Light control of evening vertical migrations by *Chaoborus punctipennis* larvae

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Abstract

Light control of vertical migration was examined with sonar recordings of the evening migration of *Chaoborus punctipennis* larvae. Frequently, a slow, upward drift in the afternoon preceded the rapid ascent of larvae. Movement out of the sediments was not consistently related to a fixed light intensity or rate of relative light change. Light intensities were variable at the initiation of and during the upward migration, whereas the beginning of rapid ascent was closely correlated with the timing of a relative light change of $1.7 \times 10^{-3} \, s^{-1}$. The close relationship between the rate of relative change in light intensity and the rate of upward movement including the afternoon drift supports the stimulus-velocity hypothesis that once larvae leave the sediments the speed and direction of the migration pattern is primarily regulated by relative light changes. Second- and third-instar larvae migrated at higher light intensities than fourth instars, but did not differ in their rate of movement in relation to light change.

Light is widely regarded as an important factor regulating the diel vertical migration of planktonic organisms (*see* Ringelberg 1964; Forward 1976, 1988; Haney 1988). Despite early and continued research on the influence of light on vertical migration (e.g. Clarke 1933; Clarke and Backus 1956; Siebeck 1960; McNaught and Hasler 1964), the mechanisms of light control are still poorly understood.

In the present study we set out to examine the validity of several hypotheses of light control of vertical migration. *Chaoborus punctipennis* was selected as a test organism since the third- and fourth-instar larvae generally exhibit clear patterns of migration and their vertical movements can be monitored in detail with sonar (Northcote 1964). We chose lakes in which *C. punctipennis* was the only chaoborid species present. We focused our study primarily on winter–spring periods when *Chaoborus* larvae were present as fourth instars and when there would be the least influence of factors associated with thermal stratification.

Light hypotheses

From the numerous ideas on the regulatory influence of light on migration we identified four hypotheses for consideration here. One of the earliest ideas was that migrating animals stay within a range of optimal or "preferred" light intensities (Ewald 1910; Rose 1925; Russell 1926, 1934). According to this *preferendum hypothesis* diel vertical migrations result from zooplankton tracking the daily changes in light intensity, possibly by alternating positive and negative phototactic (Rose 1925) or geotactic (Swift and Forward 1988) responses or changing swimming speed (Rudjakov 1970) above and below a preferred intensity.

Two contrasting hypotheses deal with light as the initiating cue for vertical migration. The *absolute intensity-threshold hypothesis* postulates that the evening-upward and morning-downward movements are elicited through a lower threshold of light intensity for positive phototaxis and an upper threshold of light intensity for negative phototaxis (e.g. Boden and Kampa 1967; Forward et al. 1984; Sweatt and Forward 1985). In contrast, Ringelberg (1964) found that the positive phototactic response in *Daphnia* was initiated by relative changes in light intensity and suggested that exposure to a threshold level of relative change in light intensity provided the stimulus for upward vertical migrations. This *relative stimulus-*

Table 1. Summary conditions for the study of fourth-instar *Chaoborus punctipennis* larvae in Barbadoes Pond. I is light intensity (W m^{-2}), LE is the leading edge of the migrating *Chaoborus* population, PI is the point of inflection of migration (i.e. point at which the phase of rapid migration began), and EC (m^{-1}) is the vertical extinction coefficient for downwelling light.

	Range I at LE	I at LE at PI	EC
3 Jan 77	5.35×10^{-10}–2.60×10^{-9}	6.86×10^{-10}	1.79
8 Feb 82	1.37×10^{-4}–1.08×10^{-3}	3.40×10^{-4}	0.77
20 Feb 79	1.12×10^{-6}–3.73×10^{-5}	2.41×10^{-5}	0.92
8 Mar 77	2.24×10^{-5}–3.39×10^{-4}	2.30×10^{-4}	1.15
10 Apr 84	1.76×10^{-5}–6.01×10^{-5}	1.98×10^{-5}	0.74
17 Apr 79	2.43×10^{-5}–4.18×10^{-4}	1.11×10^{-4}	0.91
6 May 79*	2.03×10^{-6}–1.14×10^{-4}	1.68×10^{-4}	0.60
4 Oct 79†	2.88×10^{-1}–1.81	1.20	0.85
16 Oct 79†	1.29×10^{-2}–5.90×10^{-2}	1.29×10^{-2}	0.83
24 Nov 79	3.40×10^{-6}–3.15×10^{-4}	3.40×10^{-6}	0.89

* Chocorua Lake.
† Second- and third-instar larvae.

threshold hypothesis has been supported by a study of migrations under arctic light conditions with *Daphnia* (Buchanan and Haney 1980) and recent experiments with marine copepods (Stearns and Forward 1984) and crab larvae (Forward 1985). The latter two studies also reported that, once initiated, the upward migration proceeds as an all-or-nothing response.

Daan and Ringelberg (1969) determined that the direction and swimming speed of *Daphnia* that swam nonrhythmically were proportional to the sign (positive or negative) and strength of the relative light stimulus. They suggested that the *stimulus-velocity hypothesis* could account for migrations of animals at slow changes in light intensity.

A major distinction between the relative stimulus-threshold and stimulus-velocity hypotheses is the absence of a threshold in the latter. Both hypotheses are more specific variations of the general *rate-of-change hypothesis* described by Forward (1988).

Description of the lakes

Barbadoes Pond (6.2 ha, Z_{max} = 16 m) is a slightly brown-stained, mesotrophic lake in the coastal plain of New Hampshire. Chocorua Lake (102 ha, Z_{max} = 9.4 m) is a clear, oligotrophic lake located on the perimeter of the White Mountain National Forest, New Hampshire. Extinction coefficients for downwelling light were <1 on most occasions (Table 1). Both lakes are stocked annually with rainbow trout (*Salmo*

gairdneri) fingerlings and have populations of the common catfish (*Ictalurus nebulosus*). Additionally, Chocorua Lake contains yellow perch (*Perca flavescens*) and smallmouth bass (*Micropterus dolomieui*). The lakes are generally ice covered from December through mid-April.

Methods

Light intensity was measured with an International Light radiometer (model IL-700). The underwater sensor was a cosine-corrected, vacuum photodiode with peak sensitivity at 505 nm and a spectral range of 395–680 nm, approximating the spectral sensitivity of *Chaoborus* larvae (Swift and Forward 1980). Light sensors were factory-calibrated annually against accepted standards (U.S. NBS). Light readings were either recorded by hand at 5–10-min intervals or integrated over 10-min intervals (10 April 1984) with a printing integrator (LiCor model 550). Light intensities and relative light changes estimated for specific times did not differ between the two methods, based on simultaneous use of both techniques of light recording during several experiments.

Vertical profiles of light made at 1-m intervals were taken every 1–2 h during the experiment. For continuous measurement the light sensor was placed at either 1- or 2-m depth. In winter, the bottom of the ice layer (generally 0.3–0.6 m thick) was considered to be the surface of the lake. To reduce light artifacts, we made under-ice

measurements of light with the light probe attached to a holder with a 90-cm-long side-arm, placing the probe well away from the ice hole (~15-cm diam). Ice was replaced in the hole. When snow was present, we also replaced snow cover around and over the hole to its original depth. Light intensities at the leading edge of the *Chaoborus* population were estimated from light intensities at the fixed depth, applying the slope of linear regressions of natural log (ln) light intensity vs. depth, significant at $P < 0.05$ or most often at $P < 0.01$. Although slopes of vertical light profiles from the same day did not differ significantly ($P < 0.05$), we used the light profiles closest to the time of the fixed-depth light measurements.

Light stimulus (S) was calculated according to Ringelberg (1964) as

$$S = (\ln I_i - \ln I_0)/dt$$

where S is the relative light change, I_0 the initial light intensity, I_i the final light intensity, and dt the time interval in seconds. As a reference value we used Ringelberg's (1964) threshold light stimulus ($=1.7 \times 10^{-3}$ s^{-1}), the rate of decrease in light at which 50% of *Daphnia magna* responded with a positive phototaxis. Light intensity and relative change in light were estimated at specific times to the nearest minute from linear regressions of $\ln I$ or S vs. time with six 5- or 10-min intervals around the desired time. Regressions were significant at $P < 0.01$. Plots of residuals were examined for these and other regressions. Log transformations corrected the slight heteroscedasticity of the stimulus-velocity data. Tests for significant differences among regression lines followed the approach of Neter and Wasserman (1974).

Zooplankton samples were collected with a closing net (12-cm diam, 150-μm mesh), a 30-liter Patalas-Schindler trap, or by pumping water through a 50-μm net with a Gusler diaphragm bilge pump and preserved in sucrose-Formalin (Haney and Hall 1973). Vertical profiles of zooplankton collected at 1–3-m intervals at the beginning and end of each study corroborated the migration of *Chaoborus* and confirmed that the sonar traces were caused by *Chaoborus* larvae. Larval instars were determined from

body length- and head capsule length-frequency distributions and comparisons of body and head capsule lengths of larvae reared into adults in the laboratory.

Movements of *Chaoborus* were monitored with a Raytheon Explorer II sonar on all dates except 8 February (Raytheon model D-19) and 10 April (Lowrance model X-15). All sonars were equipped with 200–205-kHz frequency transducers, ideally suited for the study of *Chaoborus* (Teraguchi and Northcote 1966; Wagner-Döbler and Jacobs 1987; Moore Rodenhouse 1986). Sonar recordings were made at a fixed location either through a hole in the ice or from an anchored boat. Before migration sonar recordings were made for 1 min every 10 min. During migration, the sonar was run continuously.

We determined the depth of the leading edge of the population (the upper boundary of sonar trace of *Chaoborus*) by calculating the average depth of the uppermost trace markings for each 1-min period. Chart paper speed was adjusted so that a 1-min recording was 2–5 cm long. Estimates of the velocity of *Chaoborus* movements were made over the same time intervals as the light stimulus measurements.

Because the upward migration of *Chaoborus* larvae often begins with movement out of the sediments around sunset, we originally planned to estimate the initiation time of the migration as the time at which sonar traces of *Chaoborus* were first observed above the sediments. Unexpectedly, on most dates in Barbadoes Pond *Chaoborus* larvae began to emerge from the sediments several hours before making their rapid ascents toward the surface. During these afternoon periods the *Chaoborus* larvae that entered the water column remained near the bottom, "drifting" slowly upward at a few centimeters per hour. It is not certain whether the slow drift upward represents an unusual migration sequence for *Chaoborus* or whether it is simply not noted with less sensitive, conventional capture techniques. We assumed that the more dramatic rapid ascent described in our study corresponds to the beginning of evening migration generally detected from plankton samples. To estimate the initiation time of migration on

days that had the "drift," we determined the time of intersection of linear regressions of time vs. depth of the leading edge of the population drawn through the early, slow phase and later, rapid phase of the migration. This point of inflection was considered the time of initiation of the rapid phase of migration.

Barbadoes Pond develops anoxia below the thermocline in midsummer, where second- and third-instar *C. punctipennis* larvae spend the day. These conditions were present on the two October sampling dates. During all other periods we examined, however, fourth-instar *Chaoborus* larvae were present, and there was >3 mg liter^{-1} of dissolved oxygen in bottom waters. We confirmed with plankton and Ekman dredge samples that fourth-instar *C. punctipennis* larvae were buried in the sediments at midday. Population densities of fourth-instar *Chaoborus* larvae in Barbadoes Pond estimated from Ekman dredge samples were (mean ± 1 SD) 2,710±860 ($n = 3$) (8 March 1977) and 3,720±1,190 ($n = 3$) larvae m^{-2} (20 February 1979). Comparisons of *Chaoborus* densities in the sediments and at night in the water column indicate that 38 and 31% of the total *Chaoborus* populations migrated on the above two dates.

Results

Preferendum hypothesis—If *Chaoborus* larvae track a fixed light intensity or narrow range of intensities, the light intensity at the leading edge of the population should remain relatively constant throughout the migration. In the preferendum hypothesis one might also expect that if animals undergo some light adaptation during upward migration, light intensities would increase with time in the stratum of the migrating population.

We found a variety of patterns of light intensities at the leading edge of the migrating *Chaoborus* populations (Fig. 1). The least variation occurred on 10 April, with irregular variations in light intensity of <71% during the migration. More frequently, light increased (24 November and 3 January), decreased (8, 20 February, and 6 May), or changed irregularly (8 March and 16 October) by as much as two orders of

magnitude (Table 1). There was also great variation among dates in the light intensity at the leading edges of the populations, generally in the range of 10^{-4}–10^{-6} W m^{-2}. On one occasion (3 January) with thick ice and heavy snow cover, *Chaoborus* migrated at extremely low light intensities (5.3 × 10^{-10}–2.6 × 10^{-9} W m^{-2}). Although not directly comparable to the data for fourth instars, second- and third-instar *Chaoborus* larvae were found at the highest light intensity (1.3 × 10^{-2}–1.8 W m^{-2}). We conclude that our data do not support the preferendum hypothesis.

Intensity-threshold hypothesis—On three occasions we began our measurements before *Chaoborus* larvae began to move out of the sediments. Light intensities at the lake bottom when *Chaoborus* emerged from the sediments were 1.1 × 10^{-3} W m^{-2} on 8 February in Barbadoes Pond, 1.7 × 10^{-4} W m^{-2} on 6 May in Chocorua Lake and 2.0 × 10^{-5} W m^{-2} on 10 April in Barbadoes Pond. These light intensities vary over about two orders of magnitude and are higher than the estimates of Swift and Forward (1988) for the upward movement of fourth-instar *C. punctipennis* larvae in the laboratory and in the field (3 × 10^{-6} W m^{-2}). Light intensity was also variable at the time of initiation of the rapid evening migration. Light values at the leading edge of the fourth-instar *Chaoborus* population at the estimated inflection times ranged between 1.1 × 10^{-4} and 3.4 × 10^{-6} W m^{-2} and on one occasion 6.9 × 10^{-10} (Table 1). Thus, overall, our observations are inconsistent with the hypothesis that the migration, considered as either movements from the sediments or rapid migration in the water column, begins at a fixed threshold of absolute light intensity.

Stimulus-threshold hypothesis—There does not appear to be a single threshold of light change for releasing *Chaoborus* from the bottom sediments. Relative light change at the time larvae began to move into the water column was well below the threshold value of Ringelberg in Barbadoes Pond (2.6 × 10^{-4} and 4.0 × 10^{-4} s^{-1} on 8 February and 10 April, respectively), but higher (2.7 × 10^{-3} s^{-1}) in Chocorua Lake.
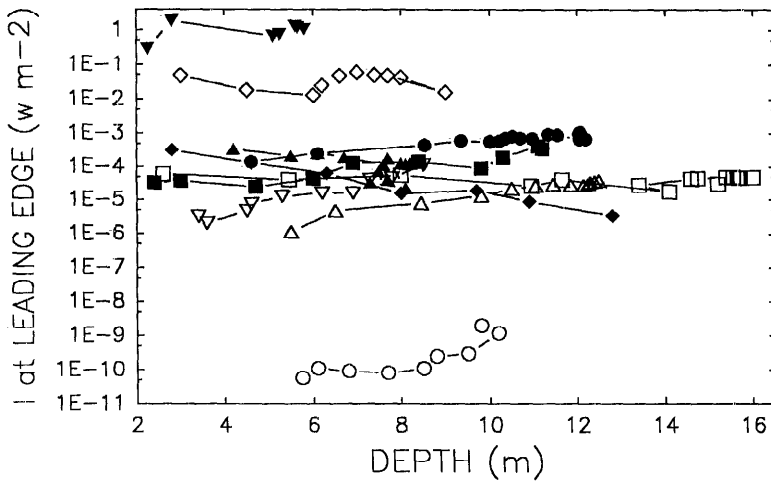
If there is a threshold value of relative

Fig. 1. Light intensity at the leading edge of the fourth-instar *Chaoborus punctipennis* population during the course of 10 evening migrations in Barbadoes Pond and Chocorua Lake: O—3 January; ●—8 February; △—20 February; ▲—8 March; □—10 April; ■—17 April; ▽—6 May, Chocorua L.; ▼—4 October; ◇—16 October; ◆—24 November. Second and third instars present on 4 and 16 October.

light change at which the rapid upward migration is initiated, then the time of the initiation of vertical migration should correspond to the time at which the threshold light stimulus was exceeded. For all dates examined the vertical migration of *Chaoborus* began within minutes (max 12 min) of Ringelberg's (1964) threshold of relative light change (Fig. 2). There was a highly significant relationship ($P < 0.001$) between the time of initiation of the rapid migration of second, third, and fourth instars and the time of Ringelberg's threshold value. The regression line did not differ from the 1:1 line (Fig. 2), for the regression slope was 0.98 and the standard errors of the intercept
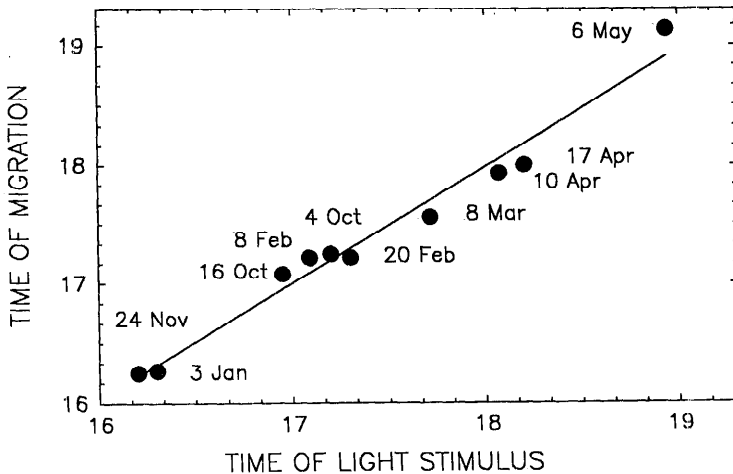

Fig. 2. Relationship between the time of migration, i.e. the point of inflection (rapid ascent) in the *Chaoborus* migration (PI_t) and the time at which the relative light stimulus threshold, 1.7×10^3 (RS_t), was first reached. Times have been corrected to standard time. The date of the experiment is indicated beside each data point. Linear regression (error ranges are ± 1 SE): $PI_t = 0.30 \pm 1.05 + 0.98 \pm 0.06 \times RS_t$; $r^2 = 0.98$, $n = 10$, $P < 0.001$.
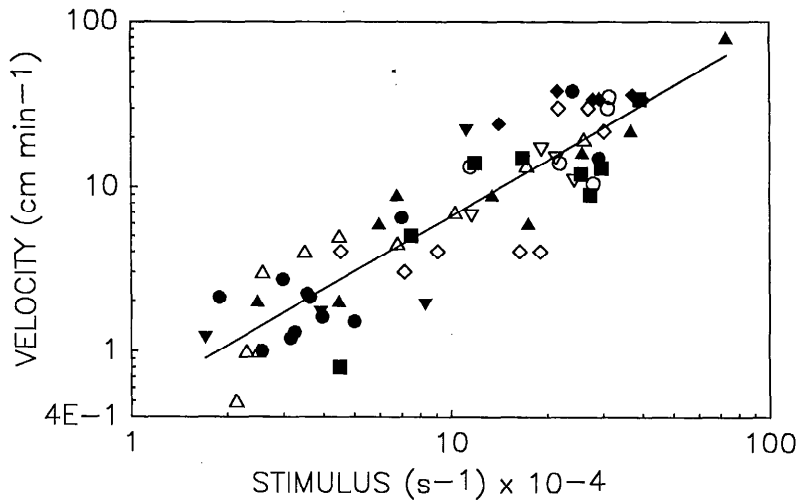
Fig. 3. Relationship between displacement velocity (*V*) and relative light change (*S*) during the evening migrations of *Chaoborus* larvae. Symbols and dates as in Fig. 1. Linear regression: $\log_{10} V = -0.31 \pm 0.24 + 1.127 \pm 0.069 \times \log_{10} S$; $r^2 = 0.80$, $n = 66$, $P < 0.0001$.

included the origin. Thus, this threshold value (1.7×10^{-3} s^{-1}) is a good predictor ($r^2 = 0.98$) of the time at which *Chaoborus* larvae begin their rapid upward ascent. The close correlation of stimulus threshold and the time of rapid upward movement is consistent with the stimulus-threshold model.

Stimulus-velocity hypothesis—To test the stimulus-velocity hypothesis, we examined the relationship between the rate of upward movement of the upper population boundary and the rate of relative light change. We included in this analysis the period of slow, upward drifting movements in the late afternoon.

Displacement velocity and stimulus value are highly correlated over a wide range of population movements and light change (Fig. 3). The unexplained variability is relatively small ($r^2 = 0.80$), considering the large number of different dates and range of conditions covered in the migrations studied. Surprisingly, there is no deviation from this relationship at 1.7×10^{-3} s^{-1} relative light change—the threshold value suggested in Fig. 2. This result indicates that there is no threshold stimulus level for the upward movement of *Chaoborus*. Instead, *C. punctipennis* larvae appear to adjust their migration rate as a continuous function of the relative rate of light change from the slowest

(0.5 cm min^{-1}) to the fastest (80 cm min^{-1}) rates of movement.

There was no significant effect of age on the swimming speed–light relationship for the second, third, and fourth instars. A linear regression of log *S* and log *V* run separately for the second and third instars ($n = 12$) was significant ($r^2 = 0.58$, $P < 0.002$), but did not differ significantly ($P > 0.50$) in slope or intercept from the fourth-instar data (Fig. 3).

It is difficult to determine whether the correlation between stimulus strength and displacement velocity is a causal relationship for both of these variables generally increase with time during the migration. Fortunately, we monitored a *Chaoborus* migration in detail on a day in which a late-afternoon storm caused irregular and abrupt shifts in the light stimulus strength and sign before and during the evening migration (Fig. 4). Data from the single migration fit closely ($r^2 = 0.93$) a log-log regression (Fig. 5) that does not differ significantly ($P > 0.10$) from the regression with the other combined dates (Fig. 3). Two of the three brief downward movements of the population caused by the sudden increases in light fall on the same regression line, extended to describe downward displacement as a function of positive light stimulus.
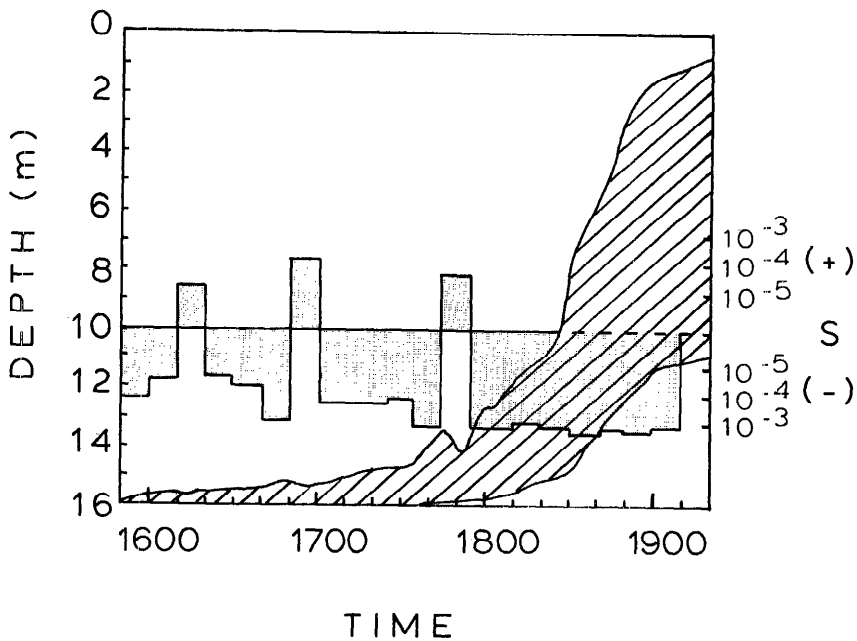
Fig. 4.   Relative light changes (*S*, in shaded area) during the evening migration of fourth-instar *Chaoborus punctipennis* larvae. Shaded area indicates *Chaoborus* population with leading and trailing edges. Barbadoes Pond, 10 April 1984.

These results strongly support the stimulus-velocity hypothesis for light control of migration and suggest that light-induced responses exert precise control of the migration velocity and direction. These results also indicate that downward movements during the evening migration are the results of active movement of *Chaoborus* rather than passive sinking.

Discussion

In agreement with Swift and Forward's (1988) field study, we found no support for the hypothesis that vertical migration of fourth-instar *C. punctipennis* larvae is a simple tracking of light intensity. Evidence from both studies could be used to support the stimulus-threshold hypothesis. Swift and Forward (1988) found a mean light stimulus of 1.3×10^{-3} s^{-1} in the 5-min period preceding the first appearance of *C. punctipennis* larvae during the evening migration in Crane Pond ($Z_{max} \sim 3.5$ m). In the New Hampshire lakes the rapid ascent of the leading edge of the fourth-instar larvae began at an average (± 1 SD) stimulus of

$1.5 \pm 0.6 \times 10^{-3}$ s^{-1}. When we included the slow upward movement of larvae in the afternoon, however, the stimulus-threshold hypothesis was rejected as inappropriate, since there was no threshold value for relative light change at which there was a corresponding abrupt change in migration rate.

Some of our other conclusions concerning light control of *Chaoborus* migration are opposite those of Swift and Forward (1988) who found that the initiating cue for vertical migration was absolute light intensity and that there was no relationship between relative light change and the velocity of movement. There appear to be several reasons for these differences. We based our conclusion that fourth-instar *Chaoborus* do not use absolute light as a cue for migration on the large variation in light at the times of emergence from the sediments (50-fold) and the 500,000-fold difference in light intensity at the time of rapid migration over all of the sampling dates. On 75% of the sampling dates (8 February–6 May), however, a period comparable to the 3-month span in their study, there was much less variation

(17-fold) in light intensity at the time of rapid ascent. Differences in the population parameters used in the two studies also must be considered. Most of their conclusions were based on relationships between light and the peak population (location of maximal density) of *Chaoborus* larvae, whereas we have dealt exclusively with the leading edge of the population.

In fact, average light intensities at the leading edge of the Crane Pond *Chaoborus* population have about the same range (3 × 10^{-6} to 1.4×10^{-4} W m^{-2}) as our values for fourth-instar larvae, except for our January series (*see Table 1*). Finally, methodological differences may be important. Swift and Forward (1988) found no relationship between rate of light change and velocity of movement using the population peaks from larvae caught in three nets at 15-min intervals. We found a significant stimulus-velocity relationship using continuous sonar recording that allowed the detection of gradual movements of larvae near the bottom and resolution of movements during the migration on a fine time scale.

Zooplankton vertical migration generally implies a simple cycle of individual plankters migrating toward the surface and returning to the deep water, although such an event is rarely recorded in nature. Migration patterns are generally based on interpretations of statistics from population samples, discontinuous in space and time. Estimates of the patterns and rates of migration are influenced by the sampling design and may be in serious error if animals do not migrate in synchrony (Pearre 1979). An advantage of tracking populations with sonar is that it can provide a continuous record of migration with fine temporal and spatial detail.

No single statistic completely describes the vertical movements of a population. We examined sonar traces of the upper population boundary since it was an easily identifiable feature. It was also a more sensitive measure of movement and migration initiation than population midpoint, which cannot be estimated until late in the migration when the lower boundary of the population emerges from the sediment. The leading edge of the population may also have ecological significance. Since animals along
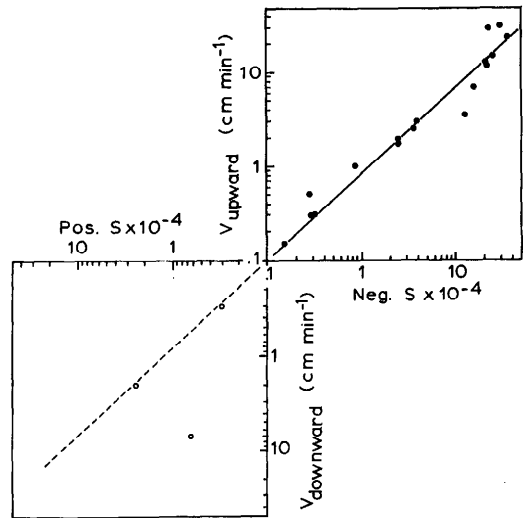

Fig. 5. Relationship between the displacement velocity (V) and relative light changes (S) s^{-1} of fourth-instar *Chaoborus punctipennis* larvae during the evening migration on 10 April in Barbadoes Pond. Linear regression: $\log_{10} V = 3.567 \pm 0.23 + 0.90 \pm 0.07 \times \log_{10} S$; $r^2 = 0.93$, $n = 17$, $P < 0.0001$. The three downward displacement values are not included in the regression. Displacement velocities and light stimulus values were estimated for corresponding 10-min intervals from 1550 to 1900 hours.

the uppermost border are the most highly illuminated segment of the population, the leading edge should be subject to the most intense visual predation. On the other hand, there could be nutritional benefits from participating in the initial contact with food resources during the evening migration, in terms of the selection as well as abundance of food.

The densities of *Chaoborus* traces on the sonar recordings were generally similar throughout the migrating population, suggesting that larvae were not strongly stratified during migration (Wagner-Döbler and Jacobs 1987). We have confirmation on only one date. On 10 April, triplicate, 30-liter Schindler traps taken at the leading edge, middepth, and trailing edges revealed remarkably uniform vertical distribution of the migrating *Chaoborus* of (mean ± 1 SD) 6.5±4.9, 8.7±4.2, and 7.4±4.2 larvae (30 liters)$^{-1}$, respectively.

Light responses based on the leading edge of the population cannot be applied directly to other portions of the population, since

animals in the lower regions of the population are exposed to lower light intensities during the migration than are animals at the leading edge. For example, on 10 April (*see* Fig. 4), fourth-instar *Chaoborus* larvae at the well-defined trailing edge of the migrating population began migrating at $\sim 2 \times 10^{-7}$ W m^{-2}, <1% of the light intensity at the upper boundary. If we assume that the migrating larvae at the trailing edge moved in response to light, they must have been dark adapted at this low light intensity (Swift and Forward 1980). The trailing edge began to emerge from the sediments about 10 min before the estimated inflection time for the leading edge and at a relative light change of 2.1×10^{-3} s^{-1}.

Initially, we suspected that if *Chaoborus* larvae are subjected to crepuscular bouts of predation by fish the vertical regions of the migrating population may show some morphological distinction, such as size of the larvae. Samples of the migrating *Chaoborus* population on 10 April taken at the leading edge, middle, and trailing edge of the population, however, revealed mean body lengths (± 1 SD) of 8.3 ± 1.2, 8.6 ± 0.5, and 8.7 ± 1.1 cm, respectively, that increased slightly with depth of the population, but did not differ significantly (paired t-tests, $n = 30$, $P > 0.10$).

We could find no consistent light intensity associated with the leading edge of the population at the time rapid ascent began. Fourth-instar *C. punctipennis* larvae began their rapid migration over a broad range of light intensities, generally between 3.4×10^{-6} and 3.4×10^{-4} W m^{-2}. On one occasion under extremely low underwater light caused by snow-covered ice, *Chaoborus* started moving rapidly upward at light intensities about three orders of magnitude lower than on other dates, but at about the same relative light change as under brighter light conditions. Thus, unlike *D. magna* (Daan and Ringelberg 1969), *Acartia tonsa* (Stearns and Forward 1984), and crab larvae *Rhithropanopeus harrisii* (Forward 1985), the responsiveness of the *Chaoborus* larvae to the rate of change in light did not appear to be altered by the previous light history of the animals.

Considering the enormous variation in patterns of diel migration of freshwater and marine zooplankton (Haney 1988), we might expect more than one mechanism of light regulation. Some of these variations can be seen by applying a useful model of Forward (1985) that separates the influence of light sequentially into premigration light adaptation, initiating cue, and orienting cue. According to him, adaptation to the light intensity before the migration controls readiness to migrate, with the greatest sensitivity to light change occurring when light is near the lower intensity threshold. The close correspondence of the timing of migration and the relative light change under a wide range of light conditions in our study suggests very little influence of premigration light intensity on the timing of the rapid *Chaoborus* migration.

The initiating cue for vertical migration seems to be absolute light intensity for the marine chaetognath *Sagitta hispida* (Pearre 1973; Sweatt and Forward 1985). Adult *A. tonsa* (Stearns and Forward 1984) and stage IV crab larvae *R. harrisii* (Forward 1985) are similar to the *Chaoborus* in the present study, however, for they begin their evening ascent in response to relative light changes. Once initiated, orienting cues are unnecessary for the upward migration of *Sagitta* since it occurs as an all-or-none response requiring no further change in light intensity (Sweatt and Forward 1985). Crab larvae, on the other hand, require continuous light change to sustain upward movement, but their rate of ascent is unaltered by light once the migration begins. The *Chaoborus* larvae in our study differed from all of the above-mentioned marine species for they responded to light changes in both the rate and direction of migration. From our field observations we cannot distinguish whether the responses to light changes during migration are phototactic or geotactic, as indicated by Swift and Forward's (1988) laboratory experiment with a reversed light field.

From the results of our study and previous ones we propose that the evening migration of *Chaoborus* can be separated into three phases, each with different controls.

The first phase often involves movement of the larvae from the sediments into the water. LaRow (1968) suggested that within the sediments the larvae undergo a circadian pattern of movements that brings the animals to the mud surface near dusk, where they enter the water in response to a threshold light intensity (Swift and Forward 1988) or other factors as suggested in this study. *Chaoborus* larvae may also spend the day above the sediments in deep lakes (e.g. Fedorenko and Swift 1972; Carter 1977) or during periods when bottom waters are anoxic (Teraguchi and Northcote 1966; Baker et al. 1985; second and third instars in this study). The second phase, upward vertical migration, involves a direct response in speed and direction of migration to relative change in light in the late afternoon and evening. As *Chaoborus* larvae near the surface they slow down and enter a more stationary nocturnal phase that has received little study. *Chaoborus* as well as other zooplankton may be inhibited from moving close to the surface of the lake by full moonlight (Hall et al. 1979; Gliwicz 1986; Moore Rodenhouse 1986).

Such depth adjustments may be in part responses to predation by visually feeding fish (Luecke 1986). It has also been suggested that night depth of *Chaoborus flavicans* larvae is determined by preference for a range of hydrostatic pressures, modified by avoidance of high nighttime light intensity (Wagner-Döbler 1988). We have observed that *Chaoborus* larvae in clear acrylic columns stop upward migration or sink 10–30 cm for 5–8 min while eating large prey such as *Daphnia* (unpubl.). Prey type may be important, for *Chaoborus* requires more time to digest *Daphnia* than *Diaptomus* (Giguere 1986). These observations suggest that the type and abundance of food may also influence nighttime location after upward migration. Such effects should be most pronounced when the animals encounter strata of prey near the end of the migration as the influence of light change wanes.

Our results clearly indicate that the swimming rate of *Chaoborus* larvae strongly depends on light changes that probably pro-

vide a visual cue for movement as well as a refuge from visual predation. In our attempt to simplify we have concentrated primarily on the upward migration phase during periods of minimal thermal and chemical stratification. A valuable next step would be to examine the role of light with increasingly complex conditions such as anoxia, a wide range of prey abundance, and contrasting amounts of visual predation.

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