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An account of a preliminary mechanistic model of swimming behaviour in *Daphnia*: its use in understanding diel vertical migration

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Key words: *Daphnia*, diel vertical migration, model, phototaxis

Abstract

This preliminary mechanistic model of normal swimming and phototactic behaviour in individual *Daphnia* was constructed using data and assumptions based on experiments and observations. Swimming under constant light intensity is characterized by short periods of upward movements alternating with equal periods of downward movements. Two oscillators are proposed that generate these phases in swimming. Unexpected shifts in depth, as observed in *D. magna* and *D. 'longispina'*, are also present in the swimming of the computer daphnid and thus seem to be inherent to the underlying mechanism. As in real daphnids, during relative decreases in light intensity of low velocity, positive phototactic upward swimming is stepwise. With increasing velocity in the change in light, these steps disappear. When the model is triggered by a natural increase in light at dawn, a small downward movement results. Migration distance can be increased to commonly found depths of migrating *Daphnia* by the introduction of a 'fish exudate factor' into the model, which enhances the phototactic response. Since attenuation of light in the water affects the phototactic swimming response, it also influences migration distance. The results of model calculations agree quite well with an empirical relationship between Secchi disc depth and amplitude of diel vertical migration in a number of lakes.

Introduction

The causal (proximate) explanation of diel vertical migration (DVM) in *Daphnia* is based on phototactic behaviour elicited by changes in light intensity around sunrise and sunset. A large and consistent body of knowledge about photo-behaviour in *Daphnia* is available (Ringelberg, 1987). This knowledge is largely based on laboratory experimentation in tubes, and, consequently, reactive phototactic swimming is over short distances and of short durations, as compared to vertical migrations in lakes. This confinement is often thought of as to be a disadvantage, which diminishes the relevance of the results. It has, however, no bearing on the explanation of DVM. Reaction parameters like stimulus thresholds and swimming velocities have to be used in the mechanistic explanation of migration. A photoresponse occurs as long as the stimulus, a relative change in light intensity, is of supra-threshold strength. In nature, swimming continues as long as changes in

light intensity around sunrise and sunset are of magnitudes that surpass the threshold. These supra-threshold changes last for about two hours and start about 90 min. before sunrise or 30 min. before sunset, respectively. Early morning descent and late evening ascent coincide indeed with these periods as was shown for *D. galeata* × *hyalina* in Lake Maarsseveen (Ringelberg *et al.*, 1991). So, the next step in explaining DVM in terms of phototactic behaviour is to build a model of swimming *Daphnia* based (as far as possible) on experimental evidence and to trigger the computer daphnid by sunrise and sunset changes in light intensity. It is expected that the simulated migrations show features (e.g. timing, amplitude) comparable to those of vertical migrations in lakes.

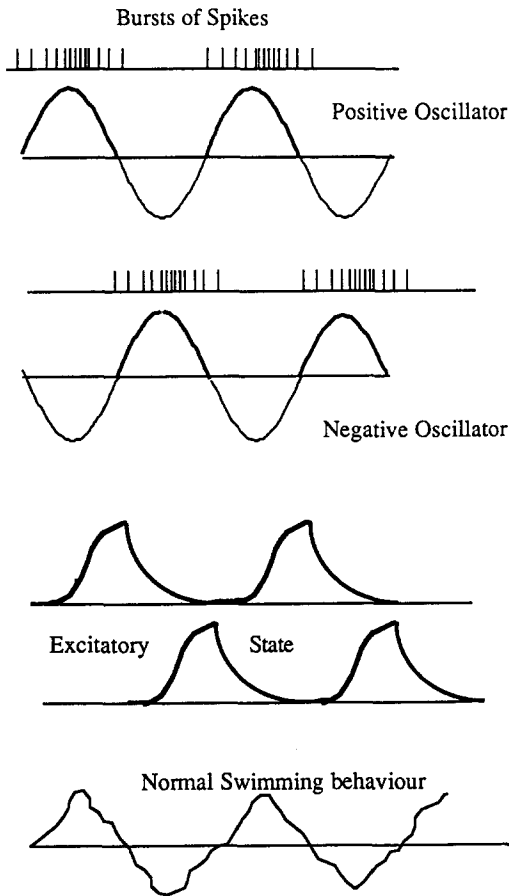


Fig. 1. Assumed physiological mechanism as the basis for normal swimming behaviour of *Daphnia* as incorporated into the model. See text.

Construction of the model

Modelling software (Stella, High Performance Systems, Inc.) was used to simulate, firstly, normal swimming behaviour and, secondly, phototactic swimming as caused by relative changes in light intensity. The integration of these two aspects makes up the essential part of the model from which conclusions about DVM can be inferred.

'Hop-and-sink' swimming in *Daphnia* consists of a stroke of the second antennae, resulting in a small upward movement, followed by a pause during which the animal sinks. When light intensity is constant, a series of strong strokes alternate with weak strokes, and result in an oscillation around a more-or-less constant depth. However, these alternating phases are irregular and sudden vertical displacements over larger dis-

tances occur. Nevertheless, autocorrelation analysis of 2–3 hour recordings in *D. magna* revealed a periodicity of about two minutes (Ringelberg, unpublished). The average duration of upward and downward phases in *D. 'longispina'* is 60.4 sec (s.d. = 16.54, n = 98) and, thus, a similar periodicity of about two minutes also seems to be present in this species. These data were obtained in experimental tubes under constant light and temperature following the method of Ringelberg (1964). (Probably, this *D. 'longispina'* from Lake Maarsveen was actually *D. galeata* or *D. galeata* × *hyalina*. Allozyme analyses, which were performed by Spaak and Hoekstra (1993), have revealed that the daphnids in this lake consist of the aforesaid taxa, which can change in relative dominance from year to year and also within a given season).

Based on this periodicity, two sinusoidal functions were assumed with default period lengths of two minutes and which were shifted in phase by 180° to model normal swimming (Fig. 1). One can imagine that in the central nervous system, two (groups of) neurons fire with a periodicity of two minutes, one group stimulating the vigour of antennal beats, the other inhibiting this activity. For reasons of simulation, spike frequency was changed into amplitude, and an excitatory state (Ringelberg, 1964) is formed in proportion to this amplitude. Excitation in sensory and nervous systems disintegrate with time, therefore, an exponential decrease was assumed. The value of the disintegration constant was calculated from the stimulus strength-stimulus duration response curve (rheobase-chronaxic curve), which was obtained from phototactic reactions (i.e. caused by relative decreases in light intensity, Ringelberg, 1993) using *D. 'longispina'*. Both positive and negative excitatory states were summed and the sum determined whether the computer *Daphnia simplicitas* swims upwards or downwards with a proportional velocity. The default amplitude of the positive and negative oscillator was calibrated in order to achieve the average normal swimming distance of 2.9 cm (s.d. = 1.39, n = 98).

It cannot be expected that the period and the amplitude of the oscillators are constant since also durations and velocities of upward and downward swimming phases vary and are normally distributed. Therefore, in the model, at randomly chosen times, the values of the period and the amplitude were replaced by values chosen randomly from normal distributions with default values as means and standard deviations of 10% about these means.

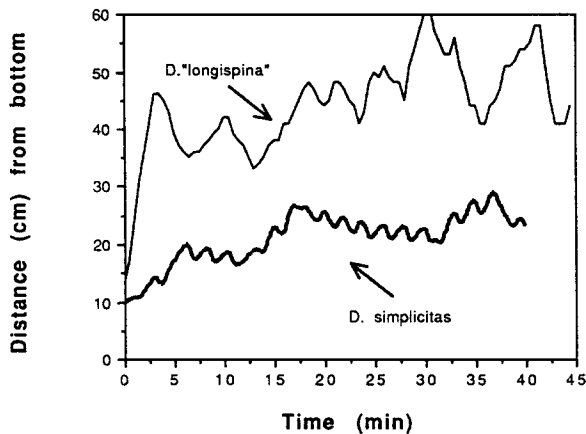


Fig. 2. An example of a swimming track of *D. 'longispina'* compared to a simulation run of *D. simplicitas*.

The second step was to incorporate phototactic swimming into the model. This was done by introducing two additional excitatory states; the first one increased proportionally to the velocity of relative decreases, while the second one was proportional to the velocity of relative increases in light intensity. Whether a phototactic swimming response does or does not occur will depend on the combination of velocity and duration of the light change. At a certain low velocity of the relative change in light intensity, an infinite duration of this light stimulus is needed because the velocity of increase in excitation equals the disintegration velocity of this excitation (see Ringelberg, 1964, 1987 for theoretical treatment). A disintegration constant used in the model, was calculated from experimental values (Ringelberg, 1993). Since it was demonstrated (Ringelberg, 1964) that the effect of relative changes in light intensity are superimposed on normal swimming, the four excitatory states were summed to obtain a final value of excitation that determined swimming direction and proportional swimming velocity.

Still, another aspect of photo-reactive swimming must be considered. If a *Daphnia* swims up or down, it experiences an increase or decrease in light intensity, respectively. The extent of this change is a function of swimming velocity and the turbidity of the water. This consequence of phototactic upward and downward swimming was also incorporated into the model by means of an extinction coefficient.

Finally, the model was run with a natural light intensity increase measured on June 18, 1989 at 0.30 m

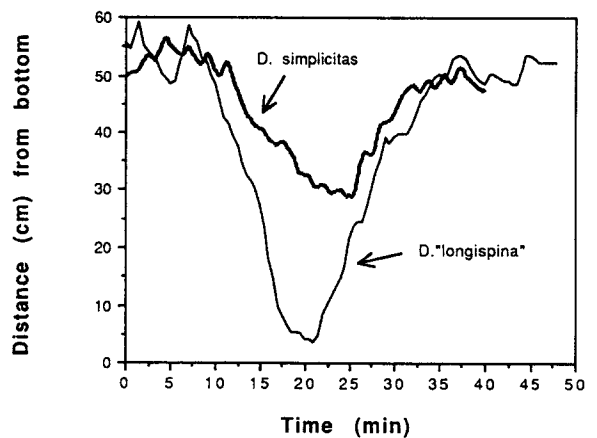


Fig. 3. Illustration showing how normal swimming may be interrupted by sudden changes in depth position without any concomitant changes in environmental conditions. Note that this occurs in both real and simulated *Daphnia*.

below the water surface in Lake Maarsveen. Absolute light intensity and relative increases, from 90 min. before until 90 min. after sunrise, were used as input. The effect of turbidity on the amplitude of migration was studied by varying the extinction coefficient in the model. The results were compared with the correlation between amplitude and Secchi-disc depths, as compiled for a variety of lakes, by Dodson (1990). Extinction coefficients were transformed into Secchi-disc depths using a formula given by Talling in George (1983).

Complete information on the functional relations and parameter values used in the model can be obtained from the author upon request.

Results and discussion

Normal swimming of *Daphnia simplicitas* and either *D. 'longispina'* or *D. magna* compares reasonably well (Fig. 2). Tracks of the latter species were smoothed for comparison because of irregularities due to 'hop-and-sink' swimming, and time lags of the observer, which were absent in the computer runs. Of special interest are sudden vertical displacements, performed by the computer *Daphnia* as well as the real species (Fig. 3). Previously, these interruptions of the regular oscillations were thought to be caused by unknown internal and/or external influences. However, it cannot be excluded that they are inherent to the basic mechanism

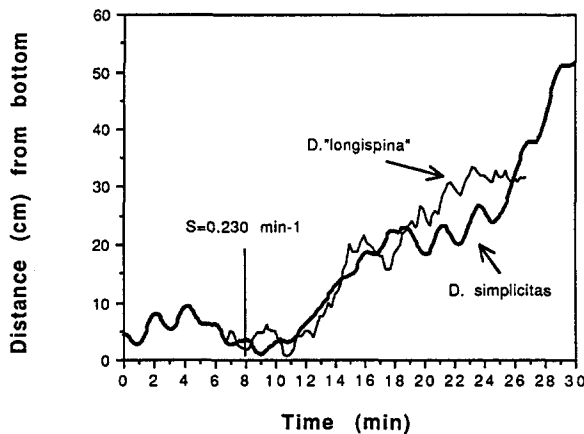


Fig. 4. An example of a positively phototactic reaction evoked by a relative decrease in light intensity ($S = 0.230 \text{ min}^{-1}$) at which stepwise upward swimming is still present in both a real and simulated *Daphnia*.

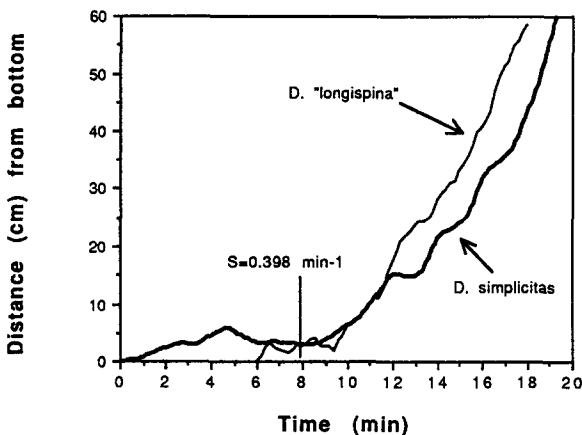


Fig. 5. As in Fig. 4 but at a higher rate of relative decrease in light intensity ($S = 0.398 \text{ min}^{-1}$). Note that the steps in upward swimming (as depicted in Fig. 4) disappear.

of normal swimming. In the model, they are the result of the stochastic succession of high amplitudes and/or long periods of either oscillator, which were accompanied by low values of the other oscillator. Of course, this interesting similarity in behaviour of the computer daphnid and *D. magna* or *D. 'longispina'* does not prove that oscillators are responsible for swimming behaviour in the real species.

Positively phototactic reactions compare well (Figs 4 and 5). As in *D. magna* and *D. 'longispina'*, at low

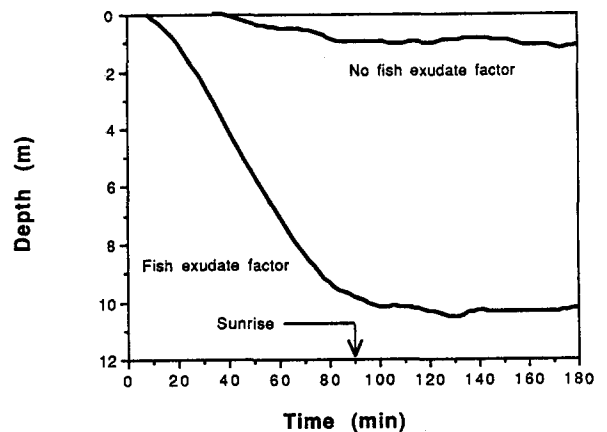


Fig. 6. A natural increase in light intensity at dawn was used to trigger the model. Without evaluation ('no fish exudate') of the excitatory state, which results from the increase in light, the amplitude of migration is small; realistic amplitudes are achieved by the introduction of an appropriate value for the excitatory state.

values of relative decreases in light intensity, upward swimming is stepwise. The upward phase of normal swimming is prolonged by the light decrease, while the influence of the negative oscillator is decreased. The periods between upward gain become shorter with increasing stimulus strength, and result in an approximated continuous upward swimming motion (Fig. 5).

The data on phototactic reactions, used to build the model, were obtained at a time when the enhancing effect of juvenile perch (*Perca fluviatilis*) on these reactions was unknown (Ringelberg, 1991). At the time of the experiments, an incidental observation (June 26–27, 1979) in Lake Maarsseveen revealed a very weak DVM with a difference in mean population daytime and night-time vertical distribution of only 1.98 m (Ringelberg, 1993). A comparable small amplitude was obtained by triggering the model with a natural light increase around sunrise (Fig. 6).

Although the mechanism of phototaxis is always functioning in the absence of fish exudates, reactivity is poor and it does not lead to extensive vertical migrations. To achieve such migrations, the excitatory states (which were elicited by relative changes in light intensity) were given greater weight than those of the oscillators. Simulated migration amplitudes were modelled as presently found in Lake Maarsseveen (Ringelberg *et al.*, 1991).

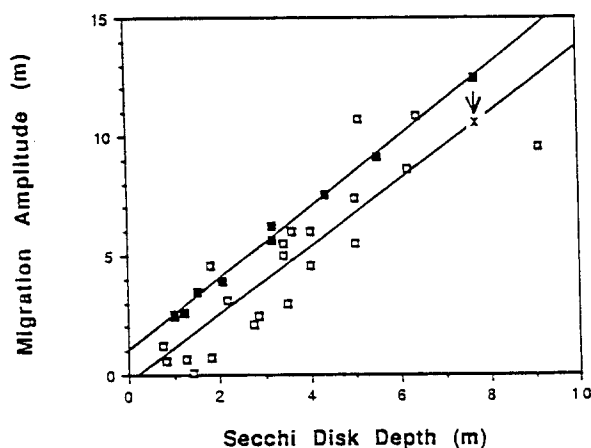


Fig. 7. Amplitude of DVM as a function of turbidity of the water as expressed by Secchi-disc depth. Open squares and the lower regression line ($y = -0.299 + 1.4092x$) are based on empirical data from different lakes as compiled from the literature by Dodson (1990). The black squares are generated by the computer model triggered by a natural increase in light intensity and different extinction coefficients. The latter were recalculated as Secchi-disc depths for comparison. The regression function is $y = 1.024 + 1.4887x$. The arrow indicates the result (x) of a computer run with an adjusted evaluation factor of excitatory states.

Finally, the model was run using different extinction coefficients. After Secchi-disc depths were recalculated, the amplitudes of migration became a function of turbidity, and this function was strikingly similar to the one published by Dodson (1990), which was based on migrations in a number of lakes (Fig. 7). The slope of the regression is important; the vertical position of the calculated regression line, which is too high in Fig. 7 as compared to the empirical one, can be adjusted quite easily to the level of the empirical one by using a slightly smaller value for the constant, evaluating excitatory states (this was done for one turbidity, see cross and arrow, Fig. 7). Evidently, the influence of water turbidity on day depth in lakes can be explained by light intensity decreases, which result from downward swimming, and thus lead to a diminished influence of relative increases in light intensity at dawn. In clear water, these decreases are smaller, as compared to more turbid water and phototactic downward swimming is less affected. Since the depth at which visual predators are able to forage is inversely related to light extinction, the adaptive significance of this property of phototaxis is evident.

Amplitudes of DVM collected for various lakes by Dodson (1990), show considerable scatter around the regression line (see Fig. 7). Since Loose (1993) demonstrated that vertical migration amplitude depends on the concentration of fish exudates, part of the variance may be explained by this factor. In the model, amplitude of migration is sensitive to the factor evaluating excitatory states, which was introduced to simulate fish exudates. Experiments on phototaxis using various concentrations of exudates, have to be conducted before the functional significance of this mechanism can be firmly established.

This preliminary mechanistic model simulates quite well, the normal swimming and photo-behaviour in individual *Daphnia*. When triggered by light intensity changes at dawn, the model simulates diel vertical migrations with several realistic properties. Therefore, it is worthwhile to continue experiments designed to evaluate the underlying physiological mechanism(s) and to refine the model accordingly.

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