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Distribution, development, and metabolism of larval stages of the warmwater shrimp, *Caridina babaulti basrensis* (Decapoda, Atyidae)

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Abstract
Peak release of zoea I larvae of the warmwater shrimp, *Caridina babaulti basrensis* (Al-Adhub AHY 1987) in the field coincided with the highest summer water temperature (33°C). Zoea I abundances did not correlate significantly with the phase of the lunar cycle ($p = 0.256$) and only slightly with time of day (day : night regimes, $p = 0.079$). Temperature correlated significantly with zoeae I larval release in the field ($p < 0.0001$). Development and respiration were measured at constant water temperatures ranging from 20 to 35°C in coordination with the temporal distribution of larvae in the field. Cumulative duration for the development of the larval phase of *C. babaulti basrensis* was 11.4, 7.7, and 6.1 days at 25, 30, and 35°C, respectively. Larvae were unable to complete development at 20°C. Respiration rate for larval *C. babaulti basrensis* increased in direct proportion to temperature, and revealed metabolic stress at high temperatures. Laboratory rearing supported field data, which indicated a constraint on the presence of stage I zoeae in the plankton at lower temperatures (20°C). Although some larval stages may be metabolically stressed at higher temperatures, rapid development rates accomplished at higher temperatures may be a likely mechanism for retention within the habitat and recruitment to the adult population.

Keywords: *Larvae, shrimp, release, development, abundance, distribution, temperature, lunar cycle,* Caridina babaulti basrensis

Introduction

Patterns in the development of the early ontogenetic stages of aquatic invertebrates have important implications in structuring adult populations. Strategies for mating (Christy 1978), larval release (Anger et al. 1994; Morgan 1990; Morgan & Christy 1994), and recruitment (Keough & Downes 1982; Nichols & Thompson 1988; Romimohtarto & Hindarti 1990; Roughgarden et al. 1988; Sandifer 1975) are vital for the successful

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propagation of decapod populations. Release of decapod larvae have been correlated to different environmental cycles based on successful avoidance of predators by these populations (Morgan & Christy 1994). Equally important are the physiological responses of decapod larvae to environmental variables, which depend on biochemical and anatomical development throughout the instar stages and are reflected by the changes in morphological features as well as shifts in the behaviour of the organism (e.g. adoption of a benthic habitat after metamorphosis). Physiological responses also depend on the developmental stage of the larva (see review by Sastry 1983). Many studies have determined larval growth and metabolism in relation to the environment, food availability, and mortality and survival rates in temperate regions (e.g. Anger 1984; Capuzzo & Lancaster 1979; Dawirs 1979; MacKenzie 1988; Sastry 1979). In contrast, there is comparatively less information on the development of warmwater decapod larvae in tropical and subtropical regions (Anger 1995; Vijayaraghavan & Easterson 1974).

In this study, we relate larval abundance in the field to larval development rates of *C. babaulti basrensis* in the laboratory. Development rates and oxygen consumption were measured at different temperatures that correspond to temperatures experienced in the field when larvae are known to be present to determine physiological viability of larvae at these temperatures. Quantitative samples from the field that correspond to the lunar cycle were collected, as well as day/night cycle, to determine whether release occurred during any of these cycles. Since the tidal cycle in the northern Arabian Gulf is of a mixed diurnal nature, this cycle would be captured in the lunar and diurnal cycles (e.g. see website for tidal information, http://www.ssc.erc.msstate.edu/Tides2D/persian_gulf.html). Hamzah (unpublished: 1980) studied various aspects of the biology and swimming activities of adult *C. babaulti basrensis*. Salman (1987a) described the larval stages of *C. babaulti basrensis* reared in the laboratory. Since then no work has been done on this species of atyid shrimp.

Materials and methods

The study area

The study area is located in the upper reaches of the Shatt al-Arab estuary (Garmat Ali), south of the Hammar Marsh (30–31°N, 47–48°E, Figure 1). The climate of the region is subtropical with distinct winter (wet) and summer (dry) seasons. The upper region of the Shatt al-Arab is oligohaline ($S = 1.3$–2.7 ppt) with a spring tidal amplitude range of 0.3–0.5 m between ebb and flood. Adult *C. babaulti basrensis* live in dense stands of hornwort (*Ceratophyllum demersum*) with another atyid shrimp, *Atyaephyra desmaresti mesopotamica* and the hymenosomatid crab, *Elamenopsis kempi* (Al-Adhub 1987; Al-Adhub & Hamzah 1987; Ali et al. 1995). Gravid female *C. babaulti basrensis* appear in the hornwort starting in March until October. Since this species is multivoltine, reproduction is continuous throughout the spring, summer, and autumn months. Each female can carry between 50 and 70 embryos, and can become gravid multiple times. This species' life cycle covers an annual cycle with five larval stages after hatching, followed by a megalopal stage, all six stages remain in the plankton from one to two weeks (Salman 1987a). The planktonic larval stages are followed by several juvenile stages until maturity where they finally reside in the hornwort (Al-Adhub & Hamzah 1987). Dense populations of gastropods also inhabit the hornwort, including *Melanopsis nodosa*, *Melanoides tuberculata*, *Theodoxus jordani*, *Gyraulus convexisculus*, and *Lymnaea tenera euphratica*, as well as many aquatic insects and mites. The zooplankton community of the Shatt al-Arab includes polychaete and oligochaete larvae, insect larvae,

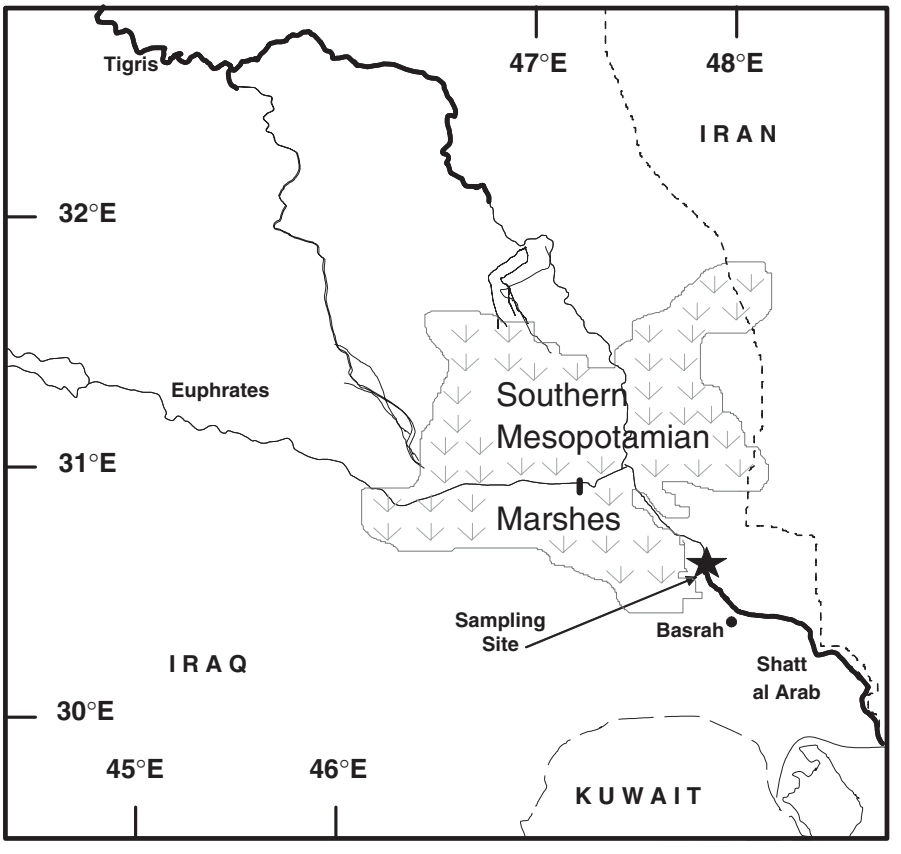

Figure 1. Map of southern Mesopotamia, Iraq, including the southern reaches of the Tigris and Euphrates rivers, and the Shatt al-Arab river system and estuary.

calanoid, cyclopoid copepods, cladocerans, ostracods, amphipods, fish larvae, and decapod larvae, including *Sesarma boulengeri*, *Elamenopsis kempi*, *Atyaephyra desmaresti mesopotamica*, and *C. babaulti basrensis* and, occasionally, harpacticoid copepods (Salman & Ali 1996; Salman et al. 1986).

Larval release and field data

Plankton samples were collected over an annual cycle, starting from the beginning of June 1988, and lasting to the end of May 1989. During 1988, samples were collected weekly from June until mid-October at quarterly lunar cycles (new moon, first quarter, full moon, and third quarter). On each sampling date, two night samples were collected between 21:00 and 23:00 h followed by two morning collections, which usually took place between 09:00 and 11:00 h. Surface (0.2–0.5 m) and bottom (10–11 m) samples during night and the daytime were collected by horizontal tows on the sampling dates. A plankton net with a 0.4 m inner mouth diameter and mesh size of 333 μm fitted with a flow-meter was used to collect the samples. Between 40 and 60 m^3 of water was filtered during each sample collection. Abundance data are presented as N m^{-2} by multiplying the abundance by 10 m, which was the water depth at the sampling site. Samples were preserved in a 4% formalin solution immediately after collection. Stages I and II zoeae were absent from the samples

by 10, October 1988. Therefore samples were collected fortnightly (new moon–full moon cycles) until mid-November, 1988 when no larvae were present in the samples. Monthly samples were collected during the winter (December 1988 to February 1989) to confirm presence/absence of larvae in the field. Stages I and II zoeae reappeared in mid-March, whence weekly samples were resumed until the end of May. Larvae were identified according to the descriptions of Salman (1987a) and counted in a 10-mL partitioned counting tray with the aid of a dissecting microscope.

Abundance data from the weekly samples (June–October 1988; 48 samples total) of stage I zoeae were used as a relative index of larval release to determine the hatching rhythms of ovigerous females. Sampling design allowed a three level model II single classification nested analysis of variance (Sokal & Rohlf 1981). The data were structured such that depth (surface/bottom) was nested within time of day (morning/night), which in turn was nested within a phase of the lunar cycle (new moon/first quarter moon/full moon/third quarter moon). To avoid temporal effects, abundance data of stage I zoeae were converted to proportions and then arcsine transformed (Sokal & Rohlf 1981). We were then able to test for significant variations in abundances of stage I zoeae among phases of the lunar cycle, time of day, and vertical distribution of zoeae with a single statistical analysis.

Development-temperature (D-T) response

Gravid females of *C. babaulti basrensis* were collected on 19 April and 11 June 1989, from Garmat Ali, a tributary linking the Hammar Marsh and the Shatt al-Arab estuary (Figure 1) and held in the laboratory in incubators at a constant temperature of 25°C and a salinity of 1.5 ppt. Development and growth rate experiments were carried out with individually reared larvae at four experimental temperatures: 20, 25, 30, and 35°C based on the range of temperatures when larvae are present in the plankton. All experiments were conducted at a constant light : dark cycle of 13:11 h. Upon hatching, larvae were individually pipetted into 20 mL of brackish water (1.5 ppt salinity) collected from the same site that the gravid females were collected and treated by freezing and thawing before use. Only healthy-looking individuals with undamaged appendages and no apparent deformities of the body or telson were used for the experiments. Twenty individuals were used for each experimental temperature run. Larvae were checked every eight hours for exuvia and mortalities. Detritus from the site where gravid females were collected was used as the experimental food. Prior to feeding, detritus was frozen at −60°C for at least 24 h before use, to eliminate any potential invertebrate predators present in the detritus. Preliminary experiments indicated that larvae did not successfully feed on fish food flakes. *Caridina babaulti basrensis* larvae also were not successful in feeding on *Artemia* sp. nauplii or natural microzooplankton (N. Idrisi, personal observation). Water and food was changed every other day for zoeal stages I, II, and III, and every day for zoeal stages IV, V, and the megalopa.

The development-temperature (D-T) relationship was calculated according to Anger (1984) and the relative rate of increase (Q_{10}) was calculated according to Lampert (1984). A model I two-way analysis of variance (ANOVA: Sokal & Rohlf 1981) was performed on the duration of development data with stage of development ($a = 6$) and temperature ($b = 3$) as main effects. Replicates in each cell were $n = 19$. Because eight hourly observations were taken during the experiments, hourly data were used for the analysis. The analysis precluded the use of the 20°C experimental temperature treatments because of missing data points for stages IV and V zoeae and the megalopa.

Table I. Number of larvae used in the metabolic-response experiments for three temperature regimes (25, 30, and 35°C). Larvae used were from four gravid females hatched on 29 June 1988. Dry weight (DW) estimates were averaged from 20 individuals per larval stage.

Larval stage	Larvae per replicate	Number of replicates per temperature	Total number of larvae in experiments	DW ± S.E (μg)
Zoea I	20–22	4	245	17.1 ± 0.18
Zoea II	12–25	4	169	20.5 ± 0.91
Zoea III	10–12	4–7	175	24.8 ± 0.16
Zoea IV	6–9	4–10	147	33.7 ± 1.03
Zoea V	5–6	6–8	109	54.1 ± 2.00
Megalopa	2–3	5–7	44	83.5 ± 3.70

Metabolic-temperature (M-T) response

Group-reared larvae used for respiration experiments were held at the same temperature and light : dark regimes as larvae in D-T experiments. Metabolic-temperature experiments were conducted on six larval stages (Table I). Respiration was measured with a Gilson differential respirometer, which includes a cooling/heating water bath system that maintains water temperature within ±1°C (Gilson, 1963). Individuals were gently pipetted into 25-mL beakers and held there for about 15 min to allow time for larvae to empty their gut contents. Individuals were then transferred to the respirometer chambers (2–6 individuals per chamber depending on larval stage). Chambers contained 7.5 mL water and carbon dioxide was absorbed with a 5% (w:v) potassium hydroxide solution. Larvae were acclimatised for 2 h during which time the respirometer was brought to equilibrium. Hourly readings were taken during each experimental run. Each experimental run lasted 3–4 h. Results were expressed as weight-specific respiration rates (μL O_2 mg DW^{-1} h^{-1} ±95% confidence intervals). A power function was used to describe the weight-specific metabolic rate–weight relationship (Lampert 1984). Q_{10} expressed as the relative rate of increase of a process rate over a temperature range was calculated for respiration rates over the experimental temperature ranges (Lampert 1984). Dry weights were made to determine weight-specific respiration. A representative sample of 20 animals per larval stage reared at 25°C were briefly rinsed in distilled water, blotted out on filter paper, and individually transferred to pre-weighed silver cups. Individual cups were then left to dry in a drying oven at 60°C for 48 h then weighed to the nearest 0.1 μg on a Cahn microbalance.

Results

Temporal distribution of larvae in the field

The breeding season of *C. babaulti basrensis* was marked by the presence of stage I zoeae in the plankton that persisted from mid-March to the first week in October (Figure 2). Peak abundances for all larval stages occurred in August and coincided with highest recorded surface water temperature (33°C) during the summer. Stages I and II zoeae were absent from samples after the first week in October (surface water temperature <20°C), and reappeared by mid-March (surface water temperature >25°C) (Figure 2). Stage III zoeae consistently appeared in the samples during the summer, then ceased to occur by mid-November, when surface water temperatures dropped below 15°C. Reappearance of stage III zoeae occurred by the end of March. Stage IV zoeae and the megalopa disappeared

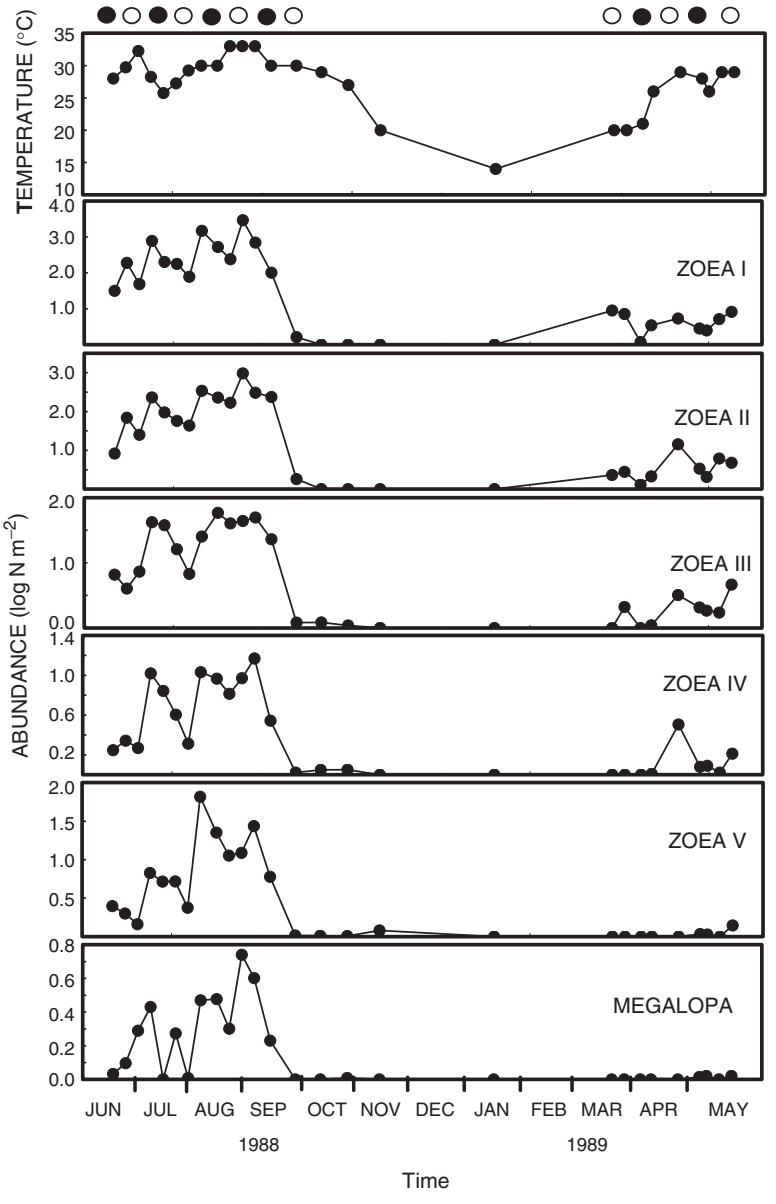

Figure 2. Surface water temperature (T, as °C) and new moon/full moon phases (upper panel) and field abundances (N, as N m^{-2}) of the larval stages of *C. babaulti basrensis* from 1988 to 1989 from the Garmat Ali sampling site (see Figure 1).

from the October samples when surface water temperature was between 25 and 30°C. Stages III and V zoeae were present in November; all stages, including stages III and V were absent in December, and were not present in the plankton until the following spring. Stage IV zoeae reappeared in mid-April; stage V zoeae and the megalopa reappeared at the beginning of May when surface water temperatures approached 30°C (Figure 2). The general trend of larval release included an upper bound of stage I zoeae abundance increasing with temperature (Figure 3). Although abundance of stage I zoeae indicated

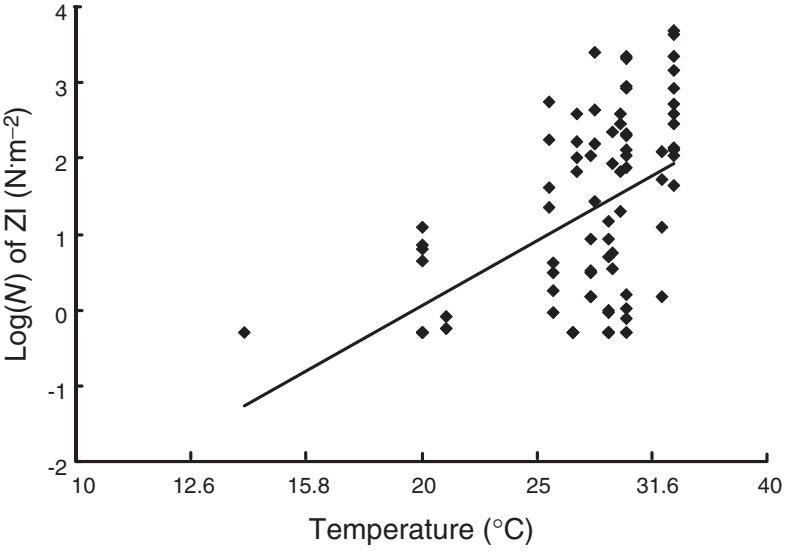

Figure 3. *Caridina babaulti basrensis*. Abundance (N, as $\mathrm{N\,m^{-2}}$) of stage I zoeae (ZI) in relation to surface water temperature (°C), logarithmic scale. $\log N = -11.07 + 8.55 \log T$, $r^2 = 0.228$, $n = 84$.

increased scatter with temperature, there was a statistically significant increase in larval release with temperature.

Caridina babaulti basrensis stage I zoeae abundances were used as an index of larval release by the adult female shrimps. A single classification nested ANOVA did not show any significant relationship with phase of the lunar cycle ($p = 0.256$) nor with time of day ($p = 0.079$), though there was higher larval release during the night. There were no apparent vertical distribution differences of stage I zoeae abundances between surface and bottom samples ($p = 0.934$), although there were slightly more stage I zoeae near the surface.

Development-temperature (D-T) response

Larvae molted successfully to the first juvenile stage at 25, 30, and 35°C (Table II). A model I two-way ANOVA revealed significant differences in duration of development at different temperatures ($F = 398$, $p < 0.0001$), stages of development ($F = 159$, $p < 0.0001$), and their interaction ($F = 22$, $p < 0.0001$). The significant interaction term from the analysis indicated a synergistic effect of temperature on developmental stage, except that stage I zoeae molted slightly over a day regardless of temperature at the three temperatures used in the analysis. For the other stages, increased temperature caused an increase in the development rate (Table II).

Development of larval stages appeared to be inhibited and do not complete development through all larval stages at low temperatures. At 20°C, all larvae molted successfully from stage I to stage II zoeae (2.1 ± 0.03 days), which is a departure from the consistent one-day rate at the higher temperatures. All larvae molted from stage II to stage III zoeae (4.87 ± 0.02 days) at 20°C. Only 20% of the larvae successfully molted from stage III to stage IV zoeae (4.89 ± 0.04 days) at 20°C; a high mortality rate, which was a departure from D-T experiments at higher temperatures. No larvae were successful in molting from stage IV to stage V zoeae. Mean development time from stage I to stage IV zoeae was 11.86 ± 0.28 days at 20°C.

Table II. *Caridina babaulti basrensis*. Duration of larval development (days ±95%) in relation to temperature for individual larval stages and cumulative duration for the complete larval phase. Q_{10} values for larval development rate (day^{-1}) for three temperature ranges for larval *C. babaulti basrensis*.

	Duration of development				Q_{10}		
Larval stage	20°C	25°C	30°C	35°C	20–25°C	25–30°C	30–35°C
Zoea I	2.104 ± 0.12	1.3 ± 0.06	1.1 ± 0.08	1.2 ± 0.08	2.61	1.40	0.84
Zoea II	4.87 ± 0.8	1.75 ± 0.18	0.88 ± 0.08	0.7 ± 0.08	7.74	3.96	1.58
Zoea III	4.89 ± 0.74	2.02 ± 0.12	0.95 ± 0.12	0.75 ± 0.06	5.86	4.52	1.60
Zoea IV	–	1.7 ± 0.1	1.1 ± 0.2	0.75 ± 0.06	–	2.39	2.15
Zoea V	–	2.17 ± 0.08	2.13 ± 0.1	1.42 ± 0.1	–	1.04	2.25
Megalopa	–	2.5 ± 0.2	1.57 ± 0.1	1.23 ± 0.08	–	2.54	1.63
Total larval duration	–	11.44 ± 0.3	7.73 ± 0.28	6.05 ± 0.18	–	2.19	1.63

Table III. Weight-specific respiration rate ($\mu L\ O_2\ mg\ DW^{-1}\ h^{-1}$) ±95% at three different temperatures and Q_{10} values for larval weight-specific respiration rates at two temperature ranges for larval *C. babaulti basrensis*. See Table I for number of larvae per experiment.

Larval stage	25°C	30°C	35°C	Q_{10} (25–30°C)	Q_{10} (30–35°C)
Zoea I	5.68 ± 1.11	9.69 ± 2.98	9.22 ± 5.7	2.91	0.91
Zoea II	7.89 ± 1.46	12.48 ± 4.42	22.15 ± 9.02	2.50	3.14
Zoea III	14.96 ± 5.25	9.5 ± 2.15	24.55 ± 9.61	0.40	6.69
Zoea IV	3.22 ± 1.94	3.61 ± 1.45	5.91 ± 1.7	1.26	2.68
Zoea V	4.98 ± 1.74	9.03 ± 2.81	1.81 ± 0.76	3.28	0.05
Megalopa	5.96 ± 1.58	5.39 ± 1.76	4.68 ± 1.38	0.82	0.75

Q_{10} for duration of development from data collected at eight hourly intervals indicated thermal sensitivity ($Q_{10} > 2.0$) at the lower temperature range for most larval stages. Larvae tended to compensate ($2.0 > Q_{10} > 1.0$) at the higher temperature range (Table II). Stages II and III zoeae were extremely sensitive to the temperature range of 20–25°C (Table II). Q_{10} remained high in stages II and III zoeae at the 25–30°C range (Table II). Q_{10} for the remaining larval stages ranged between 1.04 (25–30°C; stage V) and 2.54 (25–30°C; megalopa). Development rate for the whole larval phase showed a general compensatory response over the 25–35°C range with a Q_{10} of 1.9.

Metabolic-temperature (M-T) response

Larvae showed a typical trend of increased respiration rate with increased temperature (Table III). The exception was the megalopal stage, where mean respiration rate decreased with increased temperature, though the differences were not significant at the 95% level. Stage III was overall most sensitive with a Q_{10} of 6.69 at the 30–35°C range. Stage IV zoeae showed the greatest amount of compensatory response throughout the experimental temperature range. Whereas stage V was most sensitive at the 25–30°C range as indicated by a Q_{10} of 3.28 with the highest inhibitory response at the 30–35°C with a Q_{10} of 0.05 (Table III).

The weight-specific respiration rate to larval weight relationship was estimated for the three temperatures, 25, 30 and 35°C (Table III). The weight-specific respiration rate increased with temperature, and decreased with increased larval weight (Table III). Analysis of covariance (ANCOVA; Temperature: $p < 0.0001$; Larval Stage: $p < 0.0001$;

Interaction: $p < 0.0001$) revealed that both temperature and larval stage explained a significant portion of the variation in weight-specific respiration rates. The significant interaction term in the ANCOVA can be explained by the interference of increased larval weight per stage, which tended to reduce the effect of increased weight-specific respiration rate with increased temperature.

Discussion

Larval stages of *C. babaulti basrensis* were present in the plankton during the summer months in the Garmat Ali tributary that connects the Hammar Marsh with the Shatt al-Arab estuary when water temperatures exceeded 20°C. In the laboratory, larval *C. babaulti basrensis* successfully developed through all stages at a constant temperature range of 25–35°C. Development-temperature (D-T) response experiments indicated a decrease in duration of development with increasing temperature from stage II zoeae to the megalopa; however, stage I zoeae molted at just over one day regardless of temperature above 20°C. Stage I zoeae of other atyid shrimp have been observed to molt within one day regardless of rearing temperature (Benzie 1982; Lakshmi 1975; Salman 1987b), which may be an adaptive strategy to allow larvae to develop beyond this critical stage, independent of temperature, by being lecithotrophic and relying on lipid reserve from the egg yolk to pass through the first larval stage without having to feed. This species does not appear capable of successful development at a temperature of 20°C. The M-T responses indicated that several larval stages were physiologically stressed at higher temperatures, but temporal distributional patterns in the field suggested that the population favored larval release at higher temperatures and rapid development, likely at the expense of physiological stress.

Although duration of development changed significantly with temperature in the total larval phase of the life cycle of *C. babaulti basrensis*, the influence of temperature in relative terms is less than that observed in temperate species due to the relatively short duration of each stage. In comparison to other Caridean larvae, *C. babaulti basrensis* larval duration declined by 1–1.5 days per instar stage over the 10°C (25–35°C) range, whereas stage duration of Caridean larvae from temperate or boreal regions declined by 3–5 days over a similar temperature range (20–30°C: Knowlton 1974; 9–18°C: Criales & Anger 1986; Schultze & Anger 1997). Another major difference in development between warmwater and coldwater shrimp is lack of optional instar stages in warmwater shrimp. Caridean larvae from temperate and boreal regions increase the number of stages as molting frequency increases due to an increase in water temperatures (e.g. Criales & Anger 1986; Knowlton 1974; Schultze & Anger 1997). This phenomenon was not observed in *C. babaulti basrensis*, or in other warmwater shrimp larvae (Benzie 1982; Benzie & De Silva 1983; Fielder 1970; Lakshmi 1975; Salman 1987a, b; Vijayaraghavan & Easterson 1974), suggesting that morphogenesis may be more important than growth in warmwater shrimp larvae (see Knowlton 1974).

Metabolic rates for the larval stages of *C. babaulti basrensis* were slightly higher than those found for larvae of other decapod species (Anger & Jacobi 1985; Dawirs 1983; Jacobi & Anger 1985; McNamara et al. 1985; Mootz & Epifanio 1974; Sastry 1979; Sastry & McCarthy 1973; Sastry & Vargo 1977; Vernberg & Costlow 1966; Vernberg et al. 1981). Only a few of these studies measured respiration rates at or above 25°C (McNamara et al. 1985; Sastry 1979; Sastry & Vargo 1977; Vernberg & Costlow 1966; Vernberg et al. 1981). In these studies, temperatures above 25°C appeared to induce metabolic stress, whereas some *C. babaulti basrensis* larval stages experienced stress at 35°C.

Other than the seasonal synchrony with surface water temperature, only time of day was slightly synchronized with larval release in the field. Our results indicated a marginally insignificant difference between night and morning (time of day) abundance of stage I zoeae, but because of the large variability associated with plankton samples, it is necessary to bear in mind the possibility of committing a type II error, i.e. accepting a false null hypothesis. Assuming that there may be a difference between day and night larval releases, we observe that the greater abundance occurred in the morning samples. This suggested that female adults released more larvae between midnight and daybreak compared to the day and early evening, since night samples were collected between 9:00 p.m. and 11:00 p.m. followed by morning collection which took place between 9:00 a.m. and 11:00 a.m. The D-T response experiments showed that stage I zoeae would be present in the water column for no longer than one day at temperatures between 25 and 35°C, indicating that stage I zoeae will only be present for at most one day after hatching during the summer months. Other studies have indicated that nocturnal release of larvae is in response to predator avoidance, especially from visually responsive predators (Anger et al. 1994; Morgan 1990).

Larval release was not synchronized with different phases of the lunar cycle and therefore was not affected by spring/neap tidal cycles, which extend to this part of the Shatt al-Arab River system. This result was not surprising, considering the fact that *C. babaulti basrensis* is a sublittoral species and is able to release larvae directly into the water column without increasing their risk to predation, also this upper estuarine system experiences maximal water level change of only 0.5 m. Species that have shown synchrony to phase of the lunar cycle include crabs inhabiting intertidal zones that need to travel to the water edge to release larvae, at which point they become vulnerable to predation (Anger et al. 1994; Christy 1978; Morgan & Christy 1994, 1995). *Caridina babaulti basrensis* did not show any vertical distribution differences as has been found in other decapod species and have been linked to mechanisms of dispersal and recruitment (e.g. Sandifer 1975).

In conclusion, field observations combined with D-T and M-T experimental results suggest that water temperature is a key factor in determining the extent and magnitude of the breeding season of larval release of *C. babaulti basrensis*. Physiological responses of *C. babaulti basrensis* to temperature indicate that the larval stages are stenothermal in their temperature tolerances within the 25–35°C range, though they are metabolically stressed at the upper end of the range. Evidence to support these findings include the presence of stage I zoeae when surface water temperatures exceeded 20°C, and the occurrence of maximum abundance of stage I zoeae when surface waters had reached the warmest temperatures recorded in the field for the summer (33°C). Although stage I zoeae appeared to be relatively temperature insensitive in their D-T and M-T responses within the experimental temperature range (25–35°C), their inability to function and survive outside this range suggests the narrow thermal range to which they are adapted. The advanced larval stages show an affinity to higher temperatures, as observed from field data, although M-T responses reveal physiological stress, it appears that growth is sacrificed in favor of rapid development out of the larval phase and recruitment into the juvenile and adult populations.

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Literature cited

Al-Adhub AHY. 1987. On a new subspecies of a freshwater shrimp (Decapoda, Atyidae) from the Shatt Al-Arab River, Iraq. Crustaceana 53:1–4.

Al-Adhub AHY, Hamzah HA. 1987. *Caridina babaulti basrensis*, subsp. nov., from the Shatt-al-Arab region, Iraq (Decapoda, Caridea, Atyidae). Crustaceana 52:225–228.

Ali MH, Salman SD, Al-Adhub AHY. 1995. Population dynamics of the hymensomatid crab *Elamenopsis kempi* in a brackish subtidal region of Basrah, Iraq. Scientia Marina 59:1–13.

Anger K. 1984. Influence of starvation on moult cycle and morphogenesis of *Hyas araneus* larvae (Decapoda, Majidae). Helgolander Meeresunters 38:21–33.

Anger K. 1995. Developmental biology of *Armases miersii* (Grapsidae), a crab breeding in supratidal rock pools. I. Facultative lecithotrophy of larval stages. Mar. Ecol. Prog. Ser. 117:75–81.

Anger K, Dawirs RR. 1982. Elemental composition (C, N, H) and energy in growing and starving larvae of *Hyas araneus* (Decapoda, Majidae). Fish. Bull. 80:419–433.

Anger K, Jacobi CC. 1985. Respiration and growth of *Hyas araneus* L. larvae (Decapoda, Majidae) from hatching to metamorphosis. J. Exp. Mar. Biol. Ecol. 88:257–270.

Anger K, Spivak E, Bas C, Ismael D, Luppi T. 1994. Hatching rhythms and dispersion of decapod crustacean larvae in a brackish coastal lagoon in Argentina. Helgolander Meeresunters 48:445–466.

Benzie JAH. 1982. The complete larval development of *Caridina mccullochi*, Roux, 1926 (Decapoda, Atyidae) reared in the laboratory. J. Crust. Biol. 2:493–513.

Benzie JAH, De Silva PK. 1983. The abbreviated larval development of *Caridina singhalensis Ortmann*, 1894 (Decapoda, Atyidae). J. Crust. Biol. 3:117–126.

Capuzzo JM, Lancaster BA. 1979. Some physiological and biochemical considerations of larval development in the American lobster, *Homarus americanus* Milne-Edwards. J. Exp. Mar. Biol. Ecol. 40:53–62.

Christy JH. 1978. Adaptive significance of reproductive cycles in the fiddler crab *Uca pugilator*: A hypothesis. Science 199:453–455.

Criales MM, Anger K. 1986. Experimental studies on the larval development of the shrimps *Crangon crangon* and *C. allmanni*. Helgolander Meeresunter. 40:241–265.

Dawirs RR. 1979. Effects of temperature and salinity on larval development of *Pagurus bernhardus* (Decapoda, Paguridae). Mar. Ecol. Prog. Ser. 1:323–329.

Dawirs RR. 1983. Respiration, energy balance and development during growth and starvation of *Carcinus maenus* L. larvae (Decapoda, Portunidae). J. Exp. Mar. Biol. Ecol. 69:105–128.

Fielder DR. 1970. The larval development of *Macrobrachium australiense* Holthius, 1950 (Decapoda, Palaemonidae), reared in the laboratory. Crustaceana 18:60–74.

Gilson WE. 1963. Differential respirometer of simplified and improved design. Science 141:531–532.

Hamzah HA. (unpublished: 1980) Studies on some aspects of the biology and ecology of the freshwater shrimp *Caridina babaulti basrensis* (Al-Adhub and Hamzah) from the Shatt Al-Arab. M.Sc. Thesis, Univ. of Basrah, Basrah, Iraq.

Jacobi CC, Anger K. 1985. Effect of temperature on respiration of larval stages of *Hyas araneus* and *H. Coarctatus* (Decapoda: Majidae). Mar. Ecol. Prog. Ser. 26:181–186.

Keough MJ, Downes BJ. 1982. Recruitment of marine invertebrates: The role of active larval choices and early mortality. Oecologia 54:348–352.

Knowlton RE. 1974. Larval developmental processes and controlling factors in decapod Crustacea, with emphasis on Caridea. Thalassia Jugosl. 10:139–156.

Lakshmi S. 1975. On the early larval development of *Caridina* sp. (Crustacea, Decapoda, Atyidae). Indian J. Fisheries 22:68–79.

Lampert W. 1984. The measurement of respiration. In: Downing JA, Rigler FH, editors, A Manual on Methods for the Assessment of Secondary Productiviity in Fresh Waters. IBP Handbook no. 17, Oxford: Blackwell Scientific Pubs. pp. 413–468.

MacKenzie BR. 1988. Assessment of temperature effects on interrelationships between stage durations, mortality, and growth in laboratory-reared *Homarus americanus* Milne-Edwards larvae. J. Exp. Mar. Biol. Ecol. 116:87–98.

McNamera JC, Moreira GS, Moreira PS. 1985. Thermal effects on metabolism in selected ontogenetic stages of the freshwater shrimps *Macrobrachium olfersii* and *Macrobrachium heterochirus* (Decapoda, Palaeminidae). Comp. Biochem. Physiol. 80A:187–190.

Mootz CA, Epifanio CE. 1974. An energy budget for *Menippe mercenaria* larvae fed *Artemia* nauplii. Biol. Bull. 146:44–55.

Morgan SG. 1990. Impact of planktivorous fishes on dispersal, hatching, and morphology of esturine crab larvae. Ecology 71:1639–1652.

Morgan SG, Christy JH. 1994. Plasticity, constraint, and opimality in reproductive timing. Ecology 75:2185–2203.

Morgan SG, Christy JH. 1995. Adaptive significance of the timing of larval release by crabs. Am. Nat. 145:457–479.

Nichols JH, Thompson BM. 1988. Quantitative sampling of crustacean larvae and its use in stock size estimation of commercially exploited species. Symp. Zool. Soc. Lond. 59:157–175.

Romimohtarto K, Hindarti D. 1990. Abundance of planktonic crustacean larvae, especially decapods, in the northern Arafura Sea in relation to the monsoons. Neth. J. Sea Res. 25:585–589.

Roughgarden J, Gaines S, Possingham H. 1988. Recruitment dynamics in complex life cycles. Science 241:1460–1466.

Salman SD. 1987a. Larval development of *Caridina babaulti basrensis* (Al-Adhub and Hamzah) (Decapoda, Caridea, Atyidae) reared in the laboratory. Crustaceana 52:229–244.

Salman SD. 1987b. Larval development of *Atyaephyra desmeresti mesopotamica* (Al-Adhub) (Decapoda, Atyidae) reared in the laboratory. Inv. Peq. 51(Suppl 1):27–42.

Salman SD, Ali MH. 1996. Larval development of *Elamenopsis kempi* (Chopra and Das) (Brachyura, Hymenopsomatidae) reared in the laboratory. Scientia Marina 60:407–416.

Salman SD, Marina BA, Ali MH. 1986. Zooplankton studies: Zooplankton of North West Arabian Gulf (Khor Abdullah) and of the Shatt Al-Arab. Final Report, ROPME, submitted by the Marine Science Centre, Univ. of Basrah, Basrah, Iraq.

Sandifer PA. 1975. The role of pelagic larvae in recruitment to populations of adult decapod crustaceans in the York River Estuary and adjacent lower Chesapeake Bay, Virginia. Estur. Coast. Mar. Sci. 3:269–279.

Sastry AN. 1979. Metabolic adaptation of *Cancer irroratus* developmental stages to cyclic temperatures. Mar. Biol. 51:243–250.

Sastry AN. 1983. Pelagic larval ecology and development. In: Vernberg JF, Vernberg WB, editors, The Biology of Crustacea Vol.7 Behavior and Ecology. New York: Academic Press. pp. 214–282.

Sastry AN, McCarthy JF. 1973. Diversity in metabolic adaptation of pelagic larval stages of two sympatric species of brachyuran crabs. Neth. J. Sea Res. 7:434–446.

Sastry AN, Vargo SL. 1977. Variation in physiological response of crustacean larvae to temperature. In: Vernberg FJ, Calabrese A, Thurberg FP, Vernberg WB, editors, Physiological Responses of Marine Biota to Pollutants. New York: Academic Press. pp. 401–423.

Schultze K, Anger K. 1997. Larval growth patterns in the aesop shrimp *Pandalus montagui*. J. Crust. Biol. 17:472–479.

Sokal RR, Rohlf FJ. 1981. Biometry. W.H. Freeman and Company. San Fransisco.

Vernberg FJ, Costlow JD. 1966. Studies on physiological variation between tropical and temperate-zone fiddler crabs of the genus *Uca*. IV. Oxygen consumption of larvae and young crabs reared in the laboratory. Physiol. Zool. 39:36–52.

Vernberg WB, Moreira GS, McNamara JC. 1981. The effect of temperature on the respiratory metabolism of the developmental stages of *Pagurus criniticornis* (Dana) (Anomura, Paguridae). Mar. Biol. Lett. 2:1–9.

Vijayaraghavan S, Easterson DCV. 1974. Biochemical changes and energy utilisation in developing stages of the estuarine prawn, *Macrobrachium idella* (Hilgendrof). J. mar. biol. Assoc. India 16:275–279.