ECOLOGICAL STUDIES ON AQUATIC INSECTS. IV. ALTITUDINAL RANGE AND ZONATION OF MAYFLIES, STONEFLIES AND CADDISFLIES IN THE COLORADO ROCKIES

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The matter presented in this paper is the result of study of over five hundred vials of material collected by the authors during the summers of 1913, '14, '15 and '21, along the valley of South Boulder Creek in Gilpin and Boulder Counties, Colorado, from the Continental Divide eastward and downward to the western edge of the Great Plains. The work is supplemented by observations made by the senior author during several other summers spent in the region collecting entomostraca and making observations on climatic and physiographic conditions. The present paper is an outgrowth of, and should be studied in connection with, similar work upon the entomostraca of the region (Dodds, '17 and '20). Recognition should also be given to field work done by W. L. Brosius, who assisted with the collecting in 1913.

The area covered by these collections is of especial interest because it includes a cross section through five life zones: Upper Austral, Transition, Canadian, Hudsonian, and Arctic-Alpine. The Upper Austral is represented by an area of the plains, extending about four miles from the base of the foothills, with an elevation of about 5,300 feet above sea level. The other zones include portions of the mountain region along the creek for a distance of about 20 miles, up to its headwaters at elevations of about 11,250 feet. The topography and climate of this region are described in earlier papers.

The Material Used

The collections upon which this paper is based include both larvae and imagos of mayflies, stoneflies and caddisflies. Some of the larvae are from South Boulder Creek and its tributaries and others from 29 lakes and ponds of the same region. The imagos were collected along the streams and about the lakes by sweeping water-side vegetation with an insect net and also by catching insects as they were seen in flight. Mayflies especially were taken by the latter method, because they were seldom secured along with stone- and caddisflies from the vegetation. A collection usually includes many individuals of from one to a dozen species. The use of lantern traps was not successful, as these insects in this region fly very little at night. The larvae and nymphs were taken by straining silt from lake and creek bottoms through a net and by turning over stones, sticks, etc. and picking off the insects one by one. All insects were preserved in alcohol. Life histories of 38 species have been determined, in a few cases by field observation, but in the majority of instances by rearing insects in cages set in stream or lake. The well grown nymphs of stone- or mayflies afford little difficulty, but the caddisflies are more uncertain because of the intervention of the pupa stage.

The determination of the species, always a difficult problem for the ecologist, is especially difficult in such a case as this, where two wholly different stages of life are involved. Seldom can species of the larvae be determined without knowing the imago, especially in these western forms where descriptions of the immature stages are few and not many life histories are known. Even the imagos are imperfectly known, and at least thirty new species are included in our collections. The species were separated by the senior author, largely without attempt to assign names. During this work, types of each species were kept for comparison, and careful drawings of important diagnostic features made. Names of stoneflies and of some species of mayflies were determined by James G. Needham, and of caddisflies by Cornelius Betten and Nathan Banks. We wish to express thanks to these men for this service. Certain species of mayflies have been described by the senior author of this paper (Dodds, '23). The separation of species has been beset with many difficulties, but we feel confident that in the large majority of cases, at least, the work is substantially accurate.

The number of species collected is expressed in the following table:

TABLE I. *Number of species collected*

	Nymphs or Larvae	Imagos	Life Histories
Mayflies	18	29	12
Stoneflies	14	31	11
Caddisflies	42	55	15
Total	74	115	38

ALTITUDINAL RANGE OF THE SPECIES

The altitudinal range through which each species has been collected is shown in graphic manner in figures 1, 2, and 3. These figures also include a statement of the number of collections in which each species has appeared. Only those species for which we have secured names are included in the table, which means the omission of a goodly number of nymphs and larvae which have not been connected with any imago. In each case where both immature and imago stage of a species is known, we have included the range of both stages.

It appears at once from these figures, that there is a very definite altitudinal distribution of the species in each group, and that there is a general similarity between the groups. A somewhat extended analysis of the facts should however be made in the form of an inquiry as to the significance of

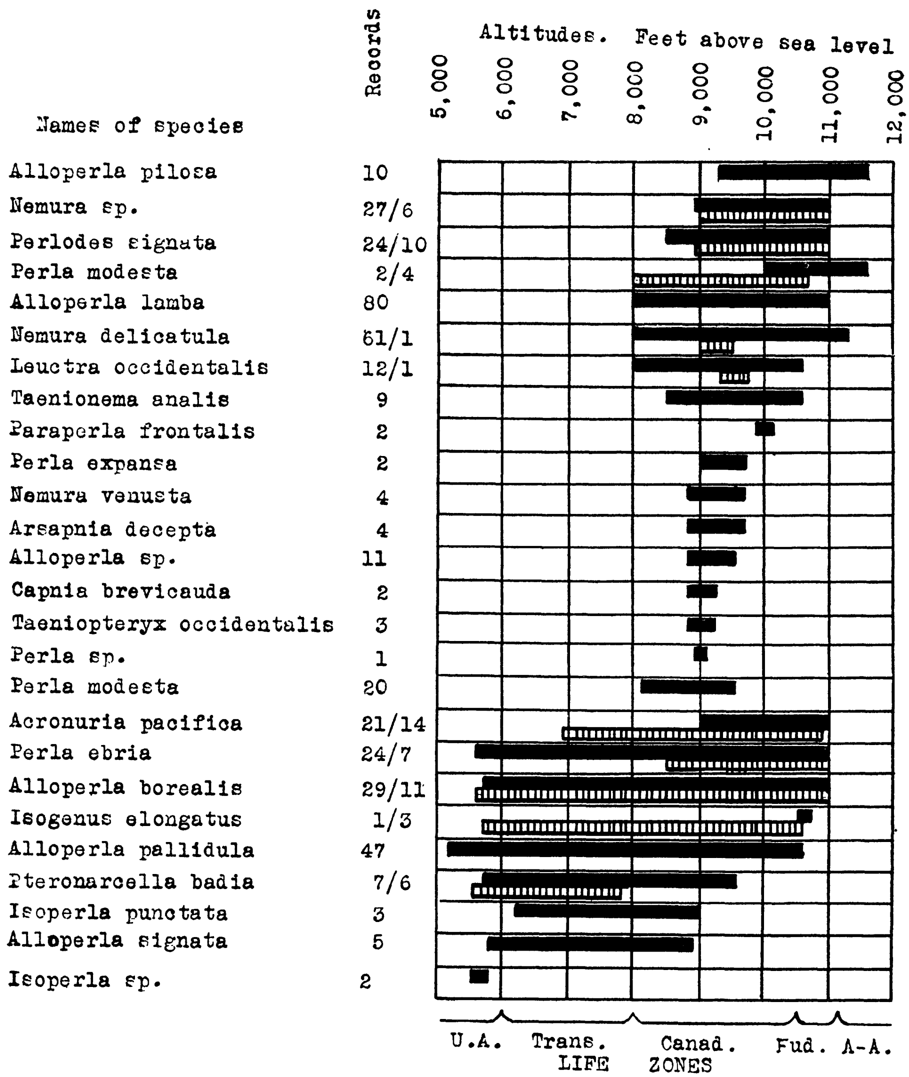

FIG. 1. Graphic representation of the altitudinal ranges of 27 species of stoneflies, together with the number of collections in which each species has appeared. The ranges of the imagos are shown by solid black, of the nymphs by cross lined bars.

the figures. First we should ask whether the range through which a given species has been collected covers its actual range, that is, have our collections been sufficiently thorough to assure us that we have not overlooked many species in altitudes where they actually live? There can be no doubt but this is the case with some species, especially those which have been collected a very few times, either because they are secretive in their habits or because they are of infrequent occurrence. It is seen from Table I that some species in their immature stages have been overlooked, inasmuch as there have been collected fewer species of nymphs and larvae than those of imagos. This is doubtless because of the more difficult and tedious means that must be employed in collecting the nymphs and larvae, as a result of which our collections contain only about half as many vials of immature forms as of imagos. Inasmuch, however, as our distribution records make use of imagos instead of larvae, using the latter only to supplement the data where a life history is known, this cannot be considered as a source of error. It may be that certain species have been overlooked in their imago stage because collections have not been made at the right date, the flying period of some species being short. This may well be the case in the lower altitudes, where some species may have passed by before the latter part of June, when we made our earliest collections. In the higher elevations, however, above 8,000 feet, the season is so short that our work, from the last of June to the beginning of September, must cover the season completely.

It should be remembered that far more collections have been made above 8,500 feet than below it. In these higher elevations we have collected repeatedly during three or four summers while the work done in the lower parts of the stream consisted of less frequent excursions, during which we were unable to cover the ground so thoroughly. It is also worthy of note that in elevations below 8,500 feet, lakes and ponds are almost wholly wanting and our collections from this region must include only those species which can live in streams. The stream-dwelling forms, however, include by far the greater number of species, even in that part of our region where lakes are common. Moreover it is also the case, that in the region below 8,500 feet the many small tributary streams so numerous in the higher altitudes are wanting and there are accordingly fewer types of homes for stream-dwelling insects in this region. The deficiency of records below 8,500 feet, while due no doubt partly to less careful collecting, is doubtless due in part to less abundant insect population here, because of less varied aquatic habitats.

There can be little doubt, however, but that the altitudinal distribution as shown in figures 1, 2, and 3 is substantially correct. Many species have been collected repeatedly at certain elevations but have never been taken at others where frequent and careful collections have been made. The general similarity of the distribution of these aquatic insects to that of the entomostraca of this same region as pictured in figure 10 of a former paper (Dodds, '17) argues in favor of the reasonableness of the picture shown in the figures of the present paper. In each case there is one group of species confined to the high altitudes, another to low, and a third including those which have an extended range from low to high. If, as is quite probable, a few species are wrongly placed in the scheme on account of inadequate collections, there is still enough definite fact to substantiate not only the general scheme of distribution of each group but also the range given for the majority of the individual species.

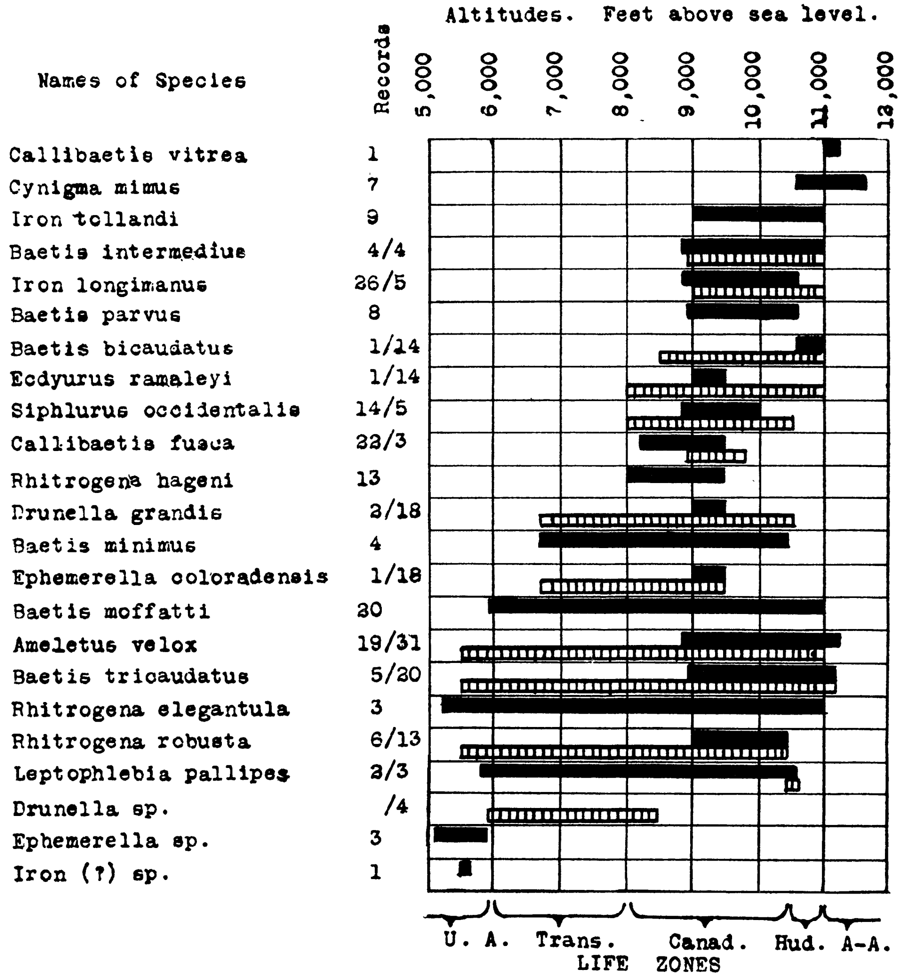

FIG. 2. Graphic representation of the altitudinal ranges of 25 species of mayflies, together with the number of collections in which each has appeared. The ranges of the imagos are shown by solid black, of the nymphs by cross-lined bars.

Altitude as a Limiting Factor

1. *The Part of the Life Cycle Affected by Altitude*

If we are to understand the nature of the ecological problems involved in considering altitude (or climate) as a limiting factor for aquatic insects, we must inquire which part of the life, aquatic or aerial (or both), is the one during which climatic barriers are effective. It may reasonably be supposed that the greater danger confronts the individual during the period of longer duration, in this instance the aquatic stage. The need for food is confined wholly, or nearly so, to this period; this is the period of growth, and the period during which the eggs and spermatozoa are nearly matured; in short, the period during which proper food must be secured and temperature conditions must be such that important metabolic activities can go on. It seems very evident that this is a stage during which climatic factors, such as determine zonation of animals and plants, must be effective.

It is not impossible, however, that there might arise during the flying season climatic conditions which would prevent the imago from depositing fertile eggs, even though conditions in the water were wholly suitable for the aquatic phase. For many animals the time of most narrowly limited toleration is the reproductive period, and it is this that limits the species to a peculiar environment; but limitations of this kind apply more frequently, not to zonal distribution on the basis of temperature, but to local distribution within the zone, based upon suitable places for deposition of eggs and rearing of young. For example, the aquatic insects under discussion are limited to regions having the proper kinds of streams or lakes, and within these regions, to the vicinity of these bodies of water.

2. *The Importance of Temperature and the Difference between Streams and Lakes in this Respect*

It is generally recognized that temperature is the prime factor in determining altitudinal zonation, though other secondary factors, indirectly connected with altitude, sometimes become confusing elements in analysis, as for example the lack of lakes in the lower part of our mountain region, in contrast to their abundance in the higher zones. To an aquatic animal, climate may be summed up as water temperature, which may mean average annual temperature, minimum winter temperature, maximum or average summer temperature, length of summer season, duration of ice covering, or some other factor or combination of factors involving temperature. In the study of zonation of entomostraca in this region, the temperature of the lakes at various altitudes was shown to afford a very reasonable explanation for the zonation of the 71 species found in the State of Colorado. In the plains region of the state, up to an elevation of from 5,000 to 6,000 feet, the lakes are free from ice for about nine months and the summer temperature of the

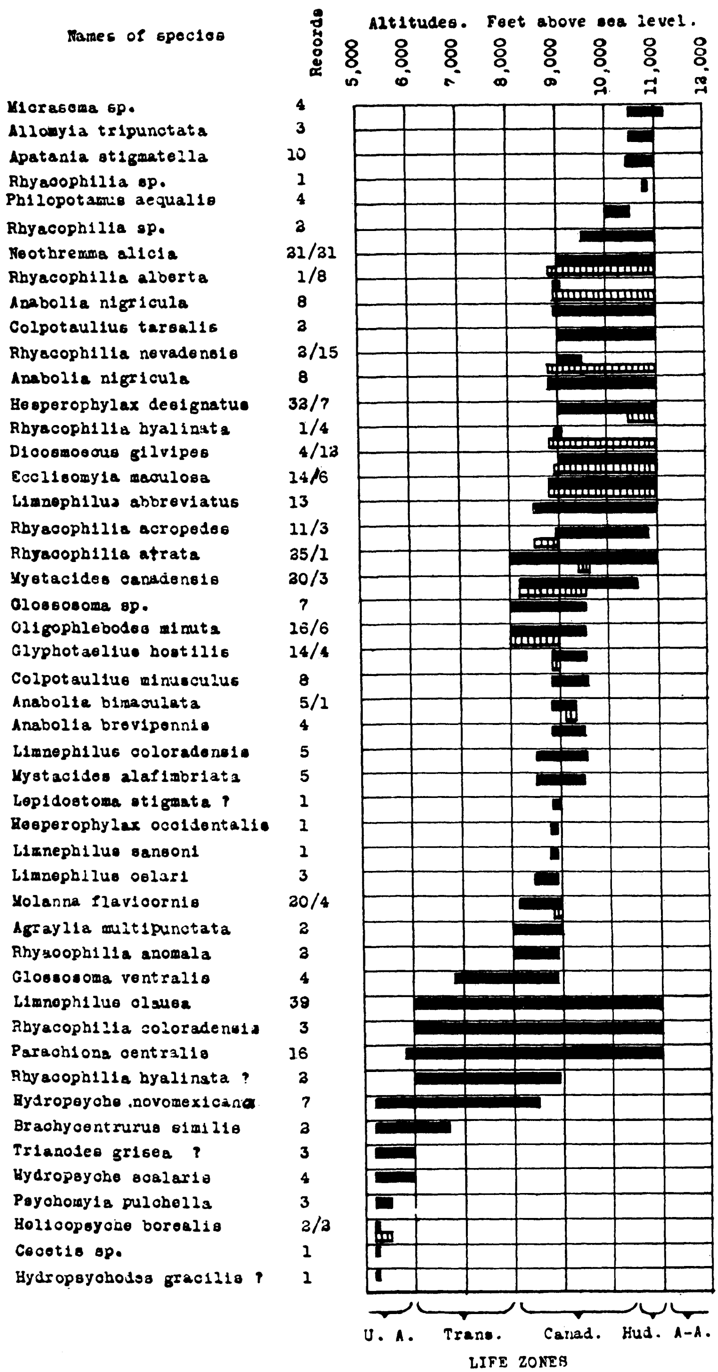

FIG. 3. Graphic representation of the altitudinal ranges of 48 species of caddisflies, with the number of collections in which each species has appeared. The ranges of the imagos are shown by solid black, of the larvae by cross-lined bars.

surface water reaches 90 degrees F. or higher, while in the highest lakes, at the headwaters of South Boulder Creek, the ice-free period may be less than three months with a maximum surface water temperature of about 50 degrees. The extremes of this range are met within the area covered by the present insect studies, and serve to explain distribution of lake-inhabiting species of insects as well as of crustacea. Winter conditions, perhaps, are of greater importance with the insects than with the entomostraca because, while the latter usually pass the winter as resting eggs, the former do so in the form of active larvae or nymphs which have hatched from eggs laid during the summer.

In the streams of the region, however, and in them live far more species of aquatic insects than in the lakes, there is not the great difference in summer temperature between higher and lower elevations in the mountains that prevails in the lakes. From temperature records kept while making our collections, we learned that the streams during July and August are only about 7 degrees F. warmer when they emerge from the foothills to the plains than they were at their headwaters, at 11,000 feet, twenty miles away, their temperature throughout this course about corresponding with that of the lakes above 10,000 feet. The effect of cold mountain streams upon stream-side vegetation is well known, for along such streams narrow borders of vegetation belonging to a colder (higher) zone frequently reach far into areas occupied by a flora of warmer zones. On such a basis, therefore, the stream-inhabiting species might be expected to show a much less conspicuous zonation than the lake dwellers.

Other factors than summer temperature are doubtless operative, among them the length of the season during which the stream is free from ice and snow, which is decidedly longer in lower than higher mountain altitudes. Moreover, the cold water fed out from the melting snow in the higher regions prevents the water in the lower regions of the stream from warming up in late spring, and thus prevents a long season of warm water such as prevails in the lakes of the same elevations. The insects of these cold streams are doubtless able to take food and grow at a low temperature, but it is probable that under winter conditions, which prevail far more than half the year in the higher reaches of the stream, they must be largely quiescent, if for no other reason, on account of the scarcity of food. Though we have made no observations in the depth of winter, nor have we been able to get definite information upon the winter conditions of the streams in the higher altitudes, it seems wholly probable that during the long winter there is no water running in the smaller streams, and that their beds, even under the heavy cover of snow, must freeze to some depth. This must be the condition at the headwaters of the streams where the average air temperature for nearly six months is below freezing, and where for about three months it never rises above the freezing point. Under such winter conditions, insects living in the streams find an environment very different from that where the stream flows at all seasons, and they probably burrow into the stream bed, as some species of lowland ponds are supposed to do in seasons of drought.

In our list of species those confined exclusively to lakes and ponds are rather few (nine) and are not numerous enough to give trustworthy data on the altitudinal range of such forms; while the difficulty is further increased by the fact that the lakes below timberline (about 11,000 feet) have bottoms very different from those above that line, a difference of great importance to animals so dependent upon the bottom as are the insect larvae.

The great majority of our species live in streams, though some of these stream-inhabiting species live also in certain kinds of lakes, and the zonation of these insects is accordingly one that applies to the streams rather than to the lakes, in contrast to the zonation of entomostraca of this region. It seems quite evident, whatever the factors which cause it, that the insect fauna of these streams exhibits a definite zonation, which, even allowing for the fact that the collections of insects are somewhat less complete than those of the entomostraca, has a definite significance, and that, moreover, there is a decided similarity between the zonation of the two groups, insects and entomostraca.

3. *Stenothermic and Euthermic Species*

In each of the three groups of insects there are represented two stenothermic groups of species, one of which is limited more or less closely to the higher altitudes, the other to the lower, and one euthermic group including a number of species which are not limited by temperature conditions and accordingly have a wide altitudinal range. This latter group includes a larger percentage of the species of mayflies and stoneflies than of caddisflies. A conspicuous feature in both the stonefly and caddisfly list, is the considerable number of species that have been collected only over a very limited range at about 9,000 feet. It would seem natural to explain by the fact that during our work we made our home at the Summer Mountain Laboratory of the University of Colorado, as a result of which more thorough collecting could be done at this elevation. An enumeration of the number of collections from different parts of our area shows that this is hardly the case, and in fact we have had the feeling that in some respects we neglected this region, because we knew that we could collect there at any time. A very thorough job of collecting was done on Crater Creek and its associated lakes, through a distance of a little less than two miles, and including elevations from 9,500 to 11,000 feet, where Mr. Hisaw collected repeatedly and carefully during two summers, so that we consider the work done here to be more thorough than in any other part of our area. Our explanation for the great number of species collected at about 9,000 feet is rather that at this elevation the valley of

South Boulder Creek broadens out into South Boulder park with a consequent wide variety of local ecological conditions. We have also had reason to suspect that if the careful collecting were done in the region below this that had been done in the higher elevations, some of these species would be found to range downward for some distance, so that the records for those species which are seemingly restricted to a narrow zone at about 9,000 feet are in all probability but the upper limits of species which range downward for some distance, though probably not to the plains.

It is evident that there is a large number of species at high altitudes, each group showing more species above 8,000 feet than below. The deficiency below this altitude may be explained, as already pointed out, by the less thorough collection here, or by the longer season which makes thorough collecting of flying forms more difficult, or it may mean that these insects are really more abundant in high altitudes than in low. In either case their abundance in high altitudes cannot be denied, and in contrast with the dwindling number of species of many other groups of animals is of great interest.

The greater variety of habitats for aquatic insects in the mountains gives a right to expect within a given area a larger number of species of such groups as are able to withstand the rigors of the climate than in the same sized area on the plains. This variety of habitat is increased along South Boulder Valley by the steep altitudinal gradient, which brings parts of several life zones within a small area.

Aquatic Insects and Life Zones

The abundance of species in the higher and colder zones of the mountains seems to have a direct relation to the general distribution of these groups. The caddisflies have their greatest abundance in the north temperate zone and decrease toward the equator (Lloyd, '21). All of these groups seem to be more abundant in our northern states and Canada than in the southern states, as indicated by the records of distribution in the *Catalogue of Neuropteroid Insects of the United States* (Banks, '07). So far as we know, no attempt has been made to assign the various species of these groups of insects to specific zones, or to characterize the fauna of the zones as mapped out by Merriam; and when this is attempted it may be found that these zones are not suitable for expressing the distribution of these animals. Reference to these zones would however be useful as a means of assigning the species to rather definite areas characterized by definite types of vegetation, which, in the absence of a better system, has a distinct field of usefulness.

Within our area the zones are very evident, each with its definite flora and characteristic mammals, birds, reptiles, amphibia, and entomostraca. The aquatic insects of the region may well be referred to this zonation. In the Arctic-Alpine zone, we have collected about 40 species of these insects, some of which seem pretty nearly confined to it while others range downward, some into the Hudsonian and Canadian zones, and still others into the Upper Austral. In the Husonian and Canadian zones there are more species than in the Arctic Alpine. The richness of the fauna of these three zones in species and individuals is evident as one collects the immature forms from the lakes and streams, where a wealth of material can be found with the slightest search. The abundance of these forms in this region has been commented on by Kellogg in his *American Insects*. In the Transition and Upper Austral zones there is an apparent decrease. It is impossible at present to define these zones on the basis of their insect population as fully or definitely as they have been defined on the basis of other groups, but it is very evident that the distribution of these species of insects does have a definite zonal significance.

Summary

1. One hundred species of aquatic insects collected between 5,200 and 11,250 feet above sea level show a definite altitudinal zonation.

2. This zonation bears a definite relation to the Life Zones of the region though the general zonal distribution of these insects has not been worked out.

3. The abundance of these insects in high altitudes, Arctic-alpine, Hudsonian, and Canadian zones, is striking, and is of interest in view of their prevalence in the northern states and Canada.

4. Temperature is the main climatic cause for altitudinal zonation of these insects.

5. Peculiarities of distribution due to topographic conditions or to secondary effects of altitude must not be confused with its direct, climatic effect.

6. Streams and lakes furnish two quite different problems in studying altitudinal zonation.

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