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Regional coexistence of four *Chaoborus* species

CARL N. VON ENDE

With 1 table in the text

Morphological characters have been suggested as indicators of past competition. Based on the LOTKA-VOLTERRA competition equations and assuming exploitation competition (sensu MILLER 1967), estimates have been made of the degree of difference in resource utilization required for species to be able to coexist (MACARTHUR & LEVINS 1967). Often size of feeding structures is used to infer differences in prey size selection. I would like to address this matter as it relates to the sizes and patterns of distribution of four *Chaoborus* species that occur in a series of lakes in the Upper Peninsula of Michigan, and exploitation and interference competition (MILLER 1967).

I have found that *C. americanus, C. flavicans, C. punctipennis,* and *C. trivittatus* occur in the 22 lakes sampled. They occur in the following combinations in different kinds of lakes. *Chaoborus flavicans, C. punctipennis,* and *C. trivittatus* are found in various combinations in the lakes with fish. *Chaoborus punctipennis* may occur alone, or with *C. flavicans,* or with both *C. flavicans* and *C. trivittatus.* Neither of the latter two species occurs alone or together without *C. punctipennis* in the lakes with fish. *Chaoborus americanus* occurs alone in stained bog lakes without fish, or together with *C. trivittatus* in clear bog lakes without fish. *Chaoborus americanus* is absent from the lakes with fish.

In comparing these species we find that they differ with respect to several other characters. First the later instars of the species that occur in the lakes with fish undergo diurnal vertical migration so that they are deep in the water during the day, and up near the surface waters at night. *Chaoborus americanus* undergoes little vertical migration (especially in the stained bog lakes), and is near the surface waters continually. Secondly, the larvae differ with respect to size (Table 1). *Chaoborus punctipennis* is

Table 1. Body length (mm) and head capsule length (mm) for fourth instar larvae of the four *Chaoborus* species. n = 30.

Species	Body length		Head capsule	
	x	SE	x	SE
C. puntcipnenis (SAY)	9.29	0.47	1.07	0.04
C. flavicans (MEIGEN)	10.78	0.29	1.35	0.04
C. americanus (JOHANNSEN)	12.42	0.47	1.57	0.06
C. trivittatus (LOEW)	12.79	0.69	1.96	0.09

the smallest; *C. flavicans* is the next largest, followed by *C. americanus. C. trivittatus* is the largest. Finally, the species differ with respect to the timing of recruitment. *C. americanus* is the first to emerge in the middle of May. Recruitment for *C. flavicans* occurs at the end of May, and at the end of June for *C. punctipennis, C. trivittatus* is the last to emerge at the end of August.

First consider the two species commonly found in this region in lakes with fish, *C. flavicans* and *C. punctipennis*. I have shown elsewhere (von Ende 1975), and others have suggested that vertical migration seems to be adaptive in minimizing predation by fish on *Chaoborus* larvae. Fish were added to a bog lake which had *C. americanus* and the fish eliminated this species from that lake (von Ende 1975). Therefore, it is not too surprising that the species that coexist with fish migrate. Stahl (1966) suggested that the size difference in the larvae of these two species should promote their coexistence by allowing them to utilize differently size prey. This has generally been considered a reasonable explanation, although never really tested. Fedorenko (1975) and Swift & Fedorenko (1975) have recently conducted extensive studies on the feeding patterns of the other two species considered above, *C. americanus* and *C. trivittatus*. They have found that the relative size of the larvae of these two species may be important at the extreme prey sizes, but generally it is the relative distribution of the different instars of the two *Chaoborus* species, and the various prey species, that are the most important factors in determining the prey taken. Once prey have been contacted by the *Chaoborus* larvae, then size, shape, and the behavior of the prey become important. However, the probability of encountering a given prey depends on the relative distribution of the two. Therefore, Fedorenko (1975) concludes that the relative size of the predators and prey in Eunice Lake is less important than their distribution, and her study only partially supports Stahl's conclusion.

I would like to suggest that there is another way to look at these conclusions of Stahl & Fedorenko so that their results do not contradict one another. It is that there is one important difference in the kinds of lakes in which these two species pairs coexist. Eunice Lake has no fish, whereas the lakes in which *C. punctipennis* and *C. flavicans* are found, contain fish. It appears in the latter kinds of lakes that these two species have become more similar in their diurnal spatial distribution by necessity. To avoid fish predation, the older instars must be in the deeper waters during the day. By feeding at night they should be subject to less fish predation. Fedorenko & Swift (1972) found spatial separation of their two species. This was primarily the result of the minimal amount of migration by *C. americanus*. Therefore, it might be argued that in a fish lake, the relative sizes of *C. punctipennis* and *C. flavicans* may be more important in the coexistence of these species because of their similar spatial distribution. They should be encountering the same array of prey at about the same time and in the same place. Under these circumstances, the differences in head capsule size may be more critical.

The difference in the timing of recruitment for these two species would seem to support this argument. Recall that *C. flavicans* emerges at the end of May and *C. punctipennis* at the end of June. This means that since both species take about the same time to develop to fourth instar, *C. flavicans* is developmentally ahead of *C. punctipennis*. In *Chaoborus* species the early instars are less different in absolute size than are the later instars (head capsule). The staggering of recruitment should serve to decrease the overlap in time of individuals of about the same size. This could be important in the early instars because they usually exhibit minimal vertical migration.

I have shown elsewhere (von Ende 1975) that *C. americanus* excludes the other three species from stained, fishless bog lakes by preying on the early instars of the other species. This is possible because of the early recruitment of *C. americanus* and the lack of migratory behavior of the older instars of this species. Under these conditions it would seem that the best way to coexist with *C. americanus,* because of the intensity of this predation (or interference competition), would be to be, at the same time, the same size as the *C. americanus* larvae, or larger. Then *C. americanus* would not be able to prey on the other species. *C. trivittatus* has apparently adopted this strategy. In the clear, fishless bog lakes, *C. trivittatus* overwinters as second or third instars. When *C. americanus* emerges in May, it is smaller than the *C. trivittatus* larvae. It does not have a chance to get a head start on *C. trivittatus.* This phenomenon does depend on there being a sufficiently low predation rate over the winter so that the *C. americanus* larvae do not eliminate the early instars of *C. trivittatus.* This presents an interesting contrast: whereas in the case of *C. punctipennis* and *C. flavicans* I argued that the separation of recruitment times may promote their coexistence by strengthening size differences, here I am suggesting that for *C. americanus* and *C. trivittatus* it is just the opposite because of interference competition. The scheduling of recruitment serves to decrease interspecific predation (interference competition), while morphological size difference minimize explotation competition. For *C. americanus* and *C. trivittatus* I am suggesting it pays to be different sizes, but not so different that one species has a predatory advantage. It should be pointed out that the difference in head capsule size may not be important in all the lakes in which these species are found, as Fedorenko (1975) has shown. This is not too say, however, that under certain conditions the size differences may be important, and this may be frequently enough to maintain it in the species. For example, one of the bog lakes in which *C. americanus* and *C. trivittatus* occur has a maximum depth of 4.5 m. The spatial overlap of the species is much greater in this lake than Fedorenko (1975) found. Perhaps head capsule size difference is more important in this case.

I would like to suggest that the combinations of characters described for the four species seem to represent adaptation to particular kinds of habitats and to a certain extent to other species. As described above, because of its small size and vertical migratory behavior, *C. punctipennis* seems well adapted for lakes with fish. Its timing of recruitment may be a response to the presence of *C. flavicans.* It is usually absent from lakes without fish. In contrast, *C. americanus* seems well adapted for lakes or pools without fish. Its early emergence may be advantageous for a species which frequently occurs in shallow pools by allowing it to get to the more hardy, later instars as quickly as possible because of stagnant waters later in the season. Its larger size is advantageous in a fishless habitat because these are usually dominated by larger zooplankton species. Finally, there would be little need for extensive vertical migration in fishless habitats. The other two species are less parochial. *Chaoborus flavicans* also emerges earlier in the summer. Occasionally, it can be found in woodland pools where early development may be necessary. Perhaps the intermediate size of *C. flavicans* allows it to survive in lakes dominated by either large or small zooplankton. It usually migrates vertically, but this may be reduced in certain lakes (Teraguchi & Northcote 1966).

Although the phylogeny of *Chaoborus* is somewhat unclear (Saether 1972), perhaps the large size of the last species, *C. trivittatus*, indicates that this was the "best" size to be considering the size array of the other three species. By being larger than both *C. flavicans* and *C. americanus*, overlap is minimized with the *Chaoborus* in both the fishless and fish lakes. Its vertical migration enables it to survive in fish lakes, and its timing of recruitment in certain fishless lakes.

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Author's address:

Dr. C. N. von Ende, Dept. of Biological Sciences, Northern Illinois University, DeKalb, Illinois 60115, U. S. A.