NO. 7

REPORT TO THE UNIVERSITY OF WISCONSIN

LAKE INVESTIGATIONS COMMITTEE

CORRELATION OF CURRENTS WITH THE DISTRIBUTION OF ZOOPLANKTON IN LAKE MENDOTA

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November 1952

UW - Lakes Inv. Comm

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Introduction

The structure of a typical inland lake is thought to consist of layers of homogen
homogeneous water. It has been assumed, and there is some supporting evidence, that horizontal variations in the plankton at a specific depth are nearly random. Ricker (1938) found that the horizontal variation in zooplankton in Cultus Lake, B.C., exceeded random variation, but that all things considered a single central station is satisfactory for sampling purposes. In Lake Nipissing, Ontario Langford (1938) sampled 10 stations in a line and found no evidence of a trend in the numbers of Daphnia. He found them randomly distributed at the surface and nearly so at one meter. On the other hand Verduin (1951) has found separate populations of diatoms in Lake Erie which were apparently related to the hydrography of the region. However, the physical dimensions of Lake Erie place it in a different class from Cultus or Nipissing.

Here in Lake Mendota we have found that significant non-random horizontal variation of zooplankton does exist. In this respect it has been more profitable to consider the lake as a small ocean, hence consisting of non-homogeneous horizontal layers. Immediately we are confronted with an entirely new concept. In an ocean water masses are formed, transported, and mixed with other water masses of different properties. The biological communities present in the water masses are transported to new locations where they may continue to reproduce or merely exist as immigrants. In a lake the situation is not quite so broad because the species present are endemic and behave as active populations. Nevertheless we shall show how even in Lake Mendota the plankton is 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. Somme (1933), (1934) reexamined 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 circulation of the Gulf of Maine to an immigrant population of Limacina retroversa, the Chaetognaths in the gulf, and 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 contributions was by Carruthers (1951) in which he proposed the term "fishery hydrography" in an effort to define the problem more exactly. Numerous other works (see references) could be cited to illustrate the point.

The Meteorology Department at Wisconsin has been studying the circulation of Lake Mendota for several years (Reports to University of Wisconsin Lake Investigations Committee, Parts I to VI). During the last two years this department has worked in close cooperation with the biologists working on the lake. Some of the products of this joint relationship are presented in this report.

Methods

Preliminary sampling showed that the horizontal variation of zooplankton in Lake Mendota was not random. The variation also exceeded by many times the sampling error. It must be noted that by variation we mean large scale changes from one location to another, not micro-variations due to foamlines and other widespread, but individually small, phenomena. The next step was to investigate the mechanism or mechanisms producing and maintaining these variations.

A typical 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. University Bay was used for this particular experiment for three reasons: It was bounded on three sides by land, its current pattern was better understood than any other region of Lake Mendota, and its size was convenient for the experiment planned. The bay was covered by a grid of 15 stations, each of which was carefully marked by a buoy. Each day for three days a team of biologists sampled the plankton and a team of meteorologists made current measurements at all stations. By simultaneous operation of both teams, the entire area could be covered in about three hours.

Daphnia pulex was the zooplankter used for the study. Since the experiment was carried out in mid-April, its vertical distribution was no obstacle. This is true because in early spring before the lake has stratified, and the surface water is quite cold, D. pulex is most concentrated at about one meter; and since the surveys were made between 9 a.m. and 12 Noon vertical migration was slight.

From the data obtained by these surveys, it was possible to construct synoptic distribution maps of D. pulex at one meter, current streamlines, and maps of horizontal velocity divergence of University Bay for three consecutive days. By horizontal divergence we mean the spreading or stretching of an area of water with the consequent vertical motion of the water to replace that lost by divergence. If one were to pour water from a pitcher onto the floor, it would diverge horizontally and converge vertically. Similarly if a liquid is sucked into a pipette from a flat dish, it converges horizontally and diverges vertically. Near boundaries, vertical motion is always associated with horizontal divergence.

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

Results

In Figure 1 the current situation at one meter for the first day of the experiment is shown by streamlines. The distance between streamlines is inversely proportional to the measured current velocity. The map is self-explanatory for the most part. The wind had been west and changed to the north during that day. Figure 2 is a map showing the distribution of vertical velocity as derived from the current measurements by use of the equation of continuity. A positive value indicates ascending water and a negative value descending water.

The map in Figure 3 shows the distribution of D. pulex at one meter on the first day of the experiment. The gradient within the bay was not steep, increasing from a concentration of 9 to 380 per cubic meter. Such low densities indicated that most of the zooplankton had been swept out of the bay by the preceding westerly winds. A little searching revealed the situation off Picnic Point where temporary auxiliary stations were established 50 yards apart. Here the gradient was sharp, going from 23 to 22,000 per cubic meter within 200 yards. Unfortunately no convergence data are available for this region, but as will be shown later, there was very likely a zone of convergence there.

By the second day (Figures 4 and 5) the situation had changed radically. The wind was from the east-northeast at approximately 20 mph. Velocities of the currents at one meter were generally about twice the previous day's values. The flow was westerly throughout the entire bay except near the bar across the head of the bay. Here a 180° reversal was observed, leading to very rapid convergence 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 were most striking but not entirely unexpected.

The Daphnia distribution map for the second day (Figure 6) shows that the mass of Daphnia off the point has moved into the bay and was still aggregated with densities up to 15,000 per cubic meter. A second cell with a density of 1,000 per cubic meter has appeared near the center of the bay mouth where convergence was occurring.

By the third day (Figures 7 and 8) the east-northeast wind had slackened to 10-12 mph. and as a result the circulation began to break down and change pattern. Here we see the convergence zone deep in the bay shifting to the south shore. The general westerly drift remains in the south half of the bay mouth, but has deteriorated somewhat in the north half. Velocities have decreased and the inflow along the point is being held close to the shore.

The southerly shift of convergence near the bar was reflected by the Daphnia (Figure 9). A tongue-like distribution began to swing out into the bay. This tongue distribution is a common pattern which has been observed before when large concentrations of plankton have met with an obstruction, whether it be a land mass or a current of water. Notice that the cell or more or less discrete group in the mouth of the bay has shifted to the north, but has not penetrated the bay to any extent.

The experiment was terminated the third day. However, more surveys carried out 9, 10, and 11 days later revealed that large concentrations still existed off Picnic Point while the bay was nearly devoid of large Daphnia. On this occasion a steady northwest wind swept the plankton across the lake toward the south shore. Then a strong east-southeast wind set up a current pattern that carried the Daphnia into the bay along the south shore. Aggregation again occurred near the bar where final concentrations reached the phenomenal values of 200,000 to 2,000,000 per cubic meter. By volume this represents 800 to 8,000 cc. per cubic meter. About this time large scale hatching of the eggs began and we believe that the largest portion of the young Daphnia representing the vernal zooplankton pulse for the whole lake originated in University Bay and the south end of the lake generally.

General Discussion

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 involved in causing aggregation 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. First, it is assumed that the Daphnia move horizontally in a random manner. This seems reasonable since pelagic animals can have no visual points of reference and must rely entirely on temperature or chemical gradients to guide them in their lateral movements. In a large inland lake such gradients may be neglected. The second assumption is that 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 existing in the lake. Laboratory experiment has verified that these animals are able to ascend or descend at a rate greater than most vertical current velocities observed in Lake Mendota, namely, 1 centimeter per second or so.

With these two assumptions in mind, we shall proceed to develop the model proposed. As a starting point we shall take the equation for the distribution of a conservative variable in the sea as developed by Sverdrup, Johnson, and Fleming in The Oceans.

A = Eddy diffusion

ρ = density of water

v = velocity of currents

s = plankton concentration

$$\frac{\partial s}{\partial t} = \frac{\partial}{\partial x}\left(\frac{A_x}{\rho}\frac{\partial s}{\partial x}\right) + \frac{\partial}{\partial y}\left(\frac{A_y}{\rho}\frac{\partial s}{\partial y}\right) + \frac{\partial}{\partial z}\left(\frac{A_z}{\rho}\frac{\partial s}{\partial z}\right) - \left(\frac{\partial (s V_x)}{\partial x} + \frac{\partial (s V_y)}{\partial y} + \frac{\partial (s V_z)}{\partial z}\right) \quad (1)$$

This expression equates the local change of concentration to the effects of diffusion and the change of flux of the variable (plankton concentration) in all three dimensions. Breaking this down we obtain equation (2):

$$\frac{\partial S}{\partial t} = \text{Diffusion} - S\left(\frac{\partial V_x}{\partial x} + \frac{\partial V_y}{\partial y} + \frac{\partial V_z}{\partial z}\right) - V_x \frac{\partial S}{\partial x} - V_y \frac{\partial S}{\partial y} - V_z \frac{\partial S}{\partial z} \tag{2}$$

In this equation the middle section is an expression of the equation of continuity which for an incompressible fluid such as water is equal to zero. However, since Daphnia tend to maintain their depth, their vertical velocity must be zero. This permits the other two parts of this equation, namely the velocity gradient in the x and y directions, to give the whole expression a finite value which represents a departure from the equation of continuity. This is the key to the whole problem. Setting $V_z = 0$ to describe no vertical motion by the Daphnia and $V_y = 0$ by taking the current in the x direction and then simplifying we obtain

$$\frac{\partial S}{\partial t} = \text{Diffusion} - S\frac{\partial V_x}{\partial x} - V_x \frac{\partial S}{\partial x} \tag{3}$$

The middle term is the horizontal velocity divergence and the last term is the horizontal transport of the plankton or advection. In words the equation reads:

Local change of concentration = Diffusion - Divergence - Advection

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 merely 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. By divergence (or convergence) we mean the lateral stretching or contraction of the water. With water alone this necessitates vertical currents, but with Daphnia we have already assumed that no vertical motion exists. Therefore convergence will tend to increase the Daphnia concentration while divergence will tend to decrease it. Since we can measure civergence, we should be able to measure the rate at which the animals are concentrated.

Trial calculations using the observed values of plankton density, plankton density gradient, and horizontal divergence have given results of the correct order of magnitude which is about all we can expect of an equation of this sort. Since the values obtained for advection and divergence may differ by one or more orders of magnitude, it is a simple matter in a particular situation to find out whether one process is dominant or both are acting at approximately equal rates.

Conclusion

The following conclusions are based on this and other similar experiments on the zooplankton distribution:

1. Horizontal variation of the zooplankton of Lake Mendota occurs in a non-random pattern.

2. Study of the pattern has revealed its close relation to the currents and especially to the simultaneous effects of divergence and the phototactic response of the animals.

3. The idea of aggregation and transport of zooplankton must be kept in mind during any attempt to sample the zooplankton of Lake Mendota and probably other lakes of similar size.

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

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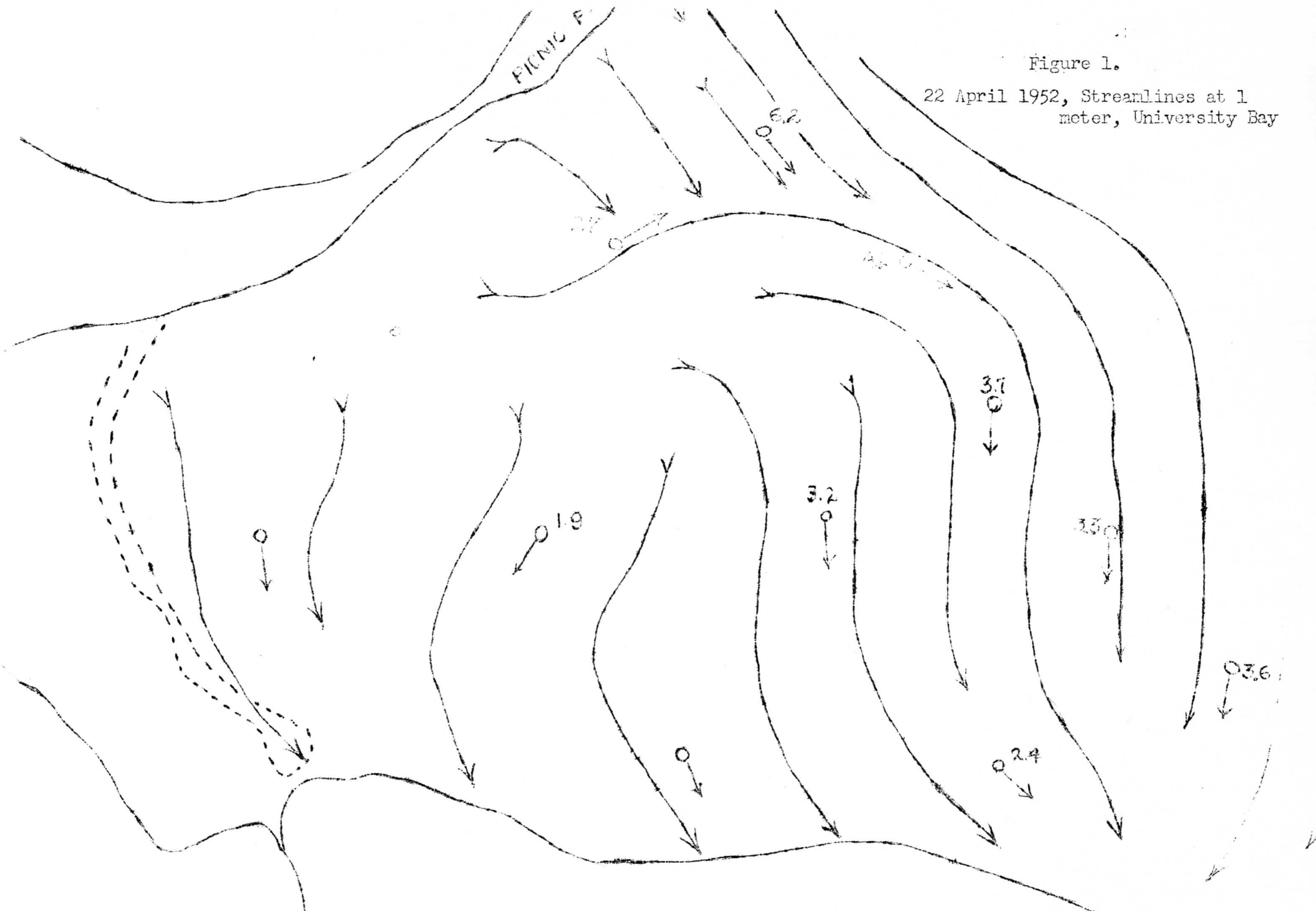
Figure 1.

22 April 1952, Streamlines at 1 meter, University Bay



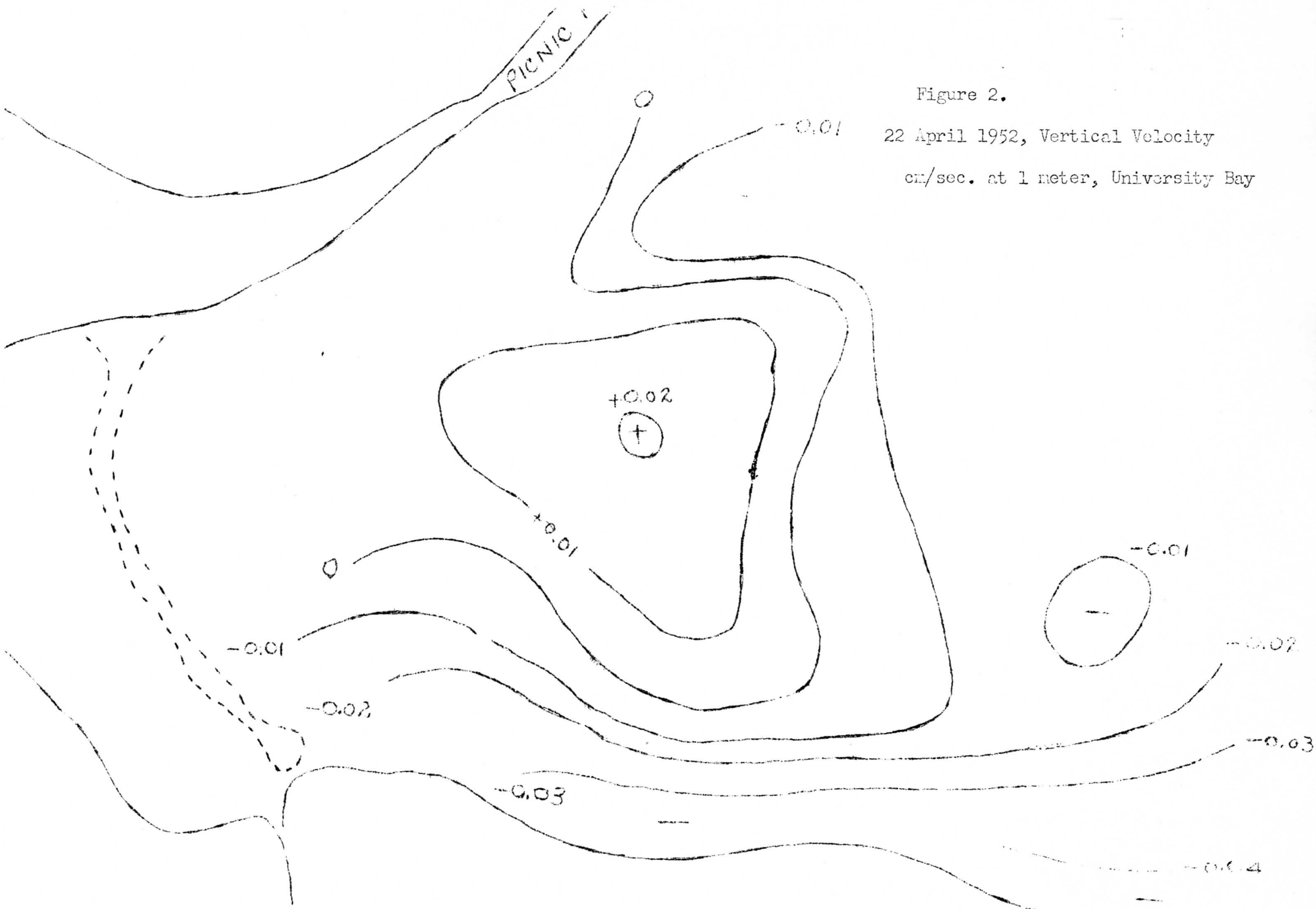


Figure 2.

22 April 1952, Vertical Velocity

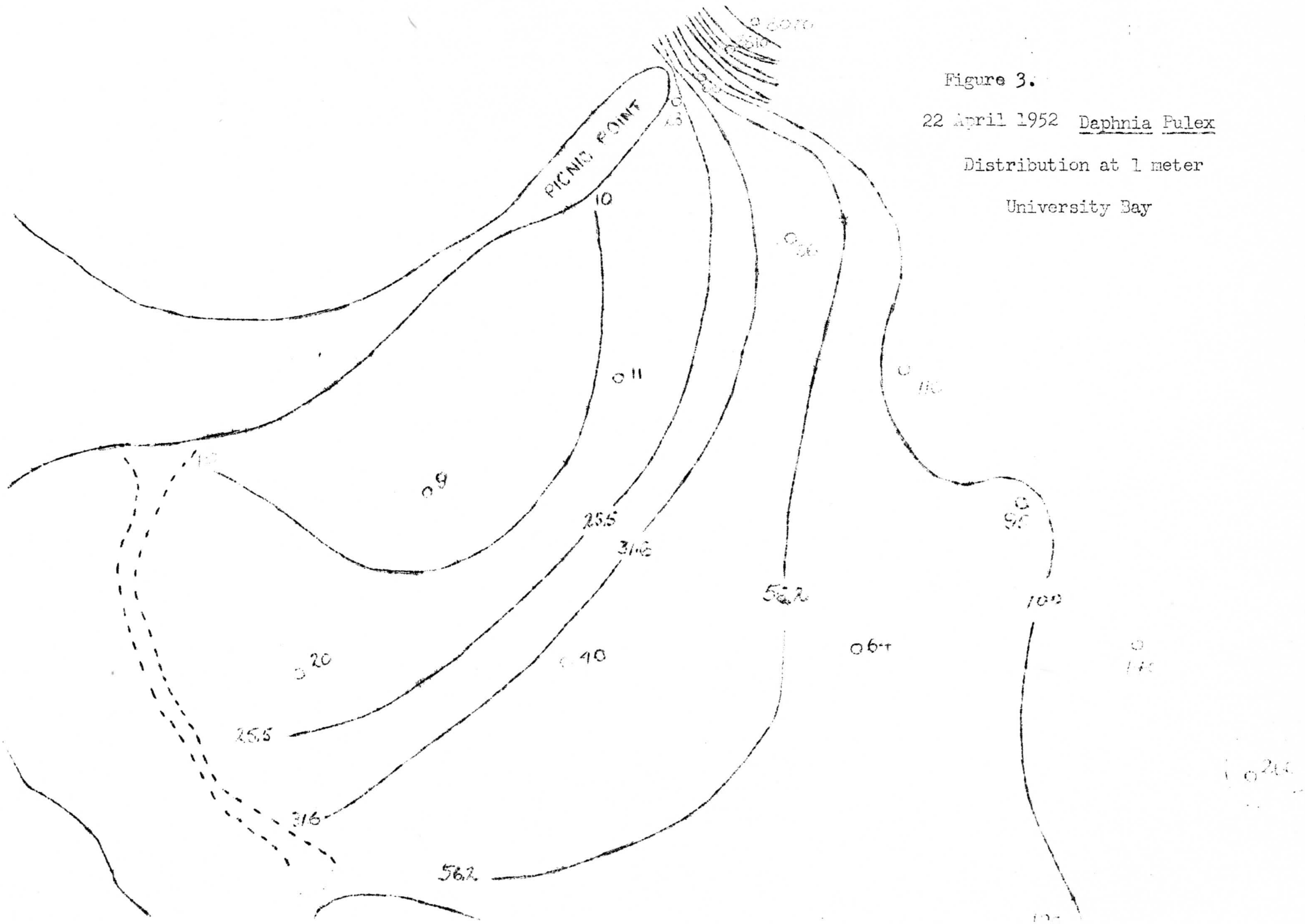
cm/sec. at 1 meter, University Bay

Figure 3.

22 April 1952 <u>Daphnia Pulex</u>

Distribution at 1 meter

University Bay



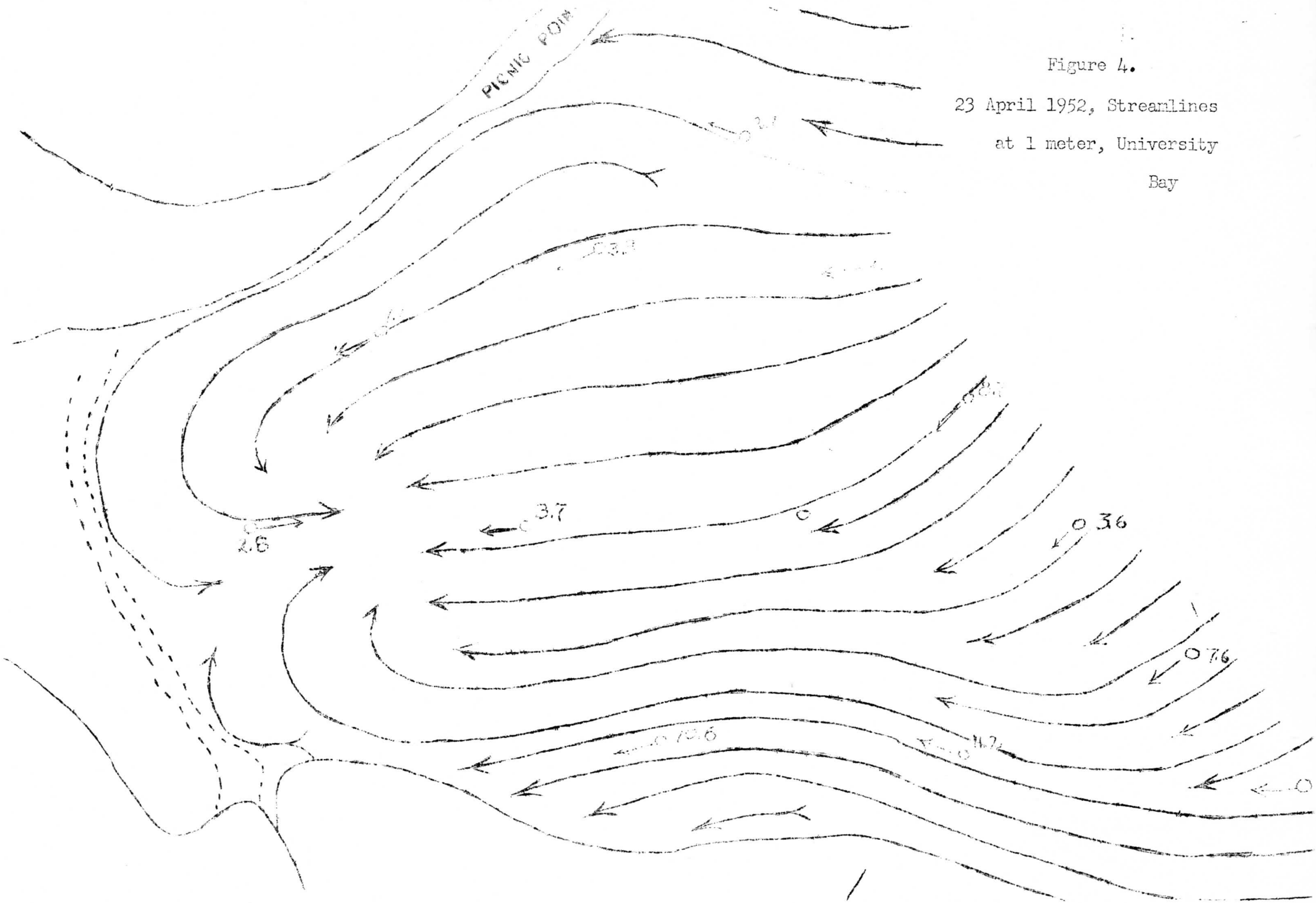


Figure 4.

23 April 1952, Streamlines at 1 meter, University Bay

Figure 5. 23 April 1952, Vertical

Velocity cm/sec. at 1 meter

University Bay

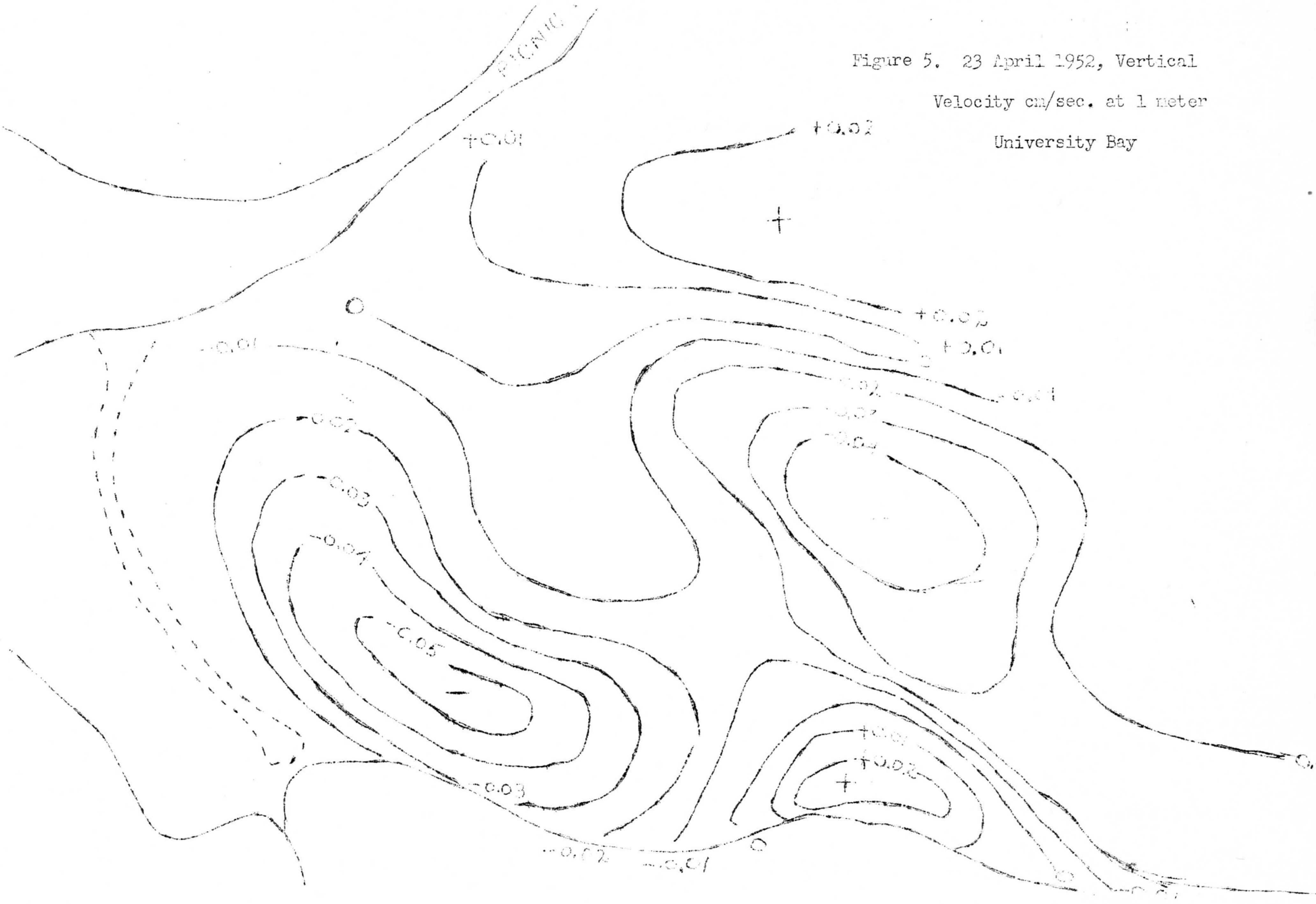


Figure 6.

23 April 1952, Daphnia Pulex

Distribution, at 1 meter,

University Bay

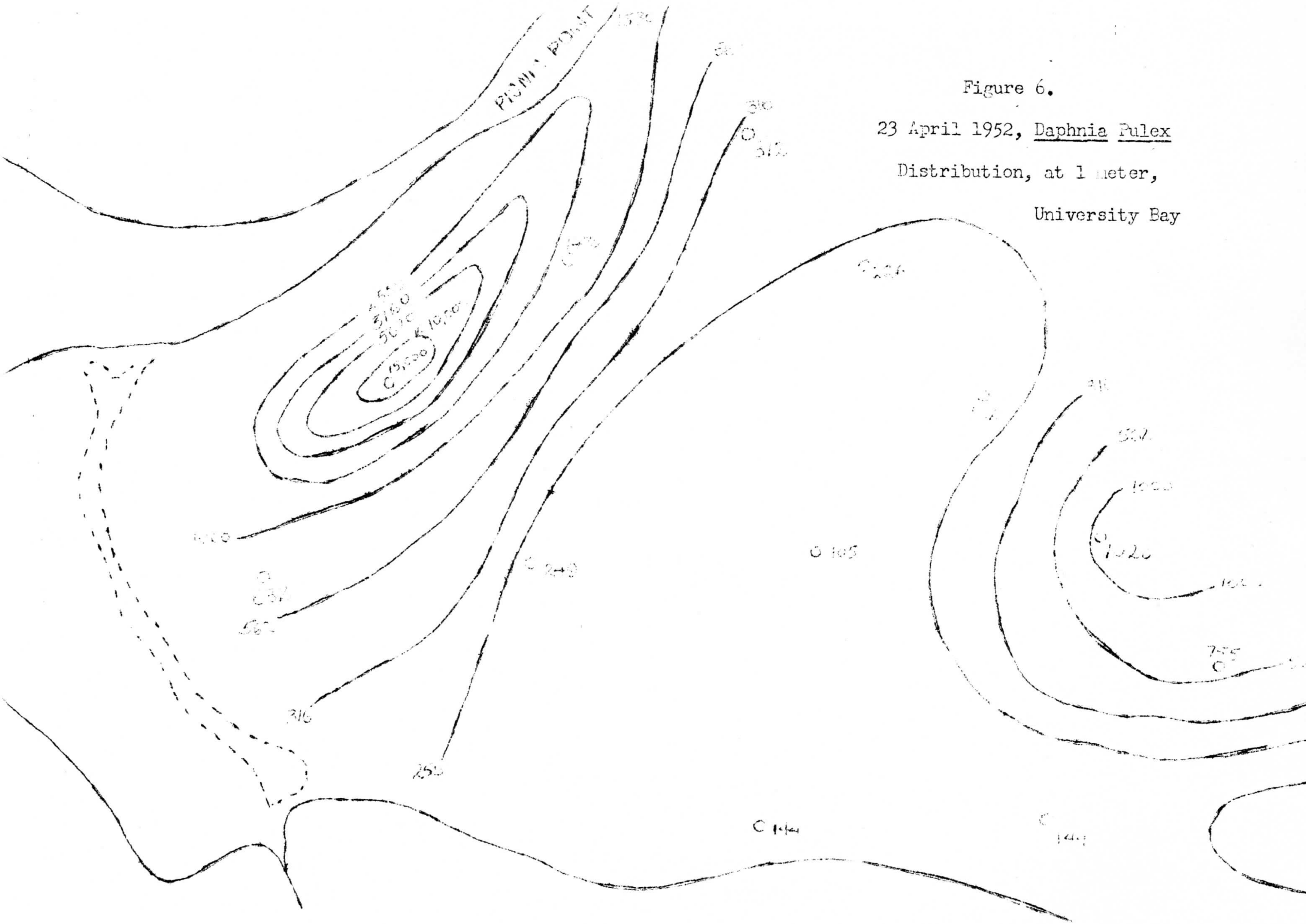


Figure 7.

24 April 1952, Streamlines at 1 meter

University Bay

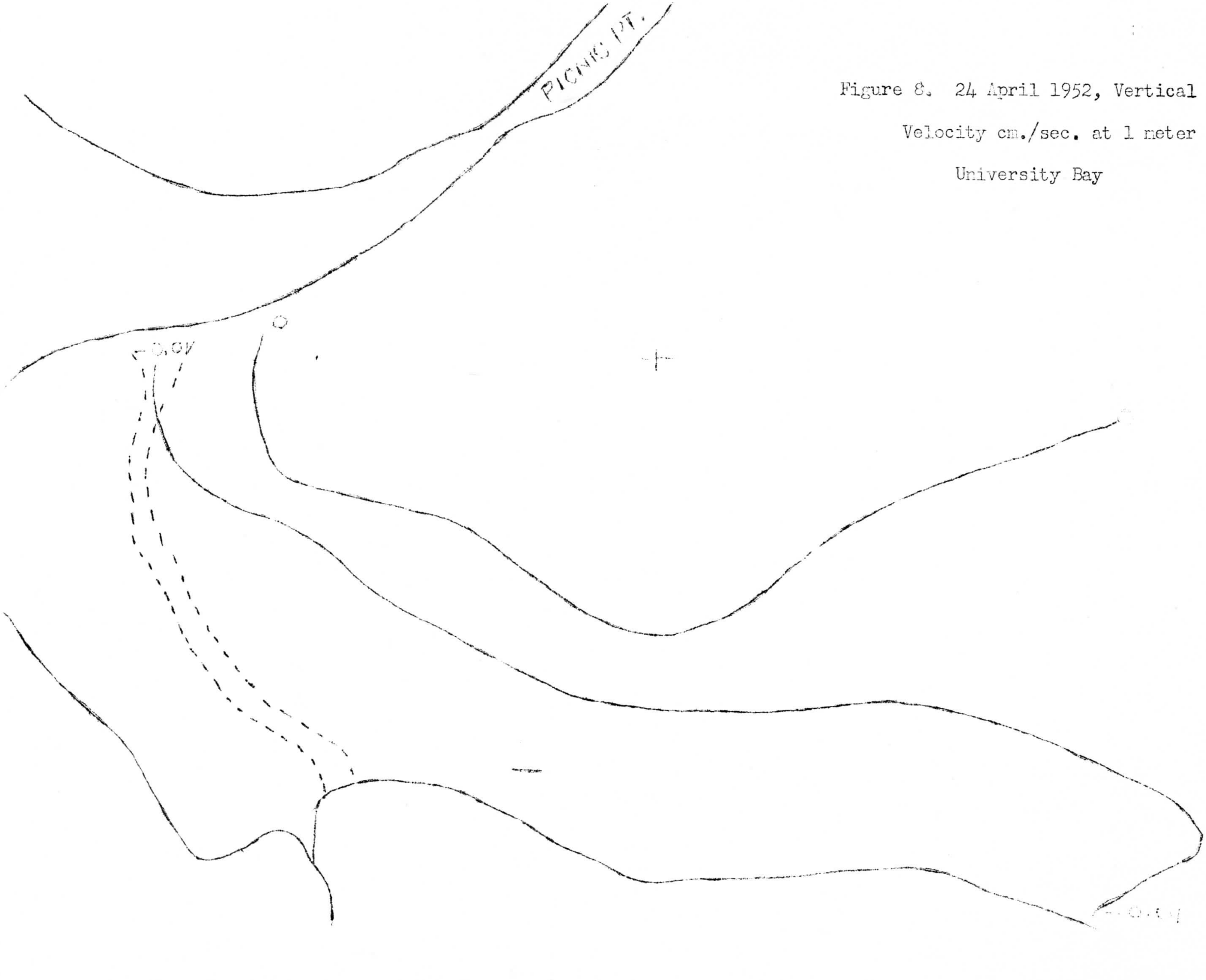


Figure 8. 24 April 1952, Vertical
Velocity cm./sec. at 1 meter
University Bay

Figure 9. 24 April 1952,

<u>Daphnia Pulex</u> Distribution

at 1 meter, University Bay