THE IMPACT OF GENETIC STRUCTURE ON THE DYNAMICS OF ZOOPLANKTON POPULATIONS

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ABSTRACT

Data on the genetic structure of parthenogenetic rotifer and *Artemia* 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 reproduction are detected among individuals collected at the same time and high variances are found between collections made at different times. In contrast, high variances in 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 to lack sexual reproduction.

Our research with parthenogenetic *Artemia* has focused on the effects of polyploidy on the dynamics of sympatric diploid and polyploid brine shrimp. Using life history characters to measure relative fitness, we show that diploids have higher fitness than polyploids under optimal conditions in the laboratory. Research in progress indicates that this situation may be reversed in stressful environments, where polyploids show a clear increase in relative fitness. These findings, although based on only three sympatric populations, correspond with the zoogeographic distribution of *Artemia* polyploidy in coastal populations. Polyploids tend to increase in relative frequency at the edges of the species' distribution in both high and low latitudes where thermal stress may be greater. In addition, our study reveals that sympatric diploids and polyploids have different responses to high salinity.

These studies demonstrate that the genetic structure of a zooplankton population may have profound effects on its life history characteristics and dynamics. We argue that the dependency of life table parameters on genetic structure is likely to be a more important experimental 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. For this reason it is clear that researchers working with parthenogenetic species of zooplankton should include genetic as well as ecological parameters in their studies of population dynamics.

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 we pose 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 organism and its environment? And finally, does the "packaging" of the genetic variation through space and time influence ecological measures of population dynamics?

To examine these issues, two series of studies from our research will be reviewed. In the first we consider the effects of genetic structure on the population dynamics and distributions of rotifer populations in temporally varying environments. In the second we examine the effects of polyploidy on the dynamics and spatial distributions of *Artemia parthenogenetica.*

I. STUDIES WITH ROTIFERS

Each of the three classes in the Phylum Rotifera has a different mode of reproduction. In this paper we will deal exclusively with the Class Monogononta whose species are typically described as cyclic parthenogens. In this mode of reproduction (KING, 1977a, KING and SNELL, 1977) diploid ameiotic parthenogenesis by amictic females produces clonal offspring whose genetic composition is identical to that of their parent. 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.
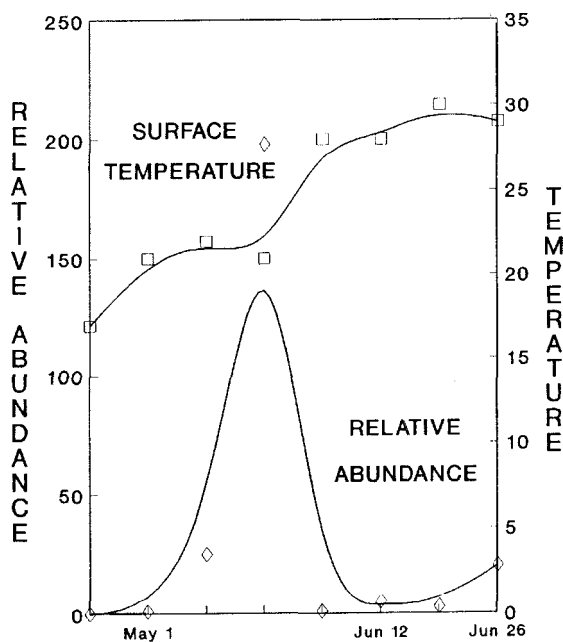

FIGURE I. Change in surface temperature and relative abundance of *Euchlanis dilatata* in Allerton Park, Illinois.

Euchlanis dilatata is a littoral rotifer with an extremely 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 of 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 shown in 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,) are expected to be higher at higher temperatures. Additionally, at the same temperature, acclimated animals are expected to have higher reproductive rates than non-acclimated animals. However, if life-history measures reflect only such Q,, and acclimational effects and experimental conditions are held constant, there should not be a significant difference between reproductive rates of clones established from different collections. Fig. 2 presents one 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 at 27°C than did clones collected on May 1. The reverse was true for clones from cool-water conditions; clones established from the May 1 collection had higher rates of increase at 19°C than did clones from the June 12 collection. These results were taken to indicate that the genetic structure of the E. *dilutata* 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 were proposed by KING (1972). In the first, temporal variation is met with physiological changes. As seasonal environmental changes progress, fitness under Model I is maintained by acclimational rather than genetic changes. The second model 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
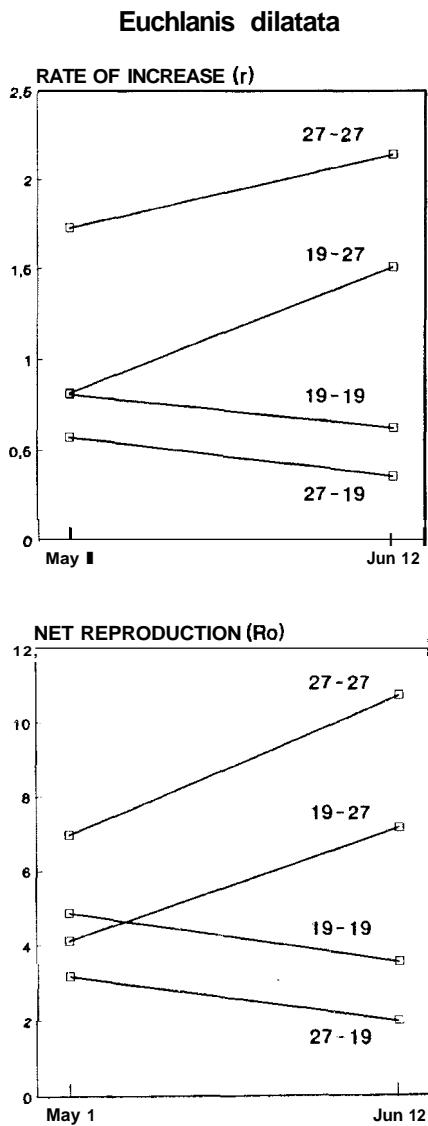
Euchlanis dilatata

RATE OF INCREASE (r)

27~27

19~27

19-19

27-19

May 1   Jun 12

NET REPRODUCTION (Ro)

27-27

19-27

19-19

27-19

May 1   Jun 12

FIGURE 2. Rate of increase (r) and net reproduction (R_0) of *Euchlanis dilatata* clones collected on May I 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.

environmental changes progress, 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 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 throughout the seasonal cycle. Given these conditions, under Model III at any given

time, clonal diversity 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 lacked direct measures of allele or clone frequencies, he could not 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 qirodi*. 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
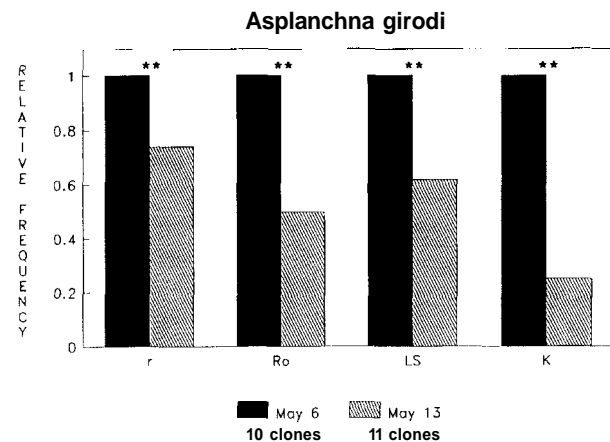
Asplanchna girodi

RELATIVE FREQUENCY

May 6 — 10 clones
May 13 — 11 clones

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

underwent a dramatic change (Fig. 3). Mean instantaneous rates of increase (r), net reproductive rates (R,), 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.

In another study, SNELL and KING (1977) measured the life history characteristics of *Asplanchna brightwelli.* 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 brightwelli.* 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 appears in the work of ARNDT (1992) 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 in lakes and ponds. 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 area of 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.
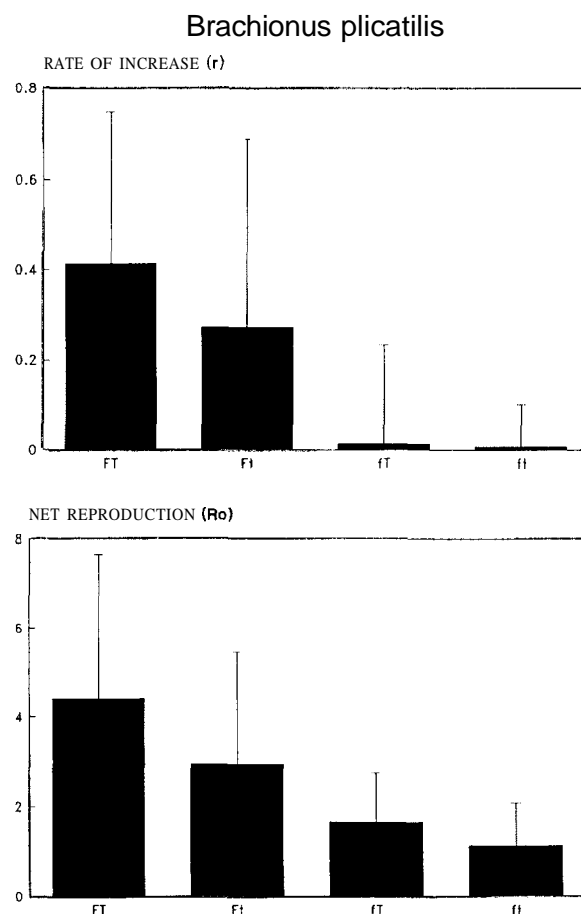
Brachionus plicatilis

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.

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,) 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
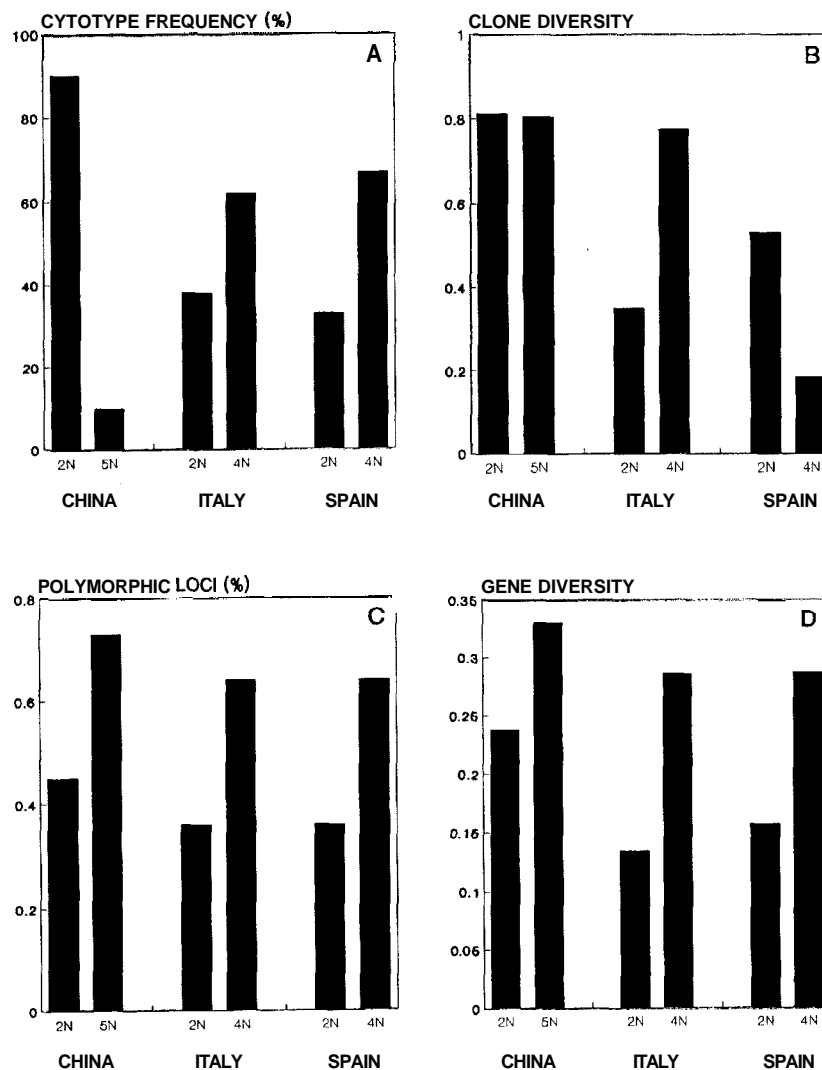

FIGURE 5. Genetic structure of sympatric diploid and polyploid clones of Artemia *parthenogenetica* from China, Italy, and Spain.

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.

II. STUDIES WITH Artemia

Members of the genus *Artemia* (Branchiopoda, Anostraca) are filter-feeding zooplankton that are widely distributed in inland salt lakes and solar salt works all over the world (VANHAECKE et al., 1987). In the New World these brine shrimp reproduce exclusively by sexual reproduction. In the Old world both obligate sexual and obligate asexual forms occur. The asexual forms are usually placed in one species, *Artemia parthenogenetica. Artemia* are capable of producing either active nauplii (ovoviviparous broods) or durable cysts (oviparous broods which are very stress-resistant), depending upon genotypic features and environmental conditions (VERSICHELE and SORGELOOS 1980, BROWNE et al. 1984). For a given genotype, cyst production tends to be induced by adverse conditions (TACKAERT and SORGELOOS, 1991; ZHANG and KING, 1993).

Our interest in A. *parthenogenetica* was stimulated by the fact that diploid and polyploid animals frequently co-occur in coastal salterns. This sympatry facilitates separating the independent influences of cytotype and environment that confound many studies of the adaptive significance of polyploidy. Details of this work are presented in ZHANG and KING (1992; 1993).

A saltern is a series of interconnected, man-made ponds used to produce salt. From the first pond, which receives a sea-water input, to the last, salinity gradually increases because of evaporation as the water flows from one pond to the next. Three populations collected from coastal salterns were used in this research. We collected cysts of one population from the Dong Fang Hong saltern on the Shandong Peninsula of NE China (KING et al., 1988a,b). Approximately 90% of the individuals from this population were diploids; the remainder were pentaploids. Cysts from the other two populations (Italy and Spain) were provided by Dr. PATRICK SOKGELOOS of the Artemia Reference Center in Gent, Belgium. The Italian population was from a saltern in Margherita di Savoia. Italy

and contained approximately 38% diploids and 62% tetraploids. Parthenogenetic members of the Spanish population were from a saltern in San Lucar, Spain that contained approximately 34% diploids and 66% tetraploids. In addition, sexual A. *tunisiana* occurred in the San Lucar saltern but will not be discussed in this paper. These data are presented graphically in Fig. 5A and, along with the other genetic aspects of that research, are discussed in more detail elsewhere by ZHANG and KING (1992). The tetraploids in this study, and perhaps also the pentaploids, appear to have an autopolyploid origin.

Approximately 50-60 individuals of each cytotype in each of the three populations were subjected to electrophoresis and scored for variation at 11 enzyme loci. Fig. 5B-D show that polyploids have consistently higher frequencies of polymorphic loci and higher gene diversities than the diploids. These results indicate that genetic divergence has occurred between the diploids and polyploids following their separation by the autopolyploid event.

Again, the central question we wish to pose is: "How do these major differences in genetic structure influence the dynamics of the two cytotypes?" This question can be addressed by examining the results of life table analyses performed under optimal conditions (25°C and 90 ppt salinity) using 20-23 randomly-selected individuals from each cytotype and population. Experimental details of this study are presented in ZHANG and KING (1993). We found that diploids from the three populations had much higher intrinsic rates of increase, higher fecundities, and faster developmental rates than their sympatric polyploids (Fig. 6). Life spans of Chinese pentaploids were shorter while life spans of Spanish tetraploids were longer than those of their sympatric diploids. No significant difference was observed between the life spans of Italian diploids and tetraploids. Most zooplankton, including *Artemia,* have relatively short generation times and in these organisms life span is seldom an important component of fitness because early reproduction accounts for the major part of the population's instantaneous growth rate.

These results indicate that sympatric diploids and polyploids in our study have significant differences in most of the life history characteristics examined. Moreover, diploids have higher relative fitness than their sympatric polyploids under optimal laboratory conditions. This observation creates a problem: if polyploids are inferior to diploids, how can the two cytotypes coexist?

To answer this question we focused on the Chinese population and examined life history responses of the two cytotypes to variation in temperature (16°C vs. 25°C) and
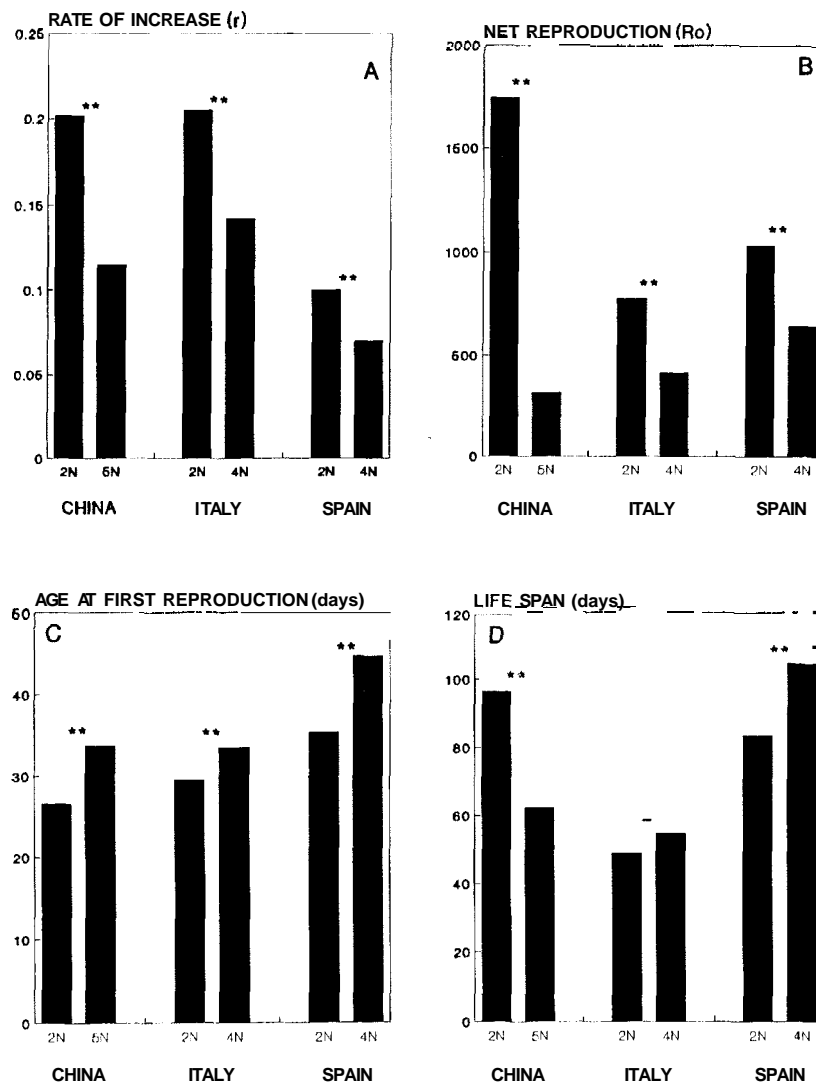
RATE OF INCREASE (r)

A

0.25
0.2
0.15
0.1
0.05
0

2N 5N   2N 4N   2N 4N
CHINA   ITALY   SPAIN

NET REPRODUCTION (Ro)

B

2000
1500
1000
500
0

2N 5N   2N 4N   2N 4N
CHINA   ITALY   SPAIN

AGE AT FIRST REPRODUCTION (days)

C

50
40
30
20
10
0

2N 5N   2N 4N   2N 4N
CHINA   ITALY   SPAIN

LIFE SPAN (days)

D

120
100
80
60
40
20
0

2N 5N   2N 4N   2N 4N
CHINA   ITALY   SPAIN

FIGURE 6. Four measures of the population dynamics of sympatric diploid and polyploid clones of *Artemia parthenogenetica* from China, Italy, and Spain. **: $P<0.01$, -: $P>0.05$ by one-way analysis of variance.

salinity (35 ppt vs. 90 ppt. Table 1). At 25°C, both diploids and pentaploids had higher developmental rates at 35 ppt than at 90 ppt; however, the pentaploid clones that produced many nauplii at 35 ppt salinity produced only cysts at 90 ppt. When salinity is low and temperature is at a stressful level (35 ppt, 16°C), the net reproduction of diploids decreases by 59% relative to our results at 25°C, 90 ppt, while that of polyploids stays almost the same.

At stressful temperatures of 0°C and 37.5°C, pentaploid nauplii, juveniles and adults have a significantly higher thermotolerance than diploids; pentaploids are able to survive a short-term lethal heat shock (42°C) and still develop to reproduce while diploids can not (ZHANG and LEFCORT 1991; ZHANG and KING, unpubl. data).

These results suggest that in the Chinese population pentaploids may have an advantage under stressful temperatures and low salinities while diploids are clearly superior under optimal conditions. Thus, coexistence of the two cytotypes may reflect both temporal and spatial separation of their optimum habitats.

This hypothesis is supported by zoogeographic distributions of diploid and polyploid *Artemia* in coastal areas. Polyploid *Artemia parthenogenetica* tend to be found at high and low latitudes near the margins of the species' distribution (ZHANG and LEFCORT, 1991). In general, marginal environments tend to be more physiologically stressful than central environments. It will be interesting to study different cytotypes from other

Table 1. Life history characteristics (mean ± SE) of Chinese diploids and pentaploids under various temperatures (T:°C) and salinities (S: ppt). Data are pooled from the three clones of each cytotype.

Characteristic	T	S	Diploids	Pentaploids	ANOVA
Net reproduction	16	35	514±86	145±24	**
	25	35	909±97	46518	**
	25	90	1241±125	197±18	**
% offspring encysted	16	35	1.2±10	25.9±9.8	**
	25	35	5.8±1.4	38.9±7.4	**
	25	90	5.3±1.4	100	**
Age at first reproduction (days)	16	35	48.7±1.2	49.3±1.4	—
	25	35	23.0±0.0	17.3±0.5	**
	25	90	29.3±1.3	34.1±1.6	**

—: $P > 0.05$

**: $P < 0.01$

environments. For instance, as found by AMAT DOMENECH (1980) in Spain, most inland salt lake populations are composed of polyploids.

CONCLUSIONS

Except under the most unusual circumstances, extensive genetic variation is a basic characteristic of natural populations. As we have shown for both rotifers and *Artemia,* one important consequence of genetic diversity is intrapopulational variation in rates of reproduction and survival. In 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 a 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, 1993).

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.

ACKNOWLEDGMENTS

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