

# THE LAW OF TEMPERATURE CONNECTED WITH THE DISTRIBUTION OF THE MARINE ALGAE

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What I have to bring before you is simply a preliminary consideration of the general subject of the geographical distribution of the marine algae together with some inquiry into the conditions immediately affecting such distribution and as possibly effecting a segregation into the larger units. In accordance with such an intention, I have started a tabulation of all the marine species and varieties, which is far from being completed as yet, but which has, however, reached a stage at which certain general statements may be made as to probable results.

The geographical distribution of the marine algae has been treated of in various ways and in many papers. It is more or less customary to make a comparison between a particular flora and other more or less corresponding floras in comparative tables, percentages of common and endemic species, etc. Certain speculations, based on such data, as to the origin of certain algal floras have also been indulged in. The result is that we have certain geographical areas fairly well marked out and certain others more or less indistinctly outlined or surmised. Certain ecologic classifications have been proposed, particularly as to zonal occurrence in varying depth, influence of varying degrees of salinity, character of the substratum, influence of surge, quiet waters, etc. Very little attention, however, has been paid to general factors controlling distribution over larger areas. We speak broadly of tropical species, or of arctic or antarctic species, of temperate species, etc., but no attempt has been made to survey the distribution of marine algae in general throughout the oceans and seas of the world and to attempt to determine the limiting factors segregating one large area from another. An attempt to determine how far our present knowledge of



species and their distribution may further such an inquiry is the object of the present paper.

Among the more general discussions, there are to be mentioned first those connected with the geographical distribution in the Arctic Ocean. Kjellman's extensive and fundamental paper 'Algae of the Arctic Sea' ('83) led the way and placed at the disposal of future students a very considerable amount of data and brought forward certain fundamental points of view as to a division of the arctic marine flora into provinces, as well as a consideration of the conditions underlying this division. This work was the result of the working over of very considerable collections of the various Swedish expeditions into the Arctic Ocean and a careful examination of all other existing data.

Later, Rosenvinge ('93, '98, '98<sup>a</sup>, '98<sup>b</sup>) published a series of papers dealing with the marine flora of Greenland, and Jónsson ('03, '03<sup>a</sup>, '04, '12) has also published on the same subject as well as on the algae of Iceland and Jan Mayen.

Finally, somewhat over twenty years after Kjellman's paper, Simmons ('05) surveyed the whole matter, revised all tabulations of the Arctic flora and brought forward further views together with a full discussion of all literature bearing upon the subject.

In these various papers and others not referred to specifically, the North Polar Sea is defined and delimited from the Northern Atlantic and Northern Pacific Oceans. The conditions under which marine algae occur in the Polar regions as well as the differences between the conditions of the various portions of its waters are also determined and discussed.

The North Atlantic has also been treated of, but more floristically than as to uniformity, or differences, of physical conditions affecting the flora. A considerable part of the discussion regarding the North Atlantic Ocean has centered about the Faeröes. Simmons ('97), Börgesen ('02, '05), Por-sild and Simmons ('04), and Börgesen and Jónsson ('05), have discussed the marine flora of these islands together with its relation to other North Atlantic floras and ocean currents. Reinke ('89), Svedelius ('01), and Kylin ('06, '07),



have considered the algal flora of the Baltic Sea and its relation to that of the North Atlantic from points of view both floristic and as to physical conditions. Harvey ('58), Farlow ('81), and Collins ('00), have dealt similarly with the algal flora of the northeastern coast of North America, and Börgesen and Jónsson ('05) have made an extended floristic comparison between the floras of the North Atlantic and those of the polar or arctic seas.

For the antarctic and subantarctic regions, the work even of floristic comparison is still hampered by incomplete knowledge. The foundations were laid by Hooker ('45) in the 'Cryptogamia Antarctica' in which there are scattered notes on distribution. Skottsberg ('06) published his 'Observations on the Vegetation of the Antarctic Sea' and later ('07) the first part of his antarctic and subantarctic work. The latter has only floristic details with notes on distribution. Gain ('12) has given a detailed discussion of the distribution of the marine algae thus far credited to either the antarctic or the subantarctic regions of the western hemisphere. Murray and Barton ('95) have given a comparison between the arctic and antarctic marine floras, and Mme. Lemoine ('12) has made a similar comparison limiting it, however, to the species of crustaceous *Corallinaceae*.

The distribution of marine algae in the warmer portions of the oceans, Atlantic, Pacific, and Indian, has not been so much considered as that of the colder portions, although very considerable floristic work has been done. Murray ('93) published a comparison of the marine floras of the warm Atlantic, Indian Ocean, and the Cape of Good Hope. Yendo ('02) has made definite statements about the distribution on the coasts of Japan. Saunders ('01) and Setchell and Gardner ('03) have dealt with the northwest coast of North America, and Schmitz ('96) and Schroeder ('12) have called attention to the relations between the marine flora of East Africa and those of the East Indies and of the central Pacific Ocean.

Various papers and floras have considered distribution, such as bathymetric zonal distribution or according to varying substratum, salinity, etc., within limited regions, prov-



inces, or districts, but no general paper has as yet appeared dealing with the distribution over the oceans in general or any definite suggestions as to the factors concerned.

The nearest approach to an attempt to account for the general facts of distribution is my own attempt (cf. Setchell, '93) to explain the main facts of the geographical distribution of the *Laminariaceae*. The plants of this family are rather inhabitants of the colder than of the warmer waters, proceeding, as it were, from the poles towards the equator, but lacking in strictly tropical waters. It was found that the *Laminariaceae* flora changed its facies with every increase or decrease of 5°C. of summer temperature, thus forming latitudinal zones controlled by temperature relations. This idea was extended to explain the demarcations of the floras of the west coast of North America by Gardner and myself (cf. Setchell and Gardner, '03) with apparent adequate reason.

In attempting to discuss the more general facts of distribution we first necessarily consider the various marine floras and their subdivisions. While the term flora has been used in all sorts of senses, both wider and narrower, to include any aggregation of plants of any region under discussion, whether larger or smaller, it generally carries a certain idea of uniformity of composition with it when used in connection with the floristics of distribution. This uniformity may, however, be only as regards region. It is desirable, here, to use the word for the aggregation of species of marine algae found in a certain region, province, or district, having a certain fairly considerable percentage of species in common throughout its extent, even of the more extended region.

The world's surface, whether land or water, is usually divided into zones of temperature, these in turn into regions, the regions into provinces, and the provinces into districts. For marine floras, the districts must be still further divided into formations, and these in turn into bathymetric or littoral belts. The bathymetric belts, in their turn, show different algal associations.



Considerable work has been done in the description of various floristic associations occurring in various depth belts and of various formations, and the special ecological relationships have been discussed and made reasonably plain. My intention, however, is to discuss the broader distribution and segregation of floras, particularly as to regions and perhaps provinces and to attempt to determine the factor, or factors, governing these.

In attempting to mark out the various floristic regions and their provinces, we are met with certain difficulties. The flora of the Arctic or Boreal region is fairly definite and has been the most carefully studied and tabulated. The provinces of the Arctic region are the Asiatic, the American, that of West Greenland, and the extended province of Spitzbergen (cf. Simmons, '05). The North Atlantic Ocean as distinguished from the Arctic has five regions, viz., those of Northwestern Europe, Southwestern Europe, and the Mediterranean-Northwest African region on the east and Northeastern North America and Middle eastern North America on the west. The Antarctic or Austral region possesses a fairly consistent flora and is not so readily divided into provinces, but the Antarctic-Magellanic province may be contrasted with the Indo-Pacific province. The South Atlantic Ocean has a flora as yet little understood, but, for the present at least, may be considered to have the regions of Southwest Africa and Southeast South America. The Northern Pacific has Bering Sea probably representing a province of the Arctic or Boreal region. Otherwise it is divided into five regions, viz., those of Northwest North America, Middle West North America, and Southwest North America on the east and the Ochotsk-Yezo region and that of East and West Honshu (or Nippon) on the west shores. The South Pacific Ocean has five regions, viz., those of Southwest South America, Middle West South America on the east and those of New Zealand and South and Southeast Australia on the west coasts. The southern portion of the Indian Ocean has two regions, viz., that of Southwest Australia and the South Africa or Cape region. The tropical waters may probably be divided into two regions, viz., the



Tropical Atlantic and the Indo-Pacific regions with their proper subdivision into provinces. Concerning these various regions, it may be said that some seem to possess very distinct and characteristic species content while others are more or less related to one another. However, it is expected that there will be a possibility of discussing this segregation at another time in more extended fashion.

Of particular interest and importance in connection with the marking off of floristic regions, are the points or areas of demarcation. Some of these are well established while others may be only more or less accurately surmised. One of these much referred to in the literature (cf. Harvey, '58; Farlow, '81; etc.) is Cape Cod on the eastern coast of Massachusetts which divides so clearly and so accurately the flora of northern New England from that of southern New England. Cadiz in Spain appears to be another point of demarcation, or possibly indication of an area, where the flora of the Southwestern European region stops, or mingles with that of the Mediterranean-Northwest African region. At Clare Island on the west coast of Ireland (Cotton, '12, p. 160) the flora "resembles that of the southwest of England," but it has elements also of a distinctly northern character. It is probably in or near a demarcation area. Similarly southern Norway and the west coast of Sweden (Kjellman, '02, '06; Svedelius, '01; Kylin, '06, '07) have a mixed flora and are in a transition region.

In Japan Cape Inuboi on the east coast of Honshu (cf. Yendo, '02, p. 181) is a demarcation point and the Strait of Sangar (cf. Yendo, '02, p. 182) is also a region of demarcation or transition. On the opposite side of the Pacific Ocean, along the western coast of North America, Cape Flattery or just south of it, Point Conception, and the region about the mouth of the Gulf of California are demarcation points or indicate transition areas (cf. Setchell, '93, p. 370; Saunders, '01, p. 393; Setchell & Gardner, '03, p. 170). In the southern hemisphere the marine flora of the Cape Region is definitely delimited both to the southwest and to the northeast and in



Australia the marine flora of the southeastern region is definitely set off from that of the southwestern region.

These various points and regions will doubtless become more definite and more of them will become established as careful investigations of the floras are made. They undoubtedly indicate that thereabouts are changes in the conditions regulating the separation of the general flora into its larger divisions and are of great importance in any inquiry as to the general factors affecting the distribution of marine algae.

Along with the mapping out of floras into regions, provinces, etc., it seems best to consider, next, the factors which seem to regulate the distribution. These have been considered by Kjellman ('83) and by others, and are summed up by Oltmanns ('05). Particularly is it desirable to consider which may be chiefly responsible for the limiting of the species within the regions or provinces.

The substratum exercises an important influence on the attached flora or benthos and that is particularly the part of the marine flora I intend to limit this paper to, since the plankton brings in certain particular factors having to do with its floating habits. Of course, benthos can only exist on its proper firmer substratum and different species differ in the nature of this. However, it is sufficiently evident that the character of the substratum limits species only locally and can by no means be considered as a factor in controlling floral regions or even floral provinces.

The motion of the water is a limiting factor in distribution, some algae preferring quiet water, some flowing, some surge, etc., but this factor, too, is clearly a local and not a general one in the distribution of the marine algal benthos.

The specific gravity of sea-water varies and with it, of course, its salt content. This variation, so far as marine algae are concerned, varies from water only slightly brackish to that (in case of exposed and shallow tide pools) of an almost concentrated solution. There is a latitudinal zonal difference here also, but it is not so great as may be found in localities at no considerable distance from one another. It



certainly seems impossible that this can be a general factor. Its local effect, however, may be very considerable.

Light varies from the equator, where it is most intense, to the poles where it is least. It very decidedly limits the distribution as to depth. Marine algae of the benthos need light and are, therefore, limited to the neritic portion of the photic zone as to their general distribution. Outside of this general limitation, however, it does not appear that the varying intensity of light can be considered as a prime factor in limiting floral regions and floral provinces, i.e., not alone.

Varying temperature, however, does act directly upon algae to limit their distribution, both locally and generally. It can easily be recognized to be the one most important factor in controlling the distribution of benthos over wide areas as well as, at times, in smaller districts or spots. We recognize that, in general, the species of the frigid zones, of the temperate zones, and of the tropical zones are sufficiently different to give an entirely different facies to each. Yet, in considering general regions, we find that they are not marked out by the same parallels as are used to mark these zones geographically. These geographical zones, however, are established more particularly as regards direction of the sun's rays and the temperature of the air rather than that of the water.

The waters concerned with the life and persistence of the algae, even of the benthos, are, relatively speaking, the surface waters, since algae seldom grow lower than at a depth of 100 meters and for the most part cease at 20-30 (or at times 40) meters. The normal decrease in temperature at such depths is slight even in temperate waters, although, at times, sufficient to account for special sporadic anomalous distribution. The range in temperature under which algae, in general, may carry on their full course of vegetative and growth activities is from  $-2^{\circ}\text{C}$ . up to the neighborhood of  $90^{\circ}\text{C}$ ., but that for marine algae is only from  $-2^{\circ}\text{C}$ . up to  $30^{\circ}\text{C}$ . (or possibly  $32^{\circ}\text{C}$ .), this being the extent of ranges for all surface waters of the ocean.

A comparison between charts in which the isotherms for surface temperature of the water of the oceans are laid off



shows a definite correspondence between certain of these lines and the boundaries of different marine floral regions as previously laid out and indicated in this paper.

From the point of view of the distribution of the marine benthos, so far as algae are concerned, it is found by practice to be satisfactory to divide the surface waters of the ocean into nine zones, as follows: Upper Boreal, Lower Boreal, North Temperate, North Subtropical, Tropical, South Subtropical, South Temperate, Lower Austral, and Upper Austral. The limiting isotherms of surface temperature chosen are those of the summer month or maxima, viz., the isotheres, which are those of February (or possibly March) for the southern hemisphere and those of August (or possibly September) for the northern hemisphere. These lines are laid down with approximate accuracy in the charts of the atlases of the different oceans published by the "Deutsche Seewarte" of Hamburg ('92, '96, '02). These isotherms are more accurate and explicit for the open ocean than for the neritic zone where the algal benthos occurs, but, with certain allowances, the zones as indicated are sufficiently accurate.

Each of the zones I have proposed covers 5°C. range of surface temperature with the exception of the Upper Boreal and the Upper Austral, each of which includes a range of 10°C. or slightly over. The zones, then, more or less arbitrarily adopted, are the Upper Boreal and Upper Austral, between the isotheres of 0°C. (or even -2°C.) to 10°C., Lower Boreal and Lower Austral between the isotheres of 10°C. and 15°C., North Temperate and South Temperate between the isotheres of 15°C. and 20°C., North Subtropical and South Subtropical between the isotheres of 20°C. and 25°C., and the Tropical between 25°C. and 30°C. (or above).

These 5°C. zones are thus laid out according to the 5° isotheres, because on inspection these isotheres approach most closely or touch the shores at the division points of floras and principal floral provinces. They have been determined empirically, and indicate, as it seems from experience in working with them, that they coincide with floral boundaries the oceans over more exactly than do any of the



winter isotherms or isocrymes, or any of those in the intermediate seasons.

For example the isothere of  $20^{\circ}\text{C}$ . passes somewhat south of Cape Cod to the eastern end of Long Island, but the shallow and more or less protected waters of Long Island Sound, Narragansett Bay, Buzzard's Bay and Vineyard Sound carry a higher temperature eastward even to the Cape Cod region. At exposed points, however, the somewhat colder waters of the ocean outside exist and exercise their influence at exposed points or in deeper waters.

Again at Cadiz, the isothere of  $20^{\circ}\text{C}$ . abruptly curves up to the coast. At Cape Inuboi, Japan, the isothere of  $25^{\circ}\text{C}$ . touches land and at the Strait of Sangar, that of  $20^{\circ}\text{C}$ . The Cape Region of South Africa is included between the isotheres of  $20^{\circ}\text{C}$ . and  $25^{\circ}\text{C}$ . Similar relations hold good on the coast of Ireland, for the  $15^{\circ}\text{C}$ . isothere comes in just north of Clare Island at about Annagh Head. On the south coast of Australia, the isothere of  $20^{\circ}\text{C}$ . touches the east coast just above Cape Howe and the south coast about Cape Arid, thus leaving the southeastern coast below  $20^{\circ}\text{C}$ . of average summer temperature and the southwestern coast above it. Although the western coast of North America has its temperature relations very much disturbed, as I shall indicate later, yet there is a fairly definite relationship to the isotheres of  $10^{\circ}\text{C}$ .,  $15^{\circ}\text{C}$ .,  $20^{\circ}\text{C}$ ., and  $25^{\circ}\text{C}$ . The arctic or boreal floristic region has a definite southern boundary in the  $10^{\circ}\text{C}$ . isothere and the subarctic in that of  $15^{\circ}\text{C}$ ., while those of the North Atlantic are bounded to the south by that of  $25^{\circ}\text{C}$ . The strictly tropical species are found almost entirely between the isotheres of  $25^{\circ}\text{C}$ . and  $30^{\circ}\text{C}$ . (or  $32^{\circ}\text{C}$ .). It is expected that a later paper will deal more definitely and in more detail with the reasons for selecting the isotheres as bounding lines for the temperature zones.

Two seeming disturbances of those zonal areas may be noted in passing; one is that the polar zones (Upper Boreal and Upper Austral) are for  $10^{\circ}\text{C}$ . interval rather than  $5^{\circ}\text{C}$ . This is in accordance with what is known of the distribution of the marine flora in the higher Arctic and the higher Ant-



arctic regions, where there seems to be no useful purpose served in segregation by assuming two zones rather than one. The second disturbance of zonal areas is through the occurrence of local areas, of greater or less extent, of water of a higher or lower temperature than is normal for the general zone. Colder waters occurring among warmer waters are found along the west coasts of North and of South America, of northwestern and southwestern Africa, and of northeastern Africa. These are due to currents or to upwellings of cold water. Their existence is well substantiated but their cause is still a matter of discussion among oceanographers. When warm waters exist among colder waters, they occur as "spots" or small areas where the higher temperature is due to comparatively local factors apart from general oceanographic conditions. Such disturbances as upwellings and spots may bring about a puzzling discontinuity in the distribution, very puzzling, indeed, until the immediate cause is discovered.

Another matter causing seeming disturbance of the limits of temperature zones proposed is the seasonal variation of the temperature of the surface waters. This is variable, but in general may be considered to hold true as follows: The seasonal surface temperature variation as plotted for 2° squares is least in the Upper Boreal, Upper Austral and Tropical zones, where it is not over 5°C. in range; is greatest in the Temperate zones where it averages nearly 15°C. and may be as great as 27 or 28°C., and is medium in the Subtropical zones and in the Lower Boreal and Lower Austral zones where it approximates 10°C.

These, then, are the principal features of temperature distribution with which we may be concerned.

In connection with the empirical establishing of the temperature zones previously outlined, I have attempted to arrange each and every species of marine algal benthos thus far described in the zone or zones to which it has been accredited. The work is not as yet by any means completed, but a general view has been obtained for the *Rhodophyceae*, *Phaeophyceae*, *Chlorophyceae*, and *Myxophyceae*, and the greater part of the



*Rhodophyceae* have been worked out in fair detail, although no percentages of absolute accuracy can be given at present. The general results are as follows:

(1) The greater part of the species are known from one zone of temperature.

(2) A considerable number of species are known from two zones of temperature.

(3) A comparatively small number are credited to three zones of temperature.

(4) Species credited as occurring in four or five zones of unlike temperature are extremely few and almost always doubtfully so accredited.

(5) There is a change of facies of the flora in each successive zone, i.e., with every increase or decrease of  $5^{\circ}\text{C}.$ , excepting in the cases of the Upper Boreal and the Upper Austral.

This means that most species are, so far as known, confined to zones of amplitude of  $5^{\circ}\text{C}.$  of summer temperature, that certain species extend over zones representing  $10^{\circ}\text{C}.$  amplitude, while a few may extend over zones representing  $15^{\circ}\text{C}.$  amplitude of summer temperature, and extremely few definitely known in zones covering over  $20^{\circ}\text{C}.$  amplitude of summer temperature.

To mention the results of the preliminary survey of the marine *Rhodophyceae* so far listed and checked, may give approximate conditions which also seem to exist in other groups. The species and varieties thus far accredited to this group number about 3,350. Of these the northern hemisphere has about 34 per cent in its extratropical waters, the southern hemisphere approximately 44 per cent, while the tropical waters have approximately 22 per cent. Of the entire number, approximately 71 per cent are confined to one zone of temperature; about 21 per cent extend over two successive zones of different temperature; about 6 per cent are accredited to three successive zones of different temperature; while between 1 and 2 per cent are accredited, but with more or less, generally very considerable, doubt, to four, or even to five, successive zones of different temperature.



Commenting on the above, it may be surmised that the percentage in one zone is high on account of many new or little known species which have been collected only once, while the percentage of species occurring in two successive zones of different temperature is low because of our incomplete knowledge. Concerning the species credited to three zones, the percentage is small but perhaps not much lower than will be found on final careful revision. Here seasonal occurrence and "spot" distribution will undoubtedly be found to be concerned in the overlapping, as it will be also in the case of overlapping in two zones. Concerning the occurrence in four or five successive zones of different temperatures the percentage although small will, with very little doubt, be decidedly decreased or even entirely erased when the doubtful cases are investigated and cleared up. There may be a fraction of one per cent still left, however, and if there is, I doubt not that some fairly simple physiological explanation of their toleration of such an extreme range of temperature will be found. The disturbances in the uniformity of regular increase or decrease in the temperature of surface waters, as referred to latitude, have already been mentioned as due to cold upwellings and spot variation according to local physical peculiarities. These disturb, of course, the zonal distribution. Where such intrusive areas of colder or warmer water are extensive, the distribution in those areas must be considered in connection with the nearest zone of similar temperature. Spot distribution also, may be so referred but only in general considerations of distribution. Otherwise it must be considered specially.

The disturbance of regular zonal distribution which must have special consideration from the zonal point of view is that which arises from seasonal variation in the surface temperature accompanied by seasonal occurrence of a certain element of the flora in some district or province of a region of the particular zone.

Seasonable amplitude varying on an average from about 5°C. to 15°C. in extent, as I have mentioned before, is found in the various temperature zones. Seasonal duration, or, at



least increased seasonal vigor in certain elements of the flora is found in all zones, a phenomenon of mixed dependence upon light and temperature. It is most marked in the Temperate zones but is to be found in the Subtropical, Lower Boreal and Lower Austral zones as well. In the Upper Boreal and Upper Austral zones its appearance is perhaps more associated with varying intensity of light than with temperature, and it is least pronounced in the Tropical zone, where it seems to be wholly dependent upon light variation.

It is certain that many boreal summer species appear as winter or early spring species in the Temperate zone and likewise certain temperate species appear during the colder season in the Subtropical zone. There is some, but apparently not very much, overlapping between the upper portions of the Subtropical zones and the Tropical zone. From the very incomplete studies thus far made, it seems that most species range through from 5 to 10°C. of temperature, that each zone has its own characteristic species and that extensions up to 15°C. for active growth and reproduction are few, if at all existent. More careful examination, however, is necessary to satisfactorily demonstrate this last point.

While the limits of the temperature zones have been founded on the isotheres or lines of average daily summer temperature, seasonal phenomena cause us to consider also the isocrymes or lines of average daily winter temperature, especially as to overlapping or transitions between the zones. The isocrymes are of especial importance in those portions of certain zones where, especially on account of strong currents, the seasonal variation is extreme, e.g., on the eastern coast of North America and on the eastern coast of Asia. In such regions there may be expected extreme expression of seasonal change of flora.

The disturbances of distribution due to upwellings cause confusion in the tabulated results unless they are to be definitely accounted for. This confusion is greatest at present in connection with the species of the central coast of California. Spot distributions also cause the species concerned to be tabulated in more than one, or, if combined with seasonal disturb-



ance, over three zones. Spot distributions are less easy to detect than other anomalous distributions but enough are sufficiently known to make apparent their influence and importance in any scheme of representation of geographical distribution.

While the distribution of any particular species of plant depends upon a complex of conditions controlling continued existence, both vegetative and reproductive, certain more general factors may be distinguished as prevailing over larger areas, while others, less general, may account for local and usually discontinuous distribution within particular provinces and districts, and as components of various formations, bathymetric belts, and associations.

Temperature has come to be considered as one of the most important of the conditions controlling, or governing, the distribution of plants and animals (cf., e.g., Merriam, '94, '98, etc.; Livingston and Johnson, '13; and others). Any biologic factor has, of necessity, two variables (cf. Livingston and Johnson, '13, p. 351), intensity and duration, and these two variables present considerable range, especially in the case of land plants. For marine plants, particularly for those species constantly submerged, the amplitude of these variables is less than for the land plants. The surface waters of the ocean, while influenced by the temperature of the air, change slowly and only within certain limits. More considerable is the variation through the influence of varying, especially seasonal, currents or upwellings. Yet on the whole the temperature variables are seemingly, at least, much less in amplitude than are those of the land. For those plants exposed during tidal changes the temperature variables may be considerable in amplitude. Yet such exposures are only occasional and of short duration, except, perhaps, for the plants of the uppermost tide limits. One matter of importance as to all factors in plants submerged entirely or for the greater portion of the time, is the uniformity of exposure to the same conditions. While the land plant may have its roots buried in the soil of one temperature and its aerial organs exposed to a considerably different temperature, the entire



surface of the submerged plant is exposed to one and the same temperature. The problem, therefore, of temperature as a physiological factor in controlling the distribution of algae, in general, and of marine algae in particular, is, as compared with that of land plants or of land animals, comparatively simple.

Any attempt to unravel the physiological basis for the control of distribution must be, at this point of the progress of the work, lacking sufficient data for conviction. The statements presented merely represent approximate optimal conditions for the duration, succession, and, therefore, continued persistence of the species of the various life zones. It seems certain that the coefficients for continued existence vary among the different species, but are restricted in the case of each species to about  $10^{\circ}\text{C.}$  in amplitude. There must be for each species a certain minimum and a maximum of optimal temperature for continued life and reproduction. It is possible that certain species may continue to exist outside these, especially if they possess powers of vegetative reproduction.

Thus far, it has been in mind to attempt to determine coefficients of efficiency as Livingston and Johnson have suggested in the case of climatic factors controlling the distribution of land plants, but no real beginning has, as yet, been made. The interval of  $10^{\circ}\text{C.}$  certainly suggests the working of the van't Hoff-Arrhenius principle as applied to vital phenomena. Taking the variation of  $10^{\circ}\text{C.}$  as the controlling interval of temperature and regarding it as an index to the summation of temperature, it may be possible in a later paper to definitely estimate the coefficients of temperature-efficiency in a fashion similar to that already suggested by Livingston and Johnson ('13) for land plants.

If the rate of the vital activities are, in general, doubled or nearly so with each increase of  $10^{\circ}\text{C.}$ , then, judging from the results of the *Rhodophyceae*, thus far tabulated, it would seem that marine algae cannot endure an acceleration greater than 2, that each species has its own definite initial temperature for efficient vegetative and reproductive activity and that such initial efficient activity may be accelerated up to the



doubling point, but not beyond it. In this way may be explained the fact that from 0°C. (or —2°C.) to 10°C. of mean summer temperature marks the limits of the Upper Boreal and Upper Austral zones. The marine algae inhabiting these zones are subjected to a range of not over 10°C. at any, or all, times. The species of the Temperate zones, enduring a mean summer temperature of 10°C. to 15°C. have a range of 10 to 12°C., probably not over, at any or all times. Similarly those of the Subtropical and Tropical zones endure a range of not over 10°C. If, therefore, tentatively, a temperature efficiency coefficient be estimated according to the formula of Livingston and Johnson ('13, p. 365) but modified by leaving out the assumption of an initial temperature higher than 0°C., viz.,  $u = 2 \frac{t}{10}$ , the efficiency coefficient in the case of the Upper Boreal and the Upper Austral zones (0 to 10°C.) will be unity to 2, in case of the Lower Boreal and also the Lower Austral (10 to 15°C.), will be 2 to 3, for the Temperate zones (15 to 20°C.), the coefficients will be 3 to 4; for the Subtropical zones (20 to 25°C.), the coefficients will be 4 to 5, and for the Tropical zones (25 to 30°C.), the coefficients will be 5 to 6. Incidentally to carry out this idea of temperature efficiency coefficients, it may be said that the application to the case of thermal algae, where I find the 10°C. amplitude rule also to apply, would carry the coefficient index up as high as 16, i.e., in the case of those species enduring highest temperatures (80°C.), and even to 18 in the case of thermal bacteria (90°C.).

In conclusion, I may say that while much detail remains to be considered and brought into order before the final data and conclusions may be published, I have reason to believe that the statements and conclusions I have either made or brought forward in this preliminary account, will probably not need be changed, at least to any great extent.

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