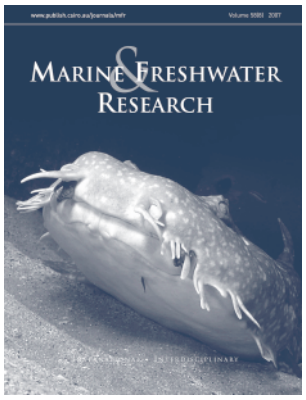
Marine & Freshwater Research

Volume 58 • Issue 8 • 2007

10.1071/MFv58n8toc



Cover

Huveneers *et al*. (p. 765) provided the reproductive parameter estimates of wobbegongs necessary for population modelling. They found that the three species of wobbegongs occurring in NSW have a synchronous triennial reproductive cycle and provided maturity, maternity, and fecundity estimates essential for adequate fisheries management and species conservation assessments.

Anger *et al*. (p. 743) studied the early life history of an endemic Jamaican stream crab. As an adaptation to unpredictable planktonic food production in the breeding habitat, *Sesarma meridies* produces large eggs with enhanced lipid reserves, allowing for food-independent larval development. These findings aid the understanding of evolutionary invasions of limnic and terrestrial environments.

CONTENTS

CSIRO PUBLISHING

www.publish.csiro.au/journals/mfr *Marine and Freshwater Research*, 2007, **58**, 743–755

Adaptive traits in ecology, reproduction and early life history of *Sesarma meridies*, an endemic stream crab from Jamaica

Klaus Anger[A,C], *Gabriela Torres*[A,B] *and Uwe Nettelmann*[A]

[A]Biologische Anstalt Helgoland, Stiftung Alfred-Wegener-Institut für Polar- und Meeresforschung, 27498 Helgoland, Germany.
[B]Carl-von-Ossietzky-Universität, 26129 Oldenburg, Germany.
[C]Corresponding author. Email: Klaus.Anger@AWI.de

Abstract. The endemic Jamaican freshwater crab *Sesarma meridies* lives in shady microhabitats on river banks, where temperature and pH are lower and ion concentrations higher than in mid-stream water. Ovigerous females were found to release up to 140 yolk-rich larvae (hatching period: 1 week; >90% at night). Larval development comprised two fully lecithotrophic zoeal stages and a feeding megalopa, which was also able to develop without food (facultative lecithotrophy). After metamorphosis in complete absence of food, juvenile crabs showed reduced body size, delayed moulting, and enhanced mortality. Endotrophic development was fuelled by internal lipid reserves; proteins were conserved as structural components of tissues and organs. Fed megalopae enhanced their protein content rather than re-stocking previously lost lipid reserves. Ecdysial biomass (CHN) losses were very low (zoeal stages: 1–2%; megalopa: 3–7%), showing an energy-saving production of thin exuviae. An extended hatching period may reduce intraspecific competition or cannibalism among juveniles; nocturnal hatching should reduce the predation on larvae. Large egg size, enhanced yolk reserves, an extended embryonic development (7 weeks at 24°C; implying a prolonged period of brood care), abbreviated and partially food-independent larval development, and reduced exuvial losses are considered as life-history adaptations to unpredictable planktonic food availability in the breeding habitat.

Additional keywords: decapod crustaceans, larval development, lecithotrophy, limnic, radiation.

Introduction

In evolutionary biology, comparative studies attempt to distinguish similarity in character states owing to phylogenetic descent (homology) from cases of independent origin (analogy), in effect, convergent evolution as a result of similar selective pressures (Harvey and Pagel 1991). Among closely related species, identical traits may provide evidence for common ancestry, whereas differences may represent recent adaptations to differential habitat conditions. However, phenotypic plasticity (i.e. intraspecific variability in response to environmental variation) (see Piersma and Drent 2003), renders this distinction sometimes difficult. This phenomenon occurs also in reproductive and developmental traits, which belong to the most important character states in phylogenetic analyses (Gilbert 2001; Hossfeld and Olsson 2003; Scholtz 2003). Comparative studies of both inter- and intraspecific variation in closely related species are therefore of utmost importance for the reconstruction of evolutionary pathways and phylogenetic relationships within and among clades. Processes of adaptive radiation are in this context particularly suitable subjects for case studies.

Among the decapod crustaceans, one of the prime examples for an adaptive radiation occurs in sesarmid crabs on the Caribbean island of Jamaica (Schubart *et al*. 1998; Graham 2003). During their transition from a coastal marine to limnic and terrestrial life styles, which took ~4 million years (Schubart *et al*. 1998), these crabs evolved various morphological, behavioural, reproductive and physiological adaptations to their new environments (Schubart and Diesel 1999; Diesel *et al*. 2000; Schubart and Koller 2005). Most of these adaptations resemble those of other Decapoda living in freshwater or on land (cf. Greenaway 1999; Adamczewska and Morris 2000; Holdich 2001).

In contrast to the evolutionarily much older crayfish and potamoid crabs, which reveal a direct development from the egg to an adult-like juvenile stage, the life cycles of the endemic Jamaican sesarmids comprise – at least in all species where this aspect has been studied – free-living larval stages, which develop in freshwater (Anger and Schuh 1992; Anger 2005; Anger and Schubart 2005). Because this phase is by origin marine planktonic, the larvae face both physical (namely osmotic) and nutritional stress in environments with low ion concentrations and poor or unpredictable plankton production. These conditions should thus select for an early appearance of osmoregulatory functions (Charmantier 1998) and larval independence from planktonic food sources (Anger 2001).

The latter assumption was confirmed in recent life-history studies on the endemic Jamaican crabs *Sesarma windsor*, *S. dolphinum*, *S. fossarum*, and *Metopaulias depressus* (Anger 2005; Anger and Schubart 2005). All of these species show an abbreviated larval development in freshwater, consistently comprising two non-feeding zoeal stages and a facultatively lecithotrophic

 10.1071/MF06176 1323-1650/07/080743

megalopa. However, the early life histories of more than one half of the endemic sesarmid species are still unknown, so that it has remained uncertain if the same reproductive, developmental and bioenergetic patterns occur in the whole clade. Further comparative studies on more of these species are therefore necessary to allow for generalisations. Corresponding traits should indicate common ancestral (homologous) character states, whereas interspecific variation may reflect derived characters that have evolved as a result of reproductive isolation and differential selection pressures (Schubart *et al*. 1998).

The present study provides the first comparative life-history data for a limnic and semiterrestrial crab from Jamaica, *Sesarma meridies*, which has only recently been described as a new species (Schubart and Koller 2005). Ecological, reproductive and developmental traits as well as ontogenetic changes in biomass and chemical composition of embryonic, larval and early juvenile life-history stages are compared with the available data from other species belonging to the endemic clade. Although similarities in several of these traits show common adaptations to fully limnic life styles, our data show also interspecific variation in some reproductive patterns.

Materials and methods

Collection and maintenance of crabs, collection of egg samples

About 40 adult *Sesarma meridies* (Fig. 1*e*), including three ovigerous females (body size ranging from 19.8 to 21.2 mm carapace width), were collected on 16 March 2004 from the Crooked River, Clarendon, southern central Jamaica (18°7.946′N, 77°18.329′W). Additional material (10 individuals) was collected from a second site in the same river, ~1 km upstream (18°7.807′N, 77°17.741′W). Water characteristics (temperature, conductivity, pH; Table 1) were measured at ~1300–1400 hours using a portable 'Combo pH and EC' apparatus (Hanna Instruments, Kehl, Germany). Concentrations of total ions (in ppt) can be estimated from conductivity (in mS cm^{-1}) using a conversion factor of 0.5 (manufacturer manual).

The crabs were transported to the Discovery Bay Marine Laboratory and subsequently maintained in freshwater kept at 24 ± 2°C and a natural light cycle. Plant materials collected from the river were given as natural food sources. Within one day after collection, five eggs were removed from each of the three ovigerous females (A, B, C) and stored frozen at −18°C for later determinations of biomass and elemental composition. The crabs were then transported to the Helgoland Marine Biological Laboratory (Germany), where they were maintained in aquaria with aerated tap water and limestones, which were added as a calcium source and as a substrate allowing the crabs to hide or to climb emersed in the air. Isopods (*Idothea* sp.) and grated carrots were provided as food. Conditions of temperature (24 ± 0.5°C) and light (12 : 12 h light : dark cycle) were kept similar to those at the collection site on Jamaica. The ovigerous females were checked at least twice daily for the occurrence of freshly hatched larvae.

Larval and juvenile rearing, feeding experiments, sampling protocol

Newly hatched larvae were pipetted to individual 100 mL Nunc plastic bowls filled with unaerated tap water (average pH 8.00; conductivity 0.41 mS cm^{-1}). Temperature and light were the same as in the maintenance of adult crabs. Cultures were checked every 12 h for moults or mortality, water was changed every 24 h.

Behavioural observations (see below) consistently showed that the zoeal stages were non-feeding, while the megalopa accepted food (*Artemia* sp. nauplii). No food was thus given throughout the zoeal phase, while megalopae were routinely fed with freshly hatched brine shrimp nauplii (density ~10–15 ind mL^{-1}) that were previously rinsed with freshwater.

In the larvae from females A and B, we tested if the presence or absence of food during the megalopa stage affected the rates of survival and development through metamorphosis, changes in megalopal body mass, chemical composition at metamorphosis, or body size in the first juvenile crab stage. Near the end of the megalopa stage (immediately after the onset of metamorphosis), samples of both fed and unfed individuals were taken for later determinations of biomass and chemical composition. Juvenile crabs from hatches A and B were individually reared (the same conditions as in fed megalopae), and the duration of successive moulting cycles was recorded through the first five instars. Further samples of larvae and juveniles were taken for a study of morphology (to be published elsewhere).

Measurements of body size, dry mass, and elemental composition

Body size (carapace width, CW) of adult crabs was measured to the nearest 0.1 mm with a Vernier calliper, the size of eggs and first-stage juveniles to the nearest 0.01 mm using a Leica MZ8 stereomicroscope equipped with a calibrated eyepiece micrometer. CW was measured between the tips of the posterior lateral carapace spines (Fig. 1*e*).

Embryonic and larval biomass was measured as dry mass (W) and contents of carbon, hydrogen and nitrogen (following the common use in the published reports, collectively referred to as CHN) per individual, as well as elemental composition (CHN in % of W; C : N, C : H mass ratios). Ontogenetic changes in biomass and chemical composition were studied during complete endotrophic development (i.e. from the egg to metamorphosis in continual absence of food, as well as in fed megalopae) (Tables 2–4). Samples of eggs or larvae were taken (*1*) within a few hours after collection of the females (early egg biomass); (*2*) immediately after larval hatching; (*3*) at the end of zoeal development; and (*4*) at the end of the megalopa stage (i.e. at metamorphosis) to the first juvenile crab stage (for development durations, see Fig. 2). Each set of W and CHN measurements in eggs or larvae comprised $n = 5$ replicate determinations with one individual each. Biomass and CHN of shed larval exuviae could be measured in only $n = 2$ replicate samples from each of the two zoeal stages and in $n = 3$ replicates with megalopal exuviae. Each of these replicate samples comprised 25 (zoeal stages) or 10 (megalopa) pooled exuviae.

Measurement of W and CHN followed standard techniques: samples of eggs, larvae or exuviae were briefly rinsed in distilled water, blotted on fluff-free Kleenex paper, and subsequently frozen for storage at −20°C in pre-weighed tin cartridges. Later, the samples were freeze-dried in a Lyovac GT-2E vacuum apparatus, weighed to the nearest 0.1 μg on a Mettler UM-3 microbalance, and analysed for CHN with a Fisons (Carlo

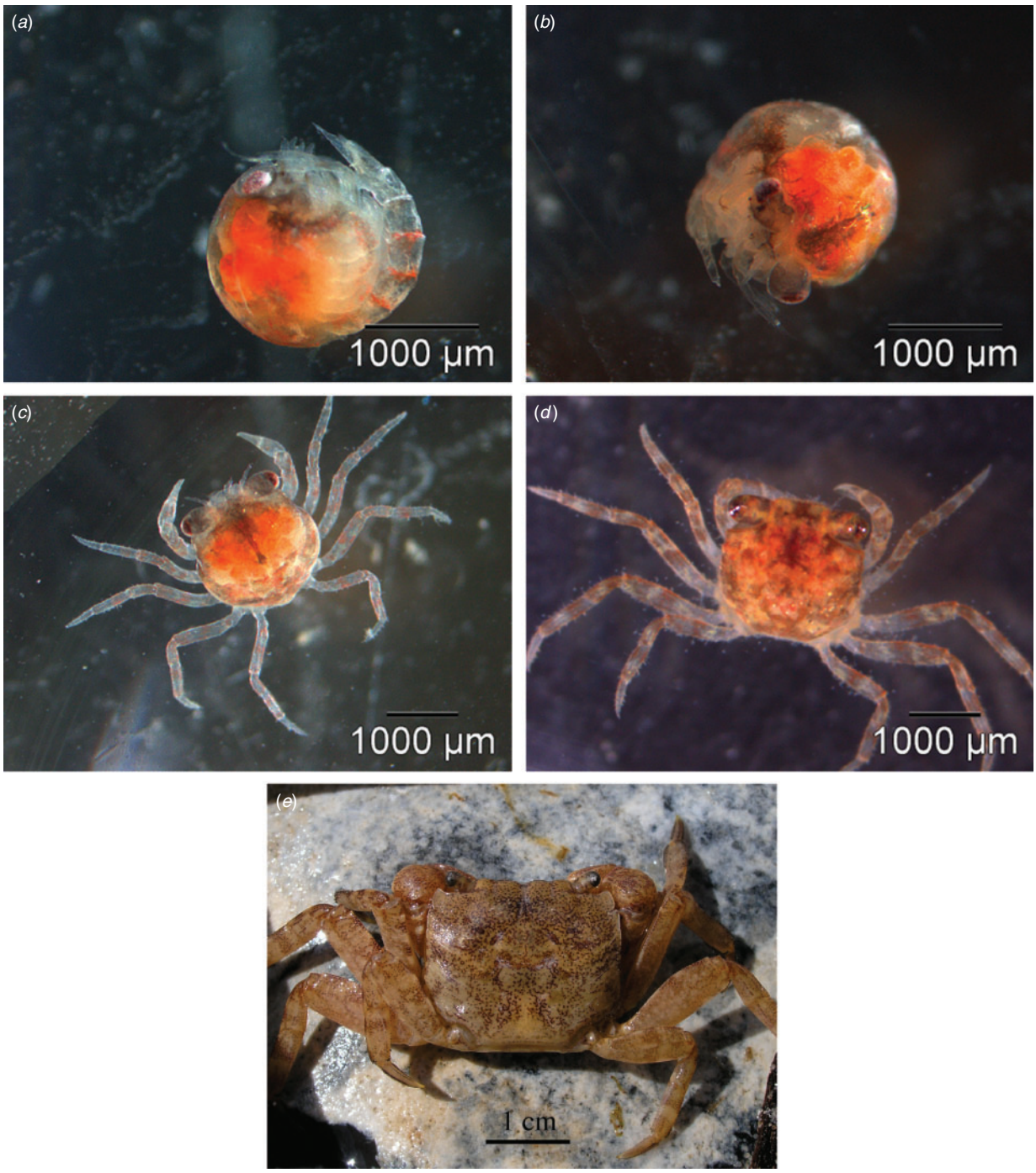


Fig. 1. *Sesarma meridies*, life-history stages; (*a–c*) larval stages (zoea I, II, megalopa); (*d*) first juvenile; (*e*) adult female.

Erba, Milano, Italy) model EA 1108 Elemental Analyser using acetanilid as a standard.

Measurements of proximate biochemical composition (total lipids, proteins)

Sufficient material for comparative measurements of proximate biochemical composition (contents of total protein and lipid) of successive larval stages was available only from hatch A. The samples were gently rinsed for 10 s in distilled water, subsequently blotted on filter paper, and stored frozen at −80°C in Eppendorf vials. After freeze-drying for 48 h, W was determined on a Sartorius MC1 RC 210 S balance (precision 0.01 mg). Thereafter, the samples were homogenised by sonication in distilled water (Branson, Sonifier, Cell Disruptor B 15; 5 strokes of 5 s on ice). Each homogenate was divided in two aliquots

Table 1. *Sesarma meridies*: water characteristics at various habitats in the Crooked River, Jamaica

'River', mid-stream water at site shown in Fig. 3*a*; 'Shaded puddles', same location, water in shallow puddles on densely vegetated, shady river banks (see Fig. 3*b*); 'Exposed pools', same location (Fig. 3*a*), but without vegetation, exposed to bright sunlight; 'Upstream site', shady river section in forest, ~1 km upstream from the other locations; $n = 5$ measurements each in the three former habitats, $n = 2$ at the upstream site

Variable		Habitats			
		River	Shaded puddles	Exposed pools	Upstream site
Temperature (°C)	Mean ± s.d.	29.6 ± 0.4	26.0 ± 1.1	32.1 ± 1.0	23.0 ± 0.2
	Range	29.2–30.2	25.0–27.7	30.3–33.1	23.1–22.8
pH	Mean ± s.d.	8.36 ± 0.08	7.12 ± 0.09	8.31 ± 0.42	7.88 ± 0.03
	Range	8.21–8.42	7.03–7.25	7.58–8.60	7.86–7.90
Conductivity (mS cm^{-1})	Mean ± s.d.	0.24 ± 0.00	0.52 ± 0.10	0.28 ± 0.09	0.34 ± 0.01
	Range	0.24–0.25	0.34–0.62	0.24–0.45	0.34–0.35

Table 2. *Sesarma meridies*: embryonic development, hatch C

Losses of dry mass (W), carbon (C), nitrogen (N), hydrogen (H) (collectively CHN), all in μg ind^{-1} and changes in elemental composition (CHN in % of W, C : N and C : H mass ratios) during the period (49 days) of development from an early embryonic stage (day of crab collection) to the day of larval hatching; embryonic biomass losses in % of initial egg W and CHN; *P*, level of significance for comparisons of mean values (n.s., not significant); note: the duration of 49 days, as well as the values of 'initial' embryonic biomass and of the biomass decrease from an early embryonic stage until hatching represent minimal estimates, because the eggs might have been laid several days before the collection of the crabs

Variable	Stage (time in days)		Embryonic loss (%)	*P*
	Embryo (−49)	Zoea I (0)		
W (μg ind^{-1})	734 ± 27	636 ± 60	13.4	<0.02
C (μg ind^{-1})	458 ± 20	378 ± 35	17.4	<0.01
N (μg ind^{-1})	56.8 ± 1.8	50.1 ± 4.7	11.8	<0.05
H (μg ind^{-1})	69.5 ± 3.2	58.0 ± 6.1	16.5	<0.01
C (%W)	62.3 ± 0.9	59.4 ± 0.2		<0.01
N (%W)	7.7 ± 0.1	7.9 ± 0.1		n.s.
H (%W)	9.5 ± 0.1	9.1 ± 0.1		<0.01
C : N ratio	8.06 ± 0.11	7.54 ± 0.06		<0.0001
C : H ratio	6.59 ± 0.02	6.52 ± 0.08		n.s.

Table 3. *Sesarma meridies*, hatch A

Changes in dry mass (W), carbon (C), nitrogen (N), hydrogen (H) (all in μg ind^{-1} and in % of W), C : N and C : H mass ratios, protein and lipid contents, and lipid : protein ratio during larval development (time, days before or after hatching); zoeae always reared without food, megalopae without (−) or with (+) *Artemia* nauplii; *P*, level of significance for comparisons of mean values − versus + (n.s., not significant)

Variable	Stage (time in days)						
	Egg (−13)	Zoea I (0^A)	Zoea I (0^B)	Zoea II (5)	Meg (−) (13)	Meg (+) (13)	*P* (− *v.* +)
W (μg ind^{-1})	589 ± 22	551 ± 22	507 ± 43	504 ± 13	478 ± 39	685 ± 14	<0.0001
C (μg ind^{-1})	353 ± 6	317 ± 11	294 ± 27	280 ± 11	227 ± 26	336 ± 7	<0.0001
N (μg ind^{-1})	42.4 ± 0.9	39.4 ± 0.8	38.0 ± 3.2	37.5 ± 0.8	35.5 ± 2.7	53.5 ± 1.4	<0.0001
H (μg ind^{-1})	52.6 ± 1.1	46.8 ± 1.9	45.9 ± 4.7	43.3 ± 1.9	34.0 ± 4.3	50.3 ± 1.1	<0.0001
C (%W)	59.9 ± 1.7	57.6 ± 1.5	58.0 ± 0.9	55.6 ± 0.9	47.4 ± 1.7	49.1 ± 0.6	n.s.
N (%W)	7.2 ± 0.1	7.2 ± 0.2	7.5 ± 0.1	7.4 ± 0.1	7.4 ± 0.1	7.8 ± 0.1	<0.001
H (%W)	8.9 ± 0.2	8.5 ± 0.2	9.0 ± 0.2	8.6 ± 0.2	7.1 ± 0.4	7.3 ± 0.1	n.s.
C : N ratio	8.32 ± 0.12	8.06 ± 0.16	7.74 ± 0.10	7.48 ± 0.18	6.37 ± 0.26	6.29 ± 0.18	n.s.
C : H ratio	6.70 ± 0.03	6.78 ± 0.03	6.42 ± 0.07	6.47 ± 0.05	6.69 ± 0.11	6.68 ± 0.01	n.s.
Lipid (μg ind^{-1})			103 ± 21	75 ± 7	46 ± 7	67 ± 7	<0.001
Protein (μg ind^{-1})			174 ± 5	167 ± 8	153 ± 6	214 ± 9	<0.0001
Lipid : Protein			0.59 ± 0.13	0.45 ± 0.06	0.30 ± 0.04	0.31 ± 0.02	n.s.

[A]First day of hatching period.
[B]Day 5 of hatching period.

Table 4. *Sesarma meridies*, hatch B

Changes in dry mass (W), carbon (C), nitrogen (N), hydrogen (H) (all in $\mu g\,ind^{-1}$ and in % of W), C : N and C : H mass ratios during larval development (time, days before or after hatching); zoeae always reared without food, megalopae without (−) or with (+) *Artemia* nauplii; *P*, level of significance for comparisons of mean values − versus + (n.s., not significant)

Variable	Stage (time in days)					
	Egg (−11)	Zoea I (0)	Zoea II (5)	Meg (−) (13)	Meg (+) (13)	*P* (− *v.* +)
W ($\mu g\,ind^{-1}$)	768 ± 60	775 ± 67	723 ± 65	694 ± 86	937 ± 63	<0.001
C ($\mu g\,ind^{-1}$)	460 ± 45	460 ± 44	415 ± 44	349 ± 53	479 ± 38	<0.001
N ($\mu g\,ind^{-1}$)	57.5 ± 4.2	58.2 ± 4.8	53.7 ± 4.3	51.3 ± 5.4	69.6 ± 4.3	<0.001
H ($\mu g\,ind^{-1}$)	70.1 ± 7.2	71.0 ± 7.0	63.2 ± 7.1	52.2 ± 8.5	71.5 ± 6.1	<0.002
C (%W)	59.8 ± 1.4	59.3 ± 0.7	57.3 ± 1.4	50.2 ± 1.5	51.1 ± 0.8	n.s.
N (%W)	7.5 ± 0.3	7.5 ± 0.1	7.4 ± 0.2	7.4 ± 0.2	7.4 ± 0.2	n.s.
H (%W)	9.1 ± 0.3	9.2 ± 0.2	8.7 ± 0.3	7.5 ± 0.3	7.6 ± 0.1	n.s.
C : N ratio	8.00 ± 0.39	7.90 ± 0.20	7.71 ± 0.41	6.78 ± 0.37	6.87 ± 0.21	n.s.
C : H ratio	6.56 ± 0.05	6.48 ± 0.04	6.56 ± 0.04	6.70 ± 0.09	6.70 ± 0.06	n.s.

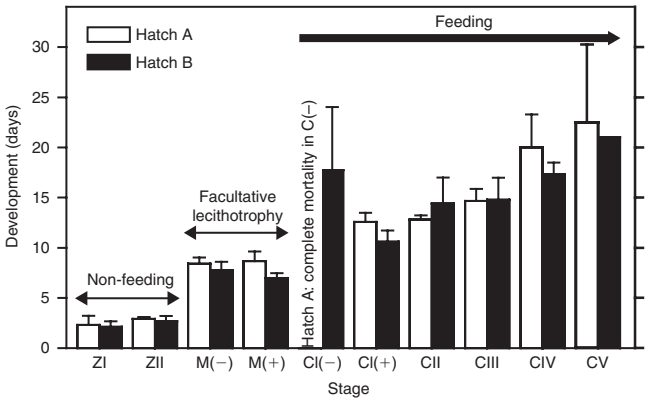


Fig. 2. *Sesarma meridies*, hatches A and B. Duration of development (mean ± s.d.) through successive larval (zoea I, II, megalopa) and early juvenile crab stages (C I–V); megalopa reared without (−) or with food (+); juvenile crabs always fed, but originating from fed or unfed megalopae respectively (no data for the − treatment in hatch A owing to complete mortality in C-I instar).

for measurements of the lipid and protein contents. The lipid content of the homogenate was determined with the sulphophosphovanillin method (Zöllner and Kirsch 1962) modified for microplates (Torres *et al*. 2007*b*). The protein content of the homogenate was determined using a BioRad (München, Germany) DC Protein Assay kit (based on the method of Lowry *et al*. 1951), which was also modified for microplates (Torres *et al*. 2007*a*).

Statistical methods

The statistical analyses followed standard techniques (Sokal and Rohlf 1995), using a JMP (version 5.1.2; SAS Institute Inc., Cary, NC) software package. Data are presented as mean values ± 1 s.d. The data were checked for normal distribution (Kolmogorov–Smirnov test) and homogeneity of variances (Levene's median test). When no significant deviations were found, Student's t-tests were used for comparisons of mean values, otherwise non-parametric Kruskal–Wallis tests. Percentage values (CHN in % of W) and ratios (C : N, C : H) were arc-sin transformed before statistical analysis. Juvenile body size was compared between two different hatches (A, B) and treatments (megalopae with or without food) using a two-way ANOVA.

Results

Habitat characteristics

Both collection sites were close to the type locality of *Sesarma meridies* (see Schubart and Koller 2005) and may thus be considered as typical habitats of this species. The Crooked River, a tributary to the Minho River, is a shallow mountain stream (Fig. 3*a*). At the river banks, there were isolated puddles and larger pools with no or only weak water flow. Numerous small fishes were observed in both the stream proper and in pools connected to it, but never in small and isolated puddles. Crabs were exclusively found under stones and boulders in or next to shallow puddles, in densely vegetated and shaded sections of the river banks (Fig. 3*b*). These microhabitats were considerably cooler (on average by 3.6°C) compared with the water in the sun-exposed stream proper (Table 1). The stagnant water in the puddles had consistently a much lower pH (on average 7.12 *v.* 8.36), while total ion concentrations (measured as conductivity) were more than twice as high.

When vegetated puddles were compared with unvegetated, mostly larger and deeper pools exposed to bright sunlight, even stronger temperature differences were noted (6.1°C higher in exposed pools; Table 1). The conductivity values were similar between these two microhabitats, but the pH values were consistently higher in exposed pools, being similar to those measured in the stream proper. The second collection site was located within an area with dense natural forest and agricultural plantations, so that the stream was almost everywhere in the shade. Here its water was on average cooler by 3°C compared with the sun-exposed downstream site (Table 1). Both the pH and conductivity values were intermediate between those in vegetated puddles and in the stream proper at the downstream site.

Duration of embryonic development, egg size

The duration of embryonic development could only be estimated for eggs from female C, which were completely undifferentiated (i.e. in an early stage of development). Hatching began 49 days

Fig. 3. *Sesarma meridies*, habitat: (*a*) Crooked River, Clarendon, Jamaica; (*b*) typical microhabitat under vegetation on river bank.

Table 5. *Sesarma meridies*: effects of (1) absence (−) or presence (+) of food during the megalopa stage, (2) of the hatch (A, B) on body size of first-stage juvenile crabs (carapace width, mm; mean ± s.d.)

Two-way ANOVA indicates highly significant effects of both food availability ($F = 59.2998$; $P < 0.0001$) and hatch ($F = 56.0782$; $P < 0.0001$); the interaction term is also significant ($F = 8.7009$; $P < 0.01$)

Food	Hatch A		Hatch B	
	Mean ± s.d.	*n*	Mean ± s.d.	*n*
−	1.81 ± 0.06	13	2.03 ± 0.09	8
+	2.04 ± 0.06	7	2.13 ± 0.03	6

later. Also, because these eggs might have been laid a few days before the collection of the crabs, the embryonic duration of 49 days, as well as our values of initial egg biomass (Table 2) represents minimum estimates. Egg size was on average 1.70 mm (measured in dropped eggs in a late developmental stage before hatching; female C).

Patterns of hatching

Larval hatching occurred throughout a period of 5–8 days, almost exclusively at night (194 *v.* 16 zoeae, or 92% night *v.* 8% day-time). The total number of zoeae produced per female varied greatly (140, 56, and 14 in hatches A, B and C). However, actual fecundity was higher, as five eggs per female had been removed on the day of crab collection, and several others were later lost during the period of embryonic development.

Patterns of larval and early juvenile development

The larval development of *S. meridies* comprised invariably two large (>1 mm) zoeal stages and a megalopa, all with conspicuous amounts of yolk remaining in the carapace region (Fig. 1). All larval stages as well as the early juveniles showed a bright red coloration, which became darker in later juveniles and adults. The latter were described as having 'a more or less homogeneous dark orange to rusty colour' (Schubart and Koller 2005). Behavioural observations showed that the zoeae never attempted to catch and ingest food (*Artemia* nauplii), and morphological inspections of the zoeal mouth parts indicated that these appendages were non-functional (for criteria, see McLaughlin *et al*. 2001). In conclusion, both zoeal stages were completely non-feeding (fully lecithotrophic), relying exclusively on internal yolk reserves. The megalopa, by contrast, responded to additions of food, capturing and ingesting prey. However, this stage also showed great amounts of remaining yolk (Fig. 1*c*), suggesting a reduced dependence on external food sources. The degree of its nutritional dependence or independence was therefore experimentally tested in treatments with or without food, comparing larvae from two females (A, B).

The duration of the zoeal stages was generally short, ranging between 2 and 3 days (Fig. 2; hatch C not included, because too few data were obtained from it). The megalopa stage lasted for another 7–9 days. Larval mortality was generally low (<5%), and the duration of development was in all stages (including the megalopa) independent of the presence or absence of food (Fig. 2). The female of origin, by contrast, did play a role: Hatch B showed consistently a slightly faster larval development than hatch A. However, this difference was not any longer apparent in the subsequent juvenile stages (Fig. 2). In both hatches, moult-cycle durations increased in successive juvenile instars, doubling from ~10–13 days in the crab I (fed treatments) to ~20–23 days in the crab V.

Although the duration of development through the megalopa stage was not affected by availability or lack of food, late effects became visible after metamorphosis. In hatch A, all crabs originating from unfed megalopae died soon after metamorphosis. In hatch B, juvenile mortality was not influenced by previous conditions of megalopal feeding or starvation, but the duration of the first crab instar showed a significant delay and an enhanced variability after megalopal development in the complete absence of food (17.8 ± 6.3 *v.* 10.6 ± 1.1 days). These effects, however, were no longer observed in instars II–V, so that their development data could be pooled for the two treatments (Fig. 2).

Besides survival and moult-cycle duration, also the body size of first-stage juveniles showed in both hatches significant effects of megalopal feeding or starvation (Table 5). Moreover, the female of origin (hatch) had a strong influence on early juvenile size, and these two factors showed a significant interaction. In crabs from hatch A obtained from fed megalopae, body size was not significantly different from that of hatch B crabs after megalopal starvation (2.04 ± 0.06 *v.* 2.03 ± 0.09 mm). Crabs obtained from fed megalopae of hatch B, by contrast, reached an average carapace width of 2.13 mm, while those from unfed megalopae of hatch A revealed only 1.81 mm (i.e. 15% smaller body size). These comparisons show a high degree of intraspecific variability in the size of early juveniles, depending on both the female of origin and the feeding conditions during the megalopa stage. The smallest crabs, however, were not viable and died soon after metamorphosis.

In conclusion, the megalopa stage was capable of food-independent development to metamorphosis (facultative lecithotrophy), but an absence of food had negative effects on juvenile fitness. Also, our data indicate a great deal of intraspecific variability in the degree of megalopal food-independence, ranging from a transitory developmental delay (hatch B) to complete mortality soon after metamorphosis (hatch A).

Changes of biomass and elemental composition during embryonic and larval development

Tables 2–4 summarise our data of changes in biomass (W, CHN per individual) and relative elemental composition (CHN in % of W; C : N and C : H ratios) during embryonic and larval development, in the megalopa stage also in relation to lack or availability of food. Hatches A and B provided comparative data for the late embryonic phase (final 11–13 days) and for complete larval development (Tables 3, 4). Additionally, changes in proximate biochemical composition (total lipids, proteins) are shown in Table 3 (hatch A only). Developmental and food-related changes in hatches A and B are illustrated in Fig. 4. In hatch C, the available materials allowed us to study only the embryonic phase (Table 2).

Embryonic development

Egg biomass varied greatly among females and in relation to the stage of embryonic development. W and CHN values in early

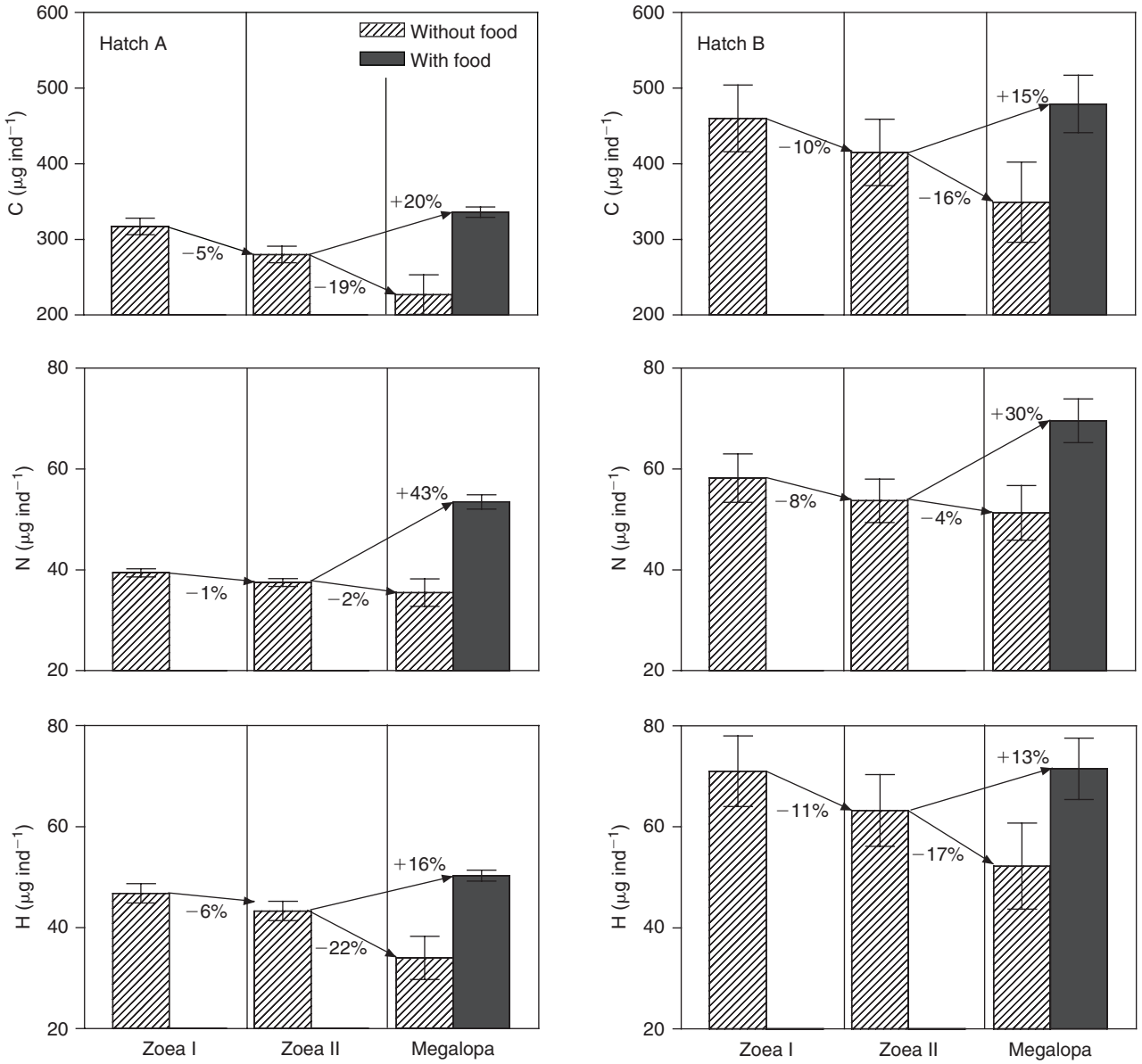


Fig. 4. *Sesarma meridies*, hatches A and B. Changes in carbon (C), nitrogen (N), and hydrogen (H), in μg ind^{-1} and as percentage values of change, during larval development from hatching to metamorphosis (zoeae non-feeding; megalopa reared with and without food).

embryos of female C (49 days before hatching; Table 2) were similar to those in female B, although the latter were in a much later stage of embryonic development (11 days before hatching; Table 4). Eggs from female A (13 days before hatching) had the lowest biomass (Table 3).

During the 49 days of embryonic development in hatch C, significant amounts of biomass were metabolised (Table 2). Losses were consistently greater in the fractions of C and H as compared with total W and N (16–17% *v.* 12–13% of initial egg biomass). As a consequence, the percentage C and H values as well as the C : N ratio decreased significantly (all $P < 0.01$), while the percentage values of N and the C : N ratio showed no significant changes (Table 2).

In late embryos from hatch A, the patterns of change in the elemental composition were similar as in hatch C (Table 3). In hatch B, by contrast, significant losses occurred only in the absolute amounts of biomass but not in the relative composition (Table 4), indicating approximately equal rates of degradation in the major biochemical constituents.

Larval biomass and chemical composition at hatching

The initial larval biomass varied greatly among the three females. Corresponding to the patterns of variation in egg biomass, larval W and CHN were generally highest in hatch B, lowest in hatch A, and intermediate in hatch C. The relative elemental composition varied much less among the three hatches (Tables 2–4).

In hatch A, we took two samples of freshly hatched larvae to check if the time within the extended hatching period (about 1 week) had an influence on biomass at hatching. Comparison of values measured on the first and the fifth day of the hatching period (Table 3; Zoea I, day 0^A *v.* 0^B) showed consistently lower values per larva on day 5 (although statistically not significant; $P > 0.05$). The fractions of N and H (% of W) increased significantly (t-tests: $P = 0.01$ and $P < 0.001$ respectively), while the percentage of C remained stable. As a consequence, the C : N and C : H mass ratios decreased significantly between day 1 and day 5 of the hatching period ($P < 0.01$ and $P < 0.0001$). As most larvae hatched on day 5, these data (0^B in Table 3) were used for all further comparisons of developmental changes in biomass and chemical composition.

Zoeal development

During the non-feeding development from hatching to the end of the zoeal phase, significant amounts of biomass were metabolised (Tables 3, 4; Fig. 4). Similar to the patterns found during embryonic development, the losses were consistently higher in the fractions of C and H *v.* total W and N. They differed also between hatches, being smaller in A than in B. The larvae from hatch A, which showed the lowest biomass at hatching, lost only 5–6% of their initially available C and H, and only insignificant amounts of N (1%). By comparison, the zoeae from hatch B (highest biomass at hatching) lost 10–11% of their initial C and H, and 8% of N (Fig. 4).

As a consequence of the patterns of loss in CHN per larva, the composition of biomass changed also proportionally. C and H (in % of W) as well as the C : N mass ratio decreased substantially, while the percentage of N and the C : H ratio changed only a little (Tables 3, 4). These patterns, in particular the decreasing C : N ratio, indicated a preferential use of lipid reserves, while the protein fraction appeared to remain stable. This indirect evidence from CHN data was confirmed by biochemical determinations in hatch A (Table 3). The lipid content decreased from hatching to the end of the zoeal phase by 27% (as a percentage of W, from 20 to 15%). The protein content, by comparison, decreased only insignificantly (from 34 to 33% of W). As a consequence, the lipid : protein ratio declined within only 5 days from 0.59 at hatching to 0.45 at the end of the zoea-II stage.

Megalopal development

Similar to the embryos and non-feeding zoeae, unfed megalopae showed a preferential use of C and H *v.* W and N, or of lipids *v.* proteins (Tables 3, 4; Fig. 4). Compared with the biomass at the end of the zoeal phase, megalopae lost 16–22% of C and H, but only 2–4% of N (Fig. 4). This caused similar changes in the relative chemical composition of biomass as in the embryonic and zoeal stages (Tables 3, 4): while the lipid fraction decreased by 39%, the protein content was reduced by only 8%, so that the lipid : protein ratio decreased from 0.45 to 0.30.

When the complete period of larval development from hatching to metamorphosis (~2 weeks) occurred in permanent absence of food, the larvae from the two hatches lost 6–12% of W and N, 23–26% of C and H, 12% of protein, and 55% of the lipid content present at hatching (Tables 3, 4). Interestingly, the losses measured during the short zoeal phase (~5 days) were slightly higher than those during the megalopa stage (7–9 days).

In treatments where megalopae were fed, biomass increased substantially (Fig. 4; both hatches and all measures of biomass, $P < 0.002$). This gain was proportionally more than twice as high in W and N than in the C and H fractions (Fig. 4). When metamorphosis was approached, fed megalopae showed higher W and N contents than at hatching (Tables 3, 4). The gains in C and H were much weaker, but they sufficed to compensate preceding losses in these fractions, reaching similar values as on the day of hatching (Fig. 4).

As a result of these patterns, the C : N ratio decreased in fed megalopae, similar to in unfed treatments (Tables 3, 4). However, the underlying causes were quite different: continued starvation caused a preferential degradation of internally stored lipids, with little change in the protein fraction. In fed megalopae, by contrast, food was preferentially used for the synthesis and accumulation of proteins rather than for a replenishment of previously lost lipids. This is consistently indicated by changes in both the C : N quotient and biochemical composition. While the lipid content of fed megalopae remained constant from the end of the zoea II to metamorphosis, the protein fraction increased concomitantly by 40% (Table 3). This lead to the surprising result that the lipid : protein ratio decreased in both fed and starved megalopae to identical final values of 0.3.

Exuvial biomass losses during larval development

As a result of low biomass of larval exuviae, we obtained only two to three replicate samples per stage, although we pooled materials from two females and two treatments. Thus, our data (Table 6) show variation among larval stages, but not among hatches or feeding conditions.

All percentage CHN values within exuvial W decreased significantly in successive stages (Table 6), indicating an ontogenetic change in the composition of the exoskeleton. The C fraction, for instance, decreased from 45% in the zoea I to 22% in the megalopa, and the sum of CHN, which is a proxy of total organic matter, decreased from 61% to 28%. This indicates an increasing proportion of inorganic matter within total exuvial W. Increasing C : N and C : H ratios suggest that there are also ontogenetic changes in the biochemical composition of the organic matter lost with larval exuviae.

When losses of exuvial biomass (per individual) are compared between successive stages, a clear ontogenetic increase can be seen (Table 6). Ecdysial losses expressed as a percentage of larval premoult biomass were highest in W (1–3% in the zoeal stages, 10–15% in the megalopa), while losses of CHN amounted to only 1–2% in each of the zoeal stages and to ~3–7% in the megalopa (Table 6).

Discussion

Ecology and reproduction

Sesarma meridies is the only known endemic sesarmid crab species that occurs in rivers draining to the south of the island of Jamaica (Schubart and Koller 2005). This suggests an early evolutionary separation from the congeners *S. windsor*, *S. fossarum*, *S. dolphinum*, *S. bidentatum*, and *S. ayatum*, which live exclusively in the northern drainage system. Three of these ‘stream

Table 6. *Sesarma meridies*, hatch A

Dry mass (W) and elemental composition (carbon (C), nitrogen (N), hydrogen (H) in μg ind^{-1} and in % of W), C : N and C : H mass ratios of larval exuviae; biomass losses in each stage (in % of larval premoult biomass); megalopa: losses related to larvae reared without (−) or with food (+)

Variable	Stage						
	Zoea I	Loss (%)	Zoea II	Loss (%)	Megalopa	(−) Loss (%)	(+) Loss (%)
W (μg ind^{-1})	6.07 ± 0.01	1.2	17.7 ± 2.00	3.5	70.5 ± 3.40	14.8	10.3
C (μg ind^{-1})	2.74 ± 0.00	0.9	4.85 ± 0.41	1.7	15.8 ± 1.10	7.0	4.7
N (μg ind^{-1})	0.60 ± 0.00	1.6	0.89 ± 0.07	2.4	2.5 ± 0.20	7.1	4.7
H (μg ind^{-1})	0.35 ± 0.01	0.8	0.55 ± 0.05	1.3	1.7 ± 0.10	5.0	3.4
C (%W)	45.1 ± 0.00		27.5 ± 0.70		22.5 ± 0.50		
N (%W)	9.9 ± 0.00		5.1 ± 0.20		3.6 ± 0.10		
H (%W)	5.7 ± 0.00		3.1 ± 0.10		2.4 ± 0.10		
$\sum$ CHN (%W)	60.70		35.70		28.40		
C : N ratio	4.58 ± 0.00		5.43 ± 0.03		6.25 ± 0.03		
C : H ratio	7.93 ± 0.06		8.87 ± 0.01		9.37 ± 0.02		

ecotypes' (in contrast to terrestrial and cavernicolous ecotypes: Schubart and Koller 2005) construct burrows in river banks, namely *S. fossarum*, *S. dolphinum* and *S. bidentatum*; the remaining species do not show this behaviour. If burrows are used not only as a shelter for adult crabs but also as breeding habitats (Anger 2005), this raises the question of where the larvae of *S. meridies* and other non-burrowing species develop.

Our observations show that *S. meridies* prefers shady semiterrestrial microhabitats under vegetation on river banks, where it hides under boulders. These habitats are cooler, reveal lower pH values, and higher total ion concentrations compared with the water in the stream proper, where no crabs could be found. Ovigerous females were exclusively observed near shallow and stagnant puddles under dense vegetation. It is therefore likely that also the larvae develop in such small isolated water bodies on the river banks. In the rapidly flowing water of the stream proper, the larvae would rapidly be flushed out of the habitat. Moreover, the stream, as well as larger pools connected to it, is inhabited by numerous small fish, which may prey on crab larvae. Hence, the choice of ephemeral puddles on river banks as a breeding habitat should protect the larvae from both irreversible advection and pelagic predation. In addition, buffered pH and enhanced ion concentrations may represent more favourable chemical conditions for larval development, as already shown for another endemic Jamaican crab, the bromeliad crab *Metopaulias depressus* (Anger and Schuh 1992; Diesel and Schuh 1993; Diesel 1997).

Breeding in isolated microhabitats such as puddles or burrows may greatly reduce larval mortality in limnic and terrrestrial sesarmids, allowing for a dramatic reduction of fecundity. On the other hand, this reproductive strategy imposes narrow limits on larval dispersal, restricting the genetic exchange among populations, and hence, favouring speciation (Palumbi 1994; Havenhand 1995).

Egg size, duration of embryonic development, hatching pattern

As in all other endemic Jamaican sesarmid crabs, for which data of egg size have become available, *S. meridies* produces few large eggs with diameters well above 1 mm (cf. Hartnoll 1964; Reimer *et al*. 1998; Diesel *et al*. 2000; Anger 2005; Anger and Schubart 2005). This is several times larger than the egg size commonly known from estuarine and coastal marine species of grapsoid crabs, and it is typically associated with an abbreviated and at least partially food-independent mode of larval development (Rabalais and Gore 1985; Anger 1995, 2001). This reproductive trait is generally considered as an adaptation to conditions with low or unpredictable production of planktonic food.

As far as this is known, the larvae of the endemic Jamaican sesarmids hatch in a morphologically advanced stage of development (Hartnoll 1964; Anger *et al*. 1995). This may explain the prolonged duration of the embryonic phase (at least 7 weeks). By comparison, tropical sesarmids with a coastal lifestyle (including *Sesarma curacaoense* and *Armases* spp. from Jamaica) require at similar temperatures only ∼2–3 weeks (Seiple and Salmon 1987; K. Anger, unpubl. data). An extended embryonic period (at least 6 weeks) was observed also in another tropical sesarmid with large eggs and an abbreviated mode of larval development, *Geosesarma perracae* (Soh 1969). This reproductive trait is most probably a prerequisite for hatching in a developmentally advanced state, implying an extension of the period of maternal brood care and a shortening of the vulnerable free-living larval phase.

As another peculiar trait, *S. meridies* exhibits an extended period of hatching from the same egg clutch (throughout ∼1 week), with highly variable numbers of larvae released per day. As later hatching larvae pass through a longer period of embryonic development, they also use larger amounts of egg biomass, hatching with slightly reduced biomass than earlier hatching siblings (Table 3). Although this effect was weak, it may have contributed to intraspecific variability in initial larval biomass.

Extended hatching patterns have been observed not only in other endemic Jamaican sesarmids (*S. windsor*, *S. fossarum*: Anger 2005; Anger and Schubart 2005), but also in various further Decapoda with large eggs and an abbreviated larval development, for example, lithodid crabs and campylonotid shrimps (Thatje *et al*. 2003, 2004). In marine species, such patterns were interpreted as an adaptive trait that may reduce pelagic predation on unusually large and visible larvae drifting in the

water column. In Jamaican stream crabs, successive hatching may reduce intraspecific predation between cohorts of juveniles, as well as cannibalism and competition for food and space among siblings. In the terrestrial bromeliad crab, *Metopaulias depressus*, by contrast, the larvae hatch within one or two nights (Anger and Schuh 1992; Anger and Schubart 2005). This may be explained by female brood-care behaviour occurring in this species, including the introduction of food items into the breeding habitat (Diesel 1997).

Although the stream crabs *S. meridies*, *S. windsor* and *S. fossarum* are similar in their extended periods of larval hatching (1–2 weeks: Anger 2005; Anger and Schubart 2005), they differ greatly in their day-night patterns. While larvae of *S. meridies* hatch almost exclusively at night, no preference for daytime or night-time has been observed in the other two species. This striking difference appears plausible when *S. meridies* and *S. fossarum* are compared. The latter species presumably breeds in narrow and dark burrows dug in river banks, where predation by visually oriented predators is unlikely to occur. Open puddles on river banks, by contrast, may expose the larvae of *S. meridies* to a higher predation risk. In *S. windsor*, the breeding habitat is unknown. This species occurs in and near limestone caves and subterranean streams (Schubart *et al*. 1997), suggesting that its larval development could take place in cryptic water-filled karst habitats. Comparable to burrowing species, darkness and lack of visually oriented predators in the breeding habitat may thus not have selected for a pronounced hatching rhythm avoiding daylight.

Patterns of larval and early juvenile development

Consistent with previous findings in other Jamaican sesarmid crab species (Hartnoll 1964; Anger and Schuh 1992; Diesel *et al*. 2000; Anger 2005; Anger and Schubart 2005), the larval development of *S. meridies* is abbreviated and partially independent of food, comprising two non-feeding zoeal stages and a facultatively lecithotrophic megalopa. This developmental sequence may thus be a common ancestral trait of the entire clade (Hartnoll 1964; Anger *et al*. 1995). However, the life cycle has not yet been studied in two of the terrestrial species (*S. jarvisi*, *S. cookei*), in the cavernicolous crab *S. verleyi*, and in the stream crab *S. ayatum*. While it is likely that all riverine species show identical patterns, it cannot be ruled out that other developmental modes could have evolved in some of the other species, for example, a further reduction of the larval phase towards a direct development as in freshwater-dwelling hymonosomatid crabs (Johnston and Robson 2005).

Similar developmental patterns as in the endemic Jamaican sesarmids may occur also in limnic and terrestrial relatives that have radiated in South-east Asia (see Sèrene and Soh 1970). This is suggested by large egg size (e.g. Soh 1969; Ng and Lim 1987) and brood-care behaviour (Ng and Tan 1995). For one of these species, *Geosesarma peraccae*, Soh (1969) also described a sequence of two zoeal stages and a megalopa, with successful development from hatching to metamorphosis in the complete absence of food. However, the degree of lecithotrophy (facultative *v.* obligatory) has remained unknown. Comparative investigations of reproductive and developmental strategies in the Jamaican and South-east Asian sesarmid clades may show similarities, indicating similar selection pressures in limnic and terrestrial invasions.

In addition to independence from planktonic food sources, the larval stages of freshwater-breeding crabs must also reveal an early appearance of osmoregulatory structures and functions (Charmantier 1998; Cieluch *et al*. 2007). While these adaptive traits have been investigated in some of the endemic Jamaican stream crabs (Schubart and Diesel 1999), no such studies have become available for their early life-history stages. Future investigations of the ontogeny of osmoregulation will enhance our understanding of evolutionary transitions from the sea to freshwater and land.

The patterns of early juvenile growth in *S. meridies*, with gradually increasing durations of successive instars, are similar to those in marine crabs (e.g. Hartnoll 1985, 2001). In Jamaican stream crabs, early juvenile fitness is also under a strong influence of previous feeding conditions and the female of origin. Food limitation during the megalopa stage causes enhanced post-metamorphic mortality, delayed development, and reduced body size of young crabs, which may affect also the subsequent development to maturity. Phenotypic plasticity in late larval and early juvenile bioenergetics make the endemic Jamaican sesarmid crabs suitable models for studies of carry-over effects (or 'trait-mediated effects': Giménez 2004), which persist through successive phases of complex life cycles (see Giménez *et al*. 2004).

Developmental changes in larval biomass, chemical composition, and exuvial loss

Our elemental and biochemical data showed that the embryos and non-feeding zoeal stages of *S. meridies* used predominantly lipid stores from remaining egg yolk as an energy source, while proteins were conserved as structural components. The same pattern was observed also in megalopae kept in continued absence of food. During completely endotrophic development from hatching to metamorphosis, the larvae lost up to 55% of their initial lipid stores, while only 12% of the initial protein content was degraded. Future biochemical investigations should elucidate if particular lipid classes or fatty acids are preferentially mobilised for the production of chemical energy, and which are conserved as indispensable components of cells and tissues. Such comparative information will help to distinguish homologous (ancestral) from ubiquitous patterns that are found also in other clades with lecithotrophic larvae.

Interestingly, fed megalopae maintained a low lipid concentration, while their protein content increased substantially. Similar patterns had been observed also in other species from the same clade (Anger 2005; Anger and Schubart 2005), suggesting that the megalopae use nutritional energy primarily for the synthesis of proteinaceous structural components of newly developing tissues and organs rather than for replacing preciously lost lipid reserves.

Besides through metabolic processes, energy losses occur also in ecdyses. Our CHN data indicate that successive larval stages produce increasingly mineralised exuviae. When exuvial losses are compared with larval biomass before ecdysis, we can see that the zoeal stages of *S. meridies* lose only 1–2% of their organic matter with the cast exoskeleton. The production

of extremely thin exuviae may thus represent an energy-saving (i.e. adaptive) trait, as in other decapod species with non-feeding larvae (Lovrich *et al*. 2003; Thatje *et al*. 2004). Losses in the megalopa stage were much higher (3–7% of premoult CHN), but still low compared with those commonly observed in planktotrophic marine decapod larvae (for review, see Anger 2001). As the megalopa stage is able to capture and ingest prey, showing benthic behaviour, it may eat small benthic food items including detritus particles (cf. Anger and Schuh 1992; Anger 2005; Anger and Schubart 2005). Hence, this stage depends less on internal energy reserves, so that it can afford to produce a thicker cuticle, which may protect it against small benthic predators.

Our study has shown a considerable degree of intraspecific variability in the biomass at hatching, which coincided with variability in egg biomass. When hatches A and B are compared, one can see that larger egg size in hatch B translated to larger zoeal biomass at hatching, reduced dependence on food in the megalopa, and eventually, enhanced survival and larger body size in the first crab stage. Our data indicate that larvae equipped with smaller amounts of lipids can partially compensate for their weak energy reserves by reducing the rate of catabolism (cf. hatches A *v.* B; Fig. 4).

Although egg size might be influenced by the nutritional condition of the female, this reproductive trait may also have a genetic basis. Food limitation in the breeding habitat should then select for an enhanced energy investment per offspring, large egg size, and an increasing degree of larval lecithotrophy. This mechanism may have been one of the driving forces in the radiations of sesarmids both on Jamaica and in South-east Asia.

Concluding remarks

The patterns of larval development in *S. meridies* show great similarity with those in other endemic Jamaican sesarmids living in freshwater or terrestrial habitats. Large egg size associated with great lipid reserves from egg yolk, non-feeding zoeal development, and a facultatively lecithtrophic megalopa stage appear to belong to the common traits of this clade, probably originating from the common ancestor. However, similar reproductive and developmental traits have evolved independently in another sesarmid clade that has radiated in South-east Asia. This suggests that evolutionary invasions of limnic and terrestrial environments are associated with similar selection pressures. Planktonic food limitation in breeding habitats may favour similar evolutionary pathways towards an abbreviated larval phase, enhanced female energy investments per offspring, and possibly, female brood care.

In contrast to the mode of larval development, the patterns of hatching show divergent evolution. In *Metopaulias depressus*, hatching occurs within 1–2 days, as in most coastal marine species, while larvae of *Sesarma* spp. hatch through extended periods of 1–2 weeks. Among the latter, also the day-night rhythm varies, suggesting differential selection pressures by visually oriented predators. This reproductive trait may thus have evolved more recently, depending on ecological niche differentiation and interspecific interactions.

The patterns of energy storage and use appear to be similar among endemic Jamaican sesarmids. However, different mechanisms (see Dalsgaard *et al*. 2003) might also occur within or between the clades on Jamaica and in South-east Asia. Further comparative life-history studies of non-marine crabs, preferably those combining laboratory and field observations, will enhance our general understanding of evolutionary processes associated with limnic and terrestrial invasions.

Acknowledgements

We are grateful to Michelina, Tanja, and three Jamaicans for help in the collection of crabs, to Karin Bickmeyer for CHN analyses, the AWI for travelling funds, and the Director and staff of the DBML for hospitality during visits to Jamaica. GT acknowledges a PhD grant from Deutscher Akademischer Austauschdienst (DAAD, Bonn, Germany).

References

Adamczewska, A. M., and Morris, S. (2000). Locomotion, respiratory physiology, and energetics of amphibious and terrestrial crabs. *Physiological and Biochemical Zoology* **73**, 706–725. doi:10.1086/318099

Anger, K. (1995). The conquest of freshwater and land by marine crabs: adaptations in life-history patterns and larval bioenergetics. *Journal of Experimental Marine Biology and Ecology* **193**, 119–145. doi:10.1016/0022-0981(95)00114-X

Anger, K. (2001). 'The Biology of Decapod Crustacean Larvae.' Crustacean Issues 14. (Balkema: Lisse.)

Anger, K. (2005). The early life history of *Sesarma fossarum*, an endemic freshwater crab from Jamaica. *Invertebrate Reproduction & Development* **47**, 63–72.

Anger, K., and Schubart, C. D. (2005). Experimental evidence of food-independent larval development in endemic Jamaican freshwater-breeding crabs. *Physiological and Biochemical Zoology* **78**, 246–258. doi:10.1086/427051

Anger, K., and Schuh, M. (1992). Bioenergetics of abbreviated larval development in the bromelid crab, *Metopaulias depressus* (Decapoda: Grapsidae). *Comparative Biochemistry and Physiology* **103A**, 507–518.

Anger, K., Schreiber, D., and Montú, M. (1995). Abbreviated larval development of *Sesarma curacaoense* (Rathbun, 1897) (Decapoda: Grapsidae) reared in the laboratory. *Nauplius* **3**, 127–154.

Charmantier, G. (1998). Ontogeny of osmoregulation in crustaceans: a review. *Invertebrate Reproduction & Development* **33**, 177–190.

Cieluch, U., Anger, K., Charmantier-Daures, M., and Charmantier, G. (2007). Osmoregulation and immunolocalization of Na^+/K^+-ATPase during the ontogeny of the mitten crab *Eriocheir sinensis* (Decapoda, Grapsoidea). *Marine Ecology Progress Series* **329**, 169–178.

Dalsgaard, J., St. John, M., Kattner, G., Muller-Navarra, D., and Hagen, W. (2003). Fatty acid trophic markers in the pelagic marine environment. *Advances in Marine Biology* **46**, 225–340.

Diesel, R. (1997). Maternal control of calcium concentration in the larval nursery of the Bromeliad Crab, *Metopaulias depressus* (Grapsidae). *Proceedings of the Royal Society of London. Series B. Biological Sciences* **264**, 1403–1406. doi:10.1098/RSPB.1997.0195

Diesel, R., and Schuh, M. (1993). Maternal care in the bromeliad crab *Metopaulias depressus* (Decapoda): maintaining oxygen, pH and calcium levels optimal for the larvae. *Behavioral Ecology and Sociobiology* **32**, 11–15. doi:10.1007/BF00172218

Diesel, R., Schubart, C. D., and Schuh, M. (2000). A reconstruction of the invasion of land by Jamaican crabs (Grapsidae: Sesarminae). *Journal of Zoology* **250**, 141–160. doi:10.1111/J.1469-7998.2000.TB01066.X

Gilbert, S. F. (2001). Ecological developmental biology: developmental biology meets the real world. *Developmental Biology* **233**, 1–12. doi:10.1006/DBIO.2001.0210

Giménez, L. (2004). Marine community ecology: importance of trait-mediated effects propagating through complex life cycles. *Marine Ecology Progress Series* **283**, 303–310.

Giménez, L., Anger, K., and Torres, G. (2004). Linking life history traits in successive phases of a complex life cyle: effects of larval biomass on early juvenile development in an estuarine crab, *Chasmagnathus granulata. Oikos* **104**, 570–580. doi:10.1111/J.0030-1299.2004.12957.X

Graham, A. (2003). Geohistory models and Cenozoic paleoenvironments of the Caribbean region. *Systematic Botany* **28**, 378–386.

Greenaway, P. (1999). Physiological diversity and the colonization of land. In 'Crustaceans and the Biodiversity Crisis'. (Eds F. R. Schram and J. C. von Vaupel Klein.) pp. 823–842. (Brill: Leiden.)

Hartnoll, R. G. (1964). The freshwater grapsid crabs of Jamaica. *Proceedings of the Linnean Society of London* **175**, 145–169.

Hartnoll, R. G., (1985). Growth, sexual maturity and reproductive output. In 'Factors in Adult Growth'. Crustacean Issues 3. (Ed. A. M. Wenner.) pp. 101–128. (Balkema: Rotterdam.)

Hartnoll, R. G. (2001). Growth in Crustacea – twenty years on. *Hydrobiologia* **449**, 111–122. doi:10.1023/A:1017597104367

Harvey, P. H., and Pagel, M. D. (1991). 'The Comparative Method in Evolutionary Biology.' (Oxford University Press: Oxford.)

Havenhand, J. N. (1995). Evolutionary ecology of larval types. In 'Ecology of Marine Invertebrate Larvae'. (Ed. L. R. McEdward.) pp. 79–122. (CRC Press: Boca Raton.)

Holdich, D. M. (2001). 'Biology of Freshwater Crayfish.' (Blackwell: Oxford.)

Hossfeld, U., and Olsson, L. (2003). The road from Haeckel: The Jena tradition in evolutionary morphology and the origins of "Evo-Devo". *Biology and Philosophy* **18**, 285–307. doi:10.1023/A:1023988119440

Johnston, K., and Robson, B. J. (2005). Habitat use by the hymenosomatid crab *Amarinus lacustris* (Chilton) in two south-eastern Australian rivers. *Marine and Freshwater Research* **56**, 37–44. doi:10.1071/MF04219

Lovrich, G. A., Thatje, S., Calcagno, J. A., Anger, K., and Kaffenberger, A. (2003). Changes in biomass and chemical composition during lecithotrophic larval development of the southern king crab, *Lithodes santolla* (Molina). *Journal of Experimental Marine Biology and Ecology* **288**, 65–79. doi:10.1016/S0022-0981(02)00596-8

Lowry, D. H., Rosenberg, N. J., Farr, A. L., and Randall, R. J. (1951). Protein measurement with the folin phenol reagent. *The Journal of Biological Chemistry* **193**, 265–275.

McLaughlin, P. A., Anger, K., Kaffenberger, A., and Lovrich, G. A. (2001). Megalopal and early juvenile development in *Lithodes santolla* (Molina, 1782) (Decapoda: Anomura; Paguroidea: Lithodidae), with notes on zoeal variations. *Invertebrate Reproduction & Development* **40**, 53–67.

Ng, P. K. L., and Lim, R. P. (1987). The taxonomy and biology of the nepenthiphilous sesarmine freshwater crab, *Geosesarma malayanum* Ng and Lim, 1986 (Crustacea, Decapoda, Brachyura, Grapsidae) from Peninsular Malaysia. *Malayan Nature Journal* **41**, 393–402.

Ng, P. K. L., and Tan, C. G. S. (1995). *Geosesarma notophorum* sp. nov (Decapoda, Brachyura, Grapsidae, Sesarminae), a terrestrial crab from Sumatra, with novel brooding behavior. *Crustaceana* **68**, 390–395.

Palumbi, S. R. (1994). Genetic divergence, reproductive isolation, and marine speciation. *Annual Review of Ecology and Systematics* **25**, 547–572. doi:10.1146/ANNUREV.ES.25.110194.002555

Piersma, T., and Drent, J. (2003). Phenotypic flexibility and the evolution of organismal design. *Trends in Ecology & Evolution* **18**, 228–233. doi:10.1016/S0169-5347(03)00036-3

Rabalais, N. N., and Gore, R. H. (1985). Abbreviated development in Decapods. In 'Larval Growth'. Crustacean Issues 2. (Ed. A. M. Wenner.) pp. 67–126. (Balkema: Rotterdam.)

Reimer, J., Schubart, C. D., and Diesel, R. (1998). Description of a new freshwater crab of the genus *Sesarma* Say, 1817 (Brachyura, Grapsidae, Sesarminae) from Western Jamaica. *Crustaceana* **71**, 185–196.

Scholtz, G. (2003). 'Evolutionary Developmental Biology of Crustacea.' Crustacean Issues 15. (Balkema: Leiden.)

Schubart, C. D., and Diesel, R. (1999). Osmoregulation and the transition from marine to freshwater and terrestrial life: a comparative study of Jamaican crabs of the genus *Sesarma. Archiv fuer Hydrobiologie* **145**, 331–347.

Schubart, C. D., and Koller, P. (2005). Genetic diversity of freshwater crabs (Brachyura: Sesarmidae) from central Jamaica with description of a new species. *Journal of Natural History* **39**, 469–481. doi:10.1080/00222930410001671291

Schubart, C. D., Reimer, J., Diesel, R., and Türkay, M. (1997). Taxonomy and ecology of two endemic freshwater crabs from western Jamaica with the description of a new *Sesarma* species (Brachyura: Grapsidae: Sesarminae). *Journal of Natural History* **31**, 403–419. doi:10.1080/00222939700770201

Schubart, C. D., Diesel, R., and Hedges, S. B. (1998). Rapid evolution to terrestrial life in Jamaican crabs. *Nature* **393**, 363–365. doi:10.1038/30724

Seiple, W., and Salmon, M. (1987). Reproductive, growth and life-history contrasts between two species of grapsid crabs, *Sesarma cinereum* and *S. reticulatum. Marine Biology* **94**, 1–6. doi:10.1007/BF00392892

Sèrene, R., and Soh, C. L. (1970). New Indo-Pacific genera allied to *Sesarma* Say 1817 (Brachyura, Decapoda, Crustacea). *Treubia* **27**, 387–416.

Soh, L. C. (1969). Abbreviated development of non-marine crab, *Sesarma* (*Geosesarma*) *perracae* (Brachyura; Grapsidae), from Singapore. *Journal of Zoology* **158**, 357–370.

Sokal, R. R., and Rohlf, F. J. (1995). 'Biometry. The Principles and Practice of Statistics in Biological Research.' (Freeman: San Francisco.)

Thatje, S., Calcagno, J. A., Lovrich, G. A., Sartoris, F. J., and Anger, K. (2003). Extended hatching periods in the subantarctic lithodid crabs *Lithodes santolla* and *Paralomis granulosa* (Crustacea: Decapoda: Lithodidae). *Helgoland Marine Research* **57**, 110–113. doi:10.1007/S10152-003-0145-3

Thatje, S., Lovrich, G. A., and Anger, K. (2004). Egg production, hatching rates, and abbreviated larval development of *Campylonotus vagans* Bate, 1888 (Crustacea: Decapoda: Caridea), in subantarctic waters. *Journal of Experimental Marine Biology and Ecology* **301**, 15–27. doi:10.1016/J.JEMBE.2003.09.010

Torres, G., Charmantier-Daures, M., Chifflet, S., and Anger, K. (2007*a*). Effects of long-term exposure to different salinities on the location and activity of Na^+–K^+-ATPase in the gills of juvenile mitten crab, *Eriocheir sinensis. Comparative Biochemistry and Physiology. A: Comparative Physiology* **147**, 460–465. doi:10.1016/J.CBPA.2007.01.020

Torres, G., Giménez, L., and Anger, K. (2007*b*). Effects of osmotic stress on crustacean larval growth and protein and lipid levels are related to life-histories: the genus *Armases* as a model. *Comparative Biochemistry and Physiology. B: Biochemistry and Molecular Biology* **148**, 117–224. doi:10.1016/J.CBPB.2007.05.011

Zöllner, N., and Kirsch, K. (1962). Über die quantitative Bestimmung von Lipoiden (Mikromethode) mittels der vielen natürlichen Lipoiden (allen bekannten Plasmalipoiden) gemeinsamen Sulfophosphovanillin-Reaktion. *Zeitschrift fur die Gesamte Experimentelle Medizin Einschliesslich Experimentelle Chirurgie* **135**, 545–561. doi:10.1007/BF02045455

Manuscript received 25 September 2006, accepted 4 July 2007