Adaptation of Rotifers to Seasonal Variation

Charles E. King


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ADAPTATION OF ROTIFIERS TO SEASONAL VARIATION

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Abstract. Most lakes display extensive seasonal variation in both their biotic and abiotic components. The question posed in this paper is how do rotifers adapt to this temporal heterogeneity? Three alternate models of population structure for temporal adaptation are advanced and considered. If the physiological state of a population varies continuously with its environment, the relative fitness of a population will be constant. To test this hypothesis, rotifers (Euchlanis dilatata) were periodically collected from nature, cloned, allowed to adapt to the laboratory environment for 10 generations, and then used in experiments to determine the intrinsic rate of population growth, $r$. The $r$ values of clones collected at different times indicated that physiological adaptation alone is not the major factor involved in adaptation to seasonal variation. Moreover, the pattern of variation in $r$ revealed genetic differences among clones collected at different times.

An alternate explanation, genetic discontinuity through time, is presented in two forms. Both models assume that different genotypes are maximally adapted to different parts of the environmental spectrum. The first model further assumes that adults of all genotypes are present throughout the spring and summer, but that the frequencies of the genotypes vary directly with the environmental variation. This model is the most likely statement of rotifer population structure if there is considerable gene flow throughout the population and if interclonal competition is not important. If either of these conditions does not hold, the population is expected to be subdivided into a number of genetically discrete units, each unit occupying a different temporal part of the environmental mosaic. An insufficient number of clones was tested to distinguish between the two models of temporal genetic polymorphism. However, the data that were obtained demonstrate that a large genetic component is necessary to explain the adaptation of E. dilatata to seasonal variation.

Extensive environmental variation is one of the most basic facts of life for any organism living in temperate lakes. Among the most notable contributors to this environmental variation are the temperature and chemistry of the water and the qualitative and quantitative composition of the phytoplankton and zooplankton. Most of these factors follow a seasonal pattern of change within an annual cycle. It is therefore apparent that any population that is present over a major part of the annual cycle must be adapted to survive in a broad range of different environments. One major pattern of adaptation has been well documented for those organisms with long lifespans. Generally it is found that populations with a generation time of 1 year or longer remain active and have a high degree of physiological homeostasis, or pass through part of the year in a relatively inactive state. The challenges facing a lacustrine population that has several short-lived generations each year are quite different. In this case, each generation exists in a different environment. Moreover, the “correct” adaptive mode in one environment may be highly maladaptive in a subsequent environment. This problem and its solution as reflected in the adaptive structure of rotifer populations form the basis of this paper.

METHODS AND RESULTS

Euchlanis dilatata is a common, littoral rotifer that reproduces both by parthenogenesis and bisexual reproduction. In the first case, parthenogenetic eggs are produced by amictic females and these eggs have a developmental time of approximately 1 day. At 22°C the generation time of this species is about 3–4 days. In contrast, the mictic female produces resting eggs by bisexual reproduction. These eggs appear to require for hatching longer periods and special conditions, such as the spring warming of the lake. Euchlanis dilatata adults are absent from northern lakes in winter and during this period the resting eggs serve as the reservoir of the population's gene pool.

Field samples

The Euchlanis dilatata used in this study were obtained in 1968 from a small (about 2-ha surface area) man-made lake at the 4-H camp in Allerton Park, 30 miles (48.3 km) southwest of Urbana, Illinois. The lake is drained each fall and then gradually refills with melted snow and rain through the winter and spring. Two types of collections were made during each of the periodic sampling visits. First, three plankton tows were taken from a low bridge at the west end of the lake. The water depth at this point is approximately 2 m. Each plankton sample was made by drawing the net, which had a 15-cm diameter, along a 6-m diagonal vector from the lake bottom to the surface. The second type of collection consisted of four 1-liter samples of the littoral vegetation at each of three sites near the bridge. All collections were made in the early afternoon and then...
taken back to the laboratory for counting and subsequent culture work.

The littoral samples were handled by placing a light directly above the open mouth of the collecting jar. *Euchlanis dilatata* is positively phototaxic and can be concentrated at the surface by this procedure. After setting up the light, 35-ml aliquots of the surface water were withdrawn from each sample at 20-min intervals for 3 hr. Counts were made of the number of rotifers in each of these aliquots and the grand mean taken as the estimated abundance per sample. All individuals in the three plankton samples were counted and the mean was taken as the estimated abundance. These estimates, along with the other collection data, are presented in Table 1. It is stressed that the absolute magnitudes of the abundance values have little meaning when taken singly. They are presented solely as indicators of the presence or absence of *E. dilatata* and to give some very rough notion of the relative abundance of animals from one sampling time to the next.

### Clone survival

The animals obtained from the field samples were first washed in the culture medium and then individually distributed to small syracuse watch glasses containing 0.5 ml of a pH 8.0 Pourriot-Gilbert medium and 250,000 cells of *Chlamydomonas reinhardtii*. The general culture techniques used in this study have been described in detail elsewhere (King 1967, 1970). Descendants from each of the isolated females were split into two groups at the end of one week. One of these groups was transferred to a 19°C constant temperature room and the other to a 27°C room. Each of the lines was maintained in mass culture, fed daily, and transferred to clean syracuse dishes at 3-day intervals.

An attempt was made to set up 25 clones for each field collection. However, on two occasions, May 1 and June 5, an insufficient number of littoral animals was obtained from the field collections and this procedure could not be followed. Two individuals were obtained and isolated on each of those dates. Preliminary work had demonstrated that a given animal and its parthenogenetic descendants either could adapt to laboratory conditions and establish a long-lived clone, or could not adapt and would become extinct within one to three generations. The proportion of clones surviving for five or more generations (approximately 2 weeks from collection for the 27°C lines) is therefore a measure of the relative ability of the animals present in the lake at any given time to exist under laboratory conditions.

Clone survival was measured with the 27°C lines because at that temperature the generation time is much shorter than at 19°C and because, using this binary yes-or-no measure of clone survival, no difference was found between the two temperatures. The results of this test of clone survival are presented in the last two columns of Table 1. These data will be referred to later; however, it is to be noted here that the *group* of animals collected at one time had a probability of survival of either 0 or approximately 1. Intermediate values were not obtained for any of the 10 groups studied.

### Population dynamics

The cultures used to measure clone survival from each collection were numbered consecutively from 1 to 25 in the order of isolation of their stem females. After clone survival was measured, the number of clones maintained from each collection was reduced to five by discarding all but the five lowest numbered surviving clones. These clones were then held for a minimum of five additional generations before use in the subsequent experiments. For the lines of each
Table 2. Intrinsic rate of increase ($r$), net reproduction ($R_0$), and expectation of life at birth ($e_b$) for the experimental clones. Each value is the mean ± standard error of three replicate experiments performed with 15 animals per experiment. Column heads indicate adaptation-experimental temperatures (°C).

<table>
<thead>
<tr>
<th>Collection date and clone</th>
<th>$r$</th>
<th>$R_0$</th>
<th>$e_b$</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>19–19</td>
<td>27–19</td>
<td>19–27</td>
</tr>
<tr>
<td>5/1 A</td>
<td>0.78±0.03</td>
<td>0.51±0.01</td>
<td>0.68±0.12</td>
</tr>
<tr>
<td>5/1 B</td>
<td>0.83±0.02</td>
<td>0.63±0.07</td>
<td>0.95±0.05</td>
</tr>
<tr>
<td>6/5 A</td>
<td>0.68±0.04</td>
<td>0.50±0.05</td>
<td>1.26±0.04</td>
</tr>
<tr>
<td>6/12 A</td>
<td>0.69±0.04</td>
<td>0.38±0.02</td>
<td>1.51±0.03</td>
</tr>
<tr>
<td>6/12 B</td>
<td>0.49±0.04</td>
<td>0.20±0.03</td>
<td>1.27±0.04</td>
</tr>
<tr>
<td>6/12 C</td>
<td>0.63±0.03</td>
<td>0.31±0.07</td>
<td>1.36±0.07</td>
</tr>
<tr>
<td>6/12 D</td>
<td>0.65±0.04</td>
<td>0.45±0.01</td>
<td>1.51±0.08</td>
</tr>
<tr>
<td>6/12 E</td>
<td>0.61±0.00</td>
<td>0.40±0.05</td>
<td>1.86±0.05</td>
</tr>
<tr>
<td>6/26 A</td>
<td>0.08±0.02</td>
<td>2.43±0.13</td>
<td>1.1±0.1</td>
</tr>
<tr>
<td>6/26 B</td>
<td>0.27±0.10</td>
<td>2.56±0.07</td>
<td>1.8±0.4</td>
</tr>
<tr>
<td>6/26 C</td>
<td>0.13±0.07</td>
<td>2.39±0.07</td>
<td>1.3±0.2</td>
</tr>
<tr>
<td>6/26 D</td>
<td>0.78±0.01</td>
<td>2.64±0.07</td>
<td>4.7±0.2</td>
</tr>
<tr>
<td>6/26 E</td>
<td>0.71±0.02</td>
<td>2.68±0.06</td>
<td>5.4±0.2</td>
</tr>
</tbody>
</table>
clone maintained at 27°C, the elapsed time from collection to experimentation was at least 4 weeks. For the 19°C lines, the elapsed time was at least 7 weeks. The purpose of this procedure was to allow sufficient time for physiological adaptation to the culture conditions so that subsequent measures would reflect genetic differences rather than adaptational differences among the clones.

To avoid the influences of maternal age on survival and reproduction which have been reported for several monogonont rotifers, including *Euchlanis dilatata* (King 1969), all experimental animals were derived from two generations of parents that were between 1.5 and 2.5 days of age when they laid the collected eggs. Within an hour after hatching, the animals to be used in experiments were transferred to individual small Syracuse watch glasses containing 0.5 ml of the food suspension described earlier. Subsequently, at 24-hr intervals, each dish was examined and scored for both survival of the rotifer and the number of eggs that it had laid. Those animals still alive were transferred to clean dishes with a fresh suspension of algae and the process was repeated until all of the animals in the cohort had died. In this way, age-specific survivorship and fecundity data were obtained. These data were used to calculate the intrinsic rate of population increase (*r*), net reproduction (*R₀* = the average number of eggs produced/lifetime), and the mean expectation of life at the time of birth (*e₀*) by the methods of Birch (1948) for the first two statistics and of Deevey (1947) for the last statistic.

Three replicate experiments with 15 animals each were run for each clone and temperature. In addition, animals maintained at 19°C were also tested at 27°C (indicated 19–27) and animals maintained at 27°C were also tested at 19°C (27–19). The results of these experiments are presented in Table 2. Data for the clones collected on June 26 could not be obtained at 19–19 and 19–27 because there was insufficient time for adaptation to laboratory conditions before the work had to be terminated in August.

Each clone shows the expected rise in the values of *r* and *R₀* with a change in experimental temperature from 19°C to 27°C. In contrast, the temperature patterns for mean lifespan are rather irregular; some clones had a significantly longer lifespan at an experimental temperature of 19°C than at 27°C, while for other clones the opposite result was obtained.

The data in Table 2 also demonstrate the importance of the temperature of adaptation. Both the *r* and *R₀* values are consistently lower at 27–19 than at 19–19. The corresponding trend was displayed in the experiments performed at 27°C; the rates of increase and fecundity are consistently higher at 27–27 than at 19–27. These observations may be used to estimate the role of physiological adaptation in the determination of *r* at either 19–19 or 27–27. It is apparent from Fig. 1 that the contribution (measured as the difference in *r* values relative to the higher value) of physiological adaptation constitutes a sizable proportion of the total rate of increase of each clone. The mean values of clones collected on different dates display an interesting pattern. At 19°C, physiological adaptation has a much greater import for the warm-water clones (collected on 6/12) than for the cold-water clones (collected on 5/1). Precisely the opposite conclusion is reached from the experiments conducted at 27°C. Each clone in this study is equivalent to a genotype, and the clear implication of these results is that the clones collected on different dates are genetically distinct.

We can approach the same question in a different context by viewing the data presented in Fig. 2. The set of circular points bounded by the solid line constitute the smallest convex set that can be obtained by plotting the mean rates of increase of each clone at 19–19 against the rates obtained at 27–27. The points obviously represent the maximum fitness of each clone at the two temperatures. We can ask what would happen to *r* if the environment suddenly warmed from 19°C to 27°C? This is equivalent to asking how the value of *r* varies between the 19–19 and 19–27 measures. The answer is given in the quadrangle of square points bounded by the dashed
Fig. 2. Variation in rates of increase among clones of *Euchlanis dilatata* at 19° and 27°C. The quadrangle delineated by the circles and unbroken line is the smallest convex set obtainable by plotting the mean rates of increase of each clone at 19–19 against *r* measured at 27–27. The quadrangle formed by the broken line and squares indicates changes in the rates of increase under conditions of rapid warming (19–19 vs. 19–27) and the quadrangle formed by the dotted line and triangles indicates changes that result from rapid cooling (27–27 vs. 27–19). Points 1 and 2 are for clones A and B of the 5/1 collection, point 3 is for the 6/5 clone, and points 4 to 8 are for clones A to E of the 6/12 collection.

![Diagram](image)

line in Fig. 2. This comparison reveals for clone 5/1–A, for example, that *r* will change from 0.78 to 0.68. However, as physiological adaptation to the 27°C temperature occurs, *r* will increase to 1.64. If the temperature then suddenly decreases, the effect on *r* is given by the 27–27 vs. 27–19 comparison made in the set of triangular points bounded by the dotted line. Again for the same clone, *r* is expected to decrease from 1.64 to 0.51 and then to increase to 0.78 as physiological adaptation to 19°C takes place. Each point in the inner two quadrangles then describes how *r* changes under a rapid environmental shift. The difference between identical points in the inner quadrangles and the outer quadrangle indicates the effect of physiological adaptation to the temperature change. In Fig. 2, physiological adaptation is measured relative to the change in *r* between two sets of temperatures, whereas in Fig. 1 the measure was the contribution of physiological adaptation to the total size of *r* observed under a single temperature.

These considerations permit us to partition the change in *r* from 19–19 to 27–27 into short-term (genetic preadaptation plus physiological adjustment) and long-term (physiological adaptation) components. The immediate change from 19–19 to 19–27 gives an estimate of the short-term component and can be measured by the ratio \([(19–27) – (19–19)] / [(27–27) – (19–19)]\). The subsequent change indicates the effect of physiological adaptation and is measured by \([(27–27) – (19–19)] / [(27–27) – (19–19)]\). These two measures are presented for each clone in columns A and B of Table 3. The corresponding calculation for changes in *r* that occur as the environment cools from 27°C to 19°C are \([(27–27) – (19–19)] / [(27–27) – (27–19)]\) for the short-term adjustment, and \([(19–19) – (27–19)] / [(27–27) – (27–19)]\) for the long-term adaptation. These measures are given in columns C and D of Table 3.

Both of the 5/1 clones adapt to a warming trend by means of physiological adaptation. In fact, for the 5/1–A clone, the mean *r*-values are actually lower at 19–27 than at 19–19, indicating an extremely tight relationship between genotype and optimum environment for which the clone was preadapted. In contrast, for the five clones collected on 6/12, only about 40% of the change in *r* is attributable to physiological adaptation.

Short-term adjustments of *r* appear to be important for both the 5/1 and 6/12 clones in adapting to a change in temperature from 27°C to 19°C. The basis of this finding for the 5/1 clones is the return of the environment to a state more compatible with the genetically preadapted optimum. Thus the May clones rely upon phenotypic plasticity derived from physiological adaptation. In contrast, the short-term component is large for the 6/12 clones under both warming and cooling trends, indicating greater genetic flexibility in the adaptation to environmental heterogeneity. In some respects, these results parallel those from the study of Jain and Marshall (1967) on two species of wild oats, *Avena fatua* and *A. barbata*. However, the comparisons made in this pa-
per are between clones of the same species. It is therefore necessary to consider mechanisms that could maintain the required degree of genetic differentiation. I shall return to this point in the discussion.

Most important in the present context is the pattern of change of r-values from one collection to the next. In making this comparison it must be recalled that the number of clones established for any one collection is small and that the numbers are not the same for all collections. Keeping this reservation in mind, I now assume that the mean growth rate observed for the clones of any single collection is a good estimate of the true mean of all clones present in the lake at the sampling time. At an experimental temperature of 19°C, the data in Table 2 indicate that the mean value of r declines from a maximum of 0.8 for the May 1 collection to a value of 0.6 for the June 12 collection. The opposite trend was observed in the experiments performed at 27°C. That is, the r-values obtained for the two clones collected on May 1 were the lowest found in any of the 13 clones examined. The clones collected on June 26 had the highest r-values at 27°C and those collected on June 12 were intermediate between the earlier and later collections.

The Duncan multiple range test (Duncan 1955) has been applied to these data. This test analyzes all possible comparisons among treatment means and therefore protects against error much better than a test based on a single comparison. The results of this test are presented in Fig. 3 for the 19°C experiments and in Fig. 4 for the 27°C experiments. The mean values of r, R₀, and e₀ are presented for each clone in these two figures along a horizontal scale such that the distance between any two points is proportional to the numerical difference between their means. Points underscored by the same line are not significantly different. Points that are not underscored by a common line are significantly different. From this analysis it is apparent that the r and R₀ values tend to be more homogeneous for clones collected at any one time than for clones collected at
different times. Moreover, the $r$-means for the various collections display little overlap. In no case, however, are the values for any one date totally distinct from those of a subsequent collection.

**DISCUSSION**

Hutchinson (1967) has extensively reviewed the research performed on morphological variation and successional changes in planktonic rotifers. The problem posed here is different in that its major focus is the adaptive structure of the population and not of the individual per se. A preliminary answer to this question is now possible for *Euchlanis dilatata* and the temperature variation of its environment. If the population is structured so as to respond to environmental variation by means of physiological adaptation alone, all $r$-values for any given temperatures are expected to be the same. The nonparametric Wilcoxon test was used to examine this hypothesis for the 5/1 clones against the 6/12 clones at 19–19 and for all three paired combinations of the 5/1, 6/12, and 6/26 clones at 27–27. In each case the one-tailed probability that the mean values of $r$ are identical was < 0.05. Thus it seems clear that physiological adaptation alone cannot be invoked to explain the seasonal adaptation of *E. dilatata*.

On the other hand, although genetic differentiation has clearly been indicated, there are not enough clones to demonstrate definitively that genetic variation is the predominant mode of adaptation. However, support for the significance of genetic mechanisms is obtainable from two basic sources.

The first source is the pattern of the $r$-values discussed in the last section. The change in $r$ from one collection to the next is consistent with the assertion made earlier that the rotifers present in the lake at one time are genetically distinct from the animals present later in the season.

Wilcoxon tests have also been performed on the $R_0$ values; the probability that the difference between the 5/1 and 6/12 means (at both 19–19 and 27–27) can be accounted for by sampling error is < 0.05. However, there was no significant difference between the $R_0$ values of the 6/12 and 6/26 clones. The reason for this can be seen by inspecting the $e_0$ values. Clones A, B, and C of the 6/26 collection have $R_0$ values that are included in the range of the fecundities observed for the 6/12 clones. However, the mean lifespans of individuals in these three 6/26 clones were much shorter and their eggs were produced much earlier in life than was the case for the 6/12 clones. These interactions between the number of eggs laid per female and the schedule of egg deposition explain the difference in $r$-values of the two groups of clones. The intrinsic rate of increase is based on both the amount and distribution of fecundity as well as on the viability pattern of a clone. For this reason $r$, and not $R_0$, is the preferable sta-
tistic to use in comparing the adaptive patterns of different clones.

Euchlanis dilatata is sometimes classed as a meroplanktonic species because it occurs in both the littoral and planktonic regions of a lake. Twice during the course of this study E. dilatata was found in the plankton. On the first occasion (June 5) the appearance followed a week of very warm weather and an accompanying rapid rise in water temperature. A smaller increase preceded the second appearance of E. dilatata in the plankton on July 3. In both cases a few planktonic males were found; males were never found in the littoral samples. No resting eggs were obtained from any of the individuals collected in the lake although they were obtained from clones that had been in culture for several generations. Other observations (e.g., Wesenberg-Lund 1930, Carlin 1943) have indicated bisexual reproduction in the planktonic phase, but in no case has a causal relationship been demonstrated between the planktonic phase and bisexual reproduction. Moreover, males and females carrying resting eggs have been found in littoral collections by Wesenberg-Lund and others.

Commonly, after bisexual reproduction rotifer populations display a drastic reduction in numbers (Wesenberg-Lund 1930). This observation was also made in the present study (Table 1). In the month following the first appearance of E. dilatata in the plankton, the population size again increased. Euchlanis dilatata was not found in either of the two collections made after the second appearance of this species in the plankton.

A final point to be made from the field collections is that the animals collected on the trip preceding the appearance of E. dilatata in the plankton could not be cultured in the laboratory. However, other cultures from earlier collections were being maintained quite successfully under the same conditions. This observation suggests an altered physiological state in the preplanktonic rotifers. None of the organisms collected in the plankton itself could be cultured (Table 1).

In summary, these observations can speculatively be taken to indicate the following sequence: first, in the spring, resting eggs deposited by rotifers in the previous year hatch. Parthenogenetic females emerge, reproduce, and are succeeded by several generations of amictic females. Meanwhile, the environment is continually changing and it is reasonable to suppose that one or more of these changes (most likely related to rotifer density or food chemistry, or both) act as environmental cues to evoke a physiological change in the littoral rotifers. Subsequently, bisexual reproduction occurs as either some or all of the animals move out into the plankton and resting eggs are produced. The bisexual reproduction is followed by the death of this first group of animals.

The first group of littoral animals is then replaced by a genetically distinct group that either hatched from a different set of resting eggs and was never sympatric with the first group of rotifers or was present at low frequency and, because of the difference in genetic background, did not respond to the stimuli inducing bisexual reproduction. This second group then increases its population size via parthenogenesis and the cycle is repeated.

Adaptive structure of rotifer populations

The consequences of alternate forms of population structure are displayed in the fitness of the population. However, the literature is replete with different, and sometimes contradictory, uses of the term “fitness” and it is therefore necessary to specify the context in which the term will be used. We can speak of “population fitness” to indicate the ability of a given clone or group of clones to exploit a specific environment. In this sense population fitness is equivalent to “adaptedness” (Dobzhansky 1968) and is measured by intrinsic rate of increase, productivity, competitive ability, or population size. In this paper, the magnitude of r will be used to measure fitness since it is probably the best single indicator of a population’s ability to exploit an environment lacking density restraints.

Measures of population fitness apply to specific environments and a clone with high fitness in one environment may have low fitness in another. To study adaptation to temporal variation, it is therefore necessary to measure change in fitness relative to a given change in the environment. In this context, fitness has no relationship to the “Darwinian fitness” or “relative selective value” measures used in simple discrete models of natural selection. In these models, each genotype is assigned a fitness value that specifies its ability to survive and reproduce relative to some standard genotype in the array. These values provide no indication of the absolute ability of a genotype to survive and reproduce in a specific environment.

Under the hypothesis of physiological adaptation to seasonal variation, the structure of a Euchlanis population can be depicted as in Fig. 5. This structure, which will be referred to as model I, provides for genetic variation in the population but stipulates that each amictic genotype follows approximately the same temporal pattern of adaptation. Moreover, the fitness of each genotype is expected to have a constant relationship to the environment even though absolute fitness (magnitude of r) will vary through time. At the end of the season, bisexual reproduction occurs, resting eggs are formed, and the adult stages die. The cycle is repeated in the next spring after the resting eggs hatch and the amictic females emerge. For reasons presented earlier, only a portion of the
adaptation of Euchlanis can be explained by physiological changes and so this model is rejected as a description of the results obtained in this study.

Model II (Fig. 6) requires that resting-egg hatching be either approximately synchronous or bimodal to match the two periods of bisexual reproduction.

\[ \begin{array}{|c|c|c|} 
\hline
\text{Comparison} & \text{Percentage difference} & \text{at} \ 19^\circ \\ \hline
5/1 \ vs. \ 6/12 & -31.1 & 19.2 \\ 6/12 \ vs. \ 6/26 & - & 16.2 \\ 5/1 \ vs. \ 6/26 & - & 32.3 \\ \hline
\end{array} \]

This model allows for genetically determined variation in the time of maximum fitness and has the added advantage of explaining a commonly observed pattern of bisexual reproduction, one period late in the spring and a second period late in the summer. Under this model a fluctuating genetic polymorphism would hold throughout the year with clone (or gene) frequencies changing more or less continuously throughout the season. Model II adequately explains the results obtained in this paper if the clones obtained in any single collection reflect only the most frequent genotypes in the lake. Genetic continuity throughout the year is maintained under this model because representatives of all genotypes in the lake would be present at each period of bisexual reproduction. Under random mating, the clones present at a high frequency in the first reproductive period would leave many offspring whereas they would leave few offspring in the late summer reproductive period. The opposite pattern would exist for those clones that had a high frequency in the second period of bisexual reproduction.

The major disadvantage of model II is that it implies a relatively small degree of interclonal competition which, if the environment is resource limited, is unlikely. Relative growth rates comparable to selective values are readily calculated on the basis of the r-measures in Table 2 by taking the ratio of the grand mean of any collection to the grand mean of a subsequent collection and subtracting the result from 1. These values are presented on a percentage basis in Table 4. At 19°C, the clones collected on May 1 have a great reproductive advantage over the clones collected on June 12. At 27°C, individuals from later collections have a reproductive advantage over those from clones collected earlier. Thus, even if there is no competition between clones, the frequencies can change rather quickly. Under competition, however, the different growth rates are expected to lead to even more striking differences in relative frequencies and, if the environment remains stable or is highly predictable from one year to the next, competitive exclusion would be likely unless there is a significant gene flow at the time of bisexual reproduction. The form of the competitive exclusion in this system would be comparable...
ADAPTATION OF ROTIFERS TO SEASONAL VARIATION

Fig. 7. Adaptive structure of *Euchlanis dilatata* under the hypothesis of complete genetic discontinuity. Fitness of any clone (A–F) varies from 0 to 1 and each clone has a different temporal point of maximum fitness relative to the environment and every other clone. Arrows indicate periods of male production and bisexual reproduction within clones such that there is no overlap in reproductive periods among clones.

... to interspecific competition (since no gene flow occurs between the amictic females) but its intensity should be much stronger because of the ecological similarity between the competing clones.

Thus, if interclonal competition is a major factor in determining the adaptive structure of rotifer clones, an alternative model would seem more likely. Under model III, depicted in Fig. 7, the frequency of bisexual reproduction is equal to the number of different adaptive maxima over an entire season. Gene flow between adaptively different clones is precluded by this model even though there may be some temporal overlap.

Although the bisexual periodicities demanded by model III are not inconsistent with recent work on the induction of bisexual reproduction in rotifers (Gilbert 1968, Birky 1969), there is little evidence for such an extreme pattern in nature. The evidence that does exist is quite circumstantial and open to other interpretations. For instance, Carlin (1943) found that the time of maximum population size of *E. dilatata* was more variable over a 6-year period in Lake Fiskby than was the time of bisexual reproduction. On the average, *Euchlanis* females were present for a period of 3 months and males for a period of 1.5 months. These data may be interpreted under the genetic discontinuity hypothesis to indicate that different clones formed the maxima in different years and that, although males were present for long periods, their genetic structure was discrete from one period to the next (as illustrated in Fig. 7).

Model III requires that the seasonal life history of a single clone be rather brief. Such life histories are known for a number of rotifers. For instance, Wesenberg-Lund (1930) has studied the monogonont rotifer *Epiphanes (= Hydatina) senta* in small temporary ponds. The resting eggs in these ponds hatch shortly after the ice cover melt. Several generations of amictic females are produced and then bisexual reproduction occurs and the adults die. This entire cycle takes place in 4–6 weeks since by that time the ponds desiccate and cease to exist. However, Wesenberg-Lund found that the same pattern occurred in exceptionally wet years when the ponds did not dry up. This observation indicates a tightly linked genetic adaptation to the normal, short-lived environment and it is not unreasonable to extrapolate the same mechanism to seasonal variation and specialization as required by model III.

Under model III the resting eggs of different clones would hatch at different times. Wesenberg-Lund (1930) has related hatching of the resting eggs of several species to water temperature. It therefore requires only a small extension to speculate on the existence of differential temperature sensitivities for hatching cues among clones of the same species.

Both models II and III are consistent with the data obtained in this study. Both, however, are extreme statements of the genetic polymorphism over a season and it is likely that the true structure of rotifer populations, at least of the genus *Euchlanis*, lies somewhere in between. Physiological adaptation and developmental flexibility undoubtedly have a role, but it seems likely that this role is to add noise to the genetically determined components of fitness so that some gene flow occurs between clones of different adaptive modalities. Without such gene flow it is difficult to understand the morphological unity displayed by most rotifers over an entire season. But, it should be recalled that many rotifers (including *E. dilatata*) tend toward a cosmopolitan distribution. It is not reasonable to assume a significant amount of gene flow between Europe and North America, yet the same morphological homogeneity of *Euchlanis* exists between continents as between seasons in the same lake. Thus, if the hypothesis of seasonal genetic discontinuity proposed in this paper is accurate, it does not create a new problem; it simply extends a zoogeographical paradox to a single lake. And, in the latter form, the problem is an eminently approachable one.

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