

Developmental biology of *Armases miersii* (Grapsidae), a crab breeding in supratidal rock pools. I. Facultative lecithotrophy of larval stages

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ABSTRACT: Starvation resistance in the larvae of a grapsid crab, *Armases miersii*, that breeds in supratidal rock pools in Jamaica was examined by point-of-no-return (PNR) and point-of-reserve-saturation (PRS) experiments. *A. miersii* shows an abbreviation of larval development (only 3 zoeal stages) and a high degree of lecithotrophy in the zoea I and II stages. In complete absence of food, larval development is possible from hatching to the zoea III stage. The potential for endotrophic development decreases during ontogeny: the zoea I is, in principle, entirely independent of food, without significant effects of starvation on survival; the zoea II shows significantly higher mortality under continued lack of food (since hatching) and delayed development after initial temporary starvation; the zoea III can also develop independently of food, but only if the preceding stages were fed continuously. Hence, no PNR or PRS can be given for individual zoeal stages of this species. Late effects of early feeding or starvation indicate that lecithotrophy in *A. miersii* is only facultative, i.e. food is not essential in the beginning of larval life, but it will be taken up when available. Conspicuous intraspecific variability in the degree of lecithotrophy was observed in larvae originating from 2 different females. In a hatch with particularly high endotrophic potential (but not in nutritionally more vulnerable larvae), development was significantly faster under starvation. This effect is interpreted as a change in energy partitioning: lack of food may induce a signal for switching from growth (accumulation of exogenous energy) to rapid mobilization of internal reserves (accelerated development, termination of the nutritionally vulnerable planktonic larval phase). Feeding after initial starvation may cause inverse effects, i.e. slower development, replacement of utilized reserves, and accumulation of additional energy for later stages. This switching should occur only in facultatively lecithotrophic larvae that have sufficient internal energy reserves to allow for this opportunistic bioenergetic strategy. Compared with most planktotrophic marine decapod larvae, the zoeal stages of *A. miersii* show higher starvation resistance and endotrophic potential. These ontogenetic traits are considered adaptations to breeding and larval development in a short-lived, nutritionally unpredictable habitat.

KEY WORDS: Crab larvae · Tropical rock pools · Starvation resistance · Lecithotrophy · Abbreviated development

INTRODUCTION

Since Rathbun (1897) described *Sesarma miersii* as a new species from Great Abaco Island, Bahamas, only a few further specimens of this apparently rare grapsid crab have been found, and its biology and life cycle remained virtually unknown. In his recent review of American Grapsidae, Abele (1992) lists only Key West (Florida) and the Caribbean islands of

Cuba, Hispaniola, Jamaica, and Swan Island as sites of later findings of *S. miersii* (now attributed to a new genus, *Armases*). Hartnoll (1965) did not find this species on Jamaica, although he conducted an extensive ecological and taxonomical study of marine grapsid crabs. Thus, the record by Rathbun (1918) for Jamaica appeared to be doubtful. Since Chace & Hobbs (1969) identified Rathbun's Jamaican material as *Armases* (*Sesarma*) *roberti*, Abele (1972) concluded that 'S.

miersii is not known from Jamaica'. Later in 1972, however, a single individual was found there by S. & J. Peck in a nearshore cave in Runaway Bay (Abele 1992), and Guinot (1988) included it in her list of cavernicolous crab species.

The reason why *Armases miersii* has been found only very rarely, and why practically nothing is known about its life cycle, can be found in the behaviour ecology of this species. Near the Discovery Bay Marine Laboratory (Jamaica), it lives on coastal limestone formations, where it remains hidden in narrow crevices, between mangrove roots, or in other cryptic habitats during the day. It is active at night, foraging in ephemeral supratidal rock pools. Like most Grapsidae, it can run very fast and hence hides quickly when it is disturbed by torch light or other human activity. Oviparous females release their larvae in these rock pools (Schuh & Diesel in press), regardless of salinity conditions (Anger 1995, this issue). Although breeding of *A. miersii* in other environments cannot be excluded at present, frequent observation suggests that supratidal rock pools represent a typical breeding habitat for this species.

Armases miersii has an abbreviated larval development with only 3 zoeal stages, and the larvae are tolerant of a wide range of salinities (Anger 1995; for review of developmental patterns in grapsid crabs see Rabalais & Gore 1985). Since the physical and nutritional conditions in small ephemeral rock pools are highly variable and unpredictable, these ontogenetic traits may be prerequisites for breeding in such a harsh environment (Rabalais & Cameron 1985). Moreover, in a study of larval growth and chemical composition, K. Anger & K. Schultze (unpubl.) showed enhanced initial energy reserves (yolk remaining from the egg) in early larvae of *A. miersii*. This suggests a high potential for lecithotrophic development and hence, independence from food. Similar developmental adaptations to breeding in small, short-lived water bodies were found also in the closely related crabs *Sesarma curacaoense* (Anger unpubl.) and *Metopaulias depressus* (Anger & Schuh 1992), and in an ocypodid crab that breeds in rainfall puddles of semi-arid coastal habitats (Rabalais & Cameron 1985).

In the present investigation, starvation resistance and endotrophic potential of *Armases miersii* larvae was examined by point-of-no-return (PNR) and point-of-reserve-saturation (PRS) experiments (Anger & Dawirs 1981, Staton & Sulkin 1991). The capability of larvae to survive and develop in the absence of planktonic food is compared with that of other grapsid crab larvae (Staton & Sulkin 1991, Anger & Schuh 1992) and with planktotrophic marine decapod crustacean larvae belonging to other families (Anger 1987).

MATERIAL AND METHODS

In March 1993, oviparous *Armases miersii* females were collected at night from supratidal rock pools on the northern shore of Jamaica, transferred to the nearby Discovery Bay Marine Laboratory, and maintained in aquaria with seawater (ca 35‰ salinity) kept at constant temperature (25°C) and a natural (approximately 12 h light:12 h dark regime). When larvae hatched, they were removed from the aquaria with wide-bore pipettes and reared as described below, under the same temperature and light conditions.

Two types of experiments were carried out with the larvae, following the procedures described in detail by Anger & Dawirs (1981): PNR and PRS experiments (see Fig. 1a). In PNR experiments, larvae were, in parallel sub-experiments (treatments), initially starved for different lengths of time (1 to 6 d, treatments S1 to S6); thereafter, they were fed freshly hatched *Artemia* sp. (San Francisco Bay Brand™) nauplii. In PRS experiments, the larvae were fed initially for differential periods (treatments F1 to F5) and then deprived of food. Both types of experiments also included continuously fed and starved control groups (FC, SC; see Fig. 1a). Water and food (where applicable) were changed daily. The larvae (25 individuals per treatment) were reared individually in glass vials with ca 25 ml of seawater. The experiments were checked twice daily for moults and mortality, at 08:00 and 20:00 h.

One series of PNR and another of PRS experiments was carried out with freshly hatched zoea I larvae (Expts 1 and 2, respectively). Since larvae originating from different females had to be used in these experiments, 6 treatments (FC, SC, F1, F2, S1, S2) were repeated in order to recognize the possible occurrence of intraspecific variability in starvation resistance. Another series composed of both PNR and PRS treatments began with freshly moulted zoea III larvae which had been fed continually until reaching this stage (Expt 3). Only Expt 1 was conducted through metamorphosis to the first juvenile crab; the others were terminated when the last larvae metamorphosed to the megalopa stage or died.

Statistical analyses of survival rates and development durations followed standard methods described by Sokal & Rohlf (1981) and Sachs (1984). Since goodness-of-fit *G*-tests showed that development data within treatments sometimes deviated significantly from a normal distribution, non-parametric tests were used for their analysis. Kruskal-Wallis *H*-tests were used in multiple comparisons of mean values (non-parametric ANOVA), and Mann-Whitney *U*-tests for pairwise comparisons. Contingency tables (survival data) were analyzed following a stepwise test procedure (STP *G*-tests for homogeneity) described by Sokal & Rohlf (1981, p. 728).

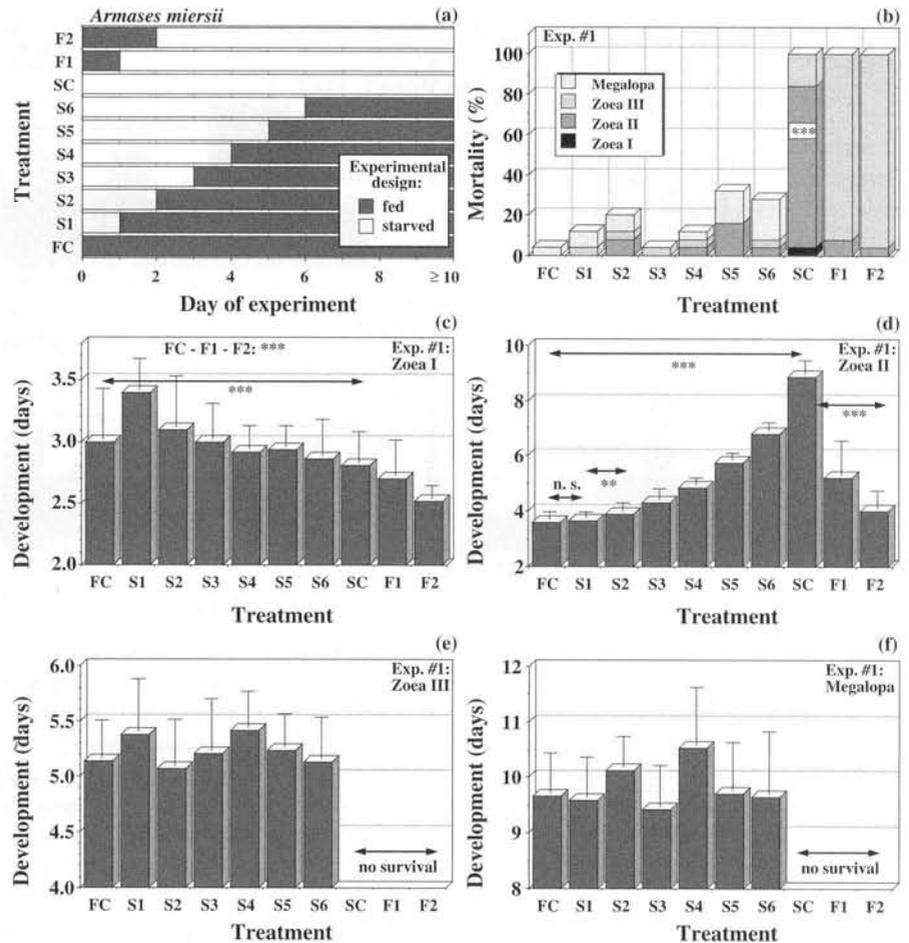


Fig. 1. *Armases miersii*. Expt 1: Point-of-no-return (PNR). (a) General experimental design, with treatments of temporary feeding (F1, F2, etc.) or starvation (S1 to S6) and continuously fed and starved control groups (FC, SC). (b) Cumulative mortality in larval stages (%; n = 25 per treatment). (c) to (f) Duration of development ($\bar{x} \pm SD$) in the zoea I to III and megalopa. *, **, ***: probability of error for rejecting the null hypothesis, with $p < 0.05$, < 0.01 , and < 0.001 , respectively; n.s.: not significant ($p > 0.05$); H: Kruskal-Wallis tests for multiple comparison of mean values; G-test for homogeneity in contingency (% mortality) data

RESULTS

Survival rate

Originally, these experiments were designed to determine critical points, the PNR and PRS, in the first zoeal stage. However, in 2 experimental series with material originating from 2 different females, almost all larvae developed successfully at least to the second zoeal instar. Some individuals (20% in Expt 1, 8% in Expt 2) reached the zoea III stage in the absence of food (SC treatments). Thus, the larvae of *Armases miersii* revealed a high degree of lecithotrophy, and the PNR shifted out of the zoea I moult cycle, close to the transition between the zoea II and III stages. The amount of yolk persisting from the egg was so large that the PRS was also outside the zoea I stage, i.e. its 'reserve saturation' was already reached during embryogenesis.

While initial periods of temporary starvation did not significantly influence mortality in the zoea I, survival was affected in later stages in some cases. This trend was weak and not statistically significant in the first

hatch (Expt 1; Fig. 1b), but it was conspicuous in Expt 2 (Fig. 2a). Zoea II mortality in the latter experiment was significantly higher in the SC, F1 and F2 than in the F3 to F5 and FC treatments of the same experiment. Likewise, overall mortality in Expt 2 treatments was higher than in corresponding Expt 1 treatments (cf. Figs. 2b & 1a). All these differences indicate that the second hatch was more dependent on food (less lecithotrophic) than the first. However, median duration of survival in SC groups did not differ significantly between Expts 1 and 2 (Fig. 3a).

Mortality in the zoea III and megalopa stages (the latter ascertained only in Expt 1) was not significantly influenced by initial starvation periods of up to 6 d, provided the larvae were fed thereafter (Figs. 1b & 2a). However, temporary initial feeding periods of less than 5 d did not suffice to allow for later food-independent survival to the megalopa stage.

These patterns indicate in both hatches that the degree of lecithotrophy decreased during larval development; in SC treatments (larvae starved continuously from hatching), the zoea I stage showed, in principle, complete independence of food, and there was still

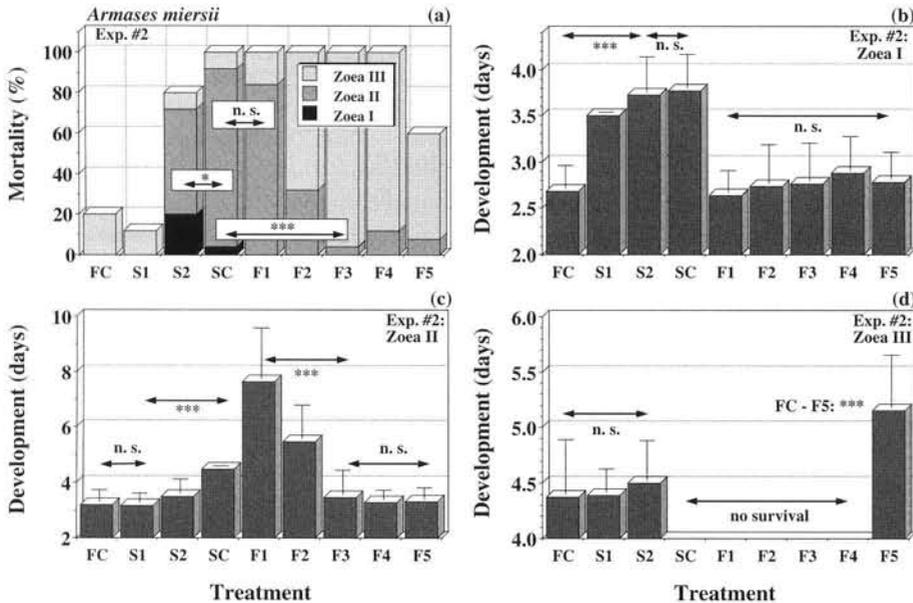


Fig. 2. *Armases miersii*. Expt 2: Point-of-reserve-saturation (PRS). (a) Cumulative mortality in larval stages (%; $n = 25$ per treatment). (b) to (d) Duration of development ($\bar{x} \pm SD$) in the Zoea I to III. Abbreviations, significance levels and statistical tests as in Fig. 1

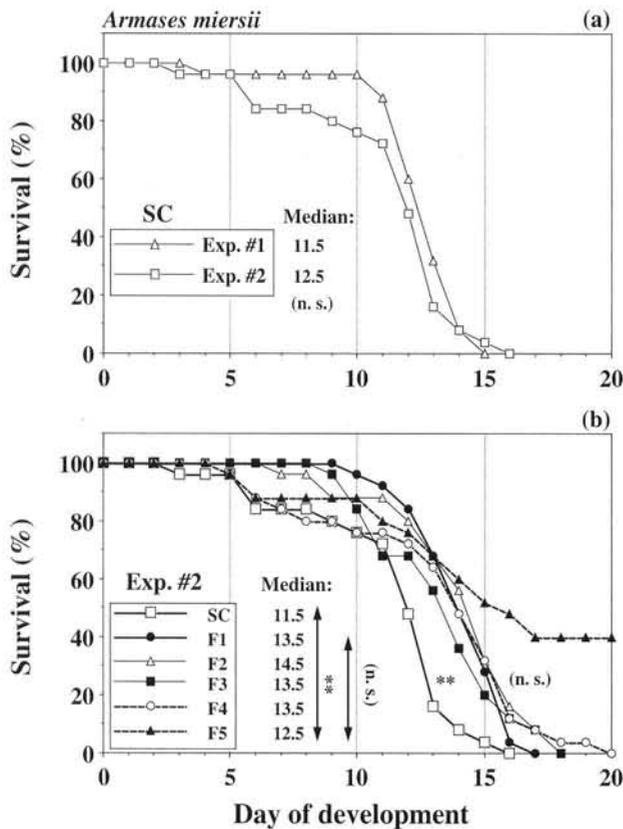


Fig. 3. *Armases miersii*. (a) Course of survival in the continuously starved control groups (SC) of 2 different hatches (Expts 1 and 2). (b) Course of survival in PRS treatments of Expt 2. Median time of survival (in d); statistical comparison by Mann-Whitney U - (pairwise) or Kruskal-Wallis H -tests (multiple); $n = 25$ per treatment. Abbreviations and significance levels as in Fig. 1

some ($\leq 20\%$) survival in the zoea II, whereas the zoea III showed complete mortality. However, when food was available for the first 5 d (i.e. from hatching to the end of the zoea II stage; treatment F5), 40% of the zoea III were able to survive and successfully develop into megalopa in the absence of food (Fig. 2a).

In Expt 3, the larvae were subjected to PNR and PRS treatments only after reaching the zoea III stage under optimum (FC) conditions. Mortality varied among treatments in this experiment in a haphazard manner, without showing a recognizable relationship to feeding or starvation (Fig. 4a). In the SC group (comparable with the F5 treatment in Expt 2), 44% of the larvae survived to the megalopa stage.

Duration of development

Effects of feeding or starvation were in general more conspicuous in rates of development than in survival. When the duration of the zoea I instar in PNR treatments (i.e. after initial starvation) is compared in Expts 1 and 2, different response patterns were observed. In the first hatch, zoea I development was slightly faster after prolonged or during continuous starvation (S4 and SC; Fig. 1c), whereas it was significantly slower in the second hatch (Fig. 2b). In both experiments, however, initial starvation periods of ≥ 2 d caused a highly significant delay in the development of the zoea II stage (H -tests and pairwise U -tests: all $p < 0.01$). Later stages showed no significant effects of PNR treatments (Figs. 1d to f & 2c, d).

PRS treatments (initial feeding followed by starvation) caused partly contradictory effects in the 2 exper-

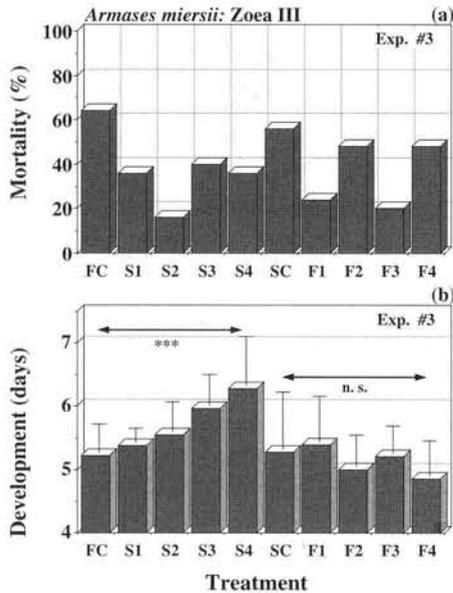


Fig. 4. Expt 3: PNR and PRS. (a) Cumulative mortality in zoea III (%; $n = 25$ per treatment). (b) Duration of development in zoea III. Abbreviations, significance levels and statistical tests as in Fig. 1

iments that began at hatching of the zoea I. In Expt 1, the zoea I stage lasted significantly less time in PRS groups (F1, F2) than in the continuously fed control (FC; Fig. 1c). However, no such effect was observed in Expt 2 (Fig. 2b). As an example of another difference between these experiments, only 1 or 2 d of initial feeding of the zoea I (F1, F2) in Expt 1 significantly shortened the duration of zoea II development during subsequent absence of food, as compared with the continuously starved control (SC; Fig. 1d). In the second experiment, in contrast, zoea II development appeared to be faster in the SC than in the F1 treatment (Fig. 2c). However, this difference was not statistically significant, since there was very low survival (2 and 5 individuals, respectively) in these 2 sub-experiments.

Median survival time in initially fed larvae (F1 to F5; Expt 2) was significantly longer than in the SC group (Fig. 3b). These late effects of early temporary feeding periods clearly indicate that the zoea I eats and converts food from hatching, i.e. its lecithotrophy is only facultative. Starvation following short feeding periods (F1, F2) consistently caused a delayed development in the zoea II as compared with the continuously fed controls (FC; Figs. 1d & 2c). This effect of late starvation was much stronger in Expt 2 than in Expt 1, again indicating a lesser degree of lecithotrophy in the second hatch.

Development duration in the zoea III and megalopa stages (the latter ascertained only in Expt 1) was not significantly influenced by initial temporary starvation

periods of up to 6 d (Fig. 1f). However, in larvae that were initially fed for 5 d and starved thereafter (F5 in Expt 2), the zoea III was significantly delayed compared with the FC group (Fig. 2d).

In Expt 3, duration of development in the zoea III showed a significant increasing trend with increasing length of initial starvation (S1 to S4; Fig. 4b). Larvae in the continuously starved control, however, developed significantly faster than in the S4 treatment (i.e. after re-feeding). In PRS treatments (F1 to F4), duration of zoea III development tended to decrease slightly with increasing length of initial food availability, however, this trend was not statistically significant (Fig. 4b).

DISCUSSION

Like the closely related crab species *Sesarma* sp. (a presently undescribed species endemic to the Gulf of Mexico; Zimmerman & Felder 1991), *S. reticulatum* (from the North American Atlantic coast; Costlow & Bookhout 1962), and *S. rectum* (from the Caribbean and Brazil; Fransozo & Hebling 1986), *Armases miersii* has only 3 zoeal stages and, hence, an abbreviated larval development compared with most other Grapsidae (Rabalais & Gore 1985). In *A. miersii* (Anger & Schultze unpubl. obs.) and *S. reticulatum* (Staton & Sulkin 1991), clear signs of lecithotrophy were observed. Larval development of *A. miersii* is possible in the absence of food from hatching to the zoea III stage and, thus, *A. miersii* larvae are much more independent from food than those of most other marine decapods (McConaughy 1985, Anger 1987). The endotrophic potential in *A. miersii* is also higher than in *S. reticulatum*, where only the second zoeal stage can be reached during starvation (Staton & Sulkin 1991). However, the degree of developmental abbreviation and larval lecithotrophy in *A. miersii* is exceeded by that in other Jamaican grapsids, *S. curacaoense* (Anger & Schultze unpubl. obs.) and *Metopaulias depressus* (Anger & Schuh 1992), and probably also by that in a North American ocyropodid, *Uca subcylindrica* (Rabalais & Cameron 1985). These species have only 2 zoeal stages, which are non-feeding in *M. depressus* and *U. subcylindrica* and, thus, are completely independent of external food sources. In *A. miersii* and *S. curacaoense*, in contrast, late effects of temporary feeding treatments indicate that zoeal lecithotrophy is only facultative.

Facultative lecithotrophy provides a great nutritional flexibility. When planktonic food is available, early zoeae will accumulate exogenous energy reserves. These reserves will be available for later stages and, thus, increase their independence from future feeding conditions. When food is lacking, on the other hand,

large internal energy reserves remaining from the egg (yolk materials) allow for an alternative strategy: development may be accelerated by rapid mobilization of internal reserves. This will increase the nutritional vulnerability of later stages, but it helps to terminate the critical planktonic phase in a shorter time.

Such switching in energy partitioning may explain some seemingly paradoxical results in the present study. In the larvae of the first hatch (Expt 1), which was particularly resistant to starvation, zoea I development was significantly shorter (compared with that in the continuously fed control, FC) when starvation commenced at hatching (SC group) or after only brief initial feeding periods (F1, F2 treatments; Fig. 1c). Here, lack of food in the presence of sufficient internal reserves may have induced a switch in energy partitioning, from growth to accelerated endotrophic development.

On the other hand, when feeding followed brief initial starvation (S1, S2 treatments), food availability seems to have induced an inverse change, to decelerated development. This delay could give the larvae an opportunity to replace used internal reserves and accumulate additional exogenous energy. This presumed effect might also explain the developmental delay in the S1 group, compared with both the starved and fed controls (Fig. 1c), and it may be responsible for slower development in initially starved and re-fed zoea III, compared with continuously starved sibling larvae (Fig. 4b).

In the second hatch, no acceleration of development occurred in any of the temporarily or continuously starved treatments (Fig. 2). The response pattern in this hatch resembled that known from most planktotrophic marine decapod larvae (Anger 1987); effects of nutritional stress suggest that these larvae had less internal energy reserves than those of the first hatch. Thus, relatively scarce yolk material (although sufficient for endotrophic development to the second zoeal stage, in a few individuals even to the third zoeal stage; Fig. 2a) may not have allowed for a switching in energy partitioning, as suggested above. This would leave only the regular response of starved planktotrophic larvae, saving energy by reducing metabolic processes and, hence, developmental rate. This delayed development response was also observed in initially starved zoea III (Expt 3; Fig. 4b) and in starvation-resistant (first hatch) larvae after a prolonged absence of food (response only in a later stage; Fig. 1d).

As in *Sesarma curacaoense* (Anger unpubl. obs.), the zoeal stages of *Armases miersii*, during their ontogeny, show an increasing dependence on food. The amount of yolk remaining from the egg is sufficient only for facultative lecithotrophy, i.e. for survival and development during temporary periods with insufficient exter-

nal food. However, in the bromeliad crab *Metopaulias depressus*, which breeds in small rainwater reservoirs in leaf axils of Jamaican bromeliad plants (Hartnoll 1964), the zoeal stages are non-feeding (obligatory lecithotrophy) and only the megalopa shows facultative lecithotrophy (Anger & Schuh 1992). Thus, due to a higher maternal energy investment, the larvae of this species can develop from hatching through metamorphosis even in complete absence of food.

In summary, starvation resistance and potential for endotrophic development are much higher in the early larval stages of *Armases miersii* than in most other marine decapod larvae (including those of the salt marsh crab *Sesarma reticulatum*), but weaker than in the semiterrestrial *S. curacaoense*, which lives in temporarily dry mangrove swamps (Chace & Hobbs 1969), and much less developed than in the fully terrestrial species *Metopaulias depressus*, which lives in mountain forests of interior Jamaica, completely independent of the marine environment and of its food sources. Like *Uca subcylindrica*, *A. miersii*, in its ontogeny, is well adapted to breeding under the physically harsh and nutritionally unpredictable conditions prevailing in ephemeral habitats of the marginal zone between sea and land. Hence, this species is a paradigm of a beginning and partially successful invasion of terrestrial and freshwater environments by originally marine crabs.

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