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CORRELATION OF CURRENTS WITH THE DISTRIBUTION OF ADULT *DAPHNIA* IN LAKE MENDOTA

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ABSTRACT

Simultaneous observations of current pattern and distribution of *Daphnia pulex* indicate that in Lake Mendota this zooplankter is concentrated by wind-induced convergence. Theoretical examination of this hypothesis yields results which compare favorably with observations.

In general it has been assumed that inland lakes are horizontally homogeneous. As a corollary, the lateral variation of plankton at a specified depth has been regarded as approximately random. Ricker (1938a, b) found that the horizontal variation in zooplankton in Cultus Lake, B. C., exceeded slightly the random variation. In Lake Nipissing, Ontario, Langford (1938) sampled 10 stations in a line and concluded that there was no trend in the numbers of *Daphnia*.

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1 This project was supported by a grant from the University Research Committee of the Graduate School; funds were administered by the Lake Investigations Committee, University of Wisconsin.
He found them randomly distributed at the surface and nearly so at one meter. On the other hand, Verduin (1951) found two distinct populations of diatoms in the western end of Lake Erie which were apparently associated with the hydrography of the region. However, the physical dimensions of Lake Erie place it in a different class from Cultus or Nipissing.

In Lake Mendota we have found large horizontal variations of zooplankton. This is evident in Figs. 3, 6, 9–12. We shall show how the zooplankton is mechanically concentrated and transported from one location to another.

This sort of problem is not new to oceanographers. Damas (1905) considered the problem for the Norwegian Sea, and Sønme (1934) re-examined this area and gave a more adequate explanation of the maintenance and transport of calanoid populations as related to the movements of the water in this Sea. More recently Redfield (1939, 1941) and Redfield and Beale (1940) described the relation of the Gulf of Maine circulation to an immigrant population of Limacina retroversa, the chaetognaths in the Gulf, and to a calanoid community existing there with a limited connection to the open ocean. Russell (1935, 1939) has used certain planktonic species as indicators of water movements in the North Sea. Sverdrup and Allen (1939) showed the relationship of diatom distribution to the water masses and currents off the California Coast. One of the most recent contributors to this problem is Carruthers (1951). Numerous other studies could be cited to illustrate the point.

Methods. Preliminary sampling indicated the existence of considerable horizontal variation of the zooplankton in Lake Mendota. The variation in samples from one location to another frequently ranged through several orders of magnitude and was greater than the variation among replicate samples at one station. By variation we mean gross changes rather than microvariation due to foamliness (Stommel, 1949). The mechanism or mechanisms which produce and maintain these variations were then investigated.

An experiment which shows the movement and aggregation of zooplankton under the influence of wind-driven currents was conducted in University Bay during the spring of 1952. This Bay was used for this particular experiment for three reasons: it is bounded on three sides by land, its current pattern was better understood than that of any other region of Lake Mendota, and its size was convenient for the planned experiment. The Bay was covered by a grid of 15 stations, each of which was carefully fixed by a buoy. At the same time each day, for three days, the zooplankton was sampled and the
current was measured at all stations. Zooplankton samples, taken with the Clarke-Bumpus plankton sampler, averaged about 600 l each. Currents were measured by the drag method (Putnam, et al., 1949). The entire area could be covered in about three hours.

*Daphnia pulex* was the zooplankter used for the study. In early spring, before the Lake has stratified, *D. pulex* is most dense at about one meter. There is little or no diurnal vertical migration (Birge, 1895). From these data it was possible to construct one meter synoptic maps of *D. pulex* concentration, currents, and vertical velocity (Bryson and Suomi, 1952) for three consecutive days.

In this experiment, only large adult *Daphnia* representing the winter population were counted. This procedure automatically eliminated the factor of biological production. The death rate was not known, but no evidence of unusual mortality during this period was observed, as it was two weeks later.

**Results.** In Fig. 1 the current pattern at one meter for the first day of the experiment is shown by streamlines. The wind had been west and had changed to the north during that day's survey. Currents had a general southerly set and were relatively weak. The distribution of vertical velocities (Fig. 2) shows that upwelling was occurring in the center of the Bay while sinking was general along the south shore.

**TABLE I.—WIND DATA, 1952**

<table>
<thead>
<tr>
<th>Date</th>
<th>Prevailing Direction</th>
<th>Av. Velocity (mph)</th>
<th>Date</th>
<th>Prevailing Direction</th>
<th>Av. Velocity (mph)</th>
</tr>
</thead>
<tbody>
<tr>
<td>April</td>
<td></td>
<td></td>
<td>May</td>
<td></td>
<td></td>
</tr>
<tr>
<td>16</td>
<td>W</td>
<td>6.8</td>
<td>1</td>
<td>NW</td>
<td>6.5</td>
</tr>
<tr>
<td>17</td>
<td>W</td>
<td>9.5</td>
<td>2</td>
<td>ENE</td>
<td>9.8</td>
</tr>
<tr>
<td>18</td>
<td>WSW</td>
<td>8.7</td>
<td>3</td>
<td>SSW</td>
<td>6.1</td>
</tr>
<tr>
<td>19</td>
<td>WSW</td>
<td>5.9</td>
<td>4*</td>
<td>WSW</td>
<td>11.2</td>
</tr>
<tr>
<td>20</td>
<td>S</td>
<td>5.0</td>
<td>5*</td>
<td>W</td>
<td>14.0</td>
</tr>
<tr>
<td>21</td>
<td>SSE</td>
<td>12.0</td>
<td>6</td>
<td>NW</td>
<td>13.0</td>
</tr>
<tr>
<td>22*</td>
<td>NNW</td>
<td>11.5</td>
<td>7*</td>
<td>ESE</td>
<td>14.4</td>
</tr>
<tr>
<td>23*</td>
<td>ENE</td>
<td>16.0</td>
<td>8</td>
<td>NE</td>
<td>10.3</td>
</tr>
<tr>
<td>24*</td>
<td>NNE</td>
<td>9.8</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

* Dates of plankton surveys.

Fig. 3 shows the distribution of *D. pulex* at one meter for the same day. Within the Bay the concentration varied from 9 to 380/m³. Such low densities indicated that most of the zooplankton had been swept out of the Bay by the preceding west winds. The concentration gradient was directed as expected, namely increasing toward the region of convergence, with the lowest values in the region of upwelling.
Figure 1. April 22, 1952. Current streamlines (spaced inversely proportional to velocity) for one meter level in University Bay; station values cm/sec.

Figure 2. April 22, 1952. Vertical velocity distribution at one meter level in University Bay (cm/sec).
After the organized survey was completed, reconnaissance to locate the main mass of plankton showed that it was situated off Picnic Point. Auxiliary stations were set up 50 yards apart and samples were taken at one meter. Here the gradient was extremely steep, and concentrations as high as 22,000/m³ were found. Unfortunately no hydrographic data are available for this region, but as will be shown later, convergence was probably occurring.

By the second day (Figs. 4 and 5) the current pattern had changed radically. The wind was from the east-northeast at 16 mph (Table I), and velocities of the currents were generally about twice those of the previous day. The flow was westerly throughout the entire Bay except near the bar at its head. Here the current was upwind, leading to high convergence values immediately out from this station and probably all along the bar. Some convergence was also occurring near the center of the Bay mouth. The effects of this change on the zooplankton distribution were striking but not entirely unexpected.

The *Daphnia* distribution for the second day (Fig. 6) shows that the mass of *Daphnia* off the Point moved into the Bay and was still concentrated with densities up to 15,000/m³. A second cell with a density of 1,000/m³ appeared near the center of the Bay mouth where convergence was occurring.
Figure 4. April 23, 1952. Current streamlines (spaced inversely proportional to velocity) for one meter level in University Bay; station values cm/sec.

Figure 5. April 23, 1952. Vertical velocity distribution at one meter level in University Bay (cm/sec).
Figure 6. April 23, 1952. Distribution of *Daphnia pulex* adults at one meter in University Bay (no./m²; contours drawn on logarithmic scale).

Figure 7. April 24, 1952. Current streamlines (spaced inversely proportional to velocity) for one meter level in University Bay; station values cm/sec.
Figure 8. April 24, 1952. Vertical velocity distribution at one meter level in University Bay (cm/sec); values are station numbers for reference purposes.

Figure 9. April 24, 1952. Distribution of Daphnia pulex adults at one meter in University Bay (no./m³; contours drawn on logarithmic scale).
By the third day (Figs. 7 and 8) the wind was north-northeast and had slackened to 10 mph; as a result the circulation pattern began to change. The general westerly drift persisted in the southern half of the Bay mouth but deteriorated somewhat in the northern half. Velocities decreased and the inflow along the Point held close to shore. Deep in the Bay the flow curved southward. Except along the southern shore, vertical velocities were practically zero.

The change of current pattern was reflected in the *Daphnia* distribution (Fig. 9). The heavy plankton concentration near the Point swung southward and began to disperse. Maximum concentrations decreased from 15,000 to less than 2,000/m$^3$. There was a northwestward shift of the cell in the mouth of the Bay.

Although this experiment was terminated on the third day, more surveys of the *Daphnia* distribution were carried out May 4, 5, 7, and 8, but only a few samples were taken on the last day. This later series was made as follows: The glass plate of an underwater viewer was marked off in one-inch squares so that *D. pulex* could be observed...
The winter individuals could be recognized immediately by their whitish color due to a microsporidial disease. There was no reason to believe that the incidence of this disease varied from one location to another. The number per square inch of viewer was estimated several times at each stop, and the results were plotted as shown in Figs. 10, 11, and 12. The authors do not intend to imply that this direct observation method is quantitatively comparable to sampling with the Clarke-Bumpus plankton sampler. However, direct observation gives the pattern of distribution over a large area whereas sampling yields detailed information over a limited area.

On May 4 (Fig. 10) a heavy concentration of Daphnia was observed off Picnic Point, and concentrations of four or more per square inch were noticed in the south central region of the Lake. A tongue of moderate concentration (2 per square inch) extended deep into University Bay (bottom center of map). By the next day, May 5, the west-southwest wind had shifted to due west and had increased in velocity (Table I), the great mass of D. pulex had reached the south shore, and the tongue in University Bay had moved out completely (Fig. 11). Concentration of the crustaceans had occurred, and it
was estimated by direct observation that there were 10 per square inch. On May 6 the wind was from the northwest, but by the next day it was east-southeast at an average speed of 14 mph. This shift was quickly reflected in the distribution of *D. pulex* (Fig. 12). There were high concentrations off Picnic Point again, and deep in the Bay there was an extremely heavy concentration. In the central region of the Lake there were streaks of high concentration which alternated with bands of somewhat lower concentration. The streaks appeared to be associated with foamlines where there is generally convergence of the surface water. As shown in Fig. 12, the estimated values in and out of the streaks varied from 4 to 10 per square inch. On the same day the west end of the Lake had a relatively sparse population with only two cells of high concentration apparently trapped in the southwest corner. First evidence of a mortality of the winter population of *D. pulex* was observed this same day along the south shore at the west end of the Lake. The numbers of dead *Daphnia* were such that the bottom appeared whitish in depths of one to two meters along nearly one-half mile of shoreline.
On the following day, May 8, no general survey was made, but the plankton mass in University Bay was even more concentrated due to the northeast wind. Samples were taken with the Clarke-Bumpus sampler in this region and also in the center of the mouth of the Bay. Table II gives the results.

**TABLE II.—** *D. pulex* Concentration on May 8, 1952

<table>
<thead>
<tr>
<th>Station</th>
<th>Estimated No. per sq. in. of viewer by direct observation</th>
<th>Actual Nos. per m² by sampling at 0.5 to 1.0 m</th>
</tr>
</thead>
<tbody>
<tr>
<td>Head of Bay</td>
<td>20+</td>
<td>2,000,000 (adults)</td>
</tr>
<tr>
<td>Mouth of Bay</td>
<td>0.05–0.1</td>
<td>15,000 (mostly juveniles)</td>
</tr>
</tbody>
</table>

Following examination of the hydrographic data it appeared likely that the accumulation of this tremendous mass of plankton was due to mechanical processes rather than to "swarming" of the animals themselves.

**Theory.** It is quite clear from this experiment as well as from other similar surveys that the concentration of *Daphnia* at a particular location may change by several orders of magnitude within 24 hours. In the light of the close correlation of the movements and aggregation of the zooplankters with the movements of the water, it seems reasonable that the explanation of the variations in concentration is related to the physical forces at work.

We have attempted to construct a mathematical model of the process which causes concentrations of *Daphnia* and other plankters to appear and move about the Lake. Naturally such a model is idealized and will have limits in its application, but up to the present it is the best explanation we have of the phenomena that do occur.

The theory is based on two assumptions:

1. It is assumed that the *Daphnia* do not exhibit purposeful horizontal motion. This is reasonable since pelagic animals can have no visual points of reference and must rely on thermal or chemical gradients to guide them in their lateral movements. In Lake Mendota horizontal temperature gradients may reach 1°C in 100 m, but usually they are less. It is doubtful if an animal as small as *D. pulex* ( approximately 1 mm in length ) could detect such a gradient.

2. The *Daphnia* orient themselves vertically by the light gradient from the surface. Vertical temperature and chemical gradients that occur later in the season only modify this orientation. This means that the *Daphnia* will tend to maintain their depth in spite of vertical currents in the Lake. Laboratory experiments have verified the fact that these animals are able to ascend or descend at a rate greater than most vertical current velocities observed in Lake Mendota, namely, 1 cm/sec or so.
With these two assumptions in mind, we shall take the equation for the distribution of a conservative variable in the sea as developed by Sverdrup, et al. (1946) and alter it so that it expresses the distribution of a known nonconservative variable, namely \( D. pulex \):

\[
\frac{\partial s}{\partial t} = \frac{\partial}{\partial x} \left( \frac{A_x}{\rho} \cdot \frac{\partial s}{\partial x} \right) + \frac{\partial}{\partial y} \left( \frac{A_y}{\rho} \cdot \frac{\partial s}{\partial y} \right) + \frac{\partial}{\partial z} \left( \frac{A_z}{\rho} \cdot \frac{\partial s}{\partial z} \right) - \left[ \frac{\partial (s \cdot v_x)}{\partial x} + \frac{\partial (s \cdot v_y)}{\partial y} + \frac{\partial (s \cdot v_z)}{\partial z} \right],
\]

(1)

where \( A \) is coefficient of eddy diffusivity, \( \rho \) the density, \( v \) the current velocity, and \( s \) the plankton concentration. This expression equates the local change of concentration to the effects of diffusion and the net flux of the variable (plankton concentration) in all three dimensions. Rewriting, we obtain

\[
\frac{\partial s}{\partial t} = \text{Diffusion} - \frac{s \left( \frac{\partial v_x}{\partial x} + \frac{\partial v_y}{\partial y} + \frac{\partial v_z}{\partial z} \right)}{\partial x} - \frac{\partial s}{\partial x} - v_x \frac{\partial s}{\partial y} - v_z \frac{\partial s}{\partial z}.
\]

(2)

From continuity considerations, the expression in parentheses must be zero. However, since \( Daphnia \) tend to maintain their depth, their vertical velocity must be zero. This gives the whole expression a non-zero value which represents a departure from the equation of continuity. This is the key to the whole problem.

Let \( v_z = 0 \) to describe no motion by the \( Daphnia \), and \( v_y = 0 \) by assuming the \( x \) direction to be that of the current. Simplifying, we obtain:

\[
\frac{\partial s}{\partial t} = \text{Diffusion} - s \frac{\partial v_x}{\partial x} - v_x \frac{\partial s}{\partial x}.
\]

(3)

The middle term on the right is the horizontal velocity divergence, and the last term is the horizontal transport or the advection of the plankton.

This equation says that the local change in concentration is due to the combined effects of diffusion, advection, and horizontal divergence. Diffusion acts only in the direction of decreasing concentration. Therefore it always tends to destroy variation and produce uniformity. Advection implies that variations already present will be transported past a given location according to the direction and magnitude of the currents. It cannot produce the variations. Horizontal divergence is the process that produces variation. With water alone this necessitates vertical currents, but with \( Daphnia \) we have already assumed that no
**TABLE III.—Numerical Examples**

<table>
<thead>
<tr>
<th>Sta.</th>
<th>Dates</th>
<th>April</th>
<th>S</th>
<th>V</th>
<th>cm/day</th>
<th>$\frac{\partial S}{\partial x}$</th>
<th>Div.</th>
<th>Adveective term</th>
<th>Divergence term</th>
<th>Sum</th>
<th>Observed Change</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>cm/day $\times 10^4$</td>
<td>$\times 10^{-2}$</td>
<td>Daphnia/cm</td>
<td>Daphnia/m$^3$/day</td>
<td>Daphnia/m$^3$/day</td>
<td>Daphnia/m$^3$/day</td>
</tr>
<tr>
<td>9</td>
<td>22–23</td>
<td>9</td>
<td>1.5</td>
<td>−39.</td>
<td>0</td>
<td>+59,000</td>
<td>0</td>
<td>+59,000</td>
<td>+59,000</td>
<td>0</td>
<td>+59,000</td>
</tr>
<tr>
<td>9</td>
<td>23–24</td>
<td>15,000</td>
<td>1.7</td>
<td>+23.</td>
<td>0</td>
<td>−20,000</td>
<td>0</td>
<td>−20,000</td>
<td>−20,000</td>
<td>0</td>
<td>−14,300</td>
</tr>
<tr>
<td>37</td>
<td>22–23</td>
<td>48</td>
<td>2.4</td>
<td>−0.083</td>
<td>0</td>
<td>+200</td>
<td>0</td>
<td>+200</td>
<td>+200</td>
<td>0</td>
<td>+201</td>
</tr>
<tr>
<td>37</td>
<td>23–24</td>
<td>249</td>
<td>1.6</td>
<td>0</td>
<td>−4.3</td>
<td>+1,070</td>
<td>0</td>
<td>+1,070</td>
<td>+1,070</td>
<td>0</td>
<td>+1,640</td>
</tr>
<tr>
<td>35*</td>
<td>23–24</td>
<td>312</td>
<td>1.6</td>
<td>−0.86</td>
<td>+4.3</td>
<td>+1,400</td>
<td>−1,300</td>
<td>+100*</td>
<td>−228</td>
<td></td>
<td></td>
</tr>
<tr>
<td>24</td>
<td>22–23</td>
<td>11</td>
<td>0.52</td>
<td>−0.22</td>
<td>$+4.3$</td>
<td>+110</td>
<td>−47</td>
<td>+63</td>
<td>+1,460</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

*Difference of two large numbers. An error of 300 in prediction represents a 20% error in either calculated term which is not in excess of the error to be expected.*

† Gradient probably greater, but data missing at edge of *D. pulex* mass off Picnic Point; zooplankton contributing to this change undoubtedly came from beyond region of survey.
vertical motion exists. Therefore convergence will tend to increase the Daphnia concentration while divergence will tend to decrease it. Since we can measure convergence, we should be able to measure the rate at which the animals are concentrated.

As a numerical example we shall take several sets of data from the charts. A certain amount of judgment in the choice of data is necessitated by the limited size of the experiment. For example, data from the mouth of the Bay could not be used because the gradients up-current were not known. Since the current velocity decreases at night, the average current and divergence values were arbitrarily reduced by one-half. Starting, then, with the plankton concentration and gradient for the first of a pair of days, Table III compares the expected change with that actually observed in the subsequent 24 hours.

The results in Table III show that advection is dominant at Station 9 in both cases and at Station 37 for April 22–23. Divergence is dominant of Station 37 for April 23–24. At Station 35 both processes are operating at similar rates but in opposite directions. The calculation for Station 24 is presented to show how extrapolation of the plankton gradient beyond the region of survey may lead to erroneous results. Thus one or the other or both of these processes may be important in the distribution of the zooplankton.

Acknowledgement. The authors would like to express their appreciation to Peter M. Kuhn and Charles R. Stearns for invaluable assistance on the project.

Conclusions:

1. Large horizontal variations of the zooplankton in Lake Mendota do exist.

2. Study of the zooplankton distribution reveals its close relation to the currents and especially to the simultaneous effects of divergence and the phototactic response of the animals.

3. The combined processes of mechanical concentration and transport of zooplankton must be kept in mind during any attempt to sample the zooplankton population of Lake Mendota and probably other lakes of similar size.

4. The phenomenon may be described by an equation which can be evaluated from actual field measurements of plankton concentration and current velocity distribution.

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