THE ROLE OF ZOOPLANKTON VERTICAL MIGRATION IN STRUCTURING THE PHYTOPLANKTON COMMUNITY

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ABSTRACT

Development of a model to predict the effectiveness of zooplankton grazing on phytoplankton requires knowledge of the factors which regulate the depth distribution of both communities. In this study, model lake systems (columns) were evaluated for their usefulness in the study of depth control of zooplankton populations. Simple linear regression and multiple regression analyses were employed to develop predictive models based on these studies under controlled laboratory conditions and in the field. Zooplankton depth regulation was further tested under continuous light in arctic lakes and ponds as well as in experimental columns.

The influence of light and food concentration was examined with the experimental columns under controlled conditions. Food concentration strongly regulates the day-depth distribution of Daphnia populations. At high food densities the population mean depth approaches the surface waters and at low food levels the population is found in the deep water. This relationship was described by a linear regression equation. Vertical movements resulting from food changes were almost immediate, although differences were found between long-term and short-term responses. The relationship between temperature changes and population mean depth was also defined. Absolute light intensity was not an important regulator of day-depth and vertical migration in temperate or arctic zooplankton. However, the rate of evening migration in temperate zooplankton and the daytime displacement velocity of arctic zooplankton populations was closely correlated with the relative light change. Implications of these results to models of depth control and grazing by zooplankton are discussed.

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INTRODUCTION

The deterioration of water quality resulting from massive algal growths presents a difficult problem in lake management. Long-term reduction in algal growth can be expected when the load of limiting nutrients entering a lake is reduced (Edmondson, 1970; Schindler, 1974). However, such management programs are generally costly and for many lakes impractical. Other means of controlling unwanted algal blooms through the use of copper sulfate and lake destratification are often unsuccessful or may create other ecological "side effects" such as fish kills (Sawyer, et al., 1968).

The high rate at which zooplankton can remove lake phytoplankton was demonstrated by Haney (1973), where in a small eutrophic lake the zooplankton community grazing exceeded 100% per day, i.e. the entire lake volume was filtered free of small algae each day. Other studies have also found evidence that zooplankton can reduce populations of certain species of phytoplankton (Goldman, et al., 1968; Porter, 1973).

Recently Lampert and Schober (1978) demonstrated the importance of zooplankton grazing as a mechanism capable of regulating both the timing and size of algal blooms in nature. Several management programs based on the enhancement of zooplankton grazers as biological controls have been proposed by Shapiro (1978).

Models to predict the impact of zooplankton grazing generally assume grazing to be constant throughout the lake and largely ignore the spatial heterogeneity of both phytoplankton and zooplankton communities (Patten, 1968). It has been widely observed in both freshwater and marine systems that zooplankton make daily excursions into the upper water at night and back down into the deeper strata during the morning. Such vertical migrations result in regular temporal and spatial changes in the grazers. Thus, before a realistic model of zooplankton grazing can be developed, it is important to understand the major factors which regulate the depth distribution of phytoplankton and zooplankton.

The depth distribution of phytoplankton is normally limited by light to the upper euphotic zone and is relatively stable throughout the day. In contrast, diel patterns of movement must be considered when describing zooplankton distribution. Diel vertical migration can be viewed as consisting of two phases: 1) the transient phase or rapid vertical movement at dawn and dusk, and 2) the stationary phase or relatively stable phase which occurs both during the day and night.

To date, the twilight transient phase has been most thoroughly studied and evidence suggests the relative rate of change in light is the dominant controlling factor (Ringelberg, 1964; Ringelberg, et al., 1967). Similarly, changes in light appear to act as the trigger regulating the timing of diel changes in the rate of feeding by migrating zooplankton (Haney and Hall, 1975).

Little is known about the factors which control the depth distribution in the stationary phase. Least difficult is the prediction of the night time stationary phase, since most studies indicate that migratory zooplankton generally move into the uppermost strata at night and remain there until daybreak. The depth of populations during the daytime stationary phase is not easily predicted and has received little study. Field studies such as those of McNaught (1966) and Kikuchi (1938) of factors controlling depth distribution of planktonic crustaceans were inconclusive because of the variability of uncontrolled factors. In the laboratory, studies can be carried out under controlled conditions to more clearly elucidate the environmental and physiological factors which regulate the daytime stationary phase (e.g. Itoh, 1970; Kikuchi, 1938). However, the results of these studies are not easily verified in nature due to the continually changing light conditions. For example, rapidly increasing light which initiates the dawn transient phase may move the population into a zone above or below the day depth, since a period of equilibrium to daytime conditions is necessary before the day-depth will be achieved. Similarly, sub-threshold light stimuli in the late afternoon may interfere with day-depth control. Thus, such oscillating

light conditions may cause continuous shifts between the transient and stationary phases and an overlap of control factors of the two phases. Ideally suited for in situ tests of day-depth control of zooplankton vertical distribution are the light conditions of the arctic summer, when the sun is always above the horizon and daily oscillations in light are negligible.

The objectives of this study include first an evaluation of the use of model lake systems (columns) in the laboratory to study diel vertical migration. The role of light as a control factor and the extent of diel vertical movements of laboratory populations were compared to the results of field studies. Secondly, the influence of light, food concentration and temperature on day-depth of zooplankton was examined with the experimental columns in the laboratory and in the field. These relationships with light and temperature were further tested in lakes and ponds in the Arctic. Implications of the results of these investigations to other studies and to models of depth control and grazing are discussed.

LABORATORY METHODS

Description of the Migration Room

Column studies in the laboratory were conducted in a controlled light and temperature room (DVM Room) with either artificial overhead fluorescent lighting or natural lighting from a west-facing window (Fig. 1). Five clear plexiglas (Lexan) columns (10 x 10 x 230 cm) were placed at the end of the room opposite the window and behind a 200 cm high dark curtain, to allow light to enter the columns from overhead, thus approximating the light transmission characteristics of a lake. Light measurements were made with an International Light Radiometer (IL-700, SEA-400 vacuum photodiode) and continuously recorded on a Hewlitt Packard stripchart recorder. During experiments the photocell was positioned at 160 cm depth outside the column.

Overhead fluorescent lights were used in the experiments with constant light conditions. To provide uniform and diffuse light to all columns in the constant-light studies, columns were arranged under a circular opaque-white plastic dome (4-ft. diam.).

Visual observations of the number of animals present were made in each 10 cm depth interval in the column. To facilitate the rapid counting of animals, observations were recorded with a portable cassette tape recorder and later played back to register data on data sheets. After some practice a total "scan" of a column could be made in less than one minute. Counts were made after dark using a hand-held fluorescent lamp equipped with a dark red filter to minimize disturbance to the animals.

Water used in the DVM Room columns was taken from Roselawn Pond, a small farm pond near Durham, New Hampshire. This pond was chosen because of its relatively unstained water and zooplankton dominated by *Daphnia*. Water for each set of experiments was transported to the laboratory in plastic carboys and filtered through a 50 μm net before use in the columns.

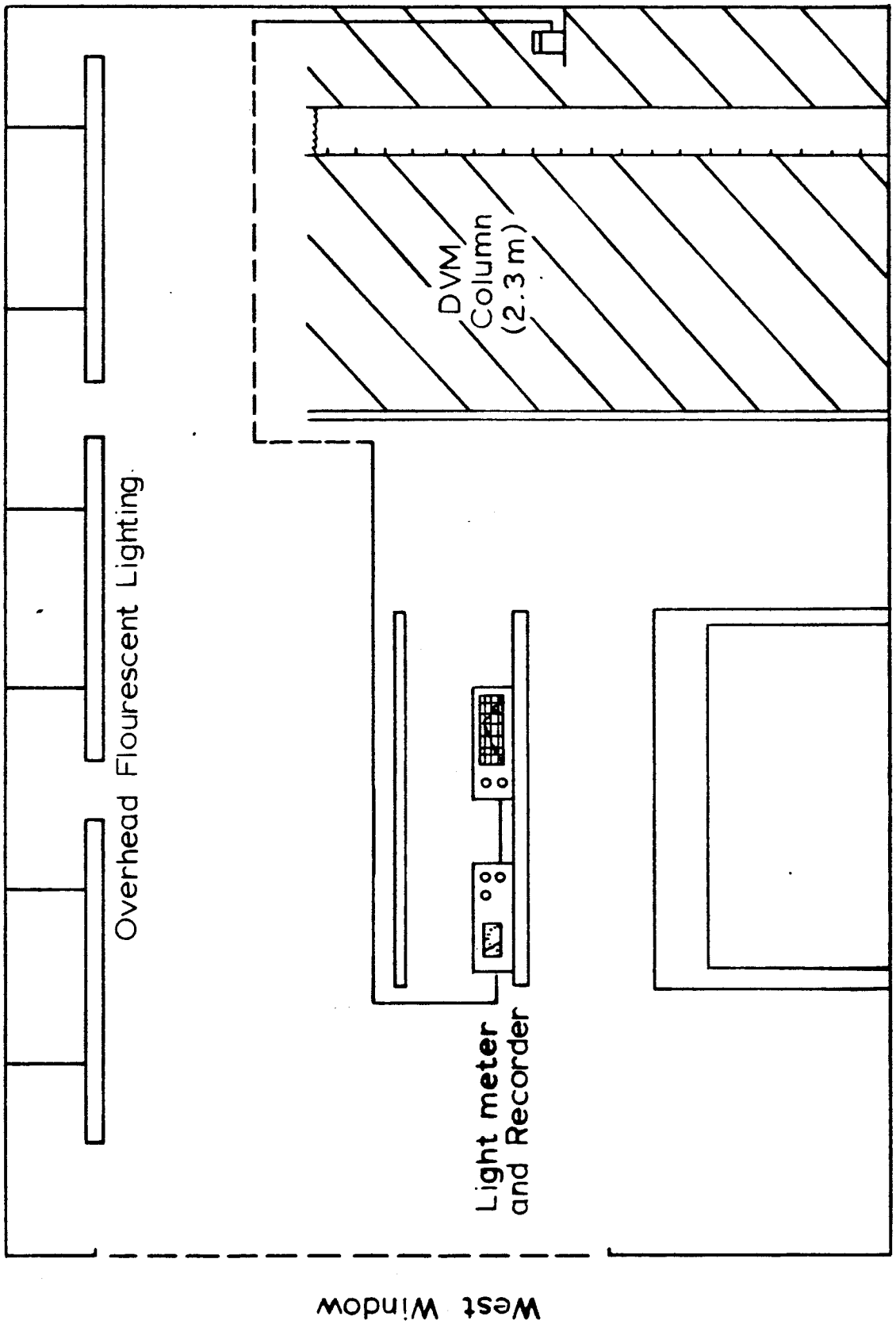

Figure 1. DVM Room illustration arrangement of columns and lighting.

About 50 Daphnia of similar size and reproductive condition were used in each column. Animals were allowed 12-24 hours acclimation before the experiment. Daphnia were grown in cultures in the DVM Room under the same light and temperatures as those used in the experiments.

Measurement of Food

Food used to maintain Daphnia cultures and to adjust food levels in the columns was taken from rapidly growing goldfish-algal cultures dominated by Scenedesmus. These cells (5-10 μm) were usually present as single cells or 2-cell colonies. Also present were unidentified unicellular green algae (2-5 μm) and bacteria.

Food concentration was determined by two different methods. Dry weights were determined by passing water collected from the columns through a 50 μm Nitex mesh and then through a preweighted 0.45 μm Millipore filter. Filters and particulate matter were then oven-dried at 103°C for one hour and reweighed on a Cahn Microbalance. Regular monitoring of food levels was conducted with a Coulter Electronic Particle Counter. Samples for the particle counts were taken at four depths in each of the columns (55, 115, 180, and 225 cm). Triplicate counts were made on each sample. Using open window settings on the counter, particles ranging in size from 1-2 μm to 50 μm were counted. Coincidence corrections were made for counts at high cell densities. Comparison of food concentration at the four depths provided a check on the homogeneity of food within the columns. Food density for each column was calculated as the average of these depths. Coulter counts of the goldfish tank algal culture were approximately 30% higher than counts made with a haemocytometer in which all visible algal cells were included. This is probably due to the inclusion of non-algal particulate in the Coulter counts, such as detritus and bacteria. To permit estimates of dry weights from cell concentrations, the relationship between these two variables was determined for a series of dilutions of the stock

algal culture. Algal densities were then estimated from the derived linear regression (r=0.999).

Passive bubbler systems were installed in the columns for the constant daylight study to prevent sinking and stratification of food, since the experiments were continued for 10 days. The bubbler system was designed to create very gentle currents which would circulate food particles, but which would not influence the distribution of Daphnia. In this system air was pumped into the bottom of an open glass tube (2.5 m long, 3 cm diam.) positioned vertically in one corner inside the column. The rising air bubbles force a small quantity of water to the top of the tube and into the surface water in the column. Food added to the column was evenly distributed within 0.5-1 h. However, water currents generated by the bubbler had no measureable effect on the depth distribution of the animals (Fig. 2).

General Experimental Approach of Food Regulation Studies

Three sets of experiments were used to examine the effect of light and food on day-depth in the columns. First, a series (5-7 May) was run with natural light changes and variable low food concentrations (91-2,500 cells ml^{-1}). In this series day-depths were chosen from 1030 to 1600 h during which time the least vertical changes in the population distribution was seen. Food concentration was determined every 3-5 hours during the experiment. All columns were isothermal with temperatures ranging from 14.5-18.0 °C. Dissolved oxygen concentrations were determined at the termination of the experiment using a dissolved oxygen probe (Yellow Springs Instruments Co.). Oxygen in columns B-E was above 50% saturation at all depths with no vertical gradient (Table 1). In column A, values near 100% saturation were recorded near the bottom.

Secondly, the effects of varying food concentration under constant light conditions were examined by artificially maintaining constant daytime light intensity with overhead fluorescent lighting. The arrangement of the columns for these experiments is shown in Fig. 1.

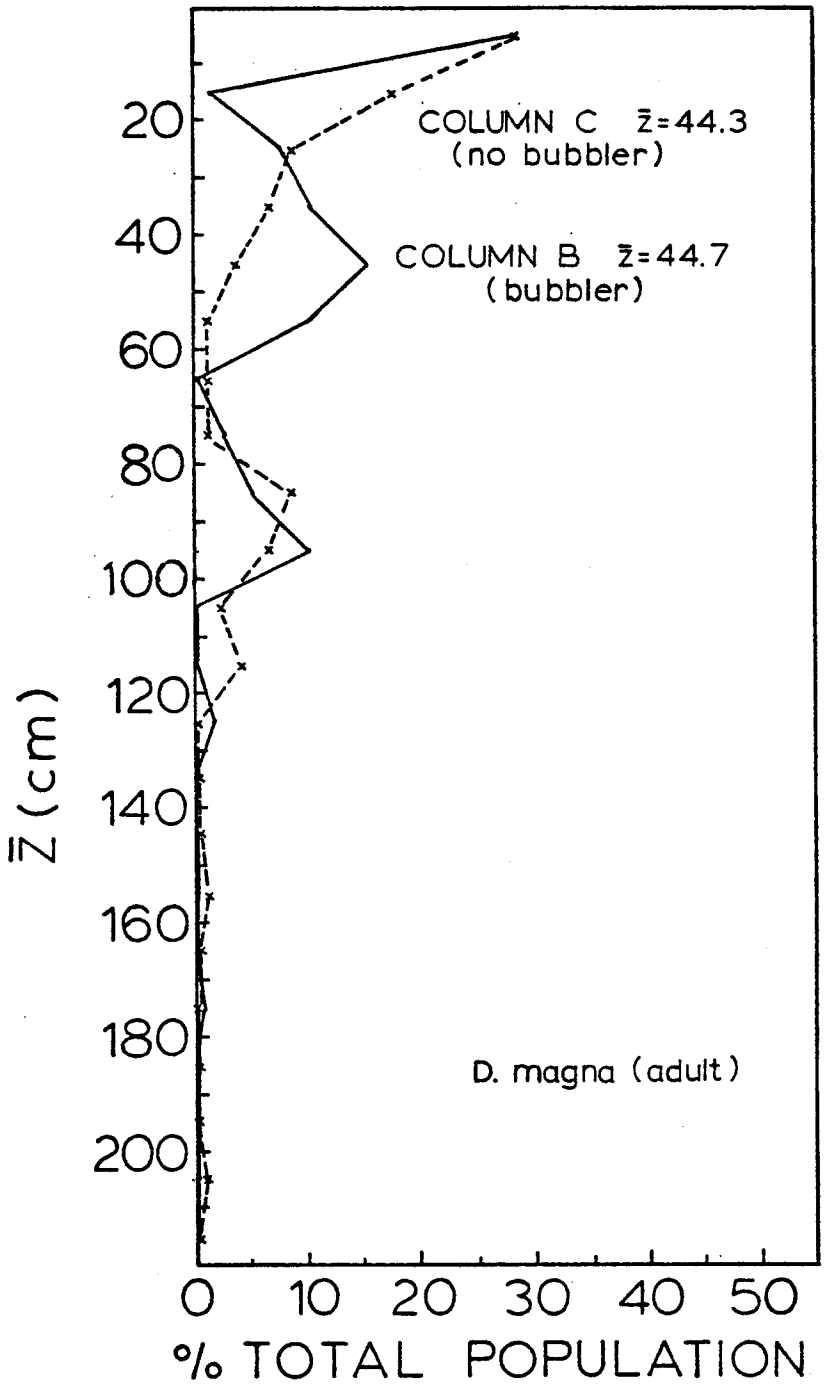

Figure 2. Comparison of the vertical distribution of adult Daphnia magna in columns with and without the water circulating system. Animals were introduced into columns 15-XII-76 at 1600 h and observations were made at 1040 h, 16-XII-76.

Table 1

Concentration of dissolved oxygen in Columns A-E on 8 May 1976 (1640 h). All columns were isothermal at 18°C.

Depth (cm)	Dissolved Oxygen (mg ℓ^{-1})				
	Column				
	A	B	C	D	E
10	6.4	5.2	5.1	6.5	6.5
50	-	5.5	4.9	6.1	6.0
100	8.5	6.3	6.0	6.8	6.9
150	-	6.7	6.2	7.2	6.6
200	9.2	6.9	6.1	6.8	6.4
230	9.3	6.7	6.0	6.7	6.1

To permit animals to undergo normal patterns of DVM, overhead lights were turned on at 0900 h and turned off at 1500 h each day. In this way all columns were exposed to the natural light changes from 1500-0900 h. Artificial light levels entering the columns through the plastic diffuser dome suspended above the columns (Fig. 3) ranged from 1.0×10^{-4} to 1.5×10^{-4} w cm^{-2}, which was about ten times the ambient natural light intensity in the DVM Room during this "noon" period. Day-depths were calculated as the average of 3-5 mean depths ($\bar{Z}$) determined at 1-h intervals between 1030-1530 h. Each day samples were taken with a syringe from each column at 35 cm and 220 cm depths for Coulter counts of food concentration. Food concentrations for the entire column were calculated as averages of the two samples. Following the final count of Daphnia for the day, additions of concentrated food were made to each column to adjust for losses of the previous 24 h due to grazing and sedimentation.

A third set of experiments were conducted to determine the short-term effects of fluctuating food concentration on the mean depth of the population. In this series concentrated food was injected into a population of Daphnia and the response of the distribution statistics ($\bar{Z}$ and quartiles) were observed at frequent intervals during the first hour.

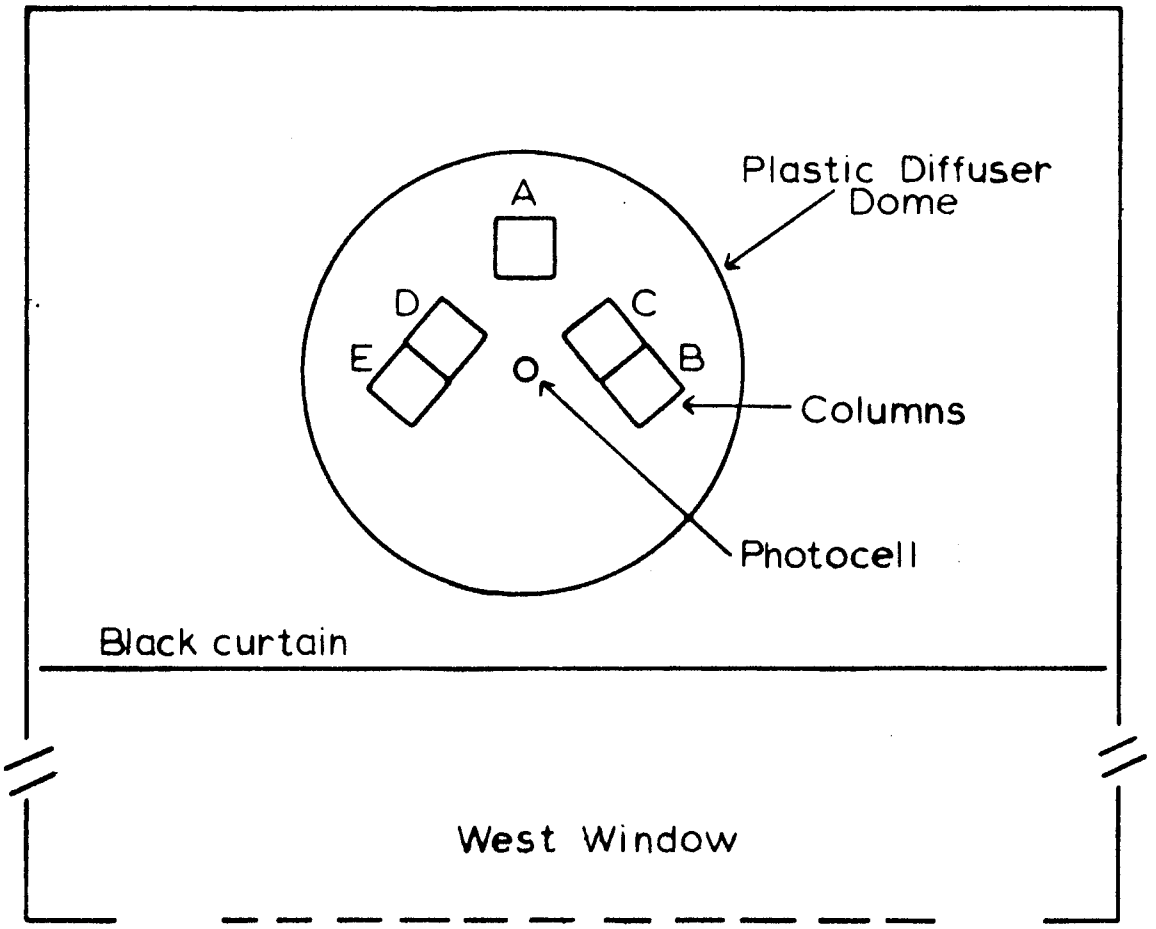

Figure 3. Arrangement of DVM Room columns and plastic diffuser for the constant daylight experiments.

FIELD METHODS

Description of Column Studies in the Arctic

The field study experimental apparatus consisted of plexiglas columns of various sizes (10 x 10 x 120 cm, 15 x 15 x 120 cm) filled with water and placed centrally in a blackened chamber constructed out of black plastic with a hole ∿ 100 cm diameter in the ceiling to allow incident lighting from above (Fig. 4). The purpose of arranging the experimental chamber and columns in this manner was to create a vertical gradient of mostly diffuse light and imitate the light environment of a pond or lake. An outer light-tight chamber surrounded the experimental chamber, and the investigator could look through slits in the walls of the experimental chamber and observe the plexiglas columns without disturbing the zooplankton.

Before each experiment, the plexiglas columns were filled with filtered (151 μm) water from a nearby lake or pond. Water was collected from Toolik Lake at Toolik and from a low center, polygon thaw pond at Barrow. The extinction coefficients of the water varied between locations and with season, however, water in the columns has little chance to alter the quality or intensity of incident light because a large portion of the light in the experimental chamber is diffuse light.

Zooplankton populations of up to 100 individuals of approximately the same size were placed in each column and allowed to acclimate to the light environment for at least 24 h. Zooplankton were usually collected from local ponds and lakes and immediately sorted and placed in the columns after their ambient water temperature equilibrated with the column temperature. It was assumed that the zooplankton rapidly acclimate to the new food concentrations (Geller 1975, Rigler 1961) and light conditions (Clarke 1930, Heberdey 1949, Ringelberg 1969, Viaud 1938) of the columns.

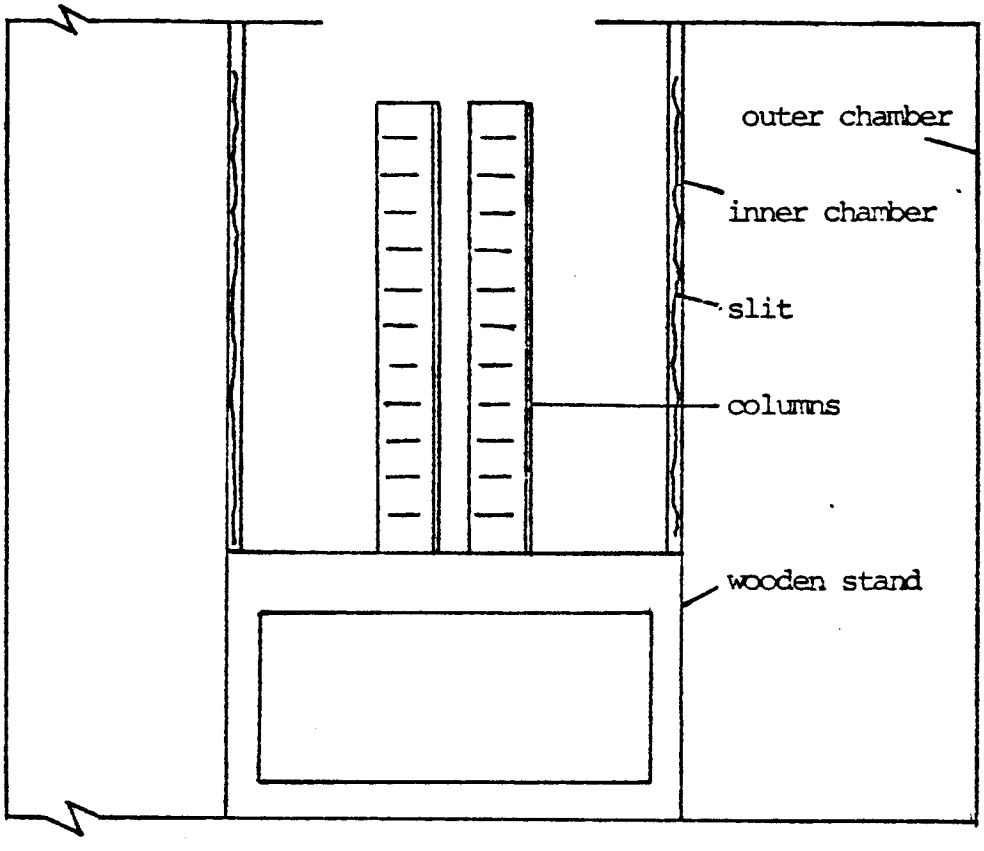

Figure 4. Experimental columns used in the arctic field studies.

After each series of observations, the temperature profile was measured and a 2 ml aliquot of an algal culture (approximately 2×10^6 cells) was usually added to each column at this time, depending on the feeding schedule of the experimental animals.

Lake and Pond Studies in the Arctic

Field lake studies were done about 200 miles north of the Arctic circle in a circular, bay-like sub-basin of the Toolik Lake lake basin. The sub-basin is cut off from the rest of Toolik Lake by a gravel bar, 1.5 meters below the water surface, blocking the bay entrance. The area of the sub-basin is $\sim$4 hectares and has a maximum depth of 31 meters. The sub-basin is bordered by low, tundra-covered foothills to the north, west, and south, and by Toolik Lake to the northeast. Samples were taken from one station (depth 20 meters) near the center of the sub-basin.

Zooplankton d.v.m. samples were collected with a modified plankton closing net (153 μ) consisting of a circular cloth collar approximately 40 cm long extending from the metal hoop (30 cm diameter) at the mouth of a standard plankton net to a second metal hoop attached to the net bridle apparatus. Except for the first series of samples on June 20th, all samples were collected as follows. The closing net was lowered rapidly, bucket-end first, to the lower depth of the depth interval being sampled, and then towed vertically upward until it reached the upper depth of the depth interval being sampled. Then, a brass messenger, sent down as the net was towed upward, released the collar which fell down across the mouth of the plankton net and effectively stopped the net from collecting more plankton as it was towed the rest of the way to the surface. Two samples were collected in each depth interval and combined. In the first series, on June 21st, the samples were collected by towing the closing net obliquely through the depth interval being sampled, then closing the net after it had been towed a given distance. Only one sample was taken from each depth interval. All the samples were preserved in 4% formalin - 5% sucrose solution.

Numbers of Heterocope septentrionalis, Daphnia longiremus, D. middendorffiana, Bosmina coregoni, and Holopedium gibberum in each sample were counted directly. The samples were then diluted to 30 mls and the Cyclops scutifer and Diaptomus tyrelli in three 1 ml subsamples from each diluted sample were counted and these totals averaged. All stages of D. longiremus, D. middendorffiana, Bosmina, and Holopedium were counted; only the copepidite and adult stages of Heterocope, Diaptomus and Cyclops were counted.

Pond studies were carried out in shallow polygon pools on the coastal tundra near Barrow, Alaska. Details of Toolik Lake and of the polygon ponds are described elsewhere (Buchanan 1978).

Miniature tow-net samplers were constructed, mounted on a calibrated stick, and used to sample zooplankton populations in shallow ponds. Each miniature sampler was lowered to the desired depth, towed for a given distance at a constant speed ($\sim$.5m/sec) and raised. Care was taken that no animals were collected while the sampler was raised or lowered. Animals were counted immediately and then released. (Adult daphnids were distinguished from juveniles by the presence of a brood pouch.) A small hand net (area 104 cm^2, $\sim$500 µm netting) was used to sample the sparse populations of Pond S. A series of plastic cylinders, each 5 cm long with 330 µm netting on one end (3.14 cm^2 area), were mounted at 5 cm intervals on the calibrated stick and used to sample the dense populations in Pond W. In Pond Y, the sampler used was a rectangular plexiglas frame (area 2 x 30 cm, and 5 cm deep), backed on one side with 330 µm netting and on the other with a plexiglas cover that could be remotely opened or closed when the sampler was underwater. The frame was divided into four sections, each 2 x 5 cm, with plexiglas cross-pieces so that incoming animals were separated into 5 cm depth intervals.

Light Measurements

Continuous recordings were made of whole light using an International Light Radiometer (model IL 700) and a Hewlett-Packard strip-chart recorder. The detector of the radiometer was a vacuum photodiode (IL model SEA-400) with a spectral range of 240 to 750 nm. The probe which houses the photodiode has a dome-shaped, quartz, glass diffuser located above the diode and the probe's detection characteristics approximate the transmittance properties of a water surface, i.e. it does not detect much light at angles of incidence larger than 80° and the relationship between angle of incidence and response is close to the lambertine, or cosine, response curve. The sensor housed in the probe was maximally sensitive at 400 nm and had a fairly flat response curve over the visible light range. Chart recordings of continuous light measurements were analyzed in the following manner: for light curves with few or no fluctuations (e.g. clear sky, heavily overcast sky with stratus clouds), absolute light intensities were read off the graph at 10 minute intervals. For rapidly fluctuating light curves (e.g. broken cumulus in a clear sky), absolute light intensities were read at every "peak" or "valley" in the curve, at intervals of one minute or more. Measurements of the light intensity at four wavelengths were made frequently during some of the experiments in order to characterize diel changes in the quality (color) of incident light. Narrow band filters were used with transmittance peaks at 365 nm (near UV), 428 nm (violet-blue), 500 nm (bluegreen), and 569 nm (yellow). The 365 nm, 428 nm, and 569 nm filters corresponded to the three absorbance peaks of the photopigments in daphnids (McNaught 1971).

Calculation of Stimulus Values and Mean Depth

Light stimulus or relative change in light was calculated after Ringelberg (1964) as: $S = \frac{\ln I_t - \ln I_o}{dt \text{ (sec)}}$, where I_o is the

initial light intensity and I_t is the light intensity at time t. Positive values indicate light intensities which are increasing and negative values decreasing light. Mean depth or effective mean depth (Haney and Hall 1975) is a weighted measure of the average depth distribution of a population and has the advantage of expressing the vertical distribution changes as single statistics rather than as a distribution. It was calculated as:

$\bar{Z} = \frac{\Sigma N_i d_i}{\text{Total N}}$, where N is the number of animals recorded at depth i and d is the depth of the observation. Quartiles were calculated according to Pennak (1943).

Statistical Methods

To describe mathematically the relationship between independent variables such as light, temperature and food density and dependent variables such as mean depth of the population or displacement velocity, simple linear regression and multiple regression analyses were applied to the data. Correlations and regressions were generally considered significant at the 95% probability level. Significance of regressions was determined for the field columns and *in situ* studies data by the correlation coefficients of the regressions and for the DVM Room data by comparing the F-values from analysis of variance tests run on the regressions.

For each set of data, attempts were made to fit all combinations of untransformed and $\log_{10}$-transformed X and Y variables. Since regression analyses require constant variance of the dependent variable, the residuals from each regression were examined in scatter plots for homoscedasticity. The best regression model for the data set was chosen on the basis of the correlation coefficients and/or the F-value from the anovas run on the regression. Also, the influence of transformations of the data on the homoscedasticity was always considered. The general approach of regression analysis used in this study follows Zar (1974).

RESULTS AND DISCUSSION

Laboratory Studies: Regulation of Day-Depth by Light and Food

Light Conditions in the Columns

Several aspects of the light conditions in the Migration Room in the columns were examined to test the similarity of the experimental light conditions with those in a natural lake. First concern was with the quality of the light in the columns and in the field. Color series were run with narrow band filters in the columns and within a few minutes again outside. The series was run at noon and at sunset to provide the greatest range of light quality changes. Percentages of yellow and blue light in the field and in the columns is remarkably similar at noon (Fig. 5). At sunset, however, yellow becomes the dominant color in the columns, whereas blue predominates in the field, probably due to the lack of skylight in the DVM Room. Also contrasting in the two systems is the importance of ultraviolet light. At both noon and sunset UV light is much reduced in the columns, which is quite likely a result of the filtering effect of the windows and the Lexan plastic columns. Light penetration in each of the experimental columns was also examined at each of the wavelengths (Figs. 6-10). The light quality in the five columns was very close. In all columns the greatest light penetration was in the yellow range and the least in the UV. All wavelengths showed an exponential decrease with depth, as might be expected to occur in a lake lacking vertical stratification of light absorbing matter.

The absolute vertical light gradient in the columns was compared to that of two lake systems in order to equate the two light environments. Fig. 11 illustrates the similarity of the columns to the lake. The pattern of whole light penetration in the columns follows very closely that of the natural systems. The range of light intensities experienced by an animal migrating 200 cm in the column is roughly equivalent to a vertical excursion of 4 m in the lake.

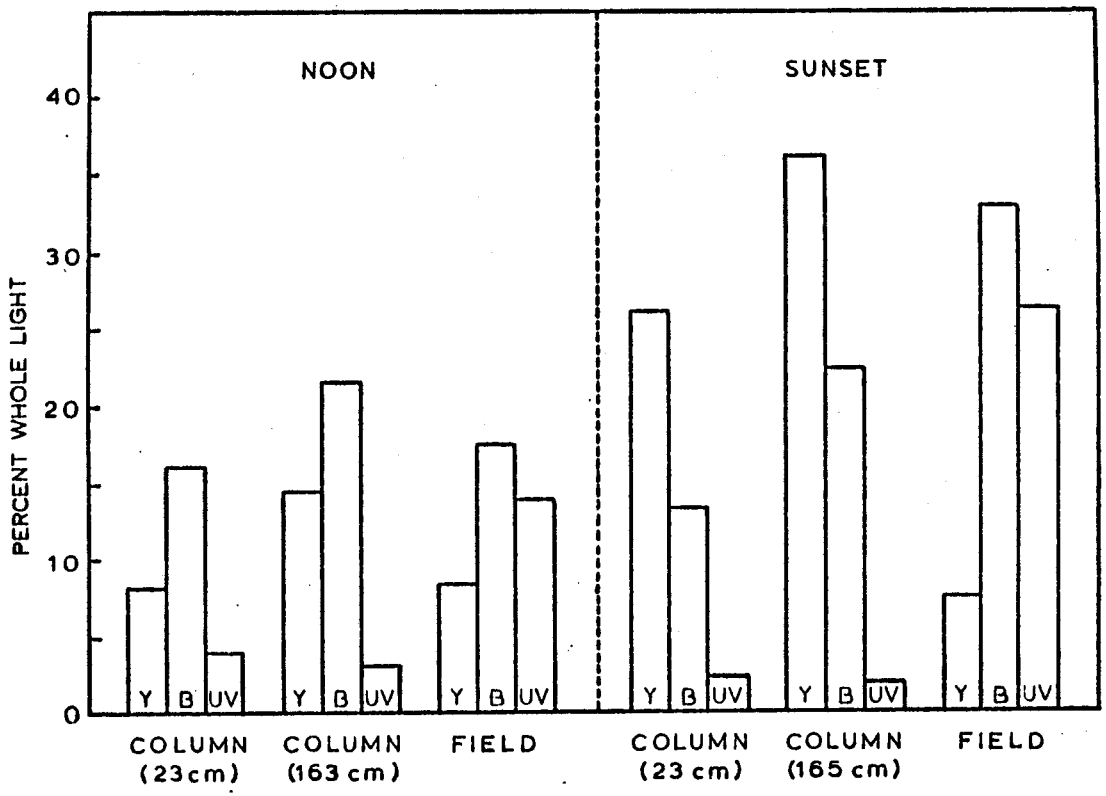

Figure 5. Spectral distribution of light in the DVM Room and outside under natural light expressed as the percentage of light measured without a filter (whole light). Peak transmittance of narrow band filters: ultraviolet (365 nm), blue (428 nm) and yellow (569 nm). Measurements taken within a 15-min. period at noon (1245-1300 h) and sunset (1814-1833 h) on 12 April, 1976.

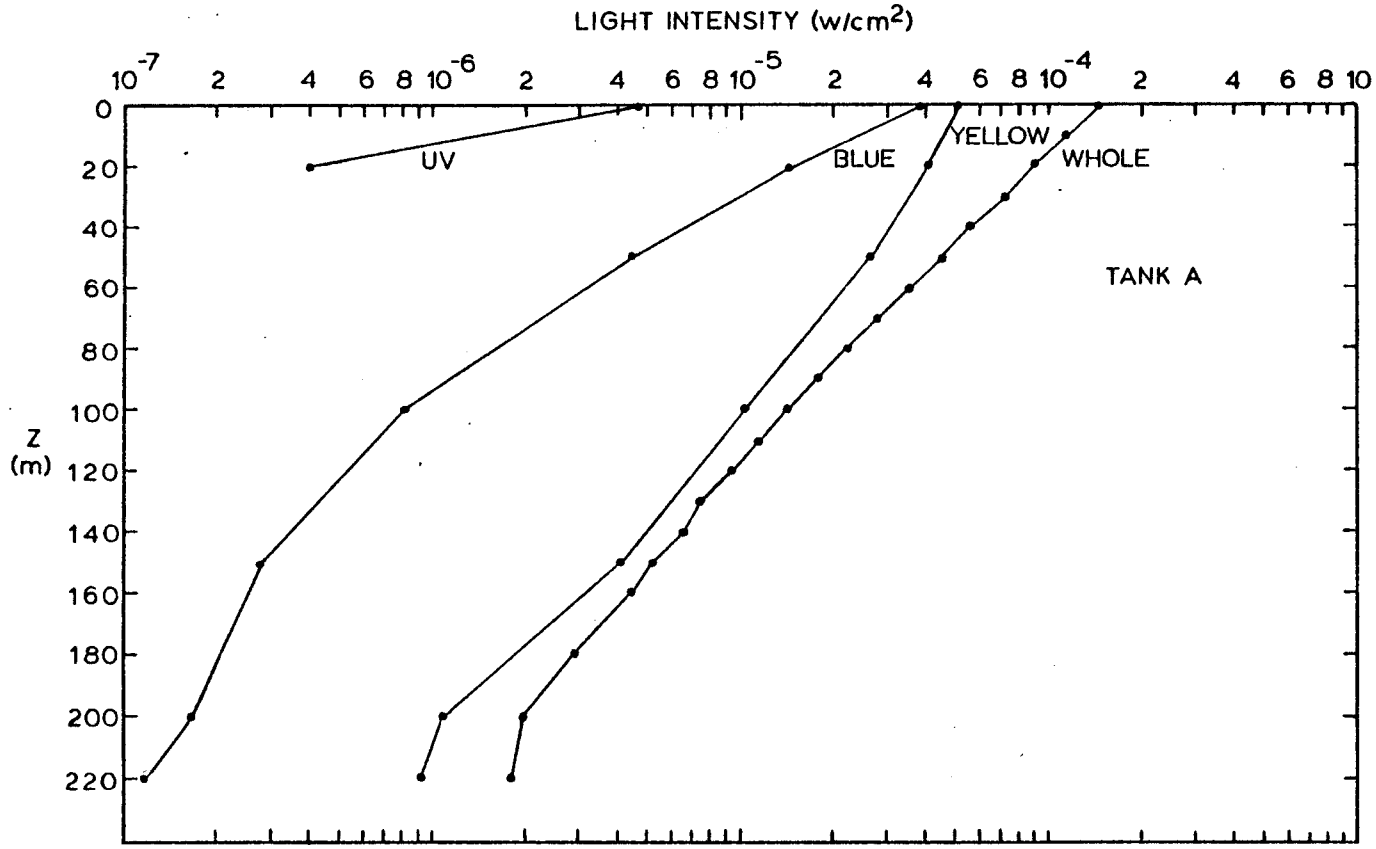

Figure 6. Light transmission of various wavelengths in the DVM Room column A. Measurements taken with natural light from west window at 1300 - 1400 h. Peak transmittance of filters: whole light, i.e. no filter, only glass diffuser (400 nm), ultraviolet (365 nm), blue (428 nm) and yellow (569 nm).

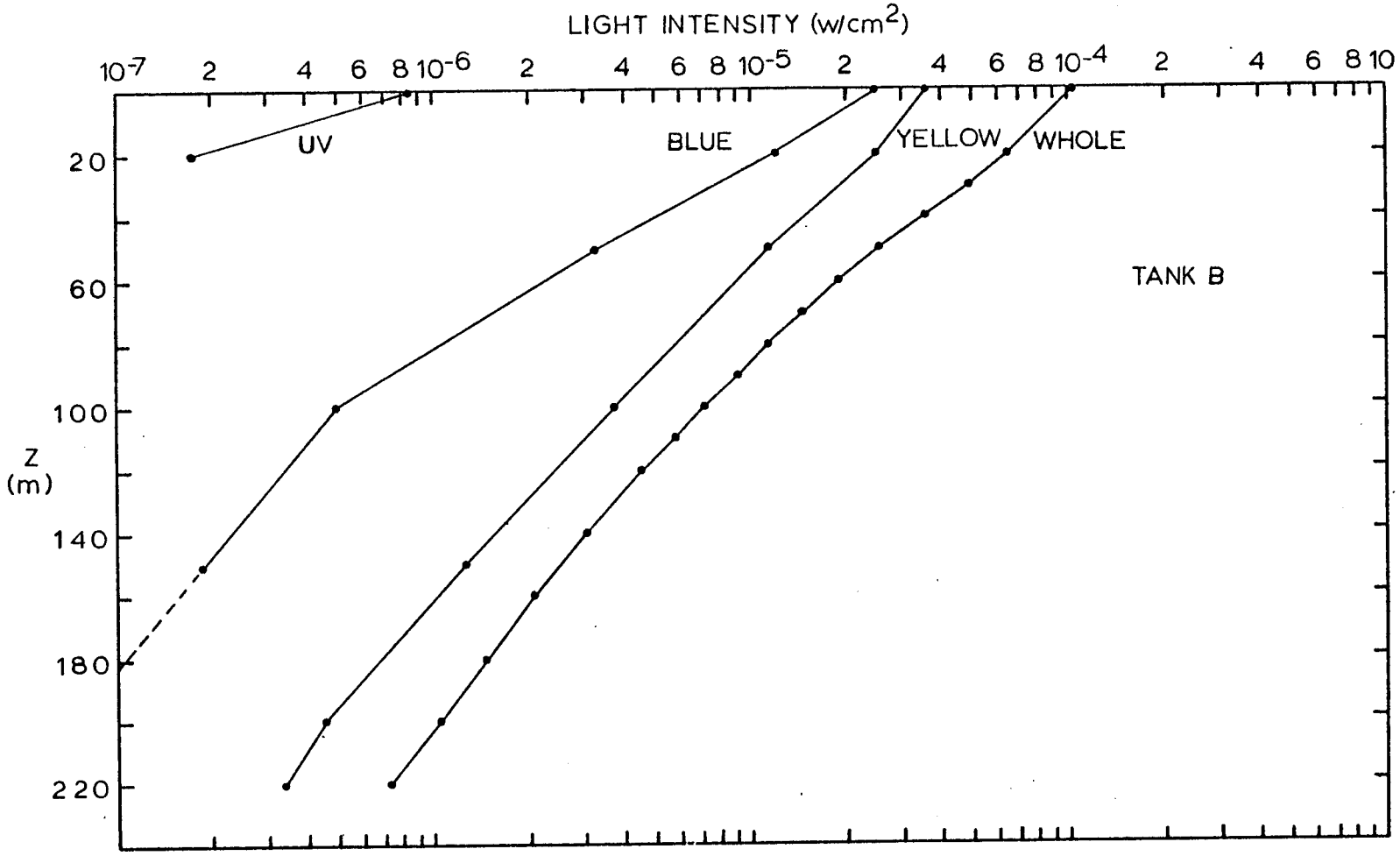

Figure 7. Light transmission of various wavelengths in DVM Room, Column B. See Fig. 6 for additional details.

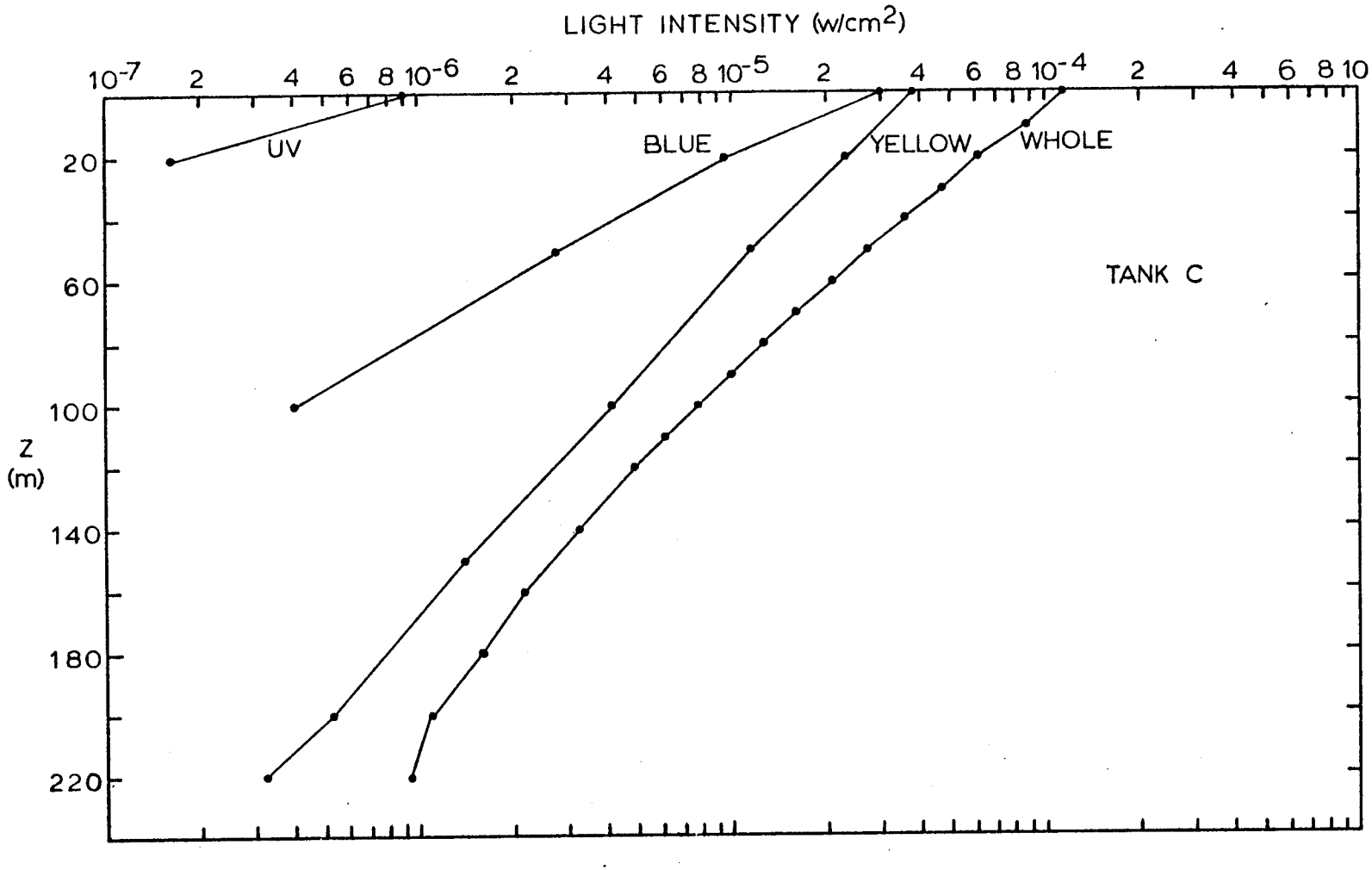

Figure 8. Light transmission of various wavelengths in DVM Room, Column C. See Fig. 6 for additional details.

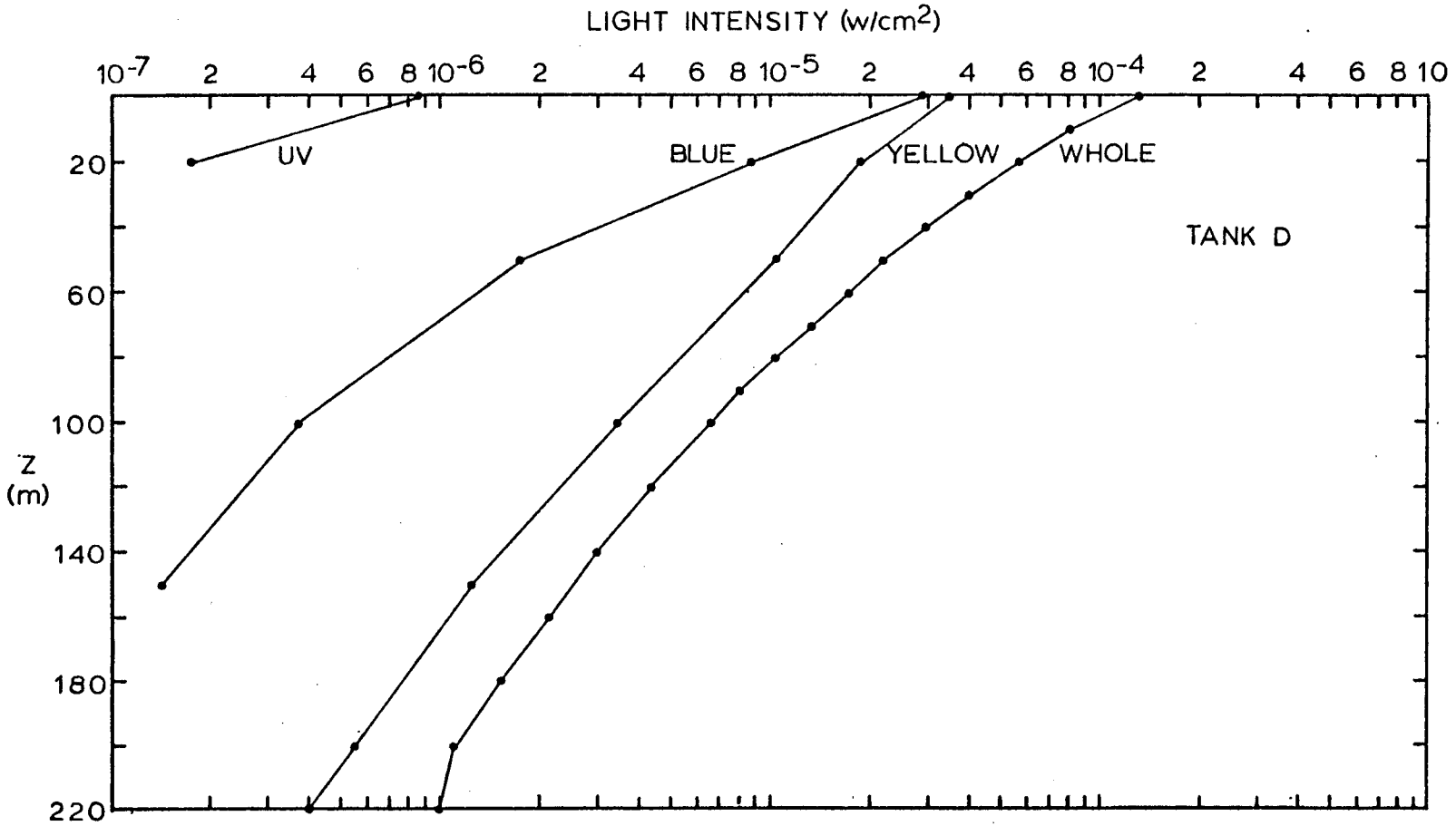

Figure 9. Light transmission of various wavelengths in DVM Room, Column D. See Fig. 6 for additional details.

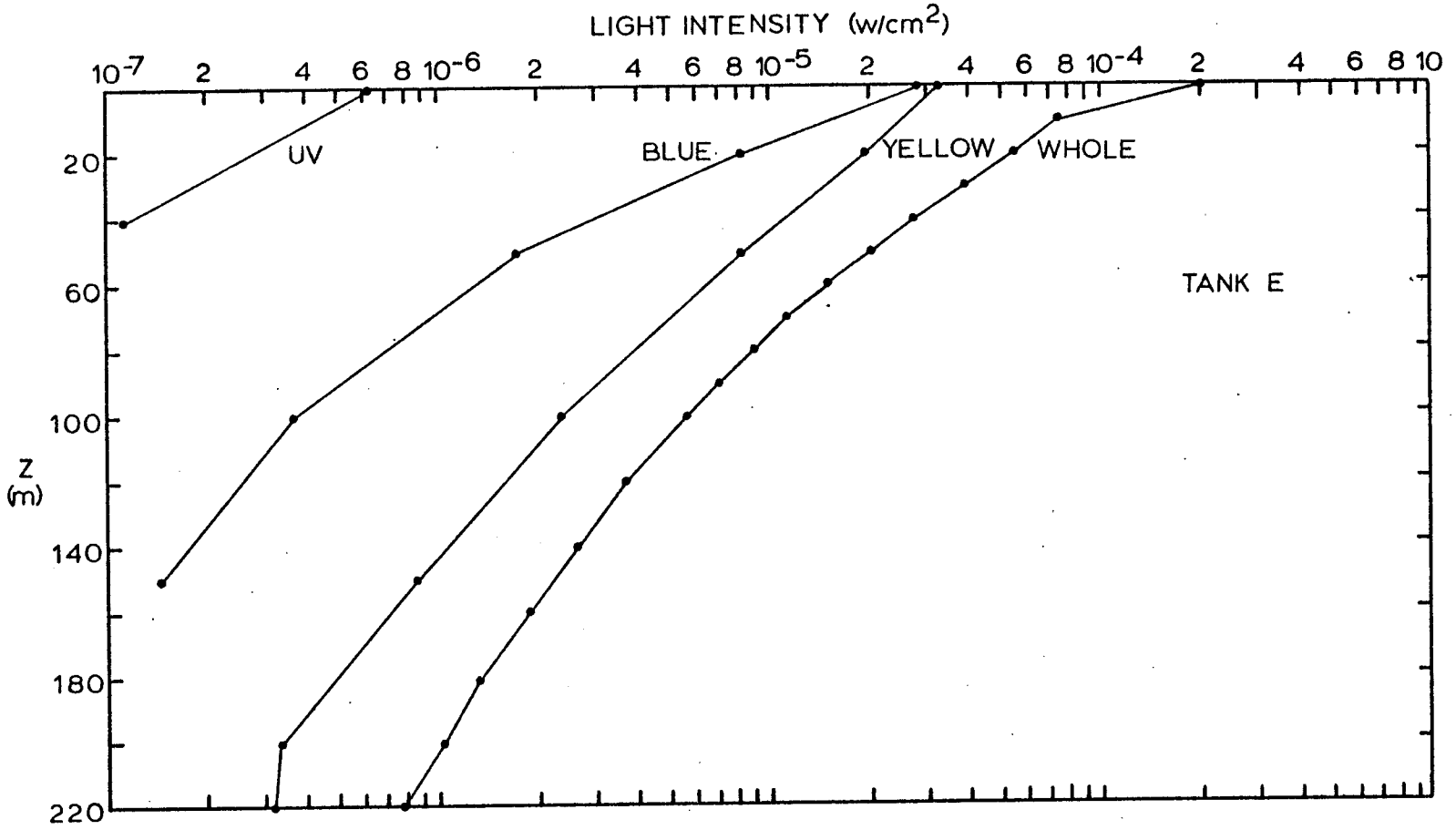

Figure 10. Light transmission of various wavelengths in DVM Room, Column E. See Fig. 6 for additional details.

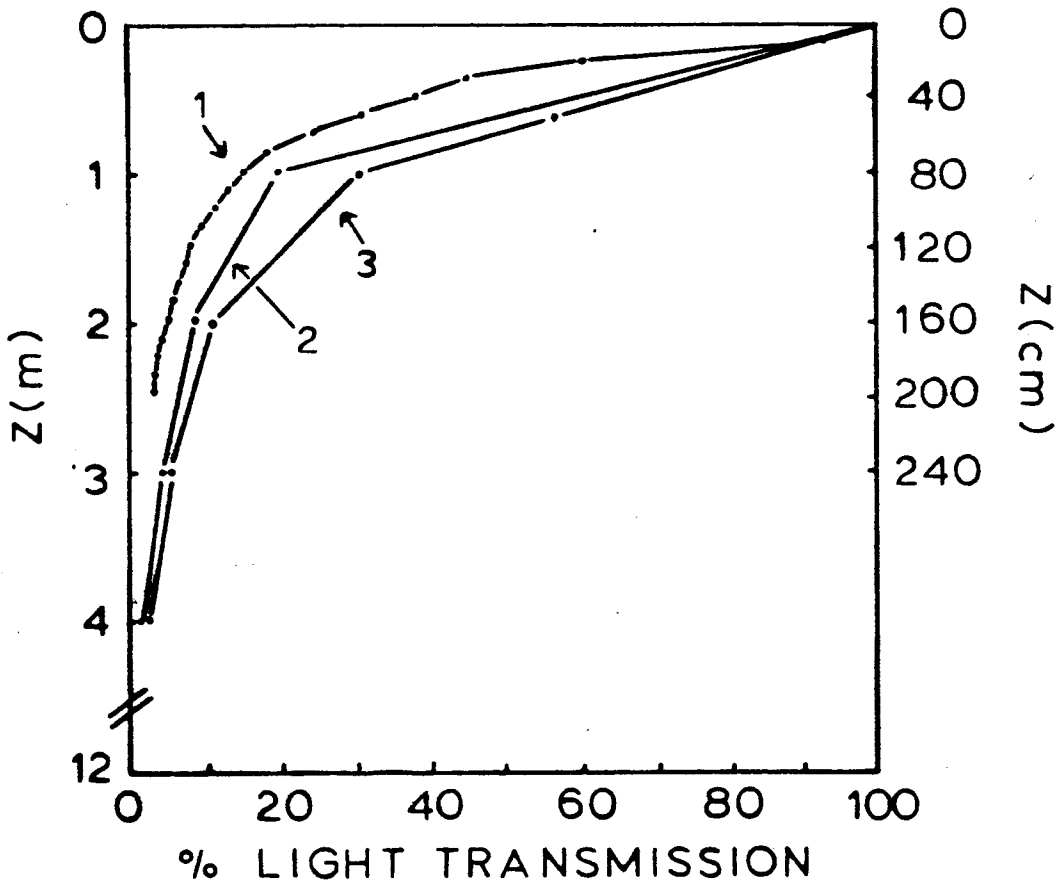

Figure 11. Percentage light transmission in the DVM Room column C (1) and in two natural lakes, Barbadoes Pond, N.H. (2) and Lake Chocorua, N.H. (3). DVM Room column C (17-I-77, 1516 h), Barbadoes Pond (16-X-78, 1800 h) and Lake Chocorua (6-V-79, 2000 h). All cloudless days.

In addition to the absolute light intensity, the influence of the changes in relative light intensity or light stimulus (Ringelberg 1963) was another important consideration of this study. It was first important to ascertain whether 1) the range of stimulus values recorded in the DVM Room approximated those in nature and 2) the stimulus values are the same at various depths in the columns. No differences were seen in the pattern of stimulus changes in the sunset period at any of the depths in the column and the range of values (approximately 5×10^4 sec^{-1} to 1.9×10^3 sec^{-1}) were essentially the same (Fig. 12) as those observed in previous field studies (Haney and Hall 1975) (Fig 13). Thus, light recorded at a single depth in the columns was used to estimate the relative light changes experienced by animals at all depths.

Pattern of DVM Activities in the Columns with Natural Light

One of the first objectives of this study was to determine whether Daphnia in the model lake systems (columns) in the DVM Room would exhibit daily changes in their vertical distribution comparable to the diel vertical migration in the field. Animals were introduced into the columns approximately 12 hr before observations of their depth distribution were begun. Food levels were held relatively constant by additions of agal suspension to each column every 12-15 hr. Food levels were monitored daily with the Coulter Counter.

Daphnia populations in the columns underwent a pronounced diel pattern of movement as illustrated with columns C and D (Figs. 14 and 15). The vertical shifts in mean depth followed the pattern generally observed in the field with maximum depth of the population in the day and minimum mean depth at night. The upward rise of the population began on the first day about noon and on the second day shortly after 0800 h. This type of early morning upward drift has been reported elsewhere for lake (Haney and Hall 1975) and marine (Ringelberg 1964) zooplankton. Replication in the

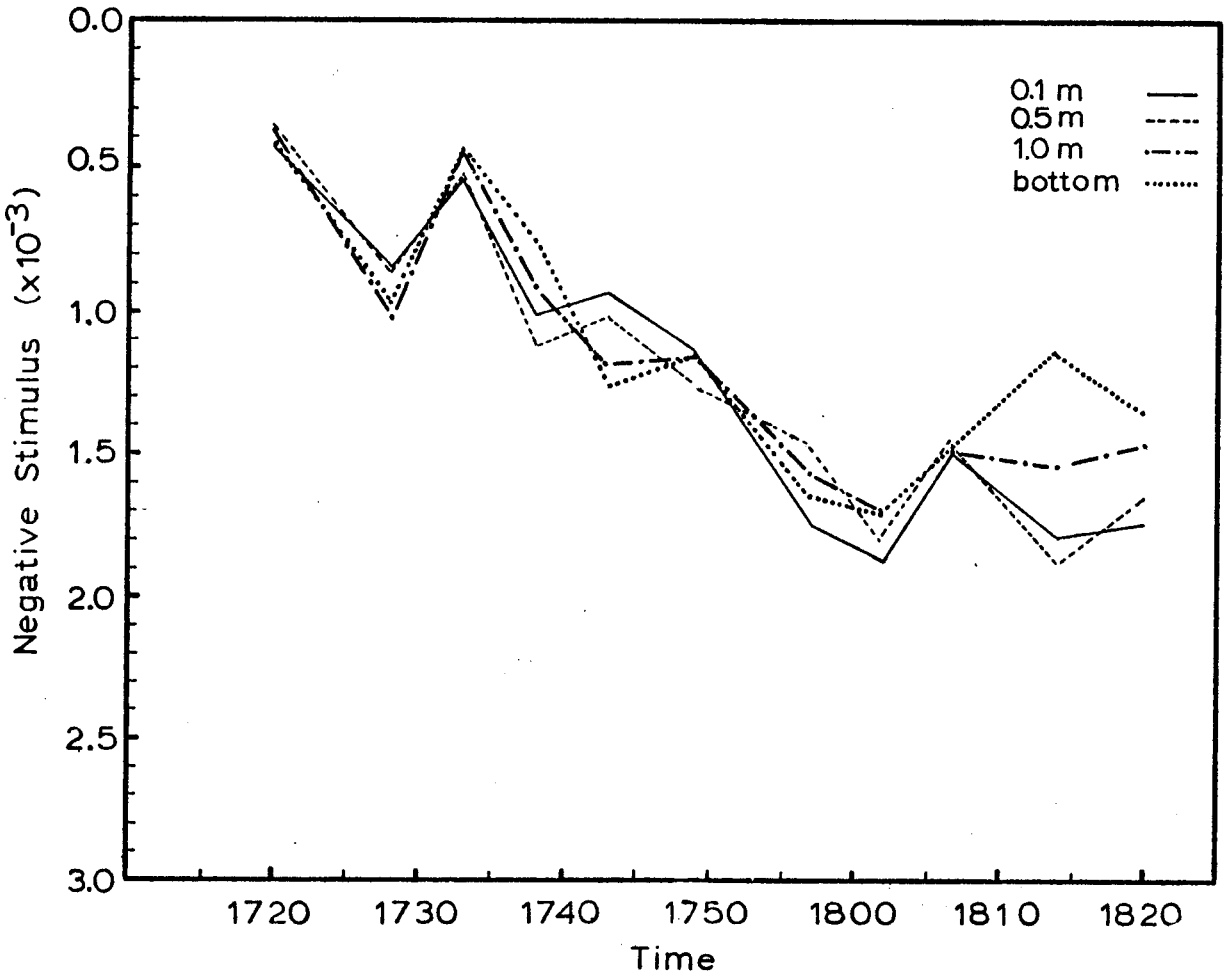

Figure 12. Light stimulus values measured at four different depths in DVM Room column A. R.S. represents the light stimulus threshold 1.7 x 10^{-3} of Ringelberg (1964). Cloudy conditions on 17-III-76.

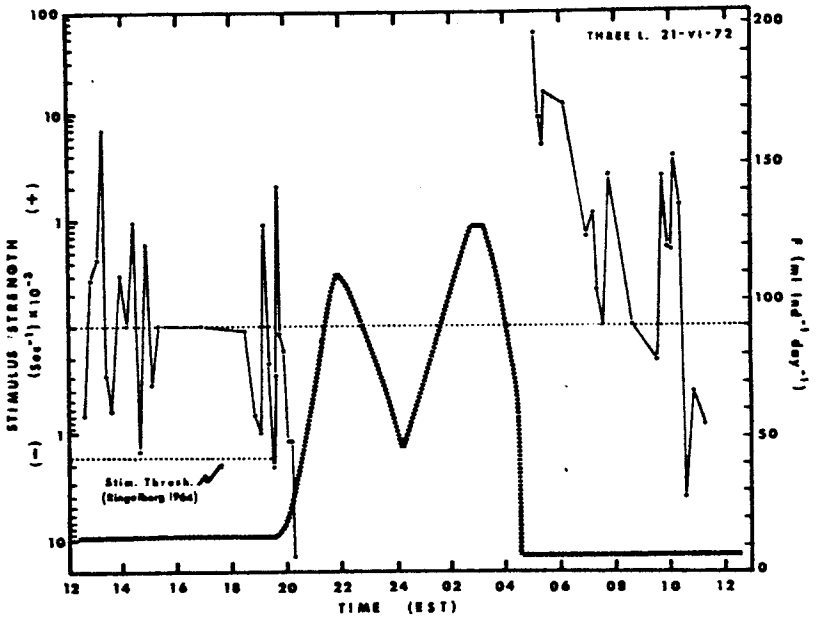

Figure 13. Comparison of light stimulus values and Daphnia pulex filtering rates in Three Lakes, Michigan. From Haney and Hall, 1975.

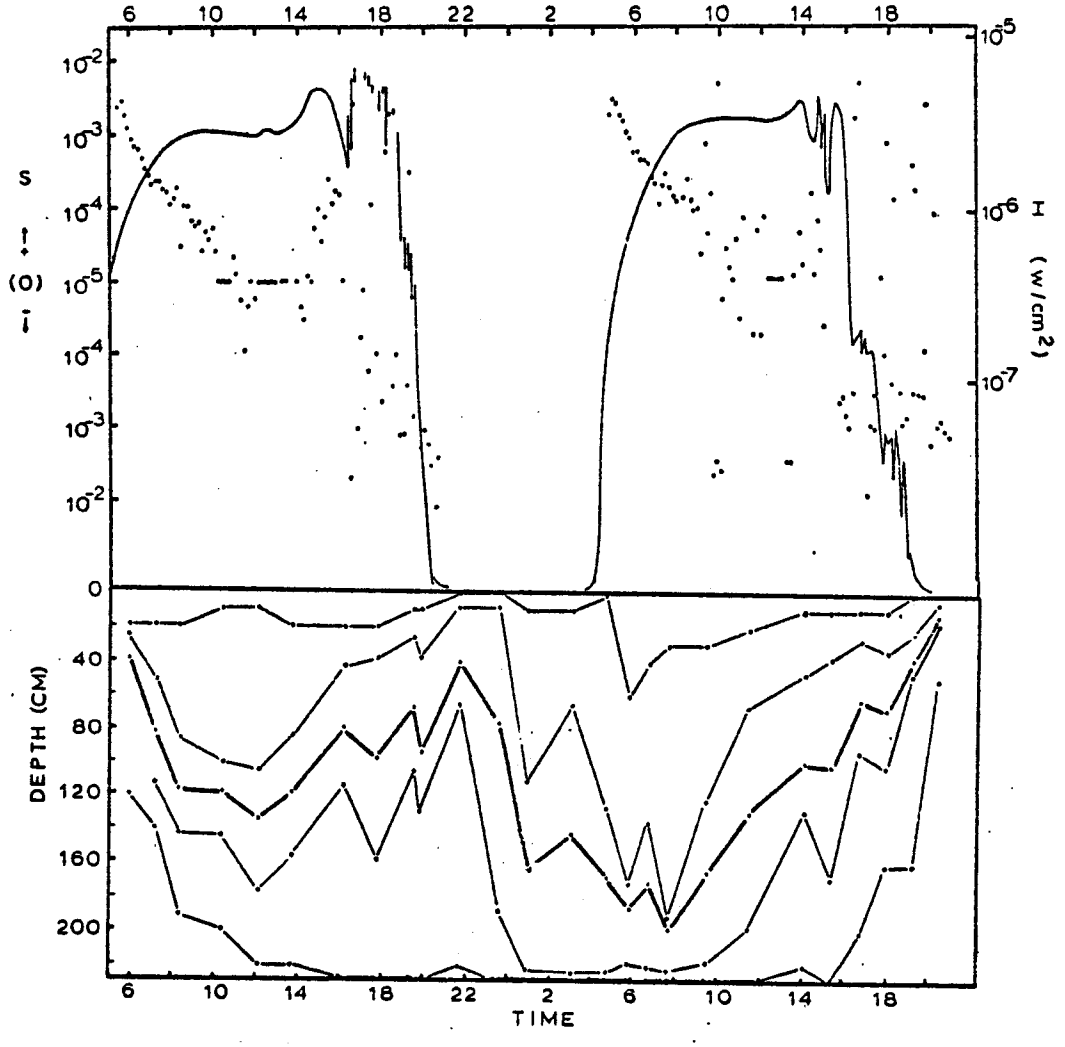

Figure 14. Diel changes in the population quartiles and $\bar{z}$ of Daphnia magna and concomitant light changes in DVM Room column C. Average food concentration 550 cells ml^{-1}. Water temperature 14-15°C. 5-6 May, 1976. Light intensities represented by continuous line. Positive and negative stimulus values (relative light change/sec) are solid dots. Quartile lines at the surface and bottom are 0% and 100%, respectively. Heavy solid line in bottom panel is the population mean depth ($\bar{z}$).

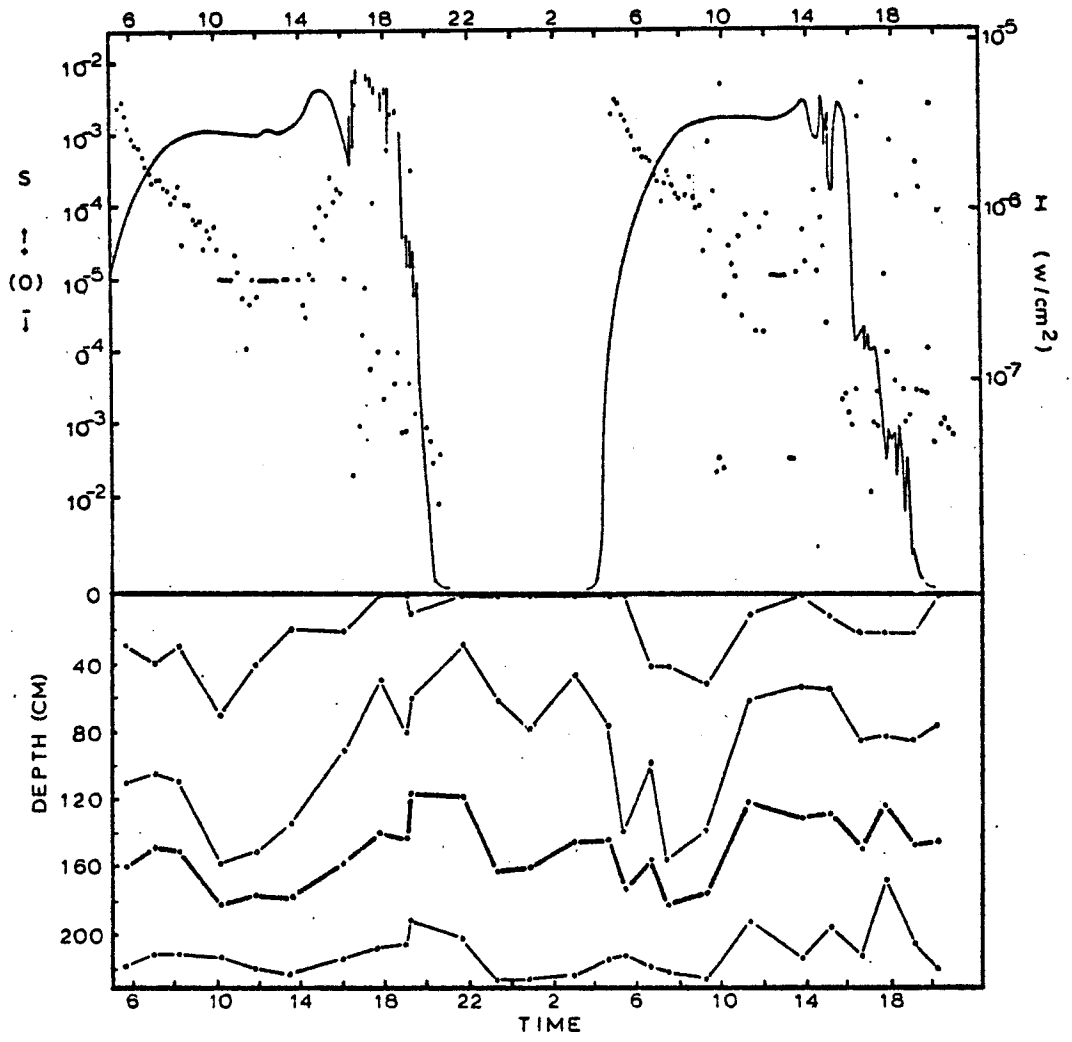

Figure 15. Diel changes in population quartiles and $\bar{z}$ of Daphnia magna and concomitant light changes in DVM Room column D. Average food concentration 905 cells ml^{-1}. Water temperature 14-15°C. 5-6 May, 1976. Light intensities represented by continuous line. Positive and negative stimulus values (relative light change/sec) are solid dots. Quartile lines at the surface and bottom are 0% and 100%, respectively. Heavy solid line in bottom panel is the population mean depth ($\bar{z}$).

other columns was very close to column C and average mean depth changes for columns B-E show essentially the same pattern (Fig. 16). In column A, however, D. middendorffiana exhibited a comparable diel pattern, but at a consistantly shallower mean depth suggesting a different behavior of this arctic zooplankter (Fig. 16). Population quartiles closely follow the changes in $\overline{Z}$, indicating that the diel movements are not limited to one part of the population. The range of diel mean depth changes in this series is from 85 cm to 180 cm or roughly equivalent in terms of light gradient (Fig. 12) to 1.7 m to 3.6 m in a lake. These movements are similar to vertical migrations observed in the field, e.g. 3.5 m for D. pulex in mesotrophic Three Lakes, Michigan (Haney and Hall 1975) and 0.28 m to 1.52 m for D. galeata mendotae in the eutrophic Lake Mendota, Wisconsin (McNaught and Hasler 1964). Thus, Daphnia in the columns have a similar pattern and amplitude of diel vertical migration to animals in the field.

Influence of Light on the Timing of DVM and Rate of Vertical Displacement

Previous work with Daphnia has shown that the diel vertical migration may be timed by the relative change in light intensity (Ringelberg 1964, Ringelberg et al., 1967). The relative light change or stimulus also appears to regulate the timing of vertical migrations in the field (Haney and Hall 1975). Thus, to further evaluate the effectiveness of the model system in allowing Daphnia populations to undergo daily migrations in the laboratory the role of light as a timer or zeitgeber was examined.

The pattern of migration in the columns is unimodal, with the upward movement occurring about 0800-1000 h (Figs. 14-16). At this time the light stimulus shifts from positive to negative values and remains for a time at its lowest levels (approx. 1000 - 1400 h). There is no apparent relationship at this time between the upward displacement and changes in absolute light intensity. The switch in vertical movement of the population appears to occur in

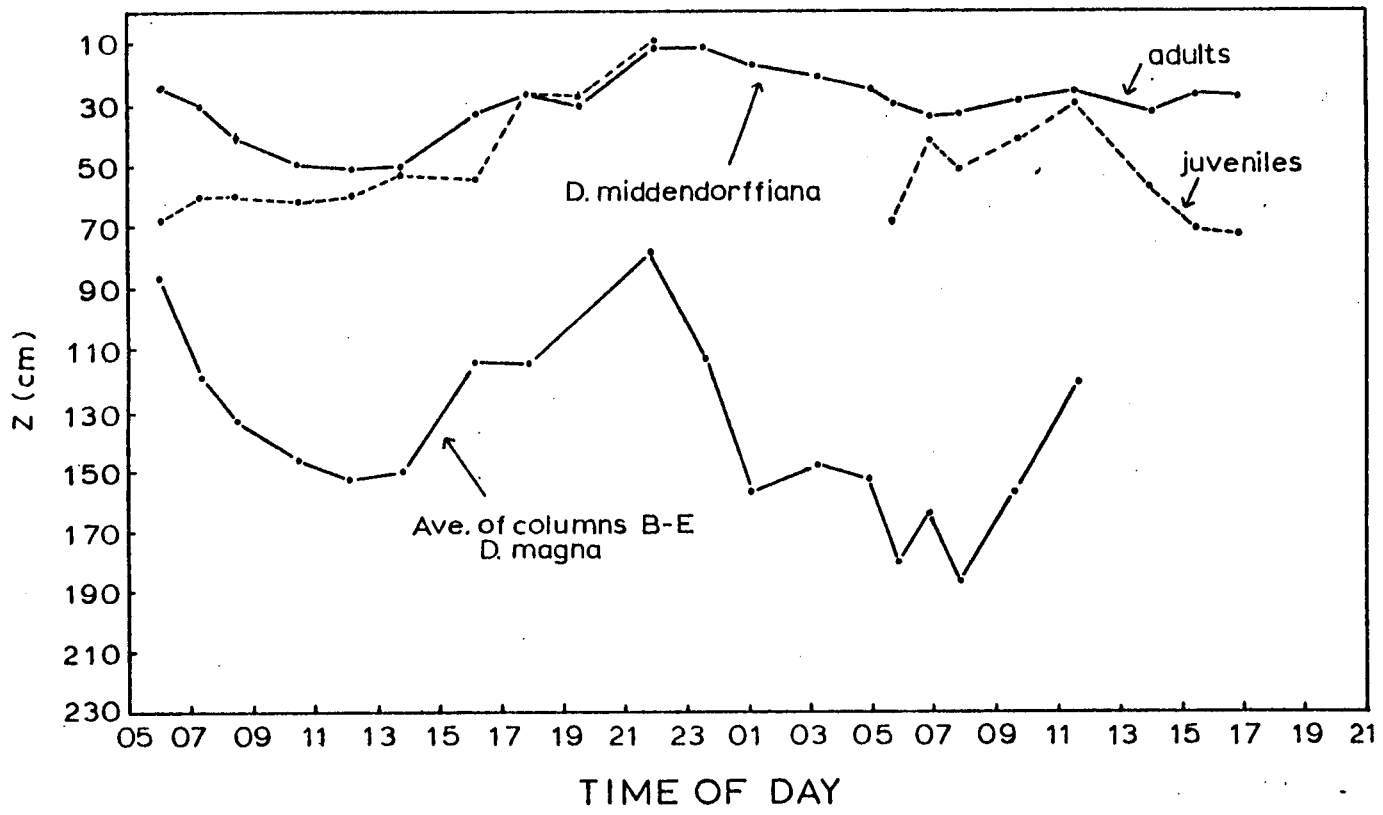

Figure 16. Comparison of diel mean depth ($\bar{z}$) changes for D. middendorffiana in column A and D. magna (average z of columns B-E). Water temperature 14-15°C. DVM Room, 5-6 May, 1976.

response to the change in stimulus sign and may result from a release from a strongly positive stimulus (increasing light intensity) which directs the negative phototactic downward swimming to a weakly negative light stimulus (decreasing light intensity) which initiates a positive phototactic upward swimming. It is also possible that the stimulus sign change may act as a zeitgeber for an endogenous rhythm which then directs the upward movement. Further studies under controlled light conditions are needed to clarify this mechanism.

Relative light changes have also been found to closely correlate with the rate of vertical movement in both the positive and negative phototactic responses of D. magna (Ringelberg 1964). This relationship was also examined for the natural light series in the columns. Displacement velocity was calculated as the change in mean depth per unit time. Average stimulus values were calculated for the corresponding time intervals. Linear regression models were applied to the data with and without log transformations. Since Daphnia may exhibit diel changes in photosensitivity (Ringelberg and Servaas 1971) the data were treated in three groups (a.m., noon, p.m.) to examine for possible differences in the effect of light stimulus according to the time of day. In four of the five columns the strongest relationship of stimulus to displacement velocity occurred during the evening period (Table 2). Regressions for columns A and E were significant at $p < 0.05$. Pooled data for all columns gave non-significant regressions of light stimulus and rate of vertical movement during the morning and noon periods, but a significant relationship in the evening (approx. 1600 - 2130 h). The significant regressions were:

$Y = 31.27X + 0.21$ Column A (p.m.)

$Y = 83.74X + 0.064$ Column E (p.m.)

$Y = 47.58X + 0.198$ Columns A-E (p.m.)

where: Y = displacement velocity (cm sec^{-1})

X = light stimulus (sec^{-1})

Table 2

A comparison of the correlation coefficients and analysis of variance F values for linear regressions of light stimulus against vertical displacement velocity. Column A is for Daphnia middendorffiana and Columns B-E for D. magna. Columns A-E represents the combined data from all columns. Approximate time designations: AM (0600-1030 h), noon (1030-1600 h), PM (1600-2130 h). Asterisk indicates significance at $p < 0.05$.

Data File	Time	N	Correl. Coeff. (r)	F
Column A	AM	6	0.29	0.36
	Noon	6	0.05	0.01
	PM	6	0.90*	8.13*
Column B	AM	6	0.09	0.04
	Noon	6	0.13	0.08
	PM	6	0.51	1.43
Column C	AM	6	0.02	0.00
	Noon	7	0.32	0.02
	PM	6	0.57	1.93
Column D	AM	6	-0.23	0.23
	Noon	7	0.71	5.01
	PM	5	0.14	0.06
Column E	AM	6	0.38	0.69
	Noon	7	0.51	1.74
	PM	6	0.93*	27.5*
Columns A-E	AM	30	0.06	0.09
	Noon	33	-0.07	0.17
	PM	29	0.38	4.28*

These results suggest that the upward movement in the morning and noon periods is under the control of factors other than the change in light intensity. Also, unlike the results of Ringelberg (1964) in which a log-log relationship was found between stimulus and displacement velocity, in this study log transformation of the data resulted in lower F values and correlation coefficients.

Effect of Light Intensity on Day-Depth

For the 5-7 May series in which population distributions were recorded under natural light changes in the DVM Room, regressions were run of light intensity measured at 160 cm depth in the columns and the mean depth for the D. magna population (columns B-E). Highest correlations were found for columns B and C, although none of the regressions were significant at $p < 0.05$ (Table 3). Light intensity was therefore not a significant factor in determining the day-depth of the column populations.

Effect of Food Concentration on Day-Depth with Natural Light

The influence of food concentration on $\overline{Z}$ was first examined using low food densities and natural light changes in the DVM Room. In this series (5-7 May), columns D and E differed from the other columns with respect to the effect of food density on day-depth. Linear regressions applied to untransformed and log-transformed data resulted in a best fit with log $\overline{Z}$ vs food, with $r = -0.29$, $N = 26$, $F = 2.18$, not significant at $p < 0.05$. In contrast, columns B and C exhibited a highly significant ($p < 0.01$) dependency of day-depth on food concentration described by the regression equation: $X = -0.31\ Y + 3.01$, $r = -0.86$, $N = 26$, $F = 121.0$ where: $X = \log \overline{Z}$ (cm) and $Y = \log$ food conc. (cells ml^{-1}).

Effect of Food and Light Intensity on Day-Depth

Since in the May series both light and food were measured along with the depth distribution of Daphnia, multiple regression analyses

Table 3

Linear regressions of light intensity (x variable) against $\overline{Z}$ (Y variable) for the "noon" periods of 5-6 May 1976 experiments in the DVM Room. E-7 = $X10^{-7}$

Column	N	Correl. Coeffic.	Slope	Intercept
A	7	-0.06	-2.15 E-7	1.10 E-2
B	6	-0.90	-4.38 E-8	7.60 E-6
C	6	-0.53	-3.51 E-8	6.78 E-6
D	6	-0.13	-7.28 E-9	3.40 E-6
E	6	-0.51	-1.82 E-8	5.18 E-6

were performed on the data from columns B and C which had shown significant linear regressions of food concentration and day-depth. Four significant regressions were found for the log-transformed and untransformed data (Table 4). The best-fit model was with: log $\overline{Z}$, log food concentration and light intensity, in which food concentration and light intensity together accounted for 85% (r^2) of the variability in mean depth of the population. Thus, addition of light as a variable resulted in an improvement over the simple linear regression ($r^2 = 0.74$). A correlation coefficient was found between light and time ($r = 0.49$, $N = 20$). Time of day was therefore not included as variable in the multiple regression analyses because of this autocorrelation.

Effect of Food Concentration on Day-Depth under Constant Daylight

To examine possible influences of the variable high food concentrations on the light conditions within the columns, light intensities were measured in each column to compare the vertical gradients of absolute light and extinction coefficients of the water in relation to the food concentration in the columns. Absolute light intensities were consistantly higher at all depths in column A than in the other columns (Table 5), whereas, light intensities showed no consistant differences in columns B-E. Since column A had the highest food level, the greater light intensity in this column was probably due to a position effect under the plastic dome, rather than an effect of the high food concentration which should have decreased the light transmission. Further evidence that the varied food concentrations had no important influence on the light environment of the columns is seen in vertical light extinction at six different levels in the columns (Table 6). Values were essentially identical at all depths and in all of the columns. Three general food concentrations were used in the beginning of the series (approximately 1×10^5, 5×10^4, 1×10^4 cells ml^{-1}) and although food additions were made throughout the experiment to maintain these

Table 4

Multiple regression statistics computed for the variable food concentration (cells ml^{-1}) and light intensity (ω cm^{-2}) on mean depth $\bar{Z}$ (cm). df is degrees of freedom for t test, t is the computed t-value for the respective variable and r is the multiple correlation. Data from D. magna in columns B and C, DVM Room, 5-6 May 1976. E7 = $X10^7$

Dependent Variable	df	Independent Variable 1	Independent Variable 2	Intercept	Part. Reg. Coeff. 1	Part. Reg. Coeff. 2	r	t-1*	t-2*
Log $\bar{Z}$	17	Log Food	Light	2.95	-0.275	-42901	0.92	-8.97	-5.30
$\bar{Z}$	17	Log Food	Light	392.89	-84.65	-1.18 E7	0.90	-7.90	-4.16
Log $\bar{Z}$	17	Log Food	Log Light	2.33	-0.274	-0.094	0.88	-7.19	-3.53
$\bar{Z}$	17	Log Food	Log Light	221.97	-84.23	-25.20	0.86	-6.73	-2.88

*t critical ($P < 0.05$) = 2.11

Table 5

Vertical profiles of absolute light (whole light diffuser #62) in the five columns with varying food concentrations on 3-II-77. Cell densities (no. ml^{-1}) in each column: A(7.4×10^4), B(1.14×10^4), C(9.83×10^3), D(4.74×10^4), E(5.70×10^4).

Depth (cm)	Light Intensity (ω $cm^{-2} \times 10^{-5}$) Column				
	A	B	C	D	E
0	14.98	10.37	11.73	13.07	12.05
10	11.48	8.24	8.91	8.20	7.56
20	9.23	6.48	6.23	5.68	5.55
30	7.34	4.93	4.76	4.07	3.94
40	5.64	3.58	3.63	3.00	2.77
50	4.60	2.57	2.76	2.23	2.04
60	3.58	1.91	2.10	1.74	1.52
70	2.83	1.48	1.63	1.34	1.15
80	2.25	1.15	1.27	1.04	0.90
90	1.80	0.92	0.99	0.82	0.72
100	1.43	0.72	0.76	0.67	0.57
110	1.17	0.58	0.61	-	-
120	0.96	0.45	0.49	0.43	0.37
140	0.66	0.31	0.33	0.30	0.26
160	0.45	0.21	0.22	0.22	0.19
180	0.30	0.15	0.16	0.15	0.13
200	0.20	0.11	0.11	0.11	0.10
220	0.18	0.07	0.09	0.10	0.08

Table 6

Comparison of vertical extinction coefficients for different depth intervals in five columns with varying food concentrations. 3-II-77. See Table 5 for food densities.

Depth (cm)	Vertical Extinction Coefficients (m^{-1}) Column				
	A	B	C	D	E
0-20	5.28	5.26	5.35	5.47	5.43
0-50	2.27	2.30	2.32	2.40	2.39
0-100	1.27	1.29	1.30	1.33	1.34
0-140	0.97	0.99	1.00	1.02	1.02
0-200	0.75	0.75	0.76	0.76	0.76
0-220	0.68	0.70	0.70	0.70	0.71

levels there was some decrease in food concentration in all columns by the end of the series (Table 7).

Linear regressions were run using the three daily $\overline{Z}$ estimates against the food concentrations measured in each column on that day. The relationship of food concentration to day-depth under the constant daytime light intensity was highly significant as described by the equation:

$$Y = -0.555 \times 10^{-5} X + 1.861 \qquad r = 0.91,\ N = 30,\ F = 126.0$$

(F critical $p < 0.05 = 4.20$)

where: $Y = \log \overline{Z}$ (cm)

X = food concentration (cells ml^{-1})

Although vertical movement of a population during midday is less pronounced than during the twilight periods when active migration occurs, endogenous rhythms could result in vertical displacement even under constant light conditions. To test for possible time dependency with the 1040 - 1530 h period of day-depth sampling, a multiple regression was computed for this series using time of day and food concentration as the independent variables. Time of day made no significant contribution to the multiple regressions, indicating the relative stability of $\overline{Z}$ during the period of observations. However, the addition of three observations made before 1040 h gave a significant effect of time on the day-depth changes. The derived equation was:

$$Y = 2.25 - 5.45 \times 10^{-6} X_1 - 2.80 \times 10^{-4} X_2 \qquad r = 0.86,$$

$t_1 = 8.73$, $t_2 = 2.25$, $df = 30$ ($t_{critical}$ $p < 0.05 = 2.04$)

where: $Y = \log \overline{Z}$ (cm)

x_1 = food concentration (cells ml^{-1})

x_2 = time of day (0000 - 2400)

This reflects a gradual upward movement of the populations in the early morning. Thus, although day-depth is most strongly influenced by food concentration, time of day earlier than 1040 h also contributes to a lesser degree to the change in day-depth. This observation of a time-dependent movement of animals under constant light conditions

Table 7

Comparison of food levels in the five columns in the variable food-constant daytime light experiments from 24-I to 3-II-77.

Column	Initial Food Conc. (cells ml^{-1})	Final Food Conc. (cells ml^{-1})	Mean Food Conc. (cells ml^{-1})
A	1.01×10^5	7.40×10^4	8.96×10^4
B	1.15×10^4	1.05×10^4	1.14×10^4
C	1.08×10^4	1.05×10^4	9.83×10^3
D	5.30×10^4	3.83×10^4	4.74×10^4
E	5.54×10^4	4.45×10^4	5.70×10^4

suggests an endogenous component in the control of daytime population depth.

Effect of Food Concentration on Day-Depth for Combined Series

The influence of food concentration over the entire range of food levels measured was examined by combining the data of the May (natural daylight) and January series (constant daylight). The data plotted on a linear scale draws attention to the rapid decrease in $\overline{Z}$ with increasing food concentration at low food concentration and the slower change at higher food concentrations (Fig. 17).

As suggested by the exponential appearance of the data, a semi-log transformation of the data resulted in the best fit to a linear regression and the following regression equation:

$$Y = 272.68 - 50.98X \qquad r = 0.93,\ N = 41,\ F = 262.0,\ (F \text{ critical } p < 0.05 = 4.08)$$

where: $Y = \overline{Z}$ (cm)

X = log food concentration (cells ml^{-1})

In this highly significant regression (Fig. 18), 86% of the mean depth variation can be accounted for by changes in food concentration. The remarkable closeness of fit of the two sets of data from separate experiments, with different light conditions and different populations of Daphnia, adds support to the generality of the regulatory role of food concentration.

Short-term Effects of Changes in Food Concentration

The strong correlation between day-depth and food concentration indicates food may have an important regulatory influence on the vertical distribution of Daphnia. Since the previous experiments with food concentration were carried out over periods of days, populations of Daphnia appear to make adjustments during that time to different food levels in the columns which involve changes in their depth distribution. To determine the rapidity with which such adjustments are made, additions of algal suspension were made to the columns and the vertical distribution of animals recorded.

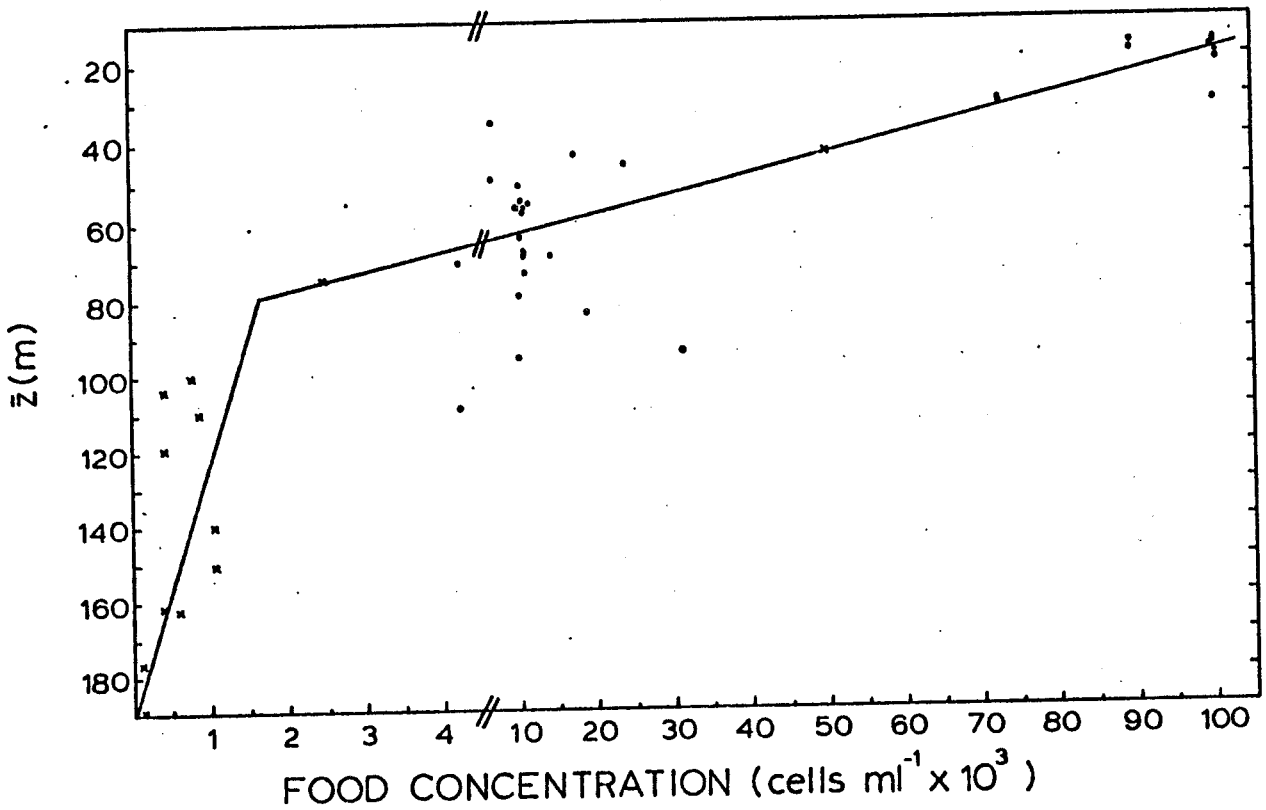

Figure 17. Relationship of mean depth and food concentration for adult Daphnia magna populations in DVM Room columns. All observations made during midday (1040-1530 h) from two experiments, with natural light changes (x) and constant daytime light (·). Lines through data points drawn by eye. Water temperature in all experiments 14-16°C.

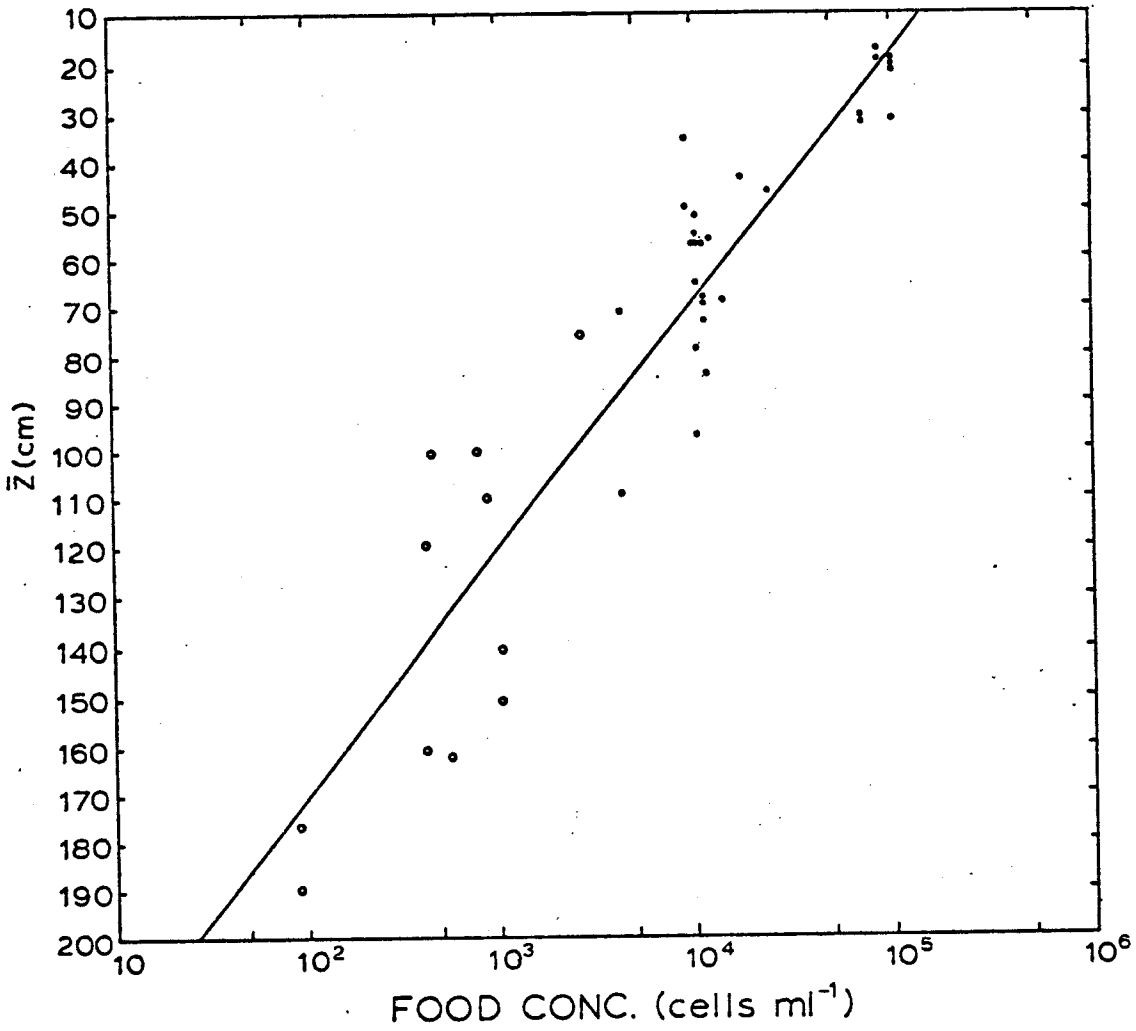

Figure 18. Relationship of mean depth and $\log_{10}$ food concentration for adult D. magna populations in DVM Room columns. All data are daytime observations (1040-1530 h) from experiments with natural light changes (0) and constant daytime light (·). Line drawn is the least squares best fit for the combined data (Y = 272.68 - 50.98x). Water temperature in all experiments 14-17°C.

Paired columns B - C and D - E were used, allowing columns C and E to act as controls (no food additions) during the first part of the experiment (0800 - 1500 h). During this time additions of concentrated food were made to the surface of columns B and D every 4-5 h and the response in the population distribution was recorded at hourly intervals. Previous food dispersion experiments had demonstrated that food added to the surface of the columns was evenly dispersed in less than 1 h. To determine the response on a finer time scale, at 1500 h food was injected into the control columns C and E and the distribution recorded every 5-10 minutes. Since populations of D. magna were those used in the 5-6 May series, food levels in all columns were low (< 2000 cells ml^{-1}). Initial food concentrations in columns B and D were approximately 1300 and 1500 cells ml^{-1} respectively and in control columns C and E approximately 500 cells ml^{-1}.

Upward movements of the D. magna populations in response to food additions were rapid, with maximum changes occuring within the first hour (Fig. 19). The same pattern of response was seen at all depths below the surface (0%), although the 75% quartile in column D showed some delay to the first food addition. About 2-3 h after each food addition depth distributions returned to levels only slightly higher than before the food was added. Depth changes in control columns C and E changed little during the same period (Fig. 20). In both columns B and D vertical displacement responses to the 5 ml food addition were greater than to the 2 ml addition (79 vs 59 cm in column B; 96 and 88 cm vs 72 cm in column D). These changes in mean depth in response to average elevations of food concentration in the columns estimated as 139 - 348 cells ml^{-1} are much greater than would be predicted from the food concentration vs mean depth relationship derived in the earlier experiments (Fig. 18), where these food additions should result in vertical shifts in $\overline{Z}$ of approximately 2-5 cm. The rapid change in $\overline{Z}$ which overshoots the predicted change, followed by a return to a mean depth only slightly

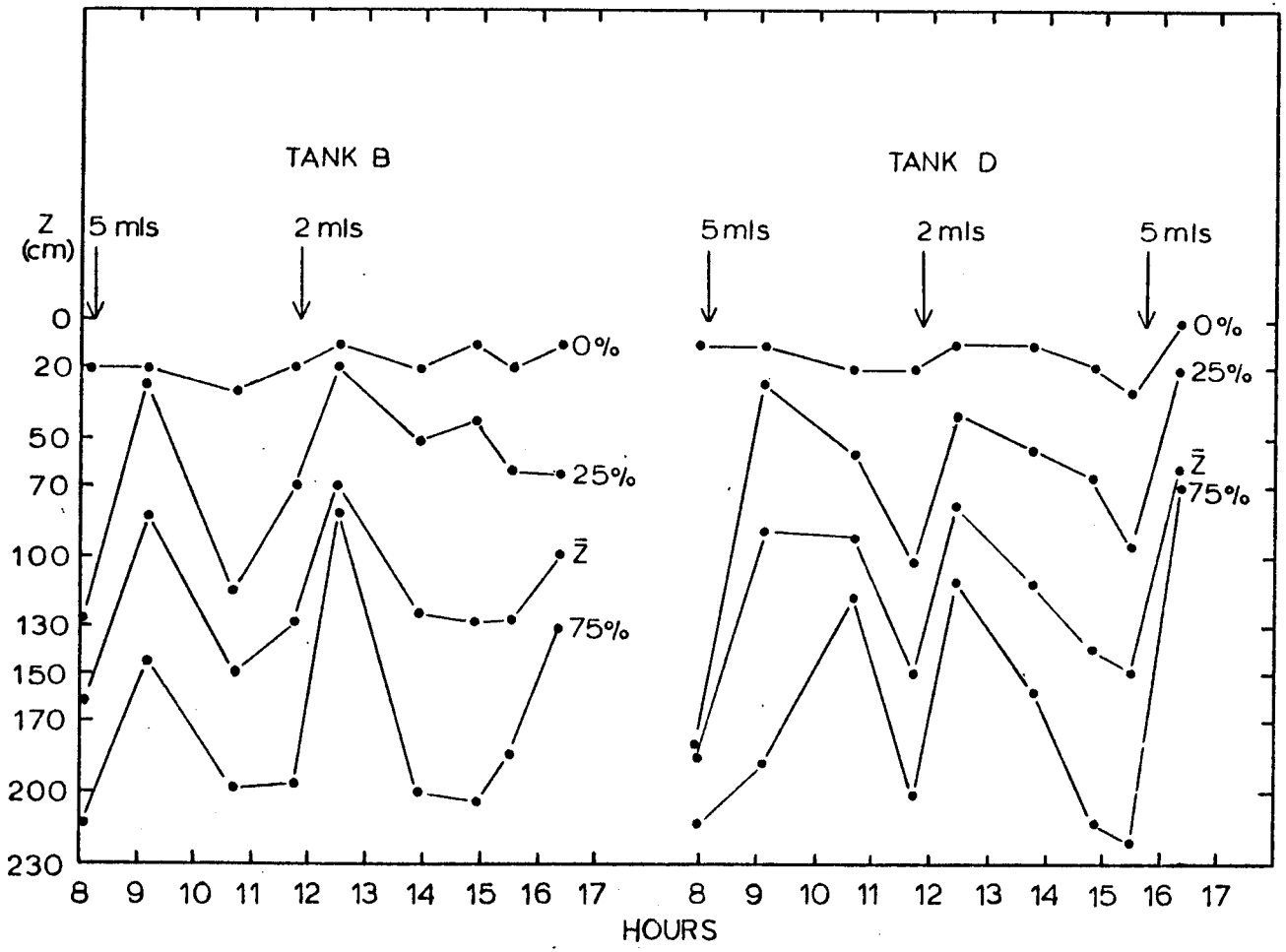

Figure 19. Response of Daphnia magna populations to additions of concentrated algal suspension. Percentages represent population quartiles.

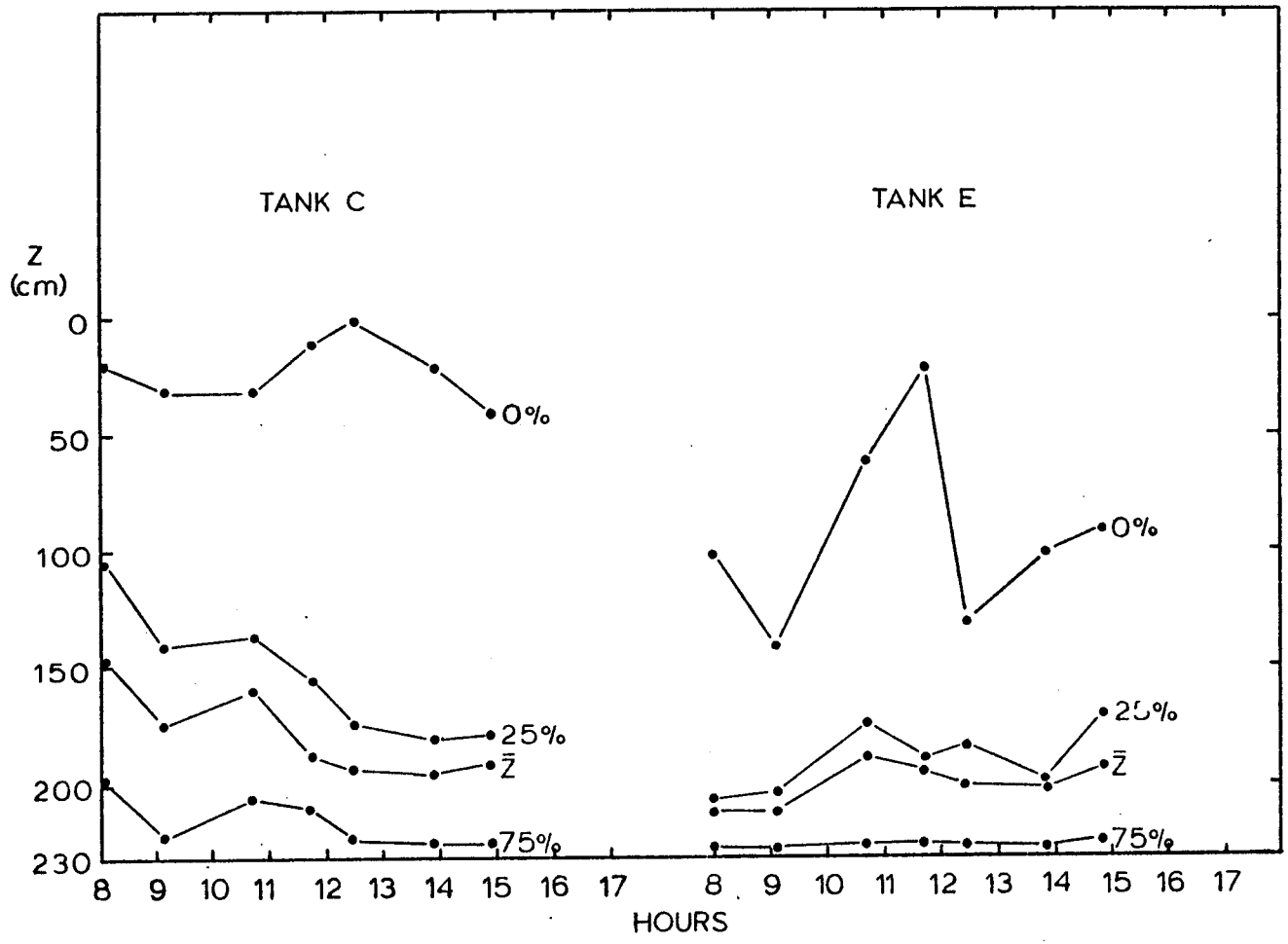

Figure 20. Distribution of Daphnia magna populations in control columns C and E which received no food additions. Percentages represent population quartiles. Water temperature 14.5°C.

higher than the prefood addition level, suggests that the Daphnia may be exhibiting a type of hunger response. Similar responses have been seen with starved Daphnia when they are presented with high food concentrations in which elevated feeding rates generally last less than one hour (Geller 1975). After 1-2 h animals have made an adjustment to the altered food density which is in closer agreement with the linear regression model. For example, in column B mean depth changed 12.5 cm 3 h after the 5 ml food addition vs a predicted change of 5.3 cm and 4.5 cm after 2 ml of food were added vs the predicted 2.3 cm change.

The immediate effects of food addition are seen in Fig. 21. Upward movement was recorded almost immediately and the mean depth of the population continued to gradually shift over the next 30 minutes. The total upward movement in mean depth was essentially the same in both columns (column C 23.8 cm vs column E 24 cm).

Although differences in food density produced no detectable alteration in the light transmission characteristics of the columns (Tables 5-6), one might explain the upward movement of Daphnia in response to food added to the surface water as a reaction to other food-related changes in water quality, such as changes in color or odor of the water, toward which the animals are attracted. In this situation the location of the stimulus (near the surface) provides an orientation cue. Another possible mechanism is that the food triggers an increase in feeding and swimming activity which is non-directed. Due to the normal vertical body orientation and hop-sink swimming mode of Daphnia this heightened activity results in greater hops and is translated into a net upward movement. These hypotheses were examined in a third experiment in which, to avoid changes in orientation cues above the population, food was injected near the bottom of the column. In this population of D. middendorffiana 90% of the animals were located below 200 cm (N = 200). Food concentration at the start of the run was about 350 cells ml^{-1}. The depth distribution of the Daphnia were recorded at 2-5 minute intervals for the first 20 minutes and 10-20 minute intervals until

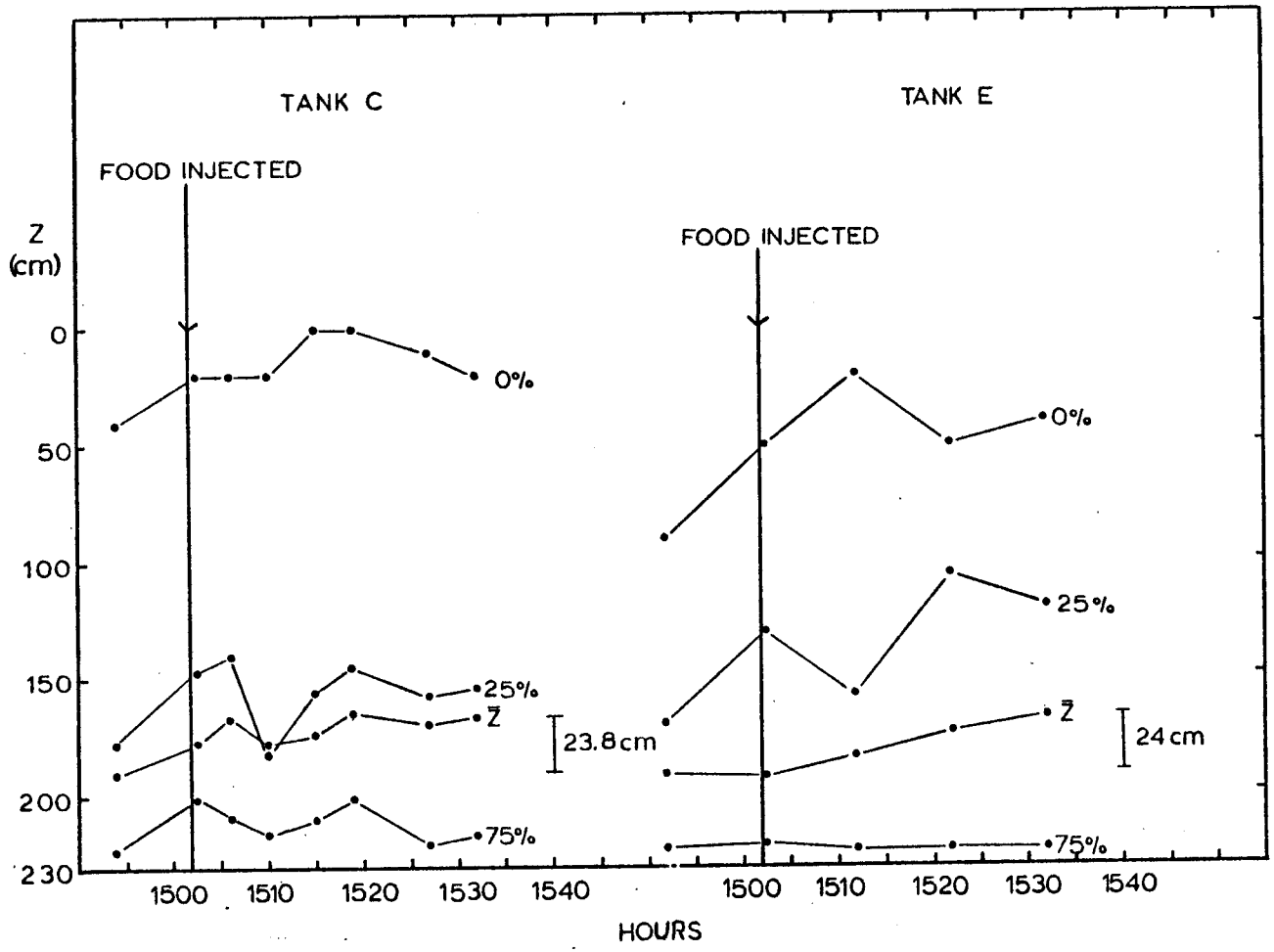

Figure 21. Short-term response of Daphnia magna populations to 5 ml additions of concentrated algal suspension. Percentages represent population quartiles. Water temperature 14.5°C.

60 minutes. The population $\overline{Z}$ had an upward displacement of 7 cm within the first 5 minutes and by 10 minutes after food addition had reached its maximum displacement of 31.9 cm (Fig. 22). Most of the mean depth change was due to movements of Daphnia from the 210-220 cm and 220-230 cm depths, where at 10 minutes the population was reduced to 40% and 20%, respectively. The almost immediate upward shift in mean depth and movement of animals well above the level of food injection (note the 5 percentile) before food could have diffused into these depths (i.e. within the first 10 minutes) supports the hypothesis that the vertical displacement of animals is a result of an increase in swimming activity rather than a directed response to altered orientation cues. The short-term cyclic response suggests this is related to the hunger response seen in Daphnia feeding experiments where high feeding rates of starved animals return low rates in 30-60 minutes. This hypothesis of short-term reactions does not, however, explain the mechanism behind the long-term relationship of mean depth to food concentration.

Field Studies: Day-Depth Studies Under Continuous Arctic Light Conditions

Since the primary objective of this study was to examine the day-depth regulation by zooplankton, field experiments were carried out in the unique Arctic environment where the effect of light on day-depth could be examined over long uninterrupted periods with minimal disturbances associated with sunset and sunrise periods when rapid changes in the distribution of populations occur.

Daytime regulation of zooplankton depth distribution has been frequently attributed to a relatively simple photoresponse of animals to light which involved compensatory swimming movements that maintain the zooplankton in a constant or preferred zone of light intensity (Rose 1925, Russell 1927 and others). This "preferendum hypothesis" predicts then that incident light intensity changes are correlated with the changes in vertical distribution of the population over time. In our field study special emphasis was placed

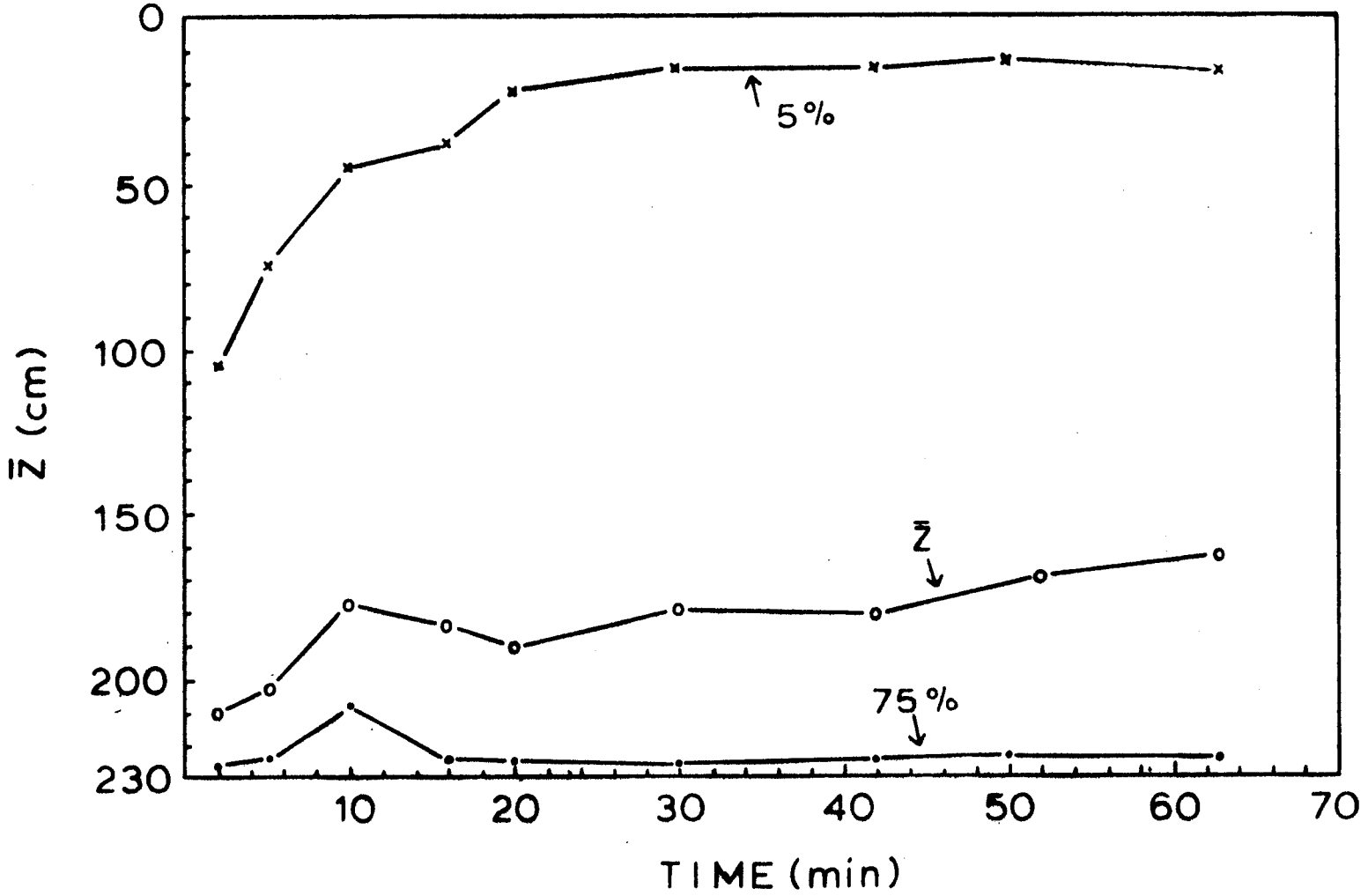

Figure 22. Changes in mean depth and population quartiles of Daphnia middendorffiana in response to a food injection at 230 cm depth in the column. Water temperature 14.5°C.

on testing the validity of this hypothesis as well as examining other factors such as temperature and relative light change. The influence of food level was not observed in the field studies.

In Situ Lake Studies

Seven diel studies of the vertical distributions of lake zooplankton were done at Toolik and Resolute Bay (Table 8). On 11 - 12 August and 21 - 22 August at Toolik, nights were dark except for very faint undetectable lighting from the stars, the moon, and the aurora borealis. Under longer photoperiods, the sun did not go far enough below the horizon to create dark nights and incident light intensities at midnight ranged from 3.4 - 4.6 x 10^{-5} watts cm^{-2}. Under continuous sunlight, midnight intensities were 2.5 - 2.7 x 10^{-4} watts cm^{-2} (6 - 7 July, Toolik) and 4.6 x 10^{-4} watts cm^{-2} (5 - 6 August, Resolute Bay). Temperature profiles and the concentrations of particulate matter in the lakes remained almost constant throughout the studies. The oxygen profile was measured in the 20 - 21 July study and also did not change during the study.

Vertical migrations of up to 17 m in the deeper lakes were predicted by the preferendum hypothesis for zooplankton studied under continuous sunlight and long day photoperiods. The preferred zone would fall between the highest and lowest isopleths of light intensity that did not meet the water surface or lake bottom. In ponds and shallow lakes, the light isopleths regularly meet the lake surface and bottom even in continuous light, and migrations through most of the water column are predicted by the preferendum hypothesis. The most striking feature of these studies is the lack of diel vertical migrations under continuous daylight, i.e. continuous sunlight and long day photoperiods (Figs. 23 and 24). The actual range of vertical movement was rarely more than 2 m in deep water and usually less than .5 m in shallow waters (Table 9). In addition, diel changes in the mean depth were frequently in reverse of the

Table 8

Maximum change in mean depth ($\bar{z}$) over 24 hours for lake zooplankton at Toolik (Toolik Lane, Lake E-1) and Resolute Bay (Ruins L.). Photoperiod was calculated from the Smithsonian Meteorological Tables, 1918. Maximum change in depth of light isopleths were calculated from measurements of incident and underwater light intensity, and are equivalent to the maximum change in $\bar{z}$ predicted by the preferendum hypothesis.

Photoperiod	Max. Change in Light Isopleths	Species	max. change in $\bar{Z}$ (m)
Ruins Lake	5-6 VIII 73		
LD 24:0h	(1.5m)**	D. middendorffiana	.16
Lake N-5	6-7 VII 77*		
LD 24:0h	(2.0m)**	D. middendorffiana (6th)	.16
		" (7th)	.10 (R)
Toolik Lake	20-21 VII 76		
LD 22.7:1.3h	9-13.5 m	D. middendorffiana	2.76 (R)
		D. longiremis cephela	1.30
		D. tyrelli	.78
		B. longirostris	1.57
		H. septentrionalis	.68
		H. gibberum	2.14
		C. scutifer	1.24
Lake E-1	23-24 VII 77		
LD 22:2h	7-9 m	D. longiremis typica	2.22
		B. longirostris	1.49
		H. gibberum	.86
		D. tyrelli	1.18
Toolik Lake	27-28 VII 76*		
LD 20.9:3.1h	12-17 m	D. middendorffiana	2.91 (R)
		D. longiremis cephela	1.25
		H. gibberum	1.46
		B. longirestris	1.37
		D. tyrelli	.17
		C. scutifer	.48 (R)
		H. septentrionalis ♀	3.90 (R)
		" ♂	2.62 (R)
Toolik Lake	11-12 VII 75*		
LD 19.2:5.8m	(7m)**	D. tyrelli	.91
		B. longirostris	.09
		nauplii	.21 (R)
		C. scutifer	1.34 (R)
Toolik Lake	21-22 VIII 75*		
LD 16.5:7.5h	(10m)**	D. tyrelli	.35
		H. septentrionalis	3.40
		nauplii	.35
		C. scutifer	.03 (R)

* noon and midnight series only
** all isopleths are interrupted by surface or bottom, maximum depth of station is given in parentheses
(R) mean depth, $\bar{Z}$, was deeper in the water column at midnight

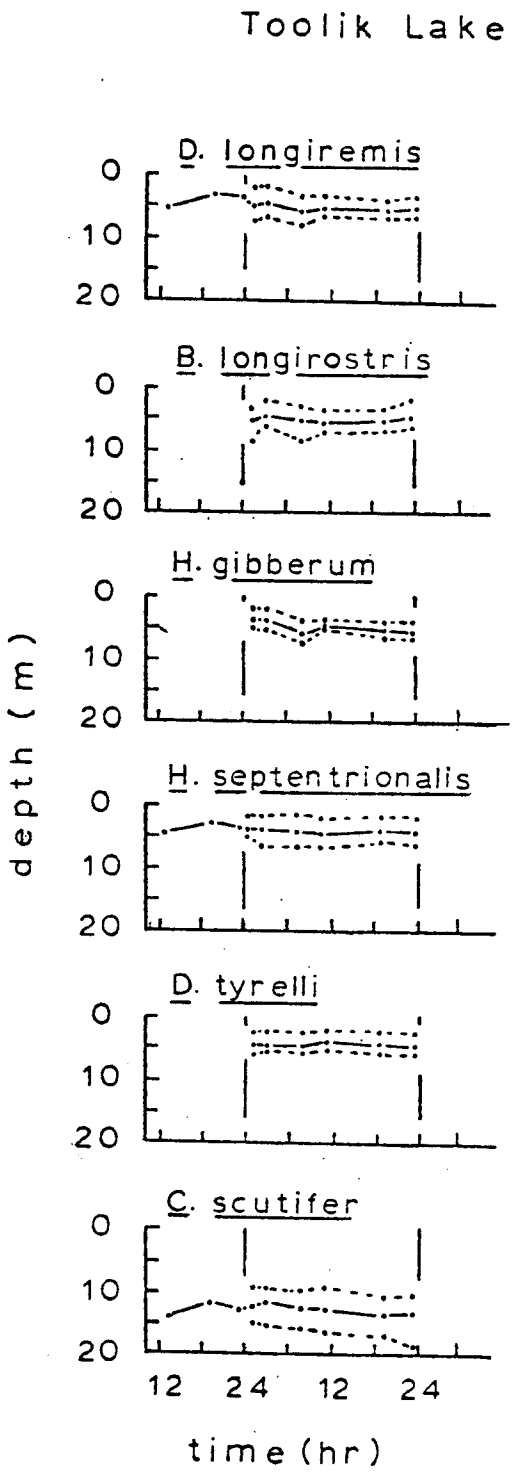

Figure 23. Depth distributions of zooplankton, 20-21 VII 76, Toolik Lake. ---- = quartiles, ——— = mean depth.

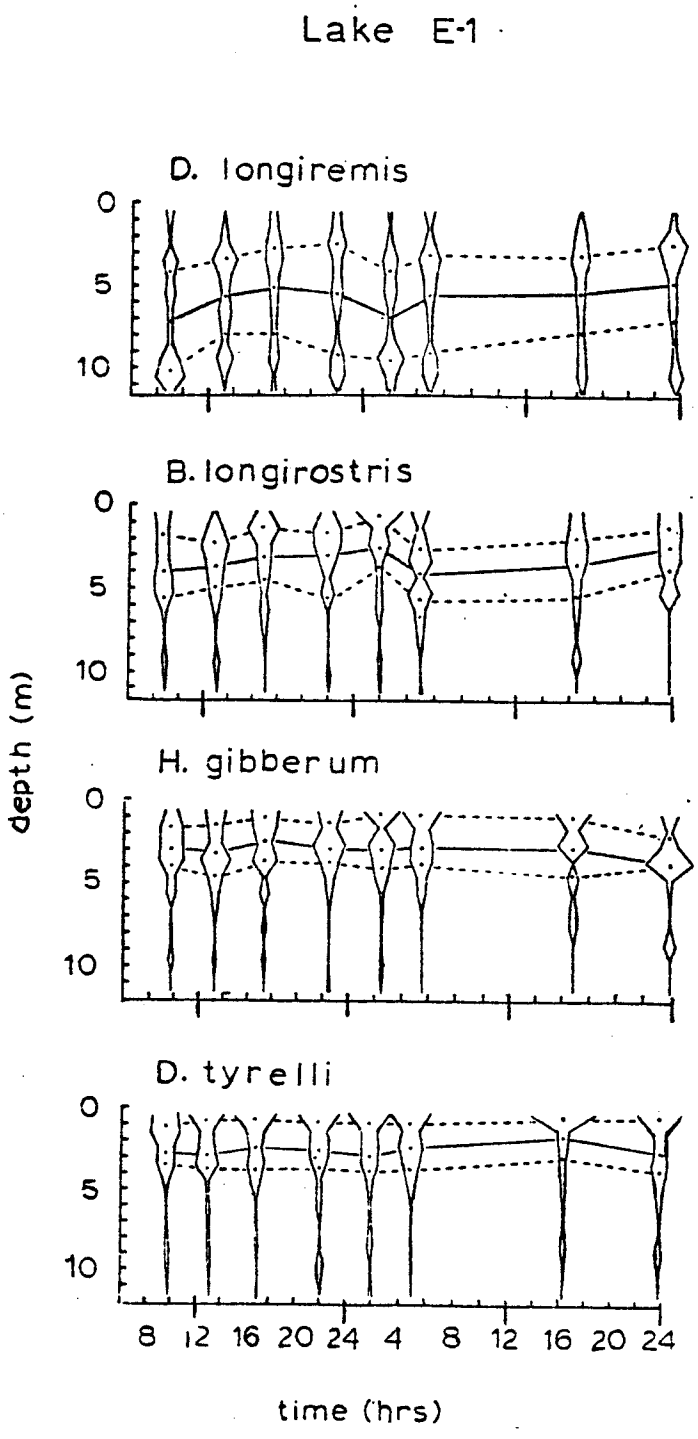

Figure 24. Depth distributions of zooplankton, 20-21 VII 76, Toolik Lake. ---- = quartiles, —— = mean depth, width of kite = % population.

Table 9

Correlations of mean depth ($\bar{z}$) and quartiles (25, 75%) with the log of the incident light intensity (I_o) for lakes. NS = nonsignificant correlation ($P \leq 90\%$); S = slightly correlated ($P \leq 95\%$).

Lakes	Species	Corr. with log I_o 25%	$\bar{z}$	75%
20-21 VII,	D. longiremis cephela	S	S	NS
Toolik L.	D. middendorffiana	NS	NS	NS
df = 4	B. longirostris	NS	NS	NS
	H. gibberum	S	NS	NS
	D. tyrelli	NS	NS	NS
	H. septentrionalis	NS	NS	NS
	C. scutifer	NS	NS	NS
23-24 VII,	D. longiremis typica	NS	NS	NS
Lake E1	B. longirostris	NS	NS	NS
df = 6	H. gibberum	NS	NS	NS
	D. tyrelli	NS	NS	NS
5-6 VIII,	D. middendorffiana	NS	NS	NS
Ruins L.				
df = 4				

direction predicted by the preferendum hypothesis or showed no consistent pattern of change.

Samples were taken at frequent intervals in the 20 - 21 July, 23 - 24 July, and 5 - 6 August studies, and sufficient data points were available so that population mean depth and quartiles could be regressed against incident light intensity. Because underwater light intensity is a logarithmic function of the incident light intensity, mean depth was actually correlated with the logarithm of incident light rather than the absolute incident intensity. All of the correlations between the depth parameters and intensity were nonsignificant ($P < 0.05$) (Table 9). H. gibberum and D. longiremis cephela showed weak correlations ($P = 0.10 - 0.05$) on 20 - 21 July. However, no correlation was found for H. gibberum at a similar photoperiod (23 - 24 July), and D. longiremis showed a similar diel range in mean depth in a longer photoperiod (27 - 28 July). Apparently diel changes in the absolute light intensity has little influence on the vertical distributions of populations in low arctic lakes.

In Situ Pond Studies

Three diel studies of the vertical distributions of zooplankton in shallow (20 - 30 cm) thaw ponds were conducted at Barrow, under continuous sunlight. The range of incident light intensities experienced during the three studies were similar, i.e. Pond W, $.14 - 7.56 \times 10^{-3}$ watts cm^{-2}; Pond Y, $.076 - 7.83 \times 10^{-3}$ watts cm^{-2}; and Pond S, $0.59 - 6.87 \times 10^{-3}$ watts cm^{-2}. Unlike the lake studies, temperatures fluctuated in a diel cycle in all of the ponds. The temperature cycle was closely related to the light cycle in Pond W and Y, but not in Pond S. The absolute temperatures observed in the Pond W study (1.3° - 5°C) were much lower than those of Pond Y (3.9° - 12.2°C) and Pond S (8.5° - 14.5°C) studies. D. pulex were found in Pond W and Y; D. middendorffiana and B. paludosa were found in Pond S.

A diel vertical migration was observed in Pond W (Fig. 25A), but not in Pond Y (Fig. 25B) or Pond S (Fig. 26). Absolute light intensity apparently was not the cause of the migration because the range of light intensities that was experienced in Pond W was similar to those in Pond S and Y. Correlations between temperature and mean depth were found in the Pond W population ($P < 0.01$), and slopes of the regression lines were steep, i.e. +2.45 cm per °C for adult and +1.75 cm per °C for juvenile D. pulex (Fig. 27A). These correlations strongly suggest that the low temperatures which were experienced only in the Pond W study may have caused the migration. Because of the close relationship between light and temperature in Pond W, the effect of the low temperatures on mean depth was seen as a diel cycle of migration. Diel fluctuations of light and temperature were also closely related in the Pond Y study, but the warm temperatures which were experienced did not affect mean depth (Fig. 27A). In the Pond S study, a correlation between temperature and mean depth was found for D. middendorffiana but not for B. paludosa. Despite the high level of significance of the correlation for D. middendorffiana ($P < 0.01$), the slope of the regression line was not steep (i.e. -.8 cm per °C) which indicates that the actual effect of temperature on mean depth was weak. A diel cycle of migration caused by temperature fluctuations was not obvious.

Temperature effects on mean depth influenced the relationship of light intensity and mean depth. When temperature affected mean depth and light and temperature were closely related, a correlation between light intensity and mean depth was found in Pond W (Fig. 27B). In the absence of a temperature effect on mean depth, no correlation was observed between light and mean depth for the same range of light intensities in Pond Y (Fig. 27B). The result of a weak temperature effect on mean depth and a weak relationship between light and temperature was no correlation ($P < 0.05$) between light intensity and mean depth in Pond S.

Results of the pond studies, summarized in Table 10, strongly

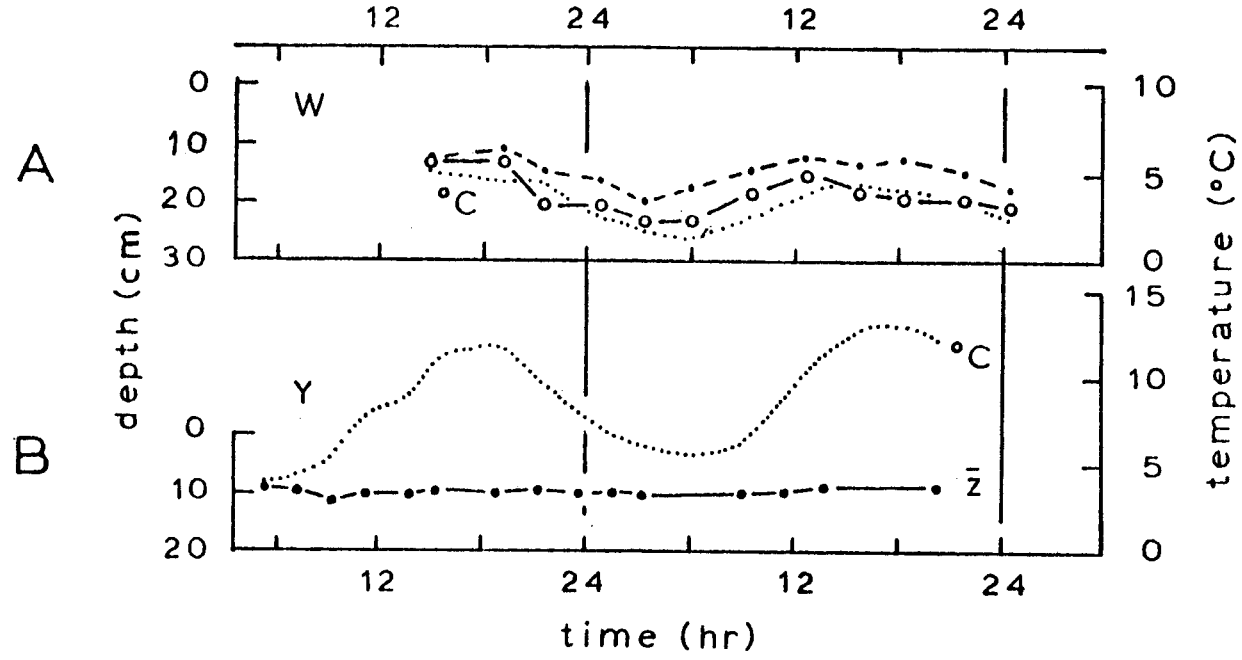

Figure 25. In situ diel studies of pond Y and W at Barrow. A: Pond W, 26-27 VII 75, D. pulex. ·---· = mean depth of juveniles; ——— = mean depth of adults; ···· = °C. B: Pond Y, 3-4 VIII 76, D. pulex, ·——· = mean depth of adults; ···· = °C.

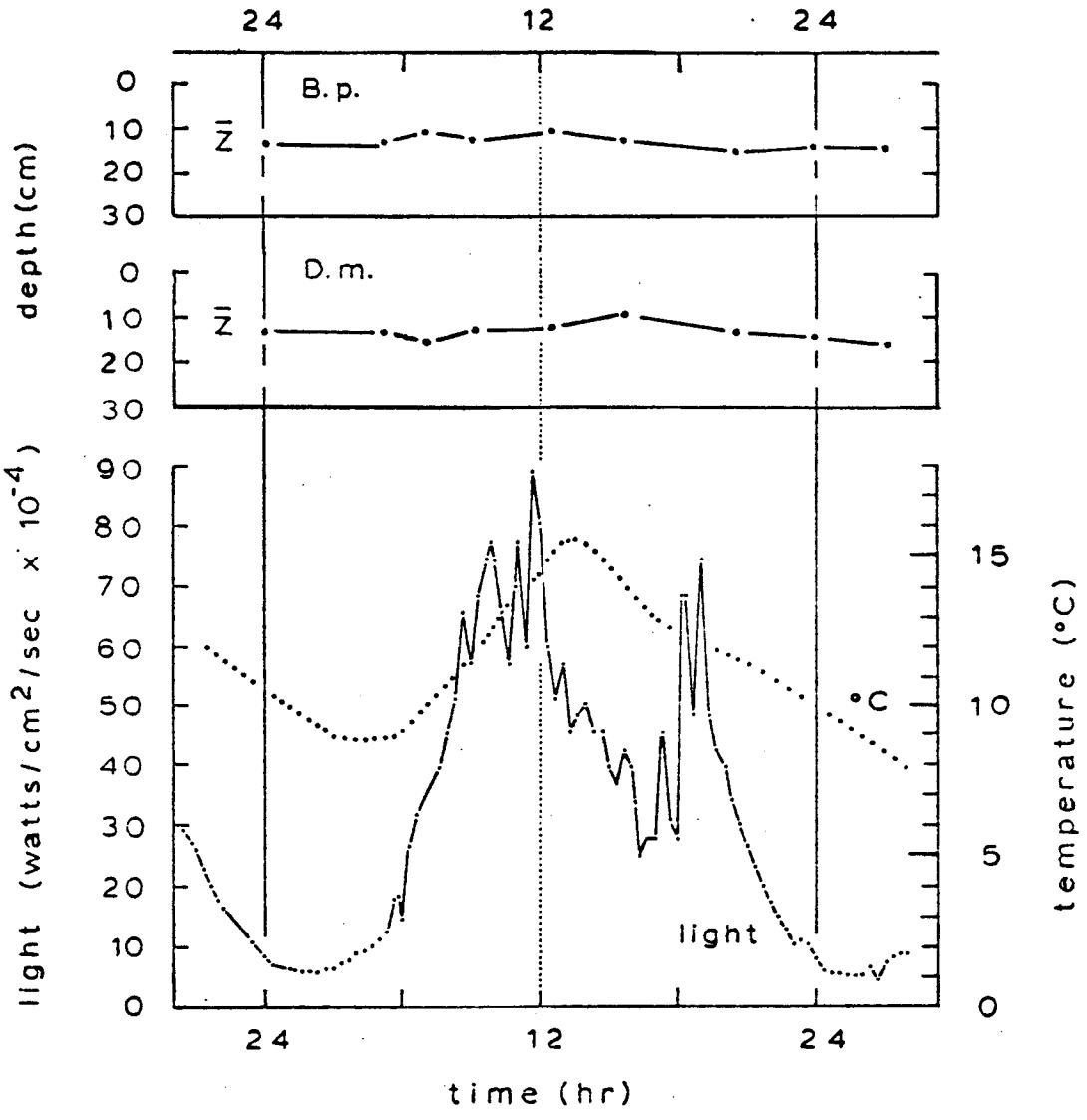

Figure 26. In situ diel studies in Pond S at Barrow. $\bar{z}$ = mean depth; B.P. = Branchinecta paludosa; D.M. = Daphnia middendorffiana.

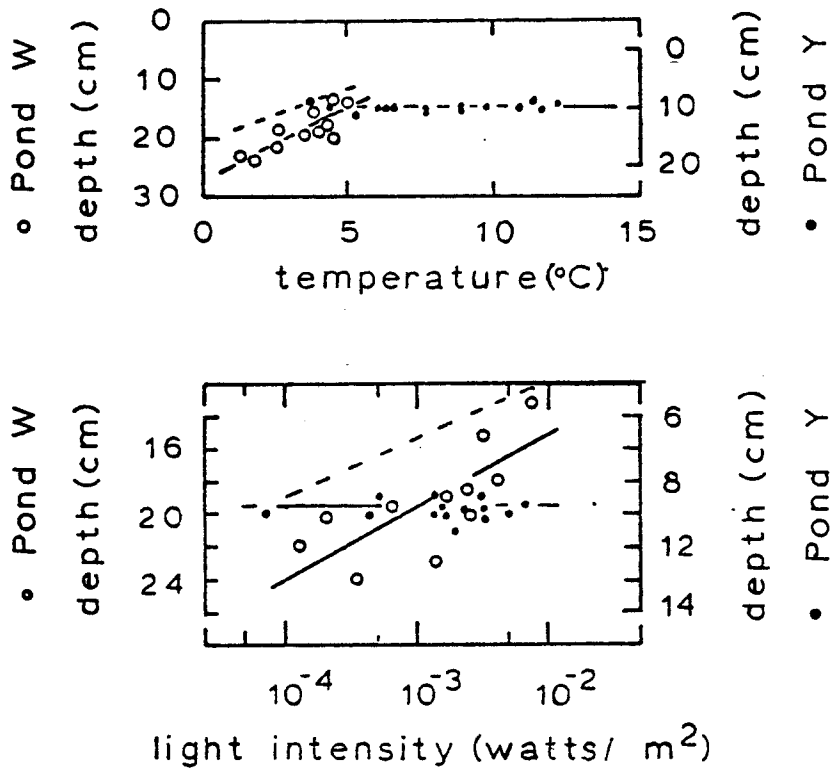

Figure 27. Pond Y and W, Barrow, Alaska. A: Correlations for temperature and mean depths. o = adults Pond W, • = adults Pond Y, solid lines = regressions for adults, dashed line = regression for juveniles of Pond W. B: Correlations for light intensity and mean depth. See A for symbol explanation.

Table 10

Correlations of mean depth with temperature (°C) and the log of the incident light intensity (I_o) for ponds. NS = nonsignificant correlation ($P \leq 90\%$); S = slightly significant ($P \leq 95\%$), ** = highly significant ($P \leq 99\%$).

		mean depth correlations		
Ponds (Barrow)	Species	°C	log I_o	df
6-8 VII,	D. middendorffiana	**	S	7
Pond S	B. paludosa	NS	NS	8
26-27 VII,	D. pulex (adult)	**	**	9
Pond W	D. pulex (juvenile)	**	**	9
3-4 VII,	D. pulex (adult)	NS	NS	13
Pond Y				

suggest that temperature rather than light regulates vertical migrations when they occur in shallow ponds under continuous sunlight. In comparison, light fluctuations of at least two orders of magnitude did not affect the distributions.

Column Studies

Light intensities at different depths in the lakes and in the experimental chamber were measured in order to compare light extinction in these two systems. Fig. 28 presents light curves measured on the same day in the experimental chamber and in Lake E-1, and suggests that light gradients in the 120 cm columns are comparable to the light gradient in the top 5-6 m of Lake E-1. A total of 42 populations representing eight species indigenous to Toolik and Barrow were studied in columns under conditions ranging from continuous sunlight at the summer solstice to long day photoperiods with measurable nighttime light intensities (i.e. continuous daylight). Differences between midnight and noon light intensities ranged from 39 fold near the solstice to 261 fold in the long day photoperiods. As in the pond studies, water temperatures fluctuated, and at times the temperature cycle was closely related to the diel light cycle. Food concentrations were not constant, but were above 5×10^4 cells ml^{-1}, and hence did not influence swimming behavior (Horton et al., 1979) or mean depth. Other environmental conditions remained fairly constant.

Table 11 summarizes the data from the column studies. Three of the studies are presented in Fig. 29. A significant correlation between temperature and mean depth was found in 61.9% of the populations studied. The slopes of the regression lines for these correlations ranged from -5.99 to +5.63 cm per °C, indicating that the effect of temperature on mean depth varied. Increasing temperatures rapidly depressed the mean depth when large positive slopes were found, and rapidly raised the mean depth when large negative slopes were found. Small slopes indicate that temperature had a minimal but significant effect on mean depth. When population

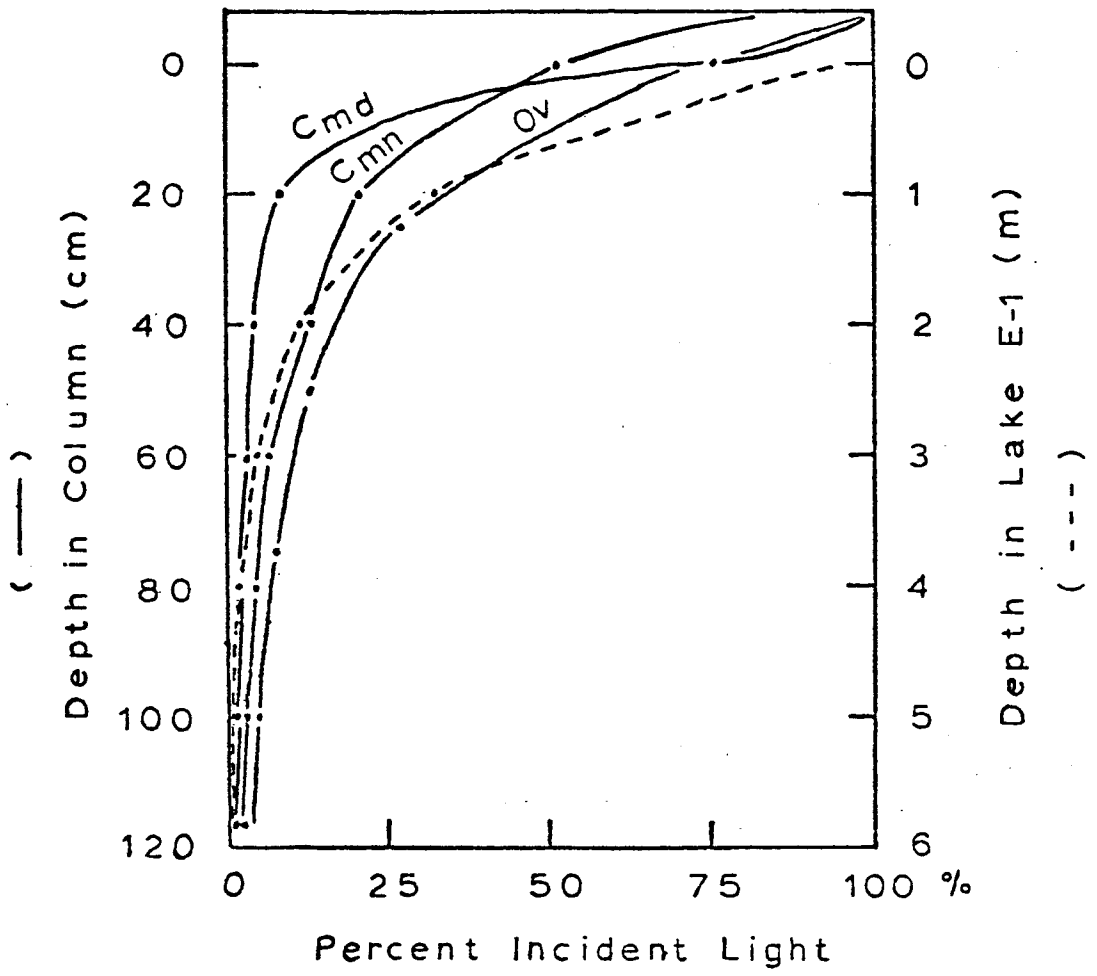

Figure 28. Light intensity versus depth in Lake E-1 (---) and in experimental chamber (——). C = 100% clear weather; OV = overcast; mn = midnight; md = midday. Light intensity measurements were made around noon and midnight in Lake E-1, but because the two extinction curves were nearly identical they were combined in this graph.

Table 11

Correlations of mean depth ($\bar{z}$) with temperature (°C) and the log of incident light intensity (I_o) for the columns. NS = nonsignificant correlation ($P \leq 90\%$); S = slightly significant ($P \leq 95\%$); * = significant ($P > 95\%$); ** = highly significant ($P > 99\%$). [1]studied at Barrow (all the other studies done at Toolik.) [2]See figure 10.

		$\bar{z}$ corr. with:		
Date	df	log I_o	°C	species
11-12 VI 77	12	**	**	D. middendorffiana (jv)
11-12 VI 77	18	**	**	"
26 VI 76	10	**	**	"
8-9 VII 77	20	**	**	D. middendorffiana (ad)
8-9 VII 77	20	**	*	"
8-9 VII 77	20	**	**	D. middendorffiana (jv)
20-21 VII 77	23	**	**	D. pulex (ad)
8-9 VII 77	20	**	**	D. longiremis typica (ad)
23 VII 77	11	**	*	"
26 VI 76	10	*	*	D. longiremis cephela (ad)
20-21 VII 77	23	*	**	"
26 VI 76	10	*	*	B longirostris (ad)
19-20 VI 77	19	*	NS	D. middendorffiana (ad)
25 VI 76[2]	14	*	NS	D. middendorffiana (jv)
29 VI 76	9	**	S	D. longiremis cephela (ad)
19-20 VI 77	19	S	**	D. middendorffiana (jv)
27 VI 76	9	NS	*	"
28 VI 76	9	NS	**	"
28 VI 76[2]	9	NS	*	"
29 VI 76	9	S	**	"
8-9 VII 77	11	NS	**	"
29-30 VI 77	16	NS	*	D. pulex (ad)
24 VII 77	17	S	**	D. longiremis typica (ad)
25 VII 77	12	NS	**	"
27-29 VII 76	8,9	S	*	"
11-12 VI 77	14,12	NS	*	P. hazeni
29-30 VI 77	16	NS	*	"
29-30 VI 77	16	NS	**	B. paludosa
13 VII 77	11	NS	*	"
29-30 VI 77	16	S	NS	D. middendorffiana (ad)
27 VI 77	9	NS	S	" (jv)
29 VI 76[2]	9	NS	NS	" (ad)
20-21 VII 77	23	S	S	D. longiremis typica (ad)
29-30 VII 77[1]	12	NS	NS	D. middendorffiana (jv)
29-30 VII 77[1]	12	S	NS	D. middendorffiana (ad)
29-30 VII 77[1]	12	NS	NS	"
13 VII 77	11	NS	S	D. pulex
28 VI 76[2]	9	NS	S	D. longiremis cephela (ad)
27 VI 76	9	NS	NS	"
13 VII 77	11	NS	NS	"
29 VI 76[2]	9	NS	NS	B. longirostris (ad)
20-21 VII 77	23	NS	NS	H. septentrionalis

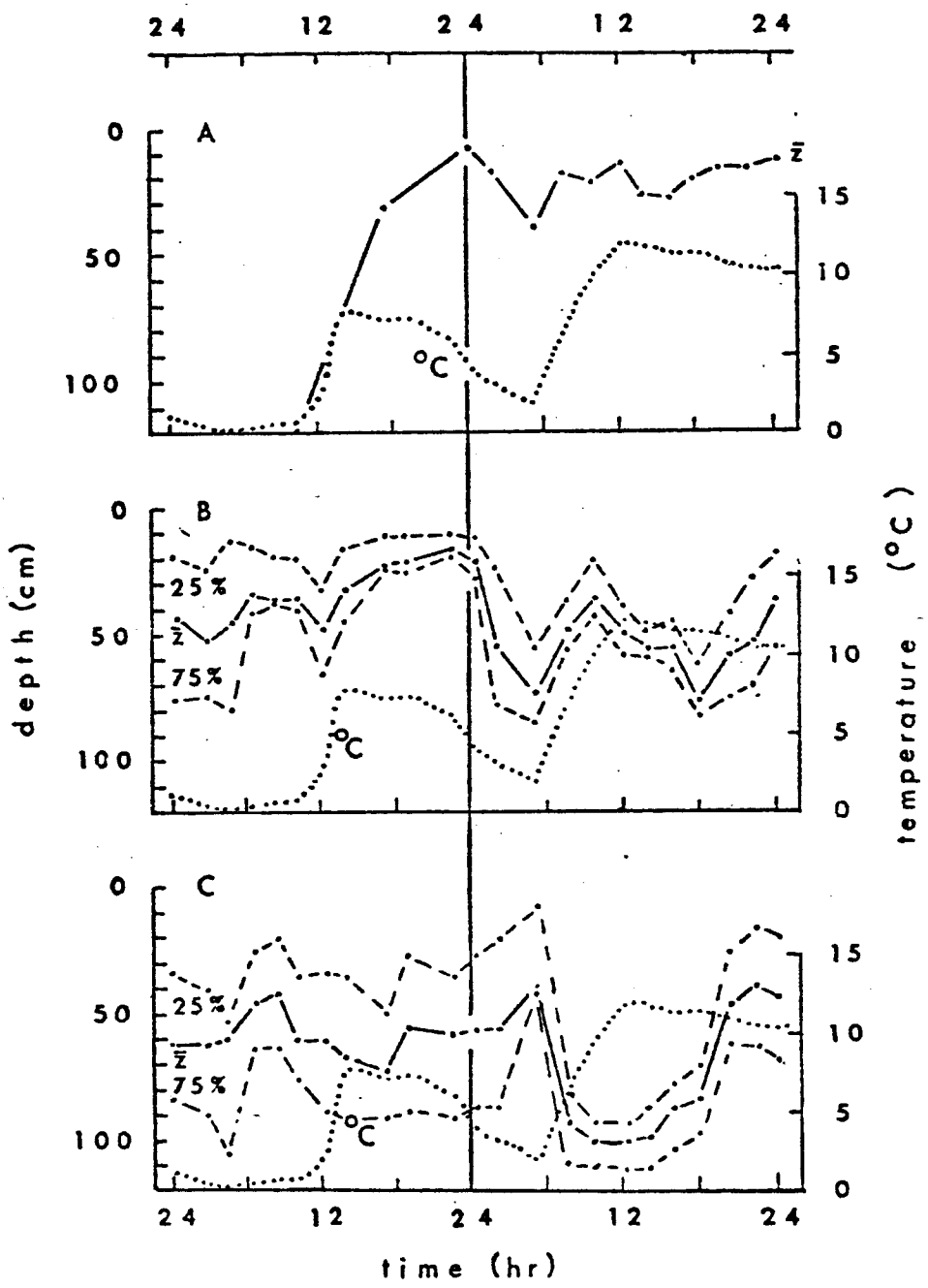

Figure 29. Column studies at Toolik, Alaska. $\bar{z}$ = mean depth; 25%, 75% = quartiles; °C = temperature. A: Bosmina longirostris, adults, 29 VI 76. B: Daphnia middendorffiana, juveniles, 28-29 VI 76; C: Daphnia longiremis cephela, adults, 28-29 VI 76. See table 6 for correlation coefficients of light and mean depth, and temperature and mean depth.

mean depth was strongly affected by temperature, a correlation between light intensity and mean depth sometimes was found (Table 11) and appears to be the result of a close relationship between incident light intensity and temperature in the columns. This temperature effect on the relationship between light intensity and mean depth was also seen in the pond studies and a diel cycle of migration occurred because of the 24 hour cycle in the light and temperature fluctuations.

In 31.0% of the studies, no correlations were observed between mean depth and light and between mean depth and temperature, and demonstrate that in the absence of a temperature effect on mean depth, absolute light intensity does not affect mean depth. These results contradict the preferendum hypothesis which predicts diel migrations in the column populations.

In 7.1%, or 3 out of 42, of the populations, a significant correlation was found between light intensity and mean depth but not between temperature and mean depth. It is interesting that these three populations were studied at the solstice or just afterwards, when diel fluctuations in light intensity were smallest and the preferendum hypothesis predicts the smallest migrations. Other factors may possibly be influencing mean depth in these studies.

Experimental Study

Water temperatures of four column populations were artificially cooled to experimentally test the effect of temperature on population mean depth. Columns were cooled by slowly and regularly adding ice to the top of the columns. Melt water sank and rapidly mixed with the warmer water of the columns. In each of the four column populations (two *D. longiremis* typica, one *D. pulex*, and one *D. longiremis* cephela), cooling by ice altered the mean depth of the population. When ice addition was stopped, the columns warmed and populations returned to previous levels (Fig. 30).

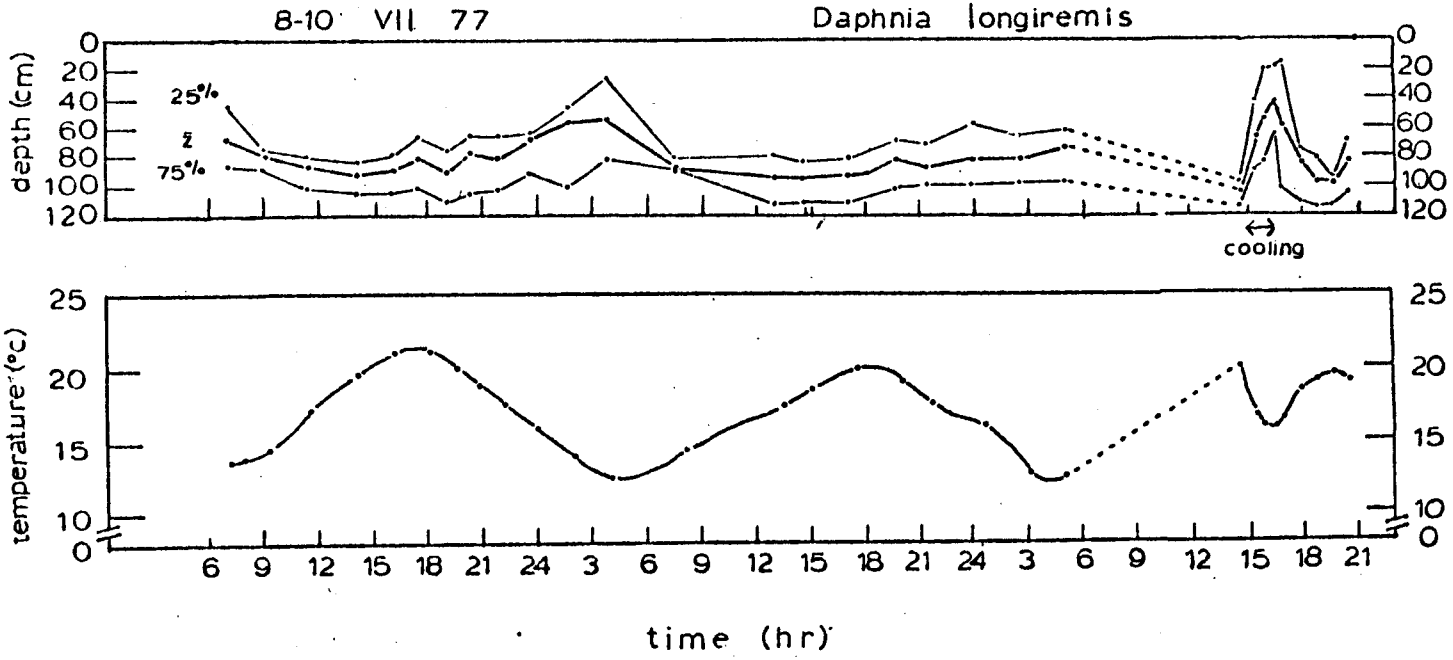

Figure 30. Experimental study of temperature effects on D. longiremis vertical distribution (see text for details). $\bar{z}$ = mean depth; 25%, 75% = quartiles.

Relationship of Light Stimulus to Vertical Displacement in Arctic Columns

In the DVM Room studies with D. magna the vertical displacement velocity was closely correlated with light stimulus during the evening period, but had no relationship during the daytime periods. Thus, it was of interest to determine whether this control on the speed of change in the population distribution also was effective under continuous light conditions. Both arctic zooplankton (D. middendorffiana and Bosmina coregoni), which were collected from the deep, clear Toolik Lake, showed a significant relationship between light stimulus and displacement velocity (Table 12). However, the temperate species which was imported to the arctic from the DVM Room culture (D. magna) did not show a significant correlation between these variables. This suggests that the arctic zooplankton have special adaptations to the arctic light environment which enable them to regulate their rate of population movement in the same fashion as the temperate species, i.e. using the relative rate of light change. Since the changes in light intensity are generally much less (stimulus values are lower) in the arctic in midsummer, such an adaption may simply involve a greater ability to perceive light changes. Such adaptations may be lacking in temperate zooplankton such as D. magna.

Table 12

Relationship between vertical displacement velocity and light stimulus (relative light change) in arctic column studies conducted at Toolik Lake, Alaska, 24-30 June 1976. *Daphnia middendorffiana* and *Bosmina coregoni* were collected from Toolik Lake and *Daphnia magna* was introduced from New Hampshire.

Species	Dependent Variable	Independent Variable	df	r	F	signif.
D. middendorffiana	velocity	stimulus	38	0.51	13.1	$P < 0.01$
Bosmina coregoni	velocity	log stimulus	15	0.68	13.1	$p < 0.01$
D. magna	velocity	log stimulus	35	0.15	0.83	N.S.

GENERAL DISCUSSION

Relevance of the Field Studies to Previous Temperate and Arctic Research

Evidence from the *in situ* and column studies of freshwater zooplankton exposed to continuous light and long day photoperiods in the Arctic demonstrated that diel fluctuations in light intensity do not cause diel vertical migrations. The results strongly suggest that absolute light intensity in the form of a preferred zone of light does not control daytime depth distributions of zooplankton populations.

The results of this investigation contradict earlier work conducted by Bogorov (1946) in the Arctic. Near the Arctic Circle, Bogorov observed a midnight increase in the numbers of zooplankton in the surface waters of the the White Sea, and he concluded that diel vertical migrations had occurred in continuous sunlight. In the Barents Sea which is north of the White Sea, Bogorov found no diel vertical migrations in continuous sunlight. He attributed the migrations in the White Sea to the greater fluctuations in light intensity over 24 hours and the lower intensities at midnight near the Arctic Circle. Although Bogorov mentions that surface waters are affected by tides in the White Sea which is surrounded by land and has a narrow opening into the Barents Sea, he does not investigate tidal effects on zooplankton vertical distribution. Rapid change in a number of environmental parameters are usually associated with tidal fluctuations in these circumstances (King 1969), and Turgeon (1976) demonstrates that zooplankton vertical distributions are affected by tides. Tides also affected the open waters of the Barents Sea, but considerable vertical mixing occurs (Zubov 1932, in Bogorov 1946) and large environmental changes were probably not experienced as a result of tidal fluctuations.

Digby (1961) studied the vertical distributions of zooplankton in two Spitzbergen fjords (79°N and 80°N) under continuous light, and his data and conclusions contradict each other. In an earlier

paper (1960), Digby predicted that diel fluctuations in light intensity would cause vertical migrations in zooplankton populations exposed to continuous sunlight. On several dates in July and August, Digby sampled the zooplankton distributions on one to three occasions over 24 hour periods. After pooling his data, Digby compared time of day to the depth interval in which the maximum density of each species was found (population maxima) and concluded that diel vertical migrations had occurred. Mean depths (a more sensitive and accurate estimate of population distribution) were calculated for the populations Digby sampled, using only the observations in which large numbers of zooplankton were present. When this was done, correlations did not occur between light intensity and population mean depth (Table 13), and the vertical distributions that Digby observed were apparently not controlled by absolute light intensity.

When light stimuli were too weak to stimulate diel vertical migrations, temperature was an important control of the vertical distribution and movements of zooplankton populations. Significant correlations between temperature and mean depth were found in 1 of the 3 pond studies and 26 of the 42 column studies conducted under continuous sunlight and long day photoperiods at Toolik and Barrow, Alaska. No clear differences were observed between the temperature responses of the Arctic species (D. middendorffiana, B. paludosa and P. hazeni) and the more temperate species. The mean depths of most species were relatively unaffected by temperature over a middle range, and were depressed when temperatures went above or below this middle range. Species differences were most clearly seen between the "pond" and "lake" species at Toolik. For a wide range of temperatures, D. middendorffiana and D. pulex, which are both typically found in ponds at Toolik, maintained high mean depths in the columns whereas the two races of D. longiremis, which are found in lakes in the Toolik region, maintained lower mean depths over the same temperature ranges (Fig. 12).

D. middendorffiana, which was repeatedly studied in the columns during 1976 and 1977, demonstrated an ability to acclimate to

Table 13

Reanalysis of Digby (1961). Correlations of mean depth and log of incident light intensity. NS = nonsignificant correlation ($P \leq 95\%$).

Correlation of mean depth with surface light intensity[1]

	Sorgat 1956 (0 - 50m series)"			Adventfjord 1948 (0 - 50m)"		
Species	Average Mean Depth	r	Signif.	Average Mean Depth	r	Signif.
Calanus VI ♀	25.9m	-.357	NS	20.8m	.391	NS
Calanus V	21.0m	.244	NS	22.5m	.545	NS
Calanus IV	21.4m	.147	NS	20.2m	-.483	NS
small Aglantha	13.8m	.245	NS			
Sagitta	24.8m	.192	NS			
Limacina	9.5m	-.204	NS			
Themisto	31.9m	.173	NS			
Crab larvae	20.1m	.086	NS			

changing environmental temperatures. The critical temperature above which the mean depth of D. middendorffiana was depressed by increasing temperatures shifted to a warmer temperature as pond temperatures increased in July (compare June and July data for D. middendorffiana in Fig. 12). No shift was seen in either race of D. longiremis (Fig. 31). However, both races are usually found at or below the thermocline in deep lakes in the Toolik area and because they did not migrate, the populations as a whole did not experience warm temperatures in the summer. D. longiremis typica were collected from above (0 - 3 m) and below (8 - 10 m) the thermocline in Lake E-1 on 24 July and observed in columns on 25 July, 1977. Mean depths of the individuals collected from the deeper waters were approximately 28.5 cm deeper in the column than those of individuals collected from surface waters, suggesting that individuals within non-migratory lake populations are acclimated to different temperature ranges.

In temperate regions, rapid changes in light intensity cause the downward, sunrise migration of zooplankton (Ringelberg 1964, McNaught and Hasler 1964, Haney and Hall 1975), and the extent of the migration initially determines the day depths of the populations. However, light stimuli for the phototactic swimming response are subthreshold during the daytime and other factors assume control of the vertical distributions of zooplankton. Kikuchi (1930, 1937), Plew and Pennak (1949), Brooks (1964), and others have observed seasonal variation in daytime vertical distributions of zooplankton in temperate lakes and oceans and have suggested that zooplankton respond to seasonal changes in the temperature gradients of these systems, although the sunrise migrations may have confused their results. Parker (1902), Kikuchi (1938) and others have demonstrated the influence of temperature on population mean depth under constant conditions in the laboratory. This investigation demonstrated the temperature effects on population mean depth in situ and in the absence of diel vertical migrations. This investigation also demonstrated that absolute light intensity does not control the

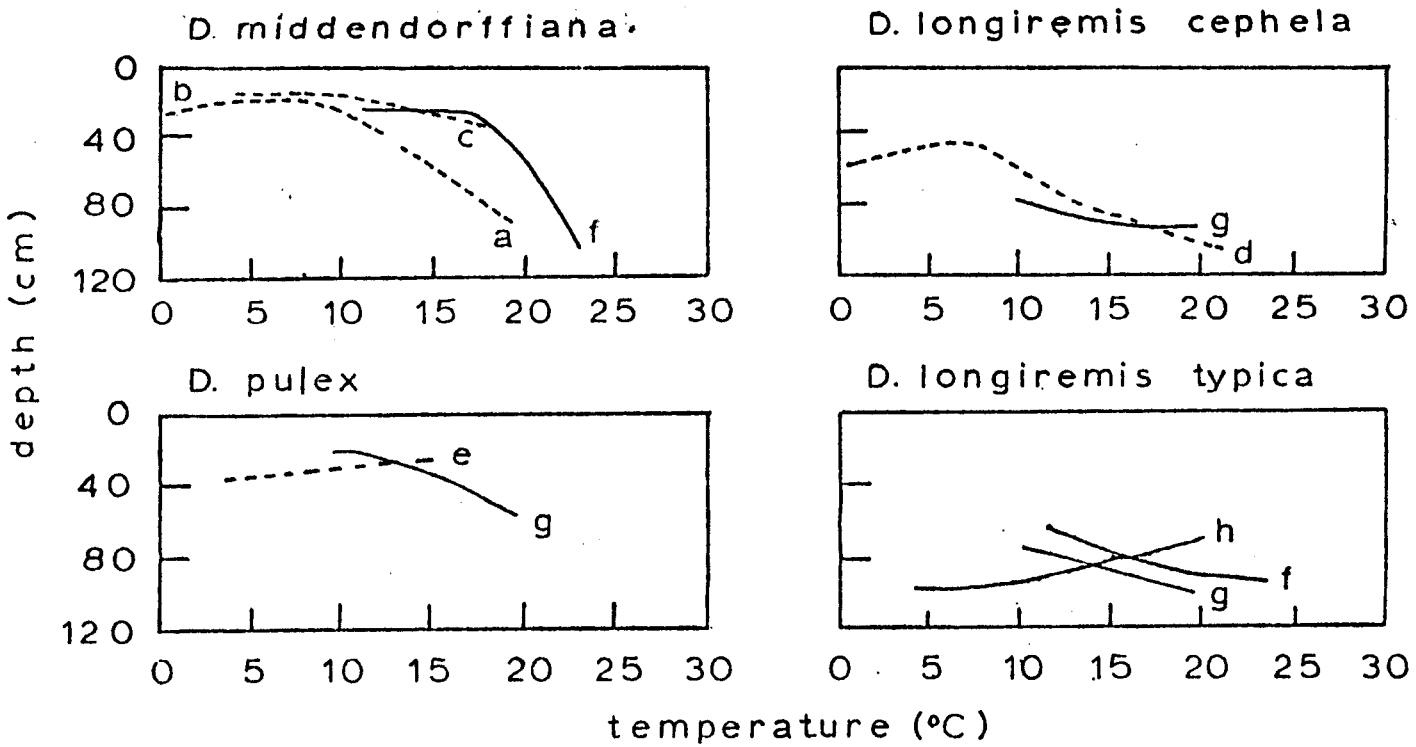

Figure 31. Relationship between mean depth ($\bar{z}$) and temperature for four species indigenous to Toolik. Solid lines = June studies; dashed lines = July studies; a = 11-12 June 1977; b = 19-23 June 1977; c = 24-25 June 1976; d = 24-30 June 1976; e = 29-30 June 1977; f = 8-10 July 1977; g = 20-21 July 1977; h = 23-24 July 1977.

daytime vertical distributions of zooplankton populations exposed to natural light fluctuations. The preferendum hypothesis, therefore, does not adequately explain the primary control of zooplankton vertical distribution during the daytime.

Implications of this Study to Models of Depth Control and Grazing

In this study we have concentrated on identifying some of the important factors which regulate the daytime depth of zooplankton. Results of the DVM Room investigations indicate the importance of food concentration in the regulation of day-depth. Also, the rate at which the population moves is independent of light changes in midday, but becomes a function of light stimulus in the evening. Arctic animals appear to employ this "evening" mechanism in the control of their rate of vertical displacement throughout the day. Both the *in situ* and column field studies under continuous light in the arctic demonstrate that temperature may also regulate day-depth. In all of these studies, absolute light intensity appeared to have no important role in depth regulation of the zooplankton.

Because of the complexity of the DVM phenomenon, this study has dealt with one simplified aspect (day-depth control) of a multi-compartmental model needed to describe the diel changes in zooplankton vertical distribution. Many factors which were not considered in this investigation, such as thermal and chemical stratification, age and molt state of the animals and food quality effects, e.g. filamentous vs non-filamentous algae, are probably also important in nature and need to be considered in further research as the complexity of the model systems is increased.

A control model describing the factors regulating zooplankton grazing has been proposed (Fig. 32). Although it is premature at this time to propose a parallel model of the factors regulating day-depth and the diel vertical migration of zooplankton, the relationships defined in this study should contribute toward the achievement of this goal and of the eventual coupling of the two models to predict the effect of zooplankton grazing in nature.

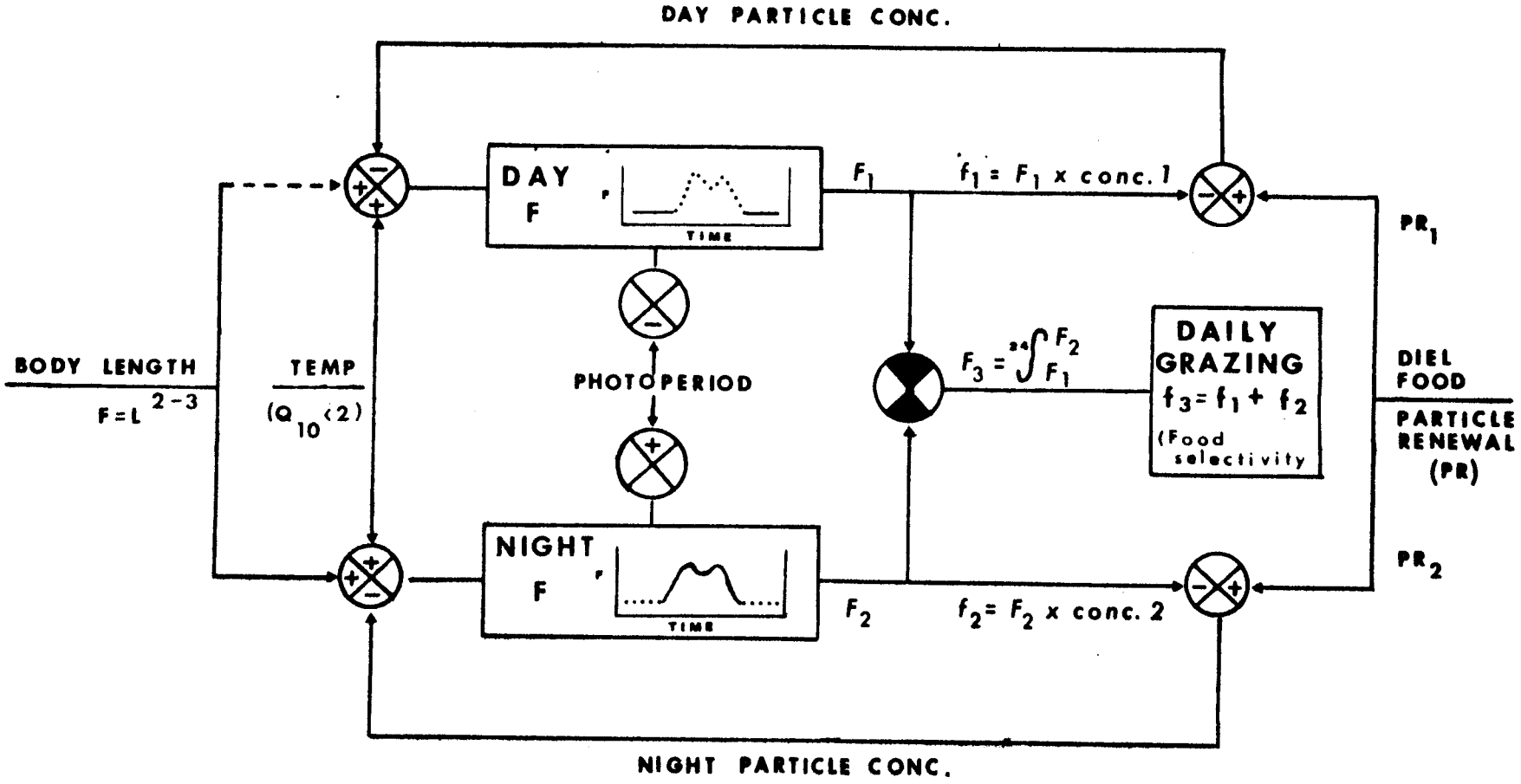

Figure 32. A control model describing the regulation of zooplankton grazing by food concentration, temperature, body size and photoperiod.

SUMMARY OF RESULTS

1. A method was developed to study factors influencing the vertical distribution of zooplankton under controlled conditions.
2. Light transmission characteristics of the model lakes (2.3 meter columns) closely approximated natural lakes. Light characteristics were nearly identical in all columns. Due to the lack of skylight laboratory columns received less ultraviolet light at noon and less blue light at sunset than is present in incident light in the field. Relative light changes (light stimulus) in the columns were comparable to those measured in nature.
3. Daphnia populations in the laboratory columns exhibited diel vertical changes similar to vertical migrations in lakes with maximum mean depth at noon and minimum mean depth at night.
4. The effects of light intensity and food concentration on day-depth of Daphnia populations were examined in the laboratory columns. The influence of light and temperature were tested under continuous light in lakes and ponds and in columns in the arctic.
5. Rate of vertical displacement of the Daphnia populations was correlated with light stimulus during the evening period in the laboratory under temperate light conditions. Under continuous light in the arctic only arctic zooplankton species showed this linear relationship between speed of movement and relative light change.
6. Absolute incident light intensity and mean depth of the zooplankton populations were related with linear regression analysis. Light intensity was generally not a significant factor in controlling day-depth in either laboratory or arctic field populations.
7. Food concentration had a highly significant effect ($r = -0.86$) on day-depth in the laboratory columns with natural light changes and low food densities. Addition of light as a second variable in a multiple regression was an improvement over the simple linear regression, the two factors accounting for 85% (r^2) of the variability in mean depth.

8. A highly significant linear regression ($r = 0.91$, $n = 30$) was found for the effect of high food concentration on day-depth under constant daytime light. Some time dependency was found with population mean depth if observations before 1040 h were included in the multiple regression of mean depth vs. food concentration and time of day. This reflects the gradual upward movement of Daphnia in the columns under constant light, indicating the importance of endogenous control of day-depth.
9. The combined data of the high and low food concentration experiments were described with a highly significant ($p < 0.001$) linear regression: mean depth (cm) = $272.68 - 50.98 \cdot \log_{10}$ food conc. (cells ml^{-1}), in which 80% of the mean depth variation was accounted for by food concentration.
10. Investigations were made of the short-term effects of food concentration. Additions of food resulted in almost immediate upward movements of the Daphnia population at all depths, with maximum response after about 1 h and a sinking to lower depths only slightly higher than the original level after about 2-3 h. The final depth established after 2-3 h is roughly the mean depth predicted by the linear regression model of mean depth is food concentration (see 9 above). This "overshoot" response to food additions appears to be related to the hunger response previously reported in feeding studies with Daphnia.
11. Diel studies of vertical distributions of zooplankton populations were carried out under continuous light and long day photoperiods in the Arctic.
12. In situ studies were done at Toolik, Alaska; Barrow, Alaska; and Resolute Bay, N.W.T. Populations were also studied in plexiglas columns, surrounded on four sides by a light tight chamber and exposed to natural light from above.
13. Population mean depth frequently was affected by water temperature fluctuations which caused vertical movements in the population mean depths (1 of the 3 pond studies, 26 of the 42 column studies). Temperature fluctuations which affected mean depth were not regular and not necessarily diel.

14. No correlations between incident light intensity and mean depth were observed in the *in situ* lake studies. Temperature profiles remained almost constant in these studies. One of the three pond studies and 15 of the 42 column showed significant correlation between incidents I_o and $\bar{z}$; however, these correlations were accompanied by correlations between temperature and mean depth (except in 3 column studies). In view of the strong correlations of light and temperature which were found in the ponds and columns, and the fact that the apparent light effects were not consistent, it was concluded that temperature actually caused the changes in $\bar{z}$ in these studies.
15. From the arctic investigations it was concluded that absolute light intensity was not a major factor controlling the depth distribution of zooplankton under continuous or long-day photoperiods. This contradicts the preferendum hypothesis of diel vertical migration and day-depth control. The data of Digby (1961) are reanalyzed and the conclusions of Digby (1961) and Bogorov (1946) are questioned.
16. Implications of the results of this study to models of depth control and grazing by zooplankton are discussed.

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