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The Effect of Temperature and Density on the Amplitude of Vertical Migration of Daphnia Magna

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THE EFFECT OF TEMPERATURE AND DENSITY ON THE AMPLITUDE OF VERTICAL MIGRATION OF DAPHNIA MAGNA

A Thesis
Presented to the Faculty of the Department of Biological Sciences of the State University of New York College at Brockport in Partial Fulfillment for the Degree of Master of Science

by
Michael John Calaban
January 1981
THESIS DEFENSE
FOR

Michael J. Calaban
Master's Degree Candidate

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ABSTRACT

The effects of thermal stratification (temperature and density changes) on the amplitude of vertical migration of Daphnia magna were studied under controlled conditions in acrylic tubes. Vertical migration was inhibited in thermally stratified columns. Changes in water density alone did not affect vertical movement. Abolition of the descending blue dance could not explain the results because of the use of a light source with a spectrum shifted to the red region. The magnitude of vertical migration may be reduced by an avoidance reaction to large but commonly observed differences in temperature encountered in temperate lakes during summer stratification.
Since the discovery of the phenomenon of vertical migration over a century ago, a preponderance of literature has evolved to explain its occurrence. A host of physical factors affect the vertical migration of plankton, depending upon the species involved and environmental characteristics. Light has always been considered as a major factor, if not the ultimate factor in controlling vertical migration. As early as 1877, it was believed that since the crustacean eye was adapted to low light intensities, migrating plankters sought regions which were best suited to them (Hutchinson 1967). More recently, avoidance of visually oriented predators (Zaret and Suffern 1976), the metabolic and demographic advantages of residing in cooler water (McLaren 1963, Enright 1977) and the facilitation of transport to areas of higher phytoplankton biomass (Isaacs et al., 1974) have been offered as hypotheses explaining vertical migration. What possibly began as a simple expression of photic sensitivity may have acquired additional significance due to niche diversification, metabolic advantages, increased fecundity and prey-predator responses.

Instead of investigating ultimate or proximal causes of vertical migration, another approach was taken. We attempted to determine if there were factors that could limit the extent of vertical migration of zooplankton. During summer stratification an obvious change in physical (i.e., temperature, light, density) and chemical (oxygen, pH) factors occurs with depth. The existence of a deep cold layer
overlaid by a shallow warmer layer of water and the thermally induced
density differences associated with summer stratification are well
known. The hypothesis tested was that thermal stratification in an
acrylic tube affects the amplitude of vertical migration of a
active swimmer. More specifically, the effects of temperature and
density on the extent of vertical migration in Daphnia magna were
investigated in a series of controlled laboratory experiments.
MATERIALS AND METHODS

*Daphnia magna* were cultured at a temperature of 20°C in erlenmeyer flasks containing a mixture of dechlorinated tap water (50%), filtered Lake Ontario water (50%) and sheep manure (~10 g) wrapped in cheese cloth. Cultures were maintained under fluorescent light (Sylvania Cool White) at an intensity of \(0.91 - 1.69 \times 10^{-2}\) μW/min and a Light:Dark cycle of 15L:9D.

The experimental and control chambers were divided into ten 12-cm sections to facilitate the counting of organisms (Fig. 1). A nylon screen (0.5-mm mesh) ~5 cm above the bottom of each column allowed fine particulate matter to pass through the mesh and collect on the bottom of the column. The bottom half (54 cm) of the experimental column was enclosed in a water jacket, through which cold water could be circulated from a Lauda K-2/RD water cooler. This created a cold hypolimnion and the required experimental temperature difference between the two columns.

The experimental and control chambers were housed in a dark room. The same photoperiod used to culture the organisms was used in all experiments. Light was supplied to each column by a 60W G.E. soft white incandescent bulb, situated directly above the top in an open cylinder 31 cm from the surface of the water. The spectral distribution of this bulb is shifted toward the orange-red portion of the spectrum. The cylinder served to channel the majority of the light in a vertical
plane. Because this enclosed light caused a heating problem in the top few centimeters of water, fans were employed to remove excess heat through perforations in the front and back of each cylinder. Also, a water filter placed above the surface was used in conjunction with the fans to absorb excess heat. These two methods combined to effectively limit heating in the top 2 cm of the column to 1-2°C.

Temperatures at different depths were recorded with calibrated mercury thermometers placed in neoprene stoppers. The mean of four readings, taken over the length of the experiment, was used to plot temperatures.

Each experiment was run over a period of 24 hr with an acclimation period of equal duration. Fifty plankters per column per experiment were used. The positions of organisms in each of the ten sections were recorded every 2 hr, except at simulated sunrise and sunset, where readings were taken 15 min before and 15 min after those times.

Position of each individual had to be recorded in the dark phase without seriously disrupting behavior. A low wattage lamp with a red filter was used to quickly count organisms during the dark phase since Daphnia have a reduced sensitivity to red light (Hutchinson 1967, p. 761). No change in behavior was observed.

In determining whether zooplankton distribution was controlled by density effects, a series of experiments were devised in which salts (NaCl) were added to the experimental column. The density measurements were standardized by measuring the density of distilled, deionized water with a 50-ml pycnometer over a range of temperatures (5.8, 6.1, 6.2, 21.8, 23.9, 23.9°C) with a calibrated thermometer (0.1°C divisions).
A correction for barometric pressure at the latent point of vaporization was made during the temperature calibration. Comparison by regression analysis of the measured densities with those of Hutchinson (1967) (for pure water) indicated equal slopes between measurements with Y-intercepts displaced by .002 g/cm³. This value was used as a correction factor.

The density of culture water used in all experiments was measured over a similar range of temperatures. A graph of density versus temperature was prepared, allowing rapid determination of the differences in density between cold (5°C) and room temperature culture water. The concentration of salts required to increase the density of room temperature water to that of water at 5°C was based on the assumption that 1 g/l salt will increase density by .00085 g/cm³ (Ruttner 1952). The final density after addition of the salts was checked with the pycnometer and found to closely agree with the calculated density.

The effects of salts on swimming behavior were observed by conducting an experiment with the experimental column filled with saline water and the control filled with normal culture water. Next, the experimental column remained isothermal, but a bottom salt layer was introduced through a tygon tube situated on the bottom of the column. The saline water pushed up the less dense fresh water, creating a halocline and the same density barrier as was found in the maximum thermal density experiment but without any temperature effects. By addition of methylene blue to the salt layer, the extent of diffusion of the salts was observed to be minimal (see Appendix, Fig. 1).

Finally, the experimental column was maintained at different
temperatures but at equal densities. This was accomplished by chilling the bottom layer of water with the cold water bath, then adding salt water at room temperature but of equal density on top. The salt water was slowly added via a tygon tube situated above a removable plastic shelf on top of the cold hypolimnion waters. The shelf was carefully removed once the layer was added. The temperature of the epilimnion was precisely maintained by the addition of a second water jacket, enclosing the upper 66 cm of water (the epilimnion). The extent of mixing between the cold and warm layers was again observed with methylene blue indicator and found to be minimal (see Appendix, Fig. 2).

Results are presented as the depth of the average individual (Worthington 1931). Ninety-five percent confidence intervals were calculated for each observation in the experimental and control columns in all experiments. In Figure 2, the depths of the average individuals are plotted with their 95% confidence intervals. In all other figures, the mean 95% confidence interval of all observations was calculated for the experimental and control columns and is reported in the figure legend.
RESULTS

In each experiment a reverse migration (i.e., movement upward during the day, descent at night) was exhibited. This migration pattern is caused by the emittance of long wave radiation by the incandescent light source employed (Wilson 1980, Smith and Baylor 1953, McNaught and Hassler 1964). This behavior is reinforced by the starved conditions of the organisms used in the experiments (Hutchinson 1967).

The often statistically significant differences in daytime position of the depth of the average individual in many experiments are caused by differences in amounts of light energy entering the surface waters of the column. The variability in amount of light impinging on the surface water of the columns is caused by differences in thickness of the water filter and construction of the aluminum cylinder used to direct light and variable energy outputs of the incandescent bulbs (e.g., Appendix, Table 1).

(A) Equal Thermal Conditions (Fig. 2)

Both chambers were set at equal temperatures (24.5 ± 0.5°C) to determine whether any variation existed in the migratory behavior of D. magna between the control and experimental columns. The vertical migration pattern throughout the 24-hr test period was not significantly different between the two columns.
(B) Minimum Temperature Difference (Fig. 3a)

In this experiment the control and epilimnion of the experimental column were maintained at a temperature of \(12.0 \pm 1.0^\circ C\). The hypolimnion was cooled to \(5.0 \pm 0.3^\circ C\) establishing a thermal gradient of \(7.0^\circ C\) in the metalimnion (60-70 cm).

The experimental population migrated throughout the column, crossing the \(7.0^\circ C\) temperature gradient and into the cold hypolimnion. The control population migrated throughout the length of the column.

(C) Intermediate Temperature Difference (Fig. 3b)

The control and epilimnion of the experimental column were maintained at a temperature of \(17.0 \pm 0.5^\circ C\). The hypolimnion was again at a temperature of \(5.0 \pm 0.3^\circ C\), creating a thermal gradient of \(12^\circ C\) in the metalimnion (60-70 cm).

The vertical distribution between the two columns was significantly different. The experimental population migrated to an average depth that was at all times above the metalimnion. The control population freely migrated throughout the length of the column.

(D) Maximum Temperature Difference (Fig. 3c)

The control and epilimnion (upper 60 cm) of the experimental chamber were maintained at a temperature of \(22.0 \pm 0.5^\circ C\). The hypolimnion of the experimental column was cooled to a temperature of \(5.0 \pm 0.3^\circ C\) establishing a thermal gradient of \(17.0^\circ C\) in the metalimnion (60-70 cm).

The vertical migration patterns between the experimental and
control populations were significantly different. The experimental group, being at all times above the thermally induced density barrier and cold water layer, did not descend past the metalimnion. The control group migrated, as before, throughout the entire length of the isothermal column.

(E) Effects of Salts on Behavior (Fig. 4)

To determine whether the elevated salt concentration had any effect upon the migratory behavior of *D. magna*, a test was run with the experimental column completely saline and the control filled with normal culture water. Enough NaCl was added (2.7058 g/l) to increase the density of the fresh culture water at 23.9°C to its density at 5°C. The concentration of NaCl used, 0.0462 molar, was well below the threshold concentration (0.072 molar) found to induce immobilization in *D. magna* (Anderson 1948). Furthermore, Anderson found that *D. magna* have a relatively high tolerance to NaCl, concluding that the only toxic effects are when "concentrations are high enough to exert an unfavorable osmotic balance."

The vertical migration pattern did not significantly differ between the saline and normal column.

(F) Equal Temperatures, Different Densities (Fig. 5a)

A chemically induced density gradient was established in the isothermal experimental column. The control contained normal culture water. Enough salts were added (3.0588 g/l) to the bottom layer (lower 54 cm) of water to increase the density of the water at 25.0°C to that of fresh culture water at 5°C. Thus, the same density barrier
was established as in the maximum temperature difference experiment but without any temperature effects.

The distribution of *D. magna* throughout the test period did not significantly differ between the salt stratified experimental column and freshwater control. Organisms readily passed through the halocline and into the bottom saline layer.

(G) Equal Densities, Different Temperatures (Fig. 5b)

To separate the effects of temperature from density, a thermal gradient was established in the experimental column by cooling the bottom layer (66-120 cm) to 5°C and by adding a saline epilimnion (22.0°C) of equal density to the bottom layer. Organisms, therefore, faced the same temperature differential as in the maximum temperature difference experiment but without any density effects. The isothermal control was again filled with normal culture water.

The vertical distribution of *D. magna* was significantly different between the experimental and control chambers. The downward movement of *D. magna* stopped at the metalimnion. Vertical movement throughout the control was evident.

(H) Cold Acclimation (Fig. 6)

A cold (6.0°C) epilimnion was maintained over a warm (15.0°C) slightly denser saline hypolimnion. The methodology of Kibby (1971) was used to cold acclimate the organisms at 5°C.

The experimental population immediately migrated through the cold layer and into the warm hypolimnion. Organisms maintained this position throughout the entire experiment. Twenty-eight hours into
the experiment, the temperature of the epilimnion was raised to 15°C; organisms then rapidly ascended into that region.
DISCUSSION

In Smith and Baylor's (1953) experiments, an increase in intensity of blue or white light induced a descending blue dance. However, the photoresponse of *D. magna* is temperature dependent with the blue dance apparently eliminated under 10°C. Thus as the population moved downward, in response to the increasing intensity of blue or white light, into a thermocline, the dance assumed red characteristics and no further downswimming occurred. If individuals moved up out of the cooled region, they immediately started a descending blue dance and returned to the cold water. Smith and Baylor (1953) believed that no other barrier restricted the population at the thermocline.

The mechanism of Smith and Baylor to explain the cessation of vertical migration into a cold region could not be invoked in this study. With a constant light intensity shifted to the orange-red portion of the spectrum, *D. magna* moved upward toward the light (Smith and Baylor 1953). By utilizing an incandescent bulb with spectral distribution shifted toward the orange-red portion of the spectrum, the temperature effect on photoresponse was separated from any potential effect of the thermocline by not allowing the population to reach the thermocline during the light portion of the light-dark cycle. That is, the population of *D. magna* was up away from the thermocline during the "day." They moved downward only after the light was shut off. Thus it was during a period of absence of light that the
population encountered the cold water of the hypolimnion and stopped their vertical movement downward (Fig. 3). It is not possible to argue that a temperature dependent photoresponse is responsible for the cessation of the vertical movement in the population in the absence of light stimulation.

Sinking rates and distribution of passive organisms, such as planktonic algae or sedimenting particles, are influenced by thermally or chemically induced density changes with depth (Wetzel 1975). However, among larger and more powerfully swimming organisms, it is generally thought that the increased frictional forces caused by these density changes are not great enough to affect vertical distribution. For example, Bosch and Taylor (1973), working with the estuarine cladoceran Podon polyphemoides in Chesapeake Bay, observed that "the podonids were observed to migrate downward, despite the presence of a sharp halocline, which because of the thermal homogeniety of the water, also represented a pycnocline." Similarly, the experiments in this study indicate that density differences normally encountered in thermally stratified lakes did not affect the extent of vertical migration of D. magna (Fig. 5a).

The limitation of the extent of vertical migration by temperature has been observed in two species of motile phytoplankton, Cachonina niei and Amphiidinium carteri (Kamykowski and Zentana 1977). Maximum descent of each phytoplankton species corresponded to their lowest tolerable growing temperature.

In zooplankton, Kikuchi (1937) has demonstrated that an upward vertical migration of a hypolimnetic form of Daphnia stops when the
warmer water of the epilimnion is encountered. This behavior is apparently independent of illumination. It is evident that in this and in comparable cases of hypolimnetic species upward migration stops when a certain temperature is reached (Hutchinson 1967, p. 783).

Similarly, the existence of epilimnetic species implies that vertical migration out of the epilimnion into cold water does not take place. The abolition of the descending blue dance in colder waters is often suggested as the mechanism by which cessation in vertical migrations of epilimnetic forms occurs (Hutchinson 1967, p. 784). However, this mechanism can not explain the results in this study. The magnitude of vertical migration in these species may be reduced by an avoidance reaction to large but commonly observed differences in temperature encountered in temperate lakes during the summer.

An avoidance reaction to stress-inducing temperature changes in an organism is not unexpected. Our data can not demonstrate that a stress is exerted on the organism as it moves into the colder water. However, Bishop (1968), working with cladocerans restricted to the 5 to 12-m region (epilimnetic species?) of Cayuga Lake and with copepods having a large amplitude of migration (~30 m), found that respiratory rates of cladocerans placed in cold hypolimnetic water changed fourfold, whereas those of copepods placed in the epilimnion changed only twofold. This suggests that the cladocerans restricted to the warm epilimnion in Bishop's study are more affected (stress?) by temperature changes than are the copepods.

The range of temperatures an organism will tolerate, in particular the lowest temperature tolerated by D. magna, is dependent on its
recent thermal history. In figure 3c, acclimation was at 23°C for 24 hr; migration occurred between the 23°C and 12°C region but not into the 5°C water. In figure 3a, acclimation temperature was at 12°C for 24 hr; the organisms now moved readily throughout the 7°C temperature gradient into the 5°C hypolimnion. A shifting downward of the lowest temperature tolerated with cooler acclimation temperatures was evident.

The experiments in this study have indicated that D. magna's vertical migration is modified and inhibited by encounters with large temperature differences. The lower range of tolerable temperatures will also change with different acclimation temperatures of the organism. The avoidance of cold water in the experiments appears to be an acclimation effect. However, this movement into cold water might not have been expected considering that the optimum temperature of development for D. magna is 25°C (Brown 1929).

In the last experiment, an attempt was made to clarify whether the avoidance of large changes in temperature was an acclimation effect or was perhaps a genetically controlled "preference" for warmer waters. Organisms were acclimated for 4 months in 5°C water (Kibby 1971) and then placed in an upper cold layer (6.5°C) overlying a warmer (15°C) salty layer. In effect, the organism had a choice of cold or warm water. Even though the organisms were acclimated at 5°C and placed initially in the upper cold water layer, they still avoided the cold water by moving immediately into the lower warmer layer of water and staying there for as long as the cold layer existed (Fig. 6). Because the descending blue dance is eliminated
under 10°C (Smith and Baylor 1953), it can not be the cause of the downward movement. This preference for warmer water was strong enough to override the organisms' normal positive phototaxis to the incandescent bulb.

The behavior of *D. magna* suggests that a genetically controlled preference for warmer temperatures, closer to its optimum of development, exists in this species. By acclimation the organism can exist and will survive at a lower temperature but given the choice will move to warmer water. To clarify this point, in the last experiment (Fig. 6) the temperature in the epilimnion was increased 24 hr into the experiment from 6.5°C to 15°C (i.e., the epilimnion and metalimnion were equal in temperature at 15°C). Unlike before, *D. magna* moved immediately into the warmer epilimnion.

In Mirror Lake, New Hampshire, two cold stenothermic rotifers (*Conochilus dossuarius* and *Kellicottia bostoniensis*) are restricted in distribution to the cold hypolimnion during summer stratification (Fig. 8 and 10). With autumnal mixing and cooling of the epilimnion to isothermal conditions, these two species are distributed uniformly throughout the water column of Mirror Lake (Fig. 7 and 9). The rotifers in the hypolimnion and/or their descendents obviously move into the upper waters of Mirror Lake. This movement into the upper region of Mirror Lake is analogous to the movement into the upper region of the experimental column after isothermal conditions are established.

The avoidance of large temperature changes is suggested as one potential mechanism explaining temporal and vertical distributions of
at least stenothermic zooplankton. Certainly the experiments in this study do not completely invalidate Smith and Baylor's temperature dependent photoresponse as a mechanism of limiting vertical migration. Light has also been suggested as affecting vertical separation of *Diaphanosoma sarsi* and *Diaphanosoma modigliani* in Lake Toba (Ruttner in Hutchinson 1967). The experiments in this study do suggest, however, that another mechanism, temperature avoidance, can limit vertical migration in *D. magna*.

The biological mechanisms of predation and competition (Brooks and Dodson 1965, Hall *et al.* 1976, Snell 1979), in part, determine the structure of zooplankton communities. Temperature avoidance by zooplankton and ultimately the physical thermal structure of a lake offer another mechanism of structuring a zooplankton community within lake ecosystems and may account, in part, for the vertical patterns of niche response surfaces observed by Makarewicz and Likens (1975, 1978) in Mirror Lake, New Hampshire.
LITERATURE CITED


Wilson, J.B. 1980. The three dimensional response to light of crustacean zooplankton from the Laurentian Great Lakes. Abstr. 23rd Conf. on Great Lakes Res. Queens University, Kingston, Ontario.


Fig. 1. Diagram of experimental chamber.
Fig. 2. Vertical migration of _D. magna_ depicted as the depth of the average individual. Thermal conditions are equal in the experimental and control column (T = 24.5 ± 0.5°C). Error bars represent 95% confidence intervals.
Fig. 3. Vertical migration of *D. magna* under different thermal conditions. Values are plotted as the depth of the average individual. Mean 95% confidence interval for experimental (*x* ± 6.8 cm); mean 95% confidence interval for control (*x* ± 9.4 cm).
Fig. 4. Vertical migration of D. magna depicted as the depth of the average individual showing the effects of salts on swimming behavior. Water in the experimental column is saline while the control is filled with fresh water. Mean 95% confidence interval for experimental ($\bar{x} \pm 6.9$ cm); mean 95% confidence interval for control ($\bar{x} \pm 8.5$ cm).
Fig. 5. Vertical migration of D. magna with (A) an isothermal experimental column with a chemically induced density layer and (B) a thermally stratified experimental column with no density difference in the column due to addition of salt to the warm upper layer. Controls contain only fresh water. All values represent the depth of the average individual. Mean 95% confidence interval for experimental ($\bar{x} \pm 8.1$ cm); mean 95% confidence interval for control ($\bar{x} \pm 9.5$ cm).
Fig. 6. Vertical migration of cold acclimated D. magna. At point A, epilimnetic temperatures were raised to 15°C. Mean 95% confidence interval ($\bar{x} \pm 6.3$ cm).
Fig. 7. Seasonal distribution of Conochiloides dossuarius in Mirror Lake, New Hampshire.
Fig. 8. Vertical migration of Conochiloideas dossuarius depicted in quartile curves and the depth of the average individual.
Fig. 9. Seasonal distribution of Kellicottia bostoniensis in Mirror Lake, New Hampshire.
Fig. 10. Vertical migration of Kellicottia bostoniensis depicted in quartile curves and the depth of the average individual.
APPENDIX
Table 1. Intensity of light in each column for the salt experiment (Fig. 4) expressed in footcandles $\times 10^3$. 1-foot candle $= 6.5 \times 10^{-5} \text{ly/mm}$.

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Table 2. Suggested research.

1. Epilimnetic species of Cladocera should be studied in both laboratory and field. In the lake situation, the magnitude of vertical migration should be closely measured with temperature throughout the year. Laboratory experiments should be devised to determine preferred temperature ranges for each species. In addition, species seasonal distributions should be compared with changes in the thermal structure of the water column and with the species preferred range of temperatures.

2. The role of acclimation in cladocerans should be studied further. Individual species should be acclimated over an extended period of time and over a range of temperatures. Shifting of preferred temperature ranges with different acclimation temperatures is an extremely important factor in allowing species to survive changing environmental conditions.
Fig. 1. Extent of diffusion between top and bottom layers of equal temperature but different density. Bottom layer is saline containing methylene blue indicator.
Fig. 2. Extent of diffusion of a warm upper saline layer as measured by methylene blue indicator.