THE EFFECT OF WATER TEMPERATURE AND DISSOLVED OXYGEN CONTENT ON THE RATE OF GILL MOVEMENT OF THE HELLGRAMMITE *CORYDALUS CORNUTUS*[1]

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ABSTRACT

The rate of gill movement of the Hellgrammite *Corydalus cornutus* as a function of water temperature and dissolved oxygen content has been measured. The specimens were introduced into open, water-filled vessels subsequent to partial removal of dissolved oxygen from the water. Measurements of gill-movement rate were made with a hand tally counter and electric timer, while dissolved oxygen content determinations were accomplished by the Winkler technique. Gill movements increased 0.026 ± 0.018 beats per second with each parts per million decrease in dissolved oxygen content. Gill movements increased 0.188 ± 0.081 beats per second with each degree Centigrade increase in temperature. This latter value is consistent with van't Hoff's rule. Observations of the specimens showed that there was a strict sequence to gill movement and that, under certain conditions, bubbles formed at the presumably inoperative spiracles. Dissections were performed to investigate the cause of this bubble formation and gas was found to fill the major portion of the closed tracheal system.

The work reported in this paper began as a laboratory exercise in an advanced insect physiology course. Inasmuch as reliable quantitative data were collected and a literature search indicated that there had been little previous work done on this subject, it was decided to expand the effort put into the project and publish the results. The results include graphical representation of the quantitative relationships mentioned in the title and, in addition, descriptions of observations made on certain responses and behavioral characteristics of the insects studied.

METHODS AND MATERIALS

The experimental animals used were larvae of the dobsonfly or hellgrammite, *Corydalus cornutus* (L.). The experimental procedure began with the introduction of an 800-ml glass beaker, nearly full of tap water, into a vacuum oven. No heating was involved and the oven was used merely as a convenient means of

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introducing the water into a partially evacuated environment of known pressure. The same results could have been obtained with a vacuum flask, drying tube, pressure gauge, and vacuum pump or aspirator. After introduction of the beaker, the pressure in the oven was reduced until the gauge reading was −29 psi. The beaker was left in the oven under this reduced pressure for time periods varying from 1 to 2 hr. Even though the water boiled at room temperature at this reduced pressure, there was generally 500 to 600 ml left in the beaker when it was removed from the oven. An item of technique should be mentioned at this point. In order to remove the water from the vacuum oven at a temperature close to the temperature of the aquarium in which the experimental larvae were kept (25 C), the water had to be at a temperature of from 30 C to 35 C when it was introduced into the oven since the low pressure and rapid evaporation rate had the effect of lowering the temperature of the water.

When the beaker was removed from the oven, a larva was introduced and the rate of its gill movement was measured with a hand tally counter and an electric timer. A sample of the water was then taken in order to immediately determine the dissolved oxygen content by the Winkler technique (Welch, 1948). Laboratory compressed air was then passed through a gas dispersion tube and bubbled through the water until a significantly different rate of gill movement was measured. Checks on the rate of gill movement had to be made with the gas dispersion tube removed from the water since the larvae had a persistent tendency to wrap themselves around the tube and not move their gills at all. Once a new rate of gill movement was observed, a sample of water was removed and measured for dissolved oxygen content. This procedure was repeated until the water in the beaker was depleted.

The difficulty with controlling the temperature of the water has already been mentioned. During the last two repetitions of the experiment the temperature of the water was kept constant to within ± 0.5 C. In addition, in order to determine the effect a variation in temperature might produce, a run was made in which the temperature of the water bath was raised while the oxygen content was held constant.

During this run the temperature of the water reached 38 C for about 10 min. The specimen seemed to suffer no ill effects from its exposure to this temperature for such a short time, since it appeared to function normally for at least the following week.

RESULTS

The results of the temperature and oxygen content runs, as shown graphically in figures 1 and 2, indicate that rate of gill movement varies directly with temperature and inversely with dissolved oxygen concentration. Although fewer data were obtained than would be desirable and although considerable scatter is evidenced by these points, a straight line was fit to both sets by the method of least squares.

The method of least squares was used, of course, to pick the best possible straight line to fit the available data. Other statistical techniques can be used to determine the accuracy of the slope of line fit to a set of experimental data. Such techniques are elucidated in Hoel (1961). Briefly, when a few data points are obtained and plotted and a curve is fit to them by the method of least squares, the slope of this curve varies with the total number of data points collected and with the inherent probabilities associated with random data collection. The possible values of the slope of a line fitted to a given set of data points varies as a "t" distribution. Therefore a "t" test can be applied, for any desired confidence level, to determine the accuracy of the experimentally determined slope. Such a test, for a 95 percent confidence level, was applied to the data shown in figures 1 and 2.

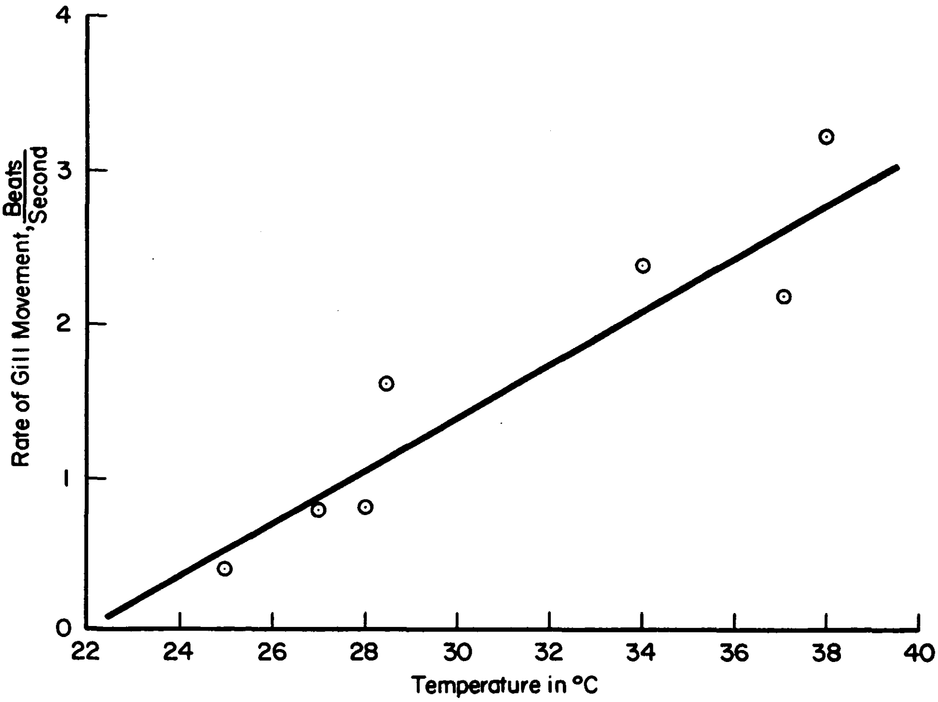

FIGURE 1. Effect of temperature on rate of gill movement.

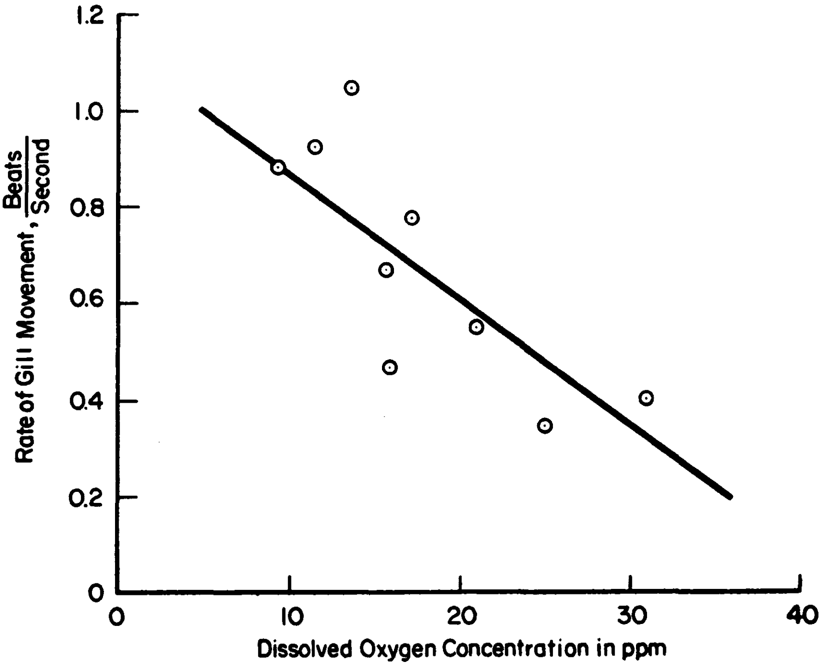

FIGURE 2. Effect of dissolved oxygen content on rate of gill movement.

DISCUSSION

The increase in rate of gill movement with increasing water temperature is consistent with van't Hoff's rule which states that a rise of 10 degrees will approximately double the rate of a chemical reaction. In the present instance the rate increase for a 10-degree rise in temperature, i.e., the Q_{10}, has a value of 1.88 ± 0.8 which is close to the theoretical value.

The increased gill movement shown with decreasing oxygen tension is less well understood. Although the tracheal gills of aquatic insects are of value in obtaining dissolved oxygen from the water, they appear to augment rather than replace cutaneous respiration in these forms. In experiments with caddisfly larvae and mayfly naiads where the gills have been entirely removed, oxygen consumption by the insect has continued at the normal rate, except in water very poor in oxygen (Wigglesworth, 1953). Even at very low oxygen concentrations, Wingfield (1939) found that naiads of the mayfly, *Cloeon dipterum*, with the gills removed, could exist normally if the water was artifically stirred. He concluded that the function of tracheal gills in this insect is mainly to drive the water over the true respiratory surfaces. Even a reduction of oxygen uptake of an aquatic insect moved from running to still water may not indicate reduced gill function for, as Balke (1957) points out, larvae in running water used almost twice as much oxygen as those in quiet ponds, presumably as a consequence of the added effort in moving about against the current of the running water. We have found no recorded studies on the hellgrammite or any other aquatic member of the Order Neuroptera in the literature of insect respiration.

In addition to the quantitative results presented, several aspects of the insects' responses that are worthy of mention were observed. The first of these is that one of the larvae was seen to "preen" or "comb" its gills with its mandibles. This activity could be valuable in food collection since a large volume of the organisms on which the insect feeds would be expected to pass by in the stream of water directed by the insect's gills and some of these would be expected to adhere to the gills. On the other hand, this activity might be more valuable in respiration, since it would result in removable of debris from the gills and thus facilitate exchange of gases.

Another observed phenomenon was the rather strict sequence in which the gills moved. Not all the gills moved together as might have been expected. Instead, for the specimens studied, gill movement appeared to originate with the third pair. Sometimes they moved by themselves and sometimes the fourth pair moved simultaneously with the third pair. Whenever the third pair of gills beat, the first and second pair beat immediately afterwards in almost all cases. This delayed movement had the appearance of peristalsis. At times of extreme stress, all the gills moved, with the third, fourth, and all posterior pairs moving together followed closely by the first and second pairs.

The third observation of interest concerned the only specimen that died during the early experiments. The insect involved was the only one that was placed in the water before the pressure was reduced and the oxygen removed. In this case the run was made with the water in an Erlenmeyer vacuum flask connected through tygon tubing to an aspirator on a water tap. As the pressure was reduced, gas bubbles were seen to form at the insect's presumably inoperative spiracles and then rise to the surface. Two alternative hypotheses were proposed in an attempt to explain this phenomenon. The first is that gas was present in the immature tracheal system. The second is that gas was dissolved in the liquid filling the tracheal system and the observed bubble formation represented the degassing of this liquid brought about by the reduced pressure in the vacuum flask.

To check these hypotheses, two larvae were dissected and examined under a binocular microscope. The dissections of these live, presumably normal, hellgrammite larvae revealed that though the majority of the tracheal system, includ- the fine branches within the tracheal gills, was gas-filled, the main tracheal trunks and the connections to the spiracles were fluid-filled. The spiracles were of the lip-closing type (Kelsey, 1957) and apparently tightly closed. One intact specimen which was tightly squeezed failed to show any bubbles through the spiracles. The presence of air in the closed tracheal system of several diverse aquatic insects has been noted by several workers (cf. Wiggelsworth, 1953) where it appears shortly after hatching, presumably as the result of selective secretion or fluid absorption by the tracheal epithelium. The finding of gas in the tracheal system favors the first hypothesis mentioned above.

SUMMARY

The rate of gill movements in the aquatic larvae of the dobsonfly increases with increasing water temperature and decreases with increasing dissolved oxygen content of the water. Quantitatively, gill movements increase 0.188 ± 0.081 beats per second per degree Centigrade which corresponds to a Q_{10} value of 1.88 ± 0.8. Gill movements increase 0.26 ± 0.018 beats per second with each part per million decrease in dissolved oxygen content. The tracheal gills of the hellgrammite move in sequence, with movement appearing to originate with the third pair. The closed tracheal system of the larva is partially gas-filled. Ordinarily no gas passes through the closed spiracles, but under a vacuum of -25 psi, gas escapes from the spiracles.

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