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STUDIES OF GROWTH IN THE NORTH-EASTERN AREA.

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FOR nearly forty years the International Council has been engaged on the investigation of the conditions of life of those animal populations which, by their annual renewal and growth, support the great sea fisheries of northern Europe. To a very great extent this study in marine biology has been built up on the ideas and methods which the science of population has created for the study of human communities. In the biological study of the effects of human activity on the sea, however, the problems assumed another shape when it became evident that in all those activities which we style hunting and fishing events will not depend merely on the changes, fluctuations or reductions in the number of hunters or fishermen, but also on the magnitude of the stock of living organisms on which the activity is based. We distinguish, therefore, between two different populations. On the one hand there is the human population of hunters, or fishermen, on the other the stock or "populations" of living organisms, and in the simultaneous study of both of these populations, their growth or decline, lies the most important task of the biological science of population, and its application to all problems of marine biology.

The approach to these studies was made by means of the hypothesis which seemed so daring forty years ago, but which, in an increasing degree, has proved so fertile, namely, that the catches of the fishermen can be regarded as representative, relative measures of the then existing stock of those species of fish of which the catches are composed. As a method the application of this hypothesis obtained a considerably enhanced importance, since means were successfully found for determining ages by the study of growth-zones in different organs of the fish, bones, scales or otoliths. By this means the catches of the fishermen could not only be made to yield representative information concerning fluctuations or changes in the size of the fish populations but it was also possible by analysing the age and growth of the fish in the catches to study the movement within the population from year to year. The stock of fish was thus analysed for its composition of year-classes, and in the study of fluctuations in this composition from the one year to the other there arose the conception of changes, governed by law, of such a nature as to make definite prognoses possible, and which were confirmed by the experiences of succeeding years. Hence this biological method seems to have received its experimental verification.

A desire has now arisen for discussion of the ideas and experience which must be said to form the foundation of this doctrine of population, namely, our methods of studying growth and growth-rate. This desire I do not regard as indicative of doubt or lack of confidence in the results hitherto achieved. Rather it arises from uncertainty over the question of whether we can probe further into the causative connexion between growth and *milieu*, and set for ourselves new and far-reaching aims. If this opinion of mine is correct our task at this meeting will be, before all, that of studying the question whether there is any vagueness of opinion as to the validity of our theoretical basis or the application of our methods. For this reason it may, perhaps, be expedient to glance briefly at our terminology for the ideas of growth and growth-rate and at the mathematical functions which have been employed to describe or characterize these ideas. In the hope of contributing to an understanding of this Dr. Per Ottestad has drawn up a very brief summary of the terms employed in the literature. This summary is printed in connexion with my presentation of the problems which have been predominant in growth investigations, especially those in the North-Eastern Area.

In various publications I have emphasized that the modern doctrine of population owes its origin to the introduction, by Robert Malthus, of the conception of time, the movement in the study of populations, just as Galileo did in mechanics. But in the formula for the exponential growth $y = m \cdot a^t$ the time unit taken by Malthus was not a quantity chosen at random. It was founded on the biological conception of "the period of duplication" and the formula, therefore, applied to organisms which according to experiment doubled their populations at regular intervals. This, in the case of the North American pioneers, was estimated at 25 years, and in Pasteur's experimental studies of the multiplication of yeast-cells at periods of 15 minutes. This gives rise to the question of whether the formula constructed by Malthus can be applied to those types of organisms, the reproductive mechanism of which is distinguished by a progeny of thousands or millions of germs in each generation.

There is another biological experience associated with Malthus's formula. It assumes that the surrounding world, the *milieu*, contains unlimited possibilities for growth throughout a number of generations. In other words, that "checks", or as Malthus puts it, "restrictive forces", do not occur in the environment. The new experimental biochemistry has succeeded in showing as correct that where a constant *milieu* of this kind is successfully maintained there also a population of yeast-cells or bacteria can grow according to the exponential law of growth. Biochemistry has also shown that the constants of the *milieu* do not only presuppose a surplus of "means of subsistence", but also that the effect of the organisms themselves on the *milieu* through their excretion of the products of metabolism must be removed if the growth-rate is not to stop or be retarded. Actually, there is yet a third assumption which is of an entirely biological nature, and this must not be overlooked if the problems of growth are to be understood. This is the growth of the individuals within the population. The individuals which make up the populations do not grow according to the exponential law. That their reproductive mechanism leads to a definite "duplicating period" is due to the fact that their individual growth follows an entirely different course and, practically speaking, reaches certain "prescribed bounds" in a limited growth. The growth of the population throughout a number of generations, therefore, takes place, in reality, in the form of cycles, periodic cyclic movements, along the growth curve.

From the very beginning it has been common knowledge in natural history that in the majority of cases in the growth of both individuals and populations, a distinct difference in growth-rate can be observed in the individual periods of the growth. Raymond Pearl has attempted to describe this experience in the following words:—

"Growth occurs in cycles. Within one and the same cycle, and in a spatially limited area or universe, growth in the first half of the cycle starts slowly but the absolute increment per unit of time becomes steadily smaller until the end of the cycle."

Graphically, it has been possible to illustrate this growth by curves which show, *inter se*, considerable differences but which, however, present such a characteristic relationship that they can be described under the common designation of S-shaped or sigmoid curves. In the sigmoid growth there is a continually fluctuating growth-rate, first increasing and then decreasing. Many biologists have been occupied with the idea that the increasing numbers of cells or individuals first seem to stimulate each other's growth, and then to retard it. Efforts have been made to find an analogy for this process in the chemical reversible reactions which are symbolized by the sign $\rightleftharpoons$ in which, simultaneously, but with fluctuating power or rapidity, certain chemical combinations are formed and again decomposed. The new experience of the influence of the organisms on the composition of the *milieu* has seemed to strengthen this point of view, and in that interesting book "Principles of Biochemistry" T. B. Robertson has endeavoured to show, on the assumption that the phenomena of growth can be regarded as autocatalytic reactions, that this theory results in an illustration of the events by a sigmoid curve. In this connexion Robertson, Pearl and Reed have attempted to develop a mathematical function for sigmoid growth, as Dr. Ottestad has explained more fully in his summary.

According to Ottestad these formulae will have to be regarded as an attempt to adapt a mathematical function to certain phenomena the existence of which has been revealed through experience. And the functions have then been applied to an "extrapolation" beyond experience, e. g., to predictions of future events in the growth of the populations. For this purpose a number of constants are introduced into the functions, and by this means it has become possible to produce an approximate similarity between the constructed constants and those which are found purely empirically. I do not, by any means, wish to dispute or reduce the value of these efforts. They are useful so long as it is borne in mind that they can only be regarded as heuristic, hypothetical methods, and that they cannot postulate anything concerning events abstract from experience.

It is of fundamental or principal importance to biologists to remember that the problems of growth do not lend themselves to representation by any kind of mathematical functions, which, through their constants, should be capable of reflecting the sum total of the factors which control the course of the growth. This would be to arrogate a "complete understanding" of the phenomena of life, or to construct the origin of the organisms. The task must therefore be to present a descriptive illustration of the course of the events, and it is this which Ottestad has endeavoured to do by taking as a basis the ordinary statistical rules for such graphical illustrations of the statistical experiences and their analysis.

The question then arises: For what purpose can this statistical method be applied in biological research? It is my belief that this question can best be answered if it is viewed in the light of von Liebig's famous Law of the Minimum, the law of the master reaction. The value of this law to the study and understanding of the problems of growth lies in the fact that no attempt is made to disvover all the factors which play a part in the life of the individuals, but that, on the contrary, an effort is made to discover one definite factor or group of factors decisive, in the particular case, for changes in the growth of an individual or population.

Liebig's law, as is well known, was developed for the study and practice of agriculture, and it rested, in reality, on a general conviction that there is an accord between the growth of the organisms and the surrounding *milieu.* Where science can discover and follow the master reaction which, in the particular case, elicits a change in the growth, there it can understand the course of the events. The first step must therefore be, by analysis of the many-sided reality, tentatively to make a selection of the factors which, hypothetically, can be accepted as controlling the events. It is clear that the study of the plants growing on the land has this advantage that these organisms can be observed throughout their lives and that, therefore, the correlation of growth and a particular *milieu* can be constantly controlled. The organisms in the sea, on the other hand, are continually in motion during their lives and can thus be exposed to a number of different environments. This fluctuating correlation of the organisms and their environments can only with difficulty, and in exceptional cases, be controlled in free nature, while experiments with animals in captivity cannot always make up for observation in natural surroundings. It is, therefore, of prime importance to glance briefly at the experiences gained from the study of the growth of land plants, assuming while we do so that growth phenomena are of such general and fundamental significance that they must everywhere reveal important common features from which conclusions can be drawn for the understanding of marine organisms also. We will attempt such comparisons by considering the growth of the coniferous trees, the spruce and pine (*Picea excelsa* and *Pinus sylvestris).*

Every forester is convinced that he can gain from the annual rings shown in a tree stump a great deal of information about the condition and growth of the tree, — its life-history. Thus, he can discover that particular historical events, such as felling for the purpose of thinning out the trees in a "densely populated" wood, or ditching in marshy ground where the trees were stagnating, have caused radical changes in the growth of the trees. This ancient lore was greatly enriched, as we well know, by the new and exhaustive investigations carried out in forestry during the last generation. Most famous are the American studies of the gigantic trees known as *Sequoia gigantea* in California, and the whole of the historical research which used the ring system of the trunks for the registration or dating of historical events.

For us, however, the following results of the Swedish investigations into the growth, at various seasons of the year, of spruce and pine trees are of most interest. Romell, the Swedish forester, found that the top shoot (la pousse terminale intacte d'un nombre de jeunes arbres marqués) showed a brief seasonal growth, commencing as a rule in May and ending in the course of 2—3 months. During this period the top shoot grows in a manner which can be illustrated by a characteristic sigmoid curve. The course of this growth, as regards time, is remarkably akin to that found by fishery research from a study of the scales of herring and species of cod in Norwegian coastal waters. The growth shows a close correlation with the temperature. It begins earlier in southern than in northern habitats of the pine, and in the case of this species it was possible to establish a progressive movement from south to north in the Swedish districts in which it was studied. The growth of the spruce tree, on the other hand, proved to be so dependent on local surroundings that the influence of the climate in the direction of north to south could not be established.

In another series of investigations Langlet has studied the correlation of growth with the chemical changes. He found, as a universal rule, that the water content falls in the autumn or, in other words, that the dry substance then increases. At the same time the tree's store of starch declines, also its acidity and often the volume of chlorophyll, while sugar, fat substances, reserve cellulose, tannins and catalase increase. These changes, which seem to occur simultaneously and in conjunction with each other, are signs of the passing of the plants into the winter resting stage, that is to say, an onset of hardening in the tree.

When these events were studied by comparing the trees in different latitudes from north to south in Sweden it proved that in the northern areas the trees held more dry substances — sugar — substances which are extracted by petroleum ether and catalase. The dry substance thus discloses the physiological variability of the plants, and it was possible in the course of these investigations to reveal a continuous variation in the pine in respect of these physiological characters. In tests involving transplantation of the pine from northern to southern areas it was possible to establish, in some cases, that the content of dry substance was hereditary.

We can hardly fail to notice the harmony between the experiences from forestry and the investigations and problems which in recent years have preoccupied international co-operation for the study of the sea. And this comparison with forestry has had that significance for marine research that our belief in the influence of the environment on growth phenomena is strengthened by experiences which have not encountered the same difficulties as those which arise in connexion with the study of organisms in the sea. In all studies of the growth of fish the greatest difficulty is perhaps that which is to be found in the fact that, during their migrations, the fish change their environment and we are unable to follow their movements closely. Nor, in marine biology, are we able experimentally to change the environment of the animals as forestry can do in the case of trees, which can be transplanted from one habitat to another. In the papers by Einar Lea and Per Ottestad which follow this paper of mine a number of illuminating examples will be found of the many problems which have confronted the study of marine growth, and which have undoubtedly contributed so much towards a widespread feeling that this branch of study is beset with overwhelming difficulties.

It is understandable, therefore, that the history of the studies of growth in reality denotes a series of attempts to overcome these difficulties, and that these attempts have, in actual fact, consciously or unconsciously, been constrained to pursue the method we have referred to, of making a selection from among the many events in nature in order to arrive at a simplification of the problems, whereby, in given cases, it must be assumed that large groups of factors are of no importance, while an individual factor can be proved to control definite changes in growth from locality to locality.

If we compare, from these points of view, the various geographical areas within the waters in which international co-operation is effected we shall observe that, *inter se*, they are separated from each other in such a manner that both natural conditions, and fisheries from area to area, exert a different influence on the growth phenomena. In individual areas, such as the southern part of the North Sea, the fishery — the catch — plays a much greater part than in any of the other areas. In the northernmost areas, and especially in the North-Eastern Area, the growth of the fish, at least hitherto, has been comparatively independent of human intervention in nature and has been determined by natural conditions in the *milieu*.

The consciousness that human activity in the North-Eastern Area must be considered as a restrictive factor of the second order for the fish, in any case as regards the growth of important species, had its origin in the discovery that the fluctuations in the age composition of the Norwegian herring and cod populations, from one year to another, far surpassed, in quantitative respects, the effect which fishing could be proved to exert. The growth phenomena are thus, as a matter of course, alternations between the organism and the external *milieu*, but the difficulty of proving this lies, as pointed out, in the movements of the organisms, the fish, across great areas of sea, within which variations in important conditions of life occur, such as temperature, salinity, and abundance of animals on which the fish subsist. Fishery research has, therefore, been constrained to enlist all available means of elucidating the life history of the fish in order to arrive, in each case, at the comparison between the biological phenomena and the particular *milieu*. The following brief references to the literature are given to illustrate how this has been done.

1. In the two first years of its life the **herring** is assumed to have a local habitat, and as there are young herring along the whole of the Norwegian coast it has been possible to compare the growth of these young herring in the various parts of the coastal waters. Lea has proved that the growth of the herring in the coastal waters of southern Norway takes place during the period April to September, while it stagnates between October and March. The optimum growth-rate occurs in May—June. Ottestad has compared the growth of herrings in their second summer from the south-west with that of the same group from north Norway and found a marked correlation with the sea surface temperature of these areas. In the southern area he found the same results as those of Lea. In the northern area the growth seems to cease as early as the latter half of August. These results remind us very strongly of the Swedish investigations of the top growth of young fir-trees in the Swedish forests at different latitudes. The growth must be considered as a series of growth-cycles of different duration according to the factors of past and present environments, varying therefore in the species, populations and individuals.

2. Lea has made the interesting observation that the scales of the young herring from north Norway have rings which are sharply defined, whilst herring from the southern part of the west coast have scales with more vaguely defined rings, and he has termed these two different scale-types "northern" and "southern". Runnstrøm has carefully studied a large material to test this statement and "agrees with Lea as to the correctness of his view" and he claims that it is therefore possible, by the study of the scales of older herring, to discover their growth-history in relation to the different environments which the species have visited in past years. By this means it was hoped to make a rational analysis and discover the connexion conformable to law between growth-rate and particular factors in the surrounding world. We are indebted to Lea, Ottestad and Runnstrøm for their interesting contributions to the solution of the difficult and complicated problem of whether the varying growth which is noticeable on the coast of Norway is due to gradual changes in natural conditions, particularly temperature; or if it is rooted in more permanent types of growth which are comparable with the conceptions of hereditary races which have played such a great part, especially in the studies of the herring tribes. It is agreed that the spawning shoals are composed of growth-types from the different areas of the coastal waters. Thus, these growth-types do not live separately from each other, at any rate not all the time, as they are found to be mingled together when they are on the spawning grounds. Another feature common to all growth-types in the Norwegian coastal waters is that there is also a perfectly parallel fluctuation in the year-classes. The particularly abundant 1904 year-class thus greatly dominated the whole of the Norwegian herring population.

3. On the other hand, the exhaustive analysis of herring samples collected from many different parts of the Norwegian Sea indicates a great variation in conditions of life, which expresses itself in a corresponding difference in growth. Thus the fjords, the coastal waters proper, the open (oceanic) sea, the winter's spawning grounds, are all different, and they constitute, therefore, a series of environments which denote a great influence on the growth of the organisms. In the study of the characteristic difference of the winter rings in the different areas, and by the measurement of the breadth of the growth-zones on the herring scales attempts have been made to reconstruct the connexion between the history of the migrations of the herring and that of their growth.

Of the highest interest are the essays made by Lea to prove the migration of the coast herring to "oceanic" stages at various ages, some at the age of 1½ to 2½ years, others of 4½ or 5½, all according to the size attained at these ages. In the investigations carried out by Lea and Runnstrøm it has also been possible to extend this analysis to the spawning shoals. A peculiar "propagative" growth has been revealed and this has enabled them to establish that the spawning or "migration to the spawning shoals" begins at different ages, in individual cases at 3 or 4 years, in others at 5 to 6 and even up to 8 years. In these investigations we have a very much more varied or complicated picture of the events in the life history of the herring and their effects on its growth history than the first investigations in the North-Eastern Area disclosed. But precisely this complication must be said to strengthen the more general conviction which, from the outset, was the guiding factor in the initiation of this line of study, namely, the belief in the indivisible connexion between growth and *milieu*.

In many respects these new observations call to mind that example most characteristic among all experiences of the revolutionary effect of a change of *milieu* on the growth, namely, the passage of the salmon from the river stages to the oceanic mode of life, or to that of the great lakes. These enormous changes in growth fully remind us of the pictures of growth which are revealed in the conifers when marshland is drained or a densely wooded area is thinned out by scientific forestry.

4. The desire to make such an analysis, previously undreamt of, of the changes in growth has, no doubt, instituted the researches undertaken in recent years with a view to a more critical valuation of the hypothesis which the pioneers of these growth studies assumed to be more or less a matter of course, namely, that there was a parallelism between the growth-zones of the herring scales and the growth of the herring itself. It is of great importance that this original assumption has now been subjected to such a searching examination as that of the two papers of Lea and Ottestad which follow this statement of mine. Even if the comparison is susceptible of correction, the points of view advanced in these papers will undoubtedly throw light on the remarkable accord or correlation, which can here be proved to exist, of the growth of the entire organism with that of the individual organs.

5. The fact that we have been able to carry our search for these analytical problems so deeply in the study of the growth of the herring populations in the Norwegian Sea is no doubt due to the circumstance that we are here confronted with organisms the growth of which, wholly or partly, is controlled mainly by natural conditions alone, while the influence of man must be assumed to be entirely negligible. The interesting question, however, has been raised as to whether fluctuations in the density of population, which are not due to human intervention but to changes in the *milieu* during the actual spawning period, and which find expression in the varying number of individuals within the year-classes, can be proved to exert any influence on the growth of the herring. It is held that this question can be answered by statistical proof that the richest and poorest year-classes have both shown the same growth in one and the same sphere of the coastal waters, and that both of them acquire another growth-type, different from the first, if they stay in another area. It is of the greatest value that this question has been raised for further investigation in the future. On a more thorough examination of the history of migration of the single individuals from one *milieu* to another the problem will perhaps prove to be even more complicated than originally appeared to be the case. But it is to be hoped that the greatly improved methods which have now been adopted will render it possible to answer the highly important question, can even the most abundant year-class of herring find such rich sources of nourishment in the North-Eastern

Area that its growth history will show no sign of "the restrictive forces of the environment", to use the expression created by Malthus?

6. Even if it should be held that growth of the herring population in the North-Eastern Area will prove to some extent to be dependent on the fluctuations in density of population which result from the varying number of individuals in the year-classes, there is undoubtedly unanimity of opinion that the catches of the fishermen do not cause any change which can be presumed to exert any influence on the growth of the herring. The same conviction was also held at the time these studies of population were begun in the other great fishery research in the North-Eastern Area, namely, that devoted to the investigation of the population of **cod** or "**skrei**". Everyone who can remember making actual observations 30 or 40 years ago on fish of this species at a length of 1½—2 metres, and who has found reason for fixing the age of these fish at 20—30 years, will have retained the idea that the cod fishery which had been carried on for centuries had not, even up to that date, changed that feature of the cod tribe which has often been called "accumulated", that is to say, a stock comparatively untouched by human fishing.

As is generally known, conditions in regard to fishing in the North-Eastern Area since that time have undergone enormous changes. The intensity of the fisheries has not merely doubled but has, in all probability, been multiplied many times. Under these circumstances it is naturally of the very greatest significance to Norwegian fishery research, and not less to international co-operation, to follow the growth phenomena of the Norwegian stock of cod, both as regards the method by which the average size of the spawning fish is investigated and the growth of the younger year-classes.

During the earliest investigations in the Norwegian Sea, in 1900 and the years immediately succeeding, it was discovered that the small fry which spring from the spawning of the cod on the coastal banks are carried and scattered by the currents over the whole great Barents Sea area. At that time there was only a coastal fishery for spawning cod, principally in the Lofoten Islands, and for the younger year-classes off the most northerly coast of Norway, namely, Finmarken. Enormous quantities of quite young stages were therefore hidden away and withdrawn from human persecution. This picture of the life history of the cod has changed very greatly during the past 10 or 15 years as a result of the operations of fleets of modern trawlers off the coast of north Norway, on the banks outside the Lofoten and Vesterålen, and the Murman coast and, finally, in the vicinity of Bear Island. I am indebted to Dr. Lundbeck for the best information I have regarding these new fishing grounds, which shows that the masses of spawning cod are now fished on the banks off the north-west coast of Norway, and that precisely those banks on which the youngest year-classes of cod grow up are those most intensively fished. Captain Thor Iversen has proved by means of a fine-meshed trawl that the number of cod in the catches on the banks south of Bear Island may consist of no less than 90 % of fish from one to two years old, which are thrown overboard by the trawlers as valueless. Experiences such as this have contributed greatly to an increased interest in the study of the growth history of the cod. Moreover, they have supported the efforts made for many years by the International Council to arrive at an international fishery convention, which was finally reached in March 1937 and which provides for a minimum mesh of 10·5 cm. for trawling in these northern waters.

From the somewhat incomplete statistics of the fishery in these waters it would appear that the draft upon the stock of cod has increased by several times its size in recent years. I consider, therefore, that it is my duty to take this opportunity to draw the attention of the Council to the important problems which this matter of the age composition of the stock of fish and its fluctuation from year to year must present to all countries which now participate in this fishery. Of equal importance are the growth problems as a means of evaluating the recent changes in the stock resulting from the increased fishery. In this connexion great significance must be attached to the information given by Gunnar Rollefsen in his paper, accompanying this report, from which it will be seen that, in his opinion, there are distinct signs in recent years of a decline in the average age of the spawning "skrei" during the great Lofoten fishery. From Oscar Sund's interesting marking experiments with spawning fish caught off Lofoten on the banks worked by the trawlers it emerges that both fisheries, the trawl fishery off the coast, and the line fishery in the coastal waters proper, take toll of the same stock. The problem, therefore, is, in a high degree, one of international importance.

For the studies of growth, moreover, it is of great interest that the investigations of the younger year-classes of cod, which are caught north of the coasts of Finmark, reveal a distinctly increased growth, which may possibly be explained by the assumption that the fishery has now reached a magnitude at which it reduces the density of population of these fish. This, therefore, must also be taken as a warning that there is indeed a great need for thorough investigation of the biological conditions of life for the economically important stocks of fish.

From the North-Eastern Area there are earlier experiences of changes in a stock of fish — an untouched or accumulated stock — namely, **plaice.** Bjerkan has observed old individuals which could be proved to have reached the age of 31 years. Where a stock of this kind has been fished these old fish have inevitably disappeared and changes in growth conditions have become apparent in the younger year-classes. It is to be hoped that further information in regard to this may be forthcoming, as was the case in respect of the early years of trawling far to the east in the Barents Sea on the banks of Cape Kanin.

With these new events the North-Eastern Area is confronted by the same problems and its fisheries by the same troubles as those which for several decades have played such a great part in the fishing industry and in fishery research in the southern parts of the North Sea.

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