Ecological Applications of Lansing's Physiological Work on Longevity in *Rotatoria*

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IT IS BECOMING REALIZED WITH increasing force that studies of productivity must deal not alone with the size of populations at various times, but also with the rates at which they increase and decline as an expression of the shifting balance between reproduction and death (*4, 7*). One of the basic needs in such studies is information about the factors which in nature are responsible for shifting this balance. Moreover, the observed distribution of organisms in lakes of various types is in part a problem of the survival of populations as determined by these factors. Attention is here directed to work by Lansing on problems of aging in rotifers because some of the data can be used in interpreting observations on natural populations. A study of extensive data on the factors correlated with the distribution of sessile rotifers in natural waters has been published (*6*), and a similar set of data on free-swimming species collected by Mr. F. J. Myers in Pennsylvania is under study by the present author for future publication. Some of the latter data are presented below in preliminary form. Carlin (*3*) has published data on seasonal cycles of many species and fluctuations in chemical and physical factors for 6 successive years in several locations in Sweden. The usefulness of life table techniques in discussing natural mortality has been demonstrated recently by Deevey (*5*). In the following pages an attempt is made to show where these diverse sets of data fit together and what problems are in greatest need of investigation.

Lansing worked variously with *Euchlanis incisa* Carlin (= *triquetra* Hudson and Gosse), *Rotaria rotatoria* (Pallas) (= *Rotifer vulgaris* Schrank), *Philodina citrina* Ehrenberg, and *Proales* sp. The results which are applicable to ecological data are summarized first, and data on the natural occurrence of the species discussed subsequently. One of the general phenomena of aging in plants and animals is the gradual accumulation of calcium. Lansing (*11*) has confirmed this for a number of organisms, including *Euchlanis incisa*.

The effect of varying the culture medium on longevity was studied (*12*):

Hydrogen ion. Increasing the pH above 7.0 without changing the salt concentration of the medium increased the length of the period of senility (*Euchlanis incisa*) somewhat without making a large change in mean life span, since only a few individuals survived beyond the period of fecundity. There was, however, a very large and significant increase in fecundity as the pH was increased from 6.0 to 9.6. This seems correlated with the distribution of the species in nature, described below.

Total salt concentration. The total concentration of salts in the standard culture medium was 0.04% (400 mg/liter). Survival and fecundity of *Rotaria rotatoria* and *Proales* sp. were studied in this and in the same medium diluted to 0.02%, both buffered at pH 9.4. Concentrations above 0.04% were markedly inhibitory to reproduction and survival of both species. The survival of *Proales* was slightly lower in 0.02%, but the rate of reproduction was much higher. Survival of *Rotaria* was considerably longer in 0.02%, while the rate of reproduction was about the same in both media.

Salt balance. Salt solutions (0.04%) were prepared with high, intermediate, and low calcium concentrations (about 97, 65, and 32 mg/liter) and correspondingly low, intermediate, and high potassium concentrations. Survival was significantly longer in low calcium than in the other two, where it was about equal. The rate of egg production was about the same in all three, but the total number of offspring per female must have been more in the low calcium. Parallel experiments holding potassium constant were not performed.

As a further test of the effect of calcium, the calcium was removed by treating with sodium citrate. The effects were spectacular. Immersion in citrate for a few minutes every day or so increased the mean life span of *Proales* sp. from 5.8 days in the control to 8.3 days.

Lansing's work on *Philodina citrina* and *Euchlanis incisa* (*13*) is in agreement with earlier work by others in showing that the mean life span is shorter for offspring born later in the mother's life than those born earlier. Hence, *orthoclones* of various ages were established and the mean life span determined. For example, eggs laid on the 8th day of a mother's life are reared, the eggs laid by these offspring on their

8th day of life are reared, etc. This is an *8-day orthoclone,* and the successive generations are designated as $8F_1$, $8F_2$, $8F_3$, etc. Two significant facts emerged:

(1) The mean life span of animals of older orthoclones became shorter each generation until it reached zero or until no eggs were laid and the line died out.

(2) The older the orthoclone, the shorter is the number of generations until extinction. The effect is reversible, as shown by establishing young orthoclones from old, nearly played-out lines. In such cases, the parental life span is quickly regained or exceeded. The oldest orthoclone which might maintain its life span is called the isoclone. In practice, the orthoclones as seen in the laboratory have either decreasing life spans (geriaclones) or increasing life spans (pediaclones) from one generation to the next. All of these lines are, of course, parthenogenetic.

The calcium accumulation may be merely symptomatic of the progressive change in some system which results in the binding of calcium in the tissues (*14*). Any explanation must account for the cumulative and reversible features as well as the apparent transmission through the egg cytoplasm, and the effectiveness of calcium in the culture medium.

G. Evelyn Hutchinson has suggested (*in litt.*) that some of the well-known cyclomorphotic phenomena observed in rotifers may be correlated with aging phenomena. Thus, the changing proportions of long-spined and short-spined or spineless animals during the season or between mictic generations are possibly the result of a change of the age of the theoretical isoclone brought about by changing temperature and chemical or biological conditions. Behrens (*1*) suggested that the length of spines in natural populations of *Keratella quadrata* is to some extent correlated with the calcium content of the water. In some investigated cases, food has seemed to be the chief factor governing cyclomorphosis. It is desirable to have a laboratory analysis made with this possibility in mind. The isoclone technique should be very useful here, and much of the conflict may be resolved by controlling factors now known to be important in aging. It is not yet known if turbulence affects rotifers in the way shown for *Daphnia* by Brooks (*2*), but the greater difficulty in culturing planktonic species, relative to littoral species, suggests dependence on some such obscure physical factor.

TABLE 1

NUMBER OF OCCURRENCES OF SELECTED SPECIES OF *Rotatoria* IN A SERIES OF LAKES OF VARIOUS pH

pH class	3.8–4.5	4.6–5.3	5.4–6.1	6.2–6.9	7.0–7.7	7.8–8.1	8.2–8.9
Species:							
Asplanchnopus dahlgreni		1	0	3			
Lindia annecta	1	1	1	2			
*Floscularis pedunculata**	1	2	2	4			
*Pseudoecistes rotifer**	1	1	0	6			
Proales fallaciosa	1	4	0	2	2†		
Proales sordida	1	5	3	5	3	3	
Keratella cochlearis			1	2	3	3	
*Sinantherina socialis**			1‡	1	6	2	3
Brachionus quadridentatus				2	1	2	
Brachionus angularis					1	2	
Asplanchnopus multiceps					3	1	

* Sessile species from the data of Edmondson (*6*); others are from unpublished data on Pennsylvania lakes.
† pH 7.0 and 7.1.
‡ Very few specimens, small colonies.

In *Philodina citrina,* which has a life span of about a month, 6-day and older orthoclones eventually die out, the 6-day line lasting for 17 generations and the 16- and 17-day lines lasting for only 3 generations under the particular experimental conditions. It is doubtless significant that the age at which the cumulative effect begins to appear is that at which growth stops (*15*). It is known that at cessation of growth calcium concentration in the tissues begins to increase. Possibly eggs are laid with an increasingly greater accumulation of calcium as the mother ages, so that the younger eggs are off to a better start. Other mechanisms are, of course, possible and perhaps more likely.

The occurrence of particular rotifer species in lakes is in many cases strikingly correlated with chemical features of the water. The nature of the correlation can be expressed conveniently in two ways—the frequency of occurrence in various classes of lakes can be tabulated to show the range and apparent optimum (Table 1), or the median concentrations of various substances can be determined and the number of occurrences above and below the median tabulated to expose any tendency to occur in particularly concentrated or dilute waters (*6,* Tables 2–6). The logarithmic nature of the pH scale introduces a certain complexity into such comparisons.

Harring and Myers (*8*) state without presenting data that hydrogen ion is the effective factor in limiting distribution and others (e.g. calcium carbonate) are not involved. This conclusion is based largely on the very sharp division which can be made between the acid and the alkaline fauna; many species have pH 7.0 as the upper or lower limit of their range of distribution and are accordingly referred to as acid or alkaline water species (Table 1). There are transcursional species which occur in both acid and alkaline waters, but many of these tend to extend further into the acid than into the alkaline range. More recent work by the writer and others generally substantiates these facts, but suggests that distribution is limited by factors other than hydrogen ion (*6* and unpublished; *17*). In lakes, there is a high correlation between pH, calcium, and bicarbonate (*9, 10*), which makes the resolution of separate effects difficult in field data. Also, the generally lower productivity of acid waters limits the size of the animal populations for reasons other than chemical tolerance.

Fortunately, some of Lansing's laboratory data, including the apparently general effect of calcium, can be related to existing data on natural populations. The effect of calcium on mortality may well explain why the fauna of soft waters is so much richer in species than that of hard waters. For instance, Myers (*16*) reported that the fauna of Mt. Desert Island included 93 species limited to acid water, 39 to alkaline water, and 145 transcursional species which occurred in both. There were 13 species which occurred in salt water. Most of the waters investigated were acid. It is very desirable to have more experimental information based on culture media in the range of salt concentration of natural waters using species of varied characteristics. Little can be said about *Philodina* or *Rotaria,* since almost nothing is known of bdelloid ecology. The author's impression is that, in nature, *Rotaria rotatoria* inhabits softer waters than any of the species of *Proales* that Lansing is likely to have had, and this agrees well with the laboratory findings, although more data are needed.

The direct effects of calcium on individual longevity are not the only ones which may be expected to affect the survival of a species in a lake, since all eggs are not equivalent. Those laid by older parents will be less effective in a survival sense than earlier eggs. A slight change in calcium concentration may be expected to have an effect on survival of the species out of proportion to its immediate effect on the individuals simply by shifting the age of the isoclone, which in turn will affect an increasing number of individuals in subsequent generations. Thus, a given rate of egg laying may be more or less effective in survival. This effect is probably amenable to a fairly simple mathematical analysis which would enable one to evaluate quantitatively the shift in terms of effective survival.

The most complete data on natural occurrence are those which concern *Euchlanis incisa.* In agreement with laboratory data, this species occurs in small numbers down to pH 6.0 in nature, but it is widespread and becomes abundant only in alkaline ponds (Table 2). It is thus classed as a transcursional species. The species occurred all through the range observed in the lakes sampled, except that it was not found in the one lake with an unusually high calcium concentration (35.8 mg/liter). This lake contained considerably fewer species than the softer ones. The largest populations were formed at concentrations of 11.7 and 8.8 mg/liter, at the upper end of the range of occurrence. These lakes may be compared with 358 in Wisconsin, investigated by Juday, Birge, and Meloche

TABLE 2

OCCURRENCE OF *Euchlanis incisa* IN A SERIES OF LAKES IN PENNSYLVANIA*

	No. of lakes		Maximum abundance	Temperature at maximum abundance (°C)
	Without	With		
pH range				
3.8–4.5	1	0	..	..
4.6–5.3	6	0	..	..
5.4–6.1	4	1	2	24
6.2–6.9	4	3	2	23
7.0–7.7	3	2	3	21
7.8–8.1	3	2	4	22
Calcium range (mg/liter)				
1– 2	2	1	1	24
3– 4	1	2	2	23
5– 6	0	0	..	..
7– 8	1	1	2	18
9–10	0	1	4	22
11–12	0	1	3	21
....	..	..	..	..
35–36	1	0	..	..

* Most of the lakes were sampled three times in one summer. Abundance in each collection was rated on a qualitative scale from 1 to 5.

(*10*), where the range was 0.13–18.8 mg/liter. On the basis of calcium alone, *Euchlanis incisa* would be able to form large populations in about 60% of these lakes. It would be interesting to know the characteristics of fecundity and mortality of this species in culture in response to variations in calcium. It is desirable to know if "alkaline" species have a higher optimal calcium concentration than others, or whether they are responding chiefly to pH within the limits of calcium found in nature. Data are needed on fecundity and survival at various concentrations of hydrogen and other ions.

Other natural phenomena may now be examined from the present viewpoint. It is highly desirable to find out whether periodic changes of any sort that happen in natural environments have the same effect as treatment with citrate. In small, moderately mineralized ponds there may be very great diurnal fluctuations in chemistry which at one time would have been thought of as deleterious, but which may actually turn out to make the maintenance of certain species possible. Such effects should be sought.

More information on the effect of temperature is badly needed, for it seems to govern the general seasonal cycles of many species. Carlin's very extensive data include measurements of a number of chemical and physical factors as well as counts of many organisms that may serve as food for some rotifers. That chemical factors modify the effect of temperature is to be expected and may account for the different seasonal occurrences of species in different kinds of lakes (*7, 18*). Indeed, there is reason to believe that interaction of temperature and salinity affects the distribution of several species which tolerate wide variation in salinity from fresh water to coastal salt water. *Notholca acuminata,* for example, is found in fresh water only in the late winter and early spring, when the water is cold, but it occurs all summer in coastal bays and ponds, where the water becomes quite warm. Data are fragmentary, and this species should certainly be investigated in the laboratory. It may be expected that survival at high temperatures will be enhanced by increasing the salt content of the medium.

In summary, it may be said that the problems of the distribution of species and the productivity of populations can profitably be thought of as problems of survival and fecundity, and this throws attention onto the physiological effects of environmental variables on the rates of reproduction, growth, and death.

The physiological mechanisms involved in the observed limitations can be determined only by properly conducted laboratory experiments, but such a laboratory study must be preceded by extensive studies of natural populations, such as those cited above, in order to find out which species are quantitatively important and which are most sensitive to environmental variations; these will be the most profitable to study. Little information of interest to ecologists will be revealed by studies of species which are rare in natural habitats or which are not limited to a more or less restricted part of the range of variation found in natural waters.

The rotifers are exceptionally useful for many kinds of physiological work, and it is likely that they will be used increasingly. The writer would like to take this opportunity to urge anyone who is contemplating a physiological study of rotifers or any other small aquatic organisms to use the above considerations in choosing his material. A little care in selecting the organisms will make the results doubly effective; it will furnish data of value to ecologists, and, further, the investigator himself will benefit by a suggestive background of observations of the behavior of the species in nature.

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