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Early growth and mortality of the Caribbean king crab *Mithrax spinosissimus* reared in the laboratory*

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Abstract

The berried females of the Caribbean king crab *Mithrax spinosissimus* (Lamarck) used in this study were collected from canals on Big Pine Key, Sugarloaf Key and Lower Matecumbe Key (south Florida, USA) on 9 August, 8 October and 15 November 1986. Viable spawns hatched as first zoeae and molted to second zoeae within ca. 10 to 12 h. Most of the larvae reached the megalopa stage 1 d later, and molted to first crab 4 to 8 d after hatching (water temperature: 27.2° to 28.8 °C). Low water temperature and/or early lack of food had a negative effect not only on stage duration, but also on the size of the early crab stages. Successful molt to first crabs occurred, however, in the absence of food. The growth rate (carapace length) between molts in early crab stages varied between ca. 20 and 30%. When provided with good water exchange, stocking density could be very high (> 22 500 individuals m^{-2}), with no increase in mortality. The highest mortality rate was recorded when the larvae molted to first crab, and the highest rates of survival were always recorded when feeding was not initiated until after 5 to 8 d after hatching. No cannibalism was observed among larvae, and cannibalism was low in early crab stages. The study indicates that to achieve viable hatches and high larval survival in rearing *M. spinosissimus,* a continuous and adequate supply of high-quality seawater is a prerequisite both in larviculture and in maintaining brooding females.

Introduction

The Caribbean king crab *Mithrax spinosissimus* is one of the largest crabs inhabiting coral reefs and rocky outcrops of the tropical western Atlantic Ocean. It is found in shallow water to ca. 180 m depth, and the known range is from the Carolinas on the east coast of the United States to the Bahamas, the Florida Keys, Nicaragua, and through the West Indies to Barbados and Venezuela (Rathbun 1925, Williams 1984). Studies on populations of *M. spinosissimus* in the Florida Keys (Hazlett and Ritschoff 1975, Bohnsack 1976) showed that it remains in crevices during the day, moves and feeds nocturnally, and usually returns to the same crevice that it occupied the day before. The larval stages and the first crab stage have been described by Provenzano and Brownell (1977). A comparison of morphological characters in larval stages within the subfamily Mithracinae has been presented by Gore et al. (1982). The sexes are dimorphic; the males reach a greater size, and their chelipeds attain massive proportions compared to those of the females. Due to its large size, non-aggressive behavior, omnivorous feeding, and market acceptability, this species has in recent years generated considerable interest for its mariculture potential. Yet little is known about the biology of *M. spinosissimus,* particularly the growth, development and behavior of individuals in early crab stages, which is critical information for the commercial mariculture of this species. This study focuses on larval and early post-metamorphosis development during the first 30 d of the life cycle.

Materials and methods

Berried females of *Mithrax spinosissimus* (Lamarck) were collected by divers at night from canals cut through oolitic limestone on Big Pine Key and Sugarloaf Key, Monroe County, south Florida, USA, on 9 August (Growth Studies 1 and 2) and 8 October (Growth Study 3) 1986. The crabs were transported in oxygenated styrofoam boxes to the Harbor Branch Oceanographic Institution (HBOI) in Fort Pierce, east Florida, the day after collection (Growth Studies 1 and 2) or later the same night (Growth Study 3).

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Selected individuals were thereafter transferred to the Indian River Marine Science Research Center (IRMSRC) in Vero Beach and were placed individually in 40-liter glass aquaria with a constant supply of seawater.

The term "days after hatching" indicates the number of days after the collection of swimming zoeae from the hatching tank, usually within 12 h after hatching.

The experiments were performed on large, shallow water-tables (equipped with drain stand-pipes), each supplied with approximately 8 l min^{-1} filtered seawater. Polyvinylchloride (PVC) rings (40 mm high), with inner diameters 106 and 51 mm (with a 500 μm screen attached to the bottom) were used for the experiments. The inner surface-area of these screens was 88.25 and 20.43 cm^2, respectively. Swimming zoea larvae were collected and held on a 300 mm diam Plexiglas ring (150 mm high, with a 500 μm mesh bottom) prior to transfer to experimental screens.

Growth Study 1 (GS 1). All swimming zoeae were siphoned into a 300 mm diam screen (with a constant supply of filtered seawater) placed on a water table. Daily random samples were taken from this screen to record larval development. Forty-two randomly selected first and second crabs (10 d post-hatch) were then transferred to 106 mm diam screens, with eight first crabs on each of four screens (906 individuals m^{-2}) and ten second crabs on one screen (1 133 individuals m^{-2}). All screens were suspended on a water table, with no water supplied to individual screens.

Growth Study 2 (GS 2). Swimming second zoeae were stocked on seven 106 mm diam screens at a density of 2 267 individuals m^{-2} (20 zoeae per screen). The screens were treated as described for GS 1. Development was monitored daily, survivors were counted, and dead individuals removed. Six days after hatching, the 14 survivors (all first crabs) on these screens were transferred to two other 106 mm diam screens (7 on each = 793 individuals m^{-2}), and 14 other individuals (all first crabs) from the same hatch (placed on a 300 mm diam screen on 16 September) were transferred to another 106 mm diam screen 8 d after hatching.

Individuals in GS 1 and 2 were fed filamentous diatoms during the first 10 d; thereafter the diet was supplemented with small pieces of macroalgae (*Enteromorpha* spp. *Gracilaria* spp., and *Ulva* sp.).

Growth Study 3 (GS 3). The swimming zoeae were collected onto a large screen on a water-table. Of these larvae, 900 were transferred the same day to twenty 106 mm diam screens for a combined study of development, growth, and density-dependent mortality, with 60, 50, 40 and 30 individuals on the screens (five replicates), which equals a density of 6 800, 5 700, 4 500, and 3 400 individuals m^{-2}, respectively (rounded to the nearest 100). Each screen was supplied with a constant flow of seawater through 4.5 mm diam aquarium-tubing. The screens were monitored daily as described for GS 2. Individuals were not fed until the 7th day after hatching. They were thereafter given the same food as those in GS 1 and 2. Sixteen days after hatching, all survivors on four screens (60), i.e., the fifth replicate of each initial density, were transferred to sixty 51 mm diam screens suspended on a water table. These screens did not have a separate water supply.

Crab exuviae were removed daily, preserved in 70% ethanol, and later measured with a stereo-microscope, equipped with an ocular micrometer. Carapace length (CL) was measured between the rostral spines and the posterior margin of the carapace.

Density-dependent mortality during early development was investigated during two additional experiments (MS 1 and MS 2). Berried females collected on 15 November, 1986 from Lower Matecumbe Key, Monroe County, Florida, were transported to IRMSRC and placed in flowing seawater.

Mortality Experiment MS 1. A hatch from 26 November was used for this experiment. The following number of larvae was placed on 106 mm diam screens (three replicates each): 200, 200, 100, and 50, which equals a density of 22 700, 22 700, 11 300, and 5 700 individuals m^{-2}, respectively (rounded to the nearest 100). The first three replicates with 200 larvae each were supplied fresh seawater through aquarium tubing (indicated by "w"). All treatments were suspended on a shallow water-table.

Mortality Experiment MS 2. This experiment was started on 2 December. The following number of larvae were placed on screens (same type as in MS 1) with four replicates: 200, 100, 50, each screen receiving a supply of seawater. Four additional screens (100 individuals per screen) were maintained in static water (0.5 liters in glass bowls), which was changed daily (indicated by "s"). The bowls were placed on the same water-table as the other screens to keep the water at the same temperature.

Individuals of Experiments MS 1 and MS 2 were not fed until Day 7 after hatching. After this time they were given large amounts of filamentous diatoms and pieces of various macroalgae.

The temperature on the water-tables was recorded daily, with an accuracy of $\pm 0.1\,C°$. The salinity was not recorded regularly, but remained very stable at ca. 36‰.

All experiments described in this study were performed using seawater filtered through a set of four big 30 μm filters.

Statistical analyses of difference between experiments were done using one-way and two-way analysis of variance (ANOVA), with no replications.

Results

Hatches of swimming *Mithrax spinosissimus* zoeae for the growth studies were obtained on 2 September (GS 1), 16 September (GS 2) and 11 October (GS 3) 1986. The sizes

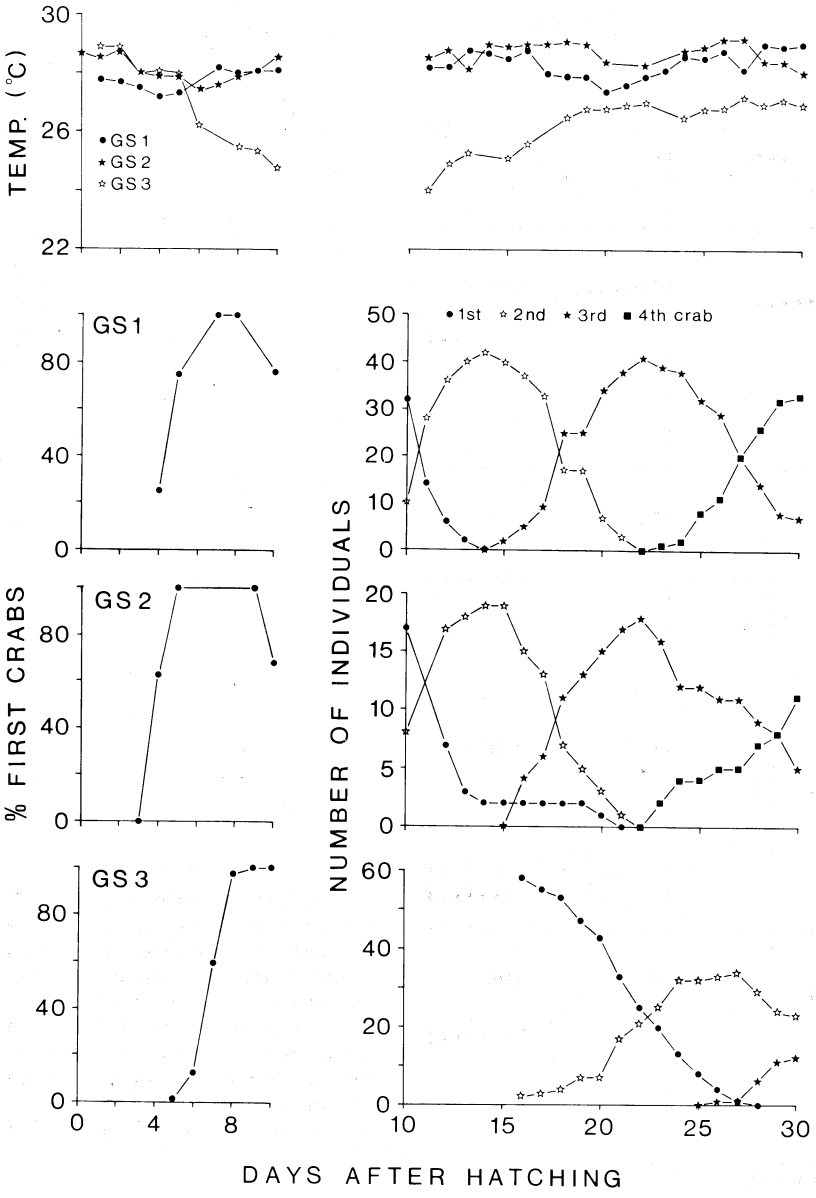

Fig. 1. *Mithrax spinosissimus.* Stage duration of larvae and young crabs of three growth study (GS) experiments

(CL) of the berried females were 81.5, 84.0, and 83.5 mm, respectively.

Mithrax spinosissimus spawns several times from the same fertilization. Second spawns from crabs kept in the laboratory were, however, much smaller and early larval mortality was higher than spawns from berried females collected from the field (own unpublished data).

Egg development and hatch size

Upon extrusion the eggs were bright orange, and gradually turned dark red during development, when near to hatching they were light brown to beige. Orange eggs on four crabs hatched after 14 to 20 d (mean = 18.0 d, standard deviation: SD = 2.8), and red eggs on eight crabs after 6 to 12 d (mean = 9.5 d, SD = 2.3). Light brown eggs on three crabs hatched after 1, 2, and 5 d.

The number of swimming second zoeae from hatches of three berried females collected from the field was counted by taking ten subsamples, each of 10 ml from each hatching container (hatches on 12 October, 18 October, and 20 November) with the following calculations on total hatch sizes; 6 930 (SD = 1 139), 10 001 (SD = 2 488), and 9 100 (SD = 1 284) individuals, respectively.

Development and stage duration

Hatching usually occurred at night and continued for several hours. The larvae were released by the fanning motion of the pleopods of the crab, accompanied by vigorous jerking of the abdomen. In most cases, larvae

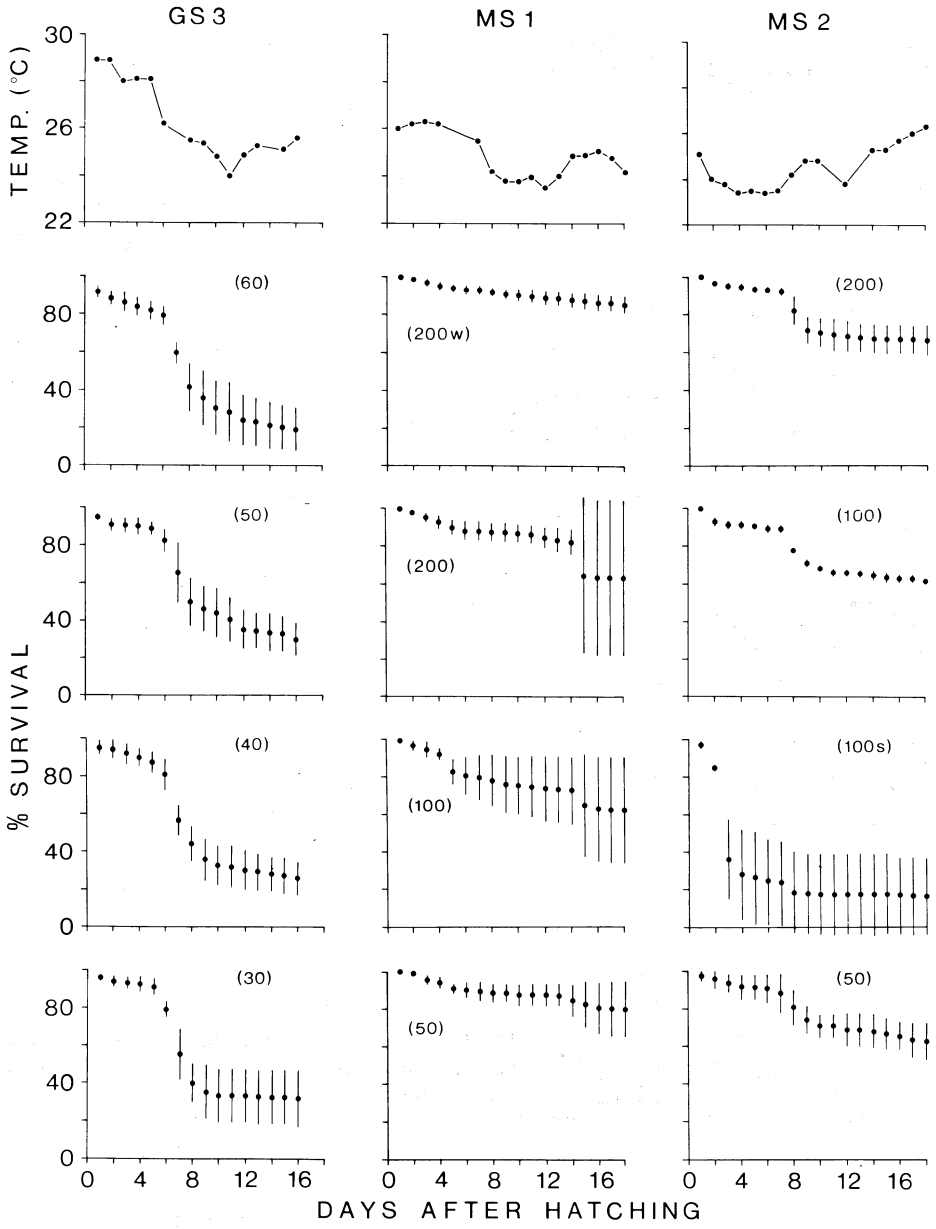

Fig. 2. *Mithrax spinosissimus.* Percentage survival (±SD) on each day for larvae/young crabs stocked at different densities. Numbers in parentheses indicate number of individuals on each 106 mm diam screen. w: Screens with separate water supply in MS 1; s: screens in static water. Number of replicates: for Growth Study (GS) 3=5, for Mortality Study (MS) 1=3, and for MS 2=4

hatched as swimming first zoeae and displayed positive phototaxis immediately after hatching. First zoeae predominated in hatches from healthy, field-caught gravid females, while the incidence of prezoeae in hatches or aborted eggs in various stages of development increased with the length of time the female was held in captivity. First zoeae molted to second zoeae within 10 to 12 h after hatching and then proceeded to the megalopa stage within 24 to 48 h. Metamorphosis to first crabs occurred 4 to 8 d after hatching (Fig. 1).

The molting-time intervals up to the third crab stage is shown in Table 1. There is little difference between GS 1 and 2 in development time of the various crab stages, but GS 3 exhibited much longer intervals. This latter study was performed at lower temperatures than the other two (see Fig. 1), and without any food supply until the 7th day after hatching.

Juvenile growth

The carapace length (CL) for the first to third crab stages is shown in Table 2. The CL increase at each molt varied between ca. 20 and 30%. The highest percentage increase was recorded between the first and second crab stages in GS 1 (30.3%), and the lowest between the second and third crab stages in GS 3 (20.8%). There were significant differences between the mean lengths of all crab stages of the three growth studies, except for the first crab between GS 2 and GS 3 (see Table 3).

Mortality

The mortality studies are shown in Fig. 2. In Experiment GS 3, larval mortality was relatively low during the first

Table 1. *Mithrax spinosissimus.* Molting-time intervals (days after hatching) of Crab Stages 1 to 3 (determined when 50% of specimens reached the crab stages) in three growth study (GS) experiments

Crab stage	GS 1	GS 2	GS 3
1	5	5	7
2	11	11	23
3	18	18	32

Table 2. *Mithrax spinosissimus.* Growth between molts. Mean length (CL) in mm (± SD) for Crab Stages 1 to 3 in three growth study (GS) experiments. *N*: number of specimens measured

Crab stage	GS 1			GS 2			GS 3		
	N	Mean	(SD)	*N*	Mean	(SD)	*N*	Mean	(SD)
1	23	1.54	(0.03)	21	1.50	(0.03)	15	1.51	(0.03)
2	39	2.00	(0.05)	15	1.90	(0.06)	15	1.84	(0.04)
3	40	2.53	(0.18)	15	2.38	(0.13)	15	2.23	(0.09

Table 3. Results of statistical analyses (one-way ANOVA) of differences between mean lengths of Crab Stages 1 to 3 in growth studies GS 1, GS 2 and GS 3

Crab stage	GS 1–GS 2	GS 1–GS 3	GS 2–GS 3
1	**	**	NS
2	***	***	**
3	***	***	***

*** = $p < 0.001$; ** = $p < 0.01$
NS ($p > 0.05$)

5 d after hatching, increasing during Days 6 to 8 as megalopa larvae metamorphosed to first crabs. Mortality declined again 10 d after hatching, when all larvae had successfully molted to first crabs. The mean mortality rate did not differ significantly between different densities ($p > 0.05$).

There was no significant difference between treatments in MS 1 ($p > 0.05$), but the survival rate was generally higher than in GS 3. The difference between the replicates was very low, and the survival rate was high in the fresh seawater treatment where all screens received a continuous water supply (200 w, Fig. 2). All individuals except six of the 147 surviving specimens on one screen with an initial number of 200 individuals (without water supply), died between Days 14 and 15. Two sharp drops in survival were recorded on the screens with an initial number of 100 individuals per screen. A large number of individuals (19) died on one screen between Days 4 and 5. This mortality rate was over 100% higher than that on the replicate screens. A second mortality event was recorded on the same screen between Days 14 and 15, and only nineteen (19.0%) survivors remained on this screen on Day 15.

The highest mortality in Experiment MS 2 (where all screens, except 100 s, had a separate water supply) was recorded between Days 7 and 10, i.e., during molting to first crabs. Mortality was very high for larvae held in static water (100 s) (water exchange, 0.5 liters per day) during the first 7 d, but stabilized thereafter. The difference in mortality rate among density treatments 200, 100, and 50 was not statistically significant ($p > 0.05$), but the static water treatments (100 s), exhibited a significantly higher mortality rate than all other treatments ($p < 0.001$).

Behavior

The megalopa larvae spent most of the time on the bottom of the screens, swimming only occasionally and short distances.

As mentioned above under "Development and stage duration", the swimming zoeae exhibited a strong positive phototaxis. This behavior was used to collect larvae through the aquarium standpipe either onto collecting screens or into larval tanks. The megalopa larvae and the young crabs are negatively phototactic, and on the screens usually hid under pieces of macroalgae during daytime.

The young crabs sometimes displayed aggressive behavior, but these encounters seldom resulted in mutilation or death. Encounters were brief, and usually one of the crabs moved away rapidly. We did not observe any larval cannibalism. Crabs were occasionally observed eating dead individuals and exuviae. We have no data on mortality resulting from cannibalism in early crab stages, but noticed that mortality resulting from cannibalism was low when enough food was supplied.

Discussion

According to Adey (1985) and Bernard and Bernard (1985), the brood-size of *Mithrax spinosissimus* varies between 7 000 and 100 000 eggs, although hatch size was not reported by these authors. Hatch-size calculations in our study were considerably lower, perhaps due to the small size of the adult females collected. However, improved handling techniques should increase the percentage of successful larvae hatched.

Provenzano and Brownell (1977), as well as Smithsonian researchers, have described a non-swimming prezoeal stage which lasted up to 12 h after hatching. In our study, we rarely observed this stage, and hatches with a high incidence of prezoeae usually resulted in high mortality. Therefore, we believe that the prezoeal hatch is an aberrant occurrence associated with stress on the females or the developing larvae. The duration of the two zoea stages was also considerably shorter than reported by Provenzano and Brownell (1977).

Crustacean molting frequency is dependent upon temperature (Allen 1972, Christiansen 1973, Anger 1984,

Dawirs 1985), diet, substrate and water circulation (Roberts 1972, Brick 1974). Bigford (1978) found that the development time and percentage survival, but not the size of the different stages of laboratory-reared *Libinia emarginata* Leach larvae was diet-dependent. Kunisch and Anger (1984), however, in a study on *Hyas araneus* (L.), found negative correlations between development time for all stages of larvae and the size of juvenile crabs. Additionally, Dawirs (1986), in a study on *Carcinus maenas* (L.) larvae, found that the biomass of newly-molted second zoeae was positively correlated (linearly) with the duration of feeding periods during the first zoea stage.

In our experiments, the development rate was considerably slower in GS 3 than in the other two growth studies (Fig. 1). The mean temperatures during GS 1, 2, and 3 were 28.0, 28.5, and 26.5 °C, respectively. However, during the first 5 d after hatching temperatures were similar in all three growth studies, and nevertheless development was also slower during this period in GS 3 than in the other two studies (Fig. 1), probably due to starvation of the larvae. The lower temperature, and possibly also the early lack of food, in GS 3 compared to the other two growth studies had a negative effect not only on stage duration, but also on the size of the early crab stages, although successful molt to first crabs occured in the absence of food. Our studies indicate, however, that after a few months the development of the GS 3 crabs was comparable with that of crabs from the other growth studies (own unpublished data). Both lecithotrophic and direct development have been reported in decapoda (McConaugha 1985). Larvae of *Mithrax spinosissimus* reject animal food, and the adult crab is mainly herbivorous (own unpublished data). Our experiments indicate a possible lecithotrophic strategy of *M. spinosissimus* larvae (see also Brownell et al. 1977).

All crab stages in GS 1 were larger than those in GS 2 in spite of similar water temperatures and the same feeding procedures during these two experiments. Anger (1984) also found some variation from hatch to hatch in the rate of larval development in relation to temperature in a study on *Hyas coarctatus* Leach. There are, however, three different aspects that should be considered in this context, namely larval density, water supply and handling. All larvae in GS 1 were kept on a 300 mm diam screen with a continuous water supply for the first 10 d, while GS 2 larvae were placed on 106 mm diam screens (without separate water supply) on the day of hatching. We did not estimate the number of larvae on the 300 mm diam screen in GS 1, but the density on this screen was considerably higher than that on the 106 mm diam screens of GS 2. Therefore handling and/or water exchange are the likely causes for the somewhat lower growth rate in GS 2. Only random samples were taken from GS 1 during the first 10 d, while all screens in GS 2 were handled every day; molts and dead individuals were removed and stages were counted. It is not possible to determine whether both or only one of these factors contributed to the somewhat lower growth rate in GS 2.

In the experiments described above and other unpublished laboratory studies, the highest mortality occurred during the first 4 to 8 d, i.e., when the megalopa molted to first crabs.

We fed the larvae a variety of natural foods, including benthic diatoms, *Thalassia testudinum*, and macroalgae such as *Enteromorpha* spp., *Gracilaria* spp. and *Ulva* sp., but the best survival rates were always recorded when feeding was initiated after 5 to 8 d.

The high mortality rate recorded in GS 3 between Days 5 and 8 (Fig. 2) may have been accentuated by infection or poisoning of the seawater in the laboratory, since high mortality rates were also recorded in all other laboratory experiments (own unpublished data) during the same period.

Total crashes (100% mortality) were recorded on some experimental screens (without a separate water supply), probably because of an accelerated infection from dead individuals caused by insufficient water supply. Partial or total crashes on some screens are indicated by very high ranges of standard deviations, which were first recorded when the larvae molted to first crab stage. The standard deviation values were generally much lower in experiments where the screens had a separate water supply. The importance of a good water exchange to avoid partial or total population crashes is illustrated in Fig. 2. Our study shows, however, that it is possible to stock the larvae and early crab stages at very high densities without any significant increase in mortality, provided they have a good water supply. Early mortality differed between hatches. An important factor is probably the condition of the larvae when they hatch. In conclusion, our study indicates that to achieve viable hatches and high larval survival in rearing *Mithrax spinosissimus*, a continuous and adequate supply of high-quality seawater is a prerequisite in both larviculture and in maintaining brooding females.

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