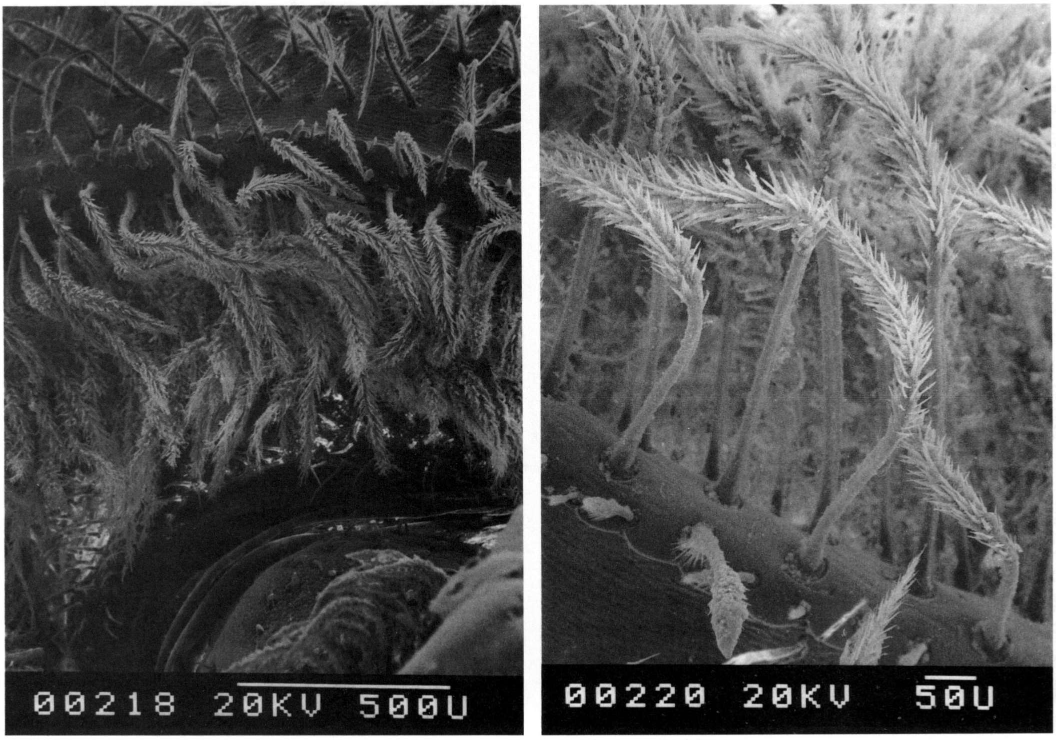

Fig. 16. *Sesarma jarvisi.* Scanning electron micrographs of plumose setae between the lower ridge of branchiostegite and the dorsal coxae.

were found from March to August (Table 4).

If the development of these juveniles took about 1–2 months, they must have hatched from January to March, that is, before the spring rainy season.

We collected a sample of 93 brood-shells in March and April 1991, containing juveniles with CW ranging from 1.3–8.5 mm (see Table 5), and representing all juvenile age classes. The calculated development period, using the CW of these juveniles (see Materials and Methods; Fig. 11) suggests a minor reproductive activity in early spring followed by a higher peak of breeding activity in late summer (Fig. 17).

Table 4. Number of ovigerous females, brood-shells with megalopae, and shells with juveniles <3-mm CW found in Windsor, Jamaica, from March–December 1991. The search activities for shells differed within months, and brood-shells were only occasionally searched for in August and December. n = no observations.

	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec*
Ovigerous females	1	2	0	0	1	0	n	n	n	1
Megalopae	0	2	0	0	1	0	n	n	n	0
Juveniles	6	4	3	2	5	1	n	n	n	0

* R. Diesel, unpublished observations.

Discussion

Sesarma jarvisi has adopted an extraordinary breeding behavior in an adverse environment, the dry karst hills of central Jamaica. After the bromeliad crab *Metopaulias depressus,* it is the second species of Jamaican endemic Sesarminae for which the breeding behavior is known. So far, these two species are the only land-breeding brachyuran crabs for which a detailed account of the breeding behavior and juvenile development in the field is available. Al-

Table 5. Number of juveniles of different size classes found in brood-shells in Windsor, Jamaica, 1991 (mean CW in mm).

	1.3–2	2–3	3–4	4–5	5–6	6–7	7–8.5	*N*
March	1	6	1	2	7	12	4	33
April	2	3	0	3	10	31	11	60

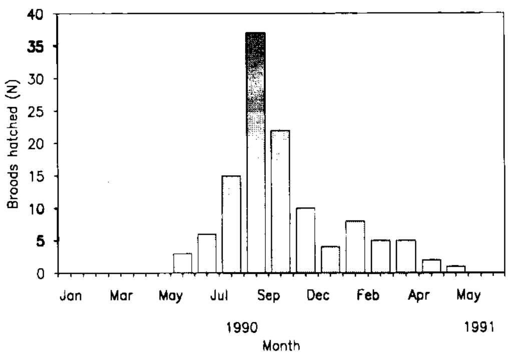

Fig. 17. Distribution of *Sesarma jarvisi* hatching dates calculated from the average juvenile size from broods found in March and April 1991.

though some information on breeding is reported for other terrestrial or fresh-water crabs (e.g., *Parathelphusa*, see Fernando, 1960; reviewed by Rabalais and Gore, 1985; Burggren and McMahon, 1988), no specific information on their early development and parental behavior under field conditions is available.

The behavior of *S. jarvisi* shows several interesting features. First, this species uses shells of land snails for larval and juvenile development. Second, females manipulate the microhabitat in the shells before releasing their larvae, by carrying water into the shells. Third, data on family composition show that the mother crab and the juveniles remain together in the shell for at least 3 months. The food items found in the broodshells, in particular the remains of millepedes, suggest that the mother crabs also feed their young.

Habitat and Distribution

The distribution of *S. jarvisi* is closely tied to areas with high precipitation (>2,000 mm annually) and wet limestone forests in western Jamaica. In pre-Columbian times, dense forests covered almost the entire island (Asprey and Robbins, 1953), and the crabs probably had a wider distribution. After the colonization of Jamaica by man and the subsequent deforestation, in many areas only isolated islands of wet limestone forest remained (e.g., Mount Diablo and Dolphin Head; Morrissey, 1983), leading to a partly disjunct distribution of the species today. The metamorphic Blue Mountains run from north to south, forming a zoogeographic barrier by dividing Jamaica's limestone layer into a small eastern plate (John Crow Mountains) and a large western plate. *Sesarma jarvisi* is restricted to the western part, where it occurs from 100-m altitude at Windsor up to 930-m at Mount Diablo, at lower altitudes than originally recorded by Abele and Means (300 m; 1977). The wet limestone forests in the east are inhabited by the same ecomorph, *Sesarma cookei* Hartnoll, a species that is larger (CW > 20 mm) than *S. jarvisi* but lives in a similar habitat (Abele and Means, 1977; R. Diesel and D. Horst, unpublished data).

Sesarma jarvisi is most common on shaded slopes and in moist valleys and is less abundant in karst depressions (cockpits) or on top of karst hills. The depressions consist mainly of eroded bauxite soil. They receive more precipitation than hill tops (Aub, 1969a), are frequently flooded (Aub, 1969b), and lack a crevice system. Therefore, these "cockpits" are unlikely to support populations of *S. jarvisi*. The hill tops are prone to desiccation by radiation, and their crevice systems may be too dry for the crabs.

The crevice system inhabited by *S. jarvisi* provides a relatively constant microclimate, with less extreme temperatures and a constant high humidity, compared to the forest floor. These microclimate conditions resemble those that prevail in the self-dug burrows of other terrestrial crustaceans, e.g., *Hemilepistus reaumuri* Audouin and Savigny (see Edney, 1958); *Uca panacea* Novak and Salmon (see Powers and Cole, 1976); *Holthuisana transversa* Martens (see Greenaway and MacMillen, 1978).

An extended crevice system also exists in areas with lower annual precipitation (e.g., at Discovery Bay), but during dry and hot periods, diel fluctuations in the relative humidity affect the microclimate in the crevice system. The occurrence of erratic drops in humidity might be one reason why *S. jarvisi* does not live in such areas, but, the distribution of the species is affected by several interconnected factors: (1) an extended rock-rubble layer of eroded limestone, common west of the Blue Mountains and less so in the John Crow Mountains, a small limestone plate in eastern Jamaica; (2) relatively constant high humidity in the crevice system, which depends on a high average precipitation and forest cover above; and (3) the occurrence of large shells of land snails. Jamaica supports 400–450 land-snail species, 95% of them endemic to Jamaica (Goodfriend, 1986a), whose distribution depends on the occurrence of limestone (the metamorphic and igneous Blue Mountains support only few species, and population densities are low; R. Diesel, unpublished data). The snail-shell size and the aperture area vary within a species depending on local annual precipitation (Goodfriend, 1986b, 1987). Shells in drier and hotter areas are smaller than those in wetter locations and have a relatively smaller aperture area (Fig. 14); shell volumes of *P. lucerna* are an average of 2.5 times higher in Windsor than in the Hellshire Hills (Fig. 3). Within the distribution range of *S. jarvisi* the apertures of shells of *P. lucerna* at Heron's Hill are almost too small for female crabs to enter (D. Horst, unpublished observation), which may explain why shells of *P. jamaicensis,* in spite of their large aperture area, were more frequently used for breeding at Heron's Hill (Table 1).

The preference of *S. jarvisi* for large shells with relatively small apertures implies that retention of moisture in the shell is a significant microclimate factor for the species. Juveniles probably require a higher ambient humidity for survival than do adults. This could be the reason that juveniles smaller than 7-mm CW were never found outside their moist brood-shells. Future experiments on the transpiratory water loss of different-sized juveniles under various humidity regimes and measurements of the humidity within various types of shells could reveal the size at which juveniles are able to leave the brood-shell for extended activities in the crevice system, e.g., to forage.

Breeding and Brood Care

During our study the release of larvae by *S. jarvisi* started during the relatively dry periods before the rainy season. According to the calculated age of juveniles found at Windsor, a major peak in breeding activity occurs in late summer and autumn. However, breeding in *S. jarvisi* appears to be distributed over the whole year. This is unlike that of the bromeliad crab, which has about the same spatial distribution as *S. jarvisi,* but whose breeding activities are strongly synchronized in spring.

Sesarma jarvisi is the smallest of the Jamaican endemic Sesarminae. Although egg size is comparable to that of other species (see Hartnoll, 1964a; Abele and Means, 1977; R. Diesel, unpublished data), it produces a very small clutch. Both small body size and small clutch size appear to be adaptations to breeding in the limited space of snail shells.

Another feature unique to the species is their ability to transport and release water into the brood shells. Water uptake from the substrate for gas exchange, drinking, or feeding using tufts of setae is a common feature in terrestrial and semiterrestrial crabs (cf. Gross *et al.*, 1966; Bliss, 1968; Hartnoll, 1973; Quinn, 1980; Felgenhauer and Abele, 1983; Wolcott, 1984), but transport to and release of the water into a "nest" (or burrow) has not been reported previously for crabs. In addition to an external water film, *S. jarvisi* may also transport water in its branchial chambers. The mechanism by which the crabs release the water into the shell remains unknown. The water held within the branchial chambers may be dumped out into the shell, by means of a water-dumping behavior like that reported for the ocypodid crab *Heloecius cordiformis* (H. Milne Edwards) (see Maitland, 1990).

Since juveniles remain in the brood-shell after metamorphosis, they are not able to forage outside and thus depend on the food resources found in the shell. We frequently observed food items of plant and animal origin in shells with young up to 5-mm CW. We have not seen mother crabs carrying food into the shell (experiments are under way), but it is reasonable to assume that the food is provided by the mother, which may care for young until they reach 6.5-mm CW. It is very likely that the percentage of broods larger than 3-mm CW attended by their mothers is higher than indicated by our data. The considerable disturbance we caused while removing rocks in the search for shells may have caused females to leave the brood-shell.

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