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OPTIMAL CONDITIONS FOR REARING THE TADPOLE SHRIMP, *TRIOPS LONGICAUDATUS* (NOTOSTRACA: TRIOPSIDAE), A BIOLOGICAL CONTROL AGENT AGAINST MOSQUITOES

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ABSTRACT. Tadpole shrimp (TPS) were reared at 15, 20, 25, and 30°C in the laboratory. Size of TPS was temperature and age dependent with more rapid development at warmer temperatures. Survivorship was inversely related to rearing temperature. Mean age at death was 24.2, 19.2, 14.3, and 11.8 days at 15, 20, 25, and 30°C, respectively. Rearing temperature (excluding 15°C) did not affect lifetime fecundity, but larger TPS laid more eggs than smaller ones. Tadpole shrimp began ovipositing earlier at higher temperatures, and at a smaller size than their counterparts in lower temperatures. Mean age at reproductive maturity was 18.8, 13.1, and 10.2 days and mean carapace length was 10.8, 11.0, and 10.3 at 20, 25, and 30°C, respectively. Embryogenesis required a minimum of 3 days for completion. Hatching rates during the first hydration decreased with increasing egg batch number produced by individuals, ranging from a mean of 74% for the first batch to 31% for the 5th batch. Cumulative hatching rates of eggs after 2 hydrations were consistent across temperatures and egg batches (79 ± 2%).

INTRODUCTION

Insect predators have not been used effectively as biological control agents for mosquitoes, partly because of lack of temporal overlap with their rapidly developing prey (Bay 1974, Collins and Washino 1985) and partly because of difficulty in mass rearing (Garcia 1973, Legner et al. 1974). The predatory tadpole shrimp, *Triops longicaudatus* (LeConte)(TPS), however, does overlap with some mosquito species that develop in temporary or intermittently flooded freshwater habitats, such as flood irrigated fields, date gardens, duck club impoundments, or natural dry lakes. This shrimp can significantly reduce populations of developing mosquitoes by larval predation and by disrupting mosquito oviposition through physical disturbance of the water surface (Tietze 1990;[2] Tietze and Mulla 1990, 1991; Fry et al. 1994).

Several life history traits of the TPS provide considerable advantages for use as a biological control agent for mosquitoes in intermittently flooded sites. Eggs hatch shortly after hydration and larvae grow rapidly (Takahashi 1977, Scott and Grigarick 1978), resulting in temporal overlap with most mosquito prey. Oviposition as early as 6 days (Fry-O'Brien, unpublished data) after hatch enables populations of TPS to survive in habitats that dry up within 1–2 wk. Fecundity of TPS is high; individuals may lay more than 1,000 eggs (Takahashi 1977). Finally, TPS lay desiccation-resistant eggs that remain viable in dry soil for extended periods (months or years) and undergo installment hatching during numerous successive floodings, enabling some TPS populations to persist during poor environmental conditions that could otherwise result in local extinction.

If tadpole shrimp are to be useful in biological control of mosquitoes in appropriate situations, a reliable production procedure must be developed. Production is a crucial component of the evaluation of a new biological control program, both in economic and technical terms (Garcia 1973, Popiel and Olkowski 1990). The egg stage of the tadpole shrimp is the preferred mode of distribution because the eggs are hardy, easy to store for extended periods, and small enough to package efficiently. Currently, there is no developed source for the large numbers of eggs needed for use in control programs.

Two approaches may be used to supply sufficient numbers of eggs: field collection of eggs from sites with known TPS populations (including managed habitats analogous to fish farms), or laboratory mass rearing. Of these 2 approaches, mass rearing may be most cost effective if TPS are reared under optimal conditions whereby high fecundity and short generation times are achieved. Field collection of eggs requires separation of eggs from soil, and unless egg densities are very high, this may be an inefficient procedure. Whichever strategy is used, cost may be mitigated somewhat by the capacity of TPS to establish permanent populations upon a single introduction with no further augmentation (Fry et al. 1994).

Development of a mass rearing program for

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[2] Tietze, N. S. 1990. The tadpole shrimp, *Triops longicaudatus* (Notostraca: Triopsidae), for biological control of mosquitoes. Ph.D. thesis. University of California, Riverside, CA.

TPS requires data on shrimp performance under laboratory conditions. Several authors have studied aspects of rearing TPS in the laboratory including competition (Weeks 1990, Weeks and Sassaman 1990), factors affecting egg hatching and lifetime fecundity in Japanese populations (Takahashi 1977), and factors affecting hatching, growth, and fecundity in a northern California population (Scott and Grigarick 1978, 1979). To determine the most appropriate rearing temperature for TPS, we examined growth, survivorship, and egg production of individuals from southern California at 4 constant temperatures. Because embryogenesis occurs in TPS after oviposition, and prior to desiccation (Hempel-Zawitkowska 1967), we conducted an experiment to determine the minimum development time required. The hatching rates of eggs from TPS reared at different temperatures were compared to identify any effect of temperature on viability. Finally, hatching rates of eggs in successive batches laid by individual TPS throughout their reproductive lives were compared to examine potential age-related differences in hatchability.

MATERIALS AND METHODS

Growth rate, survivorship, egg production, and hatching rate experiments were conducted in a glasshouse at the University of California, Riverside (UCR). The walls of the glasshouse were heavily whitewashed to decrease direct, intense light. This filtered natural light was supplemented by a mix of 40-W fluorescent and broad spectrum plant grow lights (VitaLite-DuroLite Lamps, Inc.-Duro Test Corp., North Bergen, NJ) on a 14:10 L:D cycle.

Embryo development time: An experiment was conducted to determine the minimum post-oviposition immersion time that would allow completion of embryonic development. Forty-eight 11-day-old TPS were transferred from ponds at the Aquatic and Vector Control Research Facility at UCR to individual plastic tubs (28 × 34 cm) filled with 2 liters of tap water. The water temperature was held constant at 25°C. Tadpole shrimp were fed *ad libitum* amounts of basic fish food flakes (Wardley's®, Secaucus, NJ). Tadpole shrimp were assigned randomly to one of 4 treatment groups: 1) eggs kept hydrated for 1 day prior to desiccation, 2) eggs kept in water for 3 days prior to desiccation, 3) eggs kept in water for 5 days prior to desiccation, or 4) eggs kept in water for 7 days prior to desiccation. Eggs were collected from each tub and transferred to plastic weigh boats daily for 6 days. The weigh boats were kept filled with tap water for the required treatment duration, after which the excess water was pipetted out, and the eggs in the boats were allowed to dry at room temperature (RH = 50–70%) for 7 days. Seven days after drying, the boats were refilled with tap water to hydrate the eggs. The hatching rates were determined after 48 h of hydration by counting hatched and unhatched eggs under a dissecting microscope.

Laboratory rearing: Three separate cohorts of TPS were reared in the laboratory from egg to death to determine the effect of temperature on life history traits. The cohorts were begun in April, May, and July, 1993.

Four 1.2 × 2.4 m shallow water baths were constructed from lumber and plywood and lined with double layers of 2-ply plastic. They were filled with tap water to about 15 cm depth and the temperature adjusted so that water-filled containers immersed in the baths maintained constant temperatures (±1°C) of 15, 20, 25, or 30°C. Temperatures were maintained using 2 aquarium heaters (200-W, Ebo-Jäeger) in each of the 2 warmest baths, and one circulating water chiller (AFC-3 "Turbo-Fin Plus" Fluid Chiller, Aquanetics Systems, Inc., San Diego, CA) in each of the cooler baths.

The eggs used were collected from soil of ponds containing established populations of TPS at UCR. Tadpole shrimp eggs are deposited in soil and are most abundant near the surface; therefore, the top 2–3 cm of soil in these ponds was scraped up and taken to the laboratory. Soil was spread over the bottoms of 28 × 34-cm plastic tubs set in the water baths (500 g/tub). Each tub was then filled with tap water (at the appropriate treatment temperature) to a depth of 5 cm. Two tubs (total 1 kg soil) supplied the shrimp for all but the lowest temperature treatment. Because hatch rates of TPS are very low at 15°C (Horne 1967, Scott and Grigarick 1979), 3 tubs (1.5 kg soil) were used to try to insure an adequate supply of shrimp for this treatment. Tadpole shrimp were thus kept at constant temperatures from prehatching to death.

When shrimp carapaces measured 3–5 mm in length, they were placed in individual tubs for the remainder of their lives. The 28 × 34-cm plastic tubs contained 2 liters of tap water and were immersed in the water baths. The shrimp were fed an *ad libitum* supply of cichlid minifish pellets (Nippon, Torrance, CA). Pellets were supplemented by 20 freshly heat-killed 3rd or 4th instar mosquito larvae (*Culex quinquefasciatus* Say) on alternate days. Preliminary results suggested that egg production was higher when TPS were fed mosquito larvae.

Water in the growth containers was replaced every 2 days to avoid buildups of algae and metabolic waste products. Commercial algacides were not used because they reduced TPS growth

and egg number in preliminary experiments. Tap water was held for 24 h prior to use. Water was stored in a large plastic garbage can at 30°C, in plastic buckets at room temperature, and in tubs in the 15°C water bath. All water was mixed to the appropriate experimental temperature before use.

During growth rate experiments, the midline carapace lengths of individual TPS were measured every other day using calipers. Carapace length, as opposed to wet weight, has been used by several authors to measure TPS size (Linder 1952; Scott and Grigarick 1978; Tietze and Mulla 1989, 1990, 1991), and it is used here as an estimate for total growth. One 5 × 13-cm strip of Monodur® polyester screen (mesh size 800 μm) was placed in each tub as an oviposition substrate. Eggs laid on these strips were collected and counted daily. Eggs not adhering to strips were collected by pipetting and were counted as well.

Based on the results from the egg immersion duration experiment, all eggs used in the growth and egg production study were stored underwater for 3 days to allow embryonic development to occur. They were then dried for an additional 5 days at 70% humidity in a desiccation chamber (after Hempel-Zawitkowska and Klekowski 1968), removed and stored at room temperature.

Approximately 1 month after eggs were stored, they were hydrated with tap water. The hatching rates for eggs from each individual for each sampling date were determined after 48 h, by removing the screens or loose eggs from the water and counting the numbers hatched and unhatched. Hatched eggs were split nearly in 2 and were easy to identify under a dissecting microscope by probing gently with forceps, whereas unhatched eggs were turgid and usually spherical. Some eggs were malformed, but still able to hatch, so all eggs were included in counts. The eggs remaining unhatched after the first hydration were rehydrated after being dried again under the conditions described above and the hatching rate was determined. Analysis of the viability of eggs remaining unhatched after 2 hydrations was deemed unnecessary because the overall hatching rates were very high, often approaching 100%.

The rearing procedure for TPS is summarized below:

1. Submerge eggs in 30°C H_2O. Container should have a thin (0.5-cm) layer of soil on the bottom.
2. Transfer TPS to soil-free containers when they are approximately 0.5 cm long (carapace length). Replace water (30°C) on alternate days.
3. Feed daily: *ad libitum* cichlid mini-pellets. Supplement on alternate days with fresh, heat-killed mosquito larvae.
4. Submerge thin strips of Monodur® polyester screen (mesh size 800 μm) in the containers as an oviposition substrate.
5. Remove strips daily until TPS die (approximately 2 wk), but keep them submerged in room temperature water baths for 3 days.
6. Dry strips in 70% RH desiccation chambers for 7 days.
7. Remove strips with eggs and store until use in open containers where light can penetrate.

Statistical analysis: All statistical analyses were performed using Statview™ (Feldman et al. 1988), except where otherwise indicated. In experiment one (embryo development time), comparisons of hatching rates among freshly oviposited eggs left in water for different lengths of time prior to drying were made using a Kruskal–Wallace (*H*) test. Pairwise comparisons were then made using a Tukey-type multiple comparison test for unequal samples (*Q*) (Zar 1984).

Multiple regression analysis of size and egg number by cohort was done to ensure that there were no significant differences among the 3 cohorts. Growth rates, as expressed by carapace length, at the 4 temperatures were compared using multiple regression. Tadpole shrimp age and water temperature were included in the statistical model. One-way analysis of variance (ANOVA) was used to compare the length of survival at the 4 temperatures. Pairwise comparisons were made using the Scheffe F-test. The effect of rearing temperature on individual egg production was analyzed using a Kruskal–Wallace *H* test. Because only 2 individuals in the 15°C treatment oviposited, this group was excluded from all analyses concerning egg production. All other TPS were included. Linear regression examined the effects of TPS size on egg production. Because multicollinearity is expected between the variables size and age, and temperature and size, only size was included in the regression model. We excluded observations where no eggs were laid on that particular sampling day, or if the carapace length was not measured. Both time at the onset of oviposition (measured as days after flooding) and the shrimp size at first oviposition were analyzed using one-way ANOVA. The effects of rearing temperature, age, and egg batch number on hatching rates (first hydration) were analyzed using multiple regression, although only the variable "egg batch" was included in the final model. The

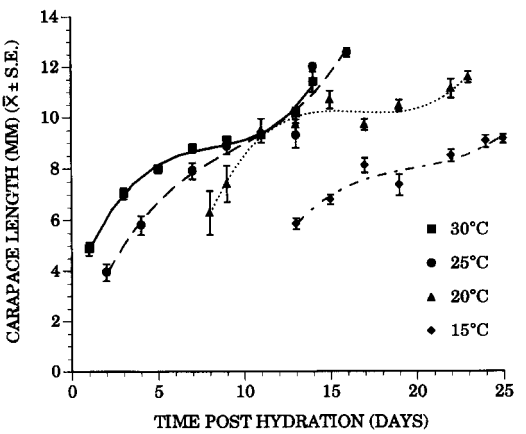

Fig. 1. Developmental rates of *Triops longicaudatus* (carapace length) at 4 temperatures. Squares = 30°C, circles = 25°C, triangles = 20°C, and diamonds = 15°C. Best fit lines are drawn using 3rd degree polynomial equations.

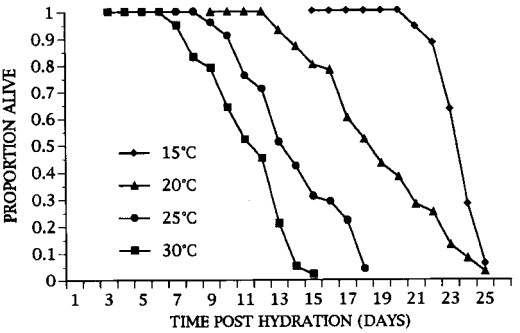

Fig. 2. Proportionate survivorship of *Triops longicaudatus* at 4 temperatures. Squares = 30°C, circles = 25°C, triangles = 20°C, and diamonds = 15°C.

same analysis was used for hatching rates in the second hydration.

RESULTS

Embryo development time: There was a significant effect of postoviposition immersion time on hatching success of TPS (H = 17.7, P < 0.001, n = 39 TPS). A minimum 3-day immersion following oviposition was required for embryonic development to be completed for hatching on a subsequent flooding episode. Hatching occurred, but was low after 1 day of immersion and differed from the hatching rates after 3, 5, and 7 days (Q = 3.58, P < 0.005). Hatching rates after 3, 5, and 7 days did not differ from one another (Q = 0.295, P > 0.5). The proportion of eggs hatching after being immersed for 1 day was 0.06 ± 0.04 (n = 858), for 3 days was 0.60 ± 0.1 (n = 658), for 5 days was 0.57 ± 0.07 (n = 646), and for 7 days was 0.57 ± 0.5 (n = 870). The mean number of eggs laid by individual TPS over the 6-day experiment was 77.7 ± 8.2.

Laboratory rearing: Regression analysis showed no difference among the 3 cohorts with regard to size, survivorship, and egg production at each temperature; therefore, these groups were pooled for analysis. Carapace length in TPS was dependent on both age (x_1) and temperature (x_2) (R^2 = 0.6, y = 0.47x_1 + 0.42x_2 − 7.34; F = 559, P < 0.0001, n = 743). Figure 1 shows the differences in mean carapace length (±SE) over the measurement period at 4 temperatures. Initially, the growth at 25 and 30°C was rapid. Twenty-four hours after hydration, the mean size of TPS in 30°C was 4.80 ± 0.26 mm, whereas the mean size of TPS in 25°C was 3.94 ± 0.34 mm 48 h after hydration. Shrimp reared at 30°C stayed larger until day 11, when TPS reared at 25°C caught up, at approximately 9.3 mm. At the 2 lower temperatures initial growth was much slower, or perhaps hatching occurred later. By day 8, TPS reared at 20°C were 6.3 ± 0.86 mm long. By comparison, TPS reared at 15°C were only 5.8 ± 0.21 mm long by day 13. The growth rate remained lower in the 2 lower temperatures for the remainder of the lifespan. With the exception of TPS reared at 15°C, they attained approximately the same sizes by death, near 12 mm carapace length. The TPS reared at 15°C, however, had a mean length of only 9.1 ± 0.18 mm at death.

Tadpole shrimp survivorship varied at the different temperatures (F = 93.7, P < 0.0001, n = 139) (Fig. 2). The mean duration of survival (flooding date until death) at 15°C was 24.2 ± 0.4 days, at 20°C was 19.2 ± 0.6, at 25°C was 14.3 ± 0.4, and at 30°C was 11.8 ± 0.4; each treatment differs significantly from the others (Scheffe F-test, P < 0.05).

Rearing temperature (20, 25, or 30°C) did not affect the total number of eggs laid by individual TPS over their lifetime (P > 0.1, n = 128). Of the TPS that oviposited, the mean number of eggs at 20°C was 85.3 ± 15.7 (n = 24), at 25°C was 85.4 ± 15.1 (n = 28), and at 30°C was 71.4 ± 14.4 (n = 39). The performance of TPS reared at 15°C, however, was so poor (only 2 oviposited) that these data were not included in the analysis. The number of eggs laid per batch by individual TPS ranged from 1 to 183, and this batch size was dependent on carapace length. Larger shrimp laid more eggs (F = 36.1, P < 0.0001, n = 128); however, a large proportion of the variance was not explained by size alone (R^2 = 0.22, y = 11.93x − 93.11).

The onset of oviposition was dependent on

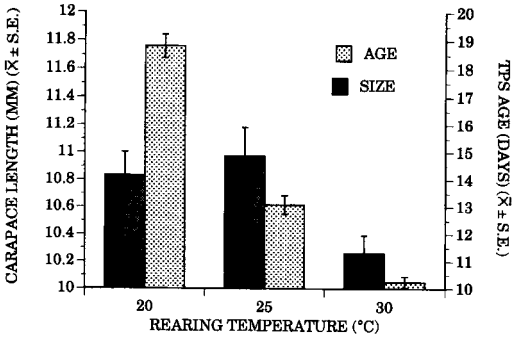

Fig. 3. Relationship between carapace length and temperature (dark bars), and age and temperature (light bars) on initiation of oviposition by *Triops longicaudatus*.

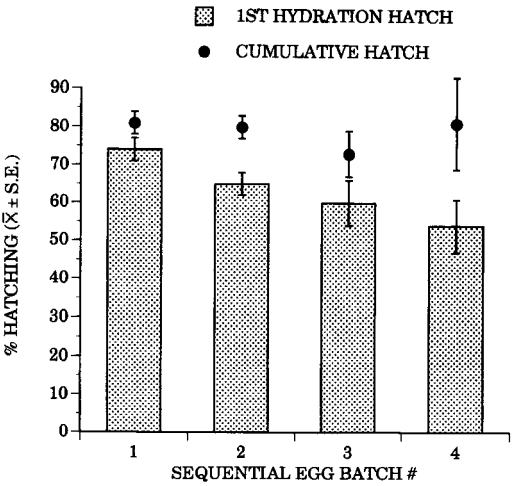

Fig. 4. Hatching rates of eggs of *Triops longicaudatus* in sequential batches during one hydration (bars), and cumulative hatching rates of eggs after a 2nd hydration (circles).

temperature (15°C excluded), as expected ($F = 194$, $P < 0.0001$, $n = 209$). The earliest oviposition was noted at 7 days postflooding in TPS reared at 30°C ($\bar{x} = 10.2 \pm 0.2$), at 9 days in 25°C ($\bar{x} = 13.1 \pm 0.3$), and at 13 days in 20°C ($\bar{x} = 18.8 \pm 0.4$). Both TPS oviposited on day 15 at 15°C. The length of TPS at first oviposition is also dependent on temperature (15°C excluded) ($F = 5.33$, $P < 0.01$, $n = 127$), although this difference may not be biologically significant (Fig. 3). Tadpole shrimp reared at 30°C first oviposited at a significantly smaller size (10.26 ± 0.13 mm) than shrimp reared at 25°C (10.97 ± 0.21 mm) or 20°C (10.83 ± 0.17).

Hatching rates of all eggs laid by adults were not affected by the rearing temperature (excluding 15°C) or TPS age, so these variables were not included in the final model. The hatching rates during the first hydration in sequential egg batches, however, did decline ($F = 5.41$, $P < 0.005$) (Fig. 4). Because temperature did not affect hatching rates, data were pooled for further analysis. The mean hatching rate during the first hydration in the first egg batches produced by TPS was 74 ± 3% ($n = 92$). Hatching rates for the 2nd, 3rd, 4th, and 5th egg batches, respectively, were: 65 ± 3% ($n = 59$), 60 ± 6% ($n = 30$), 54 ± 7% ($n = 17$), and 31 ± 19% ($n = 4$) (Fig. 4). A few TPS laid up to 8 batches of eggs. The overall mean hatching rate for eggs during the first hydration was 67 ± 2% ($n = 208$). No patterns were found in the hatching rates from the 2nd hydration with respect to age, temperature, or egg batch, but the overall mean was 56 ± 2% ($n = 161$). Cumulative hatching rates did not differ with respect to age, temperature, or egg batch. The cumulative mean hatching rate at the end of 2 hydrations was 79 ± 2% ($n = 122$) (Fig. 4).

DISCUSSION

Tadpole shrimp rearing productivity can be optimized in the laboratory by utilizing appropriate environmental conditions and egg handling procedures. For egg handling, a 3-day immersion period prior to desiccation was the minimum time needed to ensure high hatching rates. Longer immersion periods did not significantly increase hatching, and are not desirable in a rearing program where generational turnover times are important. It has been shown that high humidities during desiccation are conductive to subsequent hatching of TPS (Hempel-Zawitkowska and Klekowski 1968, Scott and Grigarick 1979). It is just as important to ensure that eggs are completely desiccated prior to hydration, as this also enhances hatching (Fry and Mulla 1992). In this study, a 1-wk desiccation period was deemed sufficient for complete drying, but it may be possible to shorten this time without adversely affecting hatching.

The 4 rearing temperatures (15, 20, 25, and 30°C) were based on reports in the literature on temperature tolerance in TPS. The prevailing temperature for hatching in TPS lies between 15 and 25°C across its range, with some authors reporting reduction of hatch below 14 or 15°C (Horne 1967, Scott and Grigarick 1979) and above 24°C (Scott and Grigarick 1979). The optimal temperature for posthatching development of TPS from northern California lies near 25°C (Scott and Grigarick 1978), but temperatures above 38°C are not well tolerated by TPS in southeastern Arizona (Hillyard and Vinegar 1972).

When TPS are reared in the laboratory, they are usually supplied with a layer of soil in their rearing containers. Survivorship at the larval stage was poor without soil (Fry-O'Brien, unpublished data), yet it may not be necessary after they develop into the adult form (in less than 24 h at 30°C). Based on these observations, eggs were hatched in soil for initiation of this experiment. However, eggs are difficult to collect from soil, so it was not added to the individual rearing tubs.

Faster growth of TPS at higher temperatures was expected in this study, and the rapid rate of development at 30°C, in particular, was notable (Fig. 1). Growth to nearly 5 mm in 24 h has not been documented in the field or in the laboratory. Scott and Grigarick (1978) reared TPS at 30°C, and they measured approximately 6 mm long by the 5th day after hatching. In this study, by day 5, TPS were approximately 8 mm long. The slower growth reported by Scott and Grigarick (1978) at 30°C may be due to to differences in response to temperature between populations of TPS collected in northern California (Scott and Grigarick 1978) versus those collected in southern California (this study). Tadpole shrimp growth was also measured in field populations in southern California by Walton et al. (1991), who found that TPS measured approximately 5 mm in length by day 7 at average daily temperatures ranging from 30 to 32.5°C. The lower growth rates in the field as compared to the laboratory may be partly due to daily temperature fluctuations in the field, or effects of competition.

The inverse relationship between temperature and survival (Fig. 2) was also expected, although survivorship was generally lower than that reported by Scott and Grigarick (1978), Weeks (1990), and Weeks and Sassaman (1990), all of whom demonstrated survivorship nearer the 1-month period seen in field populations (Walton et al. 1991). In our study, only TPS reared at the 2 lowest temperatures approached 30-day survivorship. Scott and Grigarick (1978), Weeks (1990), and Weeks and Sassaman (1990) used soil substrates in their laboratory rearing studies, and TPS are typically reared in this manner. In our study, however, soil was not added to individual rearing containers. Soil may be a source of minerals or nutrients that are not present in tap water. Therefore, lack of soil could be responsible for the relatively short-lived TPS in our study.

In spite of differential growth and survivorship at different temperatures, fecundity did not vary significantly, with the probable exception of TPS reared at 15°C, in which only 2 TPS oviposited. The fact that survival was shorter at 30°C than at the lower temperatures, yet overall egg production was equivalent, is advantageous for efficient laboratory rearing.

Tadpole shrimp size was positively correlated with egg batch size. This is also true of 2 other branchiopod species (Ivanova and Vassilenko 1987). Mean egg production in our study ranged from 71 to 85 per individual (absolute egg production range = 0–505). This is much lower than the estimate of 1,850 eggs per individual reported by Takahashi (1977) and it is also much lower than the 24-h mean of 81 eggs reported by Scott and Grigarick (1978). It cannot be determined whether nutritional requirements or some other factors contributed to this oviposition rate. Again, soil factors may have played a role in the relatively low egg production. One other possible explanation for this discrepancy is that different clonal or sexual forms, as described by Weeks (1990) and Weeks and Sassaman (1990), were used in our study. Weeks (1990) and Weeks and Sassaman (1990) showed marked differences in egg production among the lines, with means ranging from 48 to 129 (5 TPS/27 liters H_2O).

Takahashi (1977) reported TPS oviposition within 10 days of flooding (at 22–23°C), and Scott and Grigarick (1978) noted oviposition in 13 days (at 19–22°C). Those findings are supported by our study (Fig. 3), where TPS reared at 25°C and 20°C were able to oviposit as early as 9 and 13 days, respectively. At 30°C, however, TPS oviposited as early as 7 days after hydration. In this study, size of TPS at initiation of oviposition apparently varied with temperature as well. Tadpole shrimp at 30°C initiated oviposition at a smaller size than at 20 or 25°C, although the range is small (Fig. 3) and may not be biologically significant. Takahashi (1977) reported oviposition beginning when TPS carapace length exceeded 7 mm. In our study, the mean size (30°C) at oviposition initiation was 10.26 mm, whereas the smallest TPS to oviposit was 8.5 mm in length.

Tadpole shrimp in our study oviposited primarily in several temporally discrete batches of eggs. Because of this, we were able to compare hatching rates over sequential egg batches. There is a trend toward decreasing hatching rates with increasing egg batch numbers during the first hydration, but the cumulative hatching rate after 2 hydrations is relatively constant (Fig. 4). Therefore, it appears that in later batches of eggs, a larger proportion requires a 2nd hydration in order to hatch. This may be a strategy for producing some eggs that will not hatch until a 2nd or later hydration, thus spreading the reproductive risk in unpredictable habitats.

The high hatching rates reported here (cu-

mulatively > 70%) indicate high viability, which is critically important for mass production, both for the maintenance of a laboratory colony and for field distribution. Conditions in the field, though, are not likely to be as good as in the laboratory, so hatching rates of laboratory-reared eggs distributed into field settings might be lower upon each hydration, even though overall viability is high. Therefore, more floodings may be required in the field than in the laboratory to achieve high cumulative hatching rates. In fact, hatching rates of laboratory reared eggs distributed into experimental ponds in the Imperial Valley of California ranged from 12 to 19% during a single flooding (Fry et al. 1994), but in another study the mean cumulative hatching rate in field microcosms after 6 floodings was 88%. Thus, high overall hatching rates can be achieved in the field, and these will ultimately be limited by the viability of eggs that are distributed.

Conclusions: Tadpole shrimp are able to grow to maturity and produce a large proportion of viable eggs under the rearing procedure used in this study. The results suggest that 30°C is the best posthatching rearing temperature. Growth is very fast, oviposition is early, and survival is short, all without sacrificing the necessary component of fecundity. Thus, using the egg handling procedures described in combination with rearing at 30°C, the egg-to-egg generation time can be as short as 17 days (7 day minimum growth to oviposition, 3 day embryo development, 7 day egg drying).

Further research may improve rearing productivity. First, it may be possible to decrease the drying time of eggs, thus shortening the total generation time. Second, nutritional requirements of TPS must be determined to ensure maximum productivity in the system. Finally, appropriate rearing densities and rearing chamber sizes must be determined because it has been shown that TPS size is density dependent (Tietze and Mulla 1990, Weeks 1990).

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