THE EFFECTS OF CARBON DIOXIDE ON *DAPHNIA*

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ABSTRACT

In all permanent bodies of water there is a group of minute free-swimming organisms known collectively as the plankton. This includes plants (phytoplankton) and animals (zooplankton). Small fish depend entirely upon the plankton for food, as also do the whalebone whales, the largest living animals. Economically the plankton is of vast importance, the fishing industries being directly dependent upon its abundance.

To the biologist this assemblage of organisms presents a number of interesting problems, one of the most puzzling of which is the diurnal vertical migration observed in the group as a whole. These movements are correlated with night and day, so that at noon the majority are found in the deeper water, and at midnight they are nearer the surface. Superficially it appears that the movements are caused directly by light, the organisms perhaps migrating in search for a constant intensity. This explanation may be correct for the phytoplankton, but has not been substantiated for the zooplankton. Laboratory observations on the fresh-water crustacean, *Daphnia*, by von Frisch and Kupelwieser (1913), Clarke (1930, 1932) and others have not disclosed the role o[illegible] in the diurnal migrations of th[illegible]eb (1904) found that carbo[illegible] made *Daphnia* strongly [illegible] light from the side, and on this evidence suggested that diurnal variations in the carbon dioxide content of natural waters, brought about by the periodic photosynthetic activity of plants, were responsible for diurnal vertical migrations. This theory has been criticised as not having sufficient experimental proof.

The *Daphnia pulex* used in my experiments were tested for phototropic re-

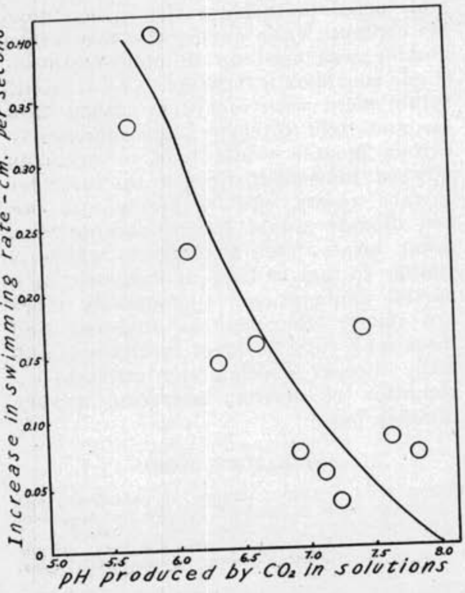

Fig. 1.—Graph showing the effect of carbon dioxide on the phototropic response to light in the horizontal plane.

sponse by placing them in a trough 46 cm. long illuminated through one end by a 100-watt lamp. The bottom was marked off in centimeters so that when animals were dropped into the middle of the trough (zero on the centimeter scale) their movement toward or away from the light could be recorded as plus or minus centimeters, respectively. Filtered Lake Michigan water at about 20°C., was used for the experimental solutions and also in the culture medium in which the animals were kept.

In the first series of experiments, which were for the purpose of finding the normal phototropic response, 2244 *Daphnia* were given one-minute trials in the trough. For the most part these were photopositive to the light source used. When similar trials were extended over a three-hour period, and the positions recorded every six minutes, the average response was much the same. The results are summarized in the tables below. A series of trials similar to those above, but using lake water charged with carbon dioxide in the trough, were next undertaken. Altogether 11 different concentrations of carbon dioxide were used, the solutions ranging from pH 5.7 with 450 parts/million free carbon dioxide to pH 7.8 with 10 parts/million. In each con-

TABLE I.—PHOTOTROPIC RESPONSE IN LAKE WATER. 1-MINUTE EXPOSURE

Positive		*Negative*	
No. of Animals	Distance	No. of Animals	Distance
2055	25918 cm.	189	1077 cm.
Average:	12.6 cm.	Average:	5.7 cm.

2244 *Daphnia* tested.

TABLE II.—PHOTOTROPIC RESPONSE IN LAKE WATER. 3-HOUR EXPOSURE

Positive Recordings	*Negative Recordings*
429	21
Average Positions: 18.6 cm.	Average Position: 11 cm.

15 *Daphnia* tested.

centration 100 *Daphnia* were tried with the result that most became strongly photopositive, many reaching the end of the trough nearest the light in less than one minute. The time necessary to travel this distance (23 cm.) was then recorded by a stopwatch, and the swimming rate in centimeters per second calculated. Each group of 100 *Daphnia* was also given one-minute control trials in lake water, either one hour before or after the carbon dioxide trials. The difference in swimming rate between control and experimental trials was then considered to be indicative of the effect of carbon dioxide on the phototropic response. This difference was significant in all trials. Figure 1 shows the results.

When trials were extended to 3 hours, as described earlier, it was found that the carbon dioxide effect persisted for about 90 minutes.

In another series of experiments the phototropic response was tested in a 46 cm. long vertical tube illuminated from above. During the trials 4 or 5 *Daphnia* were placed in the tube and their height in the solution recorded by means of a centimeter scale (0 at bottom, 46 cm. at top) at intervals of 1 hour. The animals were tested in this way for 8 hours in lake water, and the next day again tested in a carbon dioxide solution of pH 6.0. In the lake water the *Daphnia* were at an average position of 26.1 cm. for the 8-hour period. In the carbon dioxide solution the same animals averaged 33.2 cm. and the animals did not become adapted as in the horizontal illumination. Table III shows the average hourly positions of the *Daphnia*.

The same kinds of observations were then made with the light source placed to one side of the vertical tube so that it was uniformly illuminated throughout. In lake water the *Daphnia* then remained at about the same level (average—23.6 cm.) as when the light was from above. In the carbon dioxide solution, however, the situation was reversed, the *Daphnia* being nearer the bottom of the tube (average—8.9 cm.).

The experimental results described are interesting in view of the fact that natural bodies of water usually contain a considerable amount of free carbon dioxide, the amount being greater in the deeper strata of water. Philip (1927) has shown that the carbon dioxide content of a lake studied was subject to appreciable diurnal variation. At night the respiratory activities of plants and animals acted to increase the carbon dioxide content, while during the day carbon dioxide was used up in photosynthesis. If one considers a *Daphnia* to be at equilibrium point with regard to carbon dioxide and light intensity, any increase in carbon dioxide would tend to cause an upward movement toward the brighter surface waters, while a decrease in carbon dioxide would induce sinking to a lower level. This hypothesis, which is similar to that of Loeb, is suggested as a partial explanation. Undoubtedly there are many other factors involved and these may vary in effect in different animals, thereby making any ultimate explanation of diurnal migration a very complex one.

TABLE III.—AVERAGE POSITIONS OF *DAPHNIA* IN A VERTICAL TUBE ILLUMINATED FROM ABOVE

Hours	*Height in Tube* Lake Water	CO_2 solution of pH 6.0
0	21.9 cm	37.1 cm.
1	26.5	35.5
2	27.7	30.6
3	26.4	30.7
4	33.0	33.0
5	26.9	32.4
6	27.7	31.0
7	23.3	32.3
8	22.0	37.0
	Av. of 36 *Daphnia* 26.1 cm.	Av. of 35 *Daphnia* 33.2 cm.

LITERATURE CITED

Clarke, G. L. 1930. Change of phototropic and geotropic signs in *Daphnia* induced by changes of light intensity. Jour. Exp. Biol., 7:109-131.

.........., 1932. Quantitative aspects of the change of phototropic sign in *Daphnia*. Jour. Exp. Biol., 9:180-211.

Frisch, Karl von and Hans Kupelwieser. 1913. Uber den Einfluss der Lichtfarbe auf die Phototaktischen Reaktionen niederer Krebse. Biol. Zent., 33:517-552.

Loeb, J, 1904. The control of heliotropic reactions in fresh-water crustaceans by chemicals, especially carbon dioxide. Univ. Calif. Pub. Physiol. 2:1-3.

Philip, C. B. 1927. Diurnal fluctuations in the H-ion activity of a Minnesota lake. Ecology, 8:73-89.