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S. L. Tuxen: The Hot Springs, their Animal Communities
and their Zoogeographical Significance

Ejnar Munksgaard

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lived for a shorter or longer time but not the 10 or 5 hours the experiments lasted. The results from the other two springs are shown in Table VI above.

As to the pupa there is nothing particular to note. It has a spiny armature on the abdominal segments corresponding to that described by Thienemann (1936b) for *Eucricotopus* (his fig. 2); the abdominal segments 7-8 have no spines. The prothoracic horn and an anal lamella with anal bristles at the same magnification are shown in fig. 53.

Section d. *Radix ovata* Drap. f. pr. and
f. *peregra* Müll.

This snail has long been known to occur in the hot springs of Iceland; Beck's name *Limnaea geisericola* testifies to this. It is likewise mentioned by Steenstrup (1847), Mørch (1868), Thoroddsen (1891), and Bøving (1925). Mørch states that it (*f. ovata*) was found at 43°, Bøving that it occurred at "more than 40°" ("small snails"; from his collection at the Zoological Museum of Copenhagen it appears that they are *f. peregra*); but only Schwabe has tried to find out experimentally what temperatures it was able to tolerate. Personally I have very little to add, though the species is incontestably a character animal in the Icelandic hot springs and therefore might well deserve a thorough investigation. However, I was not prepared for this during my stay in Iceland.

I here follow the view, current since the publication of Bollinger's paper (1909) and accepted also by Mandahl-Barth (1938), that *Radix ovata* and *peregra* are one and the same species; however, in the Zoological Museum the material was divided into the forms *ovata* and *peregra*, and I have used these determinations in the list on p. 58-59. My material, however, does not allow of a closer investigation of the question raised by several authors, whether the shell of the snail changes its shape and appearance according to the temperature, the chemical contents, etc., of the spring; I shall merely refer to Issel 1901 p. 8-14, 1906 p. 31-34, Shadin 1927 p. 137-43, Strouhal 1934 p. 565-70, Schwabe 1936 p. 322 ff., and Yûichi Itô 1938 p. 395-404.

As regards the highest temperature tolerated by the snail I have made some few experiments with *f. peregra*. Schwabe killed a *f. ovata* "innerhalb von wenigen Sekunden" at 45.5°. However, one should be very cautious about declaring that a snail is killed. I kept a *peregra* in water at 44° for 30 seconds, when after a sudden and violent contraction it "died." But upon my return two hours later it was alive. On the other hand, two individuals of *peregra* were kept for five hours in water

with a temperature of $42\frac{1}{2}^{\circ}$ but they never recovered. In this as in other cases it applies that the resistance to high temperatures depends on the duration of the time during which the animals are subjected to them. If, therefore, we are to find out the limit for the temperature resistance of *Radix*, we must take the highest temperatures at which the species has been found as a basis; and this means 36° as regards *peregra* (see the aforementioned list) and 42° as regards *ovata*.

Chapter 5

Comparison with Other Hot Spring Areas

A great many of the numerous other larger or smaller hot spring areas of the world have been investigated zoologically, and it would be natural to compare the conditions within these areas with those of the Icelandic hot spring areas. Since, however, as I shall explain below, such a comparison cannot at present be fully carried out in the way desired (i.e. on the basis of animal communities), I can do it rather briefly. I will mention, first, the particular areas and the comprehensive works in which they are described, leaving out of consideration the large number of minor reports on animals found in hot springs.

North America.—For a number of years Brues (1924, 1928, 1932) has studied the fauna of the hot springs of North America, and his results are given in the three papers quoted above, which form one of the main pillars of our knowledge of the influence exercised by the ecological factors in the hot springs on animal life, to which I shall revert in Chapter 6. However, the material is unsuited for a comparison with the Icelandic conditions, it being impossible to find out which of the very large number of species dominated in the springs and thus could be parallelised with the community *Scatella-Eucricotopus-Radix*. Many of the species were taken in several springs (*Thermacarus*, *Ephydra*, various Chironomids, Stratiomyids, and notably many beetles), but even at best in only up to one-fifth of them; and it is not possible, either, to find out how common the species is in the individual springs. Brues was not interested in the investigation of a hot spring animal community.

Japan.—A number of minor reports are available from recent years, published by Yûichi Itô and his collaborators; most of them are written in Japanese without a summary in any European language. A comprehensive survey of the fauna of the hot springs of Japan is so far lacking.

It would seem that the snail *Anisus albus spirillum* Gould and the beetle *Laccobius oscillans* Sharp extend to the highest temperatures (45°) (Okada & Itô 1937 and ?1938, Itô 1938), but the authors do not seem to have given attention to the question as to an animal community.

North Africa.—The following reports are available from North Africa: Blanchard's (1903) and Mason's (1939) animal lists from Hammam Meskhoutine, Seurat's paper on different North African hot springs (1922), and Monod's very interesting find of the Crustacean *Thermosbaena mirabilis* in water with a temperature of 45°; *Thermosbaena* seems to be a character animal of the Tunisian hot springs (Brun 1939), but whether it is a member of a community, is not known.

Northern Italy.—In several papers, summed up in the paper of 1906, Issel gives the results of his investigations on the North Italian springs. He is the only author who is aware of the possible existence of a community, which he comprises under the designation "fauna termale" as against "fauna subtermale". He distinguishes between them at, as he says himself, an artificial temperature limit at 40°; but he points out that the difference between them is that above 40° a few species with an abundance of individuals occur, whereas below that limit the greater number of animals otherwise living in fresh water occur, but they are not particularly abundant. It is precisely the same difference that I ascertained above for the Icelandic springs. His "fauna termale" includes 3 Infusoria, 2 Rotifers, the Nematode *Dorylaimus atratus* v. Linst., the Ostracod *Cytheridea torosa* Jones, the Dytiscid *Bidessus thermalis* Germ., a *Stratiomyia* larva, and the snail *Paludestrina (Hydrobia) aponensis* v. Mart.

Sicily.—A paper by Ciofalo from 1927, which has not been available to me, is reported to deal mostly with Protozoa occurring in the Sicilian hot springs.

Kärnten (Warmbad Villach).—Strouhal (1934) treats the fauna of these springs, whose temperature, however, does not rise above 30°, and arrives at the result that in these springs we cannot speak about a special animal community; only casual species are found there, which have come from nearby cold waters.

Schlesien.—Nitsche (1932), Tischbiereck (1939), Pax (1939), and Pax & Wulfert (1941-42) give summaries of the fauna of these springs, whose temperatures do not rise above 30° (apart from two springs near Warmbrunn, which only contain *Stentor* and a couple of Rotifers), and arrive at the result that here, also, no special hot spring animal community can be ascertained, at any rate as a consequence of the temperature, but merely a cold water fauna somewhat "thinned out" by the external factors.—Pax (1942) gives a summary of the Crustaceans

occurring in the German mineral springs right up to 42.5° (cf. below), and Pax & Soós (1943) a summary of the Nematodes.

As already stated, there exist, in addition to the papers mentioned above, a large number of greater or smaller reports on some few animals or groups of animals found in some springs, but a synopsis is nowhere attempted.

A comparison may now throw light on three questions. 1) Are the animal communities throughout the world which are adapted to the highest temperatures (disregarding the chemical conditions of the spring) identical or at any rate consisting of the same animal groups (systematic or ecological), or are they composed of entirely different elements? 2) If we disregard the question as to animal communities, is it, then, identical or related species which occur at the highest temperatures? 3) Do the animals characteristic of the Icelandic absolutely hot spring community recur in identical or related species in other hot springs?

The first question, which is the most interesting, cannot be answered for the good reason that, as stated above, only from one other place is an account of a hot spring community available, namely that given by Issel for the Italian springs. Even if, on the basis of the detailed lists given in other cases (Brues), we would reconstruct the animal content of each individual spring, we should only arrive at the proportion of species, not at the proportion of individuals, which is the essential one. Unfortunately a comparison with Issel's animal communities will halt, too, because two animal groups which I have not taken into consideration as regards the Icelandic springs play an essential role in it, viz. Protozoa and Rotatoria. If we disregard them, however, his springs are found to contain: 1 Nematode, 1 Ostracod (only in a single spring), 1 beetle, 1 Stratiomyid larva, and 1 snail (a Prosobranch). In the Icelandic springs (p. 52) Nematoda were found at high temperatures, but not as character animals; the same applies to Ostracods; in addition, as character animals, two Diptera and a snail. But the Diptera are not Stratiomyids (which are absent in Iceland), and the snail is a Pulmonate. Thus we cannot speak of an absolute similarity in the systematic composition of the animal community; but there is a certain similarity (Nematoda, Ostracoda, Diptera, snails) even in view of the fact that the hot spring fauna must necessarily originate from animal groups which have representatives in fresh water! The reply to the second question will deal somewhat more fully with this problem.

In the ecological field, however, an absolute similarity might be expected, especially as regards the food. Issel (l. c. p. 51) suggests this, pointing out that the majority of species of his "fauna termale" are herbivores; as far as I can make out, this applies to them all except

Bidessus, which, like all Dytiscids, is a typical carnivore. As will be seen, all the forms of the Icelandic absolutely hot spring community, the character animals as well as those of less frequent occurrence (see p. 61), are herbivorous animals. I shall revert to the cause of this shortly.

As to the other question: whether the same animal groups are represented at the highest temperatures, more material is available for the answer, i.e. the whole large material of Brues from North America can be used. This contains, from temperatures over 40°, representatives of the following groups (orders or families; the highest temperature is added):

- Ostracoda (*Potamocypris perbrunnea* Blake, 50°; *P. varicolor* Blake, 48°; *Chlamydotheca bruesi* Blake, 42°).
- Hydrachnida (*Protzia* sp., 45°; *Thermacarus nevadensis* Marsh., 50.8° and widely distributed).
- Odonata (*Mesothemis simplicicollis* Say, 43°; others up to 41.8°).
- Chironomidae (*Chironomus tentans* F., 49°; others to 41°).
- Stratiomyidae (*Stratiomyia* spp., 43°; *Odontomyia* spp., 47°; ?*Oxycera* sp., 47°).
- Tabanidae (spp., 43°).
- Ephydriidae (*Ephydra* ?*pectinulata* Cress., 43°).
- Dytiscidae (*Bidessus affinis* Say, 42.5°; *Coelambus thermarum* Darl., 44.5°; *Agabus* spp., 42°).
- Hydrophilidae (*Ochthebius* spp. 44.5°; *Tropisternus* spp., 42°; *Paracymus subcupreus* Say, 44.8°; *Philydrus hamiltoni* Horn, 45.5°; *Laccobius agilis* Rand., 43°; other Hydrophilids, 40.8°).
- Heteroceridae (*Heterocerus* sp., 41.2°).
- Amphibia (*Scaphiopus hammondi* Baird, adults to 38.4°, when frightened to 45°; *Rana pretiosa* Baird & Gir. 41.6°, adults and tadpoles).

In the Japanese springs the following animals are found at temperatures above 40°:

- Stratiomyidae (*Stratiomyia japonica* v. d. W., 48.8°).
- Hydrophilidae (*Laccobius oscillans* Sharp, 45.5°).
- Pulmonata (*Anisus (Gyraulus) albus spirillum* Gould, 45.5°).

- Nematoda (to 44.5°, Northern Italy, Issel; (to 48.5°, China, Hoeppli & Chu, doubtful¹²); *Dorylaimus carteri* Bast. and *Chromadorita leuckarti* de Man to 43°, Germany, Pax & Soós)¹³.
- Annelida (*Nais* to 43°, North Africa, Blanchard).
- Ostracoda (*Cypris balnearia* Moniez to 50.5°, North Africa, Moniez; to 51.5°, *ibid.*, Mason; *Cytheridea torosa* Jones to 45°, Northern Italy, Issel).
- Decapoda (*Potamon (Telphusa) fluviatile* Latr. to 44°, North Africa, Blanchard).
- Amphipoda (*Thermosbaena mirabilis* Monod to 45°, North Africa, Monod).
- Hydrachnida ("a water mite" to 46°, Arizona, Schwarz; *Eylais thermalis* Uchida to 42°, Formosa, Uchida; *Thermacarus thermobius* Sokolow, to 45°, Baikal Lake, Sokolow).
- Ceratopogonidae (*Dasyhelea tersa* Joh. to 51°, Java, Mayer).
- Stratiomyidae (*Stratiomyia* sp. to 45°, Northern Italy, Issel).
- Dytiscidae (*Bidessus geminus* F. to 42°, Italy, Issel; *B. thermalis* Germ. to 45°, Italy, Issel; North Africa, Mason).
- Hydrophilidae (*Laccobius sellae* Sharp to 45°, Italy, Issel; *Helochares normatus* Lec. to 46°, Arizona, Schwarz; *Coelostoma hispanicum* Küst. to 45°, North Africa, Mason).
- Hydroscaphidae (*Hydroscapha gyrinoides* Aubé to 46°, Italy, Issel; *H. natans* Lec. to 46°, Arizona, Schwarz).
- Pulmonata (*Radix pereger* Müll. to 46°, Europe, Brues from old, though doubtful, records; *Melanopsis etrusca* Villa to 41°, Northern Italy, Issel).
- Prosobranchiata (*Paludestrina aponensis* v. Mart. to 46°, Northern Italy, Issel).
- Amphibia (*Rana esculenta* L., tadpoles, to 43°, North Africa, Blanchard).

In the above lists Protozoa and Rotatoria, which according to Issel occur up to c. 51° and 45° respectively, have been disregarded; so far too little is known about the distribution of these animals as regards hot springs.

It will be seen that some special groups of fresh water animals recur in the lists, while others are entirely absent. Among the Vermes, both

¹² The animals were taken in a well 13 feet above the surface of the water; the water had the temperature stated, but the sample cannot possibly have had that temperature.

¹³ Not above 40°, Hoeppli 1926.

Nematoda and Annelida are represented. Among the Crustacea, Ostracods and a few Malacostraca are found, but not the Crustaceans otherwise of common occurrence in fresh water, viz. Copepods¹⁴, Daphnia, and Phyllo-pods. Of the Arachnids, only the Hydrachnids could come into question; but of the insects, all the Heterometabola apart from dragon-flies are lacking, and within the holometabolous insects, also, many are plainly absent, thus Tipulids; Simuliids, Culicids, and Psychodids, within the Diptera, and notably all the caddis flies. Within the Molluscs some forms of snails, both Prosobranchs and Pulmonates, have specialised, but no mussels occur. At temperatures below 40° all these groups are found, many of them at temperatures between 35° and 40°; but it is thus not quite a matter of chance which species within the animal kingdom specialise at the highest temperatures; they are supplied by particular families and genera. On the other hand, not all these groups are represented everywhere, it depends, of course, on the fauna present in the surroundings. Thus the circumstance that the beetles, which play an important part in the North American, North Italian, and Japanese springs, are entirely lacking in the Icelandic hot spring fauna, is simply due to the fact that of the Hydrophilids only three species of *Cercyon* (which are dung-insects) and of water-beetles one species of each of the genera *Hydroporus*, *Agabus*, and *Colymbetes* are found in Iceland. They all occur in Iceland in springs but only up to 32°, nor have any of them been found at higher temperatures in other parts of the world. The absence of Stratiomyids must be considered in the same way: no Stratiomyid has hitherto been found in Iceland.

Thus the question put forward must be answered in the affirmative: the species occurring in the absolutely hot springs throughout the world originate from some few groups of animals, not from all the animal groups occurring in fresh water. And if we revert to the question as to the existence of an animal community in the absolutely hot springs all over the world, I think it will be possible—when the necessary investigations in this respect have been made with this problem in view—to erect an animal community of the absolutely hot springs valid for the whole world. This community will, of course, not be the same in all absolutely hot springs, but each field will include the representatives of this community which the surrounding fauna is capable of supplying. And carried a step further this again—provided it is correct—would mean that the community is no

¹⁴ Pax (1942) records a Copepod, *Paracyclops fimbriatus* Fisch. together with the Ostracod *Candona pratensis* Hartw. from the spring Spuckerl at Karlsbad, in which it lives in algæ on a rock wall which is washed every ninth second by water of a temperature of 42.5°. However, whether they are actually exposed to this temperature is doubtful, judging from the description.

relict community from an earlier warmer period, to say nothing of the period in which the earth had not yet been sufficiently cooled (as supposed in earlier times by several authors, cf. Issel 1906 p. 59, Vouk 1923), but that it is some few animal groups which physiologically have a power of adaptation to life at the high temperatures, and the representatives of these groups will then, sooner or later, immigrate into the absolutely hot springs.

Whether the above-mentioned community of the absolutely hot springs also presents an ecological uniformity, is another question just touched upon above. Issel pointed out that his "fauna termale" only included herbivorous Protozoa, while the carnivorous Protozoa did not occur at a temperature above 40°. And, as stated above, my Icelandic community consisted exclusively of herbivorous animals. However, not all the species recorded in the lists of animals found at temperatures above 40° are herbivorous, probably the worst carnivores of the fresh waters, the Dytiscids, are represented among them. The adult Hydrophilids are, indeed herbivores, but the larvæ of *Helochares* and possibly of *Laccobius* also are carnivorous (Bøving & Henriksen 1938). The larvæ of *Hydroscapha* are herbivorous (Bøving 1914), and the same applies to all the other animals mentioned in the lists except the Odonates. However, the greater number of the—lacking—heterometabolous insects as well as many of the likewise lacking Trichoptera are carnivores (Wesenberg-Lund 1943), so there would seem to be this uniformity that the herbivores more readily tolerate the high temperatures than the carnivores. This, no doubt, has nothing to do with nutrition, but is a respiratory problem: the carnivorous animals with their rapid movements require water rich in oxygen, and the absolutely hot springs will always be very poor in oxygen owing to the low oxygen tension of hot water. It is therefore quite obvious, too, that torrenticole forms are absent from the absolutely hot springs.

The third question, finally, whether the species of the Icelandic animal community of the absolutely hot springs recur in other hot springs, is easily answered, and it is obvious, according to the above, that it must be answered in the affirmative. Of the two species of Vermes, *Monhystrera filiformis* has been found in several German hot springs (up to 28°, Strouhal 1934, Tischbierck 1939, Pax & Soós 1943), whereas *Rotylenchus multicoloratus* is not known from other hot springs. *Cyprinotus salinus* is a salt water form, but has been found in hot springs in Germany and Italy (Pax 1942). Species of *Cricotopus* have been found in hot springs in North America (to 39°, Brues 1928 and 1932). *Scatella thermarum* has allied species in Japan, North America, Kamtschatka, New Zealand, and Greenland (Tuxen 1936b). *Radix ovata* f. pr. and

f. peregra have allied species in Germany (Strouhal 1934, Tischbierneck 1939), the Pyrenees and Provence (up to 45°, Brues 1924, Strouhal 1934), England (Brues 1924), Italy (Issel 1900 and 1906), Baikal (to 47°, Shadin 1927), Japan (up to 37°, Itô 1937), North America (up to 39°, Brues 1924 and 1932). This list is hardly complete, but it shows, at any rate, that five of the six Icelandic forms belonging to this group are represented by the same or by closely related species in numerous springs all over the world.

In the lists I have drawn the lower limit at 40°, for a lowering of this limit merely to 35° would increase the lists by numerous genera, families, and orders; in other words, we should not have a picture of a hot spring community, but the ordinary picture of a fresh water community. It would take up too much space to demonstrate this in detail here; the reader may, if he likes, examine it himself from the papers to which I have referred above. But, of course, this does not mean that all fresh water animals will be able to live at all temperatures below 40°, there being large gradations as to the upper temperature limit of the different species; it only means that the fauna as a whole reveals the ordinary picture of a fresh water community. As shown above for the Icelandic spring animals, the limit may be 35° or 40°; the reason why it did not appear quite clearly is, probably, that the Icelandic fauna which is to supply the fauna of the hot springs is much poorer, and the "selection" therefore so much smaller.

Chapter 6

Some Ecological Aspects

Section a. On a possible resting period in the winter.

One of the most remarkable features of the life in a hot spring is that the surroundings, the influencing factors, are the same throughout the year, so generation may follow upon generation without interruption all the year round. On account of the individual deviations in the duration of the development, the generations will soon overlap, so at any time it will be possible to find all stages and all ages of hot spring animals. Strouhal (1934 p. 555), Nitsche (1932 p. 33), and many other authors expressly call attention to this fact. In his treatment of the hot springs of Iceland Schwabe (1936 p. 296-99) deals with the same

subject, but points out that there is a "winterliche Ruhe," as the algal layer dies away in the winter, which "letzten Endes" is due to the lack of light in the winter. This matter presents a very interesting deviation from the conditions that may be observed in hot springs in other parts of the world, so it is very unfortunate that neither Schwa be nor myself are able to give further particulars in this respect. Schwa be makes some few remarks concerning the algal carpet which I shall mention presently, but he says nothing about the animal life. For my own part my stay in Iceland in 1937 began too late, life in the hot springs being already in full progress at the time of my arrival, and since then conditions have not only prevented personal investigations on my part but for the last 5 years also every communication with fellow scientists in Iceland.

It is, however, possible to put forward some theoretical considerations, which may be useful for further investigations and which tend to show that animal life is suspended in the two months around the winter solstice; and though, of course, it is impossible to give more than suggestions in this way, I shall try to elucidate the problem as far as possible.

The three character animals of the hot springs of Iceland are at all stages of their life herbivores (*Eucricotopus*, however, hardly as imago, it being doubtful whether it takes in food at all at that stage; still Malloch states about the Chironomids (1915 p. 288) that they "procure food... on flower heads"). Hence they always have to rely on the algal layer in the springs, the existence of the Cyanophyceae being a life condition for them. During parts of their life they have, moreover, to rely on the oxygen dissolved in the water as a source of respiration; thus, in that particular also, the existence of the Cyanophyceae is a condition of life, though to a less extent than from the first point of view, since the water, which is devoid, or almost devoid, of oxygen at its source, constantly takes up oxygen along its course during the cooling (cf. p. 31-32) both in the summer and winter. In this way it will be able, at any rate at some distance from its rise, to supply the animals with sufficient oxygen for their respiration, independently of the algæ. And light, finally, is indispensable for the thriving of the algæ. It might be of interest, therefore, to clear up those two factors, the vegetation and the light, and their interrelations as well as their relations to the animals.

Vegetation of the springs. The rich algal vegetation of the springs has been mentioned repeatedly above. I brought home some few samples myself, and of these a sample from Hvammkotslaug, taken on June 24th, 1937, at 45°, contained predominantly *Phormidium laminosum* Ag., mixed with *Hapalosiphon laminosus* Cohn and *Oscillatoria* sp. It is these species which form the well-known jelly-like algal coating of stones, and they also float about freely in the hot springs. Two other samples were

derived from lower temperate springs, viz. from Skíðastaðalaug, 27°, and Sundlaug, Reykir, 30°; they are only of interest because they contained food elements for the larva of *Eucricotopus*, namely the diatoms *Nitzschia*, *Gomphonema*, *Navicula*, etc. That these three diatoms actually belong to the food elements of *Eucricotopus* is evident from the fact that they were found, together with sheaths of the Cyanophycean *Symploca thermalis* Kütz. and the unicellular Cyanophycean *Aphanocapsa* sp. (?), in the contents of the alimentary canal of the larvæ of this Chironomid taken in Sundlaug on June 5th, 1937. Whether these plants constitute the food of *Eucricotopus* at higher temperatures also (above 40°), is not known; the larvæ taken by me at such high temperatures had starved so long before they were killed (since either an attempt had been made to rear them or they had been used in respiration experiments) that their guts only contained bacteria. *Phormidium laminosum* was found in the contents of the alimentary canal of a *Scatella* larva¹⁵. It is noteworthy that even these few collections at once characterise the algal community: it is V o u k's *Mastigocladus* type (*Mastigocladus* = *Hapalosiphon*), his oldest hot spring type (V o u k 1937 p. 64ff).

The specimens recorded represent my own random collections from the springs; but the literature supplies more copious information on this subject (only absolutely hot springs are considered).

As to the diatoms opinions differ. Ø s t r u p (1920) does not give the temperatures at which the diatoms were found. K r a s s k e (1938) writes as follows: "Die höchsten Temperaturen, die S c h w a b e für lebende Diatomeen am genauen Standort einwandfrei feststellte, sind 40° C.," whereas S c h w a b e himself (1936 p. 313) says: "40° werden mit Sicherheit überschritten von verschiedenen...Diatomeen...". This last-mentioned statement is confirmed by S c h w a b e's list (p. 286-88), according to which *Achnanthes marginulata* Grun., *Diploneis interrupta* Cleve, *D. oculata* Cleve, and *Mastogloia smithi* Thw. var. *lacustris* Grun. were all taken at temperatures above 40° (at 41.5°, 44°, 42.5°, and 44° respectively). However, diatoms play, at any rate, no great role in the absolutely hot springs.

This, however, is the case to a great extent with the *Cyanophyceae*, of which *Oscillatoria proboscidea* Gom., *Hapalosiphon* (= *Mastigocladus*) *laminosus* Cohn, and especially *Phormidium laminosum* Ag. are character algae of the absolutely hot springs. *Hapalosiphon* has been found up to 65°, *Oscillatoria* only to 47°, *Phormidium* (in different species: *tenuis* Menegh., *subuliforme* Gom., *angustissimum* W. & G. S. West, *treleasei* Gom.) up to 58°. Other *Cyanophyceae* also have been found in the

¹⁵ All these algae were kindly determined by J. Boye Petersen.

absolutely hot springs of Iceland, namely *Lyngbya* spp. (up to 48°), *Plectonema nostocorum* Bonnet (up to 60°), *Schizothrix calcicola* Ag. (66°), species of *Nostoc*, *Cylindrospermum muscicola* Kütz. (54°), *Scytonema varium* Kütz. (48°), *Calothrix thermalis* Schwabe (76°), and *Dichothrix compacta* Ag. (55°). Some of the last-mentioned species were, however, taken at the edge of the springs, that is to say, probably at lower temperatures than those stated; and all of them were only found in some few of the springs investigated and are accordingly not character algae like the three first mentioned. Moreover some of these species are exclusively thermophilous in Iceland, namely *Oscillatoria proboscidea*, *Phormidium laminosum*, **P. treleasei*, **Schizothrix calcicola*, **Haplo-siphon laminosum*, **Calothrix thermalis* (*means that they have been found exclusively in hot springs outside Iceland also); thus all the three character algae are included. (Boye Petersen 1923, Schwabe 1936.)

Chlorophyceae play no role in hot springs with temperatures above 30°-35° either in Iceland or elsewhere. However, according to information from Dr. Boye Petersen, he found an *Oedogonium* floating at the surface of a spring with a temperature of 39° south of Akureyri. This is the only case of a Chlorophycean found at a higher temperature in Iceland.

Bryophyta are of no importance in the springs (Hesselbo 1918).

Illumination. The variation of the illumination in the course of the year and its influence on the assimilation of the plants have never been investigated in Iceland. In marine biology, however, this factor plays a great role as it is one of the factors which govern the production of the phytoplankton, the marine diatoms, since their assimilation and growth of course depend on the amount of light penetrating the water. It would be natural, therefore, to seek a solution of the problem in the well-known investigations carried out in Norway by Gran, Gaarder, and others, who measured the oxygen given off by the phytoplankton diatoms in a closed bottle on different days and the simultaneous growth of this plankton. For several reasons, however, these investigations are of no use for the present purpose. In Oslo Fjord and Møre the plankton production sets in at the beginning of March at the earliest, near Lofoten (70° N. lat.) not till the end of this month. But at this time of the year the algal growth of the hot springs in Iceland is in full swing, as already stated. This means that some other factors than light is of importance for the start of the growth of the phytoplankton, namely the occurrence of soluble nutritive salts in the water. This is also the reason why the phytoplankton production in Iceland does not set in till the month of May (Stee-man Nielsen 1935). However, this being so, it is a matter of fact that the quantity of the light cannot be computed in this way, it being impossible

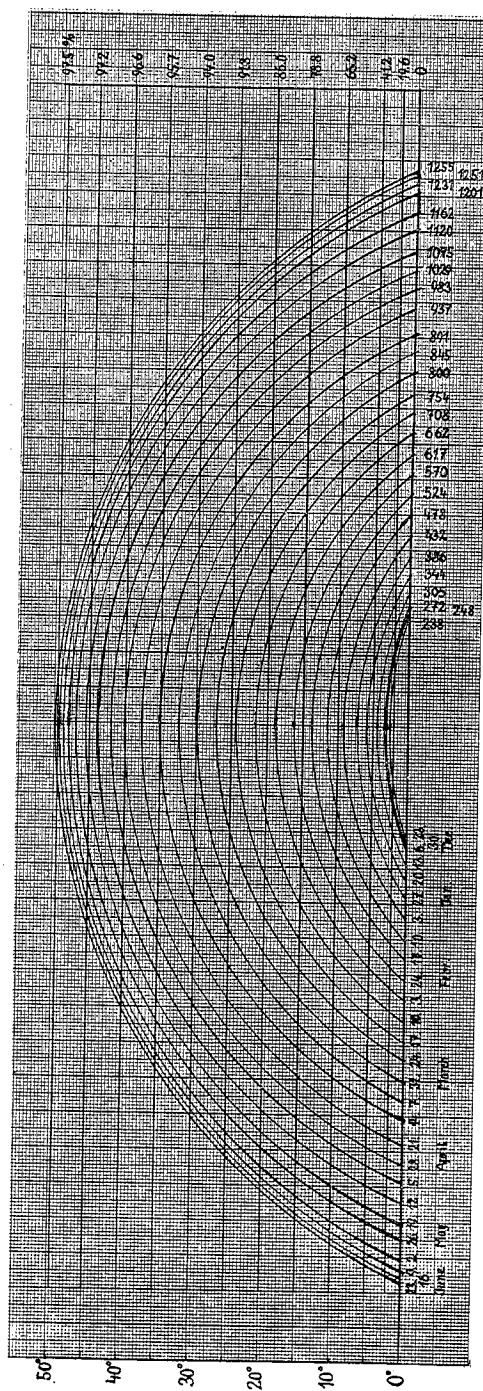


Fig. 54. Daily sun paths for Iceland in the period 23/12 1936-23/6 1937. Abscissa: left, the dates, right, length of the days in minutes. Ordinate: left, culmination height of the sun, right, the percentage of the sunlight which is refracted on passing into the water at the corresponding heights.

to ascertain it when the phytoplankton is absent, which, indeed, it is at the time at which it is of interest for the solution of the present question.

It seems evident, however, that in winter light in these latitudes is not intense enough to allow a CO_2 -assimilation to take place, but besides trying to illustrate this fact by figures it would be of interest to find out for how long time this holds good; and for this reason, direct investigations being impossible, I have tried to compute the factor of illumination on a purely theoretical basis.

The illumination of the hot springs—as throughout Iceland—differs greatly in summer and winter owing to the northerly situation of the country. To illustrate this condition, obvious in itself, I have computed how much light will penetrate below the surface of the water of a spring throughout the year. I regard the sun as the only source of light, for the light of the moon is known to be insufficient to give rise to assimilation in the plants. Furthermore, I have only taken the direct radiation of the sun into consideration, disregarding the changes of illumination due to “diffuse daylight,” that is to say, the light reflected from particles in the air and from the surface of the ground. This direct radiation is supposed to fall on a spring situated at sea-level, near Reykjavík ($64^{\circ}8'N$. lat.), and on a level open plain not surrounded by mountains. Fig. 54 shows the conditions under these schematical circumstances during the six months from December 23rd, 1936, to June 23rd, 1937. The length of the day in minutes week for week is indicated on the abscissa, after the figures for each Wednesday given in the Icelandic almanac, while the ordinate shows the corresponding culmination heights of the sun computed according to the formula $H = \delta + 90 - \varphi$ (δ = declination, φ = latitude of the place). The circular arcs, then, show the paths of the sun on the dates stated. The figures used are given in Table VII, which likewise contains the figures for Mælifell, situated in $65^{\circ}27'N$.lat. (no account, however, has been taken of the circumstance that Mælifell is situated 90 m above the level of the sea on the east side of a mountain slope, but at a distance of 7-8 km from the mountains on the other side of the valley).—In fig. 54 the horizontal lines indicate the percentage of the amount of light falling on the surface of the water which will be refracted in the water when the height of the sun above the horizon is 2° , 5° , 10° , 15° , 20° , 25° , 30° , 35° , 40° , 45° , and 49° . These figures have been computed according to Fresnel's formula $I = \frac{1}{2} \left(\frac{\sin^2 (i-b)}{\sin^2 (i+b)} + \frac{\text{tg}^2 (i-b)}{\text{tg}^2 (i+b)} \right)$, I being the ratio between reflected and incident light and i and b the angle of the incident and the refracted ray respectively with the normal at the surface of the water,

TABLE VII

| | Length of the day | | | | | | Culmination height of the sun | |
|---------------|-----------------------------|------|--------|-----------------------------|------|--------|----------------------------------|----------|
| | Reykjavík 64° 8' N. lat. | | | Mælifell 65° 27' N. lat. | | | Reykjavík | Mælifell |
| | hours | min. | Σ min. | hours | min. | Σ min. | | |
| Dec. 23. 1936 | 3 | 58 | 238 | 2 | 54 | 174 | 20° 26' | 10° 7' |
| 30. | 4 | 8 | 248 | 3 | 4 | 184 | 20° 42' | 10° 23' |
| Jan. 6. 1937 | 4 | 32 | 272 | 3 | 38 | 218 | 30° 21' | 20° 2' |
| 13. | 5 | 5 | 305 | 4 | 21 | 261 | 40° 22' | 30° 3' |
| 20. | 5 | 44 | 344 | 5 | 6 | 306 | 50° 43' | 40° 24' |
| 27. | 6 | 26 | 386 | 5 | 56 | 356 | 70° 22' | 60° 3' |
| Febr. 3. | 7 | 12 | 432 | 6 | 46 | 406 | 90° 18' | 70° 59' |
| 10. | 7 | 58 | 478 | 7 | 40 | 460 | 110° 28' | 100° 9' |
| 17. | 8 | 44 | 524 | 8 | 30 | 510 | 130° 50' | 120° 31' |
| 24. | 9 | 30 | 570 | 9 | 19 | 559 | 160° 21' | 150° 2' |
| March 3. | 10 | 17 | 617 | 10 | 13 | 613 | 180° 59' | 170° 40' |
| 10. | 11 | 2 | 662 | 10 | 58 | 658 | 210° 42' | 200° 23' |
| 17. | 11 | 48 | 708 | 11 | 48 | 708 | 240° 28' | 230° 9' |
| 24. | 12 | 34 | 754 | 12 | 36 | 756 | 270° 13' | 250° 54' |
| 31. | 13 | 20 | 800 | 13 | 25 | 805 | 290° 57' | 280° 38' |
| April 7. | 14 | 5 | 845 | 14 | 13 | 853 | 320° 38' | 310° 19' |
| 14. | 14 | 51 | 891 | 15 | 5 | 905 | 350° 13' | 330° 54' |
| 21. | 15 | 37 | 937 | 15 | 53 | 953 | 370° 40' | 360° 21' |
| 28. | 16 | 23 | 983 | 16 | 45 | 1005 | 390° 58' | 380° 39' |
| May 5. | 17 | 9 | 1029 | 17 | 35 | 1055 | 420° 4' | 400° 45' |
| 12. | 17 | 55 | 1075 | 18 | 29 | 1109 | 430° 57' | 420° 38' |
| 19. | 18 | 40 | 1120 | 19 | 22 | 1162 | 450° 36' | 440° 17' |
| 26. | 19 | 22 | 1162 | 20 | 14 | 1214 | 460° 58' | 450° 39' |
| June 2. | 20 | 1 | 1201 | 21 | 5 | 1265 | 480° 2' | 460° 43' |
| 9. | 20 | 31 | 1231 | 21 | 47 | 1307 | 480° 47' | 470° 28' |
| 16. | 20 | 51 | 1251 | 22 | 19 | 1339 | 490° 13' | 470° 54' |
| 23. | 20 | 55 | 1255 | 22 | 23 | 1343 | 490° 18' | 470° 59' |

hour between 19.6 and 41.2 %, and finally in c. $\frac{2}{3}$ hour between 0 and 19.6 %. If, now, the amount of light issued by the sun towards the spring in question every hour is denoted by x and we disregard the fact that the atmosphere absorbs an increasing part of it the lower the sun is in the sky, we shall find that the amounts of light given below, expressed in the unity x , will reach the alga in the course of the day (Table VIII):

TABLE VIII

| Dec. | | Jan. | | | | Febr. | | | | March | | | | |
|-------|------|------|------|------|------|-------|------|------|------|-------|--------|-----|-----|--------|
| 23. | 30. | 6. | 13. | 20. | 27. | 3. | 10. | 17. | 24. | 3. | 10. | 17. | 24. | 31. |
| 0.4 | 0.4 | 0.7 | 1.0 | 1.5 | 2.2 | 3.0 | 3.8 | 4.7 | 5.9 | 6.8 | 7.9 | 9.0 | 9.8 | 10.8 x |
| April | | | | May | | | | June | | | | | | |
| 7. | 14. | 21. | 28. | 5. | 12. | 19. | 26. | 2. | 9. | 16. | 23. | | | |
| 11.6 | 12.4 | 13.4 | 14.1 | 14.8 | 15.6 | 16.6 | 17.4 | 17.8 | 18.2 | 18.5 | 18.6 x | | | |

That is to say, the alga will receive c. 50 times as much light in June as in December, if x were the same figure. However, this is not the case. The amount of light which the sun would emit to the earth if no atmosphere existed, the solar constant, according to Milankovitsch (1930) is 2 cal/cm²/min. (exactly 1.946), that is to say, 120 cal/cm²/hour. But since the angle formed by the surface of the earth with the sun varies throughout the day, the amount of light this surface receives every hour will vary, also. Milankovitsch (l.c. p. 14-15) has computed the daily amount of light for some latitudes on particular days; in latitude 64° it is 17 cal/cm² on December 23rd and 1023 cal/cm² on June 22nd. On the basis of these figures we may calculate the value of x on the days in question, and then 0.4 x on December 23rd (1.8 cal/cm²) and 18.6 x on June 22nd (909 cal/cm²), or an increase of about 500 times. However, it is possible, also, to take the extinction (absorption + reflection) by the atmosphere into consideration. The transmission coefficient of the atmosphere (i.e. that fraction of the sunlight which passes through the atmosphere) is rarely 1. As an average all over the globe it has been fixed at 0.6; since Iceland on account of its northern situation and sparse population lies essentially above the average (cf. Georgi 1928 p. 59), we shall hardly be much in error if we fix it at 0.8. Milankovitsch (l.c. p. 63) has computed the daily amount of light for certain days and latitudes for a transmission coefficient of 0.8; on the basis of these I have computed x' (that is to say, x when the extinction by the atmosphere is taken into consideration) for the 27 days chosen (Table VII) and from this, again, inserted x' for the individual days in Table VIII, in

which way I arrive at the following amounts of light falling on the alga on the particular 27 days (Table IX):

TABLE IX

| Dec. | | Jan. | | | | Febr. | | | | March | | | | |
|-------|-----|------|-----|-----|-----|-------|-----|------|-----|-------|-----|--------------------------|-----|-----|
| 23. | 30. | 6. | 13. | 20. | 27. | 3. | 10. | 17. | 24. | 3. | 10. | 17. | 24. | 31. |
| 0.1 | 0.5 | 1.4 | 2.5 | 4.5 | 7.3 | 11 | 15 | 24 | 40 | 65 | 100 | 135 | 175 | 205 |
| April | | | | May | | | | June | | | | | | |
| 7. | 14. | 21. | 28. | 5. | 12. | 19. | 26. | 2. | 9. | 16. | 23. | | | |
| 250 | 295 | 350 | 390 | 430 | 465 | 500 | 525 | 540 | 555 | 570 | 580 | cal/cm ² /day | | |

That is to say, the alga receives 5000 times as many calories on the longest day as on the shortest day. The figures in Table IX are represented graphically in fig. 55. This curve shows the tendency and order of magnitude of the variation of the amounts of light; however, the figures should not be regarded as quite accurate, the deviation amounting to some few per cent., as I made the interpolation from Milankovitch's tables with approximate accuracy only. For so many other factors, which I could not consider in the computation, exert their influence that not even a high precision

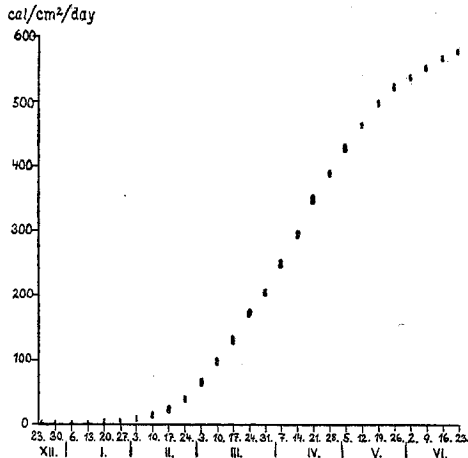


Fig. 55. The sunlight in cal/cm²/day falling on an alga just below the surface of the water on the different days.

May 7 %, and June 0 %; thus the percentage influence was the same in the months December-March. Obviously this factor will influence the amount of light utilised, though hardly to a very considerable degree. It should be noted, however, that the refraction of the diffuse daylight in the water is different from that of direct solar radiation, and cannot be computed.

3. *Clouds.* As to the "schematic" spring it is of course taken for granted that the sun shines all day from a cloudless sky. This will rarely be the case, and clouds naturally reduce the amount of light that falls on the spring very considerably, but at the same time—diffusing the light—they increase the degree of utilisation. However, the former will, of course, by far outbalance the latter. During the months in question Reykjavik received the following percentages of the amount of sunshine which it might have received: December 1.9 %, January 10.6 %, February 26.9 %, March 50.8 % (c. 50 % above the normal), April 21.1 % (c. 40 % below the normal), May 38.4 %, and June 39.0 %. Points 2 and 3 together are expressed by the albedo of the place (i.e. the ratio of the sunlight reflected from the clouds and the surface of the ground to the incident sunlight); for the whole globe it averages 40 %, but if snow and clouds are present, it increases to 60 %, while in dark places it may fall to 10 % (Wundt 1942 p. 93). At present, however, it is impossible to take its variation in Iceland throughout the year into consideration.

4. *The situation of the place.* a) The geographical situation. The "schematic" spring was situated near Reykjavik, but conditions are, of course, different in other parts of Iceland. Both the length of the day and the culmination height of the sun vary with the latitude (but not with the longitude). As an example the conditions on Mælifell (65°27' N. lat.) are given in Table VII; the culmination height of the sun is 1°19' less than at Reykjavik (so on the shortest day it is only a little more than 1° above the horizon), the length of the day also differs considerably, the shortest day being well over an hour shorter, the longest one and a half hours longer. Both these circumstances contribute to increase the difference between December and June, for the difference between the amount of light which is refracted into the spring at a culmination height of 1°7' and 2°26' is greater than at 47°59' and 49°18' (see fig. 54). b) The topographical situation. Here the height above the sea will make the days longer (at an altitude of 200 m on Mælifell I saw the midnight sun). In addition the light has to pass a thinner and clearer atmosphere, so its degree of utilisation will be greater than at the surface of the sea. However, the Icelandic atmosphere is in itself so clear that in the mountains the increase of the intensity is exceptionally small, only 5 per cent for 500 m (Georgi 1928 p. 61). An entirely incalculable change of conditions will take place according as the east, south, or west sun is hidden by the surrounding mountains and according to the height of the latter; possibly the mountains may also contribute to a better utilisation of the light by diffusing it. As a whole, however, they will contribute to increase the difference between summer and winter, since it is the lowermost part of the path of the sun, that which emits the smallest amounts of light, which they will cut off.

5) *Colour diffusion of light.* In the first place, the absorption by the atmosphere is not uniform throughout the field of light, but is greatest within the short-waved field. Thus, when the sun is lowest in the sky, it is mainly the red rays which traverse the atmosphere. This is hardly of any great importance to the green land plants, since in them the assimilation is greatest in orange-red light. Some experiences with green algæ (*Ulva*) show, however, that as to the assimilation in them the violet-blue light, also, is very important, at least just as important as the orange-red light (Gabrielsen 1940 p. 78-87; Seybold 1934). The Cyanophyceae seem, indeed, to be capable to some extent of adapting themselves to the light to which they are exposed. As a

whole it must be said that if this factor is of any importance at all, conditions would be more unfavourable to the algæ in the winter than in the summer. Secondly, the refraction of the light at the surface of the water is not uniform for all the wave fields; the differences are so small, however, that they may be disregarded. Thirdly, finally, the absorption of the light in the water is different within the different wave fields. However, to the shallow springs considered here this is of little importance, and of less importance, still, in that the algæ frequently float immediately below the surface of the water.

Thus we may conclude that the amount and nature of the light that falls on a Cyanophycean in a hot spring in Iceland varies greatly throughout the year; in the "schematic" spring it would increase c. 5000 times from December to June. It is true, that many factors have been disregarded in this computation, some of which are of great importance, especially, perhaps, the cloud covering. It seems to me, however, that in disregarding these factors I arrive at too high figures, if anything, for December and too low figures for June and, accordingly, too small a difference between December and June. I therefore think it justifiable to use them in the way done below.

Now, such small amounts of light as shown in fig. 55 for the months December and January would render it probable that there was a cessation in the growth of the algæ in these months. On this point Schwaabe makes the following statements (1936 p. 297): "In den lichtärmsten Monaten (November-Januar) kommt das Leben in Thermalbiotopen nach meinen Beobachtungen (Laugarlækur bei Reykjavík, Breiðholt S.-R.) wie in der Umgebung zum Stillstand. Vor allem sterben die assimilierenden Pflanzen ab." About a *Scytonema* carpet he says that "nach brieflicher Mitteilung kam er erst im Dezember zum Absterben." Finally, he says about *Hapalosiphon laminosum*: "Gleichzeitig mit dem hier besprochenen Schwund des *Scytonema*-Teppichs gingen auch die Bestände im heissen Abfluss bis auf wenige unscheinbare Reste zu Grunde." However, he does not state at what time of the spring the algal vegetation revives again.

On the basis of my above computation of the light conditions in the hot springs it might be possible to compute—very roughly—the oxygen production curve of the algæ in these months. For as to *Phormidium*

three colours of light, white, blue, and red, acting upon them. Disregarding this power of adaptation, I shall try to utilise his figures in a computation of the possibilities of existence for this alga.

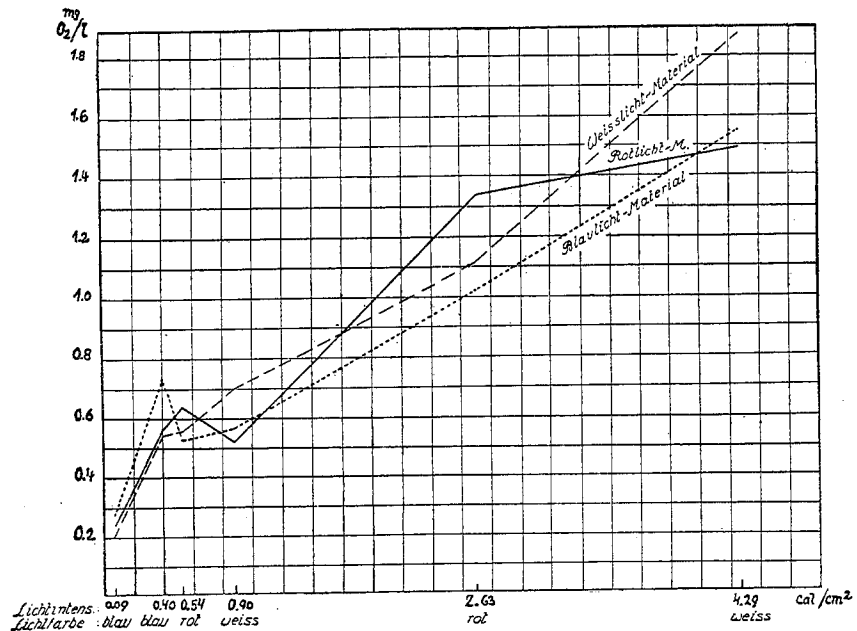


Fig. 56. The CO₂-assimilation of *Phormidium laminosum* at different intensities and colours of light. Ordinate: amounts of O₂ given off. (After Harder).

Unfortunately his figures require some recalculations in order to be convenient for my purpose. Thus he gives the light intensity in MK (Meterkerzen); it can easily be converted into gram calories (Seybold 1934 p. 612), since 1 MK = 0.000 000 225 cal/cm²/sec. = 0.00081 cal/cm²/hour. He gives the assimilation in "Assimilationswerte," which are 1000 times the amount of n/200 sodium thiosulphate (in cm³) used in titration of the oxygen given off during two hours in 100 cm³ of water. Since 1 cm³ of n/200 sodium thiosulphate corresponds to 0.04 mg oxygen, his assimilation value of 100 corresponds to 0.2 mg O₂/l/hour. Finally, the assimilation value indicates all the oxygen given off by assimilation, including that taken in again by respiration; in two cases only is this quantity of oxygen specified, and thus in these two cases only am I able to compute the amount of oxygen given off by *Phormidium* at different light intensities; and of these, one comprises only two experiments, at blue and red lights, 500 MK, and may be left out of consideration. Moreover the weight of the algæ is not stated, so I cannot give the oxygen per hour per gram algæ, but must operate with "as much of the algæ as may thrive in a litre of water." However, in the experimental series in question care was taken that in the different experiments the same number of algæ "by the eye" were found in each glass vessel.

The result of the experiments is represented in fig.*56 (after H a r d e r 1923 p. 337), in which I have substituted the light intensity in MK by cal/cm²/hour and the assimilation values by mg O₂/1/hour. The corresponding respiration is 0.2 mg O₂/1/hour = 4.8 mg O₂/1/24 hours, as the plant respire uniformly throughout the twenty-four hours of the day and night. Assuming that the curves are valid also for the intervals for which experiments are lacking, I arrive at the following quantities of oxygen *given off* on the dates selected in December-February per litre of spring water (Table X).

TABLE X

| Dec. | | Jan. | | | | Febr. | | | |
|------|------|------|------|------|------|-------|-----|-----|-------------------------|
| 23. | 30. | 6. | 13. | 20. | 27. | 3. | 10. | 17. | 24. |
| -4.6 | -4.3 | -4.0 | -3.7 | -2.8 | -1.6 | 0 | 1.8 | 6 | 15 mg O ₂ /l |

According to this the "compensation point"¹⁶ for respiration and assimilation is not reached till the beginning of February.

There are two factors, however, which have not been taken into consideration and which may cause some displacement. Firstly the temperature. H a r d e r's experiments were made at room temperature; but the high temperature of the springs will naturally affect both the respiration and the assimilation. According to B o y s e n J e n s e n (1938) the respiration in its dependence on the temperature, as long as this has no injurious influence, almost follows van't Hoff's Law; this also applies to assimilation at a high carbon dioxide tension and intense light, whereas at a low carbon dioxide tension the influence of the temperature is inconsiderable. At the high temperatures with which we are here concerned the carbon dioxide tension is no doubt low, and at any rate the intensity of light during these first months, in which the compensation point must lie, is inconsiderable, so it is probable that the respiration increases more

remain unaffected—which is highly improbable—the compensation point will be reached on February 24th.

Secondly, the ability of adaptation. It has been mentioned above that *Harder* records the existence of this ability, but his few figures cannot be considered in my computation, since he only gives the light intensities at which his material was originally kept as "Schattenlicht" and "Sonnenlicht." However, it does not seem that the difference between the oxygen production of these two materials at light of the same intensity exceeds 100 %, so this will hardly alter the result of my considerations very much. Thus, for instance, a doubling of the CO_2 assimilation in the computation for January will only shift the compensation point to January 23rd.

From this computation I think it justifiable to conclude that very probably no algal growth will take place in at least two months around the winter solstice and gradually, also, the carpet of algæ present at the beginning of this time will die, so no nourishment for the herbivores will be found in the springs. With the extinction of the algæ the source of oxygen at the mouth of the springs, where the water is free from oxygen, will likewise disappear, which, however, is a minor disadvantage farther down the overflow where the spring water is able to absorb oxygen from the atmosphere.

In what stage the animals pass the winter cannot be said. *Schwabe*, who gives some few particulars as to the algal vegetation in the winter (see above), does not state anything about the animal life except that he found *Scatella* to lay eggs "vom 4. April bis zum 4. Oktober 1932 an verschiedenen Thermenaustritten," which might mean that he did not find such specimens in the remaining part of the year. During my own sojourns in Iceland (April to August) animals were always abundantly present without distinct generation sequences.

It is, of course, possible that when the algæ at the source of the spring do not give off oxygen any more, the larvæ will change their place of residence farther down the stream where the water without the aid of Cyanophyceae will be saturated with oxygen; and as the imago stages of both insects are air breathing animals, they may quite well go back to the source of the spring again in early springtime. However, I do not consider this very probable, because sooner or later the algal layer will disappear from the overflow also, and nutrition will then be wanting and nowhere else to be had. I should think, therefore, that the insects pass the winter in a state of relaxation—as larvæ, which is the mode of wintering of Chironomids elsewhere, or as larvæ and imagines, which seems to be the mode of wintering of Ephydriids elsewhere—in the very place in which they are found in the summer. *Radix*, however, possibly

rests in a different way: it only has to crawl out of the spring to be under conditions under which snails usually pass the winter.

Section b. Heat resistance.

As to the upper temperature limit for animal life opinions agree fairly well. Brues (1932 p. 286) after his extensive investigations of the hot springs of North America combined with an immense knowledge of the literature, draws the conclusion that 51° - 52° form an upper temperature limit of organic life, higher temperatures being only tolerated by bacteria and blue-green algæ, that is to say, the lowest types of plant life. Schwabe (1936 p. 313) records 50° as a critical temperature to all living beings with the exception of bacteria and Cyanophyceae. Mason (1939), who made some death-point experiments on hot spring animals from Algeria, gives $51\frac{1}{2}^{\circ}$ as the maximum, and even for a short time only; thus *Heterocypris balnearia* Mon. is found in nature at $51\frac{1}{2}^{\circ}$, but in the laboratory it died (several hundred individuals) after two hours at this temperature, after four hours at 49° , whereas it lived for an unlimited time only at 47° . He supposes that they remain near the cold banks and only make short excursions out into the stream in which the temperature of $51\frac{1}{2}^{\circ}$ is found. (The figures agree entirely with my figures for *Scatella*, cf. p. 83-84).

Uvarov (1931 p. 17 ff), who only treats the insects, gives far more varying figures in his table, but nevertheless concludes that "the upper fatal limit is fairly uniform for various insects and lies on the average at about 50° ," which is thus in good agreement with Brues. E. Bro Larsen (1943) for *Musca* gives 52° - 53° as the limit for "instantaneous death." As stated on p. 83 a temperature of 51° causes instantaneous death (heat coma, from which they never recovered) for *Scatella* larvæ.

There is thus an astonishing agreement between the figures arrived at in different ways, and it would therefore seem probable that there were a common cause, too, of this upper temperature limit for animals of different orders. Various compilations of the cause of heat resistance in animals have been given (Cameron 1930, Uvarov 1931, Brues 1932 etc. Buletinul Institutului de Cercetari Zoologice, Bucuresti, 1932, 1933, 1934, 1935, 1936, 1937, 1938, 1939, 1940, 1941, 1942, 1943, 1944, 1945, 1946, 1947, 1948, 1949, 1950, 1951, 1952, 1953, 1954, 1955, 1956, 1957, 1958, 1959, 1960, 1961, 1962, 1963, 1964, 1965, 1966, 1967, 1968, 1969, 1970, 1971, 1972, 1973, 1974, 1975, 1976, 1977, 1978, 1979, 1980, 1981, 1982, 1983, 1984, 1985, 1986, 1987, 1988, 1989, 1990, 1991, 1992, 1993, 1994, 1995, 1996, 1997, 1998, 1999, 2000).

to me that this hypothesis gives by far the simplest explanation of the many different statements put forward in the course of time, and at the same time it affords a possibility of further exact chemical investigations of the question. The cause of the astonishing agreement between the upper temperature limits for animals of different orders might then be, that the determinators in all their anticipated differences have an upper limit of resistance even at this temperature.

Section c. The melanisation.

Lindroth (1931 p. 550) points out in a footnote that if *Scatella thermarum* is merely a melanic "Art" (oder wie man sie sonst auch nennen möge)" of *Sc. stagnalis*, and since *Lispa consanguinea*, too, occurs in a melanic form around the hot springs of Iceland, it might be supposed that "das Leben bei (sogar in) den heissen Quellen wirklich einen Melanismus zu erzielen scheint." Schwabe does not deal with the question, nor is it discussed by any other authors, as far as I know, so it cannot be seen whether it applies to any other hot spring areas; no doubt, however, it would have been observed by Brues or Issel if the thermal forms investigated by them were particularly melanically coloured. But as to Iceland the observation holds good; and it is further confirmed by my observations of *Eucriotopus sylvestris* f. *thermicola*, which was also frequently of a darker colour (cf. p. 92). However, melanism and melanism are several things; in order to elucidate the problem I will therefore treat the three forms separately.

Lispa consanguinea Loew var. *fuscipes* Ringd. (Ringdahl 1930 p. 173) does not belong to the character animals of the absolutely hot springs (cf. p. 58). It differs from the main form by being bigger and by having darker tibiae. Whether its—slight—melanism has some connection with hot springs or merely with their damp surroundings (or with the northern occurrence of the form) and whether it is of a phenotypical or genotypical character cannot be stated. Thus it loses all its importance in this respect.

Scatella thermarum Collin. On p. 65 ff I have given the views which made me return to the consideration of *thermarum* as a separate species, differing from *stagnalis* not only in colour but also in other, though minor, characters; I have also recorded my attempts to alter the type by giving it exceptional conditions for development. From this it was evident that the form could not be directly phenotypically altered, in other words, *Sc. thermarum* is genotypically different from *Sc. stagnalis* and probably a melanic mutant of the latter.

Eucriotopus sylvestris F. f. *thermicola* n. f., however, is very labile

as regards its markings; the varying distribution of the dark pigment is probably due directly to the external factors. Most likely we are here concerned with a phenotypical melanism.

In the first case we would thus be concerned with the phenomenon termed by Reinig (1937) a factorial melanism, in the second case, however, with a modificatory melanism. It is obvious that the causes, too, must be different.

The melanism of *Scatella*, being hereditary, is accordingly due to a mutation. Now, as is well known, nobody has ever yet succeeded in producing a particular desired mutation by an external influence; it is therefore not probable, either, that the heat of the springs is the direct cause of this melanic mutation, for as *Sc. thermarum* shows identic characters not only around nearly all Icelandic hot springs, but also near hot springs in both West and East Greenland, it would mean that the heat would have produced the same mutation in all these places. On the other hand, it is possible to increase the mutation frequency within a species by external influences (heat, radiation); but if this were the case here, we might expect to find other mutants also in the populations around the different hot springs, and possibly—as the conditions are only partially alike for the different springs—even a quite different mutant would predominate around some of the springs. Accordingly it is not probable, either, that the phenomenon can be explained on the basis of the power of the heat to increase the mutation frequency. The most probable supposition, I think, is that the gene or genes for melanism are recessively present in all the populations, and that in the small isolated populations around the individual springs the gene or genes have acquired a highly elective value. For in small isolated populations the scattering of variability will cause allelomorphic genes to be eliminated from the population, which after a series of generations becomes homozygotic to one of them; to which of them, is decided by chance (Dobzhansky 1937 p. 133 ff). Isolation alone cannot, therefore, explain the melanism, or if so, we must expect a dominance of different allelomorphic genes in the populations around the different hot springs—if, for instance, there are only two, melanism would be found in 50 per cent. of the populations—; but the gene or genes with which we are concerned here in

is probably due to the external factors as shown p. 92. I shall not discuss here the numerous more or less well-known experiments on exposing the pupæ of insects, especially butterflies, to heat or cold and the melanists produced in this way, but shall merely refer to the most probable theoretical explanation of the phenomenon put forward by Goldschmidt (quoted here after Giersberg 1929 and Reinig 1937), viz. that it is due to accelerating or retarding influences of heat or cold to an unequal degree on the time of development of the animal and on the formation of pigment. If the time of development is accelerated more than the formation of pigment, or it is retarded less than the latter, the animal will be light-coloured, while in the reverse cases it will be dark. The formation of melanin is due to an interaction of the factors chromogen, ferment, and oxygen; Giersberg (1929) showed that it is probably the amount of chromogen produced which is decisive for the degree of pigmentation, for the two other factors will always be present in sufficient quantities, and further that this amount is regulated from the head, in Giersberg's opinion by the nerves. Quite probably, however, it is the hormone secretion of the endocrine glands of the head which is affected (for, as will be known, chromatophore-activating hormones were demonstrated by Hanström to be produced probably in the corpora allata of many insects (cf. Hanström 1939, Pflugfelder 1941), which, it is true, do not themselves react to injection of them) since a constriction of the front part of the pupa will give rise to the development of melanists. In such cases the hormone, if any, should be chromogen-reducing and, by being put out of court, whether directly by constriction or by a stronger or weaker action of heat or cold, more or less glandular tissue being destroyed, would further the formation of melanin. On the basis of this view it would be easy to make experiments with the pupæ of *Eucriotopus sylvestris* in order to observe the development of the dark pigment. As the species is of common occurrence all over Europe, the experiments need not be made in Iceland or on *f. thermicola*.

It will be seen that the two forms of melanism may be explained in entirely different ways: in one case as due to isolation, in the other as due to the temperature; while nothing can be stated as to *Lispa*. It is therefore unjustifiable to say that life in hot springs *eo ipso* results in melanism; in principle this need not be the case at all, and quite probably the hereditary melanisms have nothing to do with the problem of hot springs.

Section d. The relation between brackish water animals and hot spring animals.

A distinct relationship between the forms found in hot springs and those living in brackish water has been pointed out by Brues (1924, 1928) and Schwabe (1936). Brues writes (1924 p. 381) that "the similarity between those two faunæ and that of the littoral zone of the sea also is very striking and cannot fail to attract the attention of any zoölogist who cares to examine the thermal fauna in any detail." The cause is found in "their ability to adjust their metabolism to the increased osmotic pressure of the medium." In 1928 (p. 215) this view is extended as follows: "Aside from temperature the most important single characteristic of thermal waters which determines the nature of its fauna is the presence of salts in solution." Schwabe, who also mentions the relationship of the plants (diatoms) of the thermal and brackish waters, gives a more cautious explanation, namely "dass die Bewohner beider über eine relativ grosse ökologische Breite verfügen müssen" (p. 326). I shall discuss the question more fully, including peripherically, also, the biotope of polluted water.

Firstly: Does the aforementioned relationship exist at all? On p. 103-04 information has been given as to what animals are found in the absolutely hot springs all over the globe. The result arrived at was that at lower temperatures the common fresh water animal community occurred, while at temperatures above 40° only representatives of some special groups were found. It is to a great extent the same groups which are seen to supply the halobiontic species (i.e. typical salt water animals), especially as regards the insects: the heterometabolous species were almost absent from the absolutely hot springs, very rarely do they have halobiontic representatives (Halobatids); Trichoptera are absent from the absolutely hot springs, only one halobiontic species has been recorded (near New Zealand, Henriksen 1934). Within the Coleoptera the fresh water families supply both halobiontic and "thermobiontic" species, whereas within the Diptera conditions are more obscure. Of the Nematoceros families mentioned on p. 105 which are absent from the absolutely hot springs, only some Culicids (*Aedes caspius* and other species) are halobiontic, but several Brachyceros families (*Empididae*, *Dolichopodidae*, etc., Karl 1930) have halobiontic representatives without being found in absolutely hot springs. *Stratiomyidae*, *Chironomidae*, and *Ephydriidae*, however, are abundantly represented in both places.

Thus the rough outlines of the interrelationship may be glimpsed, but it is not unmistakable. Conditions become clearer if we consider the genera and species in groups including both halobiontic and "thermo-

biontic" representatives. Ostracoda: No relation. Hydrachnida: No relation. Diptera Chironomidae: *Chironomus tentans* in absolutely hot springs, other *Chironomus* species halobiontic; *Eucriotopus sylvestris* is very closely related to the halobiontic *Trichocladius halophilus* (Thienemann 1925 p. 228). Diptera Ephydriidae: *Scatella thermarum* in absolutely hot springs, *Sc. subguttata* halobiontic (Brauns 1939). Coleoptera Dytiscidae: Species of *Bidessus* and *Coelambus*, which are very close allies, in absolutely hot springs, two species of *Coelambus* halobiontic (Henriksen 1934). Coleoptera Hydrophilidae: Species of *Ochthebius* and the three very closely interrelated genera *Laccobius*, *Philydrus* (*Enochrus*), and *Helochares* in absolutely hot springs, many species of *Ochthebius* and a couple of *Philydrus* halobiontic (Henriksen 1934). Coleoptera Heteroceridae: *Heterocerus* in both biotopes. Mollusca: *Paludestrina aponensis* in absolutely hot springs, many *Paludestrina* species marine. (*Radix*, however, has no marine representatives, though *Limnaea* species are reported to be able to adapt themselves to 40 ‰ NaCl (Chen-Ya-Shih 1937 p. 263)).

Thus the interrelationship is unmistakable. Next comes the question as to the cause. There are two possibilities, if it is not due to mere chance, viz.: 1) a common external factor, or 2) a common internal factor which reacts to different external factors. As stated above, Brues adhered to the first possibility, seeing the cause in the ability of the animals to adapt themselves to the higher osmotic pressure, since in hot springs, also, a high salt content is assumed to be an essential factor. A glance at my Table III will at once reveal that this is not correct, for the salt content of the hot springs of Iceland ranges from 205 to 1523 mg/l, of which even SiO₂, which perhaps is not dissociated, may constitute nearly one half or more. Thus the salt content is about 0.7 ‰ at most, that is to say that the water is fresh. Accordingly the interrelationship cannot be due to a similarity as regards the salt content; and I can see no other external factors, either, common to the highly different hot springs and to sea water.

Schwabe is inclined to accept the other possibility, speaking about "eine relativ grosse ökologische Breite." If this is correct, it would be natural to suppose that the "ecological range" would extend to other biotopes, also, than salt water and hot springs, for instance to polluted water. In much polluted water (polysaprobous and α -meso-saprobous, Kolkwitz & Marsson 1909) i.e. Tubificids and Chironomids are character animals—only the Chironomids have representatives in absolutely hot springs. Psychodids and Syrphids (*Eristalis*) are typical of polluted water without having any forms in absolutely hot springs,

while beetles of the absolutely hot springs cannot thrive in polluted water; the Ephydriids, on the other hand, have forms in both biotopes. Altogether the Ephydriids are present in any conceivable fluid biotope; for instance the petroleum fly *Psilopa petrolii* Coq., which lives in crude oil, is an Ephydriid (Thorpe 1930); Thorpe's statement is justified, that "we might have expected, if life was possible at all in an oil pool, that an Ephydriid would be the first to discover the fact."—Thus here, too, there is some similarity; precisely this circumstance, that there is only some similarity, suggests that internal, not external, factors are decisive.

It would seem natural to see such an internal factor in the permeability of the skin; Thorpe suggests it as to *Psilopa*, saying (p. 342): "the ability to live in oil depends largely on an adequate protection from contact with the medium, such as is given by an impermeable cuticle and peritrophic membrane." Little is known about the permeability of chitin. Alexandrov (1935) investigated it in *Chironomus* (*plumosus*), *Glyptotendipes*, and *Corethra*, and found that the permeability i.a. for HgCl_2 is much greater in *Chironomus* than in the other two species. All the three species examined are typical fresh water forms, so the only conclusion that can be drawn is that the permeability of the chitin to salts may differ greatly even within related forms (the first two genera). Furthermore Alexandrov found that the chitin of *Chironomus* is selective in relation to acids and bases: it is highly permeable to weak acids and bases, but hardly permeable to strong acids and bases. The difference in permeability is unexplained, but "most likely due to differences of chemical and physico-chemical properties of the cuticle" (p. 18). Possibly the different permeability of the chitin to acids and bases may account for the "ecological range," that is to say, simply as a resistance against a poisonous effect; however, it is a well known fact that the aquatic insects do not maintain their constant osmotic pressure independent of the surroundings by means of the impermeability of the chitin but by active work. Beyer (1939) has studied the phenomenon in *Ephydra* and has shown that irrespectively of whether the animals were derived from concentrations of 6 ‰ or 42 ‰ salt content, they

nection between the oxygen consumption and the osmotic regulation, point out three facts which speak for a common internal factor in connection with the osmotic regulation as a cause of the interrelationship between brackish water animals and the animals of the absolutely hot springs: 1) It has been demonstrated that the size of the anal gills, which, as is well known, have osmoregulating functions, both in Culicids and Chironomids depends on the salt content, being greatest in fresh water. In *Eucricotopus sylvestris* f. *thermicola*, which lives in very fresh water, they are very small, of the same order of magnitude as, or perhaps a little larger than, in some larvæ of *E. sylvestris* from water with a NaCl content of 1 ‰, Ringkøbing Fjord, Denmark. 2) Beyer states that the length of the respiratory tube in *Ephydra* (different species) depends on the salt content, this tube being longest in salt water. In *Scatella thermarum*, in very fresh water, it is longer than in *Sc. subguttata*, which is a marine species. 3) In the same connection Beyer states that the respiration through the skin of the Ephydrids depends on the salt content, the greater the salt content, the greater role is played by respiration through the skin. But, as stated above, *Scatella thermarum* respire to a great extent, perhaps exclusively, through the skin. All these facts suggest that the biotope of absolutely hot springs may be classed biologically within biotopes with high salt contents; and this, again, might suggest that the connection is to be found in the osmoregulative mechanism.

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