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## Influence of fish kairomones on the ovipositing behavior of *Chaoborus* imagines

**Abstract**—The phantom midge, *Chaoborus*, is a dipteran, the larvae of which occur in many freshwater habitats and are known to be vulnerable to predation by fish. The hypothesis was tested that ovipositing imagines of *Chaoborus* use chemical cues to detect predatory fish and avoid depositing eggs into waterbodies containing fish kairomones. The experimental setup consisted of cages with two small water-filled plastic containers, in which *Chaoborus* imagines could oviposit. One container was connected to a flow-through system holding fish kairomones, while the other container (the control) was connected to a flow-through system without fish kairomones. Three different *Chaoborus* species were tested: two pond-dwelling species, *Chaoborus crystallinus* and *C. obscuripes*, which do not coexist with fish, and a lake-dwelling species, *C. flavicans*, which does coexist with fish. The imagines of the two pond-dwelling species showed an ovipositing preference for fish-free water. No significant difference in ovipositing preference was found for the lake-dwelling species (*C. flavicans*). The present experiment suggests that in addition to direct predatory effects, adult oviposition behavior may contribute to the lack of local coexistence between fish and pond-dwelling *Chaoborus*.

Predation is often thought to be limited to direct, lethal effects of predators, although more recent data suggest that indirect effects can be equally important. Indirect effects include trophic linkage effects and those caused by behavioral and chemical interactions (Kerfoot and Sih 1987). Many indirect effects in freshwater communities are mediated by chemical communication, and a large number of organisms have been shown to respond in a variety of ways to chemicals or kairomones released by their predators (Havel 1987; Dodson 1989; Adler and Harvell 1990; Larsson and Dodson 1993).

Many aquatic insects have terrestrial adult stages that must return to the water to oviposit, and the selection of oviposition sites can be an important feature in determining freshwater community structure. The presence of fish could indirectly structure these communities by influencing adult choice of oviposition sites. Therefore, selection should favor adults with oviposition behavior that yields the highest juvenile survival. This particular research topic has largely been ignored by aquatic ecologists (*but see* Resetarits and Wilbur 1989; Kats and Sih 1992).

The phantom midge *Chaoborus* is a dipteran. Its larvae inhabit many freshwater habitats and are known to be vulnerable to predation by fish (Wright and O'Brien 1982). Some *Chaoborus* species have adaptations that enable them to coexist with fish. For example, *C. flavicans*, a lake-dwelling species, exhibits diel vertical migration in response to the presence of fish (Dawidowicz 1990; Tjossem 1990). In contrast, the larvae of *C. americanus*, a pond-dwelling species, do not respond to chemicals from fish, whereas the larvae of *C. punctipennis*, a lake-dwelling species, do (Barendonk and O'Brien 1996). These results suggest that the larvae of lake-dwelling species, such as *C. flavicans*, have evolved a behavioral adaptation to the presence of fish, whereas the larvae of pond-dwelling species, such as *C. crystallinus*, have not evolved such an adaptation or have lost the response. Therefore, it would be of selective advantage for adults of these pond-dwelling species to actively avoid oviposition in waterbodies with high fish densities.

Petranka and Fakhoury (1991) have demonstrated selective oviposition behavior by *Chaoborus*, but the mechanisms underlying this oviposition behavior are largely unknown, and their experimental design could not determine whether chemical or mechanical cues were important. Furthermore, they could not determine what species showed the selective oviposition behavior, although circumstantial evidence suggested that the lake-dwelling species *C. albatus* showed an oviposition preference for the fish-free pools. As the presence of fish chemicals has been shown to influence *Chaoborus* larvae and other zooplankton in a variety of ways (Dodson 1989), the goal of this study was to determine if chemicals alone can influence oviposition behavior of *Chaoborus* imagines. Three different species were tested—two pond-dwelling species, *C. crystallinus* and *C. obscuripes*, which do not coexist with fish, and a third, *C. flavicans*, which is found in lakes where fish are present. Therefore, one would predict that the two pond-dwelling species should show stronger reactions to fish kairomones than the lake-dwelling species. Selection should favor adults that avoid egg laying in a habitat where offspring would suffer higher mortality.

*Chaoborus* larvae were collected from two ponds and a lake in Schleswig-Holstein, Germany. *C. obscuripes* and *C. crystallinus* were taken from fishless ponds near Plön and *C. flavicans* from Plußsee, which contains a large planktivorous fish population (Kremser pers. comm.).

The larvae were well fed with young *Daphnia magna* and held under a 20:4 light:dark photoperiod, at  $24 \pm 1^\circ\text{C}$ , to prevent dormancy of the *Chaoborus* pupae (Bradshaw 1970; Ratte 1979).

The experimental setup consisted of five 60- × 60- × 100-cm (height) cages. Each cage was illuminated by an Osram Cyclolux lamp with a light intensity of  $36.8 \mu\text{mol m}^{-2} \text{s}^{-1}$ .

Each cage contained a hatching aquarium (30 × 10 × 20 cm [height]). The top of the aquarium was covered with a tilted glass pane leaving only a small gap (Fig. 1). Previous experiments showed that this hatching aquarium design prevented ovipositioning into the aquarium after the imagines had emerged. In front of each hatching aquarium were two adjacent 20- × 30- × 15-cm (height) black plastic containers

(Fig. 1a), as Yap et al. (1995) showed that *Aedes albopictus* preferred dark-colored jars for oviposition sites. The black containers and the hatching aquarium in each cage were randomly positioned, but their relative positions were kept the same, therefore not allowing an orientation stimulus by light or the wall of the room (Fig. 1b). Each plastic container was connected to one of two independent flow-through systems. Each flow-through system consisted of a reservoir of 36 liters with filtered fishless pond water, outside the cages, five black containers in series, one in each cage, and a peristaltic pump (Fig. 1b). The flow rate of the pumps was  $1.5 \text{ liters h}^{-1}$ . Two rudd (*Scardinius erythrophthalmus*) and two sticklebacks (*Pungitius pungitius*) were placed in one of the large containers. None of the tested *Chaoborus* species originated from the fishless pond where I obtained the experimental water. The black plastic containers and the hatching aquaria were gently aerated for 1 h a day, causing a surface disturbance of the water that prevented the growth of a bacterial film. Previous observations showed that the imagines could be trapped by such a surface film.

One hundred twenty *Chaoborus* pupae were placed in each hatching aquarium. It was impossible to determine the sex of the live pupae without damaging them; therefore, I assumed that the sexes for each replicate were randomly distributed. The experiment was run for 8 d. Once a day, dead pupae were removed and replaced with live ones. Starting the experiments with pupae had two advantages: (1) pupae are less likely to be damaged during handling than adults, and (2) the use of pupae ensured that copulation took place soon after emergence of the imagines. During copulation, the genitalia of the females should still be soft, which is an essential prerequisite of successful mating events in many dipteran species (Parma 1971). After mating, all females oviposited in one of the plastic containers.

Egg rafts were collected daily at noon and placed into a microtiter plate, to assess development time of individual egg rafts and fertilization status. In addition, this prevented later female attraction by egg rafts from earlier females. After all imagines had died, they were collected and preserved in alcohol, to determine the sex ratio for each cage.

Data from experiments with individual decisions are often essentially binomial data. Only in cases with high numbers of replicates (>50) will such data eventually approach a normal distribution (Sokal and Rohlf 1995). Therefore, I employed a two-tailed binomial exact test (SPSS vers. 6.1) to examine the differences of the data distributions. The probabilities of the  $k$  tests were combined following the method of Stouffer et al. (1949; cited in Folks 1984) rather than the method by Fisher (1954). The method after Stouffer et al. was used to combine the probabilities of the  $k$  tests. Rice (1990) stated that the Fisher method is unsuitable as a consensus test because it is more sensitive to data that refute a common  $H_0$  compared with the data that support it. Stouffer et al.'s method lacks this bias. In this test, each of a group of  $k$   $P$ -values is transformed to a corresponding standard normal variable ( $z_p$ ). A test of  $H_0$  is carried out by calculating  $Z = z_{p(\text{average})}/(1/\sqrt{k})$ . The fifth replicate of the experiment with *C. obscuripes* was not included in the analysis because of the low number of data.

In the experiments with *C. crystallinus* and *C. obscuripes*,

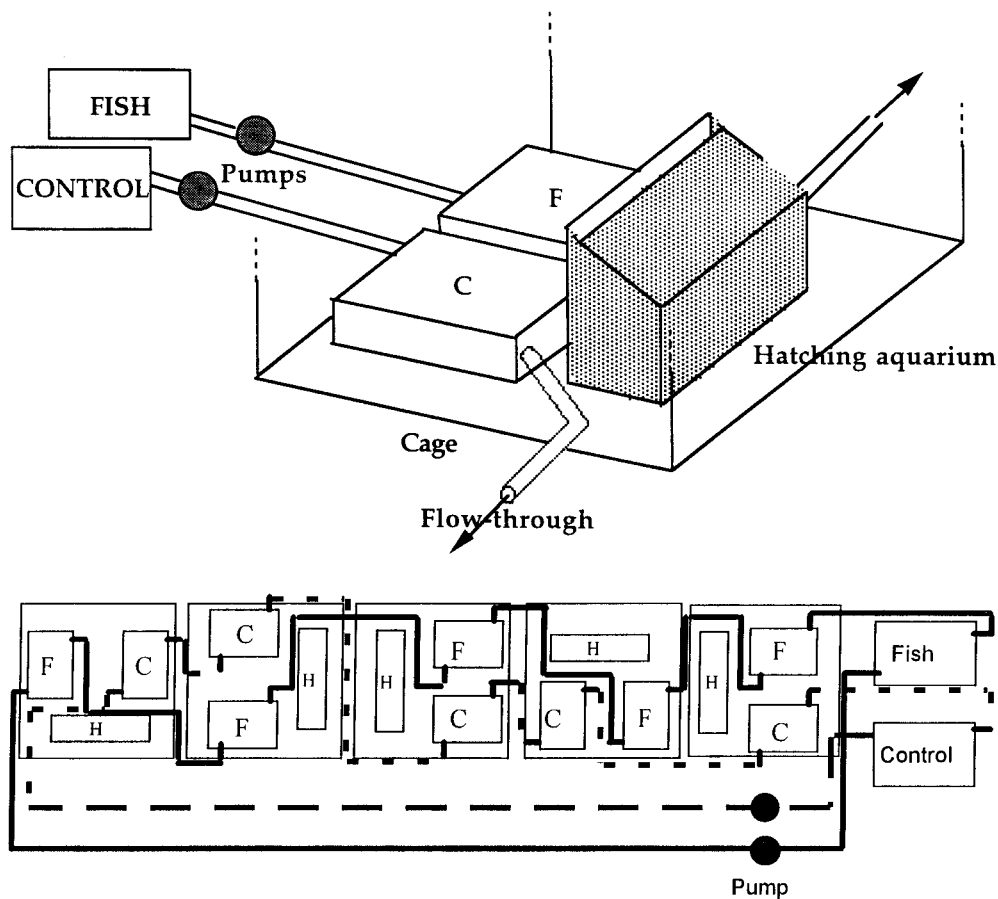


Fig. 1. (a) Design of the experimental setup. The positions of a hatching aquarium and the black containers within the cages are shown. (b) Diagram of the experimental setup showing the positions of the hatching (H) aquaria and the black containers within the cages. The black lines are the flow-through system for the fish-conditioned water (F), and the dashed lines are the flow-through system for the control water (C).

males emerged earlier, with 56.3% (SE = 3.7%;  $n = 5$ ) and 73.3% (SE = 6.5%;  $n = 5$ ) of the populations being males, respectively. After 1–3 d, nearly all imagines had emerged from the hatching aquarium and started to mate. The males caught a female when she flew into the swarm; copulation took place in flight and lasted 1–2 s. In contrast, *C. flavicans* copulation took place at the wooden frame of the cage; 47.8% (SE = 3.4%;  $n = 5$ ) of the emerged *C. flavicans* imagines were males. In the experiment with *C. crystallinus*, 94.3% (SE = 6.3%;  $n = 5$ ) of all egg rafts were fertilized and hatched, while for *C. obscuripes* and *C. flavicans*, the numbers were 86.6% (SE = 2.5%;  $n = 5$ ) and 85.7% (SE = 7.2%;  $n = 5$ ), respectively. These high fertilization rates indicate that the cage design was appropriate for successful *Chaoborus* mating.

After 2 d, the first imagines in the experiment started to lay eggs in one of the two black containers. The pond-dwelling species *C. crystallinus* and *C. obscuripes* laid significantly fewer egg rafts in the container with fish water compared to the control (Table 1). As the sex of the pupae was not determined, one replicate for both of the species contained a relatively high percentage of males, and hence the total number of oviposited eggs was considerably lower than

in the other replicates. *C. flavicans*, the lake-dwelling species, tended to prefer the containers with fish kairomones compared to the control, although this preference was not significant (Table 1). *C. crystallinus* laid an average of 64.8% of all egg rafts in the control containers, while *C. obscuripes* laid 65.7% and *C. flavicans* laid 38.5% of their egg rafts in the control containers. Females laid only one egg raft and died soon after ovipositing. At 24°C, hatching occurred approximately 3 d after laying; the developmental time of the egg rafts was the same for all species in all treatments.

This study clearly shows that the imagines of the pond-dwelling species *C. crystallinus* and *C. obscuripes* can use fish kairomones to assess the quality of oviposition sites, whereas the imagines of the lake-dwelling species *C. flavicans* do not show any preference in their ovipositing behavior. Therefore, while direct predatory effects contribute to the lack of local coexistence between fish- and pond-dwelling *Chaoborus* (von Ende 1979), the results of this study indicate that adult oviposition behavior may also play an important role in influencing *Chaoborus* species distribution. The tendency of the pond-dwelling species of *Chaoborus*

Table 1. Number of egg rafts in control and fish containers. Summary statistics are for the binomial exact test for each replicate and standard normal variable  $z_p$  for the consensus combined  $P$ -value test after Stouffer et al. (1949; cited in Folks 1984).

Taxon	Number of egg rafts in control container	Number of egg rafts in fish containers	Binomial exact test	$z_p$ (average)	Combin. after Stouffer et al.
<i>C. crystallinus</i>	33	18	0.0251	1.43	$P < 0.05$
	22	9	0.0311		
	33	19	0.0714		
	36	21	0.0637		
	12	7	0.3593		
<i>C. obscuripes</i>	12	3	0.035	1.12	$P < 0.05$
	12	3	0.035		
	11	5	0.210		
	11	7	0.481		
	1*	1	1.000		
<i>C. flavicans</i>	12	19	0.282	0.91	$P > 0.05$
	1	9	0.021		
	5	11	0.210		
	10	8	0.815		
	8	9	1.000		

\* Data not included in the analysis.

imagines to avoid habitats with fish has probably evolved in response to fish preying on the aquatic stages of these taxa.

As the design of this experiment effectively rules out the possibility that imagines could use visual or mechanical cues, chemical cues appear to be the mechanism used by *Chaoborus* to detect fish. An alternate interpretation of these results could be that mature females prefer to oviposit in water similar to the water in which they were born (i.e., water with or without fish chemicals). The only difference between the control and the fish water was the added fish chemicals; the water itself was obtained from the same pond for both treatments, and none of the organisms originated from that particular pond. Furthermore, the results suggest that fish kairomones are nonvolatile, contact oviposition inhibitors rather than volatile cues. Although the fish-conditioned water and control containers were placed next to each other, it is unlikely that volatile fish kairomones would be distributed into the air in such a sharp gradient that *Chaoborus* imagines could assess water quality of the containers while flying.

Many dipterans have contact chemoreceptors on various body appendages, including the tarsi (Stadler 1984). Petranka and Fakhoury (1991) suggest that *Chaoborus* may chemically sample water with their tarsi while positioning themselves at the water surface to oviposit. By contrast, Weber and Tipping (1993) suggest that for *Culex* species, chemoreceptors in the mouth parts may be used to assess water quality, as they observed preoviposition drinking by imagines. I observed such drinking behavior for *Chaoborus* as well, but it is uncertain which one of the proposed sensory structures the *Chaoborus* imagines use to assess water quality.

Unlike me, McPeck (1989) did not find that the fishless lake species (pond-dwelling species) of *Enallagma* damsel-

flies discriminated between fishless and fish-containing lakes. In his examination of the dispersal of adult *Enallagma* damselflies, two species found as larvae in fishless lakes and two other species found as larvae in lakes supporting well-developed fish communities all dispersed very few adults to adjacent lakes. In contrast, another species found in lakes that winterkill, and thus contain fish only periodically, dispersed large numbers of adults to adjacent lakes. He attributed species differences in the propensity to disperse to the constancy of the fish and fish-containing condition of the lakes inhabited by those damselfly species. The same may be true for *C. flavicans*, the lake-dwelling species, which generally lives in lakes with well-developed fish communities. Assuming this species has a low propensity to disperse (relative to a pond-dwelling species), this could explain the lack of any oviposition preference for *C. flavicans*. However, few data are available on the dispersal abilities of the different *Chaoborus* species (for *C. albatus*, see Lindquist and Deonier 1942); thus, further work is necessary to test this hypothesis.

This study has shown the behavioral avoidance of water containing fish kairomones by ovipositing *C. crystallinus* and *C. obscuripes*. The role of fish in structuring freshwater communities through direct predation is well documented (e.g., Zaret 1980; von Ende 1979). This study suggests a different mechanism for how predators may influence the composition of freshwater communities. Hanski and Ranta (1983) described how *Daphnia* in rock pools exist as metapopulations, and the same may be true for pond-dwelling species of *Chaoborus*. The presence of fish in a particular pond may affect not only the local pond, by discouraging oviposition, but may also increase emigration to neighboring ponds. This emigration would increase abundance and thus influence the population genetic structure of neighboring

ponds. This nonconsumptive effect of the predator may result in far-reaching (watershed-scale) direct and indirect effects since the prey are only to a small degree removed from the system. *Chaoborus* pond-dwelling species live in a fluctuating, unpredictable habitat, with a relatively short persistence time (compared to lakes). One can view ponds in the landscape as "patches of a metapopulation"; these patches are permanent and temporary ponds that periodically dry out or freeze solid from year to year. This last fact might explain why 35% of the individuals tested oviposited into the fish water, since many species that live in such unpredictable habitats show a wide variation in habitat selection behavior (Krebs 1994).

The data presented indicate that for pond-dwelling species of *Chaoborus*, selection may act at the adult stage, so that they behave to avoid fish. For the lake-dwelling species of *Chaoborus*, selection may occur at the larval stage, promoting alternative antipredator behaviors such as vertical migration and reduced movement frequency to avoid fish (Dawidowicz 1990; Berendonk and O'Brien 1996), assuming that fish predation is the ultimate cause for selective ovipositing and vertical migration in *Chaoborus*.

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