

The relations discussed may be arrived at more briefly, but less directly, from dimensional considerations. Along each stream tube, there exists for a perfect gas only one independent dimensional reference quantity, as for instance the "reservoir" pressure. All variables can be expressed in terms of that reference pressure in conjunction with one non-dimensional quantity as for instance the local Mach number. Thus the local pressure is equal to the reference pressure multiplied by a function of the Mach number, and of non-dimensional quantities representing the geometry involved. Hence the lateral pressure gradient is determined and invariant with respect to transformations not involving changes of the geometry or changes of the reference pressure and thus changes of any pressure. It follows that it must be possible to write all pertinent equations in terms of the local pressure, the local Mach number and the space coordinates, thus eliminating one dependent variable.

Among possible flows calling for application of these relations, there are jets from different "reservoirs" flowing together. Such is the flow when a propulsion jet issues into the rapidly moving air (relative to a missile or airplane) of the atmosphere. It may also be instructive to idealize boundary layer wakes by considering them as jets of a perfect gas with a lowered total enthalpy.

TURBULENCE AS AN ENVIRONMENTAL DETERMINANT OF RELATIVE GROWTH IN *DAPHNIA*

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Temporal variation or cyclomorphosis is pronounced in many limnetic races of *Daphnia*. The relative length of the head is the most variable aspect of such races of the north temperate zone. The winter and early spring generations bear short round heads resembling those characteristic of pond *Daphnia*. Individuals of midsummer generations have elongate heads, called helmets, which are often nearly as long as the rest of the body. During the period of these striking phenotypic changes reproduction is entirely asexual, which means that the genetic constitutions of all generations are almost identical. These phenotypic differences must therefore be determined by seasonally variable cytoplasmic or environmental factors, in all probability the latter.

The aim of the present investigation is precise determination of all of the environmental factors controlling cyclomorphosis. The efforts of

students in the first two decades of this century were directed toward finding a single environmental variable which controlled the relative head size. Wesenberg-Lund¹ concluded that temperature was the controlling factor while Woltereck², denying this, claimed that the level of nutrition was the prime control. The experiments of Coker and Addlestone³ in 1938 indicated, however, that different environmental factors were effective at different periods of the life history of an individual. They showed that temperature did control head size, but only during the embryonic period, some unisolated factor being involved during postnatal life. The author⁴ was able to confirm these findings of Coker and Addlestone on several species.

The rate of relative helmet growth during postnatal life can be measured by the value of k in Huxley's⁵ allometric equation, $y = bx^k$, as was demonstrated in the study⁴ of the population of *D. retrocurva* Forbes in Bantam Lake, Connecticut (1945). From April until mid-June head (y) and carapace (x) grew at the same relative rate ($k = 1$). Thereafter, helmet growth was tachyauxetic, the rate reaching a maximum ($k = 1.44$) a month later. It was still greater than unity ($k = 1.27$) at the end of the series in mid-August. Tachyauxetic growth occurred that season only when the water was above 18–19°C., but above this threshold appeared to be independent of both temperature and nutrition. Individuals of this population were cultured in laboratory vessels under conditions of temperature and nutrition which supported tachyauxetic helmet growth in the lake. Yet the helmets always grew relatively more slowly ($k = 0.52$ to 0.74) than the rest of the body in these laboratory cultures. An investigation of the effects of size of vessel⁶ and population density⁴ proved that they are not responsible for this difference between the rates of relative helmet growth in the lake and in laboratory cultures. An experimental study of the rôle of turbulence was more fruitful and forms the subject of this report.

The population of *D. retrocurva* in Bantam Lake was so small in the summer of 1946 that it was impossible to collect any experimental animals of this species. The substitution of another species was necessary, so a race of *Daphnia longispina* with apicate helmets, also present in Bantam Lake, was utilized. The shape of the helmets of this race in mid-summer can be judged from the right-hand column of figure 2. Individuals from this population were used in the investigation of the influence of population density and size of vessel, as well as that of turbulence on the rate of postnatal relative helmet growth. Some of the *Daphnia* collected on September 2 were preserved and the remainder were brought back alive to the laboratory. Twenty adults with eggs or embryos in the broodpouch were selected as parents. These adults were divided into two equal groups. One was to be maintained in turbulent water while the control group was kept in

the usual quiet water of laboratory culture vessels. The cultures were kept in two similar rectangular museum jars of dimensions $20 \times 23 \times 30$ cm. Each held ten liters of Bantam Lake water, which had been twice filtered through $10 \times$ bolting silk. The jars were placed side-by-side under fluorescent lights in a room with a fairly constant temperature. A small electric stirrer rotated a nearly straight glass rod which extended about ten centimeters below the surface of the water. The turbulence so produced was judged to be sufficient when the *Daphnia* were swept around by the current. Measurement of the amount of turbulence was not possible. The nanoplankton of the lake water reproduced rapidly enough to serve unaugmented as a sufficient source of food.

Periodic microscopic examination of the adults showed that all of them lived and reproduced in each culture. No measurements of their offspring were made during the first two weeks. The temperature fluctuated slowly between 17.2°C . and 23.1°C . The mean of the daily readings for the turbulent culture was 19.4°C ., for the control 19.3°C . At the end of this period those offspring of each culture which had matured were measured and drawn.

The difference in relative head length in the two cultures was remarkable. While the heads in the controls were of the same relative length as in all previous laboratory cultures, those reared in turbulent water had relatively longer helmets, more nearly like those found in the lake. A representative adult from this first generation of each culture is drawn in figure 2.

Accumulation of sufficient data for a determination of the relative rates of helmet growth in the two cultures was highly desirable. All the instars of the first generation constituting the population at the end of the period could not be grouped to provide this information as the temperature, hence the relative head length at birth, had been too variable. It was therefore necessary to attempt a more rigorous temperature control. The two vessels were placed side-by-side in a 60-liter water bath. First generation adults were used in this experiment. Eight from the turbulent culture were replaced in turbulent water. Ten from the control culture were replaced in non-turbulent water. The temperature in each remained between 19.4°C . and 22.4°C . during this sixteen-day experimental period, except on the first day when it reached 23.0°C . Temperature fluctuations were simultaneous in the two cultures. The mean of the sixteen daily temperature records in each culture was 21.2°C . Nutrition as judged by the color of the guts was very good during the early phase of the experiment and slowly decreased so that at its termination, although adequate, it was poorer than at the outset. This change followed the same course in both vessels. It should be emphasized here that the relative rate of helmet growth is not influenced by changes in the nutritive level.

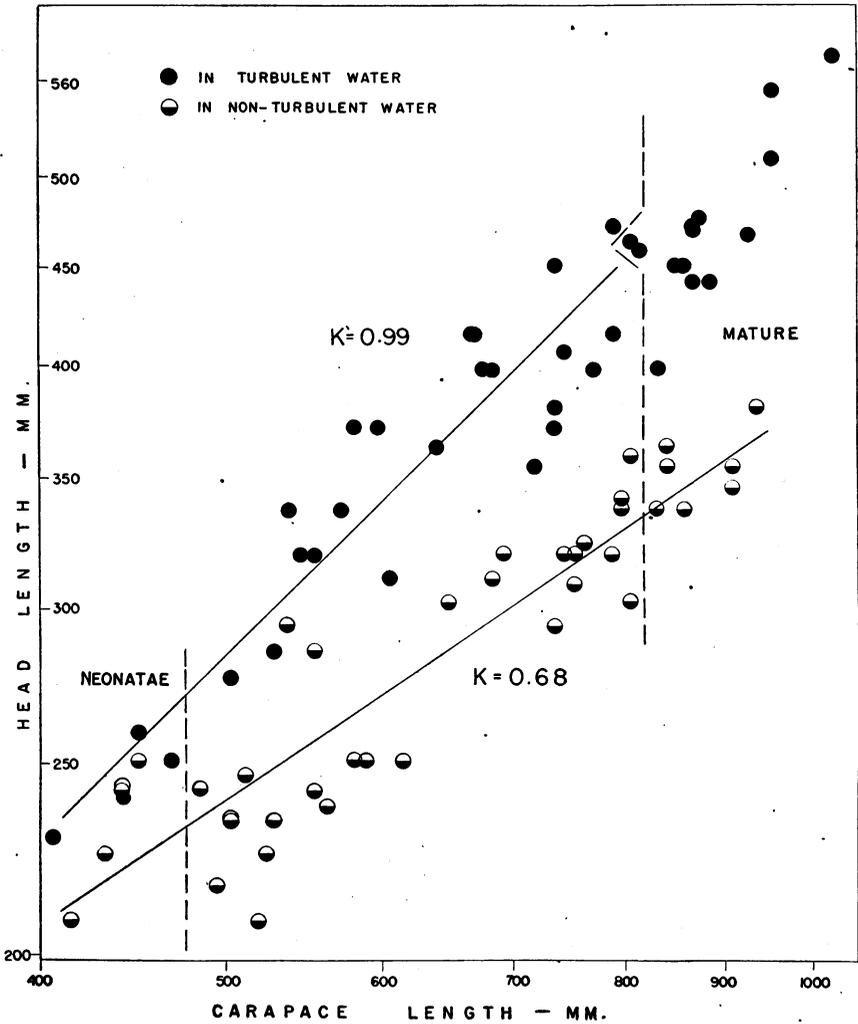


FIGURE 1.

Comparison of rates of relative head growth (*Daphnia longispina*, Bantam Lake, Conn.) in laboratory cultures with turbulent and non-turbulent water. See text for details.

Periodically a portion of the *Daphnia* population was removed from the culture vessels for examination. Each specimen was anesthetized with ethyl urethane, measured, and drawn with the camera lucida. These animals if properly treated, appeared to suffer no ill effects and were returned to the cultures. The measurements of head length and carapace length were made with an ocular micrometer. The head length was then plotted on a logarithmic grid against carapace length for each individual.

This gives a linear array of points for each culture. Measurement of the slope of the line of best fit for each array provides the k value for each culture. The details of measuring and analysis of measurements are given elsewhere.⁴ When the pre-adult rate of relative helmet growth is isauxetic or tachyauxetic, there is an appreciable fall in the rate after maturity. No change in rate is apparent when early growth is bradyauxetic. The exponent, k , for immature specimens in the turbulent water is 0.99. Calculated for all specimens in non-turbulent water it is 0.68. (Fig. 1.)

This difference between the rates of relative helmet growth in turbulent and non-turbulent cultures could be either a direct effect of turbulent water movements on the *Daphnia* or an indirect one. Turbulence might act indirectly by increasing nutrition or oxygen concentration. Yet, as pointed out above, the difference between the levels of nutrition in the two cultures at any time was small when judged by microscopic examination of the guts of the transparent living animals. Oxygen determinations using the Winkler process showed that the water in both vessels was saturated with oxygen at the end of the experiment. This leaves a direct effect of turbulence as the more likely explanation, but no definite information is available as to the manner in which it influences the growth processes of *Daphnia*. It is possible that there are environmentally conditioned differences in metabolic rate associated with different rates of relative helmet growth. This would parallel the situation in *Locusta migratoria* where the externally determined solitary and migratory phases are known to have significantly different rates of oxygen consumption.⁷

Adult *Daphnia* reared in turbulent water in the laboratory have helmets relatively larger than those reared in non-turbulent cultures but they do not attain the proportions of adults which developed in the lake at about the same temperature. A comparison of development in these three environments is given in figure 2. These camera lucida drawings are all to the same scale, except for the neonatae which have twice the linear magnification. The left and center columns contain specimens taken from the non-turbulent and turbulent laboratory cultures, respectively, while that on the right shows specimens in the Bantam Lake population at the time when the parents for the experimental cultures were collected. These parents had the appearance of the adult at the top of that column. The adults of similar size which head the other two columns are the offspring of these females which were reared under turbulent and non-turbulent laboratory culture. Development in the two laboratory cultures will first be considered. The relation of each specimen to the rest of the population samples can be checked in figure 1. More than one specimen is drawn for most size groups to illustrate the range of variation. Specimens toward the left of either column have relatively smaller helmets, appearing below the line of best fit in figure 1. Those to the right have relatively larger helmets

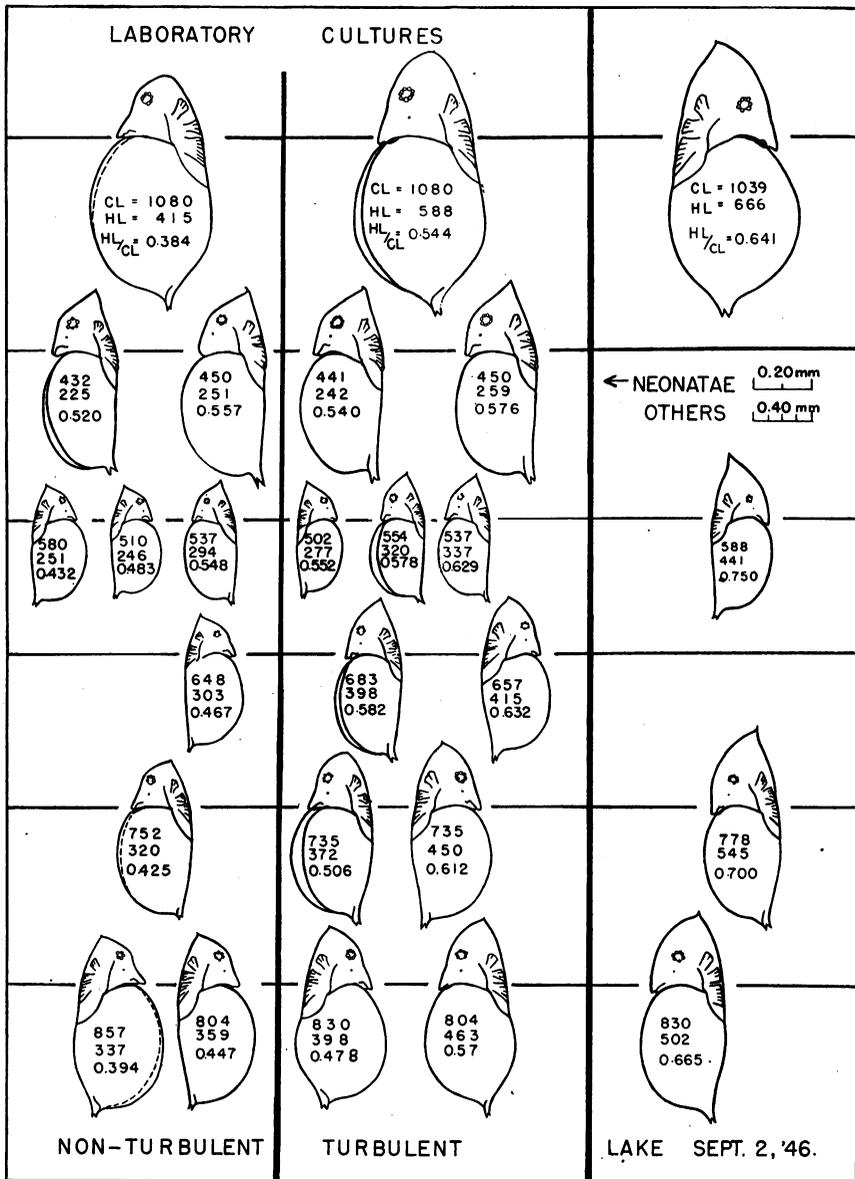


FIGURE 2.

Camera lucida drawings illustrating differences in helmet development in individuals from the same population of *Daphnia longispina* (Bantam Lake, Conn.) when reared in three different environments. The range of temperature and nutritive conditions was the same in all three. See text for details.

and those in the middle correspond to points on the curve. The relative helmet size of each *Daphnia* is given as a ratio. The effect of the different relative growth rates is apparent even on comparison of the neonatae with the next larger size group. While the newborn of the two cultures are identical, the lowest HL/CL ratio for specimens of the next larger size group in the turbulent culture is as high as the highest among the same sized individuals of the control culture. Among larger specimens the lowest HL/CL ratios in the turbulent culture are greater than the highest found in the same size group from non-turbulent water. The younger individuals in the right-hand column represent the only specimens of the appropriate instars to be found in the sparse population in Bantam Lake at that time. Unfortunately no neonatae were taken. As the temperatures at the surface, at one meter's depth and just above the bottom were 22.7°C., 21.6°C. and 20.2°C., respectively, the neonatae undoubtedly had helmets of about the same relative size as those in the laboratory cultures. If so, the helmets must have been growing relatively more rapidly than those in the turbulent laboratory culture in order to produce the higher helmets in the later instars. Although the absence of representatives of the early instars precludes an accurate determination of the relative growth rate, comparison with the laboratory growth rates should provide an approximation. The helmets in the turbulent laboratory culture were growing at the same relative rate as the rest of the body (isauxesis) since the slope of the line best fit is essentially unity ($k = 0.99$). Relative helmet growth in the lake must therefore, have been tachyauxetic ($k > 1$).

The information which this experiment provides concerning the relative rates of helmet growth under different environmental conditions is incomplete, yet it invites integration with what we know of the seasonal differences in relative growth rates in *D. retrocurva*. The helmets of the Bantam Lake population of the latter species grew isauxetically from the first of April to the middle of June 1945, under a wide range of nutritive and thermal conditions. The race of *Daphnia longispina* in the turbulent laboratory culture, well fed and at somewhat higher temperatures exhibited isauxetic helmet growth. This suggests that turbulence of the lake waters may be the factor permitting isauxesis. If so, it seems probable that turbulence is also necessary for tachyauxetic growth. Differences in the amount of turbulence might determine the rate of relative helmet growth or turbulence may be a necessary, but not a sufficient environmental factor for tachyauxesis. Further laboratory experimentation will explore this possibility. There is also hope of estimating the seasonal variation in the amount of turbulence in lakes.

One remark about the significance of turbulence in the interpretation of the biology of limnetic *Daphnia* should be made. Should turbulence prove to be a necessary environmental condition for the development of helmets

in many races it would explain the oft-noted restriction of helmeted populations to the upper, turbulent waters of stratified lakes. Those living in lower, less turbulent waters usually have shorter helmets.

Summary.—Preliminary experiments on a cyclomorphic race of *Daphnia longispina* indicate that turbulence of the water is one of the environmental factors controlling relative rate of helmet growth during postnatal life.

¹ Wesenberg-Lund, C., *Plankton Investigations of Danish Lakes*, General Part, Glydendalske Boghandel, Copenhagen (1908).

² Woltereck, R., "Variation und Artbildung," *Int. Rev. Hyd.*, 9, 1-151 (1921).

³ Coker, R. E., and Addestone, H. H., "Influence of Temperature on Cyclomorphosis in *Daphnia longispina*," *Jour. Elisha Mitchell Sci. Soc.*, 54, 45-75 (1938).

⁴ Brooks, J. L., "Cyclomorphosis in *Daphnia*. I," *Ecol. Mon.*, 16, 409-447 (1946).

⁵ Huxley, J., *Problems of Relative Growth*, New York, MacVeigh (1932).

⁶ Suggested in Coker, R. E., "The Problem of Cyclomorphosis in *Daphnia*," *Quart. Rev. Biol.*, 14, 137-148 (1939).

⁷ Butler, C. O., and Innes, J. M., "A Comparison of the Rate of Metabolic Activity in the Solitary and Migratory Phases of *Locusta migratoria*," *Proc. Roy. Soc. London, Ser. B*, 119, 296-304 (1936).

A DIRECT DEMONSTRATION OF THE PHOSPHORUS CYCLE IN A SMALL LAKE*

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It is well known that the total quantity of plankton present in the waters of a lake may undergo marked and rapid variation, so that in the course of a year a number of pulses or maximum populations may succeed each other. Juday and Birge¹ noted that such rises in the phytoplankton might occur without reducing the phosphate content of the water and that on occasions both phosphate and plankton might rise together. It has also been noted for example by Pearsall,² that rises in the population of blue-green algae may occur at the end of summer when it would seem that the phosphorus content of the water was totally inadequate to support an increased phytoplanktonic population. In an earlier paper³ much indirect evidence was assembled indicating that in Linsley Pond, a small inland lake which develops a very stable thermal stratification in summer, there is a continual liberation of phosphorus from the mud into the free water. Such of this phosphorus as enters the illuminated layers of the lake is believed to be taken up by the phytoplankton, later to be sedimented as a fine rain of particulate matter, partly no doubt dead phytoplankton, but also feces of