Movement Response of Chaoborus to Chemicals from a Predator and Prey

Thomas U. Berendonk; W. John O'Brien

Movement response of *Chaoborus* to chemicals from a predator and prey

Abstract—By means of a silhouette videotaping system we studied the frequency of movements of *Chaoborus americanus* and *Chaoborus punctipennis* when exposed to water conditioned in different ways. Four treatments were investigated: unconditioned water was used as a control; predator-conditioned water was water in which fish had been held; prey-conditioned water was water in which cladocerans had been grown; and mixed water was a mixture of predator- and prey-conditioned waters. The movement frequency of *C. punctipennis* significantly increased in prey water and decreased in predator water as compared to unconditioned water. The movement frequency of *C. americanus* significantly increased in prey-conditioned water; however, when exposed to predator-conditioned water the movement frequency was not significantly different from unconditioned water.

Predation is one of the most important ecological influences on population dynamics (Taylor 1984) and community structure (Paine 1966). Predation has been shown to be particularly important in structuring zooplankton communities (Brooks and Dodson 1965; O'Brien 1987). Predation is often thought to be limited to the direct, lethal effects of predators. However, predators may also have important indirect effects on the morphology and behavior of prey (Dodson 1988*b*). Aquatic invertebrates have been shown to respond to chemicals released by their predators (Dodson 1989*b*). The response of prey to chemicals released by predators include induction of morphological defenses (Havel 1987; Dodson 1989*a*; Black 1993), change in life-history characteristics (Stibor 1992; Black 1993), and altered behavior (Dodson 1988*a*; Tjossem 1990). Although Tjossem (1990) and Dawidowicz (1990) showed that the vertical migration of *Chaoborus flavicans* is induced by the presence of fish chemicals, studies are still lacking that specify the presence of chemicals as a key factor that influences the behavior of *Chaoborus*. Thus, although a fair amount is known about chemical response to predators, less is known about predators responding to chemicals given off by their prey.

We investigated the movement frequency of the larvae of two species of *Chaoborus* (*C. americanus* and *C. punctipennis*) in water that had been conditioned by predators and prey. *Chaoborus* is an excellent study animal for such investigations because it both preys on crustacean zooplankton and is heavily preyed upon by planktivorous fish. *Chaoborus* is a dipteran, the larvae of which occur in many freshwater habitats. *Chaoborus* is an ambush predator (O'Brien et al. 1990) that hangs motionless in the water column waiting for zooplankton prey to move within attack distance (Pastorok 1980; Riessen et al. 1984). If no prey is located within several minutes, *Chaoborus*

makes a repositioning move, presumably in an effort to move to a more favorable location. However, when in motion, *Chaoborus* is much more vulnerable to location by planktivorous fish (Wright and O'Brien 1982).

We studied the movement frequency of fourth-instar larvae of two phantom midge species. *C. americanus* larvae were collected from a small fishless reservoir on the Nelson Environmental Study Area, 15 km north of Lawrence, Kansas. *C. punctipennis* larvae were collected from Lone Star Lake, located 20 km southwest of Lawrence. Lone Star Lake is known to have fish, including large population of white crappie (*Pomoxis annularis*). All larvae were held at least 1 week in 20-liter aquaria in the laboratory at 18°C on a 14 : 10 L/D photoperiod and fed with *Daphnia parvula*. The larvae were held in aquaria in the type of water in which they would be observed. There were four types of water: unconditioned water (CONTROL), prey-conditioned predator (PREY), fish-conditioned water (FISH), and mixed water (MIX). We prepared CONTROL by adding 0.1 g liter^{-1} CaCO$_3$ to distilled water. We prepared PREY by holding daphnids and copepods in a 20-liter aquarium and feeding them with *Scenedesmus quadricauda*. We prepared FISH by holding eight white crappie in a large aquarium. The fish were fed zooplankton, but not *Chaoborus*. We mixed PREY and FISH in a 1 : 1 ratio to get MIX. All conditioned water was passed through a 0.45-μm filter and 200 ml was added daily to the appropriate *Chaoborus* aquaria after removing 200 ml of water from each aquarium.

We conducted experiments by placing 10 fourth-instar *Chaoborus* in 15 × 15 × 15-cm glass aquaria in which the four conditions were investigated (CONTROL, PREY, FISH, and MIX). Twenty-four hours before a taping session, we rinsed 10 *Chaoborus* with the appropriate conditioned (or CONTROL) water and placed them in an experimental tank. One hour before taping, we placed the tanks in position for videotaping and added 200 ml of freshly conditioned (or CONTROL) water. Larvae were used for only one taping.

We recorded three replicates of each treatment and taped each trial for 30 min. The order in which the four treatments were taped was randomized. Preliminary observations suggested that 30-min trials show the least variation in the movement frequency compared to shorter recording times. We videotaped each treatment with *C. punctipennis* between 2200 and 2400 hours because it exhibits vertical migration and feeds at night in its natural habitat. We taped *C. americanus* between 1000 and 1200 hours because it lacks extensive vertical migration and feeds throughout the day (von Ende 1979; Haney et al. 1990).

The movements of *Chaoborus* were observed with a

Table 1. Summary of ANOVA on movement frequency (variable) in response to differently conditioned waters ($n = 3$) (source of variation) for *Chaoborus punctipennis* and *Chaoborus americanus*.

	df	SS	MS	F-value	P-value
C. americanus	3	314.3	104.8	27.2	<0.001
C. punctipennis	3	542.9	181.0	92.4	<0.001

SS—sum of squares; MS—mean square.

silhouette (shadow) video photography system (Browman et al. 1989). This technique allows a large depth of field (~17 cm) and a field of view of 17 cm². This method has been used successfully in behavioral studies of fish larvae and cladocerans (Drost 1987; Browman et al. 1989). With such a system, a point source of light travels through a biconvex lens that collimates the light, which then passes through the experimental tank. A sharp silhouette of any organism in the tank is produced, which is focused on the lens of a video camera. The image was recorded on videotape with a recorder that was connected to a time-date generator and monitored on a television screen. Two of these systems were used simultaneously, one in the vertical plane and a second in the horizontal plane. For each view, we placed transparent rulers at the experimental tank in order to make measurements of size and distances from the videotapes.

The videotapes were analyzed with two frame-by-frame cassette recorders and two monitors. Tapes of the two views were analyzed in parallel in order to follow movements of individual *Chaoborus* in space and time. To avoid confounding effects of *Chaoborus* interactions with the sides of the arena, we analyzed only those animals found in an imaginary cube (10 × 10 × 10 cm) 2.5 cm from the sides of the arena. Because animals moved in and out of the imaginary cube, we noted the total animal occupation time. Total animal occupation time is the product of the number of animals in the imaginary cube and the number of seconds they remained in the cube. For the average number of movements per individual, we divided the total number of movements observed during 30 min by the total animal occupation time. The influence of the various waters on the movement frequency was checked with a parametric one-way ANOVA test followed by a posteriori comparisons using Tukey's procedure (Sokal and Rohlf 1981). The data met the assumptions of a parametric ANOVA.

We also conducted an experiment to determine whether the feeding rate of *C. punctipennis* was reduced in FISH compared to feeding in CONTROL. We placed two starved *C. punctipennis* and 30 *Bosmina longirostris* in 1-liter bioassay chambers (O'Brien and Kettle 1981). The size of *Bosmina* ranged from 0.4 to 0.6 mm, which is the preferred size range of prey of *C. punctipennis* (Pastorok 1980). We set up 12 of these chambers and submerged each in a 20-liter aquarium with CONTROL. Six aquaria were randomly chosen and every 6 h 200 ml of FISH was added. After 24 h we counted the *Bosmina* left in the chambers and in the crop of *C. punctipennis*, following
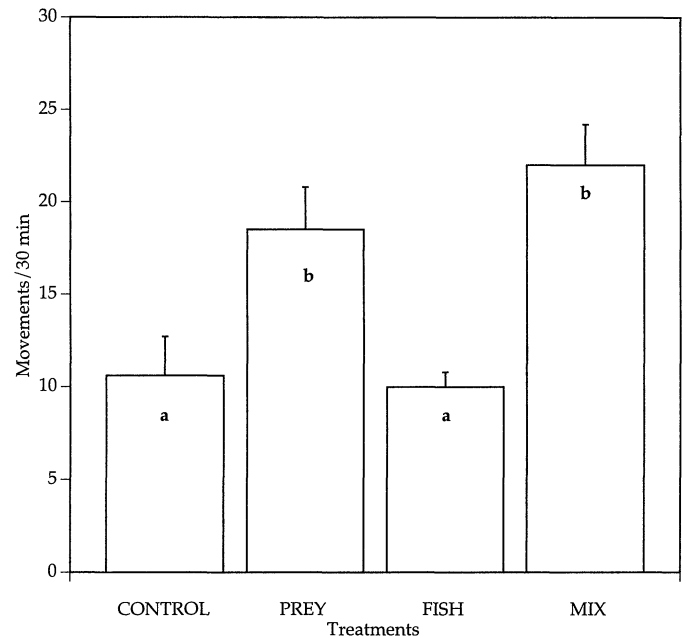

Fig. 1. Movement frequencies of *Chaoborus americanus* as a response to treatments with unconditioned water (CONTROL), prey water (PREY), fish water (FISH), and mixed water (MIX). Bars represent means of three replicates and standard error bars ($n = 3$). Bars with dissimilar letters differ significantly from each other by Tukey's procedure ($P < 0.05$).

the method of Swift and Fedorenko (1973). We used a two-tailed *t*-test to determine whether the feeding rates were significantly different. The data met the assumptions of the *t*-test.

Both *C. americanus* and *C. punctipennis* showed significantly different movement responses to the different treatments (Table 1; $P < 0.001$). The movement frequency of *C. americanus* in CONTROL averaged 10.6 movements per 30 min. *C. americanus* responded only to the treatments with prey chemicals, either in PREY or MIX, compared to CONTROL and FISH (Fig. 1).

The movement frequency of *C. punctipennis* in CONTROL averaged 18.7 movements per 30 min and was significantly higher than that of *C. americanus* (Mann-Whitney *U*-test; $U = 97.5, P < 0.05$). Also, the movement frequency response of *C. punctipennis* was more complex than that of *C. americanus*. *C. punctipennis* responded to both the PREY and FISH treatments. Compared to CONTROL, its movement frequency was significantly greater when exposed to PREY and significantly less when exposed to FISH. It also moved less in MIX than in PREY (Fig. 2).

Our experiment showed that *C. punctipennis* feeding in FISH, which supposedly reduced repositioned frequencies, ingested significantly fewer *Bosmina* per day per predator (0.7 ± 0.21 d⁻¹) than feeding in CONTROL (1.7 ± 0.21 d⁻¹) (*t*-test; $n = 6$, df $= 10$, $P < 0.01$). The number of *Bosmina* that each larva ingested was nearly equally distributed between the two individuals in each trial.

These results show that chemical cues affect the pre-

dation behavior of *Chaoborus* and that the foraging behavior of *Chaoborus* is more complex than previously assumed (Riessen et al. 1984). In the case of *C. punctipennis*, both chemicals from prey and predator alter the movement frequency. Furthermore, we found that the concentration of fish chemicals in lake water is sufficient to lower the movement frequency of *C. punctipennis*. In the case of *C. americanus*, only PREY altered the movement frequency. An increased movement frequency when prey are present makes ecological sense if such increased movement increases encounters with prey. The comparison of the feeding rates in FISH compared to CONTROL show the same effect; that is, an increased movement frequency in the CONTROL increased the feeding rate compared to the FISH.

Movement in the presence of visual predators such as planktivorous fish would be detrimental if the movement makes the *Chaoborus* more visible. Both Wright and O'Brien (1982) and Kerfoot (1982) showed that white crappie and pumpkinseed (*Lepomis gibbosus*) could locate moving *Chaoborus* at more than twice the distance of stationary larvae. Wright and O'Brien (1984) found a similar result for calanoid copepods as prey. White crappie could locate moving copepods at 3 times the distance they could locate stationary copepods. Furthermore, O'Brien et al. (1985) found that moving prey were chosen over similarly sized stationary prey by bluegill sunfish (*Lepomis macrochirus*). Martel and Dill (1995) recently showed that stationary juvenile salmon are ~10 times less likely to be attacked by piscivorous birds than are moving salmon.

Chaoborus americanus showed no change in movement pattern when exposed to fish water. This again makes ecological sense since this large *Chaoborus* species rarely coexists with fish. Hence, *C. americanus* actually has no need of characteristics that reduce predation by fish nor would it have had exposure to fish predation to evolve such characteristics.

It is widely known that chemical cues from predators can alter structures (Black 1993), life-history characteristics (Stibor 1992), and behavior of the prey (Dodson 1988*b*). However, few studies have shown chemical cues from prey having similar effects on the predator. Certainly, there are studies showing that predators use olfaction to locate their prey (Weissburg and Zimmer-Faust 1993); however, in our study, prey chemicals actually altered a component of the predator's predation behavior.

The quantities of chemicals that we produced in the PREY and FISH may have been unnaturally high. However, in experiments with water from a lake that contained fish, *C. punctipennis* had almost the same change in movement frequency as it did in FISH. Furthermore, in an experiment with water from a pond that did not contain fish, the larvae showed an increased movement frequency, although not quite to the extent of larvae in PREY. This behavior supports the conclusion that the FISH and PREY had reasonable levels of the respective chemicals.

Another interesting result was the response of *C. punctipennis* to MIX. The movement frequency in MIX was intermediate to PREY and FISH (Fig. 2). Essentially, *C. punctipennis* compromises when confronted with a 1 : 1
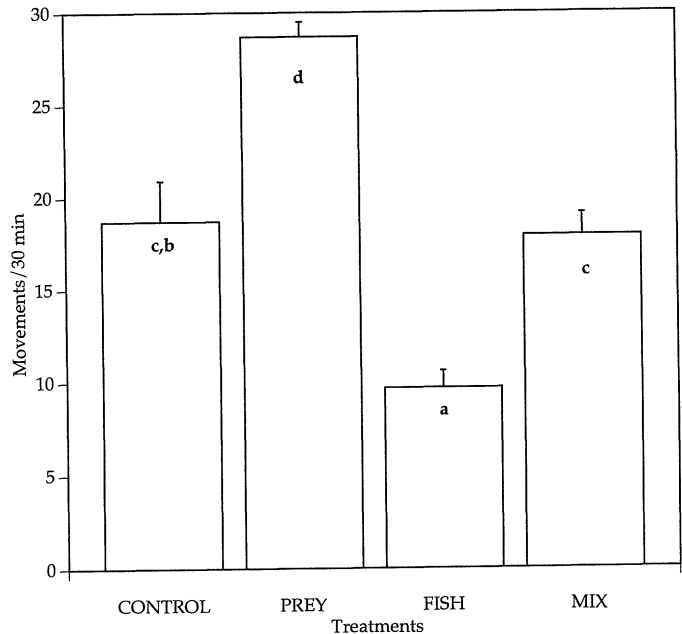

Fig. 2.   As fig. 1, but for movement frequencies of *Chaoborus punctipennis.*

mix of PREY and FISH. The reduction in movement frequency in the presence of fish chemicals has interesting implications for the prey of *Chaoborus*. Given that fish water reduces movement frequency and that prey encounter rate is reduced at lower movement frequencies, the presence of fish causes a reduction in predation on *Chaoborus* prey. This reduction in the presence of FISH was shown in the experiment in which the feeding rate on *Bosmina* was 0.7 *Bosmina* per *Chaoborus* in FISH, but was 1.7 *Bosmina* per *Chaoborus* in CONTROL.

Thus, *Chaoborus,* especially *C. punctipennis,* shows definite but subtle changes in foraging behavior in the presence of chemicals given off by its prey and predator. Other invertebrate and perhaps vertebrate predators will likely have analogous responses to their predators and prey.

Thomas U. Berendonk

Max-Planck-Institut für Limnologie
Abt. Ökophysiologie, Postfach 165
24306 Plön, Germany

W. John O'Brien

Department of Systematics and Ecology
University of Kansas
Lawrence 66045-2106

References

BLACK, A. R. 1993. Predator-induced phenotypic plasticity in *Daphnia pulex*: Life history and morphological responses to *Notonecta* and *Chaoborus*. Limnol. Oceanogr. **38**: 986–996.

BROOKS, J. L., AND S. I. DODSON. 1965. Predation, body size, and the composition of the plankton. Science **150**: 28–35.

BROWMAN, H. I., S. KRUSE, AND W. J. O'BRIEN. 1989. Foraging behavior of the predaceous cladoceran, *Leptodora kindti*, and escape responses of their prey. J. Plankton Res. **11**: 1075–1088.

DAWIDOWICZ, P. 1990. Vertical migration of *Chaoborus* larvae is induced by the presence of fish. Limnol. Oceanogr. **35**: 1631–1637.

DODSON, S. I. 1988*a*. The ecological role of chemical stimuli for the zooplankton: Predator-avoidance behavior in *Daphnia*. Limnol. Oceanogr. **33**: 1431–1439.

———. 1988*b*. Cyclomorphosis in *Daphnia galeata mendotoae* Birge and *D. retrocurva* Forbes as a predator-induced response. Freshwater Biol. **19**: 109–114.

———. 1989*a*. The ecological role of chemical stimuli for the zooplankton: Predator-induced morphology in *Daphnia*. Oecologia **78**: 361–367.

———. 1989*b*. Predator-induced reaction norms. BioScience **39**: 447–452.

DROST, M. R. 1987. Relation between aiming and catch success in larval fish. Can. J. Fish. Aquat. Sci. **44**: 304–315.

HANEY, J. F., A. CRAGGY, K. KENNETH, AND F. WEEKS. 1990. Light control of evening vertical migrations by *Chaoborus punctipennis* larvae. Limnol. Oceanogr. **35**: 1068–1078.

HAVEL, J. E. 1987. Predator-induced defenses: A review, p. 268–278. *In* W. C. Kerfoot and A. Sih [eds.], Predation: Direct and indirect impacts on aquatic communities. New England.

KERFOOT, W. C. 1982. A question of taste: *Crypsis* and warning coloration in freshwater zooplankton communities. Ecology **63**: 538–554.

MARTEL, G., AND L. M. DILL. 1995. Influence of movement by coho salmon (*Oncorhynchus kisutch*) Parr on their detection by common mergansers (*Mergus merganser*). Ethology **99**: 139–149.

O'BRIEN, W. J. 1987. Planktivory by freshwater fish: Thrust and parry in the pelagia, p. 3–16. *In* W. C. Kerfoot and A. Sih [eds.], Predation: Direct and indirect impacts on aquatic communities. New England.

———, H. I. BROWMAN, AND B. I. EVANS. 1990. Search strategies of foraging animals. Am. Sci. **78**: 152–160.

———, B. I. EVANS, AND C. LUECKE. 1985. Apparent size choice of zooplankton by planktivorous sunfish: Exceptions to the rule. Environ. Biol. Fish. **13**: 225–233.

———, AND D. KETTLE. 1981. A zooplankton bioassay chamber for lab and field use. J. Plankton Res. **3**: 561–566.

PAINE, R. T. 1966. Food web complexity and species diversity. Am. Nat. **100**: 65–76.

PASTOROK, R. A. 1980. Selection of prey by *Chaoborus* larvae: A review and new evidence for behavioral flexibility. Am. Soc. Limnol. Oceanogr. Spec. Symp. **3**: 538–554. New England.

RIESSEN, H. P., W. J. O'BRIEN, AND B. LOVELESS. 1984. An analysis of the components of *Chaoborus* predation on zooplankton and the calculation of relative prey vulnerabilities. Ecology **65**: 514–522.

SOKAL, R. R., AND F. J. ROHLF. 1981. Biometry, 2nd ed. Freeman.

STIBOR, H. 1992. Predator induced life-history shifts in a freshwater cladoceran. Oecologia **92**: 162–165.

SWIFT, M. C., AND A. Y. FEDORENKO. 1973. A rapid method for the analysis of the crop contents of *Chaoborus* larvae. Limnol. Oceanogr. **18**: 795–798.

TAYLOR, R. J. 1984. Predation. Chapman and Hall.

TJOSSEM, S. F. 1990. Effects of fish chemical cues on vertical migration behavior of *Chaoborus*. Limnol. Oceanogr. **35**: 1456–1468.

VON ENDE, C. N. 1979. Apparent exclusion of the cladoceran *Bosmina longirostris* by the invertebrate predator *Chaoborus americanus*. Am. Mid. Nat. **105**: 240–248.

WEISSBURG, M. J., AND R. K. ZIMMER-FAUST. 1993. Life and death in moving fluids: Hydrodynamic effects on chemosensory-mediated predation. Ecology **74**: 1428–1444.

WRIGHT, D. I., AND W. J. O'BRIEN. 1982. Differential location of *Chaoborus* larvae and *Daphnia* by fish: The importance of motion and visible size. Am. Midl. Nat. **108**: 68–73.

———, AND ———. 1984. The development and field test of a tactical model of the planktivorous feeding white crappie (*Pomoxis annularis*). Ecol. Monogr. **54**: 65–98.