

Sensitivity of Metabolic Rate, Growth, and Fecundity of Tadpole Shrimp *Triops longicaudatus* to Environmental Variation

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Abstract. The influence of fluctuations of ambient oxygen tensions and temperature on the rate of oxygen consumption (VO_2) was determined for the tadpole shrimp, *Triops longicaudatus*. VO_2 was oxygen dependent up to 185 torr PO_2 , and Q_{10} for oxygen consumption between 20° and 30°C was 1.9. From these results it was estimated that oxygen consumption increases more than 1100 $\mu\text{l} \cdot \text{g}^{-1} \cdot \text{h}^{-1}$ in *T. longicaudatus* for typical diurnal changes in temperature and oxygen in desert ephemeral pools. Elevated VO_2 may be coupled with increased growth rate and fecundity, because these characteristics were highly sensitive to changes in ambient temperature and oxygen tension. Depressing mean daily temperatures by 2.3°C significantly decreased body mass, whereas hyperoxia (200 torr) significantly increased growth compared to that of animals raised under hypoxic conditions (70 torr). Fecundity was dependent on animal mass and ambient oxygen tension. Thus, for a 22-day season, one *T. longicaudatus* female could produce 30 more eggs per 10 torr increase in oxygen tension and 43 more eggs per 1°C change in mean daily temperature. These results indicate that there are selective pressures for metabolic sensitivity to the high temperature–high oxygen conditions of the ephemeral environments inhabited by *T. longicaudatus*.

Introduction

Tadpole shrimp (*Triops longicaudatus* LeConte) are primitive branchiopod crustaceans that face extreme environmental conditions in the ephemeral desert pools that they inhabit. These pools are characterized by large diurnal oscillations (greater than 200 torr O_2 per day) in the dissolved gasses produced by the photosynthesis and

metabolism of their biota, and by large and rapid fluctuations in water temperature (greater than 15°C per day; Scholnick, 1994). In addition, pool water may persist for as little as 10 days during the summer when evaporation rates are high. As a result, species such as *T. longicaudatus*, which survive dry periods as dormant eggs, must complete their life cycles rapidly while experiencing extreme environmental fluctuations.

Metabolic control in tadpole shrimp presents a unique problem because of the need for rapid development in a variable environment. Only a few physiological studies have been conducted on tadpole shrimp. Horne (1971) and Scott and Grigarick (1979) reported that *Triops* eggs do not hatch until temperatures are greater than 14°C. Hillyard and Vinegar (1972) reported that oxygen consumption in immature *T. longicaudatus* was three times more sensitive to temperature than in adults. In another species of tadpole shrimp (*Lepidurus lemmoni*), metabolism was sensitive to changes in ambient oxygen tensions (Eriksen and Brown, 1980). Therefore, it is unclear what effects simultaneous fluctuations of both oxygen and temperature have on the metabolism, growth, and reproductive success of tadpole shrimp inhabiting desert ephemeral pools.

This investigation examines the influence of simultaneous fluctuations in oxygen and temperature, which occur naturally in desert ephemeral habitats, on rates of oxygen uptake in *Triops longicaudatus*. The effects of these fluctuations on growth and fecundity were also examined.

Materials and Methods

Specimens of *Triops longicaudatus* LeConte were hatched from and raised with rehydrated soils collected from four previously studied ephemeral pools near Moab,

Utah (Scholnick, 1994). Soils containing eggs from the four pools were mixed and randomly subsampled for different treatments. Animals were raised in plastic tubs (70 × 50 × 13 cm) or 10-gallon glass aquaria under cycles of temperature (18°–32°C) and light (12L:12D) to simulate summer conditions. Diets consisted of naturally occurring protozoa and algae of rehydrated soils, supplemented with commercially purchased live *Tubifex*.

Metabolic measurements

Respiration rates (VO_2 , microliters of oxygen consumed per gram wet weight per hour, standardized to STP) were determined for oxygen tensions of 77, 127, and 185 torr at 20°, 25°, and 30°C. VO_2 values were determined in a temperature-equilibrated flow-through system. The system consisted of an elevated 4.5-l water reservoir that was equilibrated with different partial pressures of O_2 and used as a pressure head to maintain constant flow. Flow was measured volumetrically and regulated by the height of the reservoir and the diameter of the tubes. Flow rates were set between 6.5 and 8 ml · min⁻¹, depending on animal size and temperature, and were held constant throughout each experiment (less than 0.1 ml change over 5 h). The oxygen content of the water was measured with an Orion oxygen meter and probe (#840 Orion Research, Boston) fitted with a 0.5-ml flow-through cell and a stir bar. Voltage output was connected to a personal computer through an analog-to-digital converter and sampled every 20 s. A 133-ml animal chamber was suspended in a water bath equipped with a thermostat and was continually stirred with an enclosed stir bar to ensure mixing. Water was collected downstream and pumped back to the reservoir with a water pump. A series of valves made it possible to measure the oxygen content of the incurrent water (water coming directly from the reservoir) or the excurrent water (water coming directly from animal chamber) without disrupting flow.

Animals of similar masses (mean of 364 ± 10.5 mg ranging from 290 to 440 mg) were given 1 h to adjust to the temperature and oxygen tensions of the chamber before measurements began. Animals were selected from simulated pools at predetermined times when oxygen and temperature levels were similar to experimental conditions. VO_2 was measured for individual animals, and each animal was measured only once. Measurement periods ranged from 3 to 4 h for each animal at a given temperature and PO_2 .

The design of the animal chamber and oxygen sampling system conformed to the principles of a single-chamber system as defined in Frappell *et al.* (1989). In this system, the time constant for the washout of oxygen for the animal chamber and from the electrode chamber ($\tau_1 + \tau_2$) was 24 min, while the time constant for the electrode circuit

alone (τ_2) was less than 2 min. Because τ_2 was reasonably small with respect to ($\tau_1 + \tau_2$) the system could be considered a single chamber in which $\tau_2 = 0$.

Measurements of growth

Growth rates of *T. longicaudatus* under natural conditions were determined in four study pools near Moab, Utah, during the summer of 1993. Animals were individually caught in a small sieve, blotted dry through the sieve, and weighed. Animals were held in a beaker containing pool water until all animals were weighed. Wet weight was determined daily by weighing 10 to 20 animals from each pool on an Ohaus portable balance (#CT 10-3, Florougham, Park, NJ).

The influence of temperature on growth rate was determined, as described above, in laboratory-simulated ephemeral pools where the average temperature was either 25.7° or 23.4°C. For the high-temperature condition (mean = 25.7°C), temperatures were cycled between 19° and 31°C by using heat lamps; the average temperature change was 0.85°C · h⁻¹. For the low-temperature condition (mean = 23.4°C), temperature fluctuated from 19° to 29°C; average temperature change was 0.65°C · h⁻¹. Animals were hatched at treatment temperature cycles, and growth rates were determined from daily measurements of wet weight. Average oxygen partial pressure of 125 ± 2 torr was maintained in each treatment by vigorously bubbling air into each tank. Temperature treatments were replicated five times with 4–5 animals in each tank at the beginning of the experiment.

Sensitivity of growth to oxygen was determined from animals raised in laboratory-simulated pools as described above at 200 ± 5 and 70 ± 7 torr PO_2 by either continually bubbling 100% oxygen or 13% oxygen, remainder nitrogen. Temperature was cycled in a manner identical to the low-temperature condition described above, and growth rates were determined by changes in wet weight per day. Oxygen treatments were replicated five times with 3–5 animals in each tank at the beginning of the experiment. Animals were hatched at treatment temperature cycles and growth rates were determined from daily measurements of wet weight.

Fecundity

Animals were raised in simulated ephemeral pools where temperature and light were cycled at 125 or 200 torr O_2 as described above. Fecundity, or egg production, was determined by chilling gravid animals (eggs were visible in brood pouches) to 8°C. When animals became hypothermic, the brood pouches opened and the eggs were released. All eggs released per female were collected and counted. Brood pouches were checked to ensure that all eggs had been liberated. This procedure resulted in zero

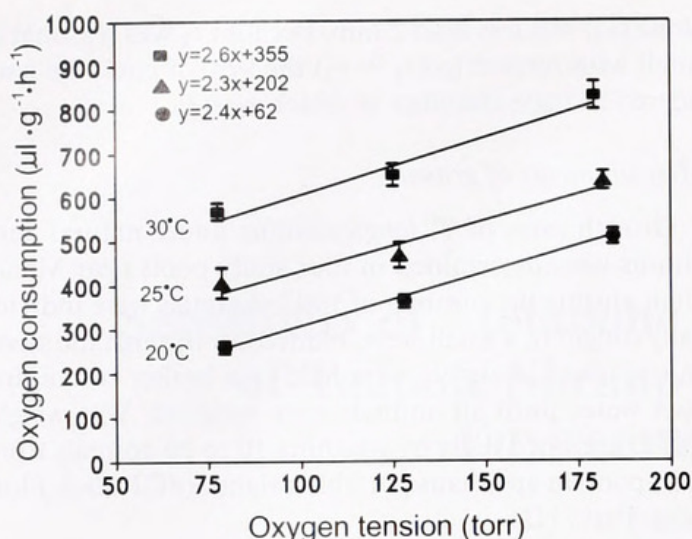


Figure 1. Mean oxygen consumption (microliters of oxygen per gram wet weight per hour) at different oxygen tensions for *Triops longicaudatus*. Values presented are means \pm SEM. Lines represent linear regressions with r^2 greater than 0.7 in all cases.

adult mortality. However, egg viability appeared to be severely compromised as a result of the “forced” release. Attempts to dry and rehydrate eggs were unsuccessful.

Statistics and calculations

An analysis of covariance was applied to the mean weights for each treatment group to determine statistical differences between growth rates. ANCOVA was weighted by the number of individuals in each tank to account for uncontrollable differences in animal number. Higher sample size was assumed to be a more accurate predictor of mean population mass and was therefore given more weight in the analysis. A probability of ≤ 0.05 was considered statistically significant.

Sensitivity of oxygen consumption to change in temperature, Q_{10} , was calculated by using the general formula:

$$Q_{10} = (M_2/M_1)^{10/(T_2-T_1)}$$

where M_2 and M_1 are metabolic rates at the higher (T_2) and lower (T_1) temperatures, respectively.

In order to reduce mass-specific effects, animals of similar masses were chosen for metabolic measurements. Because mass did not vary significantly between treatment groups ($p < 0.05$ ANOVA), VO_2 ($\mu\text{l} \cdot \text{g}^{-1} \cdot \text{h}^{-1}$) was determined by dividing oxygen consumption by wet mass.

Results

Rates of oxygen consumption (VO_2) in *Triops longicaudatus* are sensitive to changes in ambient temperature and oxygen (Fig. 1). Temperature sensitivity, or Q_{10} , at 125 torr was 1.85 between 20° and 30°C, 1.82 between 20° and 25°C, and 1.92 between 25° and 30°C. There

was a positive linear relationship between VO_2 and oxygen tension throughout the physiological range. Temperature had very little effect on oxygen sensitivity. The average change in VO_2 per torr oxygen tension was $2.5 \mu\text{l} \cdot \text{g}^{-1} \cdot \text{h}^{-1}$.

Changes in VO_2 for oxygen and temperature fluctuations typical of diurnal cycles in desert pools (Scholnick, 1994) were predicted from the metabolic responses presented in Figure 1. Metabolic rates were estimated to increase more than sixfold during a typical diurnal cycle (Fig. 2) when temperature and oxygen vary between 18° and 32.5°C and 60 and 226 torr, respectively. Therefore, animals could experience a change in VO_2 as great as $1100 \mu\text{l} \cdot \text{g}^{-1} \cdot \text{h}^{-1}$ during a single 6-h diurnal period. Growth rates in the field ranged from 97.7 to 44.7 $\text{mg} \cdot \text{day}^{-1}$ between pools (Fig. 3). The average growth rate for field animals was 53 $\text{mg} \cdot \text{day}^{-1}$, similar to the rate of about 57 $\text{mg} \cdot \text{day}^{-1}$ for animals raised in the laboratory (Fig. 4). Depressing the mean daily temperatures by 2.3°C resulted in a significant decrease in body mass ($p < 0.02$ ANCOVA; Fig. 4). On average, animals raised at the higher temperature cycle weighed over 80 mg more than those raised at the low temperature cycle after 5 days of age. At day 9, about the time when egg laying is initiated, body mass was 27% greater for animals raised at the higher average daily temperature.

Animals raised under hyperoxic conditions (200 torr) grew significantly faster (an increase of more than twofold until day 20) and were significantly larger ($p < 0.01$ ANCOVA) at every age over 5 days than animals raised under hypoxic conditions (70 torr; Fig. 5). The results for the

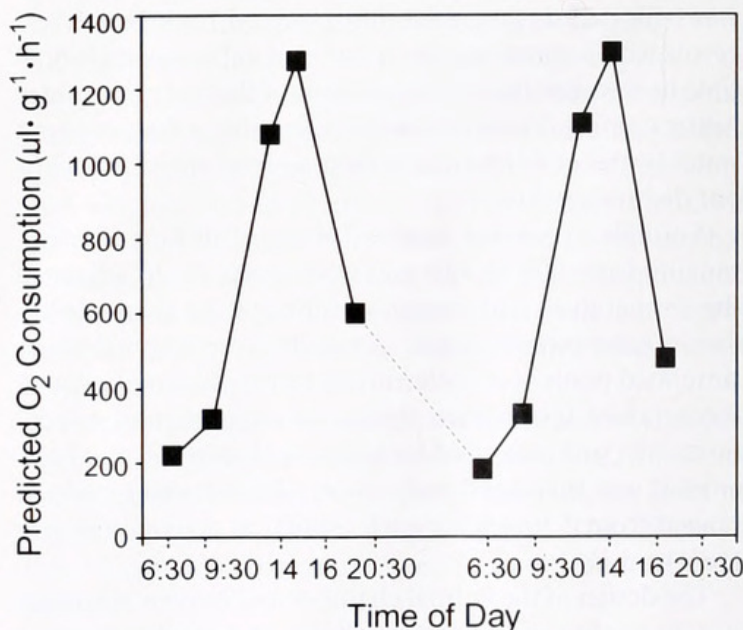


Figure 2. Predicted change in oxygen consumption rates (microliters per gram per hour) for *Triops longicaudatus* for typical diurnal fluctuations in oxygen and temperature measured in the field (Scholnick, 1994). Changes in oxygen consumption rates are based on temperature and oxygen sensitivity presented in Figure 1.

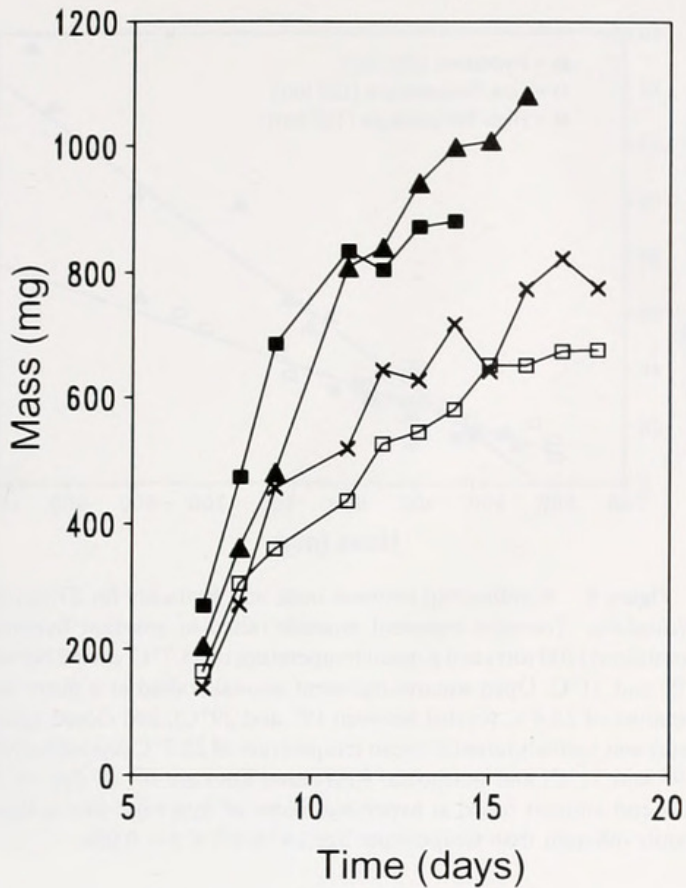


Figure 3. Growth rates for *Triops longicaudatus* from four desert pools near Moab, Utah, during the summer months of 1993. Each point represents an average wet mass of 10–20 animals in each pool.

oxygen and temperature treatments were statistically identical whether the entire growth curve (linearized using log time) or only the linear portion of the curve was used.

There was a positive linear relationship between number of eggs and wet mass (Fig. 6). At a PO_2 of 200 torr, the brood pouches of an 800-mg animal contained an average of 50 more eggs than those of a 300-mg animal. Rearing temperature (mean cyclic temperature of either 25.7° or 23.4°C) had no effect on the relationship between body mass and egg number. The slope of the regression line for animals raised at elevated ambient oxygen tensions (200 torr) was significantly greater than that of the regression line for animals raised at oxygen saturation (125 torr O_2 ; $p < 0.01$ ANCOVA).

Small changes in temperature or oxygen dramatically change the estimate of total number of eggs laid in one season (Table I). Based on the independent influence of temperature or oxygen on body mass (Figs. 4 and 5) and the relationship between body mass and fecundity (Fig. 6), an increase of 2°–3°C in average diurnal temperature was calculated to increase fecundity by about 99 eggs over a 22-day period. This estimate assumes that animals produce one brood every 3 days (estimated from Ahl, 1983) and the first brood is produced at a wet weight of 200 mg

(Fig. 6; Table I). Animals experiencing hyperoxic conditions could produce 378 more eggs over a 22-day season than animals raised under hypoxic conditions at the lower average daily temperature (Table I).

Discussion

The results presented in this study indicate that *Triops longicaudatus* maintains a high degree of metabolic sensitivity despite the wide range of environmental conditions in its natural habitat. The net effect of temperature and oxygen sensitivity is to increase oxygen consumption during the day when temperature and oxygen tensions are high. Development and fecundity are related to PO_2 and temperature, and hence to elevated VO_2 . Shortened development time and increased fecundity are critical for successful completion of life cycles in ephemeral environments.

Branchiopods are primitive crustaceans that are often prominent in ephemeral systems (Hessler *et al.*, 1982).

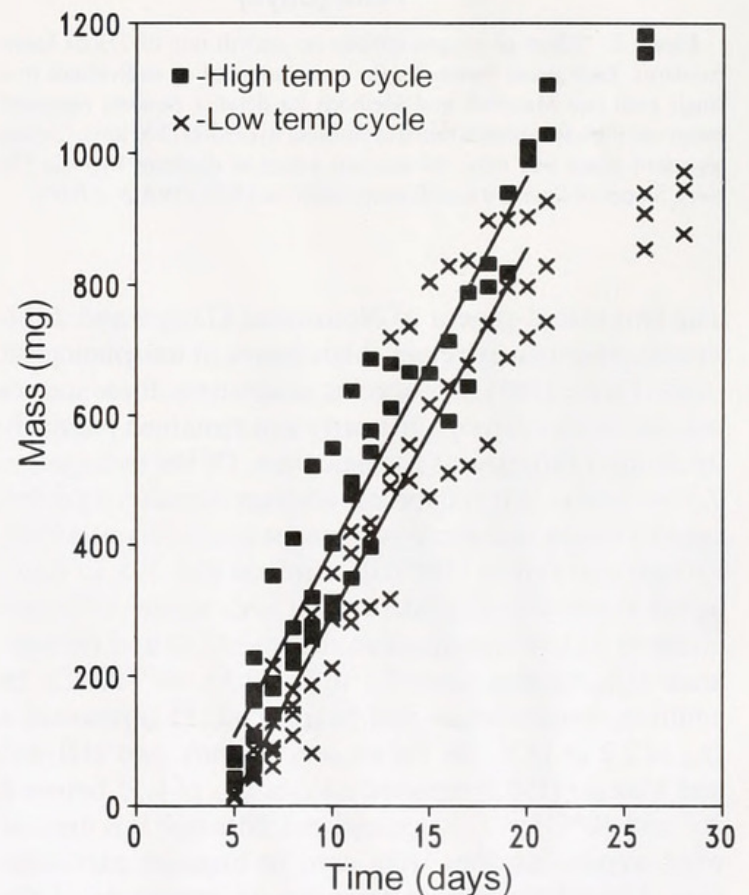


Figure 4. Effect of cyclic temperature regimes on growth rate of *Triops longicaudatus*. Each point represents the mean wet mass of all animals raised in a single pool (see Materials and Methods for details). Squares represent mean wet mass for animals raised at a mean temperature of 25.7°C, cycled between 19° and 31°C ($y = 57.7x - 190.7$, $r^2 = 0.91$). Crosses represent mean wet mass for animals raised at a mean temperature of 23.4°C, cycled between 19° and 29°C ($y = 56.8x - 271.3$, $r^2 = 0.89$). Positions of regression lines were significantly different ($p < 0.02$).

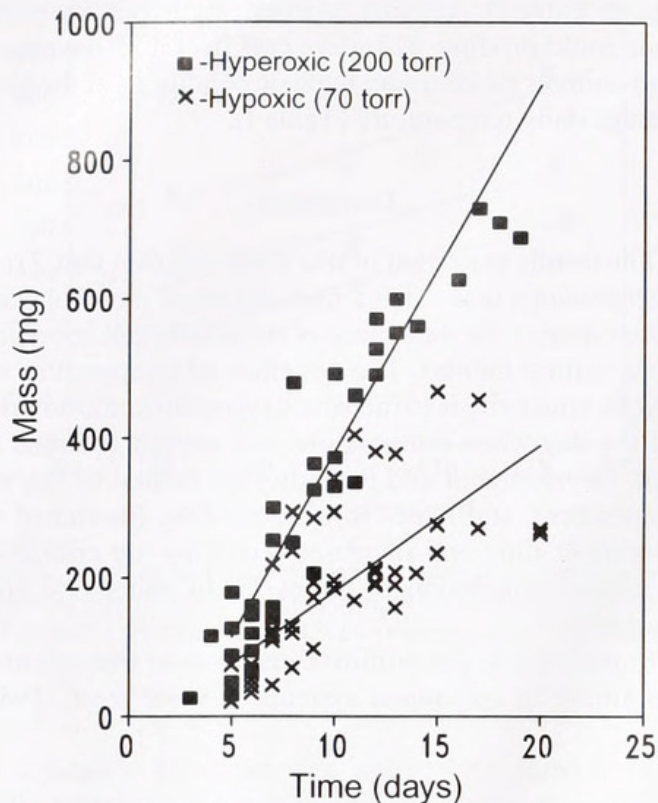


Figure 5. Effect of oxygen tension on growth rate of *Triops longicaudatus*. Each point represents the mean mass of all individuals in a single pool (see Materials and Methods for details). Squares represent mean wet mass for animals raised at constant hyperoxia (200 torr). Crosses represent mean wet mass for animals raised at constant hypoxia (70 torr). Slopes of lines are significantly different (ANCOVA $p < 0.01$).

The two extant genera of Notostraca (*Triops* and *Lepidurus*) exhibit an extremely high degree of morphological stasis (Fryer, 1985). The specific adaptations these species use may have evolved quite early and remained relatively unchanged throughout geologic time. Of the two genera, *Triops* prefers warm habitats, whereas *Lepidurus* prefers cooler regions and more permanent pools (Fryer, 1988). Eriksen and Brown (1980) determined that VO_2 in *Lepidurus lemmoni* is dependent upon both oxygen (35% decrease in VO_2 from saturation to critical O_2) and temperature (Q_{10} ranging from 2.1 to 2.7 from 18°–28°C). In addition, Shtcherbakov and Muragina (1953) reported a Q_{10} of 2.2 at 15°C for *Triops cancriformis*, and Hillyard and Vinegar (1972) reported a lower Q_{10} of 1.55 between 26° and 30°C for *T. longicaudatus*, although it is unclear what oxygen tensions were used to measure metabolic rate. The relatively high temperature sensitivity of the Notostraca suggests that diurnal fluctuations in temperature, even in vernal pools where oscillations may be less extreme (Wiggins *et al.*, 1980), may be essential to elevate metabolism and thus increase rates of growth and reproduction.

Many crustaceans from environments that regularly experience large fluctuations of oxygen and temperature

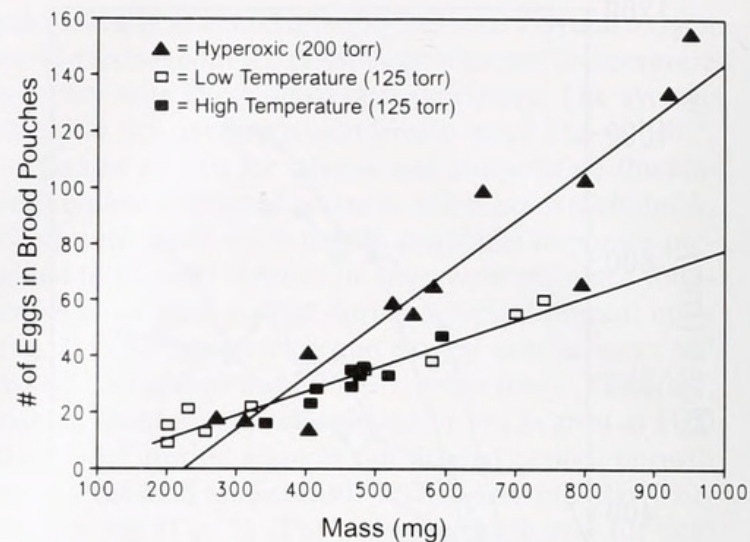


Figure 6. Relationship between mass and fecundity for *Triops longicaudatus*. Triangles represent animals raised at constant hyperoxic conditions (200 torr) and a mean temperature of 25.7°C, cycled between 19° and 31°C. Open squares represent animals raised at a mean temperature of 23.4°C (cycled between 19° and 29°C), and closed squares represent animals raised at mean temperature of 25.7°C (cycled between 19° and 31°C) and normoxia. Regression lines are for all data at 125 torr and animals raised at hyperoxia. Slope of hyperoxic line is significantly different than temperature line (ANCOVA $p < 0.05$).

are known to regulate oxygen consumption (see Taylor, 1988, for a review). Numerous mechanisms, including increasing ventilation volume and changing heart rate, pH, or the oxygen-transporting properties of the blood, have been shown to aid in the regulation of oxygen uptake. Thus, metabolic independence appears to be adaptive for many crustaceans. The results presented here suggest the opposite—that there are strong selection pressures on *T. longicaudatus* to maintain metabolic sensitivity in predictably high temperature–high oxygen environments.

Lowering the average ambient temperature by 2.3°C significantly decreased the body mass of the tadpole shrimp but did not change rate of growth except early in life (<5 days). This result suggests that temperature sensitivity before adulthood may be critical. Hillyard and

Table I

Estimated fecundity of a single female T. longicaudatus over a 22-day season

	Day first clutch oviposited	Cumulative no. of eggs laid
High temp. cycle (25.7°C)	7	287
Low temp. cycle (23.4°C)	8	188
Hyperoxic (200 torr)	7	452
Hypoxic (70 torr)	11	74

Assuming one clutch oviposited every 3 days (estimated from Ahl, 1983) and first clutch oviposited at 200 mg wet mass (Fig. 5).

Vinegar (1972) reported that, between 26° and 30°C, *T. longicaudatus* oxygen consumption rates were almost three times more temperature-sensitive in immature animals than in adult animals. Therefore, temperature sensitivity in *Triops* may be elevated immediately after hatching, when pools have recently filled and temperature fluctuations are reduced (Scholnick, 1994).

Unlike changes in temperature, changes in ambient oxygen tensions affect growth rate throughout the life of the animal. This result is not surprising considering the large metabolic oxygen sensitivity exhibited by *T. longicaudatus*. The dependence of metabolism on oxygen tension, even above saturation, suggests that oxygen diffusion is limiting VO_2 throughout the physiological range of the animal. Although an extracellular hemoglobin with a relatively high affinity for oxygen has been described for *T. longicaudatus* ($P_{50} = 6.8$ at pH = 7 and 22°–23°C; Horne and Beyenbach, 1971), the unspecialized respiratory structures (bulbous epipodite, Fryer, 1988; and entire abdominal phyllopod) in this primitive crustacean—unlike the specialized respiratory structures in more advanced crustacea—appear to be inadequate for adjusting oxygen delivery at variable oxygen tensions. In view of the high degree of morphological stasis exhibited by tadpole shrimp (Fryer, 1985) and the possible reproductive advantages of maintaining oxygen sensitivity, the selection pressure for more specialized respiratory structures is probably low.

T. longicaudatus does not appear to fit the typical pattern of an active oxygen conformer (for reviews see Herreid, 1980; Prosser, 1991). VO_2 in *T. longicaudatus* is highly dependent on ambient oxygen tensions well above oxygen saturation. Therefore, VO_2 is seemingly influenced by ambient oxygen tension at all oxygen tensions within this species' physiological range. Few studies have examined the physiological effects of hyperoxia; however, ventilation was found to decrease in both crayfish (Masabau et al., 1984) and lugworm (Toulmond and Tchernigovtzeff, 1984) in response to an increase in oxygen. In the few decapod crustaceans studied, VO_2 remains independent of oxygen tensions above saturation (Dejours and Beekenkamp, 1977; Jouve-Duhamel and Truchot, 1983). *T. longicaudatus* apparently does not stabilize VO_2 against hyperoxia. Furthermore, predawn measurements of oxygen in ephemeral desert pools (Scholnick, 1994) indicate that partial pressures of oxygen typically do not drop below 40 torr and should therefore not have a large negative effect on VO_2 .

Growth in *T. longicaudatus* is dependent on high temperature. In addition, growth and survivorship are strongly influenced by the large fluctuations of temperature and oxygen that are characteristic of these habitats (Horne, 1971; Scholnick, 1994). Horne (1971) and Scott and Grigarick (1979) found that *T. longicaudatus* eggs did not hatch until temperatures were greater than 14°C and that

the rates of hatching were highest above 22°C (Takahashi, 1977). Additionally, Scott and Grigarick (1978) reported high mortality rates and slow growth rates (about 9 times lower growth rates than those reported in this study) for animals raised at 25° or 30°C compared to those raised under diurnal oscillations, as in this study. Therefore, hatching, growth rate, and survivorship in *T. longicaudatus* all appear to be extremely dependent on the high temperature conditions characteristic of ephemeral desert pools.

A small change in average daily temperature or oxygen tension has a large effect on the total number of eggs that can be laid in a season. Calculations based on differences in mass indicate that over a 22-day season an individual can produce about 30 more eggs in response to an increase of 1°C in mean temperature. In addition, a 10-torr increase in ambient oxygen results in production of about 43 more eggs during a 22-day season. Therefore, small changes in temperature, oxygen, or both between seasons can dramatically affect fecundity and reproductive success. The dependence of initial oviposition times on temperature and oxygen would exaggerate this effect when rainfall is limited and seasons are compressed. Ahl (1991) and Seaman et al. (1991) reported a similar relationship between carapace length and fecundity for the tadpole shrimp *Lepidurus packardii* and *Triops granarius*, respectively. Although it was not possible to measure egg viability, a change in viability would be unlikely to offset the large effect of oxygen and temperature on fecundity. Food for tadpole shrimp is abundant in ephemeral pools (Dodson, 1987), suggesting that the limiting factor in these environments is not food availability but the time necessary to complete the life cycle.

The results from this investigation suggest that metabolic sensitivity in high temperature–high oxygen environments enhances the reproductive success of *Triops longicaudatus*. Shortened development times and increased fecundity are critical for success in ephemeral environments. Because VO_2 is associated with aerobic energy metabolism and appears to be diffusion-limited in *Triops longicaudatus*, the combination of hyperoxia and high temperature may engender a higher rate of energy metabolism and in turn a higher growth and reproductive output. Thus, there appear to be reproductive advantages for metabolic sensitivity to the hot, hyperoxic conditions in the ephemeral pools inhabited by *Triops longicaudatus*.

Acknowledgments

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