THE THERMAL RESISTANCE OF MAYFLY NYMPHS FROM PONDS AND STREAMS

By R. J. WHITNEY

From the Zoology Department, University of Birmingham

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(With Two Text-figures)

Temperature is a factor of great importance in determining the distribution of animals. There are many references in ecological literature to a correlation between distribution of animals and the temperature conditions prevailing in the habitats occupied by the animals. Particular instances of this correlation are the distribution of stream turbellarians (Steinmann, 1906; Thienemann, 1913) and the effects of abnormal temperature conditions on local faunas (Allee, 1923; Stephens, 1938). The great significance of temperature to the animals themselves is shown by the many physiological studies of its action on living matter (Bělehrádek, 1935), and is also evident in the ecologists' use of the terms stenotherm and eurytherm. This correlation between temperature and distribution has rarely, however, been investigated from the experimental standpoint. One line of approach has been the experimental investigation of the thermal resistances of animals from different habitats.

In this paper I shall be concerned only with the thermal resistances of aquatic animals. Some work has been done in the past relating the thermal resistances of animals to the types of habitat in which they are found. Most of this work has been done on marine animals (Richet, 1885; Frenzel, 1885; de Varigny, 1887; Meyer, 1914; Huntsman & Sparks, 1924–5). Similar work on the thermal resistances of freshwater animals from different habitats has been done by Davy (1863) on fishes, by Hathaway (1927) on fishes and tadpoles, and by Brown (1929) on Cladocera. Plateau (1872) determined the thermal resistances of some fresh-water animals which live in hot springs as well as in normal habitats. Pelseneer (1901) has related the thermal resistances of the larvae of certain marine animals to the types of habitat occupied by these animals. Runnström (1927, 1929, 1936) has determined the temperature limits for the development of several marine animals having different limits of distribution. The general principle which seems to emerge from this work is that the thermal resistance of a species of animal is related to the type of habitat from which the animal comes. Animals which are subject in nature to relatively high temperatures possess greater resistance towards experimentally imposed high temperatures. Resistance to low temperatures is usually greater in animals which normally live at low temperatures, and the range of temperature within which life is possible is greatest in animals which undergo large variations of temperature in nature. The analysis of these relations has never, however, been taken very far.

In inland waters the nymphal stages of mayflies often exhibit a very restricted distribution, the individual species being limited to one particular circumscribed habitat. Pond nymphs are usually absent from streams, and a stream species is often confined to a certain stretch of the stream. The habitats, each with its peculiar mayfly nymph fauna, differ in many factors as well as in the prevailing temperature conditions. Ide (1935), however, in an ecological survey of a Canadian stream, found that the composition of the mayfly nymph fauna changed in passing downstream from the source, and that the changes were in various ways related to the temperature conditions operating in different sections of the stream. The temperature conditions upstream were colder and less variable than the conditions downstream, and it was suggested that these differences may determine the distribution of the mayfly fauna. The upstream fauna consisted of cold stenothermal mayfly nymphs which, it was stated, would be killed by the higher temperatures which prevail downstream during spring and summer. The downstream fauna was characterized by nymphs whose growth rates would be slowed down so much by the consistently lower upstream temperatures that they would be unable to complete their development. Up to the present no experimental work which might support these conclusions has come to my notice. Physiological differences of mayfly nymphs from different habitats have, however, been found by Fox & Simmonds (1933), by Fox *et al.* (1935), and by Fox *et al.* (1937). These workers have shown that, in general, the metabolism of mayfly nymphs from still waters is lower than that of nymphs from streams. The present work was undertaken to see whether there are specific differences in the resistance of mayfly nymphs towards high temperatures and, if so, whether these differences are in any way related to the types of habitat in which the nymphs are found.

METHODS

The method which was adopted in testing the thermal resistance of a species of mayfly nymph was to transfer the animals suddenly from a temperature of 10–11° C. to various experimental temperatures. The animals were subjected to the experimental temperatures for 24 hr., and at the end of this period the percentage of animals killed by the experimental procedure was determined. The water in which the experiments were done was an artificial medium having the same alkali reserve as that of the water of the natural habitat of the species, and during the course of the experiment the water was kept saturated with air. The sizes of the animals were taken into account.

The actual procedure in an experiment was as follows. The nymphs, after collection and sorting, were transferred to the appropriate artificial medium in a shallow dish and kept for at least 24 hr. at a temperature of 10–11° C. (The artificial media were prepared from Birmingham tap water, alkali reserve 0·0003 *N*, by the addition of the requisite quantity of *N*/2 sodium bicarbonate solution. The mortality of the nymphs in the artificial media at a temperature of 10–11° C. was less than 1 % for the 4 days following collection, and they were always used in the thermal resistance experiments within this period.) A batch of twenty-two animals, of about the same size, was chosen for each experiment. Only twenty of these were used in the actual thermal resistance experiment and were treated in a manner to be described shortly. The other two, which were chosen by eye to be the largest and smallest animals of the batch of twenty-two, were used to estimate the range of size to be used in the experiment. Their lengths, from the anterior border of the head to the posterior border of the last abdominal segment, were determined under the microscope, the animals being placed alive, but without water, on a slide. This method of estimating the size of the animals made it unnecessary to measure the actual experimental animals, a procedure which might injure them and vitiate the results of the experiment. Measurement of the experimental animals at the end of the thermal resistance experiment would be incorrect, since all the animals would not normally be alive and available.

The twenty animals, chosen and graded for size as described above, were transferred as quickly as possible from the medium in which they had been living (at 10–11° C.) to the experimental vessel. The latter was a wide-mouthed unstoppered bottle of about 650 c.c. capacity. It was filled with the appropriate artificial medium and immersed up to the neck in a thermostat at the experimental temperature. Dust was excluded by a loose glass cover, perforated in the middle to enable a compressed air tube to pass through and keep the medium in the vessel saturated with air. A piece of glass rod, to which the animals could cling, was provided in the vessel. The vessel was placed in the thermostat before the introduction of the animals, and time was allowed for the medium to reach the temperature of the thermostat and to become saturated with air for that temperature. The twenty animals were introduced into the vessel together with a little of the medium (at 10–11° C.) in which they had been living. This introduction produced only a slight temporary fall (never greater than 0·2° C.) of the temperature of the medium in the vessel.

The animals were left in the experimental vessel for 24 hr. At the end of this period the contents of the vessel were tipped into a shallow dish and each animal was examined to see whether it was dead or alive. Any animal which exhibited movement during this examination was considered alive, even though it appeared moribund. Preliminary experiments showed that these apparently moribund animals usually recovered during the subsequent 4 hr. at room temperature and could therefore be considered to have survived the experimental treatment.

As a rule several of these experiments were done simultaneously. The experiments were performed on six species of mayfly nymphs which were collected from a pond and a stream at Alvechurch, Worcestershire, from streams at Frankley and Blakedown, Worcestershire, and from the River Ebble, Hampshire. Details of the nymphs and of their habitats are summarized in Table I.[1] Each species was studied between the maximum temperature at which none of the animals were killed in 24 hr. and the minimum temperature at which all of the animals were killed in this period, the resistance being determined at intervals of 2° C. within this range (occasionally at intervals of 1° C.). Ten or more experiments were usually done for each species at each temperature, although occasionally scarcity of animals reduced the number to six. The percentage of each species killed in 24 hr. at each experimental temperature is given in Table II. These values, which are the means of the experimental results, are plotted against temperature in Fig. 1, and from these curves the temperature at which 50% of each species is killed in 24 hr. has been read off and included in Table II as the thermal index.

Table I. *Details of the mayfly nymphs studied and of their habitats*

Species	Gills	Locality and its alkali reserve	Habitat	Period and temperature*
Baetis rhodani Pictet†	Motionless	Blakedown stream, 0·003 *N*	On stones in swift water	Apr.–May, 12·5° C.
Baetis tenax Eaton	„	Alvechurch stream, 0·004 *N*	„	May–June, 15·1° C.
Rhithrogena semicolorata Curtis	„	Frankley stream, 0·004 *N*	„	Mar.–Apr., 11·6° C.
„	„	Blakedown stream, 0·003 *N*	„	May, 14·5° C.
Ecdyonurus venosus Fabricius	Beating	Frankley stream, 0·004 *N*	Under stones at side of stream	Mar.–Apr., 11·6° C.
Caenis sp.‡	„	R. Ebble, 0·004 *N*	In slow weed-choked streams	May–June, temperatures not recorded
Cloeon dipterum L.	„	Alvechurch pond, 0·004 *N*	In weedy ponds	All the year, maximum June temp. 19·7° C.

* The "period" refers to the time during which grown nymphs were present in greatest numbers. The experiments were usually done during this period, which preceded the time of emergence of the subimagos by 2 or 3 weeks. The "temperature" is the maximum water temperature at the time of collection during the period.

† The species of this animal cannot be given exactly. The characters conform closely to those of *Baetis rhodani* Pictet.

‡ These animals were kindly supplied by Mr H. P. Moon of the Avon Biological Research Station, Southampton. The species was not identified.

Data concerning the temperature conditions to which the nymphs were subject in nature were obtained from the water temperatures recorded at the time of collection of the nymphs. It was from these data that the figures given in Table I for the maximum temperature to which the nymphs were exposed in nature were derived. Fig. 2 illustrates the variation of the temperature of collection, between November 1936 and June 1937, for the pond and for the stream at Alvechurch. These two habitats were separated by only half a mile.

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[1] I am indebted to Dr D. E. Kimmins of the British Museum for the identification of some of the species.

RESULTS

A comparison of Tables I and II shows that nymphs from slow-running or still waters have, in general, a greater resistance to high temperatures than animals from rapid waters. The extreme contrast is provided by *Cloeon dipterum* from a pond and *Baetis rhodani* from a rapid stream, the thermal indices being respectively 28·5–30·2 and 21·0–21·3° C. (large animals are less resistant than small animals). The other species studied have intermediate thermal indices: *Caenis* sp. (slow stream), 26·7° C.;[1] *Ecdyonurus venosus* (slow-running water at the edges of rapid streams), 26·6° C.; *Rhithrogena semicolorata* (rapid streams), 22·4–24·7° C. according to the locality; *Baetis tenax* (rapid streams), 21·3° C.

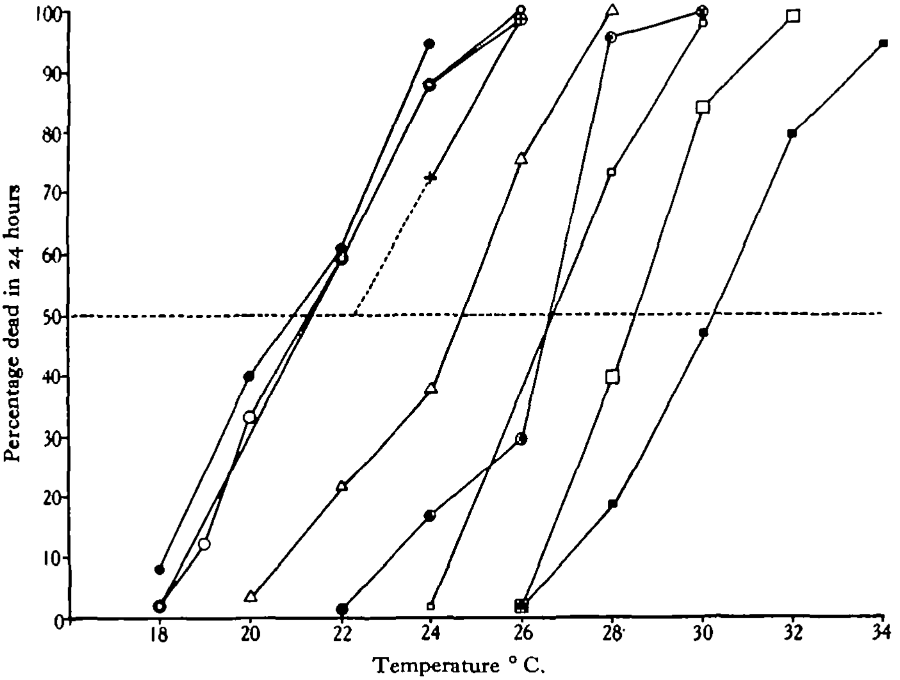

Fig. 1. Mortality of mayfly nymphs from different habitats at various temperatures. The horizontal dotted line passes through the 50 % ordinate of each graph, the abscissa of this ordinate being the "thermal index" of the species. The graph for *Rhithrogena semicolorata* from Frankley stream has been extrapolated to give the thermal index.

● *Baetis rhodani* (large);	△ *Rhithrogena semicolorata* (Blakedown);	□ *Caenis* Sp.;
○ *B. rhodani* (small);	+ *R. semicolorata* (Frankley);	□ *Cloeon dipterum* (large);
o *B. tenax;*	⊙ *Ecdyonurus venosus;*	■ *C. dipterum* (small).

The comparison of the temperatures prevailing in a pond and in a stream (given in Fig. 2) shows that the pond was subject to a maximum summer temperature at least 2·1° C. higher than that of the stream. The stream habitats also exhibit differences in the prevailing temperature conditions. This would be expected, since

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[1] The supply of animals was insufficient to test the resistance of *Caenis* sp. at 26° C. Fig. 1 makes it clear that the thermal index would probably be higher than 26·6° C. if there were a point for 26° C.

the water at the source of a stream is usually colder than the surrounding substrate and the water gradually warms up as it travels downstream by absorbing heat from its surroundings. The slower the water moves the more chance it has of taking up heat. It is by no means uncommon to record a difference of 3° C. between the water at the middle of a stream and the more stagnant water at the edges. Hence *Ecdyonurus venosus*, living under stones towards the edges of streams, experiences higher temperatures than *Rhithrogena semicolorata* which is more or less confined to a midstream position. The higher thermal resistances of animals living in slower waters is therefore correlated with the higher temperatures which these waters are known to attain during the warmer months of the year.

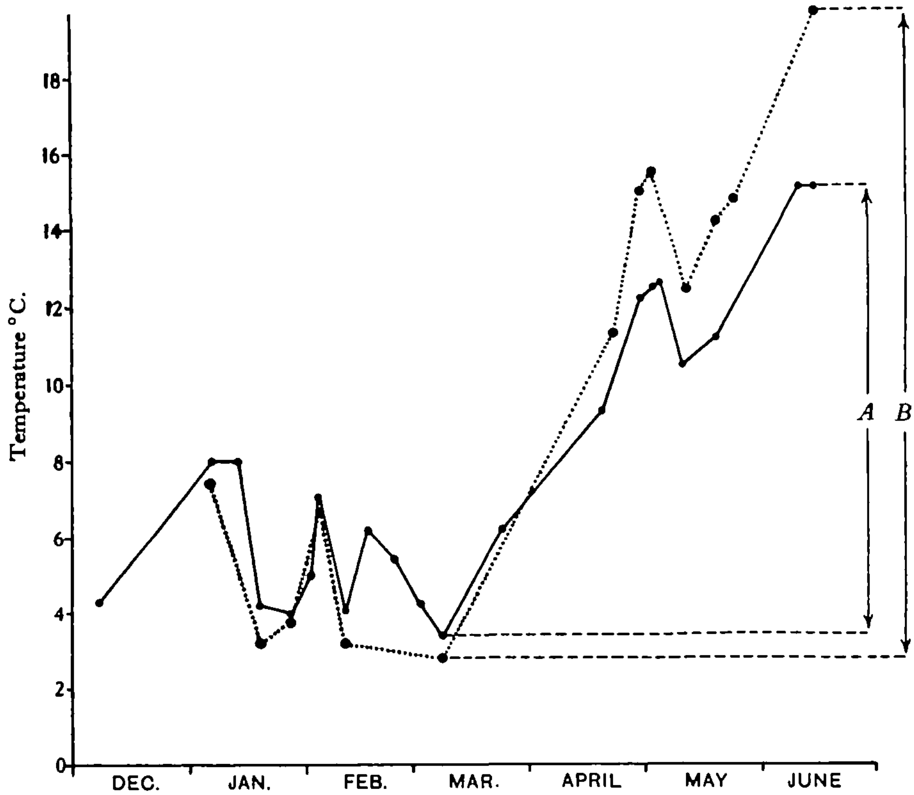

Fig. 2. Temperature fluctuations of the stream and pond at Alvechurch between November and July (1937–8). The temperature was taken between 10 a.m. and 3 p.m. on each occasion. The points on each graph are joined by straight lines. This does not imply that interpolation between the points is possible, in fact it is to be expected that the change of temperature between any two points will not be a uniform change.

——•—— Stream; ···●··· Pond; *A* Variation in stream; *B* Variation in pond.

The maximum temperature to which a nymph is subjected in nature will obviously depend on how late in the year the emergence of the sub-imago (which of course is a terrestrial animal) takes place. Table I gives the months during which grown nymphs are present in the greatest numbers. This period precedes the emergence of the sub-imago by 2 or 3 weeks. Emergence late in the year will mean that the nymphs will be subjected to the higher temperatures of late spring and summer. Comparison of Tables I and II shows that nymphs which emerge late in the year have, on the whole, a higher thermal resistance than those which emerge early in the year. The best example of this is *Rhithrogena semicolorata* from the streams at Frankley and Blakedown. The animals from the former locality have a lower thermal index than the animals from the latter locality, and the Frankley animals emerge about 1 month before the Blakedown animals. The Blakedown animals are therefore subjected to a temperature 2·9° C. higher than that experienced by the Frankley animals (see Table I). A similar state of affairs is found in the comparison of *Baetis rhodani* and *Cloeon dipterum*. The former emerges in spring, while the latter, which is present in ponds as grown nymphs throughout the year, emerges during July and August (I have found imagos in early autumn). The thermal resistance of *Cloeon* is accordingly much higher than that of *Baetis*. There are, however, exceptions to the early emergence of nymphs with low thermal resistances. *B. tenax* emerges later than *B. rhodani*, yet the thermal resistances are almost the same. The two species from the Frankley stream, *Ecdyonurus venosus* and *Rhithrogena semicolorata*, emerge at about the same time although they have quite different thermal resistances.

An effect of size on thermal resistance was found in *Baetis rhodani* and in *Cloeon dipterum*, this size factor being very marked in the latter species at the higher temperatures. In both species small animals were more resistant than large animals. The specific differences of thermal resistance cannot, however, be accounted for on the basis of size. The explanation of the size factor is at present obscure. The larger animals are, as a rule, older than the smaller ones, so that the differences may be due to age and not size. Hathaway (1927) noticed that the thermal resistance of toad tadpoles decreased with age, and this is in agreement with my result. Bělehrádek (1935, p. 201), however, after giving several examples of the effect of age on thermal resistance, remarks that younger animals are usually less resistant than old ones. He admits that there are exceptions to this statement, and I think it should be added that an aquatic stage in the life history is often compared with an aerial stage, when the physiological characteristics of the animal will probably be very different. The only work on the size factor (as distinct from the age factor) in thermal resistance that has come to my notice is that of Huntsman & Sparks (1924–5) and Sumner & Doudoroff (1938). The former authors noted in an echinoderm that the small animals were less resistant than the larger ones. They obtained the same result on one species of fish. On another species of fish, however, exactly the opposite result was obtained, small animals being more resistant than large ones. Sumner & Doudoroff found no size factor in the thermal resistance of the fish which they studied.

It was possible that the differences in thermal resistance which I found were due to corresponding differences in the efficiency of the respiratory mechanism in extracting oxygen from the water. At the high temperatures employed the water contained less oxygen than is present at normal temperatures (see Table II).

Tables I and II show that a possible deficiency in the respiratory mechanism of nymphs with low thermal indices does exist in that they lack beating gills. The correlation is particularly clear when comparing *Baetis* with *Cloeon* and *Rhithrogena* with *Ecdyonurus*. These are two pairs of structurally similar animals, and the first mentioned member of each pair has motionless gills and a low thermal index. It has been shown by Wingfield (1937) that the beating gills of *Cloeon dipterum* are necessary for the animal to maintain its normal oxygen uptake in water containing little oxygen. It was also demonstrated by Fox & Simmonds (1933) that *C. dipterum* (beating gills) could live in water of a lower oxygen concentration than that in which *Baetis rhodani* (motionless gills) was killed in a short time. Winterstein (1902, 1905) suggested that death at high temperatures is due to asphyxiation of tissues; they require more oxygen than at lower temperatures but less is available.

Table III. *The effect of extra oxygen on thermal resistance*

Species	Temp. of exp. ° C.	Aerated water		Oxygenated water		Extra survival in oxygenated water %†
		Oxygen content c.c./l.	Percentage killed in 24 hr.*	Oxygen content c.c./l.	Percentage killed in 24 hr.*	
Baetis rhodani	22	6·0	56·5 ± 2·3	28·8	46·5 ± 3·0	10·0 ± 3·8
Rhithrogena semicolorata (Blakedown)	24	5·9	41·5 ± 2·4	27·8	27·5 ± 1·4	14·0 ± 2·8
Ecdyonurus venosus	28	5·4	92·0 ± 1·7	26·4	79·0 ± 3·3	13·0 ± 3·7
Cloeon dipterum	30	5·2	56·5 ± 1·7	25·2	52·0 ± 1·7	4·5 ± 2·4

* Each value is the average of ten experiments with its standard error.

† Each value is the difference between the percentages killed in aerated and in oxygenated water, with the standard error of the difference.

It seemed likely, therefore, that stream nymphs were less heat resistant in part at least because they usually have motionless gills. I have tested this hypothesis by comparing the heat resistance of nymphs in aerated water with their resistance in oxygenated water which contains four to five times the concentration of dissolved oxygen in aerated water at the same temperature (figures are given in Table III). If the differences of thermal resistance are in fact due to differences in the efficiency of the respiratory mechanism, then provision of excess oxygen should cancel the differences. Table III, summarizing the results of the experiments on four of the species of mayfly nymphs, shows that the extra survival in oxygenated water is never greater than 14 %. This alone is not sufficient to cancel the specific differences of thermal resistance. The asphyxiation theory of thermal death cannot be said to hold, therefore, in the present instance. Amerling (1908) likewise disproved the asphyxiation theory for the death of tadpoles at high temperatures. The specific differences of thermal resistance in the case of mayfly nymphs must, therefore, be due to a more inherent property of the animal than that of the efficiency of the respiratory mechanism.

Possibilities of thermal adaptation were considered. Animals collected from a pond may have been living at a higher temperature than animals collected from a stream. The differences of thermal resistance may therefore be the result of the acclimatization of the animals from the warmer habitats to higher temperatures. In this connexion the work of Vernon (1900) and Marshall *et al.* (1935) is interesting. These authors noticed that marine animals collected during the summer months have a higher thermal resistance than animals collected during the winter months. In my experiments adaptation of this sort was not likely, since the resistance of the pond species *Cloeon dipterum* was tested during the winter when the temperature of the pond was, on one occasion, as low as 2·8° C. However, a series of experiments was undertaken to see whether a stream species with a low thermal index could be acclimatized at sub-lethal temperatures to give a higher thermal index. *Baetis rhodani* was chosen for these experiments. Each collection of animals was divided into two lots, one of which was kept at the usual temperature of 10–11° C. while the other was kept for a period of about 40 hr. at 15° C. Both lots were tested at 22° C. The results (averages of five experiments with standard errors) were:

Animals kept at 15° C. Percentage killed in 24 hr. at 22° C.—60·0 ± 3·5,
" 10–11° C. " " " —59·0 ± 2·9.

The difference (1·0 ± 4·6) is not significant. Acclimatization of *B. rhodani* to live at higher temperatures than those used in the original experiments does not, therefore, take place in 40 hr.

DISCUSSION

It is clear that among the stream mayfly nymphs the ones from swifter waters are less resistant towards high temperatures than those from slower waters. The pond nymph is more resistant than any of the stream species. There is, therefore, a relation between the high thermal resistance of nymphs from slow-running and still waters and the more extreme conditions of temperature which are known to exist in these waters. The low temperature stenothermy of animals from swift waters is emphasized by the emergence of these nymphs early in the year, that is, before the water in which they are living warms up as summer approaches. My results are therefore in agreement with those of the authors mentioned at the beginning of this paper, the thermal resistances of the animals being related to the type of habitat in which they live. I have also shown that the specific differences of thermal resistance in the mayfly nymphs are real differences (probably of a protoplasmic nature) and are not due to corresponding variations of body size or of the relative efficiency of the respiratory mechanisms.

The bearing of these results on the distribution of the mayfly nymphs is not easy to define. If the temperature differences of the environments operate through the specific thermal resistances alone, then one must assume that the adult mayfly lays its eggs indiscriminately in pond and stream and that the young mayfly nymphs are killed off in the unsuitable habitats. However, the absence of some species from parts of a stream at all times of the year (Ide, 1935) rather suggests selection of habitat on the part of the nymphs themselves. I know of no published work on the behaviour of mayfly nymphs which might account for their distribution in accordance with their thermal resistances. Moreover, there may be considerable selection of the places for oviposition on the part of the adult insects (Eaton, 1883–7;

Needham *et al.* 1935). Also, in a stream, the current tends to bring about a selective distribution of the eggs after they have been laid on account of their different rates of settling down in the water (Percival & Whitehead, 1926, 1928). Factors other than temperature may affect the distribution of the nymphs themselves. Thus Hora (1930) stresses the importance to animals inhabiting streams (including mayfly nymphs) of the organs of attachment, such as spines and suckers, which fasten them to solid objects in the stream. Another factor of importance is the available food in the different habitats. Temperature itself may act in other ways than on the heat tolerance of the nymphs. For example, the thermal limits of development may be important as they are in the case of marine organisms (Runnström, 1927, 1929, 1936). The thermal resistance of the nymphs may, therefore, be only one factor among many which are responsible for determining the distribution of the nymphs, and until these other factors have been investigated it is not justifiable to conclude that it is the deciding factor.

There is another way in which my results can be considered. References to the work of Fox *et al.* on the metabolism of mayfly nymphs from ponds and streams have already been made in the introduction to this paper. It will now be apparent that the higher metabolism of the animals from swift waters is correlated with the lower thermal resistance of these animals. This is in agreement with the principle of Child (1913) that animals possessing a high metabolism have a low resistance towards depressing agents (such as drugs) and towards lethal conditions (such as high temperature). Either these characters of high metabolism and consequent low thermal resistance are required before a species of mayfly nymph can occupy a swift-water habitat, or else the physico-chemical nature of the habitat produces in time, by selection or modification, these particular physiological traits. The case of *Rhithrogena semicolorata* suggests an intraspecific difference comparable to that described by Fox & Wingfield (1937) for the prawn *Pandalus montagui* from different latitudes. At Kristineberg (Sweden) the prawn is subjected to a maximum sea temperature of 7° C. and it cannot be kept alive in an aquarium above 11° C. At Plymouth the same species lives in the sea at a temperature of at least 15° C. and it can be kept alive in the laboratory at 17° C.

SUMMARY

1. The thermal resistances of six species of mayfly nymphs, collected from various types of habitat, have been determined.

2. Nymphs from slow or still waters have a greater resistance towards high temperatures than comparable nymphs from swift waters. This is correlated with the more extreme conditions of temperature which are known to exist in slow and still waters.

3. The interspecific differences of thermal resistance cannot be accounted for on the basis either of differences of size or of differences in the efficiency of taking up oxygen dissolved in the water.

4. In one of the stream nymphs (*Baetis rhodani*) acclimatization to higher temperatures was not possible within 40 hr.

5. The bearing of the results on the ecological distribution of the mayfly nymphs is discussed.

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