ARCTIC INVESTIGATIONS OF SOME FACTORS THAT CONTROL THE VERTICAL DISTRIBUTIONS AND SWIMMING ACTIVITIES OF ZOOPLANKTON

CLAIRE L. BUCHANAN

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ARCTIC INVESTIGATIONS OF SOME FACTORS
THAT CONTROL THE VERTICAL DISTRIBUTIONS
AND SWIMMING ACTIVITIES OF ZOOPLANKTON

BY

CLaire L. Buchanan
B.A., University of Rochester, 1972

A DISSERTATION

Submitted to the University of New Hampshire
in Partial Fulfillment of
the Requirements for the Degree of

Doctor of Philosophy

in

Zoology

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Date
Oct. 31, 1978
ACKNOWLEDGEMENTS

This work was funded at various times by the Central University Research Fund (grant #S61), the Water Resources Research Center (grant #A-044-NH), the National Science Foundation (grant #DPP76-80605).

I especially want to thank my advisor, James Haney, for the innumerable conversations we have had concerning the methods, goals and interpretations of this work, for his help in performing many of the exhausting diel studies, for his constructive criticisms of this manuscript, and particularly for giving me the valuable freedom to learn from my own mistakes. I would like to thank Alan Baker, Larry Harris, and Philip Sawyer for their patience with and interest in the evolution of the research ideas and plans of this dissertation and their research suggestions. I also want to thank them and James Taylor for their helpful comments on this manuscript. I gratefully acknowledge the encouragement, assistance, and valuable insights of Mark Mattson, Carl Watras, John Hobbie, John O'Brien, and the other members of the University of New Hampshire Department of Zoology and the RATE project; and the encouragement and support of my family.
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ABSTRACT

ARCTIC INVESTIGATIONS OF SOME FACTORS WHICH CONTROL THE VERTICAL DISTRIBUTIONS AND SWIMMING ACTIVITIES OF ZOOPLANKTON

by

CLAIRE L. BUCHANAN

The vertical distributions and movements of zooplankton populations in arctic lakes and ponds were studied. Plexiglas columns, which were surrounded on four sides by a light tight chamber and exposed to natural light from above, were used to study the vertical distributions and movements in closer detail and to measure zooplankton swimming rates. Populations did not undergo diel vertical migrations under continuous light or under long day photoperiods with dark nights. These findings contradict the preferendum hypothesis of vertical migration and daytime depth control which predicts that zooplankton populations migrate vertically to maintain a preferred zone of light intensity during the daytime. Extreme temperatures depressed the population mean depth, and diel temperature fluctuations could cause vertical movements in pond and column populations. A diel cycle was observed in the swimming rates of zooplankton populations exposed to both continuous light and long day photoperiods, with highest rates in the afternoon and sometimes in the morning. The cycle of swimming activity appears to be based in an endogenous rhythm, and could cause a slight vertical
migration in zooplankton populations when phototactic orienta-
tion cues were weak. Zooplankton were transferred north and
south to different light cycles to test the dependence of
the diel cycle of swimming activity upon light. High or low
temperatures changed the absolute rate of swimming activity
but apparently did not affect the timing of the diel cycle.
The behavior of a temperate species, *D. magna*, which was
imported from New Hampshire, was similar to the behavior of
species indigenous to the Arctic. The association of zooplankton
behavior with morphological and physiological features and
the variation in vertical distribution caused by environ-
mental and physiological factors are discussed in terms of
the selective forces on vertical migrations.
GENERAL INTRODUCTION

The Arctic provides a unique area in which to study the environmental controls of diel vertical migrations of zooplankton populations. It is generally accepted that the diel light-dark cycles in temperate and tropic regions, and especially the rapid changes in the light environment around sunset and sunrise, play an important role in regulating the diel vertical migrations. Because these light-dark cycles are never absent in temperate and tropic regions, hypotheses concerning the stimuli and mechanisms of vertical movement and the controls of depth distribution have necessarily been tested in the laboratory under artificial light responses (e.g. Heberdey 1949, Scheffer et al. 1958, Hazen and Baylor 1962, Ringelberg 1964, Waterman 1960, Siebeck 1968, McNaught 1971, Ringelberg and Servaas 1971) and the effects of environmental conditions on zooplankton light responses (e.g. Clarke 1930, 1932, Baylor and Smith 1957, Itoh 1970, Stavn 1970, Kikuchi 1930, 1931) have become more apparent, laboratory tests of hypotheses concerning diel vertical migrations have faced the necessity of simulating natural light environments in order to allow a more direct comparison of laboratory results with data from the field. In the Arctic, experimental tests of the hypotheses can be done in situ and in experimental apparatus under naturally occurring extreme light cycles.

In the Arctic during midsummer, the sun is continuously above the horizon. The rapid changes in light which are usually
associated with the evening and morning and the lack of light which is associated with the night in temperate and tropic regions do not occur. Except when altered by clouds, diel changes in light intensity are slow and light intensities remain relatively high throughout the day. When the sun begins to go below the horizon for a few hours each day, night conditions approach those at lower latitudes. However, changes in the light environment at sunset and sunrise remain slow. Several weeks before the autumnal equinox, the diel pattern of light fluctuations in the arctic is directly comparable to those in the temperate and tropic regions (figure 1). Diel studies of vertical distributions and movements of zooplankton populations conducted in midsummer, late summer, and autumn in the Arctic consequently compare the behavior of zooplankton under continuously high light intensities, alternate light-dark with a slow rate of change at sunset and sunrise, and alternate light-dark with a rapid rate of change at sunset and sunrise.

In Parts I and II of this dissertation, I present the results of several diel studies conducted in the Alaskan and Canadian Arctic during summer and autumn. Experiments were designed to test several current hypotheses concerning the stimuli and other environmental controls of diel vertical migrations of zooplankton. Part III discusses variation in vertical distributions of zooplankton and speculates on the interactions of zooplankton behavior and selective forces.
Fig. 1. Light curves for clear days at 68°N (solid line) and 74°N (dashed line). Arrows indicate sunset and sunrise on 24 July (▼ △), 24 August (▼ △), and 24 September (▼ △). Light curves for 68°N are based on measurements made with an International Light model 700 radiometer (June - August) at Toolik, Alaska, and measurements made by the Smithsonian Institution (September) (Smithsonian Meteorological Tables, 1918). Light curve for 74°N is based on measurements made with a pyranometer (Eppley model 2) at Resolute Bay, N.W.T., 1973.
PART I

THE EFFECTS OF LIGHT INTENSITY AND TEMPERATURE ON THE VERTICAL DISTRIBUTIONS OF ZOOPLANKTON EXPOSED TO CONTINUOUS LIGHT AND LONG DAY PHOTOPERIODS IN THE ARCTIC

Introduction

Light is generally recognized as the primary factor controlling the diel vertical migrations of zooplankton. These daily movements of zooplankton populations between upper and lower water layers occur at sunset and sunrise in temperate regions (e.g. McNaught and Hasler 1964, Haney and Hall 1975), and involve phototactic swimming responses to rapid changes in light intensity (Ringelberg 1964). The extent of the downward movement of the zooplankton population at sunrise initially determines the daytime vertical distributions of zooplankton populations. However, these distributions rarely remain at a constant level during daylight hours. Rose (1925), Russell (1927), and others have suggested that daytime vertical distribution is a function of light penetration in the water. They propose that zooplankton occupy an optimum or preferred zone of light intensity that moves vertically in the water column as incident light intensity increases and then decreases during the day (preferendum hypothesis). If zooplankton encounter physical barriers as they follow a zone of light intensity, they are forced to acclimate to new light intensities. However, if no barriers are encountered,
a continual movement of the population is predicted by the preferendum hypothesis and changes in the vertical distribution would correlate with changes in incident light intensity. Other workers have determined experimentally that changes in vertical distribution can be caused by temperature (e.g. Parker 1902, Kikuchi 1930, 1938, Russell 1927), angular light distribution (e.g. Schallek 1943, Itoh 1970, Siebeck and Ringelberg 1969), different chemicals (review in Russell 1927), currents (Stavn 1970, 1971), and circadian rhythms of swimming activity (e.g. Hart and Allanson 1976, LaRow 1968, 1969).

Because of the dominant role of the downward, sunrise migrations in initially positioning zooplankton populations, the effects of other factors on daytime vertical distribution are difficult to study in temperate and tropic lakes. In the Arctic, daily rates of change in light intensity are slow in continuous light and long day photoperiods, and should not stimulate the phototactic swimming responses of zooplankton. Under these light conditions, controls of daytime vertical distribution can be studied in situ.

This investigation was conducted over a 4 year period from 1973 - 1977. The vertical distributions and movements of freshwater zooplankton were studied in 1973 at Resolute Bay, N.W.T. (74°40'N), in 1975 - 1977 at Barrow, Alaska (71°18'N), and in 1976 - 1977 at Toolik, Alaska (68°37'N) (figure 2). Diel studies were done under continuous light and long day photoperiods to test the light preferendum hypothesis over a range of light cycles. Major characteristics of the light environments at Toolik, Barrow and Resolute Bay are given in
Fig. 2. Map of North American Arctic.
table 1. The difference between the sun’s angle of incidence (angle made by the zenith, the observer, and the sun) at midnight and noon is greatest at Toolik, so diel fluctuations in light intensity are greater at Toolik than at the higher latitudes during continuous sunlight conditions.

Method and Materials

The vertical distributions and movements of in situ zooplankton populations were estimated by regularly sampling at several depths in the lakes and ponds. Vertical distributions were directly observed in populations placed in clear plexiglas columns and exposed to natural changes in light. Six cladoceran, three copepod, and two anostracan species were studied in this investigation. The arctic locations where the species were studied and their geographic distributions in North America are summarized in table 2. The ponds that were studied are Ponds W, Y, and S at Barrow, and the lakes are Toolik Lake, Lake E-1 and Lake N-5 at Toolik, and Ruins Lake at Resolute Bay. Column studies were done at Toolik and Barrow.

In situ studies. Plankton closing nets (153u) were used to collect 2 samples at each depth interval from lakes in the Toolik area (Toolik Lake: 30cm diameter net; Lake E-1: 12cm diameter net). A 30 liter Schindler trap was used to collect 3 samples at each depth interval in Ruins Lake, Resolute Bay. Samples were preserved in 4% formalin with 40g/liter sucrose (Haney and Hall 1973), and later counted with a dissecting microscope.
Table 1. Major characteristics of the light cycles at Toolik and Barrow, Alaska, and Resolute Bay, N.W.T. These dates were calculated from Smithsonian Institution records, 1918, and the local terrain will affect the actual dates.

<table>
<thead>
<tr>
<th></th>
<th>Toolik (68°37'N)</th>
<th>Barrow (71°18'N)</th>
<th>Resolute Bay (74°40'N)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Difference between $\Delta$ incidence of the sun at solar noon and solar midnight</td>
<td>42°46'</td>
<td>37°24'</td>
<td>30°40'</td>
</tr>
<tr>
<td>last sunset in spring</td>
<td>May 20</td>
<td>May 12</td>
<td>April 29</td>
</tr>
<tr>
<td>first sunset in autumn</td>
<td>July 17</td>
<td>August 2</td>
<td>August 12</td>
</tr>
<tr>
<td># days of continuous sunlight</td>
<td>57</td>
<td>83</td>
<td>105</td>
</tr>
<tr>
<td>highest $\Delta$ incidence experienced, i.e. summer solstice, solar noon</td>
<td>45°10'</td>
<td>47°51'</td>
<td>51°13'</td>
</tr>
<tr>
<td>(approximate $\Delta$ above the real horizon)</td>
<td>(46°)</td>
<td>(43°)</td>
<td>(40°)</td>
</tr>
</tbody>
</table>
Table 2. List of species which were studied, and their geographic distributions. Study sites and methods are included. 
T = Toolik; RB = Resolute Bay; B = Barrow. 1 = columns, 2 = in situ.

<table>
<thead>
<tr>
<th>species</th>
<th>site</th>
<th>method</th>
<th>distribution</th>
</tr>
</thead>
<tbody>
<tr>
<td>Daphnia middendorffiana</td>
<td>T, RB, B</td>
<td>1, 2</td>
<td>arctic and alpine</td>
</tr>
<tr>
<td>Daphnia pulex</td>
<td>T, B</td>
<td>1, 2</td>
<td>widespread</td>
</tr>
<tr>
<td>Daphnia longiremis typica</td>
<td>T</td>
<td>1, 2</td>
<td>northern</td>
</tr>
<tr>
<td>Daphnia longiremis cephela</td>
<td>T</td>
<td>1, 2</td>
<td>northern</td>
</tr>
<tr>
<td>Bosmina longirostris</td>
<td>T</td>
<td>1, 2</td>
<td>widespread</td>
</tr>
<tr>
<td>Holopedium gibberum</td>
<td>T</td>
<td>2</td>
<td>widespread</td>
</tr>
<tr>
<td>Diaptomus tyrelli</td>
<td>T</td>
<td>2</td>
<td>northern</td>
</tr>
<tr>
<td>Heterocope septentrionalis</td>
<td>T</td>
<td>1, 2</td>
<td>northern</td>
</tr>
<tr>
<td>Cyclops scutifer</td>
<td>T</td>
<td>2</td>
<td>northern</td>
</tr>
<tr>
<td>Polyartemiella hazeni</td>
<td>T</td>
<td>1, 2</td>
<td>arctic</td>
</tr>
<tr>
<td>Branchinecta paludosa</td>
<td>T, B</td>
<td>1, 2</td>
<td>arctic</td>
</tr>
</tbody>
</table>
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 0.5m/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 \(104cm^2\), \sim 500u
netting) was used to sample the sparse populations of Pond S.
A series of plastic cylinders, each 5 cm long with 330u netting
on one end (\(3.14cm^2\) area), were mounted at 5cm 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 30cm, and 5cm deep), backed on one
side with 330u 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 5cm, with plexiglas crosspieces so that incoming
animals were separated into 5cm depth intervals.

Column studies. The experimental apparatus consisted of plexiglas
columns of various sizes (10 x 10 x 120cm, 15 x 15 x 120cm)
filled with water and placed centrally in a blackened chamber
constructed out of black plastic with a hole \sim 100cm diameter
in the ceiling to allow incident lighting from above (figure 3).
The purpose of arranging the experimental chamber and columns
in this manner was to create a vertical gradient of mostly
Fig. 3. Experimental chamber.
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 (15μ) 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 waters 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 hours. 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 1950, Heberdey 1938, Ringelberg 1969, Viand 1938) of the columns.

The vertical distribution of zooplankton in an experimental column was measured by counting the numbers of animals per 10cm depth interval (at .5 - 2 hour intervals). The weighted mean depth, \( \bar{z} \), was calculated in the following manner:

\[
\bar{z} = \frac{\sum (n_z \cdot z)}{N}
\]
where \( n_z \) is the number of individuals at depth \( z \), and \( N \) is the total number of individuals. Quartiles were calculated according to the method described by Pennak (1943).

After each series of observations, the temperature profile was measured and a 2ml aliquot of an algal culture (approximately \( 2 \times 10^5 \) cells) was usually added to each column at this time, depending on the feeding schedule of the experimental animals.

**Light measurements.** Continuous measurements of whole light were made from an International Light radiometer (model 700) with a vacuum photodiode, and were recorded on a Hewlett-Packard chart recorder. 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 400nm 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. For a
description of arctic light conditions, see Digby (1960).
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 photopig-
ments in daphnids (McNaught 1971).

Intensities at different depths in the lakes and in
the experimental chamber were measured in order to compare
light extinction in these two systems. Figure 4 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 5-6m of Lake E-1.

Results
In situ lake studies. Seven diel studies of the vertical
distributions of lake zooplankton were done at Toolik and
Resolute Bay (table 3). 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 $3.4 - 4.6 \times 10^{-5}$ watts cm$^{-2}$. Under
continuous sunlight, midnight intensities were $2.5 - 2.7 \times 10^{-4}$
Fig. 4. 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 3. Maximum change in mean depth (\(z\)) 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 \(z\) predicted by the preferendum hypothesis.

<table>
<thead>
<tr>
<th>Photoperiod</th>
<th>Light Isopleths</th>
<th>Species</th>
<th>Max. change in (z) (m)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ruins Lake</td>
<td>5 - 4 VIII 73</td>
<td></td>
<td></td>
</tr>
<tr>
<td>LD 24:0h</td>
<td>(1.5m)**</td>
<td>D. middendorffiana</td>
<td>1.6</td>
</tr>
<tr>
<td>Lake N-9</td>
<td>6 - 7 VII 77*</td>
<td></td>
<td></td>
</tr>
<tr>
<td>LD 24:0h</td>
<td>(2.0m)**</td>
<td>D. middendorffiana(6cm)</td>
<td>1.6</td>
</tr>
<tr>
<td></td>
<td></td>
<td>(7th)</td>
<td>0.13 (R)</td>
</tr>
<tr>
<td>Toolik Lake</td>
<td>20 - 21 VII 76</td>
<td></td>
<td></td>
</tr>
<tr>
<td>LD 22.7:1.2h</td>
<td>9 - 13.3h</td>
<td>D. middendorffiana</td>
<td>2.76 (R)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>D. longiremis cepheia</td>
<td>1.32</td>
</tr>
<tr>
<td></td>
<td></td>
<td>D. tyrelli</td>
<td>1.2</td>
</tr>
<tr>
<td></td>
<td></td>
<td>B. longirostris</td>
<td>1.57</td>
</tr>
<tr>
<td></td>
<td></td>
<td>H. septentrionalis</td>
<td>0.49</td>
</tr>
<tr>
<td></td>
<td></td>
<td>K. gibberum</td>
<td>2.14</td>
</tr>
<tr>
<td></td>
<td></td>
<td>D. scutifer</td>
<td>1.24</td>
</tr>
<tr>
<td>Lake E-1</td>
<td>23 - 24 VII 77</td>
<td></td>
<td></td>
</tr>
<tr>
<td>LD 22:2h</td>
<td>7 - 9 m</td>
<td>D. longiremis typica</td>
<td>2.22</td>
</tr>
<tr>
<td></td>
<td></td>
<td>B. longirostris</td>
<td>1.45</td>
</tr>
<tr>
<td></td>
<td></td>
<td>K. gibberum</td>
<td>0.96</td>
</tr>
<tr>
<td></td>
<td></td>
<td>D. tyrelli</td>
<td>1.58</td>
</tr>
<tr>
<td>Toolik Lake</td>
<td>27 - 28 VII 76*</td>
<td></td>
<td></td>
</tr>
<tr>
<td>LD 20.9:3.1h</td>
<td>12 - 17m</td>
<td>D. middendorffiana</td>
<td>2.01 (R)</td>
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<tr>
<td></td>
<td></td>
<td>D. longiremis cepheia</td>
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</tr>
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<td></td>
<td></td>
<td>K. gibberum</td>
<td>1.48</td>
</tr>
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<td></td>
<td>B. longirostris</td>
<td>1.37</td>
</tr>
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<td></td>
<td></td>
<td>D. tyrelli</td>
<td>1.64</td>
</tr>
<tr>
<td></td>
<td></td>
<td>C. scutifer</td>
<td>0.48 (R)</td>
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<tr>
<td></td>
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<td>H. septentrionalis</td>
<td>3.90 (R)</td>
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<td>&quot;</td>
<td>2.62 (R)</td>
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<tr>
<td>Toolik Lake</td>
<td>11 - 12 VII 75*</td>
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<td></td>
</tr>
<tr>
<td>LD 19.2:1.3h</td>
<td>7m**</td>
<td>D. tyrelli</td>
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</tr>
<tr>
<td></td>
<td></td>
<td>B. longirostris</td>
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</tr>
<tr>
<td></td>
<td></td>
<td>nauplii</td>
<td>0.21 (R)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>C. scutifer</td>
<td>1.34 (R)</td>
</tr>
<tr>
<td>Toolik Lake</td>
<td>21 - 22 VII 8*</td>
<td></td>
<td></td>
</tr>
<tr>
<td>LD 16.8:7.5h</td>
<td>10m**</td>
<td>D. tyrelli</td>
<td>0.33</td>
</tr>
<tr>
<td></td>
<td></td>
<td>H. septentrionalis</td>
<td>3.40</td>
</tr>
<tr>
<td></td>
<td></td>
<td>nauplii</td>
<td>0.35</td>
</tr>
<tr>
<td></td>
<td></td>
<td>C. scutifer</td>
<td>0.36 (R)</td>
</tr>
</tbody>
</table>

* noon and midnights series only.
** all isopleths are interrupted by surface or bottom, maximum depth of station is given in parentheses.
(R) mean depth, \(z\) was deeper in the water column at midnight.
watts cm\(^{-2}\) (6 - 7 July, Toolik) and 4.6 \times 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 17m 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 (figure 5, 6). The actual range of vertical movement was rarely more than 2m in deep water and usually less than .5m in shallow waters (table 4). In addition, diel changes in the mean depth were frequently in reverse of the 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
Fig. 5. Depth distributions of zooplankton, 20 - 21 VII 76, Toolik Lake. —— = quartiles, ——— = mean depth.
Depth distributions of zooplankton, 20 - 21 VII 76, Toolik Lake.

--- = quartiles, ---- = mean
depth, width of kite = % population.
Table 4. 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 ($P \leq 95\%$).

<table>
<thead>
<tr>
<th>LAKES</th>
<th>Species</th>
<th>25%</th>
<th>$\bar{z}$</th>
<th>75%</th>
</tr>
</thead>
<tbody>
<tr>
<td>20 - 21 VII,</td>
<td>D. longiremis cephela</td>
<td>S</td>
<td>S</td>
<td>NS</td>
</tr>
<tr>
<td>Toolik L.</td>
<td>D. middendorffiana</td>
<td>NS</td>
<td>NS</td>
<td>NS</td>
</tr>
<tr>
<td>$df = 4$</td>
<td>B. longirostris</td>
<td>NS</td>
<td>NS</td>
<td>NS</td>
</tr>
<tr>
<td></td>
<td>H. gibberum</td>
<td>S</td>
<td>NS</td>
<td>NS</td>
</tr>
<tr>
<td></td>
<td>D. tyrelli</td>
<td>NS</td>
<td>NS</td>
<td>NS</td>
</tr>
<tr>
<td></td>
<td>H. septentrionalis</td>
<td>NS</td>
<td>NS</td>
<td>NS</td>
</tr>
<tr>
<td></td>
<td>C. scutifer</td>
<td>NS</td>
<td>NS</td>
<td>NS</td>
</tr>
<tr>
<td>23 - 24 VII,</td>
<td>D. longiremis typica</td>
<td>NS</td>
<td>NS</td>
<td>NS</td>
</tr>
<tr>
<td>Lake El</td>
<td>B. longirostris</td>
<td>NS</td>
<td>NS</td>
<td>NS</td>
</tr>
<tr>
<td>$df = 6$</td>
<td>H. gibberum</td>
<td>NS</td>
<td>NS</td>
<td>NS</td>
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<tr>
<td></td>
<td>D. tyrelli</td>
<td>NS</td>
<td>NS</td>
<td>NS</td>
</tr>
<tr>
<td>5 - 6 VIII,</td>
<td>D. middendorffiana</td>
<td>NS</td>
<td>NS</td>
<td>NS</td>
</tr>
<tr>
<td>Ruins L.</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>$df = 4$</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
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 ≤ 95%) (table 4). H. gibberum and D. longiremis cephela showed weak correlations (P = 90% - 95%) 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 - 30cm) 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 x 10^-3 watts cm^-2; Pond Y, 0.76 - 7.83 x 10^-3 watts cm^-2; and Pond S, 0.59 - 6.87 x 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. paludosà were found in Pond S.
A diel vertical migration was observed in Pond W (figure 7A) but not in Pond Y (figure 7B) or Pond S (figure 8). 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 > 99%), and slopes of the regression lines were steep, i.e. +2.45cm per °C for adult and +1.75cm per °C for juvenile D. pulex (figure 9A). 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 (figure 9A). 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 > 99%), the slope of the regression line was not steep (i.e. -.8cm 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
Fig. 7. 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.
Fig. 8. In situ diel studies in pond S at Barrow. $\bar{z}$ = mean depth; B.P. = Branchinecta paludosa; D.M. = Daphnia middendorffiana.
Fig. 9. 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.
was found in Pond W (figure 9B). 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 (figure 9B). 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 5, strongly 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.** 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 \(5 \times 10^4\) cells ml\(^{-1}\), and hence did not influence swimming behavior (Peters in press) or mean depth (see part III). Other environmental conditions remained fairly constant.

Table 6 summarizes the data from the column studies. Three of the studies are presented in figure 10. A significant
Table 5. Correlations of mean depth with temperature (°C) and the log of the incident light intensity (I_o) for ponds. NS = nonsignificant correlation (P ≤ 90%); S = slightly significant (P ≤ 95%), ** = highly significant (P > 99%).

<table>
<thead>
<tr>
<th>PONDS (Barrow)</th>
<th>Species</th>
<th>mean depth correlations</th>
<th>°C</th>
<th>log I_o</th>
<th>df</th>
</tr>
</thead>
<tbody>
<tr>
<td>6 - 8 VII,</td>
<td>D. middendorffiana</td>
<td>**</td>
<td>S</td>
<td>7</td>
<td></td>
</tr>
<tr>
<td>Pond S</td>
<td>B. paludosa</td>
<td>NS</td>
<td>NS</td>
<td>8</td>
<td></td>
</tr>
<tr>
<td>26 - 27 VII,</td>
<td>D. pulex (adult)</td>
<td>**</td>
<td>**</td>
<td>9</td>
<td></td>
</tr>
<tr>
<td>Pond W</td>
<td>D. pulex (juvenile)</td>
<td>**</td>
<td>**</td>
<td>9</td>
<td></td>
</tr>
<tr>
<td>3 - 4 VII,</td>
<td>D. pulex (adult)</td>
<td>NS</td>
<td>NS</td>
<td>13</td>
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<tr>
<td>Pond Y</td>
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Table 6. Correlations of mean depth (z) with temperature (°C) and the log of incident light intensity (logI) for the columns. NS = nonsignificant correlation (P ≤ 90%); S = slightly significant (P ≤ 95%); * = significant (P > 95%); ** = highly significant (P > 99%). *studied at Barrow (all the other studies done at Toolik. See figure 10.

<table>
<thead>
<tr>
<th>date</th>
<th>df</th>
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<th>°C</th>
<th>species</th>
</tr>
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<tr>
<td>11 - 12 VI 77</td>
<td>13</td>
<td>**</td>
<td>&quot;</td>
<td></td>
</tr>
<tr>
<td>26 VI 75</td>
<td>10</td>
<td>**</td>
<td>D. middendorffiana (ad)</td>
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</tr>
<tr>
<td>8 - 9 VII 77</td>
<td>20</td>
<td>**</td>
<td>D. middendorffiana (jv)</td>
<td></td>
</tr>
<tr>
<td>9 - 9 VII 77</td>
<td>20</td>
<td>**</td>
<td>&quot;</td>
<td></td>
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<tr>
<td>9 - 9 VII 77</td>
<td>20</td>
<td>**</td>
<td>D. middendorffiana (jv)</td>
<td></td>
</tr>
<tr>
<td>20 - 21 VII 77</td>
<td>23</td>
<td>**</td>
<td>D. pulex (ad)</td>
<td></td>
</tr>
<tr>
<td>8 - 9 VII 77</td>
<td>20</td>
<td>**</td>
<td>D. longiremis typica (ad)</td>
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<td>23 VII 77</td>
<td>11</td>
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<tr>
<td>26 VI 76</td>
<td>10</td>
<td>*</td>
<td>D. longiremis cepholia (ad)</td>
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<td>20 - 21 VII 77</td>
<td>23</td>
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<td>* NS</td>
<td>D. middendorffiana (jv)</td>
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<td>D. longiremis cepholia (ad)</td>
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<tr>
<td>13 - 20 VI 77</td>
<td>19</td>
<td>S **</td>
<td>D. middendorffiana (jv)</td>
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<tr>
<td>27 VI 76</td>
<td>9</td>
<td>NS</td>
<td>&quot;</td>
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<tr>
<td>23 VI 76 2</td>
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</tr>
<tr>
<td>29 VI 76</td>
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<td>S **</td>
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<tr>
<td>9 - 9 VII 77</td>
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<tr>
<td>24 VII 77</td>
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<td>S **</td>
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<tr>
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<td>13</td>
<td>NS NS</td>
<td>H. septentrionalis</td>
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</table>
Fig. 10. Column studies at Toolik, Alaska. $\bar{z}$ = mean depth; 25%, 75% = quartiles; $^\circ$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.
Eu > o

\( z \)

\( z \)

\( 25\% \)

\( 25\% \)

\( 75\% \)

\( 75\% \)

\( \text{temperature (°C)} \)

\( \text{depth (cm)} \)

\( \text{time (hr)} \)
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 mean depth was strongly affected by temperature, a correlation between light intensity and mean depth sometimes was found (table 6) 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 (figure 11).

**Discussion**

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 (1949) in the Arctic. Near the arctic circle, Bogorov observed a midnight increase in the numbers of zooplankton in the surface waters of the White Sea, and he concluded that diel vertical migrations had occurred in continuous sunlight. In the Barents Sea which is north of
Fig. 11. Experimental study of temperature effects on *D. longiremis* vertical distribution (see text for details). $\overline{z}$ = mean depth; 25%, 75% = quartiles.
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 1949) 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. I calculated the mean depth (a more
sensitive and accurate estimate of population distribution) for the populations Digby sampled, using only the observations in which large numbers of zooplankton were present. I found that correlations did not occur between light intensity and population mean depth (table 7), 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. hazenii) 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 (figure 12).
Table 7. Reanalysis of Digby (1961). Correlations of mean depth and log of incident light intensity. NS = nonsignificant correlation (P < .05%).

<table>
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<th>Species</th>
<th>Sörgat 1956 (0 - 50m series)</th>
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<tr>
<td></td>
<td>average</td>
<td></td>
</tr>
<tr>
<td></td>
<td>mean depth</td>
<td>r signif.</td>
</tr>
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<tr>
<td>Calanus IV</td>
<td>21.4m</td>
<td>.147 NS</td>
</tr>
<tr>
<td>small Aqlantha</td>
<td>13.8m</td>
<td>.245 NS</td>
</tr>
<tr>
<td>Sagitta</td>
<td>24.8m</td>
<td>.192 NS</td>
</tr>
<tr>
<td>Limacina</td>
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<tr>
<td>Themisto</td>
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<td>.173 NS</td>
</tr>
<tr>
<td>Crab larvae</td>
<td>20.1m</td>
<td>.086 NS</td>
</tr>
</tbody>
</table>
Fig. 12. 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.
D. middendorffiana, which was repeatedly studied in the columns during 1976 and 1977, demonstrated an ability to acclimate to 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 figure 12). No shift was seen in either race of D. longiremis (figure 12). 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 - 3m) and below (8 - 10m) 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 that 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 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.
PART II

A DIEL CYCLE OF SWIMMING ACTIVITY IN
CLADOCERAN ZOOPLANKTON

Introduction

Crustacean zooplankton exposed to natural light-dark cycles undergo diel cycles of feeding (Haney and Hall 1975) and nonoriented swimming activity (Hart and Allanson 1976) in addition to their well known diel vertical migrations. Diel cycles in mandibular activity (Starkweather 1978), respiration (Duval and Green 1976, Hagerman 1969), phototactic sensitivity (Ringelberg and Servaas 1971), and polarotactic sensitivity (Umminger 1968) have also been observed under artificial light cycles in the laboratory. Most of these diel activities are associated with environmental stimuli at dawn and dusk, or with instantaneous on-off and off-on light changes in the laboratory. Large, rapid changes in light intensity evoke phototactic (light oriented) swimming reactions in zooplankton in the laboratory (Ringelberg 1964, 1969) and similar rapid changes in intensity at dawn and dusk are thought to be the stimuli of the diel vertical migrations of zooplankton. This hypothesis has been supported with correlative evidence from vertical migration studies in temperate regions (Ringelberg 1964, McNaught and Hasler 1964, Haney and Hall 1975) and tested by migration studies of arctic populations exposed to a wide range of light cycles (Bogorov 1946, Buchanan and Haney in preparation, Buchanan in preparation. The rate of change
in light intensity may also regulate the diel feeding cycle of zooplankton since onset and end of the high, nocturnal feeding activity occur when relative changes in light intensity are most rapid at dawn and dusk (Haney and Hall 1975). The environmental stimuli which time other diel activities are as yet not investigated. Other light changes that occur at dusk and dawn could stimulate behavior, for example, changes in absolute light intensity and shifts in the color (wavelength) of underwater light. In addition to environmental controls, zooplankton appear to have endogenous controls of their diel activities. Circadian rhythms of 24 - 28h have been found in several behaviors under constant light conditions (Ringelberg and Servaas 1971, Hart and Allanson 1976, Harris, 1963, Duval and Green 1976, LaRow 1968, 1969).

The purpose of this investigation was to describe the diel swimming activities of several cladoceran species under natural light cycles, and to experimentally investigate the exogenous and endogenous controls of the activity pattern.

The rate of vertical movement in zooplankton swimming was used as an index of the actual swimming velocities of zooplankton in three-dimensional space. Diel patterns of swimming activity were studied in a wide range of light cycles in arctic and temperate regions to determine the relative importance of exogenous and endogenous controls to the diel cycle of swimming activity. Correlations were made between features of the light cycle and rates of vertical movement to investigate possible zeitgebers.
Methods and Materials

Diel swimming activities of zooplankton were observed at Barrow (71°18'N), Toolik (68°37'N), and Fairbanks (64°50'N), Alaska, during the summers of 1977 and 1978. Zooplankton were exposed to natural light cycles with photoperiods ranging from LD 24:0h to LD 17:7h. For each study, zooplankton populations were collected from ponds or lakes, immediately sorted according to size and placed in 15 x 15 x 120cm plexiglas columns filled with pond or lake water filtered through a 15μm net. Populations were allowed to adjust to the column environment for at least 24 hours before observations began. The columns were surrounded by black plastic which blocked light from the sides and created a vertical light gradient in the experimental chamber. Observations were recorded on a tape recorder and later transcribed. Incident light intensity during most of the diel studies was measured with a radiometer and recorded on a continuous chart recorder. The experimental set-up is described in more detail in part I.

The rate of vertical movement was measured as follows: a zooplankter was selected on the basis of its depth in the column, and its vertical movements were visually followed for 20 - 60 seconds. The vertical distance traveled (sum of upward and downward movement) was measured against calibration marks on the face of the column. The total vertical distance traveled and the exact time (measured on a stopwatch) of the zooplankter were recorded on the tape recorder. Another animal was selected and the procedure repeated. For each set of
observations, the activities of about 5 - 10 zooplankters were measured at each of several depths in the column.

The vertical distributions of the zooplankton populations in the columns were observed following each set of swimming activity observations. The weighted mean depth ($\bar{z}$) and the 25% and 75% quartiles of the population were calculated from this data to determine if net vertical movements occurred in the column populations. The weighted mean depth is:

$$\bar{z} = \frac{\sum (n_z \cdot z)}{N}$$

where $n_z$ is the number of individuals at depth $z$, and $N$ is the total number in the water column. Quartiles were calculated according to the method described by Pennak (1944).

After each set of observations, the water temperature was measured at several depths in the column. An aliquot of an algal culture (approximately $2 \times 10^6$ cells) was added to each column at this time, depending on the feeding schedule of the experimental animals.

On several occasions, zooplankton were transferred from one latitude to another to 1) test the effect of large changes in the light cycle on the activity pattern, and 2) observe the behaviors of individuals imported from the temperate region. For each transfer, zooplankton were collected immediately before they were transported to a different latitude and placed in an insulated, light-tight container. For transfers within Alaska, zooplankton activities were observed one to three days after beginning the transfer. The
D. middendorffiana used in the studies were collected from ponds and shallow lakes, i.e. Ponds E and G in Barrow, Ballaine Lake in Fairbanks, and Lake N5 at Toolik. D. pulex were collected from a trough pond at Barrow and a roadside ditch in Fairbanks. The D. middendorffiana and D. magna imported from New Hampshire were obtained from cultures acclimated to natural light-dark cycles. The D. middendorffiana culture was originally collected at Toolik in 1976. Time spent in transit was four to seven days. In 1977, the animals were not exposed to light while in transit; in 1978, they were exposed to the natural light-dark cycles in Fairbanks for two days while enroute to Toolik. Zooplankton were allowed to acclimate to the column environment for at least 24 hours before observations were started.

One experiment was done in the arctic which attempted to compare two groups of D. middendorffiana which were acclimated to different environments but the same light cycle. D. middendorffiana were collected from Runway Pond on June 10 and acclimated to a column environment for 30 days. Individuals freshly collected from the pond were compared to column acclimated zooplankters on 8 - 10 July, 1977. During acclimation, the column environment tended to be slightly warmer than the pond. Light intensities were roughly an order of magnitude dimmer in the environmental chamber because of the steep light gradient created by the chamber. Aliquots of an algal culture (Scenedesmus sp., small unicellular green sp.) were regularly added to the column to maintain a relatively higher food concentration whereas algae concentration in the pond were low
(2.9 ug chl a/ liter on July 6). Water in the column was changed twice during the acclimation period to prevent accumulation of toxic wastes.

A standard procedure was used to analyze the results of all the diel studies. For each observation, measurements made within 30cm of the population mean depth in the column (Z) were averaged. The means were then plotted against time to determine the diel pattern of activity, and against temperature and incident light intensity to determine if correlations occurred between activity and these environmental variables. Peaks in the activity pattern were identified and used as reference points in discussing the diel patterns of activity.

When no correlation was found between temperature and activity, a high activity point was recognized if 1) two standard errors (SE) of the observation did not overlap the overall mean activity and 2) the high points were at least two SE higher than the low points on either side. Approximately two SE are equal to the 90% confidence limits for these sample sizes and the 90% confidence limit was arbitrarily chosen as the cutoff level used to recognize peaks. If visual perusal of the graphs suggested a correlation between temperature and activity, the influence of temperature on the diel pattern was determined before peaks were positively identified. Because significant correlations between temperature and activity occurred in 43% of the studies (see "Temperature effects"), high activity points were compared to the activity expected at the corresponding temperature. High activity points were tentatively selected on the basis of (2). A linear regression
was calculated between the remaining activity points and temperature, excluding the apparent high activity point.¹ If two SE of the apparent high activity points did not overlap the regression line, they were recognized as significantly high activities and peaks in the activity patterns. If only one of the two criteria was met in either the temperature influenced or uninfluenced sets of observations, the points in question were labeled as "slight peaks" in the activity pattern.

Correlations between activity and incident light intensity rarely were found (see "Light effects"). In these few cases, correlations between temperature and activity also occurred, and suggest that the correlations were a reflection of the close relationship between light and temperature in the columns and not due to an effect of absolute light intensity on activity.

The swimming activities of _Daphnia middendorffiana_, _Daphnia pulex_, and imported _Daphnia magna_ were studied in continuous light and in light-dark cycles in the Alaskan arctic and subarctic. _Daphnia longiremis typica_ was studied in continuous daylight, and _Holopedium gibberum_ was studied once in a light-dark cycle at Toolik. The majority of zooplankton indigenous to the arctic experience continuous daylight for much of their active lives. At Toolik, continuous daylight

¹One or two outliers (e.g. high activities) rarely changed the mean of 10-30 data points significantly, but when the data points are regressed against another variable (e.g. temperature) the linear regression line can be significantly altered by outliers in samples of this size. For this reason, and since I was trying to distinguish high activity points, I excluded the apparent high points from the regressions.
with light intensities greater than $4 \times 10^{-6}$ watts cm$^{-2}$, occur for roughly 80 days from mid-May until early August. During that time, overwintering resting eggs hatch, and the several subitaneous (i.e. active when released from brood pouch) and ephippial broods of the cladocerans are produced. Pond populations of cladocerans decrease in August and die after ice forms on pond surfaces in September. Consequently, pond populations experience roughly 30 - 60 light-dark cycles. Active lake populations of cladocerans are present into November at Toolik, and hence individuals experience more light-dark cycles than pond populations.

Results

Descriptions of the diel changes in swimming activity. Diel cycles in the rate of vertical movement were clearly seen in the Cladocera studied. The vertical distance traveled per unit time by an individual zooplankter is the result of upward and downward swimming and passive sinking. No attention was given in this study to the relative proportions of these three components of vertical movement since the goal of this paper was to describe the diel cycles rather than to determine how they were achieved.

When exposed to light-dark cycles, cladoceran zooplankton indigenous to the arctic (Toolik) and subarctic (Fairbanks) exhibited diel cycles in their rates of vertical movement $^{2}$

$^{2}$D. magna intensity threshold for visual orientation to a light source (Ringelberg 1964, Stavn 1971).
movement. For roughly the same photoperiod, D.middendorffiana showed evening peaks 3 - 4 hours before sunset at Fairbanks (LD 17.7:6.3h) and 8 hours before sunset at Toolik (LD 18.2:5.8h) (figures 13G, H). An evening peak 2 hours before sunset and a morning peak just after sunrise was seen in D. pulex at Fairbanks (figure 14C). Holopedium gibberum at Toolik exhibited a slight peak at sunset and a strong peak before sunrise (figure 15). D. magna imported from New Hampshire (LD 14:10h) to a similar light cycle in Fairbanks (LD 15:9h) had a strong evening peak and a slight morning peak of activity during daylight hours (figure 16C).

In continuous light prior to the summer solstice, exephippial juveniles of D. middendorffiana showed a strong unimodal cycle in the rate of vertical movement, with a daily peak at 1530h - 1930h (figure 17A, B). At the solstice, the first brood of the exephippial zooplankters had no peaks of activity at Toolik (figure 17C) and the adult exephippial animals did have peaks of activity (figure 13A). Because the activity peaks in the adults occurred at three different times during the study, it is uncertain whether the changes represent a diel cycle of swimming activity. After the solstice and before the sun began to set for long periods each day in the arctic, diel cycles of activity were evident in adult populations but not the subitaneous juveniles (compare figures 13C, D with figures 17D, E and figures 13E,F).

In this paper, photoperiod refers to the time between sunrise and sunset (i.e. L), and sunset and sunrise (i.e. D).
Fig. 13. Swimming activity of adult *Daphnia middendorffiana* at Toolik (Tk), Barrow (Bw), and Fairbanks (Fk), Alaska. Observation dates are given. ↓ = peak in swimming activity, ? = slight peak in activity, ** = temperature correlation with activity was found; in the bar below each panel, vertical lines = sunset or sunrise, shaded areas = light intensity below $4 \times 10^{-6}$ watts cm$^{-2}$ (the intensity threshold for the orientation mechanism of *Daphnia magna* (Ringelberg 1964, Stavn 1971)).
Fig. 14. Swimming activity of Daphnia pulex. See figure 13 for explanation of symbols.
Fig. 15. Swimming activity of *Holopedium gibberum*, 18 - 19 VIII 77, Toolik.
Fig. 16. Swimming activity of Daphnia magna adults (ad) and juveniles (jv) on 26 - 27 VII 78 at Toolik (A,B) and on 30 - 31 VIII 77 at Fairbanks (C). † = activity ± SE.
Fig. 17. Swimming activity of juvenile *Daphnia middendorffiana*. See figure 13 for explanation of symbols.
with figure 17F). A slight morning peak in the rate of vertical movement was sometimes observed in adult *D. middendorffiana* in continuous daylight. This peak occurred about 11 hours after the evening peak (figures 13D, E).

Adult, exephippial *D. pulex* did not show a strong diel cycle of vertical swimming activity in continuous daylight (figures 14A, B). Only slight peaks of activity could be seen at 2000h - 2200h, and sometimes about 11 hours later at 0700h - 0900h.

*D. longiremis typica* showed an evening peak of activity between 1700h - 2000h in continuous daylight (figure 18A, B). Temperature did not correlate with the rate of vertical movement in the 8 - 10 July study (temperature range 12.5° - 21.2°C), but apparently did influence the activity in the 23 - 25 July study (temperature range 4° - 20.5°C).

Imported *D. magna* were studied in continuous daylight at Toolik and in a light-dark cycle at Fairbanks. *D. magna* maintained for 1.5 weeks in continuous, presolstice light cycles (i.e. diel changes in light becoming less distinct) had slight peaks of activity around 2230h on the first day and no peak on the second day of the study (figure 16A, B). Since a diel cycle of activity was absent in *D. magna* as well as *D. middendorffiana* when both were exposed to continuous daylight at the solstice, the lack of response to whatever stimuli occur is characteristic of both nonarctic and arctic species. If a diel cycle had been found in nonarctic *D. magna* which were acclimated to continuous light cycles at Toolik, this would indicate that indigenous populations which did not
Fig. 18. Swimming activity of Daphnia longiremis forma typica on 8 - 10 VII 77 (A) and 23 - 25 VII 77 (B) and the vertical distribution in the column on 23 - 25 VII 77 (C), Toolik. 
\( z \) = mean depth of population, 25% and 75% = quartiles, 
\( = \) activity \( \pm \) SE.
show diel cycles are much less sensitive to light stimuli than nonarctic species. However, this was not the case.

Transfer studies. Comparisons of zooplankton activities in light-dark cycles and in continuous light suggested that environmental cues from the light cycle stimulate high swimming activities at certain times of the day. Diel cycles of activity in *D. middendorffiana* and *D. pulex* were weakly expressed or absent when diel changes in the light environment were minimal, whereas the cycles were distinct under a light-dark cycle. To test the relationship between light cycle and the diel cycle of swimming activity, zooplankton were transferred north or south within Alaska and studied within 3 days after they were transferred to different light cycles. Table 8 lists the pertinent light and temperature data for the transfer studies.

Features of the diel cycles in the rate of vertical movement were modified by transfers to different light cycles. Barrow *D. pulex* showed no cycle of activity under continuous light, but had an evening and morning peak of activity when transferred south to a light-dark cycle in Fairbanks (figure 19A). In *D. middendorffiana* recently transferred from continuous light in Barrow to a light-dark cycle in Fairbanks, peak rates of activity were 3 times higher (relative to the nonpeak activity rate at the corresponding temperature) The peak rates of Fairbanks *D. pulex* decreased 30% after they were transferred north to Toolik. Similarly, the peak rates of *D. middendorffiana* transferred north decreased 47% in adults and
Table 8. Light and temperature data for zooplankton transfer studied in Alaska. Barrow, 71°18'N; Fairbanks, 64°50'N; Toolik, 68°37'N.

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<thead>
<tr>
<th>change in sunlight hours</th>
<th># sunlight hours</th>
<th>population</th>
<th>max incidence</th>
<th>temperature</th>
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<tr>
<td></td>
<td>old</td>
<td>new</td>
<td>old</td>
<td>new</td>
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<tr>
<td>- 6.3</td>
<td>24</td>
<td>17.7</td>
<td>Barrow</td>
<td>Fairbanks</td>
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<tr>
<td>+ .5</td>
<td>17.7</td>
<td>18.2</td>
<td>Fairbanks</td>
<td>Toolik</td>
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Fig. 19. Transfer studies of D. pulex (A,B) and D. middendorffianna (C-E). Animals were transferred from Barrow to Fairbanks (Bw Fk), Fairbanks to Toolik (Fk Tk), and Toolik to Fairbanks (Tk Fk). Dashed vertical lines mark the times at which activity peaks occurred in the populations before they were transferred. See figure 13 for explanations of other symbols.
40% in juveniles. Besides changes in the peak rates of activity, shifts in the time of the evening activity peak were observed in Fairbanks *D. middendorffiana* which were transferred north (figures 19D, E). No shifts were observed in *D. middendorffiana* transferred south or in *D. pulex* transferred north (figures 19B, C). It was evident from these transfer studies that diel cycles of swimming activity are closely related to light stimuli associated with the light cycle.

Comparisons of the activity cycles of transferred and indigenous populations studied simultaneously suggest that populations are acclimated to their local light environments. In Fairbanks, the peak activities of *D. pulex* recently transferred from Barrow occurred about 2.5 hours later in the evening and 1 hour earlier in the morning than those of indigenous *D. pulex* (compare figure 19A with 14C). At Toolik, the peak activities of *D. middendorffiana* recently transferred from Fairbanks occurred 1 - 2 hours earlier than those of the Toolik *D. middendorffiana* (compare figures 19D, E with 17G). To summarize, animals which are transferred south responded to light stimuli earlier than southern populations and animals transferred north responded later than northern populations.

In these comparisons of indigenous and transferred populations, it was assumed that differences in photosensitivity and diel activity patterns in Alaskan populations of *D. middendorffiana* and *D. pulex* are not due to the effects of genetic differences on behavior. This assumption was never directly tested. However, *D. middendorffiana* from different
locations, which were acclimated to similar light cycles, behaved similarly which suggests that genetic differences may not heavily influence behavior. *D. middendorffiana* at Barrow and at Toolik showed similar diel cycles of swimming activity when exposed to a continuous light cycle just prior to the first sunset of the summer (compare figures 13C-F with 17D-F).

**Effects of acclimation to different habitats.** Comparisons of transferred and indigenous populations suggested that long term acclimation to local light environments can occur and will affect diel cycles of swimming activity. One experiment was done in June and early July to determine if long term acclimation to different habitats in the same light cycle can also alter diel cycles of swimming activity. *D. middendorffiana* acclimated for 30 days to the column habitat were compared with freshly collected animals in continuous daylight at Toolik. The column habitat was slightly warmer, dimmer, and had a higher food concentration than the pond habitat (see Methods and Materials).

The diel swimming activities of the column-acclimated adults and juveniles are presented in figures 13C and 17D, and the pond acclimated adults and juveniles in figures 13D and 17E. The rate of vertical movement of pond adults and juveniles correlated with temperature, whereas temperature correlation was found only in the column adults and not in the juveniles (figure 20). Therefore, the temperature cycles did alter the activity rates of the two adult groups and the
Fig. 20. Correlation of activity and temperature for adult (ad) and juvenile (jv) D. middendorffiana acclimated to the column and pond habitats, 8 - 9 VII 77. Diel cycles of activity are shown in figure 1D,E and 2C,D. o = peak activity, line through data points = regression line, average, or a combination of both.
column-raised juveniles. However, the slopes of the regression lines were less than .07 vertical cm sec\(^{-1}\) per °C and the overall patterns of diel activity were not very distorted by temperature effects. Once temperature effects were accounted for, the results suggest that long term acclimation to other factors in the two habitats did not strongly influence the diel cycles of activity, even when zeitgebers were weak. Adults in both groups showed an evening peak in swimming activity between 1700h - 2100h and tended to be active between 0000h - 0800h as well, although only the activity of the pond adults was pronounced enough to be recognized as a slight peak. Neither of the juvenile groups exhibited an evening peak of swimming activity on 8 July. The pond juveniles showed a slight peak at 1900h on 9 July, but unfortunately no data is available for the column juveniles on the 9th. The different effects of temperature on the two juvenile groups presumably are related to their dissimilar temperature histories, and suggest that long term acclimation tends to make nonpeak swimming activities constant over the range of normally encountered temperatures.

**Endogenous rhythm of swimming activity**

Hagerman (1969) did not observe an endogenous rhythm of activity in the ostracod *Hirschmannia viridis* Müller when it was held in constant dark for 72 hours. However, Hart and Allanson (1976) found an endogenous rhythm of swimming activity in the copepod *Pseudodiaptomus hessei* Mrázek when the zooplankter was held in constant dark for 36 hours. Peak swimming
activities were approximately 42 - 58% lower than peaks observed in a light-dark cycle. The occurrence of a peak in the diel pattern of swimming activities of zooplankton populations exposed to continuous light indicates that an endogenous rhythm may control the rate of activity. The rhythm might be expressed as a free-running circadian cycle of activity in individual zooplankters when zeitgebers are persistently weak and populations do not exhibit diel patterns of swimming activity (e.g. summer solstice). Studies were done with individual zooplankters transported from a light-dark cycle (New Hampshire) to continuous daylight at Toolik 10 days before the solstice. Four adult individuals did not show an obvious diel or circadian pattern of swimming activity 71 hours after exposure to continuous light (figures 21B-E). Cyclic changes in the rate of vertical movement were observed, however, the cycle period varies from 6 to 14.5 hours. Four 1st - 2nd instar individuals of D. middendorffiana which were studied as a group appeared to show a diel pattern of activity, with peaks before and after noon (figure 21A). These individuals had been released from the same brood one day prior to the start of the observations, and their activities seemed to be synchronized (i.e. variance around the mean was small). One of the individual D. magna was left in the experimental chamber and studied 8 days later. This animal, which had

4Two D. magna and two D. middendorffiana from a population collected at Toolik in 1976 and cultured in New Hampshire.
Fig. 21. A - E: swimming activity of 4 newborn D. middendorffiana (A), two adult D. middendorffiana (B,C) two adult D. magna (D,E) on 11 - 12 VI 77, Toolik. F: swimming activities of adult D. magna from 11E studied on 19 - 20 VI 77, Toolik. ↓ = peaks in activity, short vertical lines = marks denoting 8.5h intervals, horizontal line = overall average.
acclimated to the arctic for 11 days, showed a consistent pattern of activity with a cycle of approximately 8.5 hours (figure 11F). To determine if a similar but less distinct 8.5 hour cycle occurred in the first study, the 8.5h intervals were calculated (starting at 0900h on 8 June when the animals were first exposed to continuous light) and marked on figures 21A-E. Despite variation in rates and the timing of the peaks, cycles in the rate of vertical movement with roughly an 8.5h period can be discerned. In 74% of the possible 8.5h time intervals, one peak of activity occurred. In the remaining intervals, no peaks occurred. The average interpeak distance of peaks in adjacent intervals is 8.4h in *D. magna* and 8.2h in *D. middendorffiana*. Unusually high peaks of activity alternated with smaller peaks in the two adult *D. magna*, suggesting that a second endogenous rhythm with a longer period (perhaps circadian) also affects the rate of vertical movement. This second cycle apparently dampens in the absence of diel stimulation since peaks after 11 days acclimation were approximately the same rate.

These observations suggest that one, and perhaps two, endogenous rhythms influence the diel cycle in the rate of vertical movement of at least *D. magna* and *D. middendorffiana*. In the absence of a zeitgeber, the rate of vertical movement of a population of zooplankton with asynchronized cycles of activity should be fairly constant unless modified by other environmental factors, including an occasional zeitgeber. Fairly constant rates were found in *D. magna* acclimated to continuous light for 1.5 weeks and in indigenous populations
near the summer solstice at Toolik. Strong stimulation by a sporadic zeitgeber at this time should tend to synchronize the activities of individuals in a population and diminishing peaks of activity could follow at regular intervals without zeitgebers. If this hypothesis is correct, it could explain some of the variation which occurred in the timing of the peaks and in the absolute rates of vertical movement in the peaks in populations exposed to continuous light. Exposure to strong zeitgebers would cause the cycles to reset every day and a diel cycle of activity would be seen. The timing of peak activities became very precise in the middle of August (figures 13G, 19F), indicating that the zeitgeber(s) were consistently strong at these light cycles, regardless of modification by weather patterns.

Discussion

Interactions with vertical distribution of zooplankton. Harris (1963), Enright and Hamner (1967), LaRow (1968, 1969), Rudjakov (1970) and Hart and Allanson (1976) suggest that diel cycles of swimming activity influence the vertical distributions of zooplankton. LaRow (1968, 1969) and Hart and Allanson (1976) demonstrated the existence of an endogenous cycle in the swimming activity of Pseudodiaptomus hessei and Chaoborus punctipennis, respectively, which was entrained and strengthened by a diel zeitgeber. Increases in swimming activity at sunset were associated with changes in vertical distributions. Harris (1963) observed circadian cycles in the vertical distributions of D. magna and Calanus finmarchicus var. helgolandicus in a
small tank 20cm high, under both constant light and constant dark. He attributed these small vertical migrations to an endogenous rhythm of swimming activity and suggested that the rhythm is responsible for the "dawn-rise" in zooplankton which can occur in total darkness, hours before dawn. He assumed that phototactic reactions controlled the vertical distributions of zooplankton during the day and overrode any effects of an endogenous rhythm on vertical distributions. This assumption is supported by the fact that the amplitude of the circadian vertical migrations he observed for *D. magna* were approximately 2.5 times larger in constant dark than in constant light. Zeitgebers were apparently necessary to maintain the behavioral expression of the rhythm since circadian vertical migrations tended to dampen in constant light or dark. In experiments similar to those of Harris, Enright and Hamner (1967) also found a gradual decrease in the amplitudes of circadian vertical migrations for several other species of zooplankton held in constant dark.

The vertical distributions of zooplankton exposed to continuous daylight in the arctic usually were not affected by diel cycles of swimming activity. Although the activity cycle is expressed as changes in the rate, or velocity, of vertical movement, net changes in the mean depth of the populations in the columns were not usually associated with the diel cycles in swimming activity. Temperature did have an effect on the population mean depth in the columns; significant correlations found (see part I). Mean depths which were associated with peaks in swimming activity were not consistently
above or below the regression line of the correlation between temperature and mean depth. Two studies illustrating this are shown in figure 22, one from continuous daylight at Toolik and another from a light-dark cycle with a long photoperiod at Fairbanks.

When zooplankton were close to the bottom of the experimental column, diel increases in swimming activity could force the populations away from the bottom and cause a small vertical migration (figure 18C). This migration would have to be the result of larger vertical excursions by individuals during peak activities. When the mean depth of a population was located midway between surface and bottom, peaks in swimming activity occasionally corresponded to a spreading out of the population which was seen as changes in the quartiles, but the population mean depths were rarely affected. When populations were located near the water surface in the column, small migrations away from the surface (i.e. comparable to those in populations located near the bottom) did not occur. If the behaviors of populations located near the bottom, midway, and near the surface of the column are considered together, they suggest the following hypothesis: an increase in zooplankton swimming velocity during the daytime is expressed as larger vertical excursions in the column when most of the light comes in a narrow arc from directly overhead (e.g. lower half of the column) and as more frequent movement up and down within the same depth interval when light comes in a wider arc from the sides and overhead (e.g. upper half of the column). In other words, the phototactic orientation reactions
Fig. 22. Interaction of high swimming activity and vertical distribution for D. middendorffiana, 29 - 30 VI 77, Toolik (A), and for D. pulex, 3 - 4 VIII 77, Fairbanks (B). o = mean depth of zooplankton when peaks were found in the diel pattern of activity; .... = temperature (°C); z = mean depth; 25%, 75% = quartiles, solid lines in the depth versus temperature graphs are the regression lines.
of the animals can affect the expression of their diel cycle of swimming activity.

Siebeck and Ringelberg (1969) demonstrated that copepods and cladocerans orient their swimming direction with respect to contrasts in light and dark, i.e. the angular light distribution (ALD). Changes in the ALD caused directional swimming responses in zooplankton. This phototactic orientation reaction ceases at light intensities below 4 x 10^{-6} \text{ watts cm}^{-2} \text{ (Ringelberg 1964, Stavn 1970)}, and zooplankton assume non-oriented swimming positions, e.g. vertical "hopsink" in daphnids. In the columns, light-dark contrasts are provided by the edge of the skyward opening of the experimental chamber. Apparent changes in the angular light distribution are larger to a vertically moving individual near the top of the column than to an individual moving the same vertical distance near the bottom of the column. Cues for the phototactic orientation responses, then, are stronger near the top of the column. Since diel cycles of swimming activity caused the least change in distributions of zooplankton near the top of the column, the influence of the diel cycles on the vertical distributions appears to be inversely related to the strength of the cues for phototactic orientation. At light intensities below 4 x 10^{-6} \text{ watts cm}^{-2} \text{ (e.g. nighttime) or in environments with predominantly vertical lighting (e.g. pelagic zone of a clear water lake)}, the influence of the diel cycle on vertical distributions should be strongest. In systems such as experimental columns or ponds, the influence of the diel cycle should be weakest because of the overriding effect of the phototactic
orientation reactions, unless interactions of the zooplankters with the boundaries of their system translate some of the swimming activity into directional movements of the population. Even in the absence of light, the boundaries of very shallow systems could also dampen the effect of the diel cycle of swimming activity.

Distinction must be made between vertical migrations caused by phototactic swimming reactions and by rhythms of swimming activity. As they are currently understood, the in situ vertical migrations of zooplankton at dawn and dusk are phototactic swimming reactions to changes in light. Ringelberg (1964) demonstrated that an increase in swimming velocity is not required to accomplish the phototactic swimming reaction in Daphnia. Zooplankton can also undergo vertical migrations in the absence of cues for the phototactic swimming reaction (this study, Harris 1963, Esterly 1917, Enright and Hamner 1967). A diel cycle of swimming activity, based in an endogenous rhythm, appears to be the cause of the migrations. Observations of zooplankton in the arctic demonstrate that the diel cycle is expressed as changes in the swimming velocity and suggest that the behavior is more kinetic (not oriented to an environmental cue) than tactic (oriented to a cue).

Zeitgeber. The dependency of the cycle of swimming activity upon light is evident in its diel nature, the effect of transfers to different light cycles, and the dampening of the activity cycle around the solstice in continuous light. Since the cycle of swimming activity was observed when changes in
light intensity were too slow to stimulate the phototactic swimming reactions which produce diel vertical migrations, the mechanisms of these two responses may be different and may have different zeitgebers. Peaks in swimming activity did not correspond to obvious zeitgebers such as absolute light intensity or maximum rates of change in intensity. Peaks were observed near the midday maximum light intensity as well as the midnight minimum. Evening peaks typically occurred after the maximum negative rates of change in intensity, and morning peaks before the maximum positive rates. (Under light-dark cycles in Fairbanks, maximum rates occasionally corresponded with the evening peak activities but usually occurred after the peaks.)

Despite variations in timing, peak activities in the arctic occurred close to midnight around the solstice and earlier in the day on either side of the solstice (e.g. figures 13, 17). This suggests an association with a particular angle of incidence of the sun (angle created by the zenith, the observer and the sun), since the sun reaches maximum heights above the horizon at the summer solstice in the northern hemisphere and is progressively lower after the solstice. On clear days, different angles of incidence of the sun have characteristic light intensities, ratios of light wavelengths, and strengths of polarized light. Changes in these light features are known to modify the swimming orientation and velocity of zooplankton (e.g. Stavn 1970, Ringelberg 1964, 1969, Heberdey 1949, Smith and Baylor 1953, Waterman 1960, Hazen and Baylor 1962). Light incident on an horizontal
surface (e.g. water surface) decreases as the sun approaches the horizon, and shifts towards shorter wavelengths because of the absorption and light scattering properties of the atmosphere. (A similar shift in color was found in the experimental chamber housing the columns.) Skylight is strongly polarized in a circle around the sun and 45° distant from the sun, and when the sun angle of incidence approaches 90° in the west, an arc of polarized light can be found in the sky running from the northwestern and southeastern horizons up to the zenith. Weather strongly modifies the light features associated with the sun angle of incidence. Light under a heavy overcast has a higher proportion of blue light (personal observation) and is not polarized. Also, the relative rates of change in light intensity are slower (personal observation). Weather modifications could cause significant changes in any stimuli from the light environment and are probably partly responsible for the variation observed in the timing of the peak activities, regardless of what zeitgeber is perceived by zooplankton.

Evidence that weather modifications of the light environment can change the timing of the peak was clearly seen in several studies and especially on 23 - 25 July, 1977 (figure 18B). 23 July was partly cloudy until 1330h and 100% clear through the 24th until 0830h on the 25th when the sky again became partly cloudy. At 1330h on the 25th, a large storm front moved across Toolik, causing a rapid change in all aspects of the light environment. Peak activities on the 23rd and 24th occurred at 1750h and 1950h, respectively.
On the 25th, it occurred at 1430h, within 1 hour of the storm's onset and 3 - 5 hours earlier than previous days. Weather modifications of light also influenced the absolute rate of activity during the peak. The transfer studies discussed earlier indicated that peak rates are related to the strength of the stimuli and are affected by long term acclimation to the light environment. The peak rates of activity, observed in diel studies at Toolik which encompassed two or more evenings with different weather patterns, were also dissimilar. For example, in the 8 - 10 July study, the peak rate of *D. longiremis* forma typica was 0.236 vertical cm sec$^{-1}$ on the 8th which was almost 100% clear, whereas the peak rate was 0.115 vertical cm sec$^{-1}$ on the 9th and occurred when the sky was cloudy to partly cloudy. Temperature at both peaks was 20°C. When skies cleared about 4.5 hours after the peak on the second day, the rate of vertical movement in *D. longiremis* increased slightly and remained high until incident light intensity increased passed $5 \times 10^{-4}$ watts cm$^{-2}$ the next morning (approximately $1 \times 10^{-5}$ watts cm$^{-2}$ at the population mean depth in the column).

Further evidence of the influence of weather on the diel cycle of activity is seen when time of peak activity is plotted against the sun's angle of incidence for adult *D. middendorffiana* (figure 23). Peaks occurred in a narrow range between 61° and 68°15' on heavily overcast days. To factor out the influence of weather on the diel cycle of activity and determine if the activity peaks might be related to particular angles of incidence of the sun, observations
Fig. 23. Time of peak activity versus sun angle of incidence for *D. middendorffiana* in clear (o), partly cloudy (●), and overcast (⋆) weather. Upper solid curve = sun angle of incidence on June 21 at Toolik, lower solid curve = 11 - 12 August at Toolik, dotted curve = 29 - 30 July at Barrow, dashed curve = 3 - 4 August at Fairbanks.
made on clear days (excluding the transfer studies) were
separated from the rest and the light characteristics of the
Corresponding angles of incidence were determined from
measurements made at Toolik (table 9). For comparison, the
characteristics of the light environment for the average angle
of incidence at D. middendorffiana peak activities on heavily
overcast days are given. The average angle of incidence for
peak activities in D. middendorffiana, D. longiremis, and D.
pulex on clear days were 65°25', 69°27', and 72°20', respect-
ively, covering a total range of only 7° out of a possible
37° - 49°. The intensity of whole light incident on an
horizontal surface ranged from 3.2 - 5.6 x 10⁻³ watts cm⁻²,
and the ratio of yellow (560nm) to blueviolet (430nm) light
was 1:2.6.⁵ (At smaller angles of incidence, the ratio of
yellow:blueviolet was higher and at 90°, just prior to sunset,
the ratio was lower, about 1:5.5). These data strongly
suggest that the zeitgeber which stimulates diel peaks of
swimming activity is associated with the sun's angle of
incidence.

On overcast days, peak activities occurred at lower
light intensities and at higher proportions of blueviolet
light (table 9). Changes in the percent of polarized light
are probably not the zeitgeber of the diel swimming cycle
since peaks did occur on overcast days when light is depolarized

⁵560 nm and 430 nm were measured since Heberday (1949),
Smith and Baylor (1953), and McNaught (1971) suggest that
most cladocerans are maximally sensitive to these wavelengths.
Zooplankton are also sensitive to UV(370nm) and red (670nm).
Table 9. Average sun angle of incidence corresponding to peak activities of *D. middendorffiana* on clear and overcast days, *D. longiremis* on clear days, and *D. pulex* on clear days; and characteristic light intensities associated with the given sun angle of incidence.

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<th>OVERCAST DAYS</th>
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<tr>
<td><strong>Average sun angle</strong></td>
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<td>78°40' (3)</td>
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<td><em>D. longiremis</em></td>
<td>69°27' (3)</td>
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<td><em>D. pulex</em></td>
<td>72°20' (1)</td>
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<tr>
<td><strong>Light intensity (watts/cm²)</strong></td>
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<td>79°</td>
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</tr>
<tr>
<td>blueviolet</td>
<td>7.8 - 4.5 x 10⁻⁴</td>
<td>~2.4 x 10⁻⁴</td>
</tr>
<tr>
<td>yellow</td>
<td>3.0 - 1.4 x 10⁻⁴</td>
<td>~6.1 x 10⁻⁵</td>
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<tr>
<td>Ratio yellow:blueviolet</td>
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<td>~1 : 3.9</td>
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by clouds. The absolute light intensity or absolute ratios also did not seem to be the zeitgeber. It is probable that the zeitgeber is the relative rate of change in one or more features of the light environment, for example the ratios of different wavelengths of light or the rate of change in one wavelength. Laboratory studies would tend to support this hypothesis: although the effects of color shifts on the swimming velocities of zooplankters has not been quantified, they are known to cause changes in the swimming behaviors (Smith and Baylor 1953).

**Possible importance of light history.** The light histories of zooplankton seem to influence their sensitivity to the zeitgeber(s) of the diel cycle of swimming activity. This was evident in the transfer studies, where transferred populations and indigenous populations responded differently to light stimuli. Zooplankton transferred south from continuous light to a light-dark cycle had lower activity peaks than the indigenous populations. The importance of light history was also evident in the diel swimming activities of adult and juvenile *D. middendorffiana* at Toolik. Presolstice juveniles, which had been exposed to light-dark cycles as ephippial embryos, had distinct diel cycles of swimming activity in continuous light. When they matured, these individuals showed diel cycles of activity when zeitgebers strengthened in late July and early August. Juveniles which were brooded and released near the solstice did not have a diel cycle of activity in continuous light. When they matured,
these individuals had a weak pattern of activity in August relative to transferred animals. Apparently, the light cycles to which embryos are exposed affects the sensitivity of those individuals after they hatch.

**Temperature influences.** In 13 of the 30 studies, temperature correlated with the rate of vertical movement, and temperature cycles modified the overall patterns of swimming activity. A 10°C increase in temperatures above 15°C could increase non-peak swimming activities as much as 130%, however the percent increase was usually lower. The absolute effect of temperature on nonpeak swimming activities apparently depended upon the temperature history of the zooplankters, i.e. temperature range to which the zooplankton were acclimated. In these studies, temperature did not appear to affect the timing of the peaks in the diel cycle of swimming activity, and suggests that the biological mechanisms which respond to environmental stimuli and initiate the diel cycle of activity are temperature independent.
PART III

A REVIEW OF THE CAUSES OF VARIATION IN DIEL VERTICAL MIGRATION

The vertical distributions of zooplankton populations exposed to arctic light cycles are controlled by factors such as temperature, angular light distribution, and diel cycles of swimming activity, besides the obvious influence of the physical boundaries of the water body (parts I and II). Correlations between absolute light intensity and population mean depth are rarely observed, indicating that acclimation to changing light intensities occurs rapidly in zooplankton and the vertical distributions of populations are usually not affected by a wide range of absolute light intensities. Investigations of daytime depth controls which were not presented in parts I and II indicate that age structure and food concentration influence population vertical distributions (Haney and Buchanan in preparation). Older individuals of cladoceran species tend to be lower in the water column than younger individuals over a wide range of temperature (figure 24). Starved populations of both predators and grazers tend to be dispersed in the water column and have deeper mean depths than well fed populations (figures 25 and 26). Thus, environmental and physiological factors appear to have important roles in regulating the vertical distributions of zooplankton during daylight hours.
Fig. 24. Correlations between mean depths ($\bar{z}$) of four age groups of *Daphnia magna* exposed to continuous daylight (June, 1976 and 1977) and temperature at Toolik, Alaska. ** indicates significance ($P < .001$). NS indicates no significance.
Fig. 25. Mean depth ($\bar{z}$) of Heterocope septentrionalis, starved and fed, during mid-summer period of continuous daylight at Toolik, Alaska. A total of 40 measurements of mean depth were made; data points represent average mean depths for $2^\circ$C intervals, $\pm$ SE. Heterocope were fed Daphnia pulex which maintained an average mean depth of 66.4 cm in the columns or Daphnia longiremis forma typica which maintained an average mean depth of 110 cm. Heterocope distribution was not significantly affected by prey distribution.
Fig. 26. Average daytime vertical distributions of *Daphnia magna* in 220 cm columns, maintained at two concentrations of *Scenedesmus* spp., 27 January - 3 February, 1977, New Hampshire. The columns were exposed to diffuse natural light from 1600h to 0800h and to a constant, artificial light from 0800h to 1600h (incident light intensity - $1.35 \times 10^{-5}$ watts/cm$^2$). A: 89,600 cells/ml. C: 9,900 cells/ml.
These results agree with vertical migration studies done in temperate regions under less extreme light cycles. Kikuchi (1930), Langford (1938), Plew and Pennak (1949), Herman (1963), Healey (1967) and others have observed seasonal variation in daytime vertical distributions of zooplankton in temperate lakes and oceans, and suggest that changes in various environmental and physiological factors caused the seasonal differences. Pennak (1944), Kikuchi (1938), Hutchinson (1967) and others have noted dissimilar daytime vertical distributions of the same species in separate lakes and attribute the dissimilarities to different environmental conditions. The phototactic reaction, expressed as rapid vertical movements in the water column, can also be modified by environmental and physiological factors. Rapid changes in light initially stimulate the reactions, however environmental parameters such as carbon dioxide, oxygen, pH, temperature, and light intensity, and physiological parameters such as age, sex and reproductive conditions will modify and even reverse the reactions (see reviews by Cushing 1951, Baylor and Smith 1957, Hutchinson 1967, Vinogradov 1970). Besides altering the behavior of individuals, environmental parameters may also modify the features which mediate behavior. For example, gross morphological features of neurons in the visual systems of clones of Daphnia magna, are reproduced identically, however finer details are not identical (Macagno et al. 1973). The relative concentrations of the four visual pigments in Daphnia photoreceptors are determined by the photic environment of the animal rather than by genetic instruction (McNaught 1971).
Overall, environmental and physiological factors seem to be responsible for much of the variation observed in zooplankton behavior.

Intraspecific variation is essential to the selection processes of evolution. Speculations on the evolutionary cause(s) of a trait assume that heritable variations (alleles) were partly responsible for the expressed variation in the ancestral trait, and the selection forces being proposed acted upon the genome of the ancestral population as well as its array of phenotypes. Behavior is one component of an organism's phenotype, but unlike structures it has no physical form. The result of interactions between an organism's sensory, nervous, effector and skeletal organs, behavior may be strongly influenced by the physiological and environmental factors which modify the structures and functions of these organs. I would like to pose the following questions with respect to zooplankton behavior: What genotypic differences within a species population produce variation in the vertical distributions and movements of zooplankton? Do selective forces act on populations to change the average behavior if little of the variation in behavior is due to heritable differences?

Several investigations of zooplankton, and primarily of cyclomorphic species, have indicated that some of the variation in zooplankton vertical distributions and movements is directly related to genotypic differences in the population. Natural populations of cyclomorphic species appear to contain polymorphic genotypes for helmet formation. Although helmet induction and growth rate are governed by environmental factors
(i.e. temperature, turbulence, light intensity, nutrition), individuals from different clones will begin helmet formation at different threshold stimuli (Brooks 1946) and produce differently sized helmets under identical environmental conditions (Jacobs 1961). Helmets are known to alter Daphnia locomotion and orientation (Jacobs 1964, 1965) and appear to affect the vertical distribution and movement of Daphnia in natural systems (Brooks 1964, Worthington 1931, Woltereck ref. in Hutchinson 1967), hence some of the variation found in the vertical distributions of cyclomorphic species may be directly related to genetic differences. Studies of other types of polymorphs show that some polymorphisms will not affect zooplankton behavior; for example, diel vertical migrations of horned and unhorned individuals of the polymorphic Ceriodaphnia cornuta are indistinguishable (Zaret 1972). Differences in diel vertical migrations of females and males have been observed (see review by Hutchinson 1967), suggesting that secondary sex characteristics affect the light responses and locomotion of zooplankton. However, no controlled studies have been conducted. Endogenous cycles, thought to be controlled by gene action (see review by Brown 1973), are known to affect light responses and swimming behaviors of zooplankton. In the laboratory, 1.8 minute cycles in swimming movements (Daan and Ringelberg 1969), 8 minute cycles and 24 hour cycles in the strength of the phototactic reaction to light stimuli (Clarke 1932, Ringelberg and Servaas 1971), 24 hour cycles in zooplankton swimming activity (Hart and Allanson 1976) and long-term cycles in swimming behavior and light responses, related to ecdysis
(molt) cycles (Clarke 1932, Haney et al. unpublished data), have been observed. Allelic differences in the endogenous cycles could create consistent variation in zooplankton behavior, however these differences have not been sought or studied. The evidence to date that relates genetic differences to behavioral variation is mostly inferential, but it does suggest that such relationships occur within species. Behavioral variation caused by genetic differences has not been demonstrated in natural populations of species.

Selective forces can shift the light responses of a population if the population contains two or more alleles which produce different behaviors (e.g. Dobzhansky and Spassky 1969). However, if behaviors are continuously modified by changes in environmental factors, it is possible that allelic expression may be masked and cannot be acted upon by selective forces. One attempt has been made under semi-controlled conditions to examine the effect of heavy selection pressure on the phototactic responses of zooplankton and the results suggest that heritable changes in zooplankton behavior are slow. Banta (1921) attempted to artificially select for and against a phototactic response (i.e. the rate at which individuals move towards a stationary, horizontal light source) in clones of parthenogenic Daphnia pulex and Daphnia longispina raised under variable conditions. He assumed that mutations in these organisms which affected their behavior would be immediately evident and could be selectively established. Banta found that no significant differences due to selection had occurred after intensive selection for up to 203
generations (about 5 years) in 11 clones, although environmental factors did modify the phototactic reactions of both species during the experiment. Banta also studied 5 clones of parthenogenic Simocephalus exspinous, a semi-benthic species, and observed an apparent heritable change due to selection in at least one strain of one clone. S. exspinous, however, is known to produce polymorphic intersexes (Banta 1939) and variant behaviors may have been produced by pleiotropic effects of the intersex genes (or by other associated polygenes or alleles) if the genes were activated by environmental stimuli.

Arctic lakes and ponds seem to offer many uncontrolled experiments of natural selection on the light responses and swimming behaviors of zooplankton, and the phototactic response in particular. During most of their active life, zooplankton in the arctic are exposed to continuous daylight and do not undergo rapid vertical movements. During these 2-4 months, random mutation and selection could lead to changes in the phototactic sensitivity of arctic populations. Many zooplankton species found in the Arctic, however, began to show phototactic responses at roughly the same threshold stimuli that evoke vertical movements in a temperate zooplankton, Daphnia magna, suggesting that phototactic sensitivity has not changed drastically in arctic populations. Changes in arctic populations may be slow because of a masking effect of environmental variation or possibly because selection pressures are ineffective or counteract each other. In addition, the phototactic mechanisms (ocelli, compound eyes) could be conservative traits.
A number of ecologically important behaviors are mediated by the rhabdomeric eyes of zooplankton, including the dorsal light reaction, shore avoidance, daytime spatial orientation, somersaulting (fright) reaction, and the phototactic reaction (to rapid changes in light), and many mutations in the eyes may not be readily incorporated in a species' gene pool.

Despite the multi-phyletic origins of zooplankton and their range of sensory receptors, nervous systems, skeletal systems, and swimming behaviors, representatives of most phyla show phototactic behaviors and undergo diel vertical migrations, suggesting a number of selective advantages favored the development of diel vertical migrations (Hutchinson 1967). Population studies have pointed out the selective advantages of vertical migration in modern communities and have stimulated much speculation on the evolutionary causes of vertical migrations (see review in Vinogradov 1970). Such hypotheses are stimulating and heuristically useful, but are limited since they cannot be tested (Peters 1976). Experimental research associating behaviors with morphological and physiological features should improve our perception of the mechanisms of vertical migration. Investigations of selection on allelic frequencies of these features could help identify the selective forces which modify migration behavior. With this kind of information, we can speculate more knowledgeably about the present evolution of diel vertical migrations and perhaps stimulate testable ideas about the mechanisms and ecological importance of this behavior.
SUMMARY

1. Diel studies of vertical distributions and swimming activities of zooplankton populations were carried out under continuous light and long day photoperiods in the Arctic.

2. *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.

3. 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.

4. 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. 1 of the 3 pond studies and 15 of the 42 column showed significant correlation between incidents $I_0$ 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.
5. Conclusion: zooplankton populations did not undergo diel vertical migrations under continuous light or long day photoperiods because of diel fluctuations in absolute light intensity. 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.

6. Diel cycles of swimming activity, measured as the average rate of vertical movement of individual zooplankters, were clearly seen in long day photoperiods. Under continuous light, most of the Cladocera showed diel cycles of swimming activity at Toolik, Alaska, except around the summer solstice.

7. Temperatures above the acclimation temperature could significantly increase swimming activity but did not apparently change the timing of the cycle.

8. Observations of populations before and after transfers to different latitudes (i.e. different light cycles) indicate that environmental cues from the light cycle stimulate the peak swimming activities. Comparisons of the activity cycles of transferred and indigenous populations which were studied under the same light cycle suggest that populations are acclimated to their local light environment.

9. Long term acclimation to different habitats in the same light cycle did not show a strong influence on the diel cycles of swimming activity, after the effect of temperature acclimation was factored out.

10. An asynchronous, endogenous rhythm of swimming activity was observed in imported *D. magna* and *D. middendorffiana*.
individuals exposed to continuous light at the summer solstice at Toolik. The cycle period was approximately 8.5 hours. A second rhythm with a longer (possibly circadian) rhythm may have occurred during the days immediately after the zooplankters were imported, but it dampened in less than 8 days.

11. Diel cycles of swimming activity did not affect vertical distributions of zooplankton populations when phototactic orientation cues were strong. In dim light, or when phototactic cues were weak, diel cycles of swimming activity could cause small vertical movements in populations.

12. The following hypothesis was proposed: an increase in zooplankton swimming activity during the daytime is expressed as larger vertical excursions in the column when most of the light comes in a narrow arc from directly overhead, and as more frequent movement up and down within the same depth interval when light comes in a wider arc from the sides and overhead.

13. Distinction is made between vertical migrations caused by phototactic swimming reactions and by cycles of swimming activity.

14. Weather conditions modify the timing and the strength of the swimming activity peak.

15. The zeitgeber of the diel cycle of swimming activity may be related to relative changes in one or more wavelengths of light.

16. The light history of zooplankters appears to influence their sensitivity to the zeitgeber.
17. Variability in vertical distributions and movements which is related to environmental and physiological factors is pointed out.

18. Little evidence is available concerning the genotypic differences within a species population which can produce variation in the vertical distributions and movements of zooplankton.

19. Banta's work (1921) and observations of the onset of d.v.m. in arctic zooplankton suggest that a high level of environmentally-induced variation in behavior can mask genetically-related variation from selective forces.
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