* were collected from all the lakes by vertical tows with a plankton net (153 μm) on either 29 or 30 April 1978, just a few days after the ice had left the lakes. The larvae were returned to my laboratory in DeKalb and placed in a constant temperature chamber at 14 C, on a 14:10 light:dark photoperiod. Beginning 3 May 1978 and continuing for 15 days, a daily record was kept of the number of larvae pupating. Because the zooplankton communities in these lakes at this time were either at a very low density or still absent, and because long days without food would cause the large yellow larvae to pupate (Bradshaw, 1973), food was not presented to the larvae during the 15 days. Larvae that did not pupate were assumed to be the slower-developing morphs. Temperature profiles of each lake were measured at approximately 2-week intervals from 20 May until 3 August, and on 15, 16 September and 20, 21 October 1978. The degree of staining of the lakes' water was determined by a qualitative comparison of water samples.

RESULTS AND DISCUSSION

There were systematic similarities and differences in the pupation patterns of the larvae from the four lakes (Fig. 1). The final percent pupation is an estimate of the percentage of fast-developing morphs in the respective populations. The populations can be classified as high or low in terms of their final percent pupation. Forest Service and Tender had 92.9% and 98.3% pupation, respectively, whereas Marathon and Ed's had 19.6% and 39.2% pupation, respectively (Table 1). Forest Service was the only lake in which pupae were found in the field the day the larvae were collected. Within each of these pairs, the lake with the lower percent pupation on day 0 had the greater percent pupation at the end of the experiment. In Forest Service and Marathon 99% and 76%, respectively, of the fast-developing morphs had pupated on day 0, and by day 2, 95% of the fast-developing morphs in Marathon had pupated (Table 1). The difference between the two samples was that the fast-developing morphs comprised 93% of the Forest Service sample, but only 20% of the Marathon sample. The fast-developing morphs showed greater variation in the time for pupation in Tender and Ed's bogs. Fifty-three percent and 30%, respectively, of the fast-developing morphs had pupated on day 0, and by days 2 and 5, respectively, 95% of the fast-developing morphs had pupated (Table 1). Again, however, there was a large difference between the samples from Tender and Ed's bogs in the percentage of the larvae that were the fast-developing morph (98% and 39%, respectively). This rather striking difference in the proportion of morphs among the four lakes suggests that collectively they may be different from Bradshaw's (1973) vernal ponds.

Because the heritability of this polymorphism has not been studied, the effect of environmental factors on the expression of this character is unknown. If the temperatures in the 0.5-3.0 m depths (the stratum occupied by the larvae) of the lakes are compared, the lakes can be arranged in a series from warmest to coldest (Table 1). Growth of *Chaoborus americanus* larvae from first instar to fourth occurs from June to September. If we use Tender as a standard, during this time Forest Service was 6.6 C warmer on the average, Marathon 4.0 C warmer, and Ed's 0.7 C warmer than Tender (Table 1). These differences during the summer are correlated with the degree of staining of the lakes' water and the depth of the lakes. The shallow, clear Forest Service Bog was the warmest, and the darkly stained and deep Tender Bog was the coldest. If these data are compared to Figure 1, there is no correlation between the percentage of fast-developing morphs and the temperature regimes, except for Forest Service. Because Forest Service was the warmest lake and had a very high percentage of fast-developing morphs, we cannot exclude the possibility that higher temperatures accelerated development throughout the summer and, combined with the higher temperatures in May (Table 1), allowed for earlier pupation; however, the fact that the coldest lake, Tender, had the greatest percentage of fast-developing morphs suggests this effect was minimal. Higher temperatures, especially in May (Table 1), may advance development within a particular morph as seen in the fast-developing morphs from the warmest lakes, Forest Service and Marathon. Warmer temperatures, however, cannot transform a slow-developing morph into a fast-developing morph. Bradshaw (1973) showed this, but only for the fourth instar. Therefore, temperature differences

between the lakes appear to be of relatively minor importance in affecting morph frequency.

The inconsistency of the *Chaoborus americanus* pupation patterns in these lakes suggests the system is complex and that factors other than the previous spring's weather may be equally important in determining the frequency of morphs in a lake. For example, cannibalism is common in *Chaoborus* (von Ende, 1979). Variation in zooplankton production between lakes could affect cannibalism rates. One could imagine offspring of a fast-developing morph being preyed upon by fourth instars of the slow-developing morph. This would produce a shift in the frequency of the morphs, the extent of which would depend on the amount of cannibalism. Community structure also may be important in determining the amount of cannibalism if alternate prey are absent at certain critical seasons. The relative importance of cannibalism or other factors that may be affecting the frequency of the morphs is not clear at present. Understanding the role of invertebrate predators such as *Chaoborus* in structuring zooplankton communities requires understanding of the factors controlling the dynamics of these predators (Lynch, 1979). Because the dynamics of *C. americanus* populations may be related to their patterns of pupation in lakes, further investigation is required.

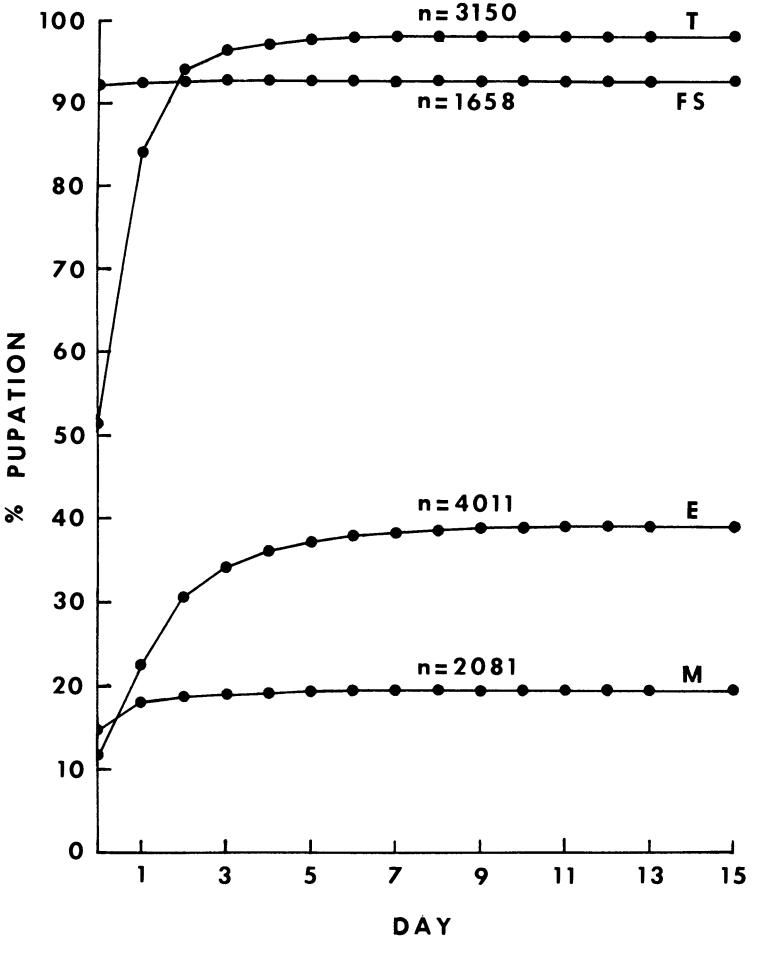

Fig. 1.—Cumulative percent pupation of fourth instar *Chaoborus americanus* exposed to long days in the laboratory. T = Tender Bog, FS = Forest Service Bog, E = Ed's Bog, M = Marathon Bog. n = sample size

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