

Life Tables and the significance of Ageing and the Age Structure of Populations

G. R. Williams

Important properties of a population affected by its age structure are:—the birth rate (which frequently varies with the age of the organism), the death rate (which usually increases with increasing age), the sex ratio (which usually alters because males and females are subject to differing risks throughout life), and behaviour (which may affect dispersal and the nature of competition).

A *life table* provides a picture of the age structure of a population. Properly constructed it will supply information about sex ratio, differential mortality between the sexes, expectation of life and the distribution of the age classes. To make useful forecasts about the fate of a population only one other parameter is required, the age specific birth rate. When all these are known a working model of the population may be built. Life tables may be prepared in three ways, and all depend upon the classification of the organisms according to their age at death. The *dynamic life table* is obtained by following the fate of a single class made up of individuals all of the same age until the last survivor succumbs. This will yield the raw data for the table, and by plotting the number of survivors against age at death a *survivorship curve* is obtained from which one may readily calculate age-specific death rates and life expectancies and the probability of an organism of any one age attaining any other. A *time-specific life table* results from taking a sample of a population and studying the distribution of all the age classes within it at that instant. When it is not possible to draw up either a dynamic or time-specific table, one may use a combination of both, a *composite life table*. These have been used for estimating annual mortality and productivity when banding and recoveries have been spread over a number of years.

If survivorship is plotted against time three types of curve may be obtained. The

first, the negatively-skewed rectangular, is shown by members of a cohort which, having been born at the same time, die more or less simultaneously after having lived out their inherited life span. The second is the simple diagonal on semi-log. co-ordinates which implies that mortality is independent of age. The third, the positively-skewed rectangular, is exhibited by populations suffering extremely heavy mortality in early life, with the few survivors living out a protracted old age. Most survivorship curves are intermediate between the first and second types. Ideally, we should draw up separate life tables or survivorship curves for each sex for each major mortality factor starting from as soon after zygote formation as possible. Unfortunately this is difficult and life tables that extend backwards from the equivalent of birth are rare.

To compare the shape of survivorship curves of animals far apart phylogenetically and in length of physiological life span, the numbers of survivors at each age may be plotted against the percentage of the mean life span. Comparative life tables have been used in the study of evolutionary rates and in the comparison of survivorship curves of some fossil and recent mammal populations.

We must distinguish between mere accretion of years and the decline of homeostasis which usually accompanies it. Medawar calls these "ageing" and "senescence" respectively and shows how the two are related: "Senescence may be defined as that change of the body faculties and sensibilities and energies which accompanies ageing, and which renders the individual progressively more likely to die from accidental causes of random incidence." Senescence is of two kinds: *innate*, and *environmental*. Examination of life tables of a number of wild animals shows that few, if any, individuals reach senility. That this should be so in natural communities, but not so in those in which the life span has been sensibly in-

creased beyond that which we would expect in the wild, is surely significant.

Environmental senescence arises from the many injuries and stresses an organism encounters throughout life; but how does *innate* senescence arise? In the simplest case the life table of a stable population subject only to constant random mortality shows that each succeeding age group is smaller than its predecessor. If, instead of being potentially immortal, members of this population die through some sudden innate degeneration after reaching a certain age, the effect upon the population will depend upon the age at which this occurs; if it happens far enough along the survival curve there will be so few animals left alive that its occurrence will probably pass unnoticed (rather like senility in wild animals). So

that the very old are but little affected by the force of natural selection. Hence, deleterious mutations may not only find a footing here, but may also accumulate. Furthermore, natural selection must tend to push heritable degeneration further and further towards the end of the reproductive period. Here then, is one way of accounting for some aspects of innate senescence. But as few animals in the wild ever survive the risks of living long enough to reach an advanced chronological age (as we can see when we compare life tables for wild and captive animals of the same species) it is understandable why senility is so rare a natural occurrence.

REFERENCE

- MEDAWAR, P. B., 1952. *An unsolved problem of biology*. H. K. Lewis, London.

The Settlement and Metamorphosis of Marine Animals

Professor E. Percival

Thorson (1) in discussing the choice of substratum by marine larvae, points out that further detailed knowledge of life cycles indicates that larvae possess more adaptability than has been hitherto assumed.

For instance, when plankton is collected by two-net, it is not unusual to take larvae of ophiuroids or echinoids, which are in process of metamorphosis, but in Lyttelton Harbour, completely metamorphosed ophiuroids or nearly completed metamorphosed spatangoids are taken near the bottom. Specimens taken nearer the surface are less changed or not at all.

That some larvae of benthic animals will readily metamorphose is shown by fully mature larvae of *Phoronis* metamorphosing in sea-water in a glass dish by no obvious stimulus. It may be that the actinotrocha does metamorphose in open water and that the adhesive surface exposed collects detritus sufficient to weight the animal and drag it down.

According to these observations, it is legitimate to regard some settlements and metamorphoses as not being conditioned by the nature of the substrate, but at the same time recent work shows that often they are not

simple, straightforward processes taking place without reference to the substrate.

Cole et al. (2) in studying settlement of oyster larvae have shown that although freedom from silt is essential, abundant settlement occurs on cultch (shells or tiles) fouled with other attached organisms, particularly recently attached oyster spat. Much less settlement takes place on clean shells. Whether settlement is encouraged by secretion into the water of some attractive substance by spat or by fully settled young has not been determined.

Observations made by Moore (3), Pye-finch (4), Knight-Jones (5) and others, show that cyprids (one of the larval phases of barnacles) move over a surface, apparently testing it. They settle readily in cracks and scratches and in angles. Settlement was found normally to be followed by metamorphosis into the young adult.

The larvae of *Elminius modestus* settled as though gregarious (*vide* oyster spat), aggregating near previously settled forms and it is suggested that an olfactory sense may play a part in bringing them together.

Miller et al. (6) showed that the settlement of the polyzoan larvae of *Bugula* (one