

# Developmental biology of *Armases miersii* (Grapsidae), a crab breeding in supratidal rock pools. II. Food limitation in the nursery habitat and larval cannibalism

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**ABSTRACT:** The grapsid crab *Armases miersii* breeds in supratidal rock pools on the northern shore of Jamaica, West Indies. In 5 replicate field experiments, temperature and salinity were monitored during the course of larval development, and the hypothesis was tested that these rock pools represent a food-limited environment for the development of planktotrophic crab larvae. Food limitation should select for and, hence, may explain, ontogenetic traits that have been observed in the early larval stages of this species: abbreviated development, enhanced initial energy reserves, starvation resistance, and potential for partially endotrophic development (facultative lecithotrophy). In a rock pool with only 1 to 2‰ salinity, *in situ* growth (measured as change in carbon content per larva) and development (occurrence of moulting to subsequent stages) were retarded, and only the zoea II stage was reached within a 6 d observation period. Successful larval development to the megalopa stage was observed in salinities ranging from 5 to 24‰ and temperatures between 24 and 32°C. Diurnal temperature variation (up to 7°C) and sudden salinity changes (up to 16‰) after heavy rain falls did not visibly influence larval growth or development. These field observations show that the larvae of *A. miersii* are very tolerant of extremely low and variable salinity and, hence, are well adapted to survive and develop under the harsh and unstable physical conditions prevailing in supratidal rock pools. Larval growth in all 5 experiments was significantly reduced and development delayed (only from the zoea III stage) under natural (unmanipulated control) conditions compared with sibling larvae that received *Artemia* sp. nauplii as an additional food source. These results provide evidence that food is actually a limiting factor in supratidal rock pools, where larvae of *A. miersii* develop. In a series of 5 replicate laboratory experiments, the possible significance of cannibalism, especially in late stages, was tested. Cannibalistic activity shows an increasing trend with decreasing endotrophic potential of subsequent larval stages, reaching a maximum in the megalopa. Thus, multiple release of larvae in rock pools may provide younger larvae as a potential food source for older conspecifics, and cannibalism may be a nutritional buffer (comparable with nurse eggs) in a food-limited breeding habitat.

**KEY WORDS:** Crab larvae · Tropical rock pools · Food limitation · Larval growth · Cannibalism

## INTRODUCTION

The semiterrestrial grapsid crab *Armases miersii* is known from the Caribbean islands, Florida, and the Bahamas (Abele 1992). On the northern shore of Jamaica, it breeds in small supratidal rock pools (Schuh & Diesel in press), where physical conditions may be variable and planktonic food production unreliable. Since *A. miersii* is the only decapod crus-

tacean that has been observed breeding in ephemeral rock pools in Jamaica, special ontogenetic adaptations should be expected in this species, allowing for its larval development in this supposedly harsh and nutritionally unpredictable nursery habitat.

Recent laboratory studies of the larvae of *Armases miersii* showed an abbreviated development (with only 3 zoeal instars), tolerance of extreme salinities (Schuh & Diesel in press), and unusually large initial energy

reserves (K. Anger & K. Schultze unpubl.). As a consequence of the latter, the zoeal stages reveal enhanced starvation resistance and facultative lecithotrophy (Anger 1995, this issue). These ontogenetic traits resemble those in some other semiterrestrial crabs (Rabalais & Gore 1985, Staton & Sulkin 1991), but they are not as far-reaching as in some Jamaican terrestrial and freshwater grapsids (Hartnoll 1964, Anger & Schuh 1992), or as in *Uca subcylindrica*, an ocyropodid crab which may show a similar breeding behaviour to *A. miersii* (Rabalais & Cameron 1985).

Plankton production in supratidal rock pools may exhibit great spatial and temporal variability, depending on pool size, depth and position (height above sea level, exposure to sunlight and wave action, shade from mangroves or other trees), and weather conditions (temperature, rainfall, wind, etc.). All these factors should influence not only the physical conditions in a rock pool at a given time, but also the duration of the existence of its water content and, hence, the time available for the development of a planktonic community which could serve as a food source for crab larvae. Such unpredictable conditions select for an abbreviation of larval development (Rabalais & Cameron 1985); however, crab larvae might rely on available food sources other than plankton, i.e. benthic diatoms, protozoans, other microorganisms which can develop very rapidly, or detritus. Thus, there is no hard evidence of food limitation (see Olson & Olson 1989 for review of this factor) and, hence, of a selective pressure toward lecithotrophy in rock pools where *Armases miersii* breeds.

Besides utilization of benthic food sources, mutual predation (larval cannibalism) could be a significant factor in the recruitment of this species. While benthic food should become important only in the megalopa stage, when the crab is able to crawl on the bottom, the assumption of cannibalistic activity also appears plausible in other stages. Freshly hatched larvae were often observed appearing in rock pools where older conspecifics were already developing and, thus, younger larvae might present a potential food source in later stages. This is in principle confirmed by a few observations of cannibalism in the field (Anger unpubl.). However, this behaviour has not been quantitatively investigated in the larval stages of *Armases miersii* and thus, its potential significance under conditions of food limitation has remained doubtful.

The present study was designed to (1) document the temperature and salinity conditions occurring in spring (March–April) in supratidal rock pools, where *Armases miersii* larvae develop; (2) test in field experiments if food is a limiting factor for the development of crab larvae in this specific breeding habitat; and (3) test in laboratory experiments if and to what extent

cannibalistic activity occurs in the larval stages of *A. miersii*.

Food limitation was tested in an experimental approach (cf. Olson & Olson 1989) based on the assumption that an experimental enrichment of the natural diet should accelerate growth and development of crab larvae in supratidal rock pools. This would support the hypothesis that starvation resistance and facultative lecithotrophy in early *Armases miersii* larvae (Anger 1995) represent necessary ontogenetic adaptations to breeding in a nutritionally unpredictable nursery habitat. Increasing cannibalistic activity, on the other hand, would provide a partial explanation of how older larval stages of this species may survive in a food-limited environment, in spite of decreasing internal energy reserves (Anger & Schultze unpubl.).

## MATERIAL AND METHODS

**Field experiments.** Supratidal limestone rock pools (ca 0.5 to 1 m above mean high water) near the Discovery Bay Marine Laboratory, northern Jamaica, were checked early in the morning for freshly hatched *Armases miersii* larvae, which were subsequently used in field experiments. During a 6 wk period (March–April 1993), 5 experiments were conducted in 4 different rock pools (1 pool was used twice, in Expts 2 and 3). In each of these 'rock pool experiments' (RPE, 1 to 5), about one-half of the larvae was pipetted out of the nursery pool and put into a plastic sieve (14 cm diameter, 15 cm high; 150  $\mu$ m mesh size) that was placed in the same rock pool. These sieves allowed the exchange of water and small particles (including microplankton) but retained the larvae and experimental food (freshly hatched *Artemia* sp. nauplii, San Francisco Bay Brand™) which was added *ad libitum* ( $\geq 10$  nauplii ml<sup>-2</sup>). The other half of the larvae was left in the rock pool as a control group without experimental manipulation. The natural food in the rock pools was checked only occasionally, since a regular non-destructive sampling from their small water volumes (ca 5 to 10 l) was impossible without disturbing the experiments; the food comprised detrital particles, unicellular algae (flagellates) and microzooplankton (mainly protozoans), but only rarely larger zooplankton such as copepods, cladocerans, or insect larvae.

At 08:00, 12:00, 16:00, and 20:00 h, the experiments were briefly checked for apparent development (i.e. occurrence of moults; the larval stages of *Armases miersii* can be distinguished in the field without using a microscope); temperature and salinity were measured with a laboratory thermometer and a hand refractometer to the nearest 0.1°C and 1‰ S, respec-

tively. Once daily (at 08:00 h), unused and dead food, and dead larvae were siphoned out of the sieves, and fresh food was added. No attempts were made to quantify mortality rates or duration of development in individual larval instars.

Five replicate samples of larvae were taken every 1 to 3 d (mostly every second day) from both the experimental and control groups. In each sample, 3 to 7 larvae (depending on their weight) were briefly rinsed in distilled water, blotted on lint-free Kleenex™ paper (for optical use), and transferred into preweighed tin cartridges. The samples were frozen at  $\leq -10^{\circ}\text{C}$  and later analysed at the Helgoland Marine Biological Station for carbon content (Carlo Erba 1106 CHN analyzer), after freeze-drying (at  $<10^{-2}$  mbar in a Leybold-Heraeus™ apparatus) and determination of dry weight (Mettler™ UM 3 microbalance, to the nearest 0.1  $\mu\text{g}$ ).

The experiments were terminated when no more sufficient larvae were available due to mortality or sampling, or when they reached the megalopa stage. The megalopa exhibits a semibenthic behaviour and often hides in small bottom crevices, so that further sampling became difficult and unreliable in this stage. Several experiments (not presented here) had to be ended prematurely, because additional new hatches appeared during the night in rock pools, where older larvae already were developing. In these cases, no safe distinction was possible between freshly hatched and older zoea I belonging to the running experiment. Moreover, younger larvae could have been eaten by older ones; this kind of cannibalism should be excluded here and tested in a separate set of experiments (see below).

**Laboratory experiments.** Larvae of *Armases miersii* were obtained from ovigerous females and reared at

constant  $25^{\circ}\text{C}$  and 32‰ salinity with freshly hatched *Artemia* sp. nauplii given as food, and a natural (ca 12 h light:12 h dark) light cycle. Only freshly hatched or moulted individuals, respectively, were used in experiments. In each of 5 replicates, 1 older larva (the 'predator') and 10 younger conspecifics ('prey') were put together in 100  $\text{cm}^3$  Nunc™ (Denmark) plastic bowls (5.5 cm diameter); within-stage cannibalism (predator and prey identical) was tested in experimental groups with 10 sibling larvae per replicate.

The experiments were checked twice daily (08:00 h and 20:00) for cannibalism, other mortality, or development (moulting). Prey larvae that had died without being eaten ('other mortality') were replaced by larvae of equal age and developmental stage taken from parallel rearing experiments; eaten prey was not replaced. The experiments were terminated when the predator died or moulted, or when all prey had been consumed.

## RESULTS

### Field experiments

Temperature in breeding rock pools varied between 24 and  $32^{\circ}\text{C}$  during the period of investigation, showing pronounced diurnal cycles (Fig. 1). Consistently lower temperatures were measured in the morning (08:00 h), and highest at noon or in the afternoon, depending on the position of a particular rock pool (i.e. the time of the day and duration of exposure to direct sunlight). Maximum variation within 24 h periods was observed in the last experiment (RPE 5), reaching up to  $6.9^{\circ}\text{C}$  difference within only 4 h (Fig. 1).

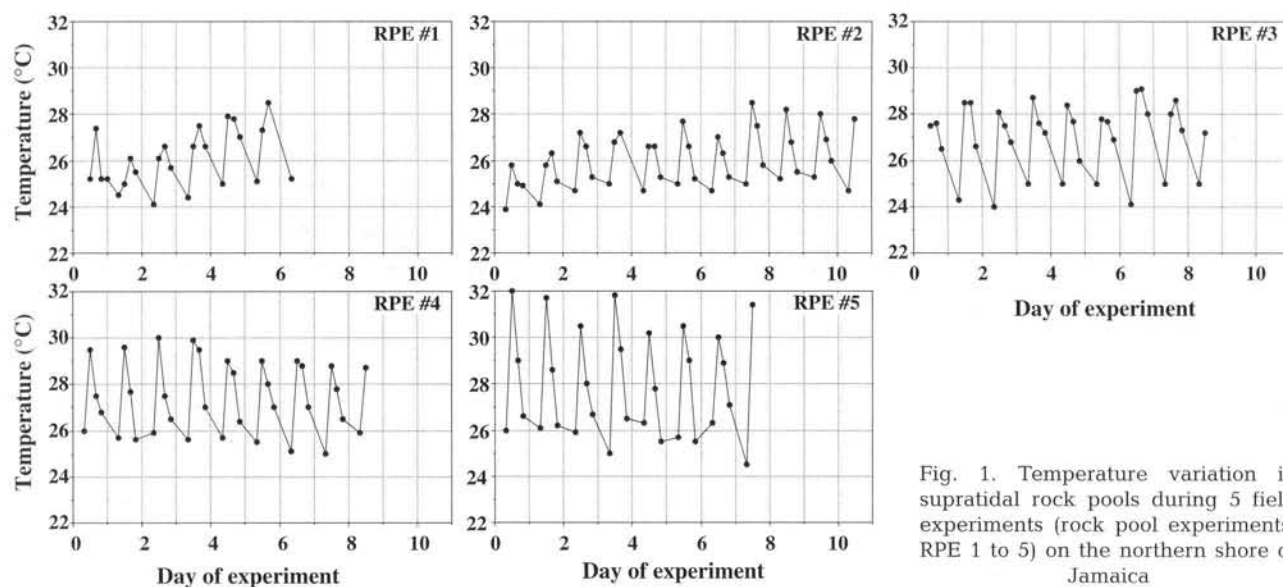


Fig. 1. Temperature variation in supratidal rock pools during 5 field experiments (rock pool experiments, RPE 1 to 5) on the northern shore of Jamaica

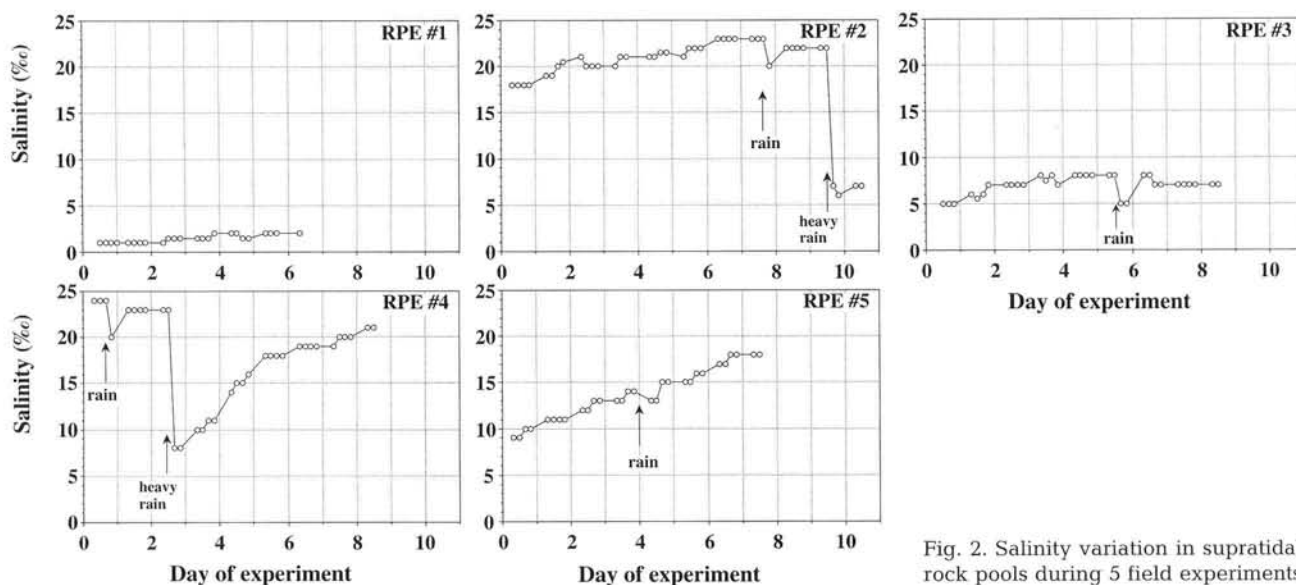


Fig. 2. Salinity variation in supratidal rock pools during 5 field experiments

Salinity showed only little daily variation in individual rock pools, except for days with heavy rainfalls, where it could drop by up to 16‰ within a few hours (Fig. 2). In smaller rock pools, evaporation caused a steady increase in salinity, reaching a maximum change of about 10‰ within less than 3 d (RPE 4; Fig. 2). Depending on the age and origin of their water body (predominantly seawater or rainwater), individual rock pools showed significant differences in salinity, ranging from 1 to 24‰.

Development and growth of *Armases miersii* larvae varied little in the different experiments, in spite of different temperature and salinity conditions (Fig. 3).

Only in RPE 1, where extremely low salinities (1 to 2‰) occurred, was development exceptionally slow, and only the zoea II stage was reached. On Day 6 of this experiment, only a few survivors were found in this pool, so that this experiment could not be continued any longer.

Larvae that received experimental food additions (*Artemia* sp. nauplii) grew in all 5 experiments consistently better than controls with exclusively natural food sources (Fig. 3). As early as 2 d after hatching, highly significant differences were measured in the mean carbon content per larva (Student's *t*-test;  $p < 0.001$ ), and these differences tended to increase during

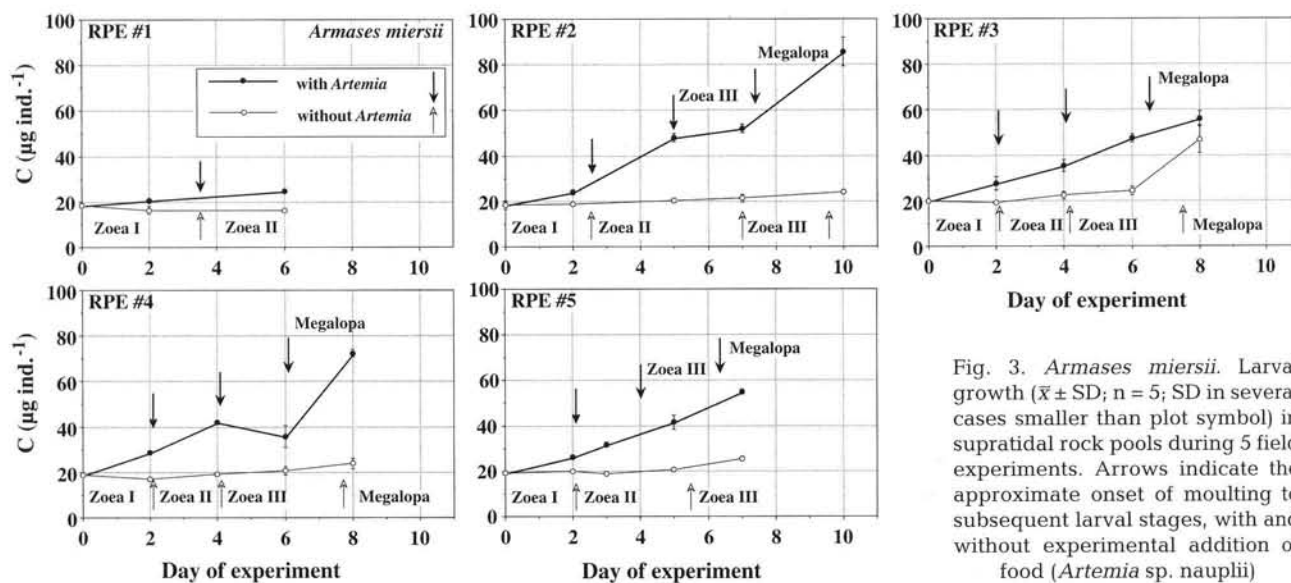


Fig. 3. *Armases miersii*. Larval growth ( $\bar{x} \pm SD$ ;  $n = 5$ ; SD in several cases smaller than plot symbol) in supratidal rock pools during 5 field experiments. Arrows indicate the approximate onset of moulting to subsequent larval stages, with and without experimental addition of food (*Artemia* sp. nauplii)



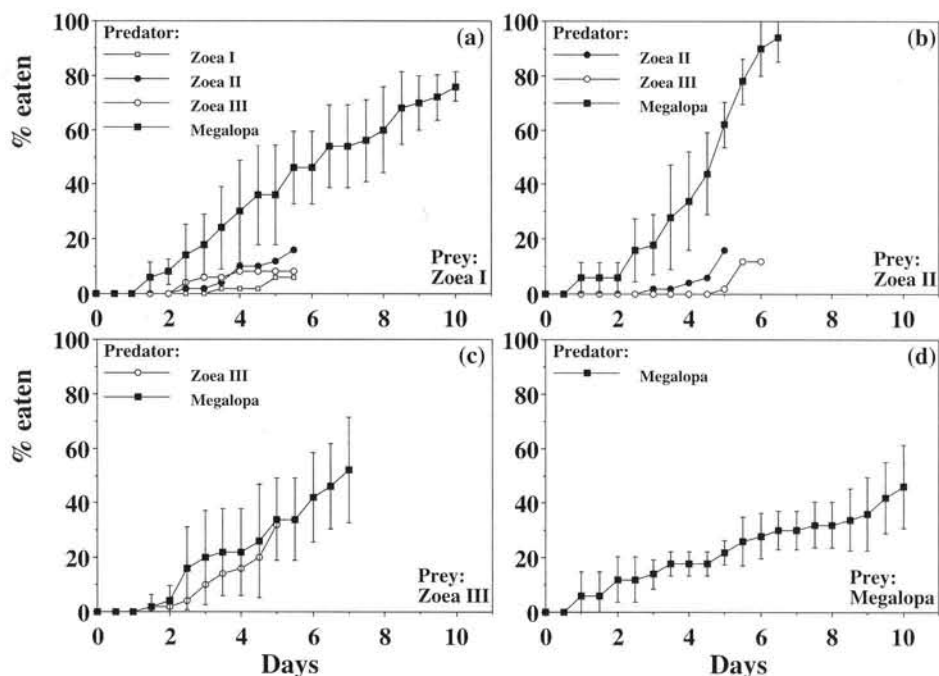


Fig. 4. *Armases miersii*. Tests for cannibalism: cumulative percentage of prey larvae eaten in laboratory experiments.  $n = 5$ , with an initial number of 10 prey individuals per replicate experiment; error bars are  $\pm 1$  SD, shown only for experiments with megalopa as predator; other SDs (smaller than in megalopa, overlapping each other) not shown for clarity of graphs

later development. Moulting to subsequent larval stages, however, occurred mostly simultaneously in the experimental and control groups, until the zoea II or III stage was reached. Delayed development became visible in the control group only in the zoea III stage or thereafter.

### Laboratory experiments

In general, cannibalistic activity tended to increase with increasing duration of development (Fig. 4). In all zoeal stages, cannibalism (both within-stage and by later-on earlier stages) usually began only after  $\geq 3$  d of the experiments, i.e. after moulting of both predator and prey to subsequent stages had commenced. Only in 2 single zoea I and II individuals (both 3 d old) was cannibalism on other larvae of equal age observed before moulting.

In the zoea III, intra-stage cannibalism began shortly before moulting to the megalopa stage, after 3 to 4 d of the experiments, followed by a steep increase thereafter (Fig. 4c). This increase was due to predation by both slightly delayed (4 to 5 d old) zoea III and those individuals that had moulted to the megalopa stage slightly earlier, eating conspecific larvae during or shortly after these were undergoing the moulting process. Thus, cannibalism among larvae of equal age and in the same stage hardly occurred in the zoea I and II, and in only a few instances in the zoea III. Predation on moulting or freshly moulted conspecifics, however, was frequently observed in all zoeal stages.

In experiments with the megalopa as a predator, cannibalism took place both within this stage (Fig. 4d) and on all earlier stages (Figs. 4a to c). Highest cannibalistic activity occurred in experiments where zoea II larvae were offered as prey (Fig. 4b), but increased steeply only after the prey individuals began to moult to the zoea III stage (after  $\geq 4$  d of the experiment). This is in contrast to relatively little predation of megalopa on older zoea III larvae (considering a high intra-stage cannibalism as a component of overall mortality in the latter; Fig. 4c). Thus, larval cannibalism was again principally related to the moulting process.

### DISCUSSION

Field experiments demonstrated that *Armases miersii* larvae are able to tolerate a wide range of *in situ* temperatures and salinities, showing successful development and growth at least between 24 and 32°C and from 5 to 24‰. Even at salinities of 1 to 2‰, development to the zoea II stage and some growth occurred, and sudden drops of 16‰ within a few hours did not exert any visible effects on development or growth. Thus, the larvae of *A. miersii* are very well adapted to developing under extremely low and variable salinities and temperature variations of (at least) 7°C within a few hours. The actual range of larval tolerance may be much higher than demonstrated in the present study, which was conducted in early spring; much higher temperature and salinity variations may occur in summer. These *in situ* observations are consistent with other laboratory experi-

iments (Schuh & Schultze unpubl.) which also showed an extremely euryhaline response.

One of the principal questions of this investigation was whether naturally available food sources in supratidal rock pools are sufficient to sustain near-to-optimum development and growth of crab larvae or if food limitation must be considered a significant factor in this habitat. Consistent trends in larval growth measured in 5 replicate experiments clearly indicate that the rock pools where *Armases miersii* females release their larvae in fact represent a food-limited nursery habitat. Thus, unusually high initial energy reserves (Anger & Schultze unpubl.), starvation resistance, and facultative lecithotrophy in early larval stages (Anger 1995) can be interpreted as ontogenetic adaptations to the particular breeding habitat of this species, i.e. as a result of selective pressure exerted by food limitation in supratidal rock pools.

These adaptations are particularly conspicuous in the early larval stages, whereas later stages (zoea III, megalopa) depend more on food (Anger 1995; see also increasingly delayed development in control groups of RPEs, Fig. 3). The zoeal stages exhibited relatively little growth, indicating a significant endotrophic component in early development (i.e. partial utilization of internal reserves), even in the presence of sufficient food. Later, when the internal energy reserves are partly depleted, uptake and accumulation of exogenous energy become increasingly important, and continued starvation will cause serious effects in later stages (Anger 1995). As a consequence of increasing feeding activity, experimental food addition enhanced growth much more in later than in early stages (Fig. 3).

This pattern of ontogenetically increasing dependence on food seems to point to a selective pressure toward further enhancement of initial energy reserves, i.e. to the evolution of full lecithotrophy. However, during the course of larval development, there is also time for planktonic microorganisms in ephemeral rock pools to develop increasingly dense populations. Thus, the zoea III might have a better chance, on average, to encounter suitable planktonic food than the zoea I. The semibenthic megalopa stage has still more possibilities to eat, since it has access to both planktonic and benthic food sources such as microorganisms (diatoms, protozoans) and detrital particles. Use of a benthic food source (sessile ciliates) was also observed in the facultatively lecithotrophic megalopa of the terrestrial bromeliad crab *Metopaulias depressus* (Anger & Schuh 1992).

Larval cannibalism might be another potentially important factor for the survival of later, less lecithotrophic stages of *Armases miersii*. Multiple release of hatching larvae was often observed in rock pools where older larvae were already developing. This

breeding behaviour should provide an opportunity to prey on younger conspecific larvae when not enough other food is available. Thus, increasing cannibalistic activity in the zoea III and megalopa stages (Fig. 4) might improve the chances of successful development in a nutritionally unpredictable nursery habitat. Comparable with nurse eggs occurring in broods of some gastropods, polychaetes, nemerteans, and other marine invertebrates (Christiansen & Fenchel 1979), larval cannibalism may serve as a buffer mechanism ensuring the survival of at least the strongest individuals to recruitment. Since water-filled supratidal rock pools are always limited in number, multiple breeding is more likely to happen with increasing density of the adult crab population. Hence, larval cannibalism may be a regulating factor in the population dynamics of this species.

It can only be speculated as to what might be the selective force that induced *Armases miersii* to choose a physically harsh and nutritionally unpredictable environment for larval release. Extremely abundant populations of small planktivorous fishes (mostly silversides, Atherinidae) that can commonly be observed foraging in the coastal fringe of northern Jamaica suggest that breeding in rock pools could be an adaptation to predation pressure. This factor is known as one of the key variables in zooplankton ecology, in particular in coastal and estuarine waters (for review, see Lazzaro 1987). While some decapod species avoid predation by following an export strategy, others show morphological or behavioural antipredatory adaptations to allow for larval retention within the adult environment (Morgan 1990, 1992). Breeding in marginal habitats such as supratidal rock pools seems to be another successful larval survival strategy. It requires the evolution of ontogenetic adaptations to highly variable conditions and, hence, predation pressure may indirectly favour the transition of marine crabs to terrestrial and freshwater environments, i.e. the conquest of land.

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