

The effects of pond duration on the life history traits of an ephemeral pond crustacean, *Eulimnadia texana*

Vivien Marcus & Stephen C. Weeks

Department of Biology, University of Akron, Akron, OH 44325-3908, USA

Key words: Conchostraca, evolution of aging, senescence, branchiopod

Abstract

We examined the relationship between pond duration and life history characters of the clam shrimp *Eulimnadia texana*, a species inhabiting ephemeral ponds in southwestern North America. Since the shrimp live in temporary habitats, we predicted that there should be high selection pressure on life history characteristics associated with rapid development (e.g., fast growth, early maturity, etc.), rather than selection for increased longevity. Pond duration was estimated using a combination of average monthly rainfall and pond size (surface to volume ratio). Shrimp that live in smaller ponds (high surface to volume ratio) in areas with low average rainfall should, on average, experience a shorter total time available for development than those in larger ponds or in areas of higher rainfall. These shrimp should have an earlier age at maturity, reduced longevity, lower fecundity, and faster growth. Five replicate populations of clam shrimp were collected as cysts from five ponds. These shrimp were raised in a common garden experiment in the laboratory. Daily measurements of growth and egg production were taken and ages at maturity and death were recorded. Shrimp from areas with higher average rainfall had slower growth, higher fecundity, greater longevity, and an earlier age at maturity than those from areas with lower average rainfall. If average rainfall is an accurate measure of pond duration, then the first three of these life history traits differ in the directions expected. However, age at maturity varied in a manner opposite to that expected, being earlier in the ponds with longer duration. Surface to volume ratio was not helpful in further resolving differences in these life history characters.

Introduction

Modern studies of the aging process have begun to incorporate ideas influenced by evolutionary biology (Service et al., 1985; Templeton et al., 1985; Friedman & Johnson, 1988; Egilmez & Jazwinski, 1989; Jazwinski, 1993; Chippindale et al., 1994). In particular, many scientists have recognized that the ultimate cause of aging is the declining force of natural selection with increased age (Williams, 1957; Medawar, 1952). There are two major theories on the population genetic mechanisms involved in the evolution of aging, both of which center on the separation of the germ line from the soma (Rose, 1991). Both theories are united under the assumption of a declining force of natural selection with increased age.

Although most of the work on the evolution of aging has been on fruit flies and nematodes (reviewed in Rose, 1991), new model organisms have also been proposed. Reznick (1993) suggested the use of ephemeral pond branchiopod crustaceans for study of the evolutionary biology of aging. These crustaceans have several qualities conducive for such study: they are small, easily cultured in a laboratory, have a high fecundity, and short generation time. Additionally, the life cycles of these crustaceans may be strongly influenced by one major abiotic factor, pond duration. Average pond duration constrains the length of life and time available for reproduction. Therefore, it would be logical to assume that pond duration is important in shaping life history characters (Reznick, 1993).

Pond duration can be influenced by a number of factors, including average rainfall, evaporation rate

(influenced by surface to volume ratio, daily temperature and relative humidity), and soil type, the first two factors potentially being the most important. Ponds with lower average rainfall and high evaporation rate should have shorter duration. Branchiopod populations that live in ponds of shorter duration should reproduce more quickly than those that live in ponds of longer duration. In the former, there should be selection for alleles that facilitate early reproduction, and since only so much time is available, it would not be expected that increased longevity would be advantageous. Therefore, one could also predict earlier senescence in shorter- than in longer-lived ponds (Reznick, 1993).

In the current study, we used the conchostracan *Eulimnadia texana* Packard to address the question of whether pond duration affects the life histories of its inhabitants. In particular, we were interested in testing the assumption that selection pressures in short-lived ponds would lead to faster growth, decreased age at maturity, lower lifetime fecundity, and early senescence (Rose, 1991). To test these predictions, life history parameters (daily growth, fecundity, age at maturity, and longevity) of these shrimp were measured and compared among five ponds that differed in average rainfall and expected evaporation rate (estimated by surface to volume ratios).

Background

The clam shrimp, *Eulimnadia texana*, is a branchiopod crustacean found in ephemeral freshwater habitats in deserts and plains of the southwestern United States. Ponds appear due to monsoon-like spring and summer rains, and vary in size and duration. The shrimp lay cysts (actually encysted embryos) which are desiccation resistant, and which remain in a resting phase when dry (Belk & Sissom, 1992). The embryos develop to a pre-larval stage, but remain dormant until the right environmental conditions are present for them to hatch.

Eulimnadia texana has a rare mating system known as androdioecy (Sassaman & Weeks, 1993) where populations consist of males and hermaphrodites. Hermaphrodites can mate with males or self-fertilize, but they cannot mate with other hermaphrodites (Sassaman & Weeks, 1993). Two morphologically indistinguishable types of hermaphrodites exist: when selfed one produces only hermaphroditic offspring (monogenic) while the other produces hermaphrodites and males in a 3 to 1 ratio (amphigenic) (Sassaman & Weeks, 1993).

Table 1. Site locations and surface to volume ratios. See text for description of calculations of S/V ratio.

Site	State	Latitude	Longitude	S/V Ratio
BAP	AZ	31° 55.821' N	109° 55.125' W	6.6
SWP5	NM	32° 31.933' N	106° 44.933' W	4.6
JT3	NM	32° 29.853' N	106° 44.448' W	3.3
WAL	AZ	31° 58.167' N	109° 07.535' W	2.6
JT1	NM	32° 29.525' N	106° 44.321' W	1.7

Materials and methods

Soil containing cysts was collected from 5 sites in New Mexico (3) and Arizona (2) in June of 1995 (Table 1). These sites were chosen on the basis of pond size differences and the presence of *E. texana*. Soil samples were randomly taken from several sites around each pool. Only the top 1–3 cm of soil was taken from any site. The soil was stored in air-tight plastic bags until needed for hydrations. Soil from each site (500 ml) was hydrated using aged tap water which was aerated for several days prior to use. Soil containing eggs of *E. texana* was placed in the bottom of 27 liter aquaria. Aged water (28 °C) was added and the mixture was stirred to stimulate the hatching of cysts. The aquaria were kept in an environmentally controlled room between 28 and 32 °C under continuous light from sun-light simulating fluorescent bulbs (Durotest, Inc.). The tanks were also aerated. Fifty milliliters of a yeast suspension (1 gm dried baker's yeast per 100 ml water) was added to each tank daily. The tanks were stirred (two times per day for 1 min) for two days after hydration.

Under our laboratory conditions, *E. texana* eggs hatch within 18–36 hours after hydration, with no additional hatches after this period (V. Marcus, pers. obs.). Therefore, age reported herein is ± 9 hours, and is based on time since hatching rather than time since hydration. Juvenile clam shrimp were individually isolated in 500 ml cups 3 days after hatching. Water for the isolation cups came from a second set of tanks with soil (known not to contain any branchiopod crustacean eggs) and aged tap water, which had been allowed to aerate for 3 days before use. Each isolate was fed 2 ml of yeast suspension on the first day of isolation, and 1 ml of yeast suspension every day thereafter. The isolated shrimp were also raised in a temperature controlled room under continuous light and consistent temperature (28–32 °C) conditions (Sassaman & Weeks, 1993). Thus, the shrimp were raised in a 'common gar-

den' style experiment where each replicate block was exposed to the same abiotic conditions.

Daily growth measurements and egg counts were performed using NIH Image software and a Power Macintosh computer. To capture an image, a shrimp was removed from its cup, and placed with a small amount of water into a petri dish. Then an image was recorded, and the shrimp was returned to the cup (the whole process usually took less than 30 seconds). Length was measured daily, starting on day 4, by measuring maximal carapace length on lateral images of the shrimp. Age at maturity was determined by the day at which developing eggs or eggs in the brood chamber were first noted in the hermaphrodites. Males were identified by the formation of claspers on the first two pairs of phyllopoas. Males, once identified, were not used further in this experiment. Daily fecundity was calculated by counting the eggs produced the previous day by each hermaphrodite. The eggs were collected from the bottoms of the rearing cups with a plastic pipette every 24 hours (at a consistent time of day) and stored for later counting. Longevity was determined by the length of time (in days) each individual survived.

The length, width, and average depth of the ponds for each population were measured. Most ponds were essentially rectangular. Therefore, from these measurements, volume (length \times width \times depth) and surface area (length \times width) were calculated to estimate the surface to volume ratios for the ponds.

Rainfall data were obtained from the National Climatic Data Center database on the World Wide Web. Average monthly rainfall was collected for Arizona (Portal, 1934–1995) and New Mexico (Jornada Experimental Range, 1914–1995). The recording stations are in close proximity (within 10 miles) to the ponds used in this study. No rainfall data was available for individual ponds.

The pools from New Mexico are located in the Jornada Range, northeast of Las Cruces. JT1 and JT3 are located on the east side of Jornada Road and are separated from one another by approximately 1 mile (Table 1). They are simple, man-made depressions in the soil, constructed to hold rainwater for cattle. The SWP5 site is on the west side of Jornada Road and is approximately 3 miles from JT3. This site is a simple, natural depression in the soil and is close to other, similarly small pools that may overflow into it in years with heavy rainfall. The pools from Arizona are located near Portal. The BAP site is nearby Portal Road (Rt. 533), and the nearest pond is approximately 0.5 miles away. The WAL site is approximately 7 miles

from BAP, located nearby Foothills Road. It is adjacent to a much larger pool, with a large earthen barrier separating the two. Both Arizona pools are also simple, man-made depressions with rectangular shapes. Since some of these depressions are man-made, they collect water from a specific area of each watershed which may not be equal for all ponds.

Statistical methods

The dependent variables used to compare populations were growth rate, lifetime fecundity, age at maturity, and longevity. Growth rate was estimated by computing the slope of daily length on the log of age. All variables were compared using a blocked, one-way ANOVA (analyzed with PROC GLM; SAS Inc., 1990) using replicates as blocks and populations as the independent variable. Blocks were considered random, whereas populations were considered fixed effects. Comparisons among geographic sites (Portal vs Jornada) were made using the CONTRAST statement of PROC GLM. Not all five populations were represented in each block; therefore Type IV sums of squares were used for tests of significance (SAS Inc., 1990). Tests of block by population interaction were not significant for any dependent variable, and therefore this factor was not included in any of the analyses reported here. Fecundity, age at maturity and longevity all required log-transformations to normalize distributions and to equalize variance among populations.

Results

Pond duration should be influenced by a combination of factors, including expected rainfall and pond drying rate. Monthly rainfall was consistently higher for the Portal, Arizona station relative to the Jornada station throughout the year (Figure 1). This difference was especially pronounced during the monsoon season (June through September; Figure 1). The second factor of pond duration, pond drying rate, was estimated by calculating a surface to volume ratio (Table 1). A high surface to volume (s/v) ratio for a pond was used to predict a faster drying time relative to ponds with a low s/v ratio. Using these estimates, pond surface to volume ratio ranged over nearly a factor of four, from large (JT1: 1.7) to small (BAP: 6.6) ponds. An overall estimate of average pond duration was calculated by separating first by average rainfall (i.e., geographic site), and then within geographic site by pond s/v ratio.

Table 2. ANOVA calculations. REP=Replicate, POP=Population, SITE=Contrast among geographic sites; AZ (BAP & WAL) vs NM (JT1, JT3 & SWP5).

Life history parameter	Source of Variation	DF	Type IV Sums of squares	F value	Pr>F
Growth	Replicate	4	36.07	24.40	0.0001
	Population	4	6.49	4.39	0.0021
	Site	1	5.35	14.47	0.0002
	Error	169	62.46		
Fecundity	Replicate	4	12.13	2.95	0.0217
	Population	4	30.96	7.53	0.0001
	Site	1	5.35	5.21	0.0237
	Error	169	173.74		
Maturity	Replicate	4	0.21	6.16	0.0001
	Population	4	0.30	8.84	0.0001
	Site	1	0.08	9.77	0.0021
	Error	169	1.45		
Longevity	Replicate	4	0.83	2.73	0.0310
	Population	4	1.98	6.53	0.0001
	Site	1	0.91	12.04	0.0007
	Error	169	12.81		

Using this method, the rankings for low to high pond duration was: SWP5, JT3, JT1, BAP, and WAL (see Figures 2–5).

Ages at maturity differed significantly among populations (Table 2), with the WAL population maturing earliest followed by JT3, BAP, and JT1 (Figure 2). The population that matured the latest was SWP5. The average age at maturity of the two Portal populations was significantly earlier than the three Jornada populations ($F_{1,169} = 9.77$, $P < 0.005$), though there was heterogeneity within each geographical region (Figure 2).

Longevity differed significantly among populations (Table 2), with the survivorship of the JT3 population being the shortest, followed by JT1. The SWP5, BAP, and WAL populations lived the longest (Figure 3). The average longevity of the two Portal populations was significantly greater than the three Jornada populations ($F_{1,169} = 12.04$, $P < 0.001$). Again, there was heterogeneity within each geographical region for average longevity (Figure 3).

Growth rate was significantly different among populations (Table 2). JT3 and SWP5 had the fastest growth rate of the five populations, whereas BAP and WAL had the slowest growth rates (Figure 4). The average growth rate of the two Portal populations was significantly lower than the three Jornada populations

($F_{1,169} = 14.47$, $P < 0.0005$), and these differences were consistent within each geographical region (Figure 4).

Total fecundity differed significantly among populations (Table 2), with the JT3 and BAP populations producing the least total eggs, while the WAL population produced the most (Figure 5). The average total fecundity of the two Portal populations was significantly greater than the three Jornada populations ($F_{1,169} = 5.21$, $P < 0.05$). Again, there was heterogeneity within each geographical region for average total fecundity (Figure 5).

Discussion

The clam shrimp *Eulimnadia texana* was used to address the hypothesis that average pond duration may affect life history characters associated with senescence. Pond drying was estimated using two factors: the pond's average monthly rainfall and surface to volume (s/v) ratio. Data for the former was only available on a regional basis, and thus ponds were grouped together by geographic site for these comparisons. In the latter, if the s/v ratio is high, the pond should dry faster, since more of the surface is exposed to evaporative water loss. Pond duration should affect the inhabitants of the ponds by restricting the expected length of life. Therefore, in short-lived ponds it is important for the shrimp to mature quickly, since the pond may not last long enough for them to reproduce if they mature slowly. The cost of this greater emphasis on early maturity can be reduced longevity (Haukioja & Hakala, 1978; Clutton-Brock et al., 1982, 1983). Evolutionary models of senescence place a high emphasis on early life history characters and a lowered emphasis on later life history, which is predicted to lead to earlier senescence (Medawar, 1952; Williams, 1957; Rose, 1991). Thus, in the current study, we tested the expectation that fast growth, early maturity, reduced lifetime fecundity, and reduced longevity would be found in the ponds with low average rainfall and high surface to volume ratios.

Although many of these ponds are man-made (<100 years old), rapid evolution in life history traits has been documented in a number of systems over periods of one to several decades (Stearns, 1983a, b; Hairston and Walton, 1986; Stockwell et al., unpubl.), and significant responses to selection have been recorded in as short as 4–7 years in populations of guppies (Reznick et al., 1990, 1997). Thus, we can expect phenotypic responses to important selective processes

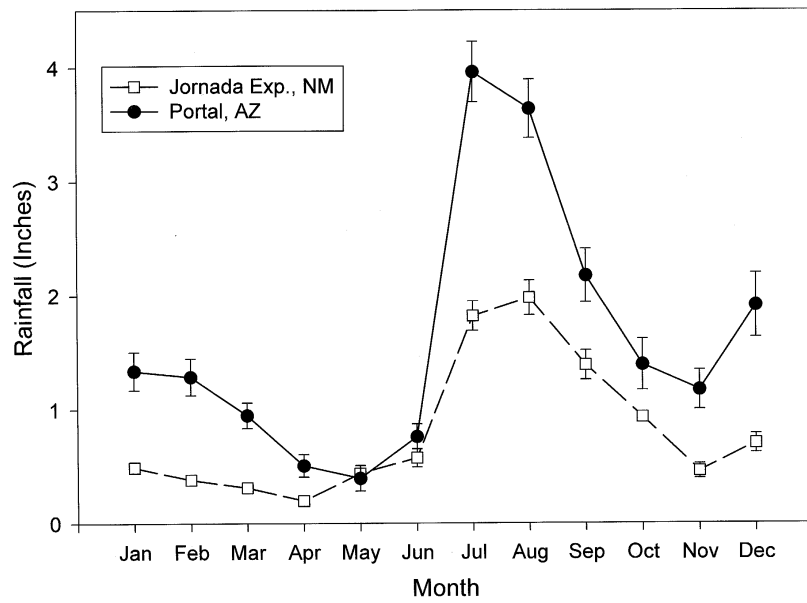


Figure 1. Average monthly rainfall for the Jornada Experimental Range, New Mexico (JT1, JT3, SWP5) and Portal, Arizona (BAP, WAL) ponds.

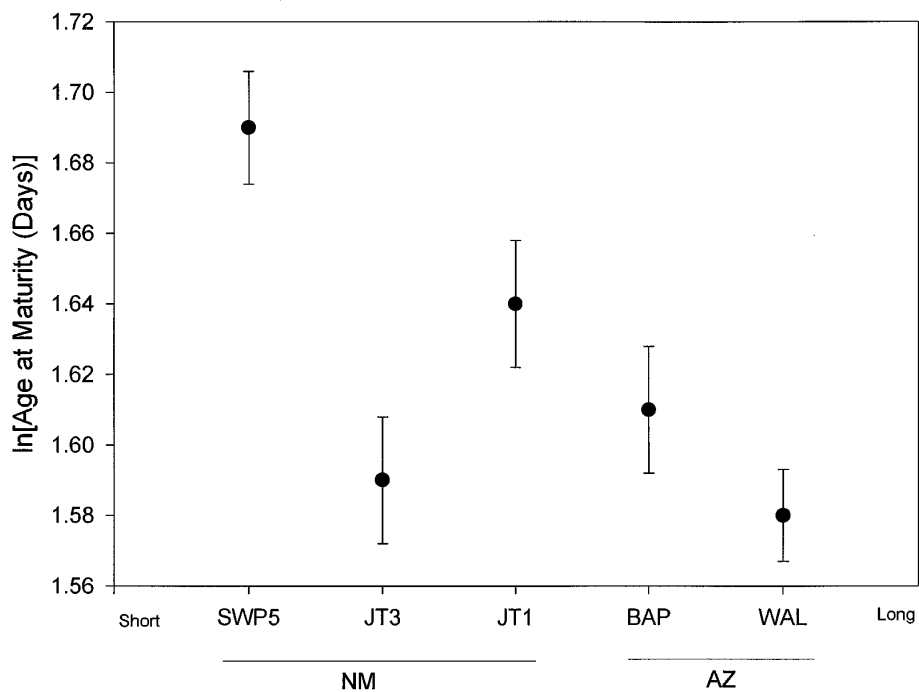


Figure 2. Natural logarithm of age at maturity per population. Population abbreviations are on the x-axis and are separated by geographic region (AZ & NM). Error bars portray one standard error of the mean.

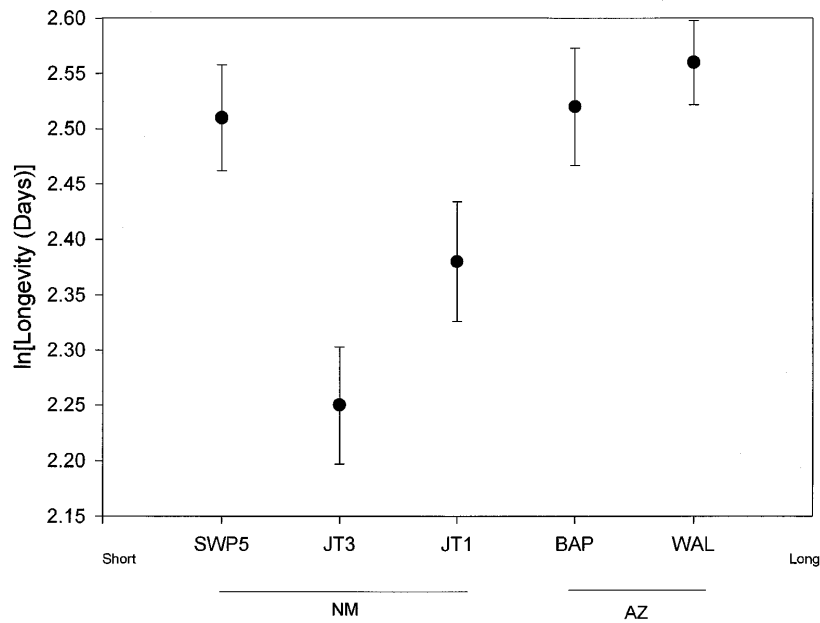


Figure 3. Natural logarithm of longevity per population. Error bars portray one standard error of the mean.

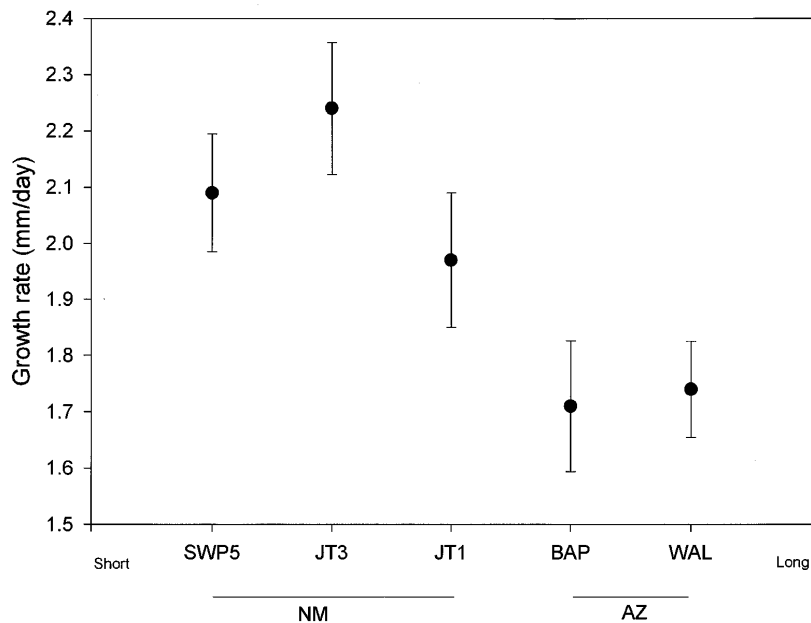


Figure 4. Growth rate per population. Error bars portray one standard error of the mean.

(such as average pond duration) even in these man-made ponds.

A faster drying pond is expected to have shrimp that mature earlier, allowing a greater likelihood of producing eggs before the pond dries. Using average rainfall

as an estimate of pond duration, the populations with higher average rainfall (Arizona populations: BAP and WAL) matured earlier than the those from New Mexico (JT1, JT3, SWP5) with a lower average rainfall. This is contrary to theoretical predictions, which assume that

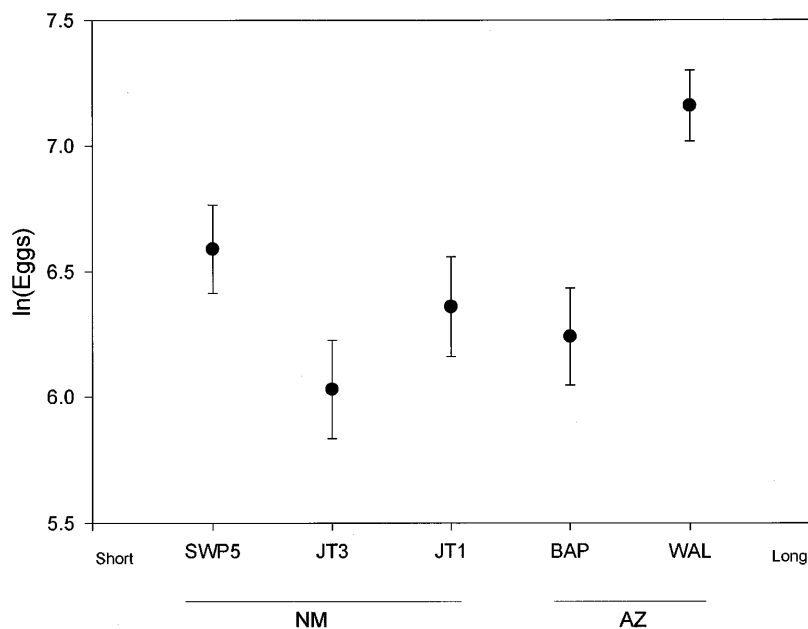


Figure 5. Natural logarithm of total fecundity per population. Error bars portray one standard error of the mean.

faster-drying ponds should select for earlier maturity. However, the ponds within regions were not consistently grouped, indicating no overall geographic effect (Figure 2). Additionally, considerations of pond size did not help to explain differences in maturity. The fastest maturing population was WAL, which also had one of the lower s/v ratios. The slowest maturing was the SWP5 population, which had the second highest s/v ratio. Clearly, age at maturity was not correlated with s/v ratios. Overall, estimates of pond duration did not sort out consistently with ages at maturity, which is an unexpected result (Reznick, 1993).

Longevity of shrimp inhabiting an ephemeral habitat, such as the ponds being studied, is also expected to be constrained by the duration of the habitat: shrimp inhabiting ponds that dry quickly should have a shorter expected life span than ones inhabiting slower drying ponds (Reznick, 1993). Over many generations, this de-emphasis on later life should result in earlier senescence in the early drying ponds (Reznick, 1993). The Arizona populations lived longer, on average, than the three New Mexico populations. If average rainfall is a good estimator of pond duration, this is consistent with the expectation that pond duration is positively correlated with longevity. However, not all New Mexico populations were consistent, with SWP5 shrimp living as long as the two Arizona populations (Figure 3).

Again, pond size was not correlated with longevity, either within or across geographic sites. The JT3 clam shrimp had the shortest longevity, even though this pond does not have the highest s/v ratio of the five ponds. The WAL population had the longest lifespan and had one of the lowest s/v ratios. Also, the JT1 population had one of the shortest life spans, but had the lowest s/v ratio. Clearly, there is no correlation between pond size and the longevity of these clam shrimp. Thus, overall there was no clear affect of pond duration on average longevity.

Pond duration may also affect other life history traits of its inhabitants, such as growth rate. If a pond has a short duration, the growth rate of the clam shrimp should be fast compared to clam shrimp in a slower drying pond because they may have to reach a certain size before they can be reproductively mature (Nijhout, 1975). Therefore, the clam shrimp from ponds of shorter duration should be selected to have a faster growth rate than those from ponds of longer duration. This expectation was met when considering the ponds by geographic region. The three New Mexico ponds (lower average rainfall) had consistently and significantly higher growth rates than the two Arizona ponds (higher average rainfall). Thus, if average rainfall is associated with pond duration, then shrimp from ponds of longer duration did grow more slowly than shrimp

from shorter-lived ponds (Figure 4). Once again, s/v ratio was not correlated with growth rate. The shrimp in the pond with the lowest s/v ratio (i.e., JT1) had a fast growth rate compared to those in ponds that had higher s/v ratios. Therefore, if average rainfall is more indicative of pond duration than s/v ratio, then these results are consistent with expectations.

Another life history trait that may be affected by pond duration is total lifetime fecundity. Ponds that last a short time may have shrimp that produce fewer eggs because of the time constraint on the longevity of the clam shrimp, as well as earlier reproductive senescence. *Eulimnadia texana* hermaphrodites display reduced egg production several days before death (i.e., reproductive senescence; Marcus, 1996; Weeks et al., in press). Shrimp from ponds of shorter duration may exhibit earlier reproductive senescence than those in longer-lived ponds. Again, this expectation was correct when considering differences in average rainfall. Shrimp from the Arizona ponds produced more total eggs, on average, than the New Mexico populations (Figure 5). However, this difference was primarily due to the greater lifetime egg production of the WAL shrimp, rather than a consistent pattern among ponds. Surface to volume ratio was again not correlated with total fecundity. Although, the population with the highest s/v ratio (BAP) had the second lowest total fecundity, and the population with the highest total fecundity (WAL) had one of the lowest s/v ratios, the remaining populations did not fit this expectation. Although a fast drying pond may select for shrimp that produce a lot of eggs early, ponds that last longer should select for shrimp that have a higher total lifetime fecundity because of the longer time available for reproduction. Considering both average rainfall and pond size, there was no consistent evidence that pond duration affected total lifetime fecundity.

Realistically, pond duration is the result of a combination of factors, including average rainfall and surface to volume ratio. For example, substrate composition may affect pond drying rate: if the soil making up the bottom of the pond is very water permeable, then a large pond might not last long, regardless of surface to volume ratio or rainfall. It is unclear how all of these factors combine to affect pond duration, and thus it is difficult to assign a weight to any single factor. Therefore, it would be preferable to gather average pond duration data for each pond directly (e.g., using remote sensing technology). The expectation of pond duration affecting life history characteristics may be a correct assumption, but our current estimates of pond

duration (via average rainfall and pond size) may be incomplete. A potential problem with measuring pond duration directly is that it may take years to do. The monsoon rains of the southwest are sporadic, and a particular pond may not fill for years. Thus, measuring pond duration in the field could be a very time consuming project.

This study was conducted using a reductionist approach: starting simply by looking at one factor, pond duration, that is expected to affect many traits. In reality, several factors are probably involved in shaping life history traits, which may confound the use of a simple model to explain variation in these life history traits. Other factors such as inbreeding depression and community composition may also have great impacts on the life history characteristics of organisms inhabiting ephemeral habitats. Therefore, additional factors such as these could have confounded any differences among populations expected by examining pond duration only.

In conclusion, the current experiment has produced mixed results in relation to expectations based on models of the evolution of senescence (Rose, 1991; Reznick, 1993). Except for growth rate, the current experiment has not produced any results that correlate well with evolutionary models of senescence. Each of the other factors (maturity, longevity, and fecundity) showed no consistent pattern with respect to the predictions of evolutionary models of senescence. Surface to volume ratio and average rainfall overall were not helpful in sorting out differences in these three life history characters. At this time, it is unclear how to combine rainfall and s/v ratios to determine pond duration accurately, nor if other important variables remain to be measured. Also, other biotic factors (e.g., competition, predation, inbreeding depression) can influence these life history traits. Additional studies that would increase pond sample size as well as directly measure pond duration would be extremely beneficial.

Acknowledgments

We thank D. Ott and J. Stinner for helpful comments on the design of this experiment, and D. Alexander, D. Ott, J. Stinner and two anonymous reviewers for critically reading earlier drafts of the manuscript. This project was funded, in part, by a Sigma Xi Grant-in-Aid of Research and by research funds from the Biology Department at the University of Akron to VM.

References

- Belk, D., & S. L. Sissom, 1992. New *Branchinella* (Anostraca) from Texas, USA, and the problem of antennalike processes. *Journal of Crustacean Biology* 12: 312–316.
- Chippindale, A. K., D. T. Hoang, P. M. Service & M. Rose, 1994. The evolution of development in *Drosophila mealongaster* selected for postponed senescence. *Evolution* 48: 1880–1899.
- Clutton-Brock, T. H., E. F. Guinness & S. D. Albon, 1982. Red deer – Behavior and ecology of the two sexes. University of Chicago Press, Chicago, Illinois, 378 pp.
- Clutton-Brock, T. H., E. F. Guinness & S. D. Albon, 1983. The cost of reproduction in red deer hinds. *J. anim. Ecol.* 52: 367–383.
- Egilmez, N. K. & S. M. Jazwinski, 1989. Evidence for the involvement of a cytoplasmic factor in the aging of the yeast *Saccharomyces cerevisiae*. *J. Bact.* 171: 37–42.
- Friedman, D. B. & T. E. Johnson, 1988. A mutation in the age-1 gene in *Caenorhabditis elegans* lengthens life and reduces hermaphrodite fertility. *Genetics* 118: 75–186.
- Hairston, N. G. Jr. & W. E. Walton, 1986. Rapid evolution of a life history trait. *Proceedings of the National Academy of Science USA*. 83: 4831–4833.
- Haukioja, E. & T. Hakala, 1978. Life history evolution in *Anodonta piscinalis* (Mollusca, Pelecypoda). *Oecologia* 35: 253–266.
- Jazwinski, S. M., 1993. The genetics of aging in the yeast *Saccharomyces cerevisiae*. *Genetica* 91: 35–51.
- Marcus, V., 1996. Senescence in the ephemeral pond crustacean, *Eulimnadia texana*. Master's Thesis, University of Akron, Akron, Ohio, 48 pp.
- Medawar, P. B., 1952. *An Unsolved Problem of Biology*. H. K. Lewis, London, 24 pp.
- Nijhout, H. F., 1975. A threshold size for metamorphosis in the tobacco hornworm, *Manduca sexta* (L). *Biol. Bull.* 149: 214–225.
- Reznick, D., 1993. New models for studying the evolutionary biology of aging: crustacea. *Genetica* 91: 79–88.
- Reznick, D., H. Bryga & J. A. Endler, 1990. Experimentally induced life-history evolution in a natural population. *Nature* 346: 357–359.
- Reznick, D., F. H. Shaw, F. H. Rodd & R. G. Shaw, 1997. Evaluation of the rate of evolution in natural populations of guppies, *Poecilia reticulata*. *Science* 275: 1934–1937.
- Rose, M. R., 1991. *Evolutionary Biology of Aging*. Oxford University Press, Oxford, 221 pp.
- SAS Institute, Inc., 1990. *SAS/STAT User's Guide, Version 6, Fourth Edition, Volume 2*. Cary, North Carolina: 1686 pp.
- Sassaman, C. & S. C. Weeks, 1993. The genetic mechanism of sex determination in the conchostracan clam shrimp *Eulimnadia texana*. *Am. Nat.* 141: 314–328.
- Service, P. M., E. W. Hutchinson, M. D. MacKinley & M. R. Rose, 1985. Resistance to environmental stress in *Drosophila melanogaster* selected for postponed senescence. *Physiol. Zool.* 58: 380–389.
- Stearns, S. C., 1983a. A natural experiment in life-history evolution: Field data on the introduction of mosquitofish (*Gambusia affinis*) in Hawaii. *Evolution* 37: 601–617.
- Stearns, S. C., 1983b. The genetic basis of differences in life history traits among six populations of mosquitofish (*Gambusia affinis*) in that shared ancestors in 1905. *Evolution* 38: 618–627.
- Templeton, A. R., T. J. Crease & F. Shah, 1985. The molecular through ecological genetics of abnormal abdomen in *Drosophila mercatorum*. I. Basic Genetics. *Genetics* 111: 805–818.
- Weeks, S. C., V. Marcus & S. Alvarez. Notes on the life history of the clam shrimp, *Eulimnadia texana*. *Hydrobiologia*, in press.
- Williams, G. C., 1957. Pleiotropy, natural selection, and the evolution of senescence. *Evolution* 11: 398–411.