STATISTICAL ANALYSIS OF QUANTITATIVE COLLECTIONS AS A MEANS OF INTERPRETING LIFE HISTORIES*

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INTRODUCTION

There are relatively few species of animals whose entire life history is known. The developmental cycles of even some of the species most commonly used for study in zoölogical laboratories have been but imperfectly traced or have been unstudied. The concept of specific life histories has not been given serious consideration by the present generation of scientists. The closing decades of the nineteenth century witnessed a revival of interest in the process of cleavage and in the early stages of embryonic or larval development because of the dominating interest in the problems of cell lineage and of experimental embryology, but this interest rarely inspired an investigation of the complete life cycle. Exception may be raised to this generalization in the case of animals of distinct economic importance. The result is that we have fairly complete pictures of the successive seasonal changes of many of the economic insects and ticks and know with a fair degree of precision the cyclic periods in the life histories of parasitic worms and protozoa which are causal agents of disease in man and other animals, but beyond these fields of investigations there has been but little progress in the interpretation of individual life histories. In part, this static condition may be traced to an unwarranted assumption that closely related forms have identical life histories. A like assumption of essential similarity invalidated many of the early researches in other fields of biological inquiry. Many of the early investigations on physiology of the invertebrates, as well as those dealing with reactions, experimental embryology, and regeneration, gave erroneous results because of the erroneous assumption that members of a given genus or other large systematic unit have identical physiological responses. In the field of experimental zoölogy, this error has been recognized and only individuals of the same species or variety, and preferably members

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from the same sort of habitat, are used in experiments that are expected to yield specific results.

In the literature on life cycles the concept of specificity of development has not yet been widely accepted. Perhaps the morphological "type" concept which dominated the zoölogical thinking of a generation ago has lingered in the minds of zoölogists who have written on topics concerning individual development. To the person whose morphological thinking permits of a non-specific generalized concept of *"the* frog" or *"the* crayfish" the inadequacy of a generalized scheme of ontogeny may not be apparent, but to the person who has collected and studied animals in the field, such generalized type concepts have little meaning, for he observes differences in structure, in habits, in reactions, and in seasonal occurrence, all of which can be explained only by underlying physiological differences. These physiological differences in turn became reflected in specific differences in development, leading to specifically recognizable life cycles.

Methods of Interpretation

Two methods have been very generally relied upon for securing data upon the life history of animals. The more important and more trustworthy of these is that of direct field observation, following the animal in its natural habitat throughout all seasons of the year. By this method, growth, transformation from one stage to another, changes in habits and in habitat, are directly observed so that a specific calendar may be prepared to record the changes in form and activity of each species under observation.

The second method is that of experimental determination of the life cycles. By this method, the animal being studied is brought into the laboratory where observations may be more easily made. Under the experimental method great discrepancies are apt to intrude due to lack of complete duplication of the natural habitat. Even under the most carefully checked laboratory conditions, it is impossible to recreate natural conditions for any but a very few organisms. Checks on animals kept under the most carefully guarded conditions frequently yield evidences of significant departures from conditions shown by controls under natural surroundings. Observations based upon animals kept under experimental conditions are never acceptable unless in agreement with controls in the natural habitat. There are numerous investigations setting forth the results of experiments designed to show the influence of relative numbers of individuals reared in a given space upon the size of the individuals. The physiological significance of these experiments must not be overlooked by any student rearing organisms in cultures for studies on the life cycles.

A third method of securing data on certain aspects of specific life histories is through the analysis of quantitative seasonal collections. This avenue to an understanding of life cycles has been relatively little used, and its possibilities have never been exhausted. Investigations that have been completed and others still in progress in the Zoölogical Laboratory of the University of Illinois give ample evidence of the value of detailed studies of quantitative collections as a supplement to field observations. The value of periodic collections becomes especially evident in studying animals from habitats that are at inconvenient distances from the laboratory.

The only limitation to the applications of this method of investigation is that of relative abundance of the organism under investigation. The method has been applied to amphibians, reptiles, fishes, crustaceans, and molluscs, and has untried possibilities in practically all of the other invertebrate groups.

Seasonal growth rate, determination of actual or relative age, ratio of the sexes, correlation of sex and size, development of secondary sexual characters, reproductive habits, seasonal limitations to growth and reproduction, changes in body form, periodic changes in habitat, are but a few of the many topics which may be investigated upon preserved quantitative materials brought from the field into the laboratory for uninterrupted analysis. Naturally, this method of analysis has its greatest value when checked by extended field observation. In turn, both field study and analysis of quantitative data are profitably directed by the observations on animals kept under experimental conditions. Thus, the minute eggs of a snail belonging to the species *Goniobasis livescens* were first observed in laboratory aquaria (Jewell, 1931), and this observation led later to their detection in the native habitat after periodic collections had demonstrated the onset of the gravid conditions in the females brought directly from the stream. Similarly, in the viviparous snails the state of development of the females in quantitative samples gives a clue to the breeding season and provides information as to the season when young are born (Lederer in unpublished thesis).

In 1916, the writer utilized seasonal collections of Acanthocephala for the interpretation of life history data. For three species of the family Neoechinorhynchidae he showed marked specific differences in periods during which these parasites dwell in the intestine of their vertebrate hosts. Two species living in the same host species were found to have entirely different seasonal periods of infestation. Either periodic changes in food habits of the final host or essential development phases of the life cycle of the parasite in the invertebrate host might be responsible for such an instance of seasonal restrictions to the occurrence of the parasites within their normal host. In the same paper, the author called attention to the fact that another species of Acanthocephala *(Neoechinorhynchus emydis)* occurs in turtles throughout the year. Individuals of this species seem to have residence in the turtle for at least a year, hence the occurrence of young and old individuals at all seasons led to the conclusion that reinfestation is continuous, not cyclic. In the course of this study on life histories of parasitic animals by analysis of periodic collections, it was found that unselected data on negative records may lead to an erroneous interpretation of cyclic occurrence, for negative records frequently indicate the total absence of a parasite in a given region rather than reflect a seasonal absence from the host.

Particularly significant life history studies on marine organisms have been conducted by British investigators working at the Plymouth Laboratory. In many of the studies that have come from that laboratory, the statistical method of interpretation has played a most important part. The researches of J. H. Orton (1928) on the oyster and the heart shell (1926) are admirable examples of life history investigations as are also those of E. W. Sexton (1924) on Gammarus and of A. C. Stephen (1929) on Tellina from the same laboratory.

Observations and conclusions derived from recapture of marked individuals have played important rôles in the study of fishes, especially the salmon, and the same method is now being widely practiced with gratifying results in the cooperative study of banded birds.

In recent years, investigators in the United States Bureau of Fisheries have made marked progress in life history investigations through an analysis of periodic collections and a combination of this method with field observations and analysis of statistical data, but space forbids an enumeration of more than a few typical references. Rich (1925) has given a summary of the studies on age and maturity of the chinook salmon. Van Oosten (1929) has completed an intensive study of the life history of the lake herring. Schroeder (1930) has assembled a great amount of information on the life history of the cod.

Other investigators working for the Bureau of Fisheries have brought forth significant results in the study of Mollusca, determining age, rate of growth, relative abundance, and reproductive habits. Characteristic of these recent contributions may be mentioned the work of Gutsell (1931) on the bay scallop and that of Weymouth and McMillin (1931) on the razor clam. A new activity in the investigation of fresh-water mussels is reflected in publications of Isely (1914) and of Chamberlain (1931) on the growth of mussels.

In many of the older biometric studies, populations of a given species of animal were measured and a normal distribution or growth curve was obtained. Occasionally, populations gave a bimodal or polymodal curve because of extreme differences in size of the sexes or segregation of age groups. In the early investigations most of such statistical analysis was made upon assemblages of individuals without regard to date of collections. The chief contribution of such a study, in fact the only end sought by many students, was the establishing of size range of the species. When seasonal collections are considered individually, they frequently yield much biological information of value. Thus, in the fishes, relative age and sex have both been found significant factors for consideration in further resolving a simple curve showing distribution in a population according to size (Van Cleave and Markus, 1929, figs. 1-3).

A series of distribution curves based upon collections made at stated intervals gives a graphic picture of rate of growth in the entire population through the progressive shifting of the modes of the population. Thus in a series of twelve monthly collections of a species of fingernail shells belonging to the genus Sphaerium, Foster in an unpublished thesis has been able to give a very satisfying picture of rate of growth, to determine the length of life of the individuals of this species, and to ascertain precisely the dates when young are being produced.

Similarly, in some species the occurrence of gravid females at all seasons of the year gives rise to the impression that the species continues to breed uniformly throughout the year. Thus, in the isopod *Mancasellus macrourus,* Markus (1930:232) found gravid females throughout the year, but a statistical analysis of his data (Markus 1930, fig. 4) revealed the fact that less than 5 per cent of mature females were carrying eggs or young through the fall and winter (September to February) while more than 50 per cent of the females taken in April carried either eggs or young. He further found a significate correlation (p. 231) between the season of the year and the number of young produced by each female.

F. N. Blanchard (1928 and 1931) has skillfully applied the statistical method in an analysis of many aspects of the life cycle of salamanders. Other similar, isolated instances of application of this method might be cited, but it is the purpose of this paper to call attention to new lines of investigation by this method rather than review the entire literature.

Morphological characters that have been considered as specific and have been used for the separation of species are interpreted in new light when studied in quantitative collections. Thus in the isopods, the number of antennal segments has been considered as a specific character (Richardson 1905:413) although Markus (1930:224) by following the growth of individuals in quantitative samples through the year has been able to correlate number of antennal segments with age through relation of segment number to the number of ecdyses.

Investigations are under way on the life cycles of a number of species of invertebrates, the extent of whose life spans has never before been determined. For several of these species it has been found that individuals of the maximum size group are wholly lacking in the quantitative samples taken during certain periods of the year. This fact indicates that these individuals have a life span of less than a year. If it took more than a year for the individuals to reach maximum size there would always be individuals of the maximum size group present in every population. In case the breeding season is restricted to a definite month, age groups when plotted would tend to fall into well defined modes, one mode for each year group.

In some groups of animals which have a sharply limited growing season and a breeding season of considerable length, size groups even if they are composed of members of the same sex do not always represent a single age group. Thus in one of the minnows it was found (Van Cleave and Markus, 1929) that some individuals hatched late in one breeding season are no larger than those hatched early in the following year, after both groups have passed through a single growing season. Many of the fresh-water fishes furnish especially favorable material for quantitative study of growth and the whole life cycle, for although the restricted growing season adds some confusion to the size groupings, composite groups of varying age are rather easily resolved into age groups by microscopic examination of the scales.

In some extraordinary instances, abnormal individuals may result from disturbed metabolism and hence may introduce elements of complication into a statistical analysis of quantitative samples. Among the vertebrates, cannibalism may lead to a type of gigantism. Such abnormalities must be considered thus and cannot be considered in the analysis of populations where normal growth is assumed.

The foregoing are but a few of the numerous instances that might be cited showing wherein an analysis of quantitative collections yields valued results in the interpretation of life cycles. The method, although by no means new, deserves more attention as a tool for the unwinding of complicated life histories than it has been accorded in the past.

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