

Experimental Evidence of Food-Independent Larval Development in Endemic Jamaican Freshwater-Breeding Crabs

Klaus Anger^{1,*}

Christoph D. Schubart²

¹Biologische Anstalt Helgoland, Stiftung Alfred-Wegener-Institut für Polar- und Meeresforschung, 27498 Helgoland, Germany; ²Biologie I, Universität Regensburg, 93040 Regensburg, Germany

Accepted 6/14/04; Electronically Published 3/3/05

ABSTRACT

In an experimental study, we compared reproductive and developmental traits of endemic sesarmid crabs from Jamaica living in landlocked limnic or terrestrial habitats. Laboratory rearing and behavioral observations showed that the larval development of *Sesarma windsor*, *Sesarma dolphinum* (both from freshwater brooks), and *Metopaulias depressus* (the bromeliad crab) invariably consists of two nonfeeding zoeal stages and a facultatively lecithotrophic megalopa. In a quantitative study of life-history processes characterizing this developmental mode, we provide for *S. windsor* first data of biomass and elemental composition (dry mass, *W*; carbon, hydrogen, nitrogen, collectively, CHN) during development from the egg through successive larval stages. These data show that larval independence of food is based on an enhanced female energy allocation in reproduction, reflected in unusually large egg size (1.45–1.70 mm), as well as high contents of C and H (about 60% and 9%, respectively) and high C:N ratios (7.6–8.4) in eggs and early larvae. During zoeal development, about 6% of initial *W* and 9% of N but 13% each of C and H were lost; similar losses occurred during megalopal development in continued absence of food. These patterns reflect the metabolic utilization of stored organic matter, with preferential degradation of lipid reserves. Fed megalopae gained greater amounts of *W* and N as compared with C and H (increments of 37% and 38% vs. 25% and 19%, respectively), indicating preferential investment of nutritional energy in proteins required for the formation of new tissues and organs, while generally decreasing proportions of CHN within total *W* suggested an increasing mineralization of the exoskeleton. Although survival and molt

cycle duration of the megalopa stage were not affected by absence of food, significant effects were found in the size of first-stage juvenile crabs, indicating a trade-off between nutritional flexibility in the last larval stage and postmetamorphic fitness. Similar patterns of development and biomass in *M. depressus* as well as preliminary data obtained for *S. dolphinum* and *Sesarma fossarum* suggest that reproductive and developmental traits may be similar in all endemic Jamaican sesarmids. These traits are interpreted as life-history adaptations to development in landlocked habitats, probably playing a key role during adaptive radiation.

Introduction

Invasions of limnic and terrestrial environments by marine organisms are among the top issues in evolutionary biology (e.g., Labandeira and Beall 1990; Little 1990; Bartsch 1996; Gordon 1998; Lee and Bell 1999). Although such radical transitions in lifestyle require major physiological and life-history adaptations to new and profoundly different habitat conditions (e.g., Burggren and McMahon 1988; Anger 1995, 2001; Greenaway 1999; Feder et al. 2000), the invasion of freshwater or land by marine species is, in some cases, a surprisingly rapid process. In two extant shrimp species from Japan, for instance, Mashiko and Numachi (1993, 2000) detected consistent physiological, developmental, and genetic differences between conspecific limnic and estuarine populations, indicating an incipient segregation into new species. Similarly, beginning morphological divergence between anadromous marine and landlocked limnic populations of a holoeuryhaline fish species could be observed 1 decade after the invasion of inland freshwater habitats, suggesting that a complete change in the frequencies of different phenotypes might occur within only about 130 yr (Klepaker 1993). Thus, continued genetic isolation of populations living at different salinities may lead to rapid speciation (Palumbi 1994; Cognetti and Maltagliati 2000; Schluter 2000).

One of the most conspicuous examples of limnic and terrestrial invasions from the sea is found on the Caribbean island of Jamaica. Geographic isolation and the availability of highly diverse ecological niches allowed here for adaptive radiations in amphibians, reptiles, crabs, and several other taxa, leading to the evolution of numerous endemic animal and plant species (e.g., Hedges 1996; Schubart et al. 1998; Graham 2003). Dif-

* Corresponding author; e-mail: kanger@awi-bremerhaven.de.

ferential speciation in small, geographically and ecologically similar regions of the island (termed “short-range endemism” [Harvey 2002] or “regionalization” [Whiting et al. 2000]) was probably enhanced by pronounced cycles of fluctuating sea levels during the Pliocene and Pleistocene, which periodically may have isolated different populations (Schubart et al. 1998). Among the decapod crustaceans, at least 10 endemic limnic and terrestrial sesarmid crab species have evolved during the past 4 million years, all originating from the same ancestor (Hartnoll 1964, 1971; Schubart et al. 1998; Schubart and Koller 2005). Morphological, developmental, and recent molecular genetic data indicate that a mangrove-dwelling euryhaline coastal species of *Sesarma*, which must have been very closely related to the extant species *Sesarma curacaoense*, colonized the island in the early Pliocene (ca. 4.5 million years ago) and gave rise subsequently to nonmarine radiation.

While numerous physiological and morphological adaptations to freshwater or terrestrial conditions have been identified in adult decapods (Burggren and McMahon 1988; Greenaway 1999; Schubart and Diesel 1999; Freire et al. 2003), much less is known about the evolution of ontogenetic adaptations in the early (i.e., embryonic, larval, and juvenile) life-history phases. Most marine decapod crustaceans develop through a series of pelagic larval stages, which are generally stenohaline, planktotrophic, and physiologically far more vulnerable than the conspecific benthic juveniles and adults (Anger 2001). Many estuarine, terrestrial, and freshwater decapods worldwide evade this problem using an “export strategy” (Strathmann 1982); that is, their sensitive early life-history stages develop in adjacent coastal marine waters, outside the habitats where the adults live. This implies that those species rely on a seaward transport of their early planktonic larvae and a subsequent return of late larval or early juvenile stages; that is, they depend on an open connection with the sea.

In contrast to an export strategy, a complete invasion of landlocked freshwater or terrestrial habitats, as in the case of the endemic sesarmid crabs on Jamaica, requires either that the larval phase is omitted (direct development) or that the larvae evolve similar adaptations to nonmarine conditions as the benthic juveniles and adults. In cases where an aquatic larval phase is retained as part of a life cycle completed independent of the sea, the physiologically sensitive larvae face environmental stress, for instance, an exposure to dramatically reduced ion concentrations. This selects for an early appearance of osmoregulatory functions that are based on the development of ion-transporting cells and tissues and an early expression of the key enzyme $\text{Na}^+ - \text{K}^+ - \text{ATPase}$ (Charmantier 1998; Cieluch et al. 2004). Hence, the attainment of such ontogenetic traits may also have played a key role in the evolution of endemic Jamaican crabs. However, no experimental data on the ontogeny of osmoregulation have become available for any of these species, so this remains an interesting topic for future studies.

As another adverse environmental condition prevailing in

nonmarine habitats, lacking or unpredictably variable plankton production selects against planktotrophy. Again, this favors the evolution of a direct (i.e., nonlarval) mode of development or, alternatively, the occurrence of free-living but nonfeeding (i.e., lecithotrophic) larvae (Anger 1995, 2001). Both of these potential reproductive adaptations require an enhanced female energy investment in the production of large and energy-rich eggs as compared with relatives with planktotrophic larvae. In fact, large egg size has been noted in several endemic Jamaican crab species (Hartnoll 1964; Anger 1995, 2001; Diesel et al. 2000). This reproductive trait alone, however, does not necessarily prove a nonfeeding mode of larval development, because egg size is not always a good predictor of egg biomass, due to variability in volume-specific energy concentrations (Anger et al. 2002), and differences in egg size do not fully account for differences in larval form (Wray and Raff 1991), which can also be seen in the occurrence of decapod taxa with large eggs but planktotrophic larvae (e.g., all nephropid lobsters [Factor 1995] and some king crabs [Kittaka et al. 2002]).

For the endemic Jamaican crab species, no observations have been reported that suggest a direct mode of development. On the other hand, experimental evidence of free-living endotrophic larvae has been provided for one of these species, the bromeliad crab, *Metopaulias depressus* Rathbun 1896 by Anger and Schuh (1992). It passes through two fully lecithotrophic (nonfeeding) zoal stages followed by a facultatively lecithotrophic megalopa (i.e., the latter stage accepts food when available, but it can also successfully pass through metamorphosis in complete absence of food). For the remaining species (all belonging to the genus *Sesarma*), anecdotal observations on the occurrence of larvae have become available (Hartnoll 1964; Abele and Means 1977; Anger 1995; Diesel and Horst 1995; Diesel et al. 2000); however, none has provided information on experimental details, rearing methods, or biomass of eggs and larvae. Inferring from generally large egg size (all >1 mm), it is presumed that most, if not all, endemic Jamaican sesarmid species might show a similar mode of larval development as *M. depressus* (Anger 1995, 2001; Diesel et al. 2000).

In this study, we provide the first experimental evidence of lecithotrophic larval development in an endemic Jamaican species of the genus *Sesarma*, namely, in the recently described *Sesarma windsor* Türkay and Diesel 1994 (redescribed by Schubart et al. [1997]). In addition, we present occasional data and observations on eggs and larvae of *Sesarma fossarum* Schubart et al. 1997, *Sesarma dolphinum* Reimer et al. 1998, and *M. depressus* (Hartnoll 1964; Diesel 1989). Since previous observations had shown that the megalopae of *M. depressus* are able to capture, ingest, and convert food (Anger and Schuh 1992), we tested in laboratory experiments with *S. windsor* whether the presence or absence of food during the time of development through the megalopa stage influenced its survival, duration of development through metamorphosis, dry mass, elemental composition (contents of carbon, nitrogen, hydrogen), or post-

metamorphic juvenile body size. An increase (or a lower rate of loss) in the biomass of fed versus unfed megalopae should indicate a successful uptake and conversion of food, while the absence of such effects would indicate that the megalopa is a nonfeeding stage, as the zoeae. Comparisons of the chemical composition of larvae in different developmental stages and treatments (with and without food supply) were carried out to provide information on the energetic costs and metabolic substrates preferentially utilized during phases of nonfeeding development in this species, as well as on biochemical changes associated with biomass accumulation by fed megalopae. Furthermore, the initial larval biomass at hatching was established for interspecific comparisons of female energy allocation in offspring production. These may correspond to species-specific differences in the degree of larval independence of planktonic food sources.

Material and Methods

Collection and Maintenance of Crabs

Most crabs used in this study were collected in Jamaica during the period March 9–22, 2003. Ovigerous females of *Sesarma windsor* were obtained from its type locality, the Mouth River, next to the Printed Circuit Cave near Albert Town in Trelawny, while those of *Metopaulias depressus* and *Sesarma dolphinum* were collected in the Dolphin Head area in western Jamaica (Hanover). Additionally, we include in this article unpublished data on biomass of eggs and larvae of *Sesarma fossarum* gathered during a previous visit (March 1991; data partially used by Anger [1995, 2001]; for more details, see Anger and Schuh 1992). In both years of study, this limnic species was collected from the upper Martha Brae River, less than a kilometer from where it rises from springs next to Windsor Cave, Cockpit Country (Trelawny).

Crabs were first transported to the Discovery Bay Marine Laboratory (Discovery Bay, Saint Ann) and subsequently were maintained in freshwater at $24^{\circ} \pm 3^{\circ}\text{C}$ with a natural light cycle and were provided with natural food sources (plant materials) collected from the Martha Brae River. Later the crabs were transported to the Helgoland Marine Biological Laboratory (Germany) and maintained in aquaria with aerated tap water with limestones added as a calcium source, at similar conditions of temperature ($24^{\circ} \pm 1^{\circ}\text{C}$) and light as on Jamaica (12L : 12D cycle), with frozen isopods and grated carrots given as food. Stones with crevices were added as a substrate to allow the crabs to hide or to climb, emersed, into the air. In ovigerous females, we checked at least twice daily for the occurrence of freshly hatched larvae.

Larval Rearing and Measurements of Size

Larvae of *S. fossarum* were obtained only in 1991; these were not reared but were used exclusively for elemental analyses of

freshly hatched zoeae. Laboratory rearing experiments were carried out with larvae of *S. windsor*, *S. dolphinum*, and *M. depressus* hatched in April 2003. Within at most 12 h after hatching, the zoeae of these species were transferred with wide-bore pipettes to individual 100-mL Nunc plastic bowls filled with freshwater previously stored in a container with limestones. The conditions of temperature and light were the same as in the maintenance of adult crabs.

Present behavioral observations (see “Results”) as well as previously published experiments with one of the species studied here (*M. depressus*; Anger and Schuh 1992) consistently indicated that zoeae of these species are entirely nonfeeding, while the megalopa stage might begin to accept food. Hence, no food was given throughout the zoeal phase, while megalopae were routinely fed in daily intervals with freshly hatched *Artemia* sp. nauplii (ca. 10–15/mL). Before the nauplii were given to the megalopae, we rinsed them carefully with freshwater using a sieve (100- μm mesh size) and a squeeze bottle.

In megalopae of *S. windsor*, we also tested whether the presence or absence of food affected survival, development time to metamorphosis, body mass, and chemical composition. From 73 larvae that were available in this species, we risked 10 individuals in a treatment without food supply. At the end of the megalopa stage (on day 10 of its molting cycle, soon after the onset of metamorphosis to the first juvenile crab stage), five unfed individuals were sampled and killed for determinations of dry mass and contents of carbon, hydrogen, and nitrogen (CHN). Another set of five replicate CHN samples was taken from a group of 10-d-old megalopae that had been reared with food. Another five unfed individuals were used for the determination of development time and survival to metamorphosis in complete absence of food. All these unfed megalopae metamorphosed successfully to juvenile crabs, so we were able to measure and compare postmetamorphic body size of juvenile crabs obtained from both fed and unfed megalopae. Juvenile size was measured as carapace width between the tips of the posterior lateral carapace spines (for illustration of crab morphology, see Fig. 1 in Schubart et al. 1997) using a Leica MZ8 stereomicroscope equipped with a calibrated eyepiece micrometer. The same technique was also used to measure egg size.

Measurements of Biomass and Elemental Composition (CHN)

Sufficient larval material for the study of ontogenetic changes in biomass (dry mass, *W*) and elemental composition (carbon, hydrogen, nitrogen [CHN]) was available from only two species, *S. windsor* and *M. depressus*. Since no quantitative data whatsoever had been available for the larval development of *S. windsor*, we studied in this species the losses of biomass and changes in elemental composition (CHN) occurring during completely endotrophic development from hatching to metamorphosis, as well as megalopal growth during development in the presence of food (*Artemia*). For *M. depressus*, a previous

study (Anger and Schuh 1992) had already quantitatively shown the consequences of feeding and starvation in the megalopa stage (with materials originating from the same female), so there was no need to repeat this experiment. By contrast, the quantification of zoeal biomass losses during the completely nonfeeding developmental period from hatching to the molt zoea II to megalopa was in the previous study only preliminary because, for technical reasons, zoeae from different females had been used (implying a possibly confounding overlap of developmental changes with variability among different hatches). Hence, we repeated here in *M. depressus* the study of ontogenetic changes in biomass occurring during the fully lecithotrophic development from hatching to the end of the zoea II stage, this time using larvae from the same female.

In both *S. windsor* and *M. depressus*, first samples for later determinations of biomass and CHN were taken within a few hours after hatching. The end of the zoeal phase was defined as the time when most (>50%) of the zoea II larvae molted to the megalopa stage (5.5 and 6.5 d after hatching, respectively), and the end of the megalopa stage as the time when most larvae within a treatment (fed or unfed) passed through metamorphosis to the first juvenile crab stage (for development durations, see Table 1).

Measurement of dry mass (W) and elemental composition (CHN) followed standard techniques: samples of individual eggs or larvae were transferred with wide-bore pipettes to small bowls with distilled water, briefly rinsed, blotted on fluff-free Kleenex paper for optical use, frozen for storage at -20°C in preweighed tin cartridges (with one individual in each), freeze-dried in a Lyovac GT-2E vacuum apparatus, weighed to the nearest $0.1\ \mu\text{g}$ on a Mettler UM-3 microbalance, and eventually analyzed for CHN with a Fisons (Carlo Erba) model EA 1108 elemental analyzer using acetanilid as a standard. In general, each analysis of egg or larval W and CHN comprised five replicate measurements, each with a single individual; in some cases, however, limitation or loss of materials allowed for only

lower replicate numbers (n , given in Tables 2 and 3 for all W and CHN data).

Statistical Methods

Our statistical analyses followed standard techniques (Sokal and Rohlf 1995), using a JMP (version 3.2.6, SAS Institute) package. Data are presented as mean values ± 1 SD. The data were checked for normal distribution (Kolmogorov-Smirnov test) and homogeneity of variances (Levene's median test). Since no significant deviations were found, we used for comparisons of mean values Student's t -test. Percentage values (CHN in percent of W) and ratios (C : N, C : H) were arcsine transformed before statistical analysis.

Results

Patterns of Hatching

In all three species studied in 2003 (*Sesarma windsor*, *Sesarma dolphinum*, *Metopaulias depressus*; no data available for *Sesarma fossarum*), hatching in the laboratory occurred in April, about 4 wk after collecting the ovigerous females. *Sesarma windsor* showed an extended period of irregular larval release. First hatching (a single larva) was observed on April 16, while the last larvae from the same female hatched 13 d later, on April 29, reaching a total number of 73 sibling larvae. Mostly, five to seven and maximally 13 larvae per day (observed on April 25) were released, while no larva at all hatched on several other days. No preference for daytime or nighttime hatching was apparent.

In *S. dolphinum*, the ovigerous female lost and ate most of its eggs. Only two larvae hatched successfully on two successive days (April 17 and 18). In the bromeliad crab, *M. depressus*, 40 larvae were released from a single female, all hatching during the same night (April 17–18).

Table 1: Duration of development through successive larval stages (days, mean ± 1 SD) and cumulative time of development (days from hatching) in three endemic Jamaican crab species

	<i>Sesarma windsor</i>		<i>Sesarma dolphinum</i>		<i>Metopaulias depressus</i>	
	Mean \pm SD	n	Mean \pm SD	n	Mean \pm SD	n
Stage development:						
Zoea I	3.1 \pm 1.6	65	2.0 \pm 0	2	4.0 \pm 0	28
Zoea II	3.3 \pm .5	55	2.0 \pm 0	2	1.5 \pm 0	19
Megalopa	10.0 \pm .6	42	7.0 \pm 0	2	8.3 \pm 1.3	14
Cumulative development:						
Hatching to megalopa	6.5 \pm 1.6	55	4.0 \pm 0	2	5.5 \pm 0	19
Hatching to crab stage I	16.7 \pm 1.8	42	11.0 \pm 0	2	13.8 \pm 1.3	14

Note. n = number of observations (individuals). Data for fed and unfed megalopae were grouped, as no statistically significant differences in their respective development durations were found.

Table 2: Biomass, elemental composition, and C : N and C : H mass ratios of eggs and newly hatched larvae of endemic Jamaican sesarmid crab species

Female (Stage)	Size (mm)			W		C		N		H		C		N		H		C : N		C : H		
	\bar{X}	SD	<i>n</i>	\bar{X}	SD	\bar{X}	SD	\bar{X}	SD	\bar{X}	SD	\bar{X}	SD	\bar{X}	SD	\bar{X}	SD	Ratio	Ratio	Ratio	Ratio	<i>n</i>
<i>Sesarma windsor</i> :																						
A (egg II)	1.60	.08	10	781	42	475	26	56.4	2.4	70.8	3.9	60.8	.3	7.2	.1	9.1	.0	8.42	.14	6.71	.02	5
B (egg III)	1.68	.03	5	789	53	450	12	58.9	1.9	69.9	2.8	57.1	2.8	7.5	.3	8.9	.3	7.63	.26	6.43	.12	4
C (zoea I)				747	27	442	18	57.5	1.5	68.8	3.0	59.1	.4	7.7	.1	9.2	.1	7.69	.15	6.42	.03	5
<i>Sesarma fossarum</i> :																						
A (egg I) ^a	1.40		1	703	29	417	18	57.1	2.1	72.2	4.8	59.4	.3	8.1	.2	10.3	.3	7.31	.14	5.79	.20	6
B (egg II) ^a				602	29	354	18	47.5	2.2	54.5	3.0	58.8	.3	7.9	.2	9.0	.2	7.46	.17	6.51	.12	5
C (egg III) ^a				561	44	313	25	44.2	2.5	43.5	3.8	55.9	.3	7.9	.2	7.7	.1	7.10	.21	7.22	.06	5
D (zoea I) ^a				581	33	333	20	47.0	2.5	48.1	3.1	57.2	.3	8.1	.1	8.3	.1	7.07	.10	6.92	.04	5
<i>Sesarma dolphinum</i> :																						
A (egg III)	1.65	.04	4	694	17	387	20	58.1	1.0	59.4	3.1	55.7	1.5	8.4	.1	8.5	.2	6.66	.23	6.52	.00	2
<i>Metopaulias depressus</i> :																						
A (egg I) ^b				430	22	262	11	32.8	1.4	38.8	1.9	60.9	.9	7.6	.1	9.0	.1	7.97	.03	6.74	.06	5
B (egg I) ^b				405	18	239	10	34.5	1.7	36.0	1.3	58.9	.6	8.5	.4	8.9	.3	6.93	.25	6.64	.20	5
C (egg III) ^b				399	24	225	11	30.0	1.7	29.7	1.8	56.5	.9	7.5	.3	7.5	.2	7.52	.21	7.59	.18	5
D (egg II)				485	4	276	3	41.0	.3	42.7	.4	56.9	.2	8.5	.1	8.8	.1	6.73	.05	6.46	.03	5
E (egg III)	1.53	.04	2	424	4	225	1	36.9	.2	32.9	.1	53.2	.2	8.7	.0	7.8	.1	6.11	.01	6.86	.01	2
E (zoea I)				407	9	216	6	35.3	.5	31.9	.9	53.0	.3	8.7	.1	7.8	.1	6.10	.29	6.76	.02	5
F (zoea I) ^b				408	24	219	16	33.4	3.8	32.0	2.4	53.6	.8	8.2	.5	7.9	.1	6.57	.30	6.83	.03	3
G (zoea I) ^b				381	10	205	9	34.5	2.3	32.1	2.3	53.7	1.1	9.1	.4	8.4	.4	5.94	.17	6.37	.20	3

Note. Biomass measured as dry mass (W), contents of carbon (C), nitrogen (N), and hydrogen (H) per individual (ind). Elemental composition, in percentage of W, C : N, and C : H mass ratios (mean values $[\bar{X}] \pm 1$ SD) of eggs and newly hatched larvae (zoea I). Egg stages: early (I), intermediate (II), late (III); *n*, number of replicate measurements.

^a K. Anger, unpublished data, partially presented in earlier work (Anger 1995, 2001).

^b Data from Anger and Schuh (1992).

Patterns of Larval Development and Behavior

Rearing experiments invariably revealed in *M. depressus*, *S. windsor*, and *S. dolphinum* the occurrence of two zoeal stages followed by a megalopa and the first juvenile crab stage. The zoeae consistently showed a complete lack of feeding response when food (*Artemia* nauplii) was experimentally offered. The megalopae, in contrast, showed a clear behavioral response to food organisms, namely, an immediate increase in locomotory and mouthpart activities resembling suspension-feeding behavior. All three larval stages showed generally sluggish and benthic behavior, remaining motionless most of the time on the bottom of the rearing bowls. When zoeae were mechanically disturbed, they exhibited a brief swimming response, using abdominal flapping rather than maxilliped beats for locomotion. By contrast, the megalopa reacted with rapid juvenile-like walking using the pereopods.

Duration of Larval Development

The durations of individual larval stages and of total larval development from hatching to metamorphosis observed in *S. windsor*, *S. dolphinum* (only occasional observations from two

individuals available in *S. dolphinum*), and *M. depressus* are summarized in Table 1. Decreasing numbers of individuals (*n*) in successive stages are mostly due to sampling for later determinations of biomass and elemental analyses and for studies of larval morphology (to be published elsewhere); larval mortality in the rearing experiments was generally low or absent. After the last zoeal molt, megalopae were fed daily with *Artemia* nauplii, with the exception of 10 megalopae of *S. windsor* that remained unfed to test for their capability to develop in complete absence of food from hatching through metamorphosis.

In *S. windsor*, not only was the pattern of hatching quite irregular but also the time of development through successive stages varied greatly. In the zoea I, most larvae (51 individuals) molted 2–3 d after hatching to the second zoeal stage, 12 individuals molted after 4–5 d, and three individuals required as much as 9–12 d to reach the same molt (one of these died in ecdysis). This great variability in the duration of the zoea I stage is reflected in a very high standard deviation (3.1 ± 1.6 d; Table 1).

The durations of the next two larval stages (zoea II, megalopa) varied much less, ranging from 3 to 4 and from 9 to 11 d, respectively. On average, metamorphosis to the first juvenile

Table 3: Developmental changes in dry mass; contents of carbon, nitrogen, and hydrogen per individual; elemental composition of *Sesarma windsor* and *Metopaulias depressus*

Stage	W ($\mu\text{g}/\text{ind}$)	C ($\mu\text{g}/\text{ind}$)	N ($\mu\text{g}/\text{ind}$)	H ($\mu\text{g}/\text{ind}$)	C (%W)	N (%W)	H (%W)	C : N Ratio	C : H Ratio	n
<i>Sesarma windsor</i> :										
Zoea I (at hatching)	747 ^A \pm 27	442 ^A \pm 18	57.5 ^A \pm 1.5	68.8 ^A \pm 3.0	59.1 ^A \pm .4	7.7 ^A \pm .1	9.2 ^A \pm .1	7.69 ^A \pm .15	6.42 ^A \pm .03	5
Zoea II (end of stage)	699 ^A \pm 41	385 ^B \pm 24	52.5 ^B \pm 2.3	59.8 ^B \pm 3.9	55.2 ^B \pm .8	7.5 ^A \pm .2	8.6 ^B \pm .1	7.33 ^B \pm .22	6.45 ^A \pm .06	5
Megalopa (not fed)	669 ^B \pm 34	327 ^C \pm 21	50.1 ^B \pm 1.8	49.0 ^C \pm 3.2	48.9 ^C \pm .7	7.5 ^A \pm .3	7.3 ^C \pm .1	6.53 ^C \pm .29	6.68 ^B \pm .03	5
Megalopa (fed <i>Artemia</i>)	957 ^C \pm 95	481 ^A \pm 54	72.4 ^C \pm 5.3	71.1 ^A \pm 8.4	50.3 ^D \pm .6	7.6 ^A \pm .2	7.4 ^C \pm .1	6.64 ^C \pm .27	6.77 ^B \pm .05	3
<i>Metopaulias depressus</i> :										
Zoea I (at hatching)	407 ^A \pm 9	216 ^A \pm 6	35.3 ^A \pm .5	31.9 ^A \pm .9	53.0 ^A \pm .3	8.7 ^A \pm .1	7.8 ^A \pm .1	6.10 ^A \pm .29	6.76 ^A \pm .02	5
Zoea II (end of stage)	368 ^B \pm 12	184 ^B \pm 4	33.3 ^B \pm 1.2	26.6 ^B \pm .6	50.1 ^B \pm .6	9.0 ^B \pm .2	7.2 ^B \pm .1	5.54 ^B \pm .11	6.93 ^B \pm .03	5

Note. Developmental changes in dry mass (W); contents of carbon (C), nitrogen (N), and hydrogen (H) per individual (ind), and in percentage of W, C : N, and C : H mass ratios (mean values \pm 1 SD) of *Sesarma windsor* (complete larval development from hatching to metamorphosis; megalopa either fed or continuously reared without food) and *Metopaulias depressus* (nonfeeding zoeal phase only). n, number of replicate analyses. Superscript letters show statistical comparison of mean values, unequal letters indicating significant differences among developmental stages in a given biomass parameter ($P < 0.05$; Student's *t*-test).

crab stage was reached 16.7 ± 1.8 d after hatching from the egg. While most individuals metamorphosed after 15–18 d, the two individuals that had taken longer in the zoea I stage required in total 21 and 25 d, respectively. Five megalopae that remained unfed since hatching reached metamorphosis after 10–11 d in the megalopa stage (mean duration 10.4 ± 0.5 d), or 16–17 d (16.6 ± 0.6 d) after hatching; the other five unfed individuals were used for measurements of biomass and CHN. Their development duration was not significantly different from that in all other megalopae that had received food and is thus included in the overall mean values given in Table 1. Natural mortality (not including losses due to sampling for studies of larval morphology or biomass) comprised in total only four individuals (one in each larval stage and the one that was initially delayed and died in the molt from the zoea I to the zoea II stage).

In *S. dolphinum*, the only two larvae obtained in the laboratory required 2 d to reach the zoea II, another 2 d to the megalopa, and 7 d to metamorphosis to the first juvenile crab stage. Hence, their total time of larval development was 11 d.

In *M. depressus*, molting to the second zoeal stage occurred invariably 4 nights after hatching, and the next molt (zoea II to megalopa) was observed only 1.5 d later. Hence, total duration of nonfeeding zoeal development from hatching to the onset of the megalopa stage took 5.5 d. The duration of the megalopa stage was 6.5–11.5 d (average 8.3 d), so the time of total larval development from hatching to metamorphosis was 12–17 d (average 13.8 d; Table 1). There was no mortality throughout larval development.

Size, Biomass, and Elemental Composition (CHN) of Eggs and Freshly Hatched Larvae

Observations of egg size (measured as largest diameter) and biomass (dry mass, W; contents of CHN; see Table 2) were only occasionally obtained from eggs that either were lost by ovigerous females or (in a single female of *S. windsor* shortly

after it had died) were removed from the pleopods. In the latter case, the eggs were in an intermediate stage of development (embryo largely differentiated but not yet with fully developed eye pigments), showing a diameter of 1.45–1.70 mm. Another female of the same species dropped a few eggs shortly before larval hatching (i.e., in a late stage of embryonic development), with a size of 1.62–1.70 mm. In late eggs of *S. dolphinum* (lost by the female), we measured diameters of 1.61–1.70 mm. In an occasional measurement of the egg size of *S. fossarum* (in an early developmental stage), a value of 1.4 mm was obtained. In *M. depressus*, two eggs were measured (both in a very late stage of development), showing diameters of 1.50 and 1.56 mm.

The data of egg biomass (W, CHN) compiled in Table 2 include those from previous studies (Anger and Schuh 1992; K. Anger, unpublished data; see “Material and Methods”). In *S. fossarum*, the eggs in an early stage of development (stage I; Table 2) were sampled only 1 night after being extruded by the female, while the precise time since egg laying was unknown in the other species. When eggs in early, intermediate, and late stages of development are compared within single species, generally decreasing trends can be seen in the values of biomass (W, CHN) per egg as well as in the percentage values of CHN (percent of W; Table 2), reflecting a consumption of organic matter throughout the period of embryonic development. This decrease generally was stronger in the fractions of C and H compared with N. As a consequence, the C : N ratio tended to decrease in later developmental stages, while the C : H ratio showed no consistent trends.

The highest values of egg biomass were consistently observed in *S. windsor* (e.g., mean W, 781–789 μg ; C, 450–475 μg), while slightly lower figures were found in *S. fossarum* and *S. dolphinum* (W, 561–703 μg ; C, 313–417 μg), and clearly lowest values in *M. depressus* (W, 399–485; C, 225–276 μg). The same pattern of interspecific variation was also observed in the biomass of freshly hatched zoea I larvae (Table 2).

The relative elemental composition of the biomass of eggs and early larvae (CHN in percent of W; Table 2) was similar

in all species, with C varying from 53% to 61%, N from 7.2% to 9.1%, and H from 7.5% to 10.3%. Since the proportions of N and H within total W were generally similar, similar indexes (mass ratios) of C : N and C : H also were obtained, ranging roughly between 5.9 and 8.4 and between 5.8 and 7.6, respectively. Similarly to the pattern observed in the absolute amounts of W and CHN per individual, *S. windsor* tended to show also, although less clearly, the highest average values in the C : N ratio (7.6–8.4); mostly lower indices (5.9–8.0) were found in *S. fossarum*, *S. dolphinum*, and *M. depressus*.

Developmental Changes in Larval Biomass and Elemental Composition (CHN)

Ontogenetic losses of biomass and CHN occurring during the nonfeeding (fully lecithotrophic) zoeal development of *S. windsor* and *M. depressus* are shown in Table 3. For the former species, subsequent losses during the facultatively lecithotrophic development of megalopae reared to metamorphosis in complete absence of food, as well as growth of fed megalopae, are quantitatively documented (Table 3) and graphically illustrated, using changes in CHN per individual as examples (Fig. 1).

In both species, significant losses of W and CHN per individual occurred during the development from hatching to the end of the zoea II stage (i.e., to the end of the fully lecithotrophic zoeal phase). These losses were considerably lower in zoeal W (6% and 9% in *S. windsor* and *M. depressus*, respectively) compared with those in C and H (13% in *S. windsor* and 15%–17% in *M. depressus*). The losses in N, on the other hand, were similar to those in W (9% in *S. windsor* and 6% in *M. depressus*). As a consequence of these differential rates of biomass utilization, there were significant changes in the elemental composition of biomass, with generally decreasing percentage CHN values (in percent of W; decrease in the N content of *S. windsor* statistically not significant), significantly decreasing C : N ratios, and slightly increasing tendencies in the C : H ratios (statistically insignificant in *S. windsor*; Table 3).

Similar losses of biomass as in the zoeal phase were also observed in megalopae of *S. windsor* reared to metamorphosis in complete absence of food (Table 3; Fig. 1). Again, the losses per individual were lower in W (4%) and N (5%, statistically insignificant) than in C (15%) and H (18%). The patterns of change in elemental composition of nonfeeding zoeae and of continually unfed megalopae also were similar, with significantly decreasing C : N and increasing C : H ratios (Table 3).

Significantly different final values of W and CHN per individual in late megalopae of *S. windsor* reared to metamorphosis either in the presence or in the absence of food (Table 3; Fig. 1) indicate very clearly that the final larval stage of this species is capable of successfully capturing and ingesting prey organisms and converting their biomass to substantial growth. Fed megalopae gained, compared with the biomass at the end of the zoea II stage, significant amounts of W and CHN per

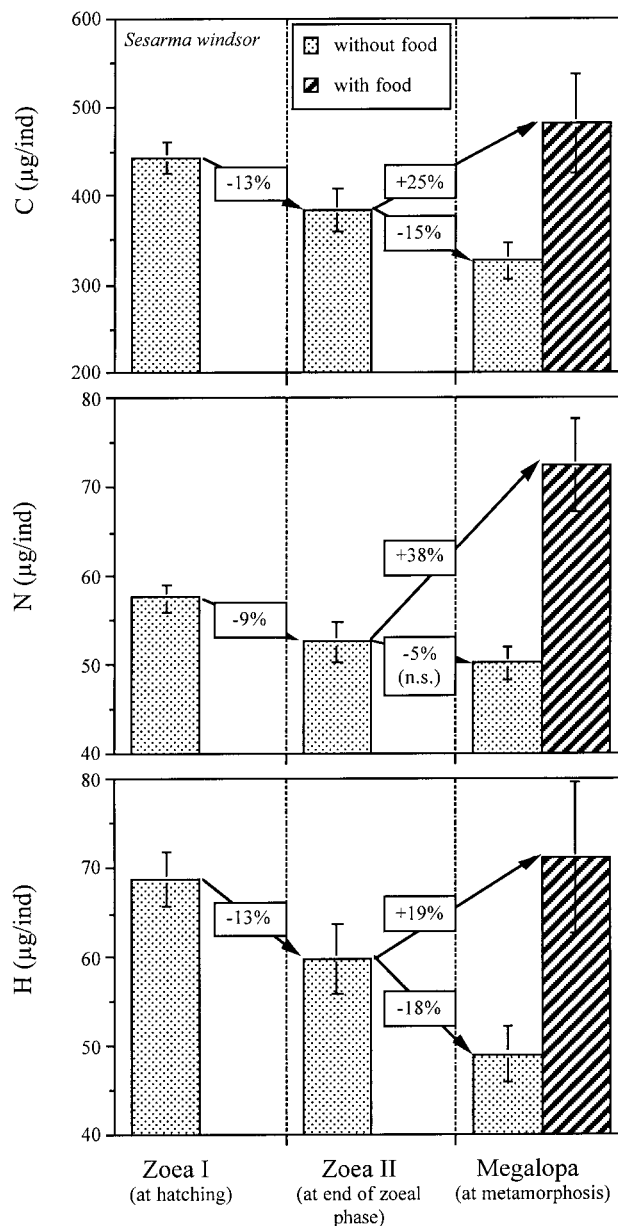


Figure 1. Changes in the contents of carbon (C), nitrogen (N), and hydrogen (H) during the larval development of *Sesarma windsor* (mean values ± 1 SD; all in $\mu\text{g}/\text{individual}$). Percentage losses shown for non-feeding zoeal development (zoea I and II combined), and for unfed megalopae, percentage gains in fed megalopae. Except for losses in the N content of unfed megalopae, all losses and gains are statistically significant (Table 3).

individual. Interestingly, the increments in W and N (37%–38%) were much higher than those in C (25%) and H (19%).

Lack or availability of food during the final larval stage was reflected not only in differential biomass and chemical composition shortly before metamorphosis but also in different body size of first-stage juvenile crabs. Juveniles that originated

from larvae that had developed from hatching through metamorphosis in complete absence of food had, on average, a carapace width of 1.98 ± 0.03 mm (range: 1.95–2.01 mm; $n = 5$). In contrast, fed megalopae developed into juveniles with carapace widths of 2.16 ± 0.05 mm ($n = 41$; range: 2.03–2.22 mm). This difference was highly significant (t -test: $t = 8.01$, $P < 0.0001$).

Discussion

Patterns of Hatching

Although this study represents only a beginning in the experimental investigation of reproductive and developmental traits in endemic Jamaican freshwater and terrestrial crab species, preliminary observations suggest a possible major difference between *Metopaulias depressus* and *Sesarma* species. While all sibling larvae produced by a bromeliad crab hatched during a single night, those from an egg clutch of *Sesarma windsor* hatched in small groups over an extended period of almost 2 wk, and the only two larvae obtained from *Sesarma dolphinum* hatched separately on subsequent nights. An extended hatching period with low numbers of simultaneously released larvae was also observed in lecithotrophic king crab larvae, where it was tentatively interpreted as an adaptive trait that may reduce larval conspicuousness, and thus, minimize posthatching mortality of large and slowly swimming demersal larvae (Thatje et al. 2003). This might be similar in Jamaican *Sesarma* species living in mountain streams or subterranean caves, although the potential predators exerting a selection pressure in those habitats are presently unknown. In *M. depressus*, on the other hand, female brood protection has been shown to mitigate predation pressure on the larvae (Diesel 1992), while great variability in age and size of siblings would probably enhance cannibalism among juvenile crabs living together at a high density (Kurihara and Okamoto 1987; Elgar and Crespi 1992; Luppi et al. 2001). The peculiar breeding biology of this species may thus favor simultaneous rather than extended hatching of sibling larvae. Another possible explanation is that *S. windsor* females, which were never observed to care for their offspring after hatching, may disperse the hatching larvae deliberately not only in time but also in space to avoid future competition. In the case of *M. depressus*, the extended brood care behavior (summarized in Diesel 1997) and continuing presence of the mother during early development make simultaneous breeding more energy efficient; dispersal of the larvae or early juveniles would be less of an issue because of the lack of suitable leaf axils. Future studies should further elucidate the developmental and physiological basis of different hatching patterns, in particular different coordination of developmental steps within embryogenesis (Lee and Strathmann 1998; Fernández et al. 2003).

Patterns of Larval Development and Feeding

In three endemic sesarmid species from Jamaica, *M. depressus*, *S. windsor*, and *S. dolphinum* (no data available for *Sesarma fossarum*), we invariably observed two zoeal stages followed by a megalopa that later metamorphosed to the first juvenile crab stage. This pattern is consistent with previous observations in *M. depressus* (Hartnoll 1964; Anger and Schuh 1992) and probably in another endemic freshwater-breeding species, *Sesarma bidentatum* (Hartnoll 1964), suggesting that this developmental sequence may be universal in this clade. It is probably an ancestral trait persisting from the coastal marine species that gave rise to the adaptive radiation of crabs on Jamaica (Hartnoll 1964; for recent discussion, see Anger 2001). Among the extant Sesarmidae occurring on Jamaica, the closest coastal relative of the endemic crabs is *Sesarma curacaoense* (for morphological and molecular genetic evidence of phylogenetic relationships, see Hartnoll 1964, 1971; Schubart et al. 1998, 2000). Like the endemic freshwater-breeding species, it has two zoeal stages and a megalopa (Anger et al. 1995).

Our observations consistently show also a complete lack of feeding response in the zoeal stages. This may be explained by previous morphological observations in *M. depressus* (Hartnoll 1964) and *Sesarma cookei* (Abele and Means 1977), which had shown that the zoeae possess only rudimentary and apparently nonfunctional feeding appendages. Preliminary data suggest the same may apply to the zoeae of *S. windsor* and *S. dolphinum* (J. I. González-Gordillo, K. Anger, and C. D. Schubart, unpublished data). Moreover, the larvae of these species are very inactive, showing swimming only as an escape reaction after disturbance.

In the megalopa stage, in contrast, our behavioral observations as well as our chemical data show clearly that the final larval stage of the species studied so far is only facultatively lecithotrophic; that is, it accepts available food but is also capable of successful development through metamorphosis if food is completely lacking. This flexible or opportunistic pattern of larval feeding had for the first time been demonstrated by Anger and Schuh (1992) for *M. depressus*. Future investigations will show whether this is another universal pattern in the early development of endemic Jamaican sesarmid crabs.

Egg Size and Initial Larval Biomass

Due to species-specific and developmental variation in scaled (volume-specific) energy contents of crustacean eggs (Anger et al. 2002), our measurements of egg size in terrestrial and freshwater crabs from Jamaica cannot immediately be compared with literature data, which have often been obtained from eggs in different or unspecified stages of embryonic development. However, there is no doubt that the endemic sesarmid crabs produce, in general, far larger eggs (all with diameters well above 1 mm) than closely related marine and brackish-water

species (all <0.5 mm; Anger 1995; Diesel et al. 2000). As a consequence, the organic biomass per egg or newly hatched larva is in the limnic and terrestrial species from Jamaica at least one order of magnitude higher than in coastal relatives (Table 2; Anger and Moreira 2004). Extremely high-percentage C and H values (53%–61% and 7.5%–10.3%, respectively) as well as unusually high C : N ratios (6–8.4) indicate that the females deposit great amounts of lipid reserves in the egg yolk. These stores of chemical energy serve as a fuel for fully endotrophic larval development from hatching through the two zoeal stages and, when necessary, also through the megalopa stage to metamorphosis.

These peculiar reproductive traits must be considered as evolutionary adaptations to life in landlocked habitats, where lacking or highly unpredictable production of planktonic food organisms selects against planktotrophic larvae (Anger 2001). Similar adaptive traits, that is, unusually large egg size, high initial biomass, high C : N ratios, and enhanced lipid reserves at larval hatching have also been observed in several marine anomuran crabs from high latitudes, where the season of planktonic production is too short in relation to long duration of larval development at low temperatures (Kattner et al. 2003; Lovrich et al. 2003). Independent evolution of lecithotrophic larvae hatching from large and energy-rich eggs in subpolar and tropical regions, as well as in marine, limnic, and terrestrial environments indicates quite clearly that planktonic food limitation rather than any other ecological factor is the principal selecting agent responsible for the occurrence of this phenomenon. High larval survival rates in freshwater and terrestrial habitats, independently of an availability of plankton, should enhance one component of the species' overall fitness, compensating for a trade-off that inevitably is associated with large egg size, the reduction of fecundity (Brommer 2000; McEdward 2000).

When egg characteristics are compared among the four species studied here, those of the bromeliad crab, *M. depressus*, consistently show the smallest size, lowest biomass (W, CHN per egg), and mostly lowest C : N ratios. Among the endemic *Sesarma* species, it appears that egg size and biomass increase in the order *S. fossarum* < *S. dolphinum* < *S. windsor*, suggesting an increasing endotrophic potential of the larval stages in this sequence of species. However, this pattern must be considered only as a preliminary observation because the presently available data do not allow for estimating the actual degree of potentially confounding intraspecific variability or plasticity, which may be high in the endemic Jamaican crabs (Anger and Schuh 1992). In future studies, these aspects should be investigated in more detail because they reflect the adaptability of a clade to diverse ecological scenarios and, hence, are important also for the understanding of the evolutionary process of adaptive radiation (Palumbi 1994; Arthur 2000; McEdward 2000; Schluter 2000).

Patterns of Larval Growth and Chemical Composition

Food-independent larval development is commonly associated with an abbreviation of the larval phase, occurring as both a reduction of the number of larval stages and as an acceleration of the rate of development through individual molting cycles (Anger 2001). This clearly is also the case in the endemic Jamaican crabs, which, as far as data are available, invariably pass through only two fast-developing zoeal stages and a megalopa, whereas most closely related marine and brackish-water sesarimid species (with the exception of *S. curacaoense*) have at least three zoeal stages (Rabalais and Gore 1985). It is striking, however, that the developmental abbreviation is restricted to the zoeal phase, while the duration of the megalopal molting cycle is similar to that in most other relatives. This suggests that the abbreviation of the zoeal phase is associated with a reduction of the planktonic (and normally planktotrophic) part of the life cycle. Together with zoeal lecithotrophy, this allows for fully food-independent early development. In contrast to the zoeal stages, the megalopa has access to benthic food sources, including detritus (Anger and Schuh 1992), and thus this stage may not require an additional female energy allocation into egg production, allowing for full lecithotrophy from hatching to metamorphosis. However, the facultative lecithotrophy of the megalopal stages of *M. depressus* and endemic Jamaican species of *Sesarma* suggests that the availability of benthic food may be highly variable, selecting for an enhanced although not maximum level of energy storage in the eggs.

The abbreviation of the planktonic larval phase may also have contributed to the rapid evolution of endemic crabs on Jamaica, as it implies a reduction of gene flow and, thus, an enhanced reproductive isolation of regional populations (Palumbi 1994; Havenhand 1995). Once the early larval stages became nonfeeding, this transition became effectively irreversible, due to substantial changes in early development, including the loss of complex feeding structures (Strathmann 1978, 1985; Wray and Raff 1991; McEdward 2000). This should have further stabilized the directionality of the radiation in Jamaican sesarimids, from an extended toward an increasingly abbreviated mode of development and from planktotrophy through facultative and, eventually, toward full lecithotrophy.

Changes in the elemental composition during the development of nonfeeding zoeae and unfed megalopae, namely, substantially decreasing percentage values of C and H, little change in N, and consequently decreasing C : N ratios, consistently indicate a preferential utilization of the lipid fraction, while proteins are degraded to a lesser extent. This pattern of chemical reserve utilization had been demonstrated before in the bromeliad crab (Anger and Schuh 1992) as well as in various other decapod crustacean species with lecithotrophic larvae (Anger 2001). In nonfeeding subantarctic king crab larvae, Kattner et al. (2003) found that neutral lipids are preferentially degraded as a metabolic substrate, whereas polar lipids are largely retained

as structural components of cell membranes. Among the fatty acids, monounsaturated and saturated compounds were utilized much more as an energy source than the essential highly unsaturated fatty acids (HUFA). Increasing tendencies in the C : H ratio (Table 3) suggest that similar patterns of lipid degradation may also occur in the lecithotrophic larvae of the endemic Jamaican crabs. However, this should be checked with direct biochemical studies, which may also reveal if independently evolved lecithotrophic larvae from different taxa (e.g., Brachyura, Anomura) and different climatic zones (tropical, subpolar) and environments (limnic, brackish, terrestrial, marine) show common patterns.

Another interesting finding is that our elemental analyses showed that fed megalopae of *S. windsor* did not preferentially restore those chemical fractions that had predominantly been degraded by the preceding nonfeeding zoal stages. The zoeae lost greater amounts of organic than inorganic matter (indicated by decreasing percentage CHN values within total body mass, *W*) and more lipids than proteins (decreasing values of percentage C, H, and C : N), which is a common pattern in unfed larvae (Anger 2001). However, the response of megalopae to subsequent feeding differed greatly from that of starved and, later, fed planktotrophic crustacean larvae. Instead of first restoring lost lipid reserves, the megalopa of *S. windsor* converts nutritional energy preferentially to proteinaceous body structures, most probably investing in the morphogenesis of new appendages, muscles, nerve tissues, cuticle, and other organs. Also, the benthic megalopa builds up a thicker and partially calcified exoskeleton, which requires an increasing uptake of inorganic matter (reflected in significantly lower-percentage C and H values in fed megalopae vs. nonfeeding zoeae; Table 3). These patterns of megalopal growth show that biomass losses occurring during zoal lecithotrophy belong to a normal developmental program; that is, they do not represent a condition of nutritional stress.

Although the internally stored energy reserves remaining from egg yolk suffice also for complete larval development from hatching through metamorphosis in continuous absence of food, without affecting survival or molt cycle duration of the megalopa, this endotrophic capacity clearly is associated with a trade-off: early juvenile crabs originating from unfed megalopae showed significantly smaller body size and may thus be inferior competitors for food and space or may become victims of cannibalism (e.g., Luppi et al. 2001). Hence, facultative lecithotrophy in the last larval stage represents a flexible strategy, allowing for successful metamorphosis under conditions of severe food limitation, while the feeding capability of this stage allows for an effective exploitation of available resources.

Concluding Remarks

Our experiments have shown that at least some endemic Jamaican crabs living in freshwater or terrestrial habitats have

undergone substantial evolutionary changes in major life-history traits, in particular, in the mode of larval development and feeding. These changes are reflected in extremely large egg size, unusual chemical composition (e.g., high C : N ratio), and great amounts of organic matter (presumably including enhanced lipid stores) remaining from egg yolk throughout the entire zoal phase. This allows for completely nonfeeding development from hatching to the megalopa stage, which still exhibits a high degree of independence from food (facultative lecithotrophy). These species release their free-living larvae in the upper reaches of mountain streams, in subterranean cave waters, or in small rainwater reservoirs collected in bromeliad leaf axils, respectively, and all those habitats have in common that they lack a production of plankton with an appropriate average particle size (for recent review of the nutritional requirements of decapod larvae, see Anger 2001). This very strongly suggests that large egg size and high initial larval biomass represent adaptive traits that were crucial for the success of the invasion of limnic and terrestrial environments. The increasing independence from the sea required irreversible life-history changes, including an abbreviation of the larval phase resulting in reduction of larval feeding structures and dispersal, all contributing to an increased reproductive isolation of regional populations and, hence, to the adaptive radiation of endemic crabs.

While the identification of these life-history changes helps to explain the developmental independence of endemic Jamaican crabs from the sea as well as the rapidity of their adaptive radiation, the evolutionary route of invasion from the sea to land and freshwater remains unresolved (Schubart and Diesel 1999; Diesel et al. 2000). When *M. depressus* and *Sesarma* species were exposed to concentrated media, Schubart and Diesel (1999) found a lack of the capability for hypo-osmoregulation. This finding supports the hypothesis that the terrestrial species evolved secondarily, and thus more recently, from limnic ancestors (which themselves originated from brackish-marine ancestors), while the opposite route, as favored by Diesel et al. (2000), is rendered unlikely. A direct descent of terrestrial crabs from hyper-hyporegulating coastal or marine ancestors (which were similar to the extant *S. curacaoense*) would require a secondary loss of hyporegulating functions on land. This is unlikely because most semiterrestrial and terrestrial crabs are in fact strong hyper-hyporegulators, while freshwater crabs may never have acquired this capability (Greenaway 1988, 1999).

Large egg size and larval lecithotrophy are generally considered ancestral traits appearing early in the clade that radiated in Jamaica (for references, see Anger 2001; Anger and Moreira 2004). Similar to the lack of hyporegulation in adult crabs, these reproductive adaptations are consistent with an evolutionarily direct transition from coastal (brackish-marine) to isolated limnic environments where the larvae are exposed to planktonic food limitation. Terrestrial brachyuran and anomuran crabs, which are believed to have evolved directly from

marine ancestors (namely, Gecarcinidae, Ocypodidae, Grapsidae, Coenobitidae, Diogenidae) normally have small eggs and follow an export strategy (Adiyodi 1988; Hartnoll 1988). Lecithotrophic and limnic larval development in terrestrial crabs such as *M. depressus*, and probably also *S. cookei* (Abele and Means 1977) and *Sesarma jarvisi* (Diesel and Horst 1995), support the view that these evolved from limnic ancestors and not from marine supralittoral ones.

It remains an open question, however, why the endemic Jamaican freshwater and terrestrial crabs did not evolve in their life histories extended spawning migrations to the sea like those exhibited, for instance, by varunid crabs (e.g., the Chinese mitten crab, *Eriocheir sinensis*; Rudnick et al. 2003) or the Christmas Island red crab (*Gecarcoidea natalis*; Adamczewska and Morris 2001). One reason may be that the Jamaican Sesarmidae show a relatively small body size and short legs. This appears to vary only little in this clade, presumably due to phylogenetic constraints (canalized traits) or as an adaptation to structural peculiarities (small crevices) of terrestrial limestone habitats on Jamaica. In addition, one may suspect that considerably larger and faster predators occurring in the lower estuaries, for example, *Callinectes* and other brackish-water and marine species (Warner 1969), may have prevented the evolution of reproductive migrations and thus contributed to the rapid radiation of sesarmids in landlocked habitats. The other way around, it is also possible that phylogenetic constraints never capacitated members of other families of the Grapsoidea with terrestrial or limnic adults (e.g., Gecarcinidae, Varunidae, or Glyptograpsidae) to produce yolk-rich eggs and thus evolve abbreviated development. Schubart et al. (2000) emphasized that all “entirely inland” forms among the Grapsoidea are species belonging to the Sesarmidae and that this is the only grapsoid family with marked reduction of larval stages and production of large yolk-rich eggs, even in the marine environment (Anger 1995; Anger and Moreira 2004; C. D. Schubart, unpublished data). These and many other remaining questions related to the biology of the endemic Jamaican crabs show that their comparative study is still promising interesting discoveries that eventually may contribute to our understanding of adaptive radiations in general.

Acknowledgments

We would like to thank Tobias Weil, Tobias Santl (Universität Regensburg), and Dr. Renae Brodie (University of South Carolina) for their assistance in the field. Karin Bickmeyer and Cornelia Püschel (Biologische Anstalt Helgoland) carried out CHN analyses. K.A. acknowledges traveling funds from the Stiftung Alfred-Wegener-Institut für Polar- und Meeresforschung, Bremerhaven. C.D.S.’s research on Jamaican crabs is funded by the Deutsche Forschungsgemeinschaft (DFG) project Schu 1460/3 as part of the priority program SPP1127 “Radi-

ations, Genesis of Biological Diversity.” Thanks are also due to the director and staff of the Discovery Bay Marine Laboratory (Discovery Bay, Jamaica), in particular to Mrs. J. Lawrence, for kind help and hospitality.

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