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Ringelberg, J.; Flik, B.J.G.

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Increased phototaxis in the field leads to enhanced diel vertical migration

J. Ringelberg and B. J. G. Flik

Department of Aquatic Ecology, University of Amsterdam, Kruislaan 320, 1098 SM Amsterdam, The Netherlands

Abstract

Downward and upward displacement velocity of diel vertical migration in Lake Maarsseveen by the hybrid *Daphnia galeata* × *hyalina*, was correlated with the relative change in light intensity at dawn and dusk, indicating a phototactic basis for these migrations. The significance of the regression function increased over a period of 4 yr. Changes in environmental factors such as water transparency and food concentration are not responsible.

Since 1989, a diel vertical migration (DVM) of *Daphnia* in Lake Maarsseveen, The Netherlands, has been intensively studied. This migration is confined to 5–6 weeks in June and July when large shoals of juvenile perch (*Perca fluviatilis*) are present in the open water (Ringelberg et al. 1991). Before 1989, day and night vertical distributions of *Daphnia* were occasionally determined, but differences in depth were small and did not suggest extensive vertical migrations. For instance on 3 August 1978, the difference in mean population depth was 1.39 m. On 26 June 1979, a date within the crucial period of migration, the mean population depth around noon was 6.9 m, and around midnight it was 4.6 m. However in 1988, day depth had increased to 10 m (noon, 15 June), and the mean depth at midnight was slightly more than 5 m, indicating a migration with a small amplitude. Also observed for the first time on 15 June 1988 were large shoals of juvenile perch in the open water. We do not exclude the possibility that these shoals were overlooked in previous years, although weekly visits to the lake had been made; in the years after 1989, shoals were always encountered.

In 1989, we began a systematic study of DVM of the hybrid *Daphnia galeata* × *hyalina*. Juvenile perch were found to prey on *Daphnia*, and the *Daphnia* migration was con-

sidered a behavioral strategy to reduce predation pressure (Ringelberg et al. 1991). Nevertheless, during the first 2 yr of our study, a considerable part of the *Daphnia* population remained at light depths great enough to permit predation. The *Daphnia* migration depth increased considerably in 1991, which was an exceptional year in that low temperatures and low algal concentrations in June retarded the *Daphnia* migration until July. At the end of June, water temperature rose and algal concentrations increased. At the same time, the juvenile perch population rapidly increased and the *Daphnia* population was decimated. The leftover *Daphnia* migrated deeper than in previous years. This increased day depth was also found in 1992.

We hypothesized that changed phototactic reactivity was the cause of the increased migration depth. There is no common agreement about external factors that cause daily vertical movements and consequently no general acceptance of any basic, physiological mechanisms. The relative change in light intensity and phototaxis has been proposed as a primary initiating cause and mechanism (Ringelberg 1964; Daan and Ringelberg 1969), and the coincidence of maximum relative changes and vertical movements in the field has been pointed out (Ringelberg et al. 1991). The role of phototaxis in DVM has been demonstrated for different species (e.g. Forward 1976; Stearns and Forward 1984; Haney 1993). However, most studies of DVM are concerned primarily with the role of predators and overlook the importance of a stimulus-response system. Therefore, additional evidence, especially from field observations, is needed to substantiate the involvement of phototaxis in DVM.

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The objective of the present study is to demonstrate from field observations the importance of the relative change in light intensity as a causal factor of DVM. We also discuss whether the change in DVM was due to altered phenotypic inductions or to genotypic selection of the phototactic response system.

Methods

Lake Maarsseveen is a mesotrophic man-made lake; details about its morphometry, physics, and chemistry are given elsewhere (Ringelberg 1981; Swain et al. 1987).

Seven (1989–1991) or nine (1992) torpedo nets were used simultaneously to collect zooplankton at 2.5-m intervals from 1.25 m to 16.25 m (1989–1991) and 21.25 m (1992). Tows were made along the longitudinal axis of the lake over the deepest area (25–30 m). Technical details about the torpedo nets are given by Swain and Royackers (1986), and sampling methods are described by Ringelberg et al. (1991). Several weeks before, during, and after the migration period, weekly standard sampling was done at noon and midnight. In addition, samples were taken at intervals of 30 min, starting 2.5 h before sunrise and ending 1 h after sunrise. In the evening, the procedure started 1 h before sunset and also lasted for 3.5 h. As far as possible, this sampling was done at the peak of the migration periods. Originally, we planned this intensive sampling program to determine the time of day that vertical displacement occurred (Ringelberg et al. 1991). However, when DVM finally began in 1991, there were not enough personnel available to execute the extensive sampling program.

Daphnia species composition in the lake varied over time. In 1989, the pelagic daphnids were called *D. hyalina* sensu latiori (Ringelberg et al. 1991). However, allozyme analysis revealed that during the migration period, the population consisted of various clones of the hybrid of *D. galeata* × *hyalina* and of *D. galeata* (Spaak and Hoekstra 1993), and the hybrid has been dominant ever since. During routine sample counting, *D. galeata* was differentiated from the hybrid, and the daphnids were designated as juveniles, adults without eggs, and gravid females. Because of its dominance, the results presented here refer only to the hybrid *D. galeata* × *hyalina*.

Light intensity was measured continuously at 0.3 m below the water surface. The sensitivity of the custom-built sensor and a Kipp recorder was high enough to begin measurements at early dawn, when an observer could just perceive the beginning of the day (light intensity, $1 \times 10^{-4} \mu\text{Einst m}^{-2} \text{s}^{-1}$). When light intensity increased sufficiently, measurements (PAR) with a LiCor Quantum sensor were also made. The custom-built sensor was calibrated by comparing its readings with the LiCor readings and extrapolating to the very low intensities at dawn. Log linearity was controlled in the laboratory and proved to be good beginning at $\sim 1 \times 10^{-3} \mu\text{Einst m}^{-2} \text{s}^{-1}$. Below that intensity, a log-log relation can be used up to $\sim 5 \times 10^{-5} \mu\text{Einst m}^{-2} \text{s}^{-1}$. The continuous light signal was digitized at 1-min intervals. Relative changes in light intensity (S) were calculated over successive 1-min intervals.

Migration behavior of juveniles differed from that of adults but the data are not presented here. Data for each adult category were combined for a regression analysis. For each 0.5 h between sample times, the vertical displacement velocity (dv) of adults with eggs and adults without eggs was calculated from their average depths. Relative changes in light intensity were averaged over the same 0.5-h periods (\bar{S}). Assuming a constant dv per 0.5-h period, average depth (d) was calculated each minute for each type of adult. The natural logarithm of the light intensity at these depths [$\text{Ln } I(d)$] was calculated from the light intensity measurements at 0.3 m and the extinction coefficient. These values were averaged per 0.5-h period [$\overline{\text{Ln } I(d)}$].

Linear regressions were made with \bar{S} as the independent variable and dv as the dependent variable. The same value of \bar{S} may be encountered before and after its maximum, although at quite different absolute light intensities (see Fig. 3). Since the lowest value of a relative change in light intensity (threshold or just noticeable change) eliciting phototactic swimming in *Daphnia magna* depends on the light intensity of adaptation (Ringelberg et al. 1967), a swimming response to S , and thus dv , might be different on either side of this maximum in relative change because the ambient light level is different. For this reason, $\overline{\text{Ln } I(d)}$ was introduced in multiple regression analysis to reduce the unexplained variance caused by this light intensity-dependent stimulus thresh-

Table 1. Results of linear ($dv = a + b \times \bar{S}$) and multiple regression [$dv = a + (b_1 \times \bar{S}) + b_2 \times \overline{\text{Ln } I(d)}$] of dv on \bar{S} and $\overline{\text{Ln } I(d)}$ averaged over 0.5-h periods. P denotes probability that (partial) regression coefficients b , b_1 , and b_2 are equal to zero; n —number of data used in calculations. Means of dv are given if linear regression is not significant; otherwise 95% confidence limits of linear regression coefficients are given.

Date	n	Regression	Significance	Equation
Sunrise, 27 Jun 89	8	Linear	NS	$dv = 2.05 + 1.64\bar{S}$
		Multiple	NS	$dv = 2.5 \text{ m h}^{-1}$ (SE = 0.35)
Sunrise, 30 May 90	8	Linear	NS	$dv = 2.75 - 1.61\bar{S}$
		Multiple	NS	$dv = 2.6 \text{ m h}^{-1}$ (SE = 0.44)
Sunrise, 11 Jun 92	8	Linear	$P(b)=0.001$	$dv = 0.87 + 35.51\bar{S}$
		Multiple	$P(b_1)=0.007$ $P(b_2)=\text{NS}$	$dv = 2.98 + 32.33\bar{S} - 0.37 \overline{\text{Ln } I(d)}$
Sunset, 29 May 90	10	Linear	$P(b)=0.033$	$dv = -0.22 + 31.47\bar{S}$ ($2.71 - b - 60.22$)
		Multiple	$P(b_1)<0.0001$ $P(b_2)=0.003$	$dv = -5.50 + 53.96\bar{S} - 0.46 \overline{\text{Ln } I(d)}$
Sunset, 22 Jun 92	8	Linear	$P(b)<0.0001$	$dv = -3.32 + 74.81\bar{S}$ ($42.43 - b - 107.21$)
		Multiple	$P(b_1)<0.0001$ $P(b_2)=\text{NS}$	$dv = -3.58 + 74.70\bar{S} - 0.05 \overline{\text{Ln } I(d)}$

old. Data were combined for both adult categories and used in the following linear and multiple regression models:

$$dv = a + b \times \bar{S}$$

$$dv = a + (b_1 \times \bar{S}) + b_2 \times \overline{\text{Ln } I(d)}.$$

a , b_1 , and b_2 are constants, and this dv is the average performance of many animals swimming out of phase. If S is a strong factor causing phototactic swimming, a significant regression coefficient (b and b_1) is expected, even though dv is a derivation of the actual response parameter—the swimming velocity.

In multiple regression, independent variables should not correlate. \bar{S} and $\overline{\text{Ln } I(d)}$ are thought to be sufficiently independent because \bar{S} depends on the sun's change in altitude over time and is independent of depth, while $\overline{\text{Ln } I(d)}$ depends on altitude, weather conditions, water turbidity, and, most importantly, depth of the animals.

Results

In Table 1 we present the results of linear and multiple regressions.

Sunrise, 27 June 1989—The animals descended, but there was no significant relation with \bar{S} or absolute light intensity, and dv was averaged (Table 1). Adults with eggs began downward movement earlier (-127 min to

sunrise) than adults without eggs (-112 min) and ended migration later (-22 and -53 min, respectively); thus, gravid females descended for a longer period (105 vs. 59 min).

Sunrise, 30 May 1990—The daphnids descended again, but there was no significant regression between dv and \bar{S} (Fig. 1A). The average dv equals that found the previous year. Neither linear nor multiple regression was significant. The slow downward movement resulted in a considerable increase in light intensity at the depth of the animals (Fig. 2), thus, animals were not migrating in response to a particular light level (isolume).

Sunrise, 11 June 1992—The adults descended more rapidly, and the regression coefficients b and b_1 are significantly different from 0 (Fig. 1C). Partial regression coefficient b_2 is not significant. The initially high downward dv before sunrise resulted in a more or less constant low light intensity at the depth of the migrating animals (Fig. 2). $\overline{\text{Ln } I(d)}$ is not a function of time ($R^2 = 0.092$, $P = 0.466$, $n = 8$) as in previous years, which explains its unimportance in multiple regression. Toward sunrise, downward migration slowed, and with the accelerating velocity of change in overhead light intensity after sunrise, the animals were found at increasing absolute light intensities (Fig. 2). However, these intensities are overestimated because part of the population migrated below the deepest sampling depth, so the average

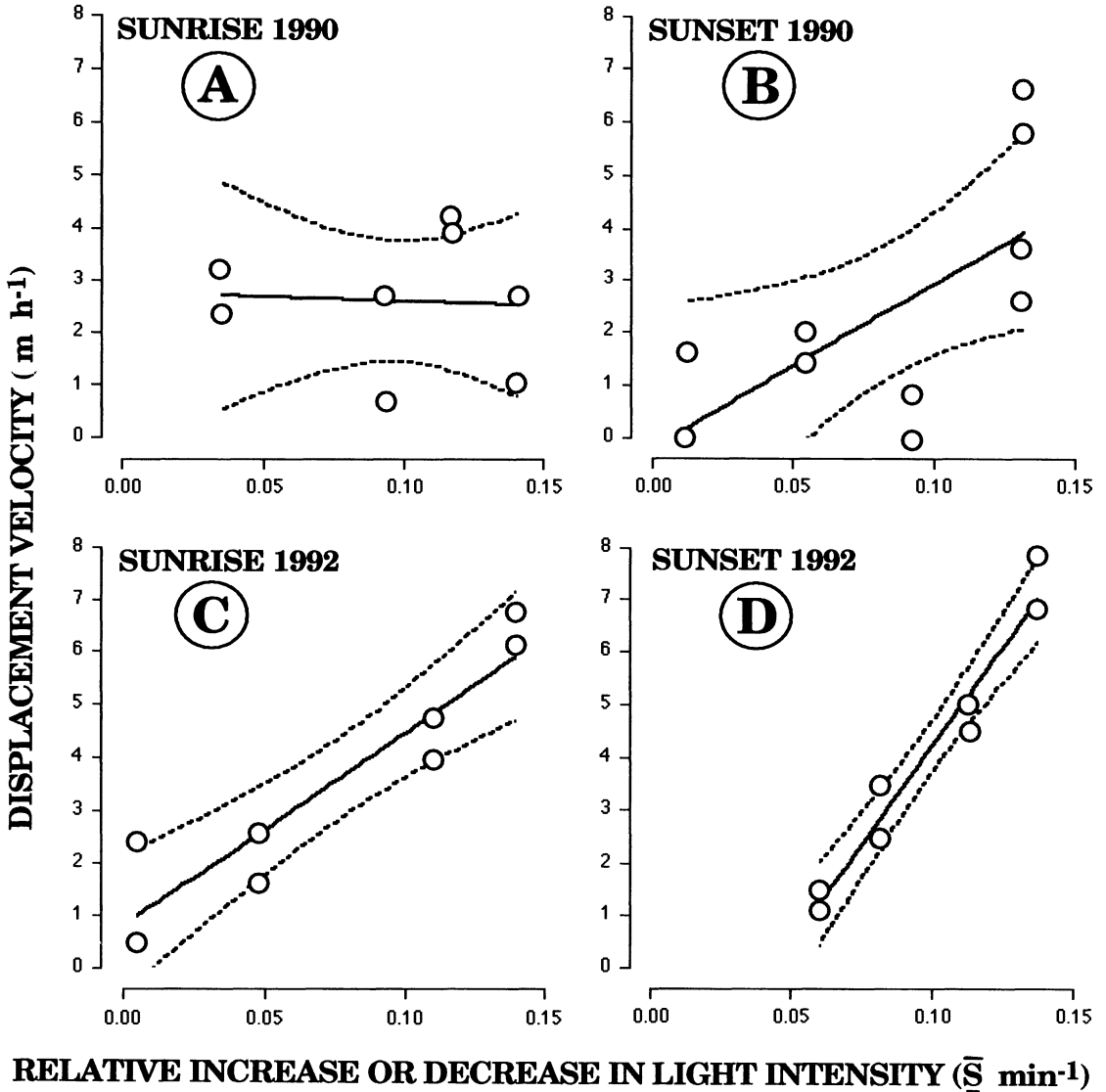


Fig. 1. The vertical displacement velocity (dv) of adult *Daphnia* as a function of the relative change in light intensity during morning descent of 30 May 1990 (A), evening ascent of 29 May 1990 (B), morning descent of 11 June 1992 (C), and evening ascent of 22 June 1992 (D). Regression lines and 95% confidence limits are presented. Regression functions are given in Table 1.

population depth we used is an underestimation.

Sunset, 29 May 1990—The dv of adults was significantly correlated with the relative decrease in light intensity (Fig. 1B). (A direct illustration of the correlation between dv and the relative decrease in light intensity is given in Fig. 3.) Prior to the maximum in relative decrease in light (~ 40 min after sunset), dv

was lower than at similar relative decreases after the maximum. Therefore, the significance of \bar{S} as a factor increased after the introduction of $\ln I(d)$ as an independent variable. Absolute light intensity accounted for part of the error variance. Upward migrations could not be passive because the animals are negatively buoyant. The animals are forced to react with active swimming. This might be why results

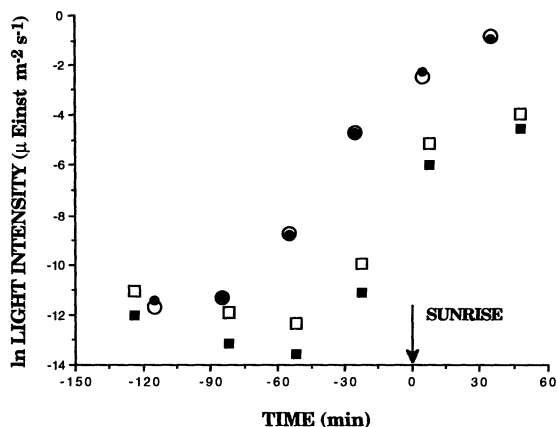


Fig. 2. Natural log light intensity [$\overline{\text{Ln } I(d)}$] at the mean depth of adults without (open symbols) and with eggs (closed symbols) during morning descent on 30 May 1990 (circles) and 11 June 1992 (squares). Migration began ~ 2 h before sunrise. The last two intensities in 1992 are overestimated because the mean depth of the population after sunrise was underestimated.

in regression between sunrise and sunset were different in 1990.

Sunset, 22 June 1992—The relative decrease in light intensity was a highly significant factor in determining dv (Table 1), as indicated by the linear (Fig. 1D) and multiple regressions. The partial regression coefficient b_2 was not significant.

Although linear regression coefficients b for sunrise in 1989 and 1990 were not significant, a formal comparison for equality of slopes (Sokal and Rohlf 1969) with the significant b for sunrise of 1992 was made. In both cases, regression coefficients were highly ($P \ll 0.001$) different from one another.

The linear regression coefficients for both sunset observations also show large differences. Nevertheless the 95% confidence limits overlap (Table 1), and a test for equality of slopes proved these regression coefficients b are the same ($0.25 > P < 0.1$). If we subject the dv of sunset 1990 and 1992 to an ANOVA

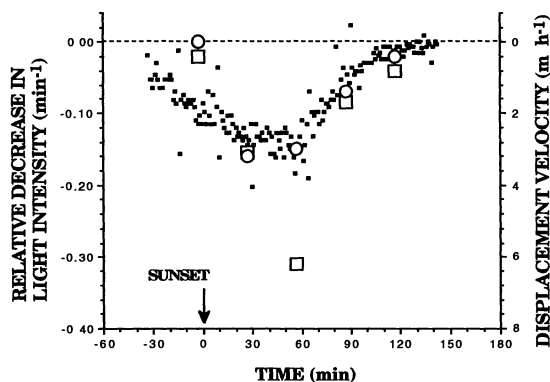


Fig. 3. Comparison of the relative decrease in light intensity (\blacksquare) and the dv of juvenile (\circ) and adult (\square) *Daphnia* in Lake Maarsseveen around sunset, 29 May 1990.

with relative decreases in light intensity and these two years as independent variables, we find a nearly significant year-effect ($P = 0.064$, Table 2). It is apparent that confidence limits for b_1 (May 1990) and b_1 (June 1992) largely overlap, and no formal test for equality was applied.

Variance in dv also changes over the years, as is apparent from the confidence limits of slopes in linear regression (Fig. 1). The difference in sunrise and sunset variance indicates a less variable behavior when active swimming is necessary for migration.

A comprehensive overview of the influence of \bar{S} from 1989 to 1992 is presented in Fig. 4. The percentage contribution to the total sum-of-squares of \bar{S} , $\overline{\text{Ln } I(d)}$, and residuals was calculated for the subsequent years.

For sunrise 1989 and 1990, the percentage contribution of \bar{S} is very small and the unexplained variance is large. In 1992, when the animals migrated faster and deeper, 79% of the total sum-of-squares can be attributed to the relative increase in light intensity. For sunset migrations, the contribution of the relative decrease in light increases from 40% in 1990 to 91% in 1992. It is evident that relative light

Table 2. ANOVA of upward dv with the relative decrease in light intensity at sunset and time (years 1990 and 1992) as independent variables. Relative light decreases were divided over two groups. Interaction was very small and pooled with the error estimate.

Source of variance	SS	df	MS	F-ratio	Probability (P)
Relative light decrease	67.89	1	67.89	41.15	<0.0001
Years	6.81	1	6.81	4.12	0.064
Error	24.82	15	1.65		

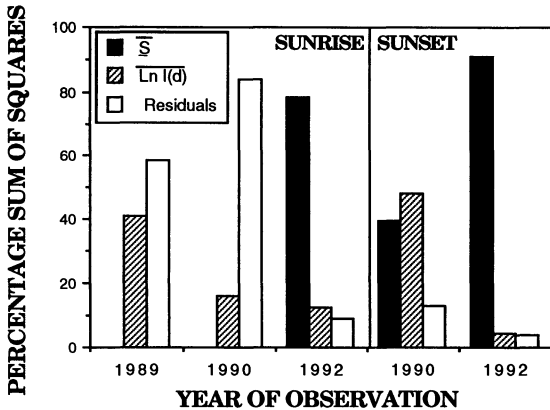


Fig. 4. For each year of observation is shown the percentage contribution to the total sum-of-squares in an ANOVA of the relative change in light intensity \bar{S} , absolute intensity $\ln I(d)$, and residuals.

changes determine the upward dv of the adult *Daphnia* in the evening.

Discussion

Since migration behavior of individuals cannot be studied in the field as yet, we have to deal with the average performance of a population. An interpretation of results in terms of physiological mechanisms can be made if experimental data on the behavior of individual animals are available, provided there is a strong enough correlation between the overall behavior in the field and the environmental factor responsible for causation of the mechanism in the laboratory. In the present study, phototaxis caused by relative changes in light intensity (see Ringelberg 1987) is considered.

Species and clone composition of the *Daphnia* "population," perhaps better called a "clone collective," changed over the years of observation, as shown by allozyme analysis (Spaak and Hoekstra 1993). After the migration period in 1989 ended, *D. galeata* increased and in 1990, during the migration period, it made up 50% of the population. The remaining 50% consisted of different clone groups of the hybrid of *D. galeata* and *D. hyalina*. In 1991, *D. galeata* disappeared from the lake almost completely. In 1992, the variation in hybrid genotypes had also decreased considerably (P. Spaak pers. comm.). Therefore, this clone collective in Lake Maarsseveen is a dynamic mosaic of genotypes, varying in composition with

time, undoubtedly due to changing forces of selection. We consider only migrations of adult hybrids of *D. galeata* \times *hyalina*.

The stimulus-response system—At sunrise in 1989 and 1990, *Daphnia* migrated downward, but no significant regression exists between dv and the relative increase in light intensity. The obvious conclusion is that light intensity is not a causal factor initiating downward migration. However, an alternative conclusion is possible.

In a study of phototaxis, Daan and Ringelberg (1969) found that at low values of relative increase in light intensity, individual *D. magna* reacted with short periods of passive sinking alternated with short periods of no vertical movement or even upward swimming. Active downward swimming occurred mainly at higher values of relative light increase. Sinking caused by continuous increase in light intensity was also found in *Daphnia longispina* from Lake Maarsseveen (Ringelberg 1993; considering results from recent allozyme analysis, experiments were probably done with *D. galeata* or *D. galeata* \times *hyalina*) and the hybrid we are dealing with here (Ringelberg unpubl. data).

With these experimental results in mind, one can suppose that downward displacement in 1989 and 1990 consisted predominantly of passive sinking. In both years, dv was ~ 2.6 m h^{-1} (Table 1), considerably lower than the sinking rate of 19.4 m h^{-1} reported by Brancelj and Blejec (1994) for narcotized animals of 2.5 mm at $22^\circ C$, which means that downward movement probably consisted of interrupted sinking and was undertaken by only a part of the population. The migration amplitude of 6.5–7.5 m in Lake Bled (Slovenia) mentioned by Brancelj and Blejec (1994) suggests the same manner of downward movement must have occurred there. Downward displacement velocities in *D. magna* ranged from 1 to 2.5 m h^{-1} , within the relevant range of relative increase in light intensity (0.055 – 0.15 min^{-1}) at sunrise (Daan and Ringelberg 1969), and consisted of interrupted movements. As in the phototaxis experiments (Daan and Ringelberg 1969; Ringelberg 1993), sinking occurred as long as relative increases in light intensity were equal to or higher than a threshold value, or rheobase, of ~ 0.055 relative light units per minute. If this value is also valid in the field, a period of ~ 2 h (Ringelberg et al. 1991) is

available for a reaction. Passive sinking, instead of active downward swimming, can be considered a sign of low reactivity. At high stimulus values in experiments, downward swimming becomes active (Daan and Ringelberg 1969). Because the velocity of sinking depends on gravity and zooplankton buoyancy (both constants), a significant correlation with the relative increase in light intensity is not expected. Nevertheless, above-threshold increases are considered stimuli that initiate and maintain reactions displayed as downward displacement.

The results of the regression analysis performed for the evening ascent in 1990 support this conclusion. An upward migration cannot be passive; therefore, dv must be a function of the relative decrease in light intensity if the latter is a causal factor. The significance of this factor was high indeed, especially in multiple regression.

A suggestion for an alternative explanation of a constant dv at dawn is given by Clarke and Backus (1956). They suggested that once downward movement was initiated by a certain light intensity, it would continue, independent of external stimulation. The existence of such a reaction has never been demonstrated in experimental studies and is unlikely from a physiological point of view. Moreover, this hypothesis is inconsistent with the significant role of the relative change in light intensity at dawn in 1992 and at sunset in 1990 and 1992.

Downward migration of *Daphnia* in 1992 was significantly faster than in earlier years (up to 7 m h^{-1} in Fig. 1C, as compared to 2.5 m h^{-1} in 1989 and 2.6 m h^{-1} in 1990) and animals moved deeper. Either reactivity or the number of reacting animals increased. Regression of dv with the relative light increase was highly significant (Table 1). In early morning, absolute light intensity at migrating depth was about constant. In the past, this would have argued in favor of the optimal light intensity explanation of DVM (Cushing 1951; Segal 1970) that is occasionally reintroduced (George 1983; Young and Watt 1993). In 1990, the dv was lower than the descent rate of isolumens, and light intensity at migration depth increased continuously (Fig. 2). Light intensity at the depth of the migrating daphnids depends on reactivity and is not the cause but the result of migration.

The regression lines, as presented in Fig. 1, suggest the absence of a threshold. In *D. magna*, Daan and Ringelberg (1969) found two types of reaction to increases in light intensity that were correlated with the mode of swimming at constant light. For one type, a distinct latent period, and thus threshold, was discernible; for the other type, an interrupted downward sinking began almost as soon as light intensity began to increase. If these types of reactions exist in *D. galeata* \times *hyalina*, a threshold would not be discernible. In addition, at the very low light intensities of dawn, a threshold lower than 0.055 min^{-1} may hold (Ringelberg et al. 1967). The sunset 1992 regression suggests the presence of a rheobase. If dv is zero in the regression equation, $\bar{S} = 0.044 \text{ min}^{-1}$, which is close to the experimentally found value, especially considering a possible lowering of threshold in the presence of fish exudates. Since field data are rough and sufficient experimental data are lacking, a too-detailed interpretation must be avoided.

At sunset 1990 and 1992, the relative decrease in light intensity was a highly significant factor determining dv . Although the slopes of the two linear regression lines differed by a factor of >2 , the regression coefficients were not significantly different, due to the large variance in 1990 (Fig. 1B). This variance could be ascribed to inhomogeneity of the reaction within the population and was strikingly different from the small variance in 1992. ANOVA showed years to be a nearly significant factor (Table 2), and, notwithstanding the results of the statistical analyses, upward dv in both years was considered different. Of course, this conclusion is supported by the substantially increased depth of migration in 1992.

Absolute light intensity was significant in multiple regression for sunset 1990 only. In *D. magna* (Ringelberg et al. 1967) and *Acartia tonsa* (Stearns and Forward 1984), the threshold of the relative change in light intensity eliciting a phototactic response increased with increasing light intensity. If the same is true for *D. galeata* \times *hyalina*, a different response to changes in light intensity, thus a different dv , might be expected at high light intensities than at low light intensities, although relative changes would be the same (cf. $dv < 0.2 \text{ m h}^{-1}$ at the time of sunset with 1.8 m h^{-1} at 85 min after sunset, Fig. 3). Thus, the absolute

light intensity may obscure a correlation of dv and \bar{S} ; for this reason, $\overline{\text{LN } I(\bar{d})}$ was introduced in multiple regression (see *methods*). However, it proved to be of minor importance.

The origin of an increased reactivity—The increased role of relative light changes in 1992 is obvious in Fig. 4. These light changes are the same from year to year, so the response of *Daphnia* must have increased. There are several ways to explain this. First, there may have been selection by juvenile perch (the predominant visual predator) during the period of migration for daphnids with a higher reactivity to relative changes in light intensity. Since fish exudates enhance reactivity (Ringelberg 1991), daphnids with a higher sensitivity to these kairomones may also have been selected for. Second, a higher abundance of perch may have increased the concentration of fish exudates in the epilimnion and consequently enhanced the phenotypic induction of phototactic reactivity. Third, environmental factors known to influence the amplitude of migration might have differed over the years.

Two environmental factors known to be of importance are the transparency of the water and the available food concentration. Amplitude of migration is positively correlated with Secchi disk depth (George 1983; Dodson 1990). Vertical extinction was measured every 2 weeks during the years of observation. Extinction was comparable during the migration periods of 1989 and 1990 and averaged 0.451 m^{-1} . In 1991, this coefficient was 0.426 at the beginning of the DVM period but increased during the migration period to values comparable with previous years. In 1992, transparency was slightly higher ($K = 0.40 \text{ m}^{-1}$). Converting this extinction into Secchi disk depth (George 1983) and substituting the value into the regression equation reported by Dodson (1990) leads to an increased amplitude of migration of 13% in 1992 as compared to 1989. The observed maximum depth at the end of the morning descent increased from 9.7 m in 1989 and 8.4 m in 1990 to 19 m in 1992, an increase of ~200%, indicating that the difference in water transparency does not explain the observed increase in migration depth.

Low food concentration tends to negatively influence migration amplitude (Johnson and Jakobsen 1987; Flik and Ringelberg 1993). Chlorophyll *a* concentrations, measured week-

ly during the periods of DVM, varied from 1.9 to 3.7 in 1990, 3.0 to 4.2 in 1991, and 1.7 to 2.7 in 1992. Although they are rough estimates of food conditions, these ranges do not provide clues to the increased migration in 1991 and 1992.

Selection by visually predating fish is implicit in the generally accepted explanation of the evolution of vertical migration behavior (Lampert 1993). Because DVM often seems to coincide with a high abundance of fish predators, ongoing selection may be presupposed, yet a convincing example of selection in operation is hard to find in the literature. At best, evidence is circumstantial.

This also holds for the present situation. Displacement velocity is the average result of swimming responses of many animals, including daphnids that do not respond or have a low reactivity. In 1989 and 1990, only part of the *Daphnia* population migrated out of reach of juvenile perch. In daytime, a considerable percentage of the *Daphnia* was found above the light threshold for visual predation ($5 \times 10^{-3} \mu\text{Einst m}^{-2} \text{ s}^{-1}$) and above a depth of 8 m, below which no 0+ perch were caught just before or during the migration periods. In 1992, however, all *Daphnia* were below the zone of visual predation and far below the 8-m depth in daytime. Therefore, it is plausible that genetic traits for higher reactivity were selected. Selection may operate through the physiological mechanism of phototaxis. Animals with a high rheobase, for instance, react later in the morning and respond for a shorter time. Consequently, descent may not be deep enough to prevent predation, as was the case in 1989 and 1990. These daphnids may have been removed from the population. The hypothesis can be tested experimentally by determining rheobase values for different clones. Also, other properties of the reaction system can be candidates of selection. Phototaxis is enhanced in the presence of fish exudates (Ringelberg 1991). Exudates must be perceived and the information must be processed in the central nervous system before reactivity to relative light changes can increase. The ability to perceive and process is certainly genetically determined and may be clone-specific. Also, this hypothesis can be tested experimentally.

Instead of genetic selection, intensified phenotypic induction may also have resulted in

an increased depth of migration in 1992. Loose (1993) observed that DVM in plankton towers depended on the concentration of a fish kairomone. Water from the epilimnion of Lake Maarsseveen (rather than water from the hypolimnion) enhanced phototaxis (Ringelberg unpubl. data). More rapid morning descent might have been the result of a higher concentration of fish exudates in the epilimnion if the number of juvenile perch had increased. Although perch was regularly fished with Bongo nets (1989–1992) and gill nets (1990, 1992) and an echosounder was used to study fish movements, we are unwilling to estimate the abundance of juvenile perch and cannot state that the number of fish was different in different years. Our impression is, however, that year-class strength did not change appreciably.

It is difficult to conclude from the present data whether genetic selection or stronger phenotypic induction was responsible for the observed increase in vertical migration behavior. Clone composition in the lake changed considerably from year to year (Spaak and Hoekstra 1993), which demonstrates that the *Daphnia* population was subjected to selecting forces, such as fish predation. Different clones of *Daphnia pulex* in a lake can have different ranges of vertical migration (Weider 1984), and Müller and Seitz (1993) reported that clones of the hybrid *D. galeata* × *hyalina* underwent DVM of various amplitudes.

It is plausible that the *Daphnia* clone collective in Lake Maarsseveen is a mosaic of genotypes with varying potentials for migration (including no migration) and that fish predators act as a selecting force. On the other hand, genotypic plasticity and fish kairomones, responsible for a phenotypic induction and control of migration, are also important. The relative influence of the two mechanisms might change from year to year and from lake to lake.

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