# ECOLOGICAL STUDIES OF AQUATIC INSECTS. II. SIZE OF RESPIRATORY ORGANS IN RELATION TO ENVIRONMENTAL CONDITIONS [1]

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While making a study of the insect larvae, mayflies, stoneflies and caddisflies of mountain lakes and streams in the Front Range of the Rockies near Tolland, Colorado,[2] it was observed that, with very few exceptions, the species living in the lakes and quieter parts of the streams had the respiratory organs larger in proportion to the size of their bodies than the larvae living in the swift streams. It was also noted that there was a tendency for the species living under stones in the stream and on pond bottoms with much decaying plant material to have large respiratory organs. These facts seem to be correlated with two things, (1) the oxygen content of the water and (2) the swiftness of the current. With these observations in mind, sudies were made to determine the relationship between the area of the respiratory surface and the body weight for the representative species of the different habitats.

## 1. Mayfly Nymphs

Mayfly nymphs were selected for the intensive study because they furnish striking examples, and also because their gill lamellae could be easily measured. We made use of nymphs that had nearly or fully attained their growth. In determining weights, nymphs which had been preserved in alcohol were soaked in distilled water until the alcohol had been removed. To prevent loss by evaporation during weighing, the nymphs were weighed in a small vial, tightly corked, and about half full of distilled water. After the container had been weighed, a nymph from which the excess water had been removed with filter paper, was placed in the vial and total weight recorded. A number of individuals of each species were weighed, and the average taken as that of the species. In determining the area of the gills,

[1] This paper is the second of a series of investigations made on aquatic insects at the University of Colorado, Mountain Biological Laboratory. It is contribution No. 73 from the Department of Zoology, Agricultural Experiment Station, Kansas State Agricultural College.

[2] Dodds, G. S., and F. L. Hisaw, "Ecological Studies of Aquatic Insects. I. Adaptation of Mayfly Nymphs to Swift Streams," Ecology, 5: 137–148, 1924.

all the gill lamellae were removed from nymphs which had been weighed, were outlined under known magnification, and the area of the drawings determined by means of a planimeter. The oxygen content of the water was

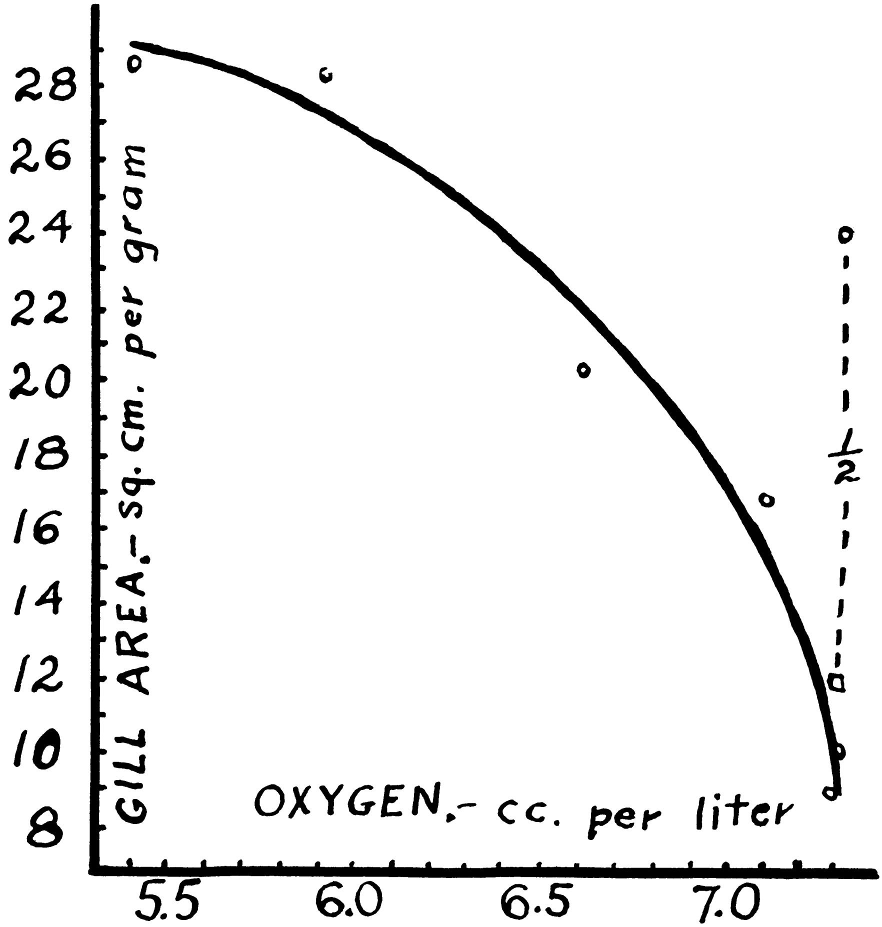


FIG. 1. Graph showing relation between gill area per unit weight and oxygen content of the water inhabited by the seven species of mayflies included in Table I. The curve as drawn passes near all of the values except one (*Iron* sp.), which lies far off. If the gill area of this species is divided by two, as explained in the text it probably should be, it falls close to the curve.

tested by the Winkler method.[3] The velocity of the current in various parts of the stream was measured by means of a glass tube bent at a right angle, as described in a former paper (Dodds and Hisaw, 1924).

[3] Birge, E. A. and Juday, C., "The Inland Lakes of Wisconsin. The Dissolved Gases of the Water and their Biological Significance," Wis. Geol. and Nat. Hist. Survey, Bull. No. 22, Sci. Series No. 7, pp. 13–21, 1911.

The relation of gill area to body weight, we express, for convenience, in square centimeters of gill surface per gram of weight. Of the seven species selected for the study the greatest gill area was 28.8 sq. cm. per gram, the least about 32 per cent of this, or 9.3. The other values range in between, as seen in the first column of table I.

The oxygen values run from 7.28 to 5.4 cc. per liter of water, the smallest being 74 per cent of the greatest, a proportionate difference much less than that between the gill areas. Reference to the first column of table I shows a definite inverse correlation between these two sets of values, with the exception of *Iron* sp., which will receive special comment later. The relation between these two sets of values is made evident by the graph shown in figure 1, where the curve as drawn, falls close to all the plotted values in such a way as to indicate clearly a significant relationship. It is of interest that so great a difference of area as 68 per cent is so definitely correlated with an oxygen difference of only 26 per cent, suggesting that possibly other factors than oxygen difference may be operative in determining gill area.

TABLE I. *Showing correlation of gill area of mayfly nymphs with oxygen content and velocity of water in which they live*

| Nymph | Sq. Cm. of Gill Area per Gram Body Wt. | Cc. Oxygen per Liter | Velocity of Water in Ft. per Second | Habitat |
|---|---|---|---|---|
| *Edyurus ramaleyi* | 28.8 | 5.4 | 0 to moderate current. | Under stones in streams and lakes. |
| *Siphlurus occidentalis* | 28.4 | 5.9 | 0 | Silty bottom of lakes. |
| *Callibaetis fuscus* | 20.4 | 6.6 | 0 | Vegetation in lakes. |
| *Baetis tricaudatus* | 17.0 | 7.1 | 0–5 | Streams and lake shore. |
| *Iron* sp. | 24.1 | 7.3 | 5–7 | Torrent. |
| *Baetis bicaudatus* | 10.3 | 7.3 | 6–10 | Torrent. |
| *Ameletus velox* | 9.3 | 7.28 | 0–1 | Clean lake and quiet stream. |

The oxygen values given here represent the average of several determinations from each locality, and figures from more than one locality of each type are included in the average value given. In all the analyses made, the amount of oxygen found was more than enough to saturate the water at the prevailing temperature and barometric pressure. At 9,000 feet altitude and a temperature of 12 degrees C., a common temperature here, the saturation point of water is about 5.2 cc. per liter, as against 7.44 per liter at the same temperature at sea level. All our readings accordingly represent varying degrees of supersaturation, the largest oxygen content found being about 150 per cent of saturation. These values do not seem to be exceptional or of special interest, except the absence of very low oxygen values, such as are found in the deeper strata of inland lakes during the summer. The absence of such values in our readings is of course due to the fact that none of our samples were taken at very great depths so that none of them represent the stagnant conditions which prevail in the deeper strata of many lakes during the summer.

The data obtained from this study (table I) show that with few exceptions those species living in the lakes and *under* stones in the stream, have larger gill areas per unit body weight than those living on the *surfaces* of stones in the swift streams and torrents, and that the exceptions have qualifying factors. *Ecdyurus ramaleyi* which has 28.8 sq. sm. of gill area per gram of body weight, lives under stones in the streams and the clean-bottomed lakes, where the oxygen content of the water was found to be 5.4 cc. per liter. *Siphlurus occidentalis* with 28.4 sq. cm. of gill area per gram of body weight, lives on the silty bottom of lakes where the oxygen is 5.9 cc. per liter. The environments of these two nymphs are similar in that the oxygen content of the water is almost the same and that a current is almost or entirely lacking. It is evident that the respiratory activities of these nymphs tend to lower the oxygen content of the water in the immediate vicinity of their bodies and some means must be provided to replenish the supply. This is done, as in the case of all mayfly nymphs living in quiet water, by creating a respiratory current by the movement of some part of the body, in these two cases by a rythmetic motion of the gill lamellae which causes a current of water to flow past.

*Callibaetis fuscus* and *Baetis tricaudatus* live in environments quite different from those of the two species just described, but similar to each other in certain respects. They have about the same ratio between the gill area and body weight, *C. fuscus* having 20.4 sq. cm. per gram body weight and *B. tricaudatus* 17.0. *C. fuscus* lives upon the vegetation of lakes where the water has been found to contains 6.6 cc. of oxygen per liter. The vegetation is a factor which differentiates this habitat from conditions under stones or on silty bottoms, and since the nymphs are usually found on it they do not come in contact with the decaying organic materials covering the bottom. This species is also a fairly active swimmer, the frequent shifting of position affording a new supply of oxygen, and when at rest, the nymphs keeping up a respiratory current by movement of the gill lamellae. *B. tricaudatus* lives on the surfaces of stones and vegetation in the stream, provided the water is not flowing more than five feet per second, and also in clear lakes close to the entrance or outlets, where oxygen has been found to be present in amounts of about 7 cc. per liter. Although *B. tricaudatus* lives in a situation where the oxygen content of the water is slightly higher than that in which *C. fuscus* is found, the most important factor is the current of the stream. *B. tricaudatus* does not carry on respiratory movements while in the stream, for the flow constantly changes the water which bathes the gills. However, when this species lives in the lakes under the conditions described for *C.*

*fuscus,* it performs respiratory movements by moving the abdomen back and forth in a horizontal position.

*Baetis bicaudatus* and *Ameletus velox* have the smallest gill area per unit body weight of any of the species studied. The former, with a gill area of 10.3 sq. cm. per gram of body weight, inhabits the torrents where the water may be flowing at the rate of 10 feet per second, while the latter, with a gill area of 9.3 sq. cm. per gram of body weight, inhabits the quiet parts of the stream and clean shores of lakes. *B. bicaudatus* is able to live in swifter water than any of the other species studied, while *A. velox* spends most of its time close to the surface where the oxygen content of the water is 7.28 cc. per liter and, while at rest, keeps up a respiratory current by moving the abdomen up and down and at the same time raising and lowering the thorax. It is almost constantly in motion, either changing position while feeding, or swimming from place to place.

*Baetis bicaudatus* holds to the bottom in the torrent where the water contains about 7.3 cc. of oxygen per liter, and is constantly being changed by the current. It seems evident that *B. bicaudatus* expends much energy maintaining its position in the torrent, while *A. velox,* perhaps, uses an equal amount in swimming, and both live in a situation where the oxygen is abundant. Another factor correlated with this, and perhaps, of equal importance, is the resistance of a large gill area to the water. Probably both of these factors have some influence upon the relationship between the gill area and body weight, but the extent and importance of each has not been determined.

Concerning the relationship of respiratory surface to body weight, *Iron* sp. is one of the most interesting of the mayflies. This nymh inhabits the torrents where the water may be flowing as fast as seven feet per second. It has a gill area of 24.1 sq. cm. per gram body weight, while the water has 7.3 cc. of oxygen per liter. This seems to be an exception to the rule pointed out in the foregoing discussion, but the large gill area can be accounted for if the specialization of the gill lamellae to form a sucker is taken into consideration. In fact, only the upper surfaces of the gills can function fully, as the lower surfaces, pressed against the bottom, form a partial vacuum and thus aid the nymph in retaining its position in the swift water. In this way the respiratory surface is decreased about one half. There is also an additional specialization which must be considered. At the base of each lamella there is a bunch of well developed gill filaments which are exposed to the water and are no doubt, functional respiratory organs. Perhaps these filaments are adaptations which compensate to some extent for the respiratory surface lost as the result of the specialization of the lamellae into a sucker. If the surface of these filaments is included with half the gill surface, the ratio between gill area and body weight would be about 12.7 sq. cm. to one gram or only a little more than for *B. bicaudatus,* which is also a torrent species. If such a value is used as is indicated by the square at the lower end of the dotted line in figure 1, it brings the value of the gill ratio for this species close to the curve where fall the values for the other species.

The data represented above seem to show a definite correlation between the relative gill area and the oxygen content of the water in which the nymph lives. There is also evident a correlation between gill area and velocity of the water, and to a certain extent, between velocity of water and its oxygen content. The higher oxygen content of rapid water certainly explains, in part, at least, the smaller gill area of species occupying such positions, but we must not lose sight of the possibiliy of a mechanical relation also, as suggested in the discussion of *Baetis bicaudatus*.

## Caddisfly Larvae

Caddisfly larvae, of which we have collected 42 species in this region, also afford an excellent opportunity for the study of the relation between gill development and external conditions, for we find a range including at one extreme species with large development, and at the other, species wholly without gills.

In comparison with mayflies, certain points of difference appear. The gills instead of being lamelliform are filamentous, and gill development may be measured by number, length and thickness of gill filaments. The fact that most species live in movable cases, only a few being naked (about 25 per cent of ours) complicates the problem for at least two reasons. First, the thin skin of the case-bearing abdomen must be of considerable importance as a respiratory surface, while the thicker, less delicate covering of the caseless type would, presumably, be much less suitable for this function. Secondly, many if not all of the case bearing species maintain a constant current of water through the case by undulation of the abdominal lateral fringe, or of the abdomen itself, insuring a constant change of water over the respiratory surface, while, on the other hand, the caseless forms are dependent upon natural currents of the water or their own migratory movements. In both groups (caseless and case bearing) there is a wide range of gill development, each group including species with no gills as well as others with a large development of respiratory filaments.

### *A. The Gills of Case Bearing Species*

Though the number of gills differs greatly in different species, and is subject to slight variation within the species, gills, when present, arise only at certain definite places on the body. There are three longitudinal rows on each side of the abdomen, *viz.* a mid ventral row, with one row above and the other below this. From these places on the abdomen, gills arise singly in some species, while in others they are in tufts, often of four, sometimes more. The largest number of places of origin of gills on one segment is 12, and the greatest total number of filaments observed in any of one species was 80 single filaments while the greatest number of filaments in tufted species was 310. In species with tufted gills the number in a tuft is smaller on the posterior segments, often being reduced to one, where the anterior segments have four or eight. In those species with fewer gills it is from the posterior segments that the gills are entirely wanting, and those of the mid-lateral row are nearly always less numerous than those of the other two.

In estimating gill development the size of the larvae should be considered, and, as in the case of mayflies, we used full grown larvae and made no attempt to study the younger stages. We have not, as for mayflies, computed the area of the gills, but have made use of the number of filaments, as giving a pretty good index of proportional gill area, because the filaments do not vary greatly in size relative to the larva. In most species the length of the filament is about equal to the length of one abdominal segment, in a few species being a little shorter and in a few somewhat longer, the longer ones being on the larger species.

It is evident that the larger species have more numerous filaments than the smaller ones, a relation which is clearly shown in figure 2, where length of larvae is plotted against number of filaments. Not only is this relation clearly shown, but it is also seen that the species fall into three groups, in each of which the same relation is evident. Group A includes 12 species whose filaments arise singly, with total numbers ranging from zero to 80; group B, 10 species with gills in tufts of 4, or total numbers from 56 to 204; while group C includes 3 species with gills in tufts of 8 and total number of filaments from 240 to 310. In each group the larger species have more gil filaments than the small ones. This is not surprising, because by a wel recognized mathematical relation, the volume of a body varies as the cub of one of its linear dimensions, while its surface varies as its square. Thu a larva 20 mm. long when compared with one of 10 mm. has a volume increase eight fold but surface of only four fold. This is significant in respec to respiratory surface and would be effective no matter what the relativ respiratory importance of the abdominal surface and gill filaments. T compensate for this difference in volume, therefore, either the gill filament must increase in length more than the larva does, or they must become mor nuerous. Failing in either of these adjustments, the larger larvae must see water with more available oxygen or make better use of their existing respiratory surface by more active current of water though the respiratory chambe or some other means of increasing efficiency.

Our observations, as partially expressed in figure 2 indicate that the nee for larger relative respiratory area has been met in the larger species chief by increase in number of gill filaments, and only to small degree by increa in their proportional size. It also seems quite evident from data which do not present in detail, that the larger species do not occupy habita with larger oxygen supply than the small ones. We have made no observ tions to determine the activity of the respiratory current, though this is clearly a desirable line of attack.

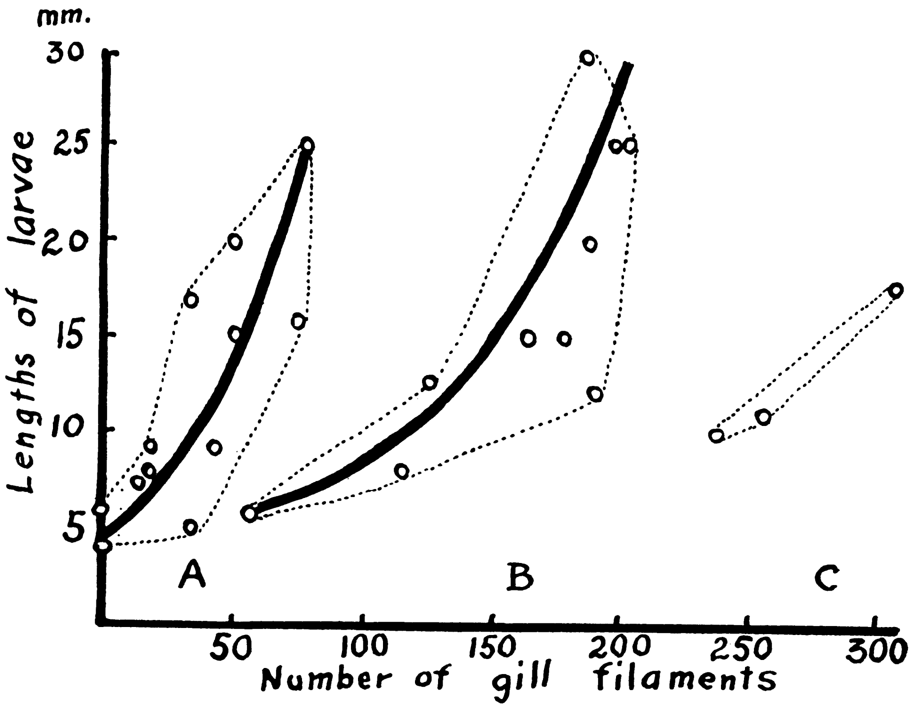


FIG. 2. Graph showing relation between length of case-bearing caddisfly larvae and number of gill filaments. Group A, species with gills arising singly. Group B, species with gills in groups of four. Group C, species with gills in groups of eight. The caseless larvae are not included in this graph.

When we seek to correlate gill development with oxygen content of the water or with swiftness of stream, such as is evident for mayfly nymphs, we do not find, on the whole, that our data give consistent results, possibly because we have not studied carefully enough the exact habitat of each species. It is not sufficient to know whether a species lives in a stream or a lake, but we must know definitely in just what part, *e.g.* whether under rocks or on top, for as shown in table I, the oxygen content varies greatly within a few inches, according to the exact situation. We do not find, as might be expected, that groups A and B differ as a whole in regard to habitat, both groups including, as far as we have been able to determine, species living in both high and low oxygen. It is true that we could select a group of species which would show a definite correlation between oxygen supply and gill development, but if we include all species in such a study, the results are not definite.

It is true that those species with less than 25 gills do live in water rich in oxygen, either on clean lake shores or upon the surface of stones in swift streams with oxygen content of about 7 cc., situations similar to those occupied by *Ameletus velox* and the two species of *Baetis,* and that most of the others of the group also live either on shores of clean lakes or in edges of swift streams. Only two species of this group are confined to lakes, two species of *Phryganeidae,* both of which live in situations inhabited by *Callibaetis fuscus,* chiefly among vegetation, where oxygen is about 6.6 cc. per liter. These are the two species in group A which have the largest number of gills, 76 and 80 respectively.

An instance where different relative gill development seems to have been of advantage is the case of L 204 and L 225,[4] both from the family Limnophilidae. A number of individuals of each species had been living in an aquarium for some time, until one day we forgot to change the water, as a result of which the latter, belonging to group B, became inactive and only a few revived when the water was changed, while none of the larvae of L 204, belonging to group C, were injured. The species which died in this case had a relative gill development of only about half of the other species. having 168 rather small gills for a body 15 mm. long against 260 average sized ones for a body of 11 mm. in the species which survived. Comparison of various species made along this line, coupled with oxygen determinations to learn the minimum amount required, would be highly instructive.

### *B. The Gills of Caseless Larvae*

In our list there are two species of Hydropsychidae and 11 of Rhyacophilidae having no cases. The two species of Hydropsychidae have many groups of branched, filamentous gills on the ventral half of the abdomen, making a total of very many filaments, affording beyond question, a larger gill area than in any of the case bearing species. These two larvae live beneath stones in the creeks, where the oxygen content is low. A large gill development seems appropriate in such situations.

Of the eleven species of Rhyacophilidae, there are five without gills, four with from 62 to 74 single gills, and two with 42 tufts of about 8 gills. We know definitely that certain of the species without gills live upon exposed surfaces of rocks and that certain of those with gills live under rocks where oxygen has been found to be less abundant, while the exact habitat of the others is not known. None of these live in lakes or ponds or slow streams.

In this family there does not appear, as among case bearing species, any relation between the size of the species and number of gills. Among caseless larvae the absence of gills, especially in larvae of fair size, is more surprising than among case bearing forms, because it might be expected that the tough

[4] These larvae, the specific names of which we do not know, are designated by numbers.

integument necessary in the caseless forms would be a much less favorable respiratory surface than the delicate cuticle of those protected by cases.

### 3. Stonefly Nymphs

Stoneflies, as a group, have poorly developed gills, many species being wholly without, while others have scant filaments, usually on the thorax. In general it appears to be the larger species which have gills, while more often the smaller ones are wholly without, and must rely upon the general surface of the body for respiration, a surface seemingly poorly adapted for such a purpose. Though we have made no special study of the habitat of each species, it is well known that all live in swift streams, and according to our observations usually under the shelter of rocks and various sorts of trash. When placed in collecting jars they die much more quickly than caddis- and mayflies. It is our impression, from a few scattered observations, that those species without gills do not live as long under such conditions as those with gills when both are confined in the same vessel.

## Conclusions and Summary

The mayfly nymphs studied show a definite correlation between gill area and oxygen content of the water, and a less distinct one with velocity of water.

The case bearing caddisfly larvae show a striking correlation between number of gill filaments and size of larvae. They do not show (as far as our investigations go) a very definite relation between number of filaments and oxygen content of the water, though some facts observed indicate the existence of such a correlation.

The caseless caddisfly larvae do not show a corelation between number of gill filaments and the size of the larvae, but some of our observations show a definite relation between number of gill filaments and oxygen content of the water.

Stonefly nymphs are very poorly equipped with gills and show decidedly less tolerance of scant oxygen supply than either caddis- or mayflies.