

GENETIC INFLUENCES ON THE NICHE BREADTH AND TEMPORAL DISTRIBUTION OF ROTIFER POPULATIONS¹

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ABSTRACT

Data on the genetic structure of parthenogenetic rotifer populations are reviewed and analyzed to address the question: "How do the dynamics of natural populations of zooplankton reflect the 'packaging' of their genetic variation?". Two distinct patterns have been found in rotifers. When the clones comprising a population undergo a seasonal succession, low variances in both rates of increase and net production are detected among individuals collected at the same time, and high variances are found between collections made at different times. Rotifers from these populations appear to be narrow-niched specialists. In contrast high variances of life history characters occur both within and between collections when clonal succession does not occur. The latter condition has been found in only one rotifer population. In that case the population appeared to be present in the lake throughout the year and the lack of sexual reproduction.

These studies demonstrate that the genetic structure of a zooplankton population may have profound effects on its life history characteristics and dynamics. The dependency of life table parameters on genetic structure is likely to be a more important variable in studies with obligate or cyclical parthenogens than in those with sexual species. Knowledge of the genetic structure is essential to correctly interpret ecological measures made on these populations.

INTRODUCTION

Until the 1970's, when isozyme electrophoresis was first applied in limnological studies, ecological research with zooplankton was conducted in a vacuum of information regarding the genetic structure of natural populations. Starting with the studies of King (1972, 1977a) on rotifers and Hebert (1974a,b,c) on cladocerans, it has become progressively more clear that zooplankton populations are assemblages of genetically diverse individuals. The question posed in this paper is: so what? Does the fact that natural populations are genetically diverse really have an important impact on the ecological analysis of these populations? Do genes do anything other than contribute to the "fine-tuning" of the relationship between the organisms and its environment? And

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finally, does the "packaging" of the genetic variation in the population through space and time influence ecological measures of population dynamics?

To examine these issues, I will focus on the effects of genetic structure on the population dynamics and distributions of rotifer populations in temporally varying environments.

THE STRUCTURE OF ROTIFER POPULATIONS

Each of the three classes in the Phylum Rotifera has a different mode of reproduction. In this paper I will deal exclusively with the Class Monogononta whose species are typically described as cyclic parthenogens. In this mode of reproduction (King, 1977a, King & Snell, 1977) diploid ameiotic parthenogenesis by amictic females produces clonal offsprings whose genetic composition is identical to that of their parents. Sexual reproduction is also known to occur in many species. Mictic (sexual) females produce haploid eggs by meiosis. If unfertilized, these eggs develop into haploid males; if fertilized, they develop into diploid resting eggs which hatch to start a new cycle of amictic reproduction.

Euchlanis dilatata is a littoral rotifer with a broad distribution in freshwater lakes and ponds of the temperate zone. It has long been a favorite for studies of population dynamics because this species also has the ability to survive and reproduce in a variety of laboratory environments (reviewed by King, 1967). Based on these criteria, *E. dilatata* appears to be a broad-niched generalist. To investigate the role of physiological acclimation in relation to niche breadth, King (1972) made a series of collections on this rotifer from a small lake in central Illinois, U.S.A. From April 17 to June 26 the surface temperature and relative abundance of *E. dilatata* underwent the changes showed in the left panel of Fig. 1. A series of clones from each collection was established, and after one week the descendants of each female were split into two groups. One group was placed at 19°C and the other at 27°C. Each group was maintained at these temperatures for ten generations and then used for life table experiments at both temperatures. That is, both the 19°C and the 27°C acclimation groups were tested at both 19°C and 27°C. These four treatment combinations were designated using hyphens to separate the acclimation and experimental temperatures. For instance, the (19-27) group was acclimated to 19°C and used in experiments conducted at 27°C while the (27-19) group was acclimated to 27°C and used for experiments conducted at 19°C.

Instantaneous rates of increase (r) and net reproductive rates (R_0) are expected to be higher at higher temperatures. Additionally, at the same temperature, acclimated animals are expected to have higher reproductive rate than that non-acclimated animals. However, if life-history measures reflect only such Q_{10} and acclimation effects and experimental conditions are held constant, there should not be a significant difference between reproductive rates of clones established from different collections. The center and right panels of Fig. 1 present two of the comparisons made in King (1972). As expected, acclimated females had higher reproductive rates than non acclimated individuals. However, clones established from collections made in June, when the water was warmer, had higher rates of increase and net reproduction at 27°C than did clones collected on May 1. The reverse was true for clones from cool-water conditions; clones

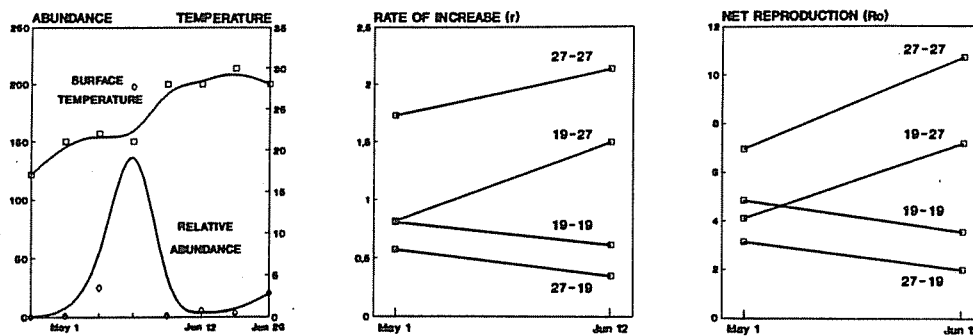
Euchlanis dilatata

Figure 1. Left panel: Change in surface temperature and relative abundance of *Euchlanis dilatata* in Allerton Park, Illinois. Center and right panels: rate of increase (r) and net reproduction (R_0) of *Euchlanis dilatata* clones collected on May 1 and June 12. Experimental treatments are identified by a pair of numbers the first of which is the acclimational temperature and the second of which is the experimental temperature.

established from the May 1 collection had higher population growth and reproduction rates at 19°C than did clones from the June 12 collection. These results were taken to indicate that the genetic structure of the *E. dilatata* population underwent seasonal changes paralleling the environmental changes. That is, instead of having one group of broad-niched generalists, King (1972) suggested that there is a seasonal succession of narrow-niched clones, each of which is optimally adapted to only a small part of the annual environmental spectrum.

Three models of the adaptive structure of rotifer populations, shown in Fig. 2, were proposed by King (1972). In the first (top panel), temporal variation is met with physiological changes. As seasonal environmental change progresses, fitness under Model I is maintained by acclimational rather than genetic changes. Consequently, all five of the hypothetical clones have the same growth patterns and total population size is simply the sum of the individual abundances of all five. The second model (center panel) envisioned adaptation to seasonal change at the population level as involving changes in relative frequencies of the different clonal genotypes in the population. Under this model, individuals representing all genotypes emerge from their resting eggs at approximately the same time. As seasonal environmental change progresses, first one genotype and then another increases in relative frequency. Model II assumes weak interclonal competition and predicts a high degree of genetic polymorphism at any single time. The third model (bottom panel) also envisioned adaptation as being dependent on genetic change. However, unlike Model II, Model III assumes strong interclonal competition and the occurrence of resting egg hatching and sexual reproduction

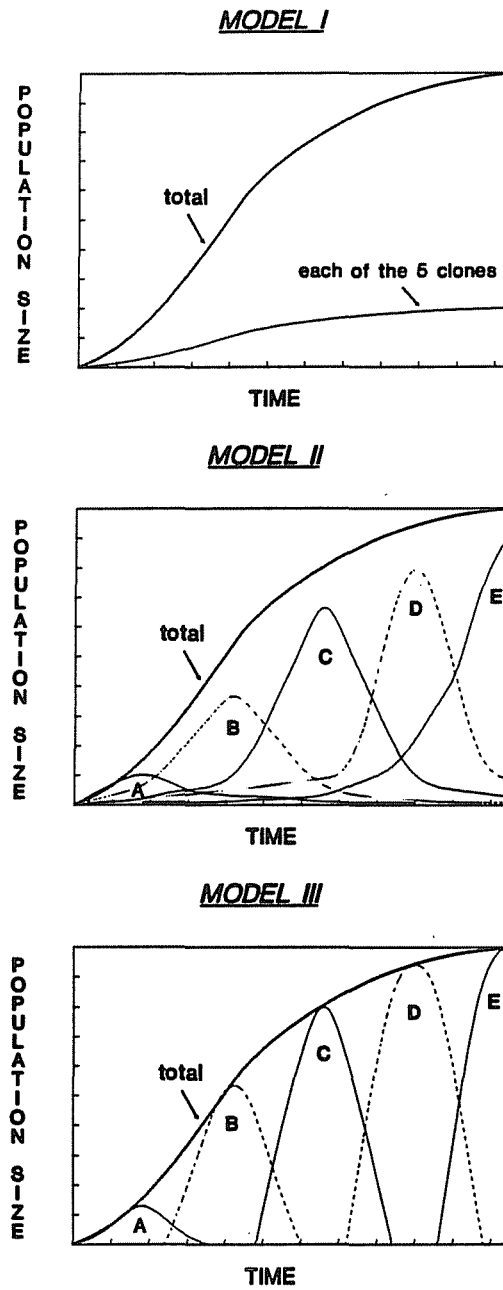


Figure 2: Models of rotifer populations structure proposed by King (1972). Top: Model I- physiological acclimation. Center: Model II- incomplete genetic discontinuity. Bottom: Model III- complete genetic discontinuity.

throughout the seasonal cycle. Under Model II clonal diversity at any point in time is expected to be much lower than in the second model.

King (1972) demonstrated that Model I did not adequately describe the adaptive structure of *E. dilatata*. However, because he had no direct measures of allele or clone frequencies, it was not possible to distinguish between the predictions of Models II and III. This problem was overcome in a later study (King, 1977a, 1980) by the application of polyacrylamide gel electrophoresis to seasonal changes of isozyme frequencies in the rotifer *Asplanchna girodi*. It was found that periods of relative stasis of genotype frequencies were followed by rapid change. The most striking of these occurred in a population that on May 6 appeared to be composed exclusively of heterozygotes for two alleles at a malic enzyme locus. One week later, on May 13, the population was dominated by homozygotes for a third allele at the same locus. Moreover, the dynamics of the population also underwent a dramatic change (Fig. 3). Mean instantaneous rates of increase (r), net reproductive rates (R_0), life spans (LS) and equilibrium population sizes (K) under standard laboratory conditions were all significantly different for the two genotypes. The two genotypes are clearly different ecotypes. This evidence supported the genetic structure proposed in Model III.

These results can be used to address the questions posed in the Introduction. It is clear that there was a radical genetic change in population structure between May 6 and May 13. However, this genetic change was not accompanied by a morphological change. An ecological investigation of this system would not have recognized the change in population structure and, therefore, would have confounded the dynamics of the two groups. The results obtained would have had an artificially high variance and lead to an inaccurate description of the system.

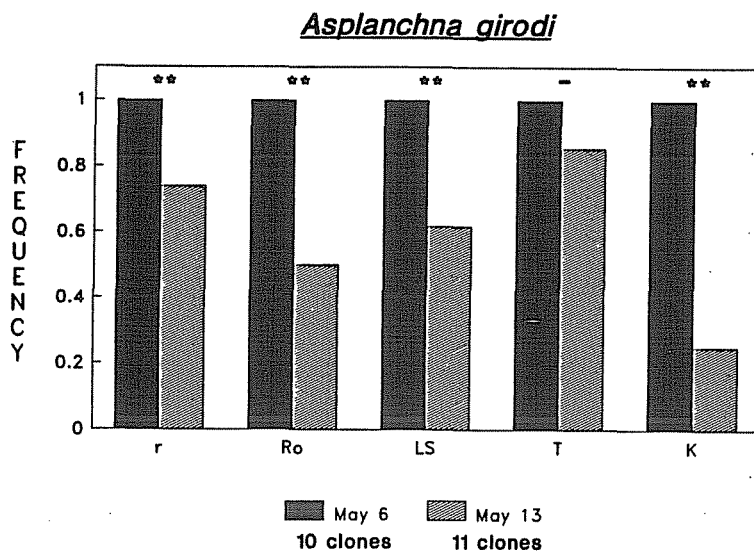


Figure 3: Population dynamics of two electromorphs of *Asplanchna girodi* collected one week apart from Golf Course Pond, Florida **: $p < 0.01$, -: $p > 0.05$ by one-way analysis of variance.

In another study, Snell and King (1977) measured the life history characteristics of *Asplanchna brightwellii*. Seven clones were studied from each of three collections at three different temperatures. Survivorship and reproductive rates were found to be more variable between than within collection dates. These results are also consistent with Model III.

The population structure described by Model III requires three elements to maintain ecological and genetic separation of clones adapted to different environmental conditions. First, there must be strong competition between ecotypes. Evidence for such competition was provided by Snell (1979) in an elegant series of experiments conducted with *Asplanchna brightwellii*. Second, there must be frequent sexual reproduction so that recombination occurs within ecotypes and very little, if any, gene flow occurs between ecotypes. There is ample evidence from natural populations that this requirement is also met; many studies have noted the frequent presence of rotifer males and females carrying resting eggs in plankton collections (see King, 1980; King and Snell, 1980). The third requirement is for frequent or continuous hatching of resting eggs to provide a source of new genetic input to the population. Until recently no information was available on this point. Important observations on resting egg hatching frequencies appear in the work of Arndt (in press) who has followed the annual abundance cycles of several rotifer species living in brackish areas of the Baltic Sea. Rotifer resting eggs have higher densities than fresh water. By contrast, in the areas of the Baltic studied by Arndt, the shells of resting eggs floated to the surface after the neonates hatched. He therefore was able to determine that resting egg hatching occurs throughout the annual cycle. These observations provide support for the third critical assumption of Model III.

It is reasonable to predict that resting egg hatching is non-random in Model III populations. That is, if a resting egg hatches at the "wrong" time, the neonate will not be able to survive because of a mismatch between its genes and environment. To prevent loss of reproductive success by the sexual parents, there should be strong selection favoring the acquisition of environmental cues to stimulate resting egg development only at appropriate times. Since the temporal structure of rotifer populations is diverse, there should be a comparable diversity in hatching cues. Unfortunately, we have almost no knowledge of the factors that initiate development of rotifer resting eggs. This topic is an important subject for future research.

A completely different genetic structure has been found for the rotifer *Brachionus plicatilis* in Soda Lake, Nevada, U.S.A. Thirty-eight composite electromorphs were identified from electrophoretic variation of three enzymes scored on 138 clones established from collections made between August, 1980 and September, 1984. In all, six of the eleven enzymes assayed were variable and, unlike the *Euchlanis* and *Asplanchna* studies previously discussed, no evidence was found for seasonal succession of electromorphs. There was uniformly a great deal of genetic variation in single collections of *B. plicatilis*, and even more variation through time. This species, unlike the rotifers we considered above, is present in the lake for the entire year and neither males nor females carrying resting eggs were found in any of the samples from this habitat. King and Zhao (1987) therefore concluded that the *B. plicatilis* in Soda Lake constituted a single population.

In a subsequent paper (Zhao and King, 1989), the question of fitness

differences among the co-existing clones was addressed. Based on life table experiments conducted with seven of the composite electromorphs at different temperatures and food levels (Fig. 4), significant heterogeneity was found for rate of increase (r), net reproduction (R_0), and mean life span (not shown) both within and between treatments. Clearly the differences among the composite electromorphs are not selectively neutral. Instead, it seems likely that directional selection may be either too weak or of too brief a duration in Soda Lake for clonal exclusion to occur. In contrast with the *Euchlanis* and *Asplanchna* populations, the genetic structure of *B. plicatilis* in Soda Lake appears to be best described by Model II. Significantly, as mentioned earlier, this is the only rotifer so far studied with genetic analysis that (a) is a permanent, year-around population and (b) for which there is no indication of sexual reproduction. This population, like some *Daphnia pulex* populations (Hebert, 1987), may be an obligate parthenogen.

In other studies of *B. plicatilis* allozymes, both Snell and Winkler (1984) and Serra and Miracle (1985) found that between-locality genetic variation was greater than within-locality variation. A particularly interesting approach was taken by Carmona, Serra and Miracle (1989), who used SDS polyacrylamide gels to score total protein variation on 42 clones from 9 coastal lagoons in Spain. Low levels of intrapopulational and relatively high levels of interpopulational variation were found in this study. Strain differences in electrophoretic genotypes have also been reported by Fu, Hirayama, and Natsukari (1990, 1991). It seems likely that the genetic structure of *B. plicatilis* (the "white rat" of the rotifer world because of its broad distribution, ease of culture, and frequent utilization in rotifer research) will be found to vary from one environmental type to another.

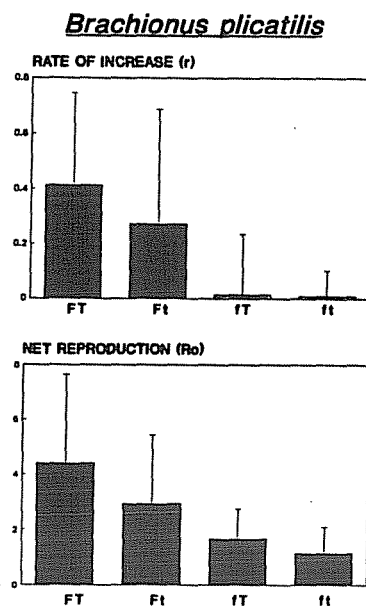


Figure 4. Population dynamics of ten clones representing seven composite electromorphs of *Brachionus plicatilis* and their standard errors. Experimental conditions: F= 300,000 cells/ml and f=60,000 cells/ml of *Dunaliella salina* at experimental temperatures of T=27.5°C and t=19.5°C.

CONCLUSIONS

Except under the most unusual circumstances, extensive genetic variation is a basic characteristic of natural populations. One important consequence of genetic diversity is intrapopulational variation in rates of reproduction and survival. From this perspective, genetic variation provides the basis for spatial and temporal population subdivision. While it is true that these relationships may be important in any population, they are particularly likely to influence the results of ecological research with zooplankton because many species have parthenogenetic reproduction.

Each individual in a sexual population is expected to be genetically unique. The problem facing the ecologist wishing to study the dynamics of a sexual population is to sample adequately its allelic combinations. Such measures will primarily reflect genic diversity at loci influencing survival and reproduction; while genes are reshuffled from one generation to the next by recombination, the distributions will seldom change very quickly. Recombination retards the effects of natural selection. By contrast, under diploid ameiotic parthenogenesis, clones transmit their genomes to their descendants without change. Under these circumstances the variance of life history measures will reflect both the variance in allelic combinations and the frequency distribution of clones in the sample. Thus the risk of inadequate sampling is potentially greater in asexual populations. Moreover, because clone frequencies in a parthenogenetic population under natural selection are likely to change more rapidly than allele frequencies in sexual population (King, 1977b), there is more potential for temporal variation in population dynamics. This problem may also be exacerbated by random genetic drift acting on clone frequencies (King, 1992).

Differences in genetic structure of the types described by Models II and III may have profound effects on the variation observed in life history measures. In some populations, such as the *B. plicatilis* in Soda Lake, many clones coexist, and the dynamics of a random sample of individuals is likely to have a high variance both within and between different collections. In other populations, such as the *Asplanchna girodi* from Golf Course Pond or the *Daphnia longispina* in El Tobar (King and Miracle ms submitted), the entire population may be dominated by one or two clones in one sample and one or two different clones at the next sampling time. Life history measures in these populations are expected to have a low variance among individuals collected at the same time and a high variance among individuals collected at different times.

These are not the small differences that would exist if genetic variation only provided the "fine tuning" for ecological adaptation. Life table experiments are mirrors held up to the population's genetic structure. Without a knowledge of that structure, the life table reflection is unlikely to provide a meaningful ecological description of the population.

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