Diel vertical migration patterns in two populations of *Chaoborus flavicans* larvae (Diptera: Chaoboridae) in response to fish kairomones

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ABSTRACT

Diel vertical migration (DVM) of larvae of the phantom midge Chaoborus flavicans *(Diptera: Chaoboridae) inhabiting a fishless pond and a fish-abundant lake (Lake Nakanuma) was studied in the field and in the laboratory. In the fishless pond, dissolved oxygen concentration and water temperature were homogeneously distributed in the vertical profiles and* Chaoborus *larvae did not show DVM. In contrast, there was thermal stratification and an anoxic layer in Lake Nakanuma, and 2nd, 3rd and 4th instar* Chaoborus *larvae exhibited DVM. Fourth instar* Chaoborus *larvae collected from the two populations were introduced into thermally stratified acrylic tubes containing 'fish water' (water conditioned by fish and containing only the fish 'smell') or control water free of fish smell after a two-day acclimatization, and the larval positions in the tubes were analysed during the day and at night. The two populations of* Chaoborus *larvae showed different DVM patterns in the control water: the larvae from Lake Nakanuma exhibited DVM, whereas those from the fishless pond did not.* Chaoborus *larvae from Lake Nakanuma responded to the fish kairomones, exhibiting marked DVM in the fish water, whereas little response to the fish smell was recognized in the larvae from the fishless pond. The presence of a difference in response between the two populations implies that they had genetically different patterns of expression of DVM and thus different behavioural responses to the fish smell. The fish smell tended to cause the* Chaoborus *larvae in the tubes to increase their depth, during both the day and night. The effects of the fish smell became ambiguous with time, suggesting microbial degradation of the fish kairomones.*

Key words: bluegill sunfish, phenotypic plasticity, predator avoidance

1. INTRODUCTION

Diel vertical migration (DVM) is a widespread phenomenon in zooplankton and phytoplankton in both freshwater and marine environments. Most zooplankton migrate to deeper layers at around dawn and swim up again at dusk, whereas some exhibit a reverse pattern (Ohman *et al*. 1983).

Many hypotheses have been proposed to explain the adaptive significance of DVM (Lampert 1989, 1993), such as metabolic and demographic advantages (McLaren 1963, 1974), population energy conservation (Geller 1986), optimal resource utilization (Enright 1977), a direct deleterious effect of light (Siebeck 1978, cited in Lampert 1989), and predator avoidance (Zaret & Suffern 1976). The most dominant hypothesis today is that of predator avoidance. Zooplankton can reduce their predation risk from visually hunting predators (fish) if they stay in the deep and dark strata during the day. However, migrating to deeper layers is disadvantageous to zooplankton because there are reduced growth rates at the cold temperatures and low food levels in these layers, and there is a swimming cost. Therefore, when night comes, zooplankton migrate upward to compensate for these disadvantages of the deeper layers by spending the night in the warm and food-rich conditions of the surface water.

Various environmental factors such as temperature change, thermoclines, turbidity, food distribution, and food abundance can modify the DVM pattern (LaRow 1970; Calaban & Makarewicz 1982; Gerritsen 1982; Johnsen & Jakobsen 1987; Pijanowska & Dawidowicz 1987; Dodson 1990; Leibold 1990). Moreover, relative changes in light intensity and chemical substances exuded by predators (the predators' "smell") are known to be proximate factors in the initiation and direction of DVM (Dodson 1988; Loose, von Elert & Dawidowicz 1993). These chemical substances are called kairomones because the prey species (the receiver of the kairomone) can benefit by using them to signal information about the presence of the predator (the chemical releaser), whereas the predator receives no benefit (Brown *et al*. 1970). Various vertebrate (fish) and invertebrate (rotifers, copepods, and backswimmer and phantom midge larvae) predators release kairomones, which induce changes in the morphology, life history traits, and behaviour of zooplankton (Larsson & Dodson 1993; Hanazato 1994).

Larvae of the phantom midge *Chaoborus* (Diptera: Chaoboridae) often occur as major zooplankton in eutrophic lakes and ponds. The larvae, especially 3rd and 4th instars, show marked DVM in environments with abundant fish (Stahl 1966; Teraguchi & Northcote 1966; Goldspink & Scott 1971; Luecke 1986), but not in environments with no or few fish (Northcote 1964;

Carter & Kwik 1977; Luecke 1986). This suggests that the presence of fish is a factor that induces DVM. Laboratory studies have indicated that kairomones released from fish induce DVM of 4th instar *C. flavicans* larvae (Dawidowicz *et al*. 1990; Dawidowicz 1993).

We analysed the effects of fish kairomones ("smell") on the DVM behaviour of *C. flavicans* larvae in two populations - one in a fishless pond and one in a fish-abundant lake - that seemed to have different responses to fish smell. In the laboratory we compared the DVM patterns of the larvae from these two populations in the presence or absence of fish smell.

2. METHODS

2.1. *Analysis of DVM of* Chaoborus *larvae in the field*

The fishless pond was located in the grounds of the National Institute for Environmental Studies (NIES, Tsukuba, Ibaraki, Japan; 36°02'N, 140°07'E). This eutrophic fish-free pond (maximum depth 4.2 m; surface area 3890 m^2) was constructed by digging in a wetland in 1980. *Chaoborus flavicans* is one of the major invertebrates in the pond, and the population has been reported to produce 10 complete and one incomplete cohort annually (Iwakuma *et al*. 1989).

Lake Nakanuma (Ryugasaki, Ibaraki, Japan; 35°53'N, 140°09'E) is a small eutrophic lowland lake (maximum depth 13 m; surface area 1.08 ha) that develops thermal stratification in summer. The lake is inhabited by a planktivorous fish, the bluegill sunfish (*Lepomis macrochirus*), and by *C. flavicans* larvae, which exhibit marked DVM (Hanazato 1992).

The vertical distributions of *Chaoborus* larvae in the fishless pond and in Lake Nakanuma were investigated by taking a series of discrete depth samples at the centre of each water body at noon (12:00) and at midnight (0:00). In the fishless pond, sampling was conducted at depths of 0, 1, 2, and 3 m on 7 October 1994. Larvae were collected by passing 12 L water samples through a 40 μm mesh net; two samples were taken at each depth with a 6.0 L Van Dorn sampler (Rigosha Co., Ltd., Saitama, Japan). The larvae in Lake Nakanuma were collected on 18 October 1994 by hauling a conical closing net (1 m long; 30 cm-diameter opening; 200 μm mesh) vertically for a distance of 2 m at 2 m intervals from the surface to 10 m depth. Samples at a depth of 10 to 12 m could not be collected because they contained too much mud. Larvae were preserved in 5% formalin solution. Larval instars were identified from the head capsule width as a criterion of instar separation and were counted under a dissecting microscope in the laboratory.

At the time of sampling, the temperature and oxygen concentration profiles of the water column were determined by means of a YSI model 54A oxygen meter (YSI Hydrodata Ltd., Hertfordshire, UK) in Lake Nakanuma and a YSI model 55 oxygen meter (YSI Hydrodata Ltd., Hertfordshire, UK) in the fishless pond.

2.2. *Experimental analysis of DVM of* Chaoborus *larvae*

2.2.1. Collection of larvae

All the experiments were carried out on 4th instar larvae of *C. flavicans* collected from the fishless pond and Lake Nakanuma in July 1994. The larvae were collected during the day by towing a plankton net (40 cm diameter opening, 300 μm mesh) from the bottom to the surface of the pond and the lake. They were then kept in an aquarium containing aged tap water at 20 °C under a 16:8 light:dark cycle for 2 days before the experiments. Neonates of the cladoceran *Moina macrocopa* were supplied as food.

2.2.2. Experimental apparatus

The experimental apparatus consisted of 30 clear acrylic tubes (1 m long, 3.0 cm in diameter) placed vertically in a transparent acrylic water bath (13 × 60 × 60 cm). This apparatus was set in a temperature-controlled room (23 °C) under a 16:8 light:dark cycle. The room was illuminated homogeneously with fluorescent lamps on the ceiling. At the start of the experiments, the larvae were put into the tubes, which had been marked with ticks at 10 cm intervals from the top to the bottom for measurement of larval depth, and had been filled with test medium. The water temperature in the lower halves of the tubes was reduced to form a thermal stratification of the water column by cooling the water bath with a thermoregulator (TAIYO Cool Mix, TAITECH Co., Ltd., Japan).

To form a light gradient in the tubes that was similar to the one present in the field, the acrylic water bath was covered with black vinyl sheeting to shield the lower half of the tubes from light. The black sheet had windows on both sides of the water bath for observation of the larvae in the lower parts of the tubes.

Swift & Forward (1980) reported that 4th instar *Chaoborus punctipennis* larvae respond weakly to red light. Therefore, we used a dim red fluorescent lamp to track DVM behaviour in the tubes during the dark period.

The larvae in the tubes were fed with the small cladoceran *Moina micrura*, which had been cultured at 20 °C under a 16:8 light:dark regime. Between 20 and 30 moinids were put into each tube just before the start of the dark period every day. Most of the prey animals were distributed in the upper, warmer parts (i.e., the epilimnion) of the tubes.

2.2.3. Experimental design

The larvae were put into tubes containing either control water or fish-conditioned water (fish water). Aged tap water in which fish had never been reared was used as the control water. The fish water was prepared as follows. Bluegill sunfish (body length: 13 to 14 cm) were reared individually for 2 or 3 days in 10 L aquaria
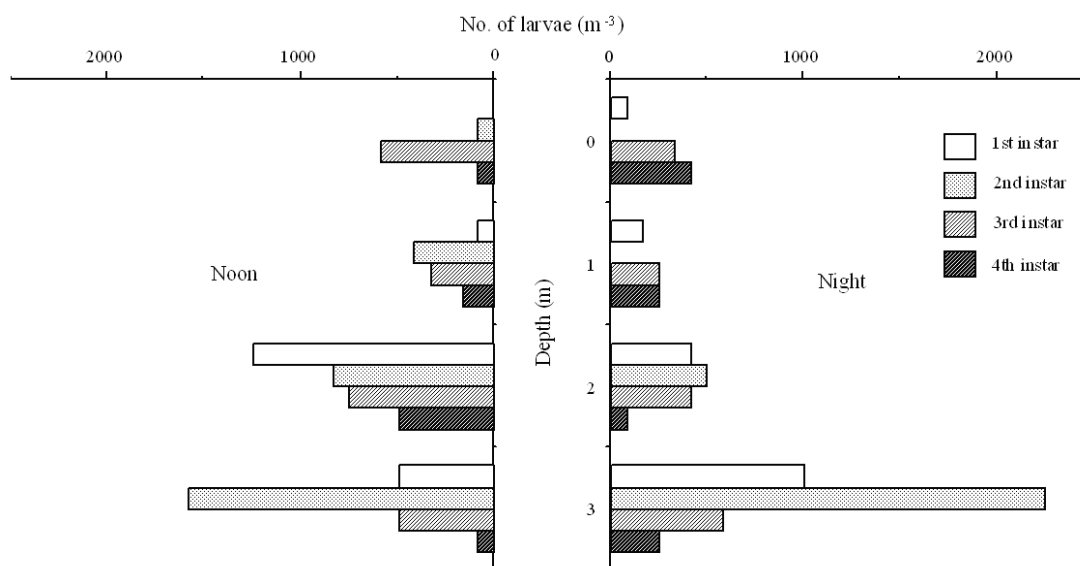
Fig. 1. Vertical distribution of *Chaoborus* larvae in the fishless pond at noon (left) and midnight (right) on 7 October 1994.

filled with aged tap water. Adequate amounts of the cladoceran *Daphnia magna* were provided daily as food. At the end of the rearing period the water was filtered with a Whatman GF/C filter to remove any particles >1 μm in diameter. The fish water was prepared just before the start of each experiment and was never replenished during the experimental period.

The following two experiments were conducted to analyse the DVM behaviour of the *Chaoborus* larvae from the fishless pond and Lake Nakanuma under conditions with or without fish smell.

In experiment 1, larvae from the two populations were kept in the tubes containing the control water or fish water at a density of one individual per tube, with a light gradient and thermal stratification (20.3 °C at the surface and 12.9 °C at the bottom). Seven replicates were prepared for each of four treatments (two populations × two culture media). The experiment was conducted for 4 days. Positions of the individuals were recorded every 3 h in the daytime (10:00, 13:00, 16:00, 19:00, and 22:00) and twice each night (1:00 and 6:00).

In experiment 2, each treatment had four replicates and the larval density was five individuals per tube. Both a light gradient and thermal stratification were formed. The depths of the larvae in the tubes were recorded once in the daytime (16:00) and once at night (4:00), and the observation was continued for 5 days.

3. RESULTS

3.1. Field data

In the fishless pond, the profiles of water temperature at noon (12:00) and at midnight (0:00) were almost the same, except at the surface, where the temperatures were 23.1 °C (noon) and 21.8 °C (midnight). The dissolved oxygen concentration, which was 4.56 mg L^{-1} at 0 m, decreased gradually to 2.51 mg L^{-1} near the bottom

at 3.5 m and did not show any marked difference between noon and midnight.

Figure 1 shows the vertical distribution of *C. flavicans* larvae in the fishless pond. There was no marked difference in the profiles of the 3rd and 4th instar larval vertical distribution in the fishless pond in between 12:00 and at 0:00 (Fisher's exact probability test, $P = 0.24$, Sokal & Rohlf 1995). The larvae tended to be distributed throughout the whole water column.

A marked thermocline was present in Lake Nakanuma at around 9 m depth. The water temperature of the epilimnion was about 22 °C and that of the hypolimnion 10 °C. The lower layers of the hypolimnion were anoxic; the dissolved oxygen concentration was <3 mg L^{-1} below 8 m depth. Differences in water temperature or dissolved oxygen were not observed between noon and midnight.

Because larval samples were not collected from the stratum below 10 m depth in Lake Nakanuma, there are no data on the density of larvae in that stratum. However, in the water column above 10 m depth, the vertical profile of *Chaoborus* larvae at noon significantly differed from that at midnight (Fisher's exact probability test, $P <0.001$, Sokal & Rohlf 1995). The larvae stayed in the low-oxygen layer (8 to 10 m) at noon, whereas they went up to 4 m depth at midnight and were not observed in the 8- to 10 m stratum (Fig. 2). The results indicate that *Chaoborus* larvae performed DVM in the lake.

3.2. DVM of Chaoborus *larvae in experimental tubes*

3.2.1. Experiment 1: one larva per tube

Lack of normal DVM behaviour (up at night and down during the day) by the larvae from the fishless pond was observed in both the control water and the fish water (Fig. 3a, Mann-Whitney U-test). Rather, the lar-
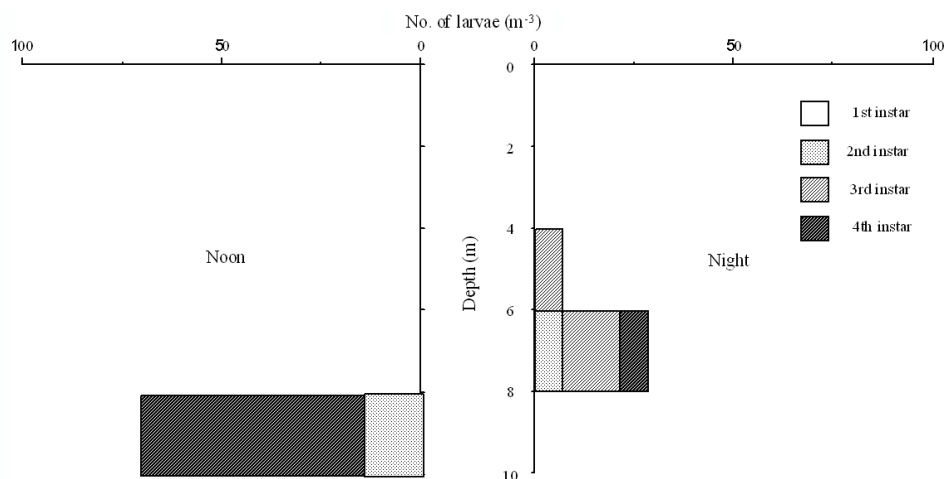
Fig. 2. Vertical distribution of *Chaoborus* larvae in Lake Nakanuma at noon (left) and midnight (right) on 18 October 1994.
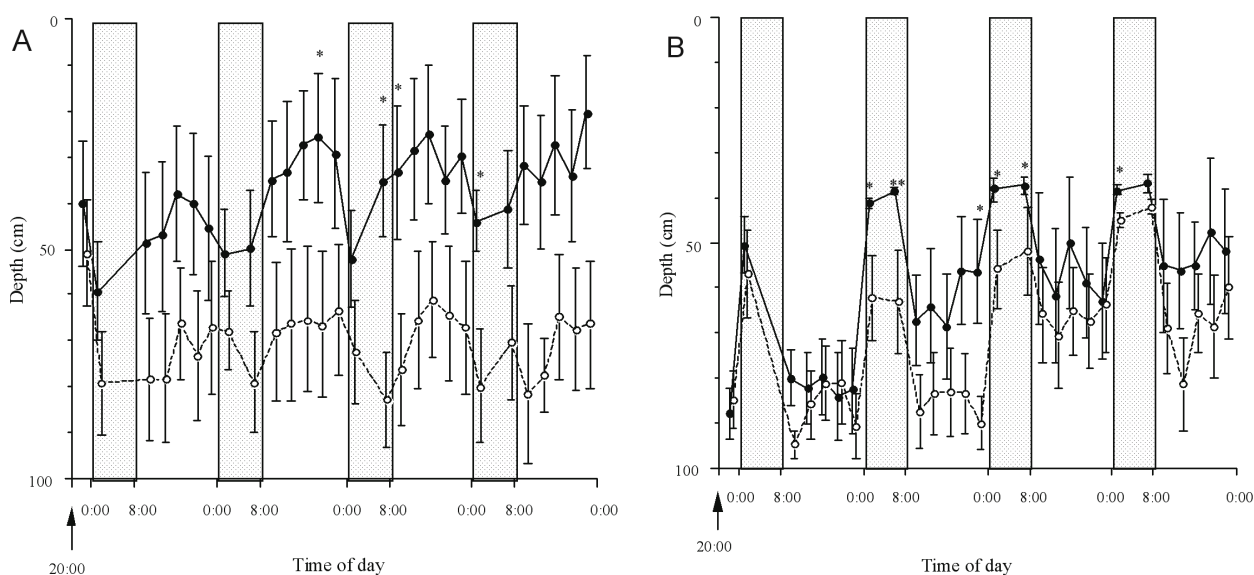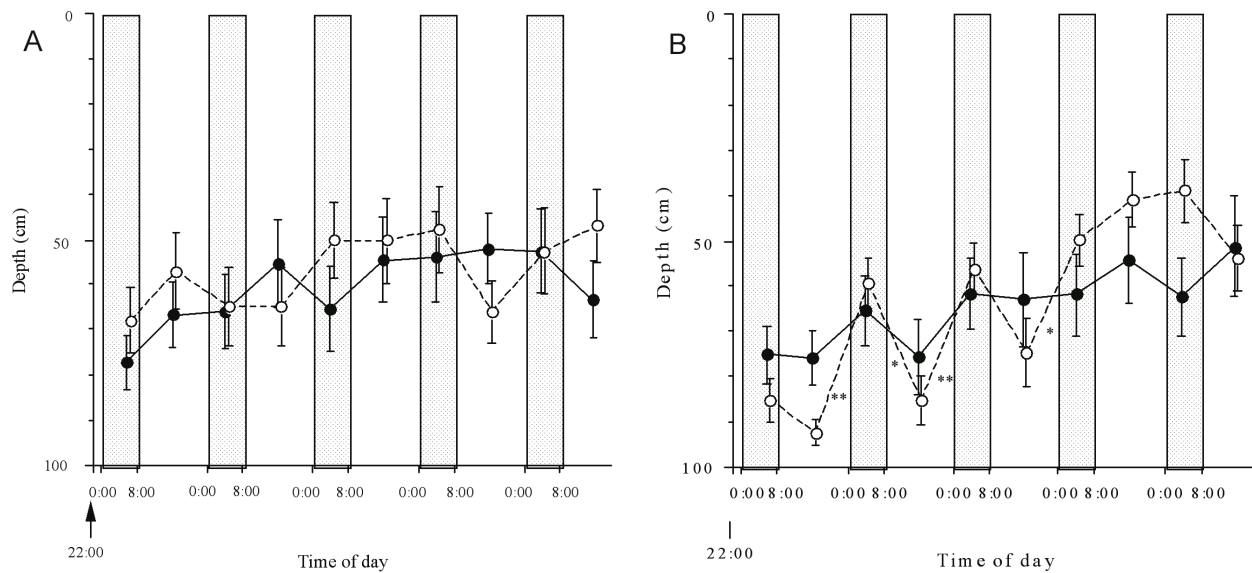

Fig. 3. Mean depths (± SE, N = 7 at the start) of larvae (**A**) from the fishless pond and (**B**) from Lake Nakanuma in the tubes containing control water (closed circles) and fish water (open circles) in Experiment 1. Shaded areas are periods of darkness. Asterisks indicate significant differences in the larval depths between the control water and fish water (Mann-Whitney U-test, * = P <0.05, ** = P <0.01). When the experiment ended more than 85% of the larvae remained.

vae slightly showed a reverse pattern. Although the fish water did not induce DVM by the larvae, it lowered the larval positions in the tubes; their positions were significantly deeper in the fish water than in the control water at times (Fig. 3a, Mann-Whitney U-test, * = P <0.05, ** = P <0.01).

The larvae from Lake Nakanuma exhibited DVM patterns in both the control water (Mann-Whitney U-test, P <0.001) and the fish water (Mann-Whitney U-test, P <0.001), and they stayed deeper in the fish water than in the control water (Fig. 3b). Larval depths between the control water and fish water were significantly different at times (Mann-Whitney U-test, * = P <0.05, ** = P <0.01).

3.2.2. Experiment 2: five larvae per tube

When there were five larvae in each tube, the larvae from the fishless pond again did not exhibit significant DVM behaviour in the control water or the fish water (insignificant day-night effect by ANOVA with repeated measurements), and there was no clear difference in their mean depths in the two types of water (Fig. 4a, ANOVA with repeated measurements, P = 0.27). By contrast, the larvae from Lake Nakanuma exhibited a definite DVM pattern in the fish water (ANOVA with repeated measurements, P <0.001), but not in the control water (P = 0.99, Fig. 4b). The mean larval depths in the two types of water did not differ significantly

Fig. 4. Mean depths (± SE, N = 20 at the start) of larvae (**A**) from the fishless pond and (**B**) from Lake Nakanuma in the tubes containing control water (closed circles) and fish water (open circles) in Experiment 2. Shaded areas are periods of darkness. Asterisks indicate significant differences in the larval depths between adjacent measurements either in the control water or fish water (Mann-Whitney U-test, * = P <0.05, ** = P <0.01). See Results for the results of Anova. When the experiment ended more than 65% of the larvae remained.

(ANOVA with repeated measurements, P = 0.73, Fig. 4b). All of the DVM behaviour (as expressed by average depth) occurred in the lower halves of the tubes (in the hypolimnion). As the experiment proceeded, the position of the larvae at noon gradually shifted upward and the amplitude of the vertical migration became smaller (Fig. 4b).

4. DISCUSSION

It is widely known that chemical substances exuded by fish induce DVM behaviour in *Chaoborus* larvae and *Daphnia* (Tjossem 1990; Dawidowicz 1993; Loose *et al*. 1993). In our experiments, DVM behaviour was induced by a fish (bluegill) kairomone in *Chaoborus* larvae from Lake Nakanuma (Figs 3b and 4b). The kairomone may be a proximate factor that induces DVM by *Chaoborus* larvae in the lake.

The fish smell tended to cause the *Chaoborus* larvae to stay deeper in the experimental tubes at both noon and midnight (Figs 3b and 4b). A similar finding was obtained in *C. flavicans* by Dawidowicz *et al*. (1990). From the standpoint of adaptive significance, however, all that the larvae have to do is to increase their depths only during the day in response to the fish smell, because larvae can reduce their vulnerability to predation by spending only the daytime in the deep and dark layer, where visually oriented planktivorous fish can hardly detect their prey. It is probable that, under our experimental conditions, the larvae responded to the fish kairomone even in the night phase. Loose and Dawidowicz (1994) demonstrated that *D. magna* exposed to higher concentrations of fish kairomone

exhibit greater DVM response and stay deeper even at night, suggesting that the degree of DVM response depends on the kairomone concentration, as is the case in the morphological response of *Daphnia* to different concentrations of predator kairomone (Parejko & Dodson 1991). Therefore, if *Chaoborus* larvae are exposed to high concentrations of fish kairomones in natural environments, they could suffer from a lack of food if they were to stay in the food-poor strata during both the day and night.

The larvae from Lake Nakanuma exhibited marked DVM in the fish water, but the pattern became more ambiguous as time passed (Figs 3b and 4b). This is presumably because, in part, the kairomone exuded by the bluegill sunfish lost its effect in a few days owing to degradation by microbes. Loose *et al*. (1993) studied the induction of DVM in *D. magna* by kairomones released from fish (*Leucaspius delineatus*, Cyprinidae) and found that the activity of the kairomones disappeared within 24 h under non-sterile conditions at 37 °C, suggesting that microbial degradation of the kairomones occurred.

The larvae from the fishless pond did not show marked DVM behaviour, either in the control water or in the fish water. Why did DVM differ between the population from Lake Nakanuma and that from the fishless pond? This can be explained by the fact that the larvae in the two populations had DVM traits that were genetically based and differed in their degree of phenotypic plasticity.

Daphnia are known to exhibit varying degrees of DVM, with a genetic component, in the absence of predators (Weider 1984; Watt & Young 1992; De

Meester 1993). Our larvae from the fishless pond did not exhibit DVM in the control water, whereas those from Lake Nakanuma did in the same water. This could be attributed to the fact that the *Chaoborus* larvae in the two populations have different genetically based DVM patterns. However, we must note the possibility that habituation of the larvae to their natural environments, with or without fish predation, persisted during the experiments despite prior acclimatization.

The different responses of *Chaoborus* larvae to kairomones suggest that the larvae have varying degrees of phenotypic plasticity in their DVM behaviour in response to different predation regimes. *Daphnia*, for example, exhibit a variety of responses (changes in morphology, life history traits, and DVM behaviour) when they are exposed to predators' kairomones, and *Daphnia* that occur in environments with abundant predators tend to be more sensitive to kairomones than those in environments with fewer predators (Parejko & Dodson 1991; Lüning 1992; Spitze 1992; Black 1993; De Meester 1993).

Adult phantom midges migrate to lakes and ponds to lay eggs and their larvae are exposed to unpredictable predation pressure that varies seasonally and among water bodies. Therefore, it should be adaptively important for *Chaoborus* larvae to have the ability to detect the presence of predators and to avoid predation behaviourally only when it is necessary. However, the poor response of our larvae from the fishless pond to the fish smell suggests that gene flow mediated by adults migrating between neighbouring populations of *C. flavicans* is limited. The environmental conditions (e.g., distance between water bodies) that limit the gene flow should be analysed in future studies.

Chaoborus flavicans in Lake Nakanuma are reported to produce fewer generations in a year than those in the fishless pond (Iwakuma *et al.* 1989; Iwakuma, unpublished data). In part, this is because the larvae in the lake migrate into the cold anoxic layer with little food in the daytime to reduce the predation risk, and this activity probably retards their development. Dawidowicz (1993) studied the DVM of 4th instar *C. flavicans* larvae introduced individually into thermally stratified tubes and found that DVM retarded larval development rates. Similar results were obtained in *Daphnia* by Stich & Lampert (1984), Dawidowicz & Loose (1992), and Loose & Dawidowicz (1994). They studied the life history parameters of *Daphnia* species under food supply and temperature conditions that simulated those that might be experienced by *Daphnia* exhibiting DVM. It is possible, therefore, that fish kairomones affect the population dynamics of *Chaoborus* by controlling larval behaviour.

ACKNOWLEDGMENTS

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