Cyst bank life-history model for a fairy shrimp from ephemeral ponds

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SUMMARY

1. Ephemeral wetland habitats provide a useful model system for studying how life-history patterns enable populations to persist despite high environmental variation. One important life-history trait of both plants and crustaceans in such habitats involves hatching/germination of only some of the eggs/seeds at any time. This bet-hedging leads to the development of a bank composed of dormant propagules of many ages.
2. The San Diego fairy shrimp, *Branchinecta sandiegonensis* (Crustacea: Anostraca), a dominant faunal element of ephemeral ponds in San Diego, California, is a suitable organism for studying the consequences of highly fluctuating environmental conditions. As a result of large-scale habitat loss, the species is also endangered, and this motivated our specific study towards understanding the hatching dynamics of its egg bank for planning conservation efforts such as pool restoration and re-creation.
3. We formulated a matrix population model using egg age within the bank to study the relationship between adult survival and reproduction, and survival in and hatching from the egg bank. As vital rates for fairy shrimp are only poorly known, we generated 48 matrices with parameters encompassing ranges of likely values for the vital rates of *B. sandiegonensis*. We calculated population growth rates and eigenvalue elasticities both for a static model and a model with periodic reproductive failure.
4. The model shows that in good filling events, population growth rate is very high and the egg bank is increased dramatically. While population growth rate is insensitive to long-term survival in the egg bank in our static deterministic model, it becomes sensitive to survival in the egg bank when a regime of periodically failed reproductive events is imposed.
5. Under favourable conditions, it was best for shrimp to hatch from eggs as soon as possible. However, under a regime where failed reproductive events were common, it was best to hatch after several pool fillings. Because conditions change from favourable to unfavourable unpredictably, variation in age within the egg bank appears to be critical for the persistence of the population. This attribute needs to be carefully considered when restoring or creating new pools for conservation purposes.

Keywords: conservation, environmental variation, fairy shrimp, life history, matrix model

Introduction

Ephemeral freshwater ponds occur in places where a Mediterranean climate is accompanied by subsurface soils that form an impermeable layer. Water from winter rains collects in depressions but remains only until the ponds dry as a result of evaporation. In southern California, U.S.A., this type of pond is defined by its vegetation and is called a vernal pool (Holland, 1978; Zedler, 1987; Holland & Jain, 1988). The number of days ponds have standing water is strongly correlated to total yearly precipitation (E. T. Bauder, unpublished data) and the pattern of rainfall

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also affects pond duration. For example, in San Diego County, southern California, mean annual rainfall has been 25.5 cm (range of 8.8–67.0 cm) in the past 150 years (E. T. Bauder, unpublished data) and ponds can fill and dry several times during the winter if rainfall is sporadic, or hold water for longer periods if rainfall is more regular (Philippi *et al.*, 2001).

All obligately aquatic crustaceans inhabiting ephemeral wetlands exhibit the same basic life-history patterns: they have fast development to maturity (days to weeks) and persist through dry phases as desiccation-resistant propagules such as shelled dormant embryos (cysts) or ephippia (Hairston & Cáceres, 1996). Dormancy ends when the appropriate environmental cues (e.g. light, temperature) occur with hydration (Brendonck, Centeno & Persoone, 1996; Brendonck, 1996; Hathaway & Simovich, 1996; Brendonck *et al.*, 1998). However, in this environment, organisms must have life-history adaptations that allow them to take advantage of ponds filling when it occurs but still 'hedge their bets' against the possibility of ponds drying before the life cycle is completed, so that only a fraction of the viable cysts hatch in any single hydration event (Brendonck, 1996; Simovich & Hathaway, 1997). As such, large numbers of cysts can accumulate in the soil after several years of reproduction. This cyst bank ensures that even if all adults die without reproducing in one or more filling events, the population will not be extirpated (Brendonck & Riddoch, 2000; Philippi *et al.*, 2001).

Cyst banks resemble the seed banks of annual plants in many ways (Brock *et al.*, 2003) and similar theoretical approaches have been used to try to predict the patterns of both hatching and germination relative to environmental conditions. Several mathematical models have been used to study questions relating to the evolutionary consequences of seed banks for annual plants (Cohen, 1966, 1968; Templeton & Levin, 1979; MacDonald & Watkinson, 1981; Schmidt & Lawlor, 1983; Ellner, 1985a,b; Brown & Venable, 1986; Venable & Brown, 1988; Kalisz & McPeek, 1992, 1993; Tuljapurkar & Istock, 1993) and egg banks in lacustrine copepods (Cáceres, 1997; Easterling & Ellner, 2000). However, only some of these models have included structure in terms of age or availability for hatching or germination in the egg or seed bank (MacDonald & Watkinson, 1981; Schmidt & Lawlor, 1983; Tuljapurkar & Istock, 1993; Cáceres, 1997; Easterling & Ellner, 2000), although

Tuljapurkar & Istock (1993) and Easterling & Ellner (2000) have shown that incorporating structure in the propagule bank in models leads to different conclusions about evolutionary consequences, compared with models ignoring it. It is therefore important to consider propagule bank structure in these models.

Spatial compartments have been considered for copepods in lakes; cysts that are near the sediment surface and are available for hatching and those that are more deeply buried in the sediment and unavailable for hatching contribute differently to the population dynamics (Easterling & Ellner, 2000). In the vernal pools of southern California, as sedimentation is negligible and the entire cyst bank is present in a few centimetres of soil, the type of spatial structure modelled for lacustrine copepods is not required. Instead, age structure in the cyst bank of these organisms is an important type of structure to be incorporated in a model, as for seed bank models for annual plants (MacDonald & Watkinson, 1981). The length of time cysts or seeds stay dormant is critical to understand the population dynamics when pool filling and drying is unpredictable enough to have any impact on reproductive success.

Ephemeral wetlands worldwide have experienced and continue to experience large-scale losses as a result of urban expansion, agricultural conversion, and other human uses of the environment. Habitat loss negatively impacts the fauna of these wetlands, such as the San Diego fairy shrimp, *Branchinecta sandiegonensis* Fugate (Anostraca: Crustacea). It is a narrow endemic, known only from San Diego county and northern Mexico (Simovich & Fugate, 1992; Fugate, 1993; Eriksen & Belk, 1999). It was described in 1993 (Fugate, 1993) and was listed as a federally endangered species in 1997, because of the loss of over 97% of its habitat. As one of the largest and most common vernal pool invertebrates, conservation of the vernal pool fauna has focused on this species in southern California.

Branchinecta sandiegonensis can be found in both deep (>30 cm) and shallow vernal pools (to 5 cm) with moderate pH, low alkalinity, and low concentrations of total dissolved solids (Balko & Ebert, 1984; Gonzalez *et al.*, 1996; Hathaway & Simovich, 1996). As cysts hatch 3–8 days after hydration, depending on the temperature, nauplii are present in the water soon after the pools fill (Hathaway & Simovich, 1996). Larvae mature in 7–20 days depending on the

temperature. Adults have lived up to 42 days in the laboratory but probably only live about 30 days in the field (Hathaway & Simovich, 1996). Females produce clutches of up to 100 cysts every other day and can produce up to 500 cysts over their lifetime (Holtz, 2003).

The duration of the shrimp's habitat is quite variable. Shallow pools frequently fill and dry several times within a single season when rainfall is low or sporadic (Philippi *et al.*, 2001). Five or more filling/drying bouts where shrimp do not survive to maturity are not uncommon (Simovich & Hathaway, 1997; Philippi *et al.*, 2001). In response to this environment, shrimp hatching patterns show strong evidence for bet-hedging to spread the risk in case mortality occurs before reproduction: individuals that do not hatch during one hydration will hatch under the same conditions in later hydration bouts (Simovich & Hathaway, 1997), and the cumulative probability of hatching over three filling events is approximately equal to the probability of a pool filling long enough for successful reproduction (Philippi *et al.*, 2001). Studies on other fairy shrimp species show that the basic life history of *B. sandiegonensis* is fairly typical of anostracans in general (Daborn, 1975, 1976, 1977; Grainger, 1981; Anderson & Hsu, 1990; Saiah & Perrin, 1990; Brendonck & Riddoch, 2000).

Plans for the protection and management of *B. sandiegonensis* require information on its habitats, physiological tolerances, life histories, general ecology, and population structure. Although crucial data for the San Diego fairy shrimp and other vernal pool species are still lacking, efforts are underway to restore degraded pools and create new ones to mitigate the destruction of other pools. These activities are considered experimental and have met with variable biological success (Bauder, 1987; Ferren & Gevirtz, 1990; Long *et al.*, 1992). No successful pool creation experiments for fauna have been reported in the literature; therefore, based on the current techniques, pool creation cannot be considered to sufficiently mitigate the loss of native habitat of pool fauna (Ferren & Gevirtz, 1990).

There are two main concerns for pool creation for fairy shrimp. The first is to ensure that shrimp populations in the created pools are self-sustaining. For example, if the pool never holds water long enough for the shrimp to reach maturity and reproduce, it is not acceptable as remediation. The second

problem is to create pools with a hydrological regime appropriate to the life-history pattern of the shrimp. Although the shrimp are known to adapt to periodic reproductive failures, the precise requirements for population persistence in terms of pool filling duration and frequency are unknown.

We chose matrix population models to study these requirements because they specifically relate demographic data to population persistence. Once the relationship between life-history parameters and population growth has been determined, specific criteria can be established for allowable remediation activities. This type of approach also allows for sensitivity analyses as a basis to decide which parameters may need to be measured more accurately in the laboratory before making management recommendations. As we are not aware of any structured population models for ephemeral pool anostracans, the aim of this study was to develop such a model and use it to identify the demographic factors on which fairy shrimp population growth is most dependent and those which allow the population to persist through multiple failed hatching events. Furthermore, we wished to compare the theoretical predictions of a model with age structure in the cyst bank with models for annual plants and those using a spatially structured cyst bank.

Methods

Matrix population models are powerful tools for using population structure to examine the interactions of various parts of an organism's life-history pattern and their contribution to population growth (Caswell, 2001). They are routinely used in conservation planning (Morris & Doak, 2002). A deterministic matrix population model projects a stage-structured population from one time t to the next time by

$$\mathbf{n}(t+1) = \mathbf{A}\mathbf{n}(t) \qquad (1)$$

where $\mathbf{n}$ is a vector of stage abundances and $\mathbf{A}$ is a constant projection matrix. The projection matrix elements are estimates of the possible transitions between stages by growth, survival, and reproduction, over one time step. The trajectory of the population through time is determined by the matrix $\mathbf{A}$. The dominant eigenvalue of $\mathbf{A}$ is the population growth rate, λ. This is the rate at which the population will grow if the parameters in the projection matrix

are constant through time and can be interpreted as mean individual fitness (Caswell, 2001). Parameters for the projection matrices can be calculated easily from a variety of types of data (Caswell, 2001).

We formulated a deterministic matrix population model for the San Diego fairy shrimp, *B. sandiegonensis*. Population structure was modelled as age structure in the cyst bank (Leslie, 1945, 1948). This formulation can be thought of as cysts using the aquatic phase of the life cycle in order to produce more cysts. A similar formulation has been used to model seed banks in plants (Schmidt & Lawlor, 1983).

The time step chosen for matrix models is often 1 year. For the fairy shrimp model, the interval chosen was time between pool filling events, which can be a few days to months or even years, but is the only natural periodicity for the species. This irregularity of filling events created some problems for interpreting the modelling results (i.e. describing what happens on a yearly basis), but greatly simplified the formulation of the model. Processes affecting cysts during dry periods are included in the model in the parameters that describe cyst survival between filling events.

The model includes categories for three age classes of cysts and allows incorporation of different hatching probabilities, survival rates, and reproductive rates for each age class of cyst. We included more than one cyst age because we were interested in investigating the effect of changing viability with time on the importance of the cyst bank. However, we have poor data on the differences in vital rates associated with cyst age and we do not know how long cysts can survive in the dry soil. Therefore, we estimated parameters for what we considered the simplest meaningful model we could create. This model has three categories of cyst age: one dry period, two dry periods, and three or more dry periods. The last category is actually a stage rather than an age class, and includes all ages from three to infinity. Parameters in the projection matrix representing transitions from one age class to the others are shown in the life-cycle diagram (Fig. 1). The matrix

$$\begin{bmatrix} H_1 & H_2 & H_3 \\ G_1 & 0 & 0 \\ 0 & G_2 & P_3 \end{bmatrix}$$

is the projection matrix for this model. Survival of the cyst without hatching (G_1 and G_2) was modelled for
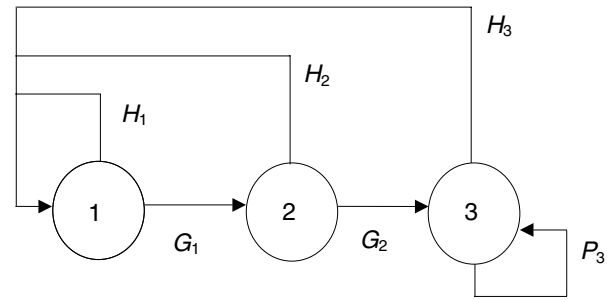

Fig. 1 Life cycle graph for cyst bank model. Circles represent cysts that have been in the soil for one, two, and three or more dry periods. The arrows represent survival to the next dry period as cysts (G_1, G_2 and P_3) or the probability of cysts hatching, growing to maturity, and adding eggs to the cyst bank (H_i).

the first and second dry periods in the soil. The probability of surviving in the cyst bank beyond the third dry period is P_3. H_i were calculated from the percentage hatching after i periods in the soil (h_i), survival to maturity after i periods in the soil (p_i), and number of female cysts produced by females hatched after i dry periods in the soil (m_i):

$$H_i = (h_i)(p_i)(m_i) \tag{2}$$

with $i = 1$, 2 and 3. Thus H_i represents the number of female cysts that each female cyst of age i contributes to the cyst bank in one pool filling.

Estimates of life-history parameters were made based on literature values for *B. sandiegonensis* (Table 1). For some of these parameters, mean and ranges of values have been reported in a single study. In some cases, such as survival to maturity, only two data points have been reported and these differ greatly. Mean values used for parameter estimation were either reported by the authors cited or were calculated from the independently reported values. Such roughly estimated parameters were adequate for this analysis because we were only interested in the basic patterns of parameter importance, not an accurate calculation of population growth rate.

The parameter P_3 is the probability that cysts will remain viable beyond the third filling event. This parameter should be calculated from the data on the maximum number of filling/drying cycles that cysts can go through before they hatch and on the distribution of hatching across these fillings. Simovich & Hathaway (1997) measured cyst hatching up to three

Table 1 Estimated parameter values for *Branchinecta sandiegonensis*. When the range of values is derived from two sources, the citation for the low end of the range is listed above the citation for the high end of the range

Parameter	Mean	Range	Source
Cyst hatch per hydration (h)	h_1: 11%	0–61%	Simovich & Hathaway (1997)
	h_2: 3%	n/r	
	h_3: 2%	n/r	
Survival to maturity (p)	42%	5–79%	Hathaway & Simovich (1996); Holtz (2003)
Fecundity per female	78 cysts	0–250 cysts	Holtz (2003)
Cyst survival in soil (G)	50%	50%	Simovich & Hathaway (1997)
Cyst longevity	n/r	Three drying events	Simovich & Hathaway (1997)

Lifetime fecundity values listed are 50% of those reported by J. Holtz (2003) to count only female cysts, assuming a 1 : 1 sex ratio. Cyst longevity is used to calculate P_3 (see text for the discussion of why no mean value was calculated for cyst longevity). n/r, not reported.

Table 2 Projection matrices and their elasticity matrices. The first row of matrices are the projection matrices (PR) and the second row are the elasticity matrices (EL) for the three population states: failed reproduction, 'mean' parameter estimates, and maximum parameter estimates

Matrix	Fail			Mean			Maximum		
PR	0	0	0	3.60	0.98	0.65	120.5	4.53	3.95
	0.50	0	0	0.50	0	0	0.50	0	0
	0	0.50	0.49	0	0.50	0.49	0	0.50	0.98
EL	0	0	0	0.92	0.03	0.00	1	0	0
	0	0	0	0.04	0	0	0	0	0
	0	0	1	0	0.00	0.00	0	0	0

fillings only. In other anostracan species, cysts can remain viable through at least 16 filling and drying cycles (Hildrew, 1985; Brendonck *et al.*, 1998), implying that the number for *B. sandiegonensis* is conservative. Because of the uncertainty about the value for P_3 we chose to vary P_3 over the full range of possible values: 0 to $(1 - h_3)$. A value of 0 for P_3 implies that the cysts are viable for up to three dry periods. A value of 1 implies that viability is infinite but the cyst bank is depleted slightly during each filling event because of hatching. With h_3 equal to 2%, we used a value of 0.49 as the 'mean' for P_3. As preliminary results showed that λ was relatively insensitive to P_3, accurate estimation of this parameter was not necessary.

All the 'mean' parameter values were used to parameterise the 'mean' projection matrix. A 'fail' matrix was also created to represent filling events in which the pool dries before reproduction occurs. In this case, no cysts will be added to the bank from the cysts that hatch, so the H_i are all zero. The other parameters were the same as in the mean matrix (Table 2). We also calculated a 'maximum' matrix of the largest possible parameter values, from the high ends of the parameter ranges reported.

The first analysis we performed on these three matrices was to calculate the population growth rate, λ. Next, we calculated an elasticity value for each parameter according to:

$$e_{ij} = \frac{v_i w_j}{\langle \mathbf{v}, \mathbf{w} \rangle} \frac{a_{ij}}{\lambda} \tag{3}$$

where $\mathbf{v}$ and $\mathbf{w}$ are the reproductive value vector and the stable age distribution of $\mathbf{A}$, respectively, and $\langle \mathbf{v}, \mathbf{w} \rangle$ is the scalar product of $\mathbf{v}$ and $\mathbf{w}$. Elasticity values indicate the change in λ that would occur if the matrix parameters are changed, in proportion to their values, over 'small' ranges (Caswell, 2001).

To assess the sensitivity of λ to changes in the parameters over their whole potential range, we methodically generated 48 matrices by changing one parameter at a time across its possible range. All parameters except the one being changed were those from the mean matrix. At least five possible values of each parameter were tested (including the minimum and maximum reported values) to generate at least

five separate matrices. For H_i the highest reported values of h, p, and m were multiplied to estimate the highest end of their ranges, and as the lowest reported value for m is 0, the low value used for all the H_i was 0. We calculated population growth rates for all these matrices.

Finally, a periodic model was created to determine how high λ has to be in the deterministic constant model to allow the population to persist through multiple fillings where total reproductive failure occurs. The periodic matrix, $\mathbf{A}_P$, was calculated according to the equation,

$$\mathbf{A}_P = \mathbf{A} * \mathbf{F}^t, \tag{4}$$

where $\mathbf{A}$ is the projection matrix for a filling event where reproduction occurs, $\mathbf{F}$ is the fail matrix, and t is the number of failed events occuring in a row. The population growth rate of the periodic matrix is the dominant eigenvalue of $\mathbf{A}_P$ raised to the $(t + 1)^{-1}$ power (Caswell, 2001). The sensitivity of λ to the matrix elements was calculated for the periodic model using the same matrices created for the methodical sensitivity analysis of the deterministic constant model. These were compared with results for the constant model. Several additional matrices were generated by trial and error to obtain matrices with $\lambda = 1$ for values of t up to 5, the maximum number of failed pool fillings that has been observed in the field.

Results

Estimated parameter values (Table 1) showed large possible ranges. The 'mean' matrix (Table 2) was calculated from the mean values in Table 1. The 'fail' projection matrix (Table 2) differs from the 'mean' matrix only in that the first row is all zeros. The parameters of the 'maximum' matrix (Table 2) were all higher than for the 'mean' matrix; number of cysts per cyst hatched from the first age category (H_1) was about 30 times the size of the value for the 'mean' matrix while the differences between the other parameters were less extreme.

The population growth rates for the 'mean', 'fail', and 'maximum' matrices were 3.7, 0.49, and 120, respectively. Elasticity values for the 'mean' matrix corresponded roughly to the size of the projection matrix values. Thus, elasticity to λ decreased from H_1 to H_3 suggesting that selection will favour hatching in

the first hydration after birth when conditions are consistently favourable for successful reproduction. In contrast, for the 'fail' matrix, when conditions were consistently unfavourable, λ was completely determined by persistence in the cyst bank (P_3). This suggests that in periods of repeated failed reproduction, there is strong selection pressure for delayed hatching. When reproductive success of cysts hatching in the first hydration after birth was extremely high, as in the 'maximum' matrix, λ was completely determined by H_1.

Analytical elasticities predicted the effect of changing parameters across their entire range reasonably well. Population growth rate was clearly most sensitive to changes in H_1 (Fig. 2a). The only parameters
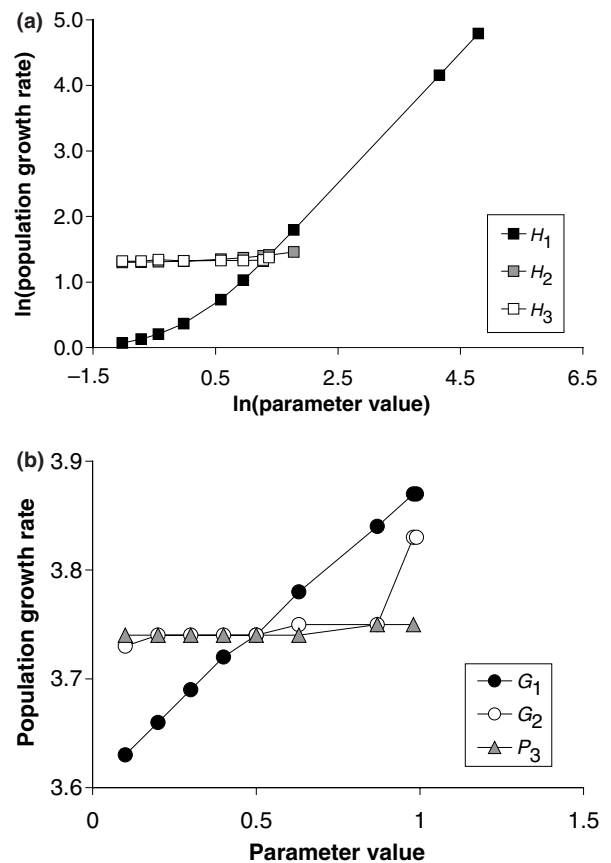

Fig. 2 Effect of large changes in parameters on the population growth rate, λ. One parameter at a time was changed over its entire possible range while all other parameters were held constant at the values for the mean matrix. (a) Natural log of H_i plotted against natural log λ. The possible parameter ranges are from 0 to 120; however, no points are plotted at 0 because these values are undefined on a log scale. (b) The parameters that can range from 0 to 1 only. For G_i, possible values range from 0.1 to 0.99, while P_3 ranges from 0 to 0.98.

that differed in sensitivity of λ compared with the elasticities were the survival in the cyst bank parameters, G_i which had equal elasticity values, but when changed across the full parameter range, sensitivity of λ to G_1 was higher than to G_2 (Fig. 2b). However, changing G_1 across its entire possible range only changed λ by about 0.2, while changing H_1 across its entire range changed λ from 1.1 to 120.

Although the deterministic constant population growth rate for the 'mean' matrix was much larger than 1, the periodic population growth rate dropped to below 1.0 when this matrix was in a regime of alternating filling events with reproductive success and failure (Table 3). The 'maximum' matrix, which had an extremely high population growth rate in the deterministic model, only had a $\lambda_P > 1$ for up to two failed reproductive events in a row. The only parameters to which the periodic population growth rate was sensitive when they were changed one at a time were H_3 and P_3. Changing P_3 could change λ_P only slightly, but by increasing H_3 it was possible to attain population growth rates of 1.0 or larger for up to five failed reproductive events.

In summary, the most important parameter for population growth in the static model is hatching from cysts that have only been in the cyst bank one dry period. In the model with periodic reproductive failures, the most important parameter for population growth is hatching from cysts that have been in the cyst bank for three or more dry periods.

Table 3 Results of the periodic model: The projection matrix used for **A** in Equation 4 is listed in the first column. The deterministic, constant population growth rate for that matrix (λ_A) is in the second column. The number of pool fillings with reproductive failure that occur in a row for each model are indicated in the periodicity column, and the population growth rate for the periodic model (λ_P) is shown in the last column. H_3 is the number of cysts produced per cyst hatched from the third age category

Matrix	λ_A	Periodicity	λ_P
Mean	3.74	**AF**	0.82
Mean	3.74	**AF**^{2}	0.65
Maximum	120.5	**AF**	1.58
Maximum	120.5	**AF**^{2}	1.07
Maximum	120.5	**AF**^{3}	0.88
Mean with $H_3 = 7.7$	3.87	**AF**^{3}	1.00
Mean with $H_3 = 16.3$	4.01	**AF**^{4}	1.00
Mean with $H_3 = 33.5$	4.42	**AF**^{5}	1.00

Discussion

Based on a matrix population model as formulated here, the life-history strategy of the San Diego fairy shrimp depends on a bank of cysts which hatch at different times and an extremely high population growth rate under good conditions. With this strategy, the shrimp can replenish the cyst bank and persist as a population despite a draw-down of the cyst bank in failed pool fillings. The bet-hedging strategy of only partial hatch in any one filling (Simovich & Hathaway, 1997) and survival through multiple years in the cyst bank is critical for population persistence through multiple failed reproductive events. The importance of a diapausing propagule bank for persistence under variable conditions has also been demonstrated for the cladoceran, *Daphnia galeata*, (Cáceres, 1997) and the annual plant, *Collinsia verna* (Kalisz & McPeek, 1992), using structured matrix models.

Climate patterns exert strong selection pressure on the life-history of aquatic crustaceans living in ephemeral habitats. Selection pressures will change depending on weather conditions, which can vary over short time scales. For *B. sandiegonensis*, the average pool in the San Diego area fills long enough to allow reproduction once in every three fillings (Philippi *et al.*, 2001). However, in an especially dry year, up to five failed fillings in a row have been observed (M. A. Simovich, personal communication) and more failed fillings may occur. Under these conditions, delayed cyst hatch will be favoured. In contrast, during cool and rainy years, pools may fill and stay filled for several weeks, allowing ample time for reproduction to occur and favouring early cyst hatch. Therefore environmental conditions for *B. sandiegonensis* populations frequently change between selection regimes favouring early cyst hatch and delayed cyst hatch. If selection pressures change like this over short time scales, individuals adapted to both types of conditions can persist in the population. Genetic diversity for hatch pattern and related traits is therefore maintained at higher levels than it would be in predictable environments.

The wide ranges of possible parameter values for vital rates of *B. sandiegonensis* (Table 1) show that not much is currently known for making informed conservation decisions. Usually, 'reasonable' parameters are those which yield a population growth rate of

about 1. It is difficult to assess how reasonable the estimated parameters are for the deterministic model because we know that λ must be $\gg 1$ to persist through failed pool fillings. Possible errors in our parameterisation of the mean model are highlighted in the periodic model. As we had to increase the number of cysts per cyst hatched in the third age category (H_3) above our 'mean' value to get a population persistence in periodic conditions – those which are poor for the shrimp but that they are exposed to regularly and obviously can survive – some of the parameter values we used may be unrealistically low.

An alternative explanation for this result is that it is uncommon for pools to fill sufficiently only once between long sets of failures; if we had used two sequential and adequate fillings in the periodic model, the population growth rates would have been higher. However, in winter 2001–2002 (the driest on record in San Diego) pools did fill in the same pattern as in the periodic model, and hence the situation in the model does occur in nature. A stochastic model that incorporated actual frequencies of different environmental conditions and the effect of these conditions on fairy shrimp vital rates would reflect the environmental variability more realistically. We are currently collecting data to parameterise such a model to continue our investigation of fairy shrimp life-history patterns under more realistic assumptions.

The significance of the older cysts to the cyst bank (H_3) in the periodic models suggests that we need to measure differences among hatching, survival, and fecundity for different ages of cyst more carefully. At this point, we only assume that these rates are lower in cysts that have been resting longer. Some evidence suggests that there may be a peak in hatching at an intermediate age (Simovich & Hathaway, 1997) or that there are several peaks across a long series of wetting events (Hildrew, 1985). We are not aware of any data on survival or fecundity of shrimp hatching from cysts of different ages. As P_3 is also an important contributor to population growth rate, we would also like to know how long cysts can survive through serial wettings and dryings. To understand why some cysts hatch and others do not, more work is needed on the physiological mechanisms that trigger hatching.

Theoretical models for diapausing organisms have shown that mean fitness will be reduced by life-history traits that enable these organisms to withstand environmental variation (e.g. Venable & Brown, 1988). Although the results on seed bank models for annual plants may not generally apply to crustaceans (Philippi, 1998), our results do support this generalisation. The population growth rate (which is a measure of fitness) was highest when H_1 was high relative to the investment in the cyst bank. In contrast, Kalisz & McPeek (1993) found that for the annual plant, *C. verna*, the seed bank enhanced population growth rate, unless favourable years were common. The impact of diapause on fitness seems to depend on the frequency with which unfavourable conditions occur.

It has been recognised for some time that seed or cyst banks create a condition where although adults die before their offspring begin reproducing, they actually exist in overlapping generations with long generation times (Templeton & Levin, 1979). The matrix model used here is formally the same as that for an organism that reproduces more than once during its life span although the shrimp lay eggs only once, the eggs hatch at different times (Schmidt & Lawlor, 1983). Through this mechanism dormancy can alter the year-to-year genetic makeup of the population (Ellner & Hairston, 1994) and its competitive relationships with other species (Warner & Chesson, 1985; Cáceres, 1997).

Our model and that of Schmidt & Lawlor (1983) assume that a propagule bank is necessary for a population to survive in a fluctuating environment and investigate how a propagule bank structure relates to other life-history traits. Schmidt & Lawlor (1983) showed that for an annual plant with a structured seed bank, sensitivity of population growth rate was higher to fecundity and survivorship than to the percentage of germinated seeds. In our deterministic model, these factors were not modelled separately, so a direct comparison between results cannot be made.

Our results have several implications for management. The first is that even when there are shrimp in a pool, the population may not be self-sustaining. Even without a mathematical model it is clear, however, that a cyst bank will eventually be depleted if there is no reproduction. Our results show that pools need to fill long enough for shrimp to reproduce in one of every two or three fillings, on average, to maintain the cyst bank. Hildrew (1985) estimated from estimates of

egg production and mortality rates that the fairy shrimp, *Streptocephalus vitreus*, needed to reproduce in one of every seven or eight pool fillings during a season with a long rainy period. However, taking environmental variability into account, reproduction was much lower in a season with a shorter rainy period, the shrimp would need to reproduce more frequently (Hildrew, 1985). Our results for *B. sandiegonensis* are more conservative than these, which may be due to the different habitat, the life history, or methods of calculation.

The second implication for management is that a wide distribution of ages of cysts should be used when inoculating new pools, because it is on differences in hatch timing that the persistence of the population depends. Soil used to inoculate new pools should be from pools that have had stable populations for several years so that the cyst bank contains older and younger cysts. Where few pools with appropriate cyst banks are available, it would not be wise to remove very much soil to inoculate others. It may be possible to inoculate pools with laboratory-cultured organisms in the future. *Artemia* is routinely cultured and sustainable cultures of several species of fairy shrimp have been kept in the laboratory (Moore, 1957; Brendonck, Uyttersprot & Persoone, 1990). Creation of an appropriately age-structured cyst bank would require putting the population through multiple filling and drying events. However, partly because of its low hatching rate, *B. sandiegonensis* is difficult to culture and the viability of laboratory-produced cysts has not yet been determined. As genetic variability is also a concern in laboratory cultures, a captive breeding programme for this species in not currently a viable option.

As cysts hatch in the laboratory under environmental conditions that they did not hatch under previously (Simovich & Hathaway, 1997), it is possible that the mechanism for hatch timing is genetic. Although the trigger for hatching is unknown for *B. sandiegonensis*, there is some evidence that hatch timing is under genetic control in the anostracan, *S. vitreus* (Hildrew, 1985) and in the cladoceran, *D. pulex* (Pfrender & Deng, 1998). Assuming that the variation in hatch timing is genetic, the third implication for management is that genetic variability in shrimp populations needs to be preserved in order to maintain enough variability in hatch pattern to sustain the population through failed filling events.

Based on allozymes, genetic variability among pools is low for *B. sandiegonensis* (Davies, Simovich & Hathaway, 1997); therefore, it is critical that efforts are made to preserve as many of the few remaining populations as possible.

The three conclusions from this study – (i) pool filling pattern needs to allow shrimp hatch in every two to three fillings, (ii) inoculum for a restored or created pool must contain cysts of varying age, and (iii) genetic variability must be preserved – need to be incorporated into planning for conservation activities and as criteria for allowable mitigation.

Acknowledgments

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