spectacular change has been in a rather older marsh which has changed from a Zosteretum in 1933 to a Spartinetum townsendii in 1957. One corner, which was a Salicornietum, is now partly General Salt Marsh and partly a Puccinellio-Asteretum. Another corner, formerly an incipient Salicornietum is now an Asteretum. An adjacent small, closed marsh has changed from a Salicornietum strictae of 1932 to an Asteretum, whilst the algal vegetation has changed from a Chlorophyceae community and a *Fucus vesiculosus* ecad *caespitosus* community to a *Pelvetia libera—Bostrychia scorpioides* community. A small marsh (Anchor marsh) has changed from a Salicornietum to a General Salt Marsh community. The more rapid changes in the closed marshes are what would be expected in contrast to the rather slower changes on the open marshes. These changes can be compared with rates of change calculated from rates of accretion and the vertical extent of the different communities.

Experimental Work on Daphnia

V. M. Stout

The first work on most animals is their discovery and identification. Observations on their natural history follow. From these have developed studies on communities and populations and for freshwater plankton such studies have been intensively carried out for some time. They have resulted in much information about the composition, distribution and growth of the populations, and on fluctuations in populations together with the relation of the fluctuations to the biological and physico-chemical environment. Much work on freshwater Cladocera as populations or communities is being carried out at present and this work fills large sections of general texts on limnology. But only within recent years has much account been taken of the relation of the physiology of the animals to the general effect on the population.

Experimental work on animals has increased recently, partly in connection with physiological work. The animals can be kept in a controlled physical and biological environment, in which one factor is varied and the effect on the animal recorded. This enables detailed examination of specific relationships, such as the effect of temperature on the growth rate or on the number of eggs produced. These results could be used more fully to try to interpret information from studies on natural populations.

There has been much experimental work with Cladocera, and especially *Daphnia*. *Daphnia* is easy to keep in cultures and in controlled conditions. The animals reproduce parthenogenetically and it is possible to experiment with a genetically stable line by breeding several generations from one individual. *Daphnia* responds differently to different temperatures and various other factors and the effects on the animal can usually be expressed numerically.

Most of the experimental work has been concerned with factors contributing to population growth or decline, and recently there has been some work on the interrelations between different species. After the publication in 1926 of Raymond Pearl's "The biology of population growth", Terao and Tanaka selected the cladoceran, *Moina macrocopa,* as a suitable animal with which to demonstrate some of Pearl's theories and determine if there was any change in the size of a population at saturation point according to the temperature. In 1928 they published three short papers with their results. The first paper gives population growth at three different temperatures and shows different-sized populations at the different temperatures (Fig. 1). The results also demonstrate that population growth was logistic as far as the observations went. Later workers have shown, however, that the experiments were terminated too soon. The two other papers by Terao and Tanaka show a variation in the rate of reproduction with temperature, and the effect of density of the population on the rate of reproduction.

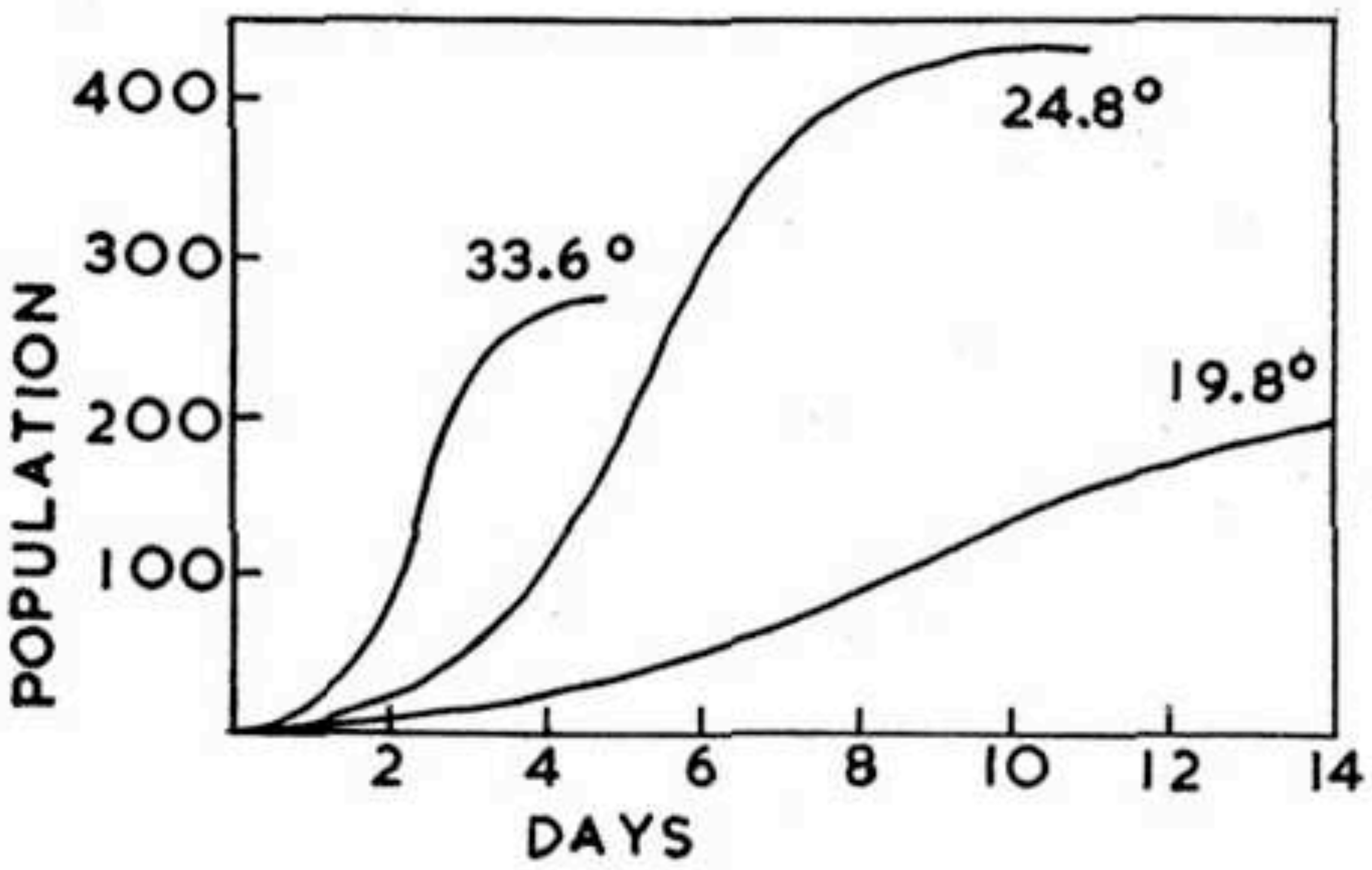

FIGURE 1.—*The population growth of* Moina macrocopa *at different temperatures (from Terao and Tanaka).*

In 1931, Berg, having worked on natural populations of *Daphnia,* was able by experimental work to correlate a seasonal variation in the number of eggs produced by each parthenogenetic female with the amount of food available. He studied the populations of various ponds and counted the average number of eggs per parthenogenetic female. The number of eggs decreased during each season up to the period of sexual reproduction. The decrease was attributed by Berg to unfavourable conditions.

During the last fifteen years, work by Pratt, Green and Frank in particular, has resulted in the following conclusions, all of which apply to animals producing eggs parthenogenetically. The density of the population, i.e., the number of animals per c.c. of medium, affects the survival of the animals. An increased proportion of animals survive with increased crowding over a wide range of densities. With intense crowding there is increased death of the young animals and survival is not as good as with slightly lower numbers.

The density of the population affects the number of eggs produced by each female. The greater the population density the lower the birth rate. At certain temperatures, the density also affects the death rate, which increases with increased density. This has been found, for example, for *Daphnia magna* at a temperature of 25° C. but not at 18° C. The effect of density on birth rate and death rate leads to two different population curves at 18° C. and 25° C. At 25° C. the effect of density on both birth-rate and death rate gives an oscillation of the population growth curve (Fig. 2). Increased number of births causes an increased number of animals, which in turn causes an increased number of deaths reducing the numbers present until a further increase in number of births takes place. The alternating fluctuations in numbers of births and numbers of deaths give the oscillation. At 18° C., the number of births fluctuates but the number of deaths is nearly constant, so that after an initial rise to a peak the population falls slightly and then remains almost stable (Fig. 3.). In neither case is the population growth expressed as a simple logistic curve, as found by Terao and Tanaka, who observed results only to the end of the initial rise.

These results show also the effect of temperature. The temperature affects the number of eggs produced by each female, the optimum temperature varying according to the species. The number of eggs decreases on either side of the optimum. It has been known for some time that young develop more quickly at a higher temperature. In correlation with density, the temperature affects the size of the population. Pratt (1943) suggested that population size is determined by two factors, the initial rate of increase, which depends on temperature, and the duration of this increase, which depends on density. For example, although *Daphnia* reproduces more quickly at 25° C. than at 18° C., populations at 18° C. attain a greater mean size (Figs. 2 and 3). At 25° C. the increase in the size of the population ceases at a smaller density. The mean population size at 18° C. is three and a half times as great as at 25° C. but the population takes a longer time to reach this

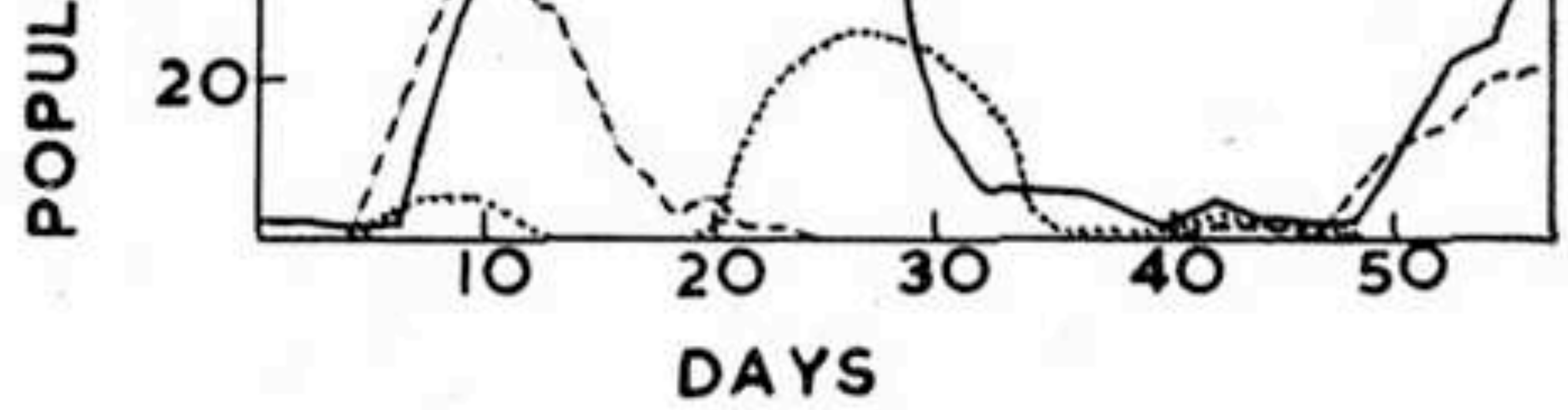

FIGURE 2.—*The density of a population of* Daphnia magna *at 25°C. (after Pratt).*
population size ————
births - - - - - - - - -
deaths ....

[*For births and deaths, the numbers were doubled and the curves smoothed.*]

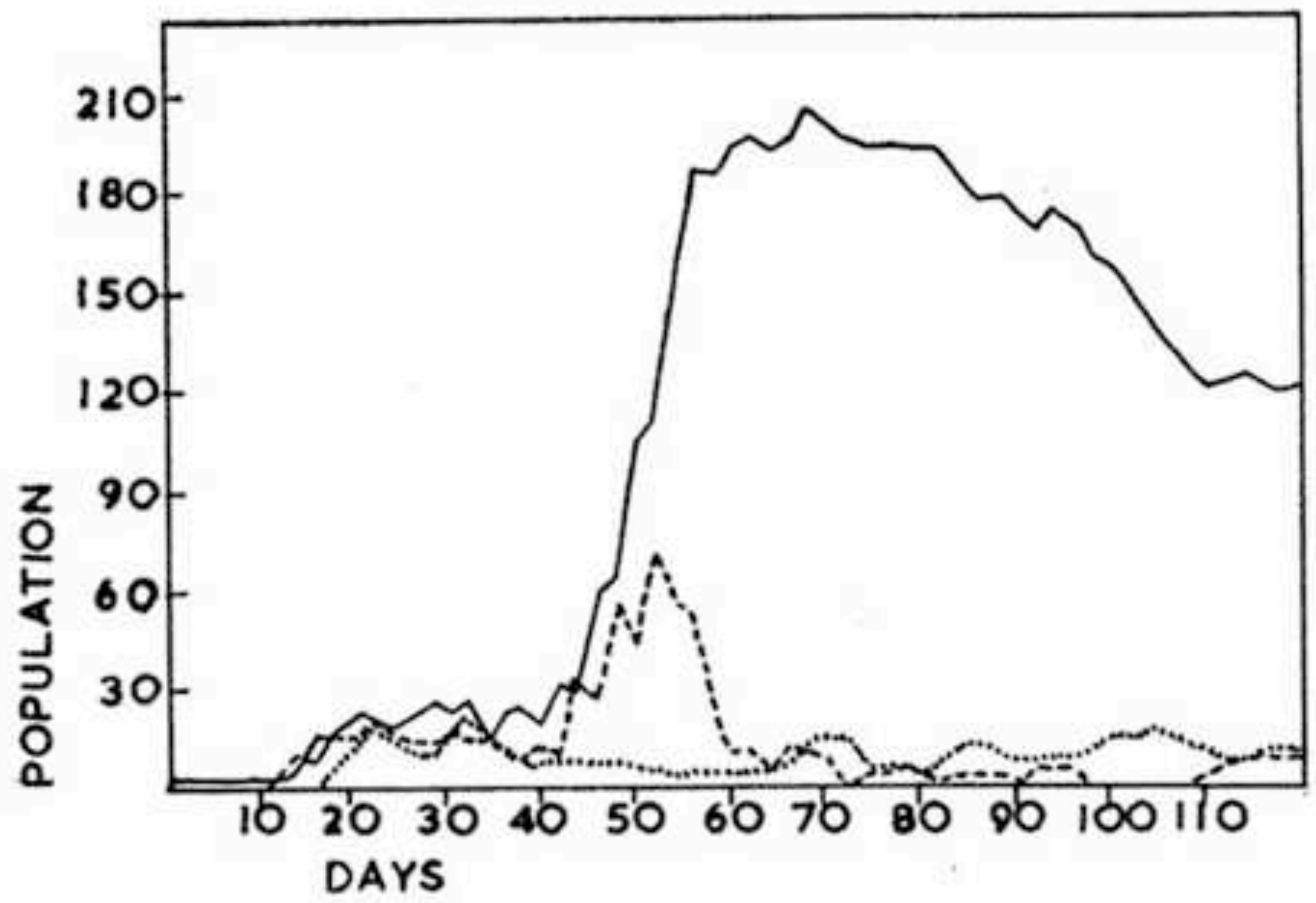

FIGURE 3.—*The density of a population of* Daphnia magna *at 18°C. (after Pratt). Legend as for Fig. 2.*

size. This information is based on experiments where food supply is constant and there is no time limit. In populations in nature, the time taken to reach mean population size may be critical.

The number of eggs produced is related to the age of the mother, the number of eggs increasing during the early broods and decreasing during the later broods. The age of the mother also affects the size of the young liberated for the young of the third brood are larger on an average than the earlier or later broods. This has a further effect, because the initial size of the young when liberated from the mother influences the instar, or age, when maturity is reached and thus when the first eggs are produced. For example, young of *Daphnia magna* measuring 0.78–0.98 mm. when liberated by the mother mature in the 6th instar, whereas young measuring 0.84–1.06 mm. mature in the 5th instar.

The number of eggs produced is directly related to the size of the mother, the larger female producing the greater number of eggs. So that if in a population the number of eggs is plotted against the length of the mother a linear graph results.

Recent studies have sought to determine experimentally the effect of one species upon another. Frank (1957) published results of keeping two species of *Daphnia* separately and together and found that, in two sets of experiments in different media, *D. pulicaria* persisted while *D. magna* died out. Frank decided that there were two limiting factors, oxygen and food.

As yet there has been little application of the results of experimental studies to natural populations of *Daphnia*. A study made by Green (1956) of a population of *Daphnia* showed that during the early summer, the length of the parthenogenetic females fluctuated together with the number of eggs, confirming his experimental results that larger females produce more eggs.

Edmondson (1955) worked on the population of an arctic lake which has a short season with only one generation of *Daphnia* each year. He correlated the changes in density of the population with the size composition and found an increase in the abundance of large animals later in the season.

Ward (1940) investigated a series of ponds and studied the fluctuations in numbers of different species of entomostraca, concluding that the composition of the population and the peculiarities of the individual species were important factors in seasonal fluctuations both in quality and quantity.

Recently Vallentyne (1957), in a review of limnology, suggested the application to limnology of Riley's quantitative approach to the dynamics of marine plankton. Riley developed theoretical equations to explain the distribution of phytoplankton and zooplankton in the western North Atlantic based on certain assumptions and tested these assumptions by the available experimental work on marine phytoplankton and zooplankton.

For freshwater Cladocera, and especially *Daphnia*, quite a lot of experimental work on animals in controlled conditions has now been done and could now possibly be related more fully to the varying state of affairs in nature.

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