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Reproductive Ecology of an Intertidal Brachyuran Crab, *Sesarma* sp. (nr. *reticulatum*), from the Gulf of Mexico

TODD L. ZIMMERMAN AND DARRYL L. FELDER

University of Southwestern Louisiana, Department of Biology, and USL Center for Crustacean Research, Lafayette, Louisiana 70504-2451

Abstract. The natural history and reproductive ecology of a presently undescribed marsh crab endemic to the Gulf of Mexico were studied in both the laboratory and the field. Weekly sampling of populations in coastal Louisiana allowed us to determine the periodicity of molting and ovarian development, as well as the seasonal variation in egg laying and size of individual egg masses. Timing of molt, egg laying, and egg hatching were monitored in individual females under simulated tidal cycles in laboratory mesocosms. Peak periods of reproductive activity in Louisiana coincide with favorable temperatures and elevated primary productivity in coastal waters. Size cohort and fecundity differ between these periods. Egg-laying, larval release, and molting observed in individual females in the laboratory and extrapolated dates of egg-laying and larval release for those in field samples exhibit a semilunar influence throughout the season. Female receptivity to mating is tied to egg-laying. Rate of embryonic development was associated with decreases and increases in egg size. Behavior related to larval release is described. Adaptive significance in relation to the intertidal marsh habitat is discussed.

Introduction

Present distributional records for the burrowing grapsid crab, *Sesarma reticulatum* (Say, 1817), suggest a range from Woods Hole, Massachusetts to Volusia County, Florida along the East Coast of the United States, and from Sarasota County, Florida to Calhoun County, Texas within the Gulf of Mexico (see Williams, 1984). The original purpose of this study was to expand upon the ecological works concerning *S. reticulatum* (which have, to date, been carried out on the Atlantic Coast; Crichton, 1960, 1974; Mulstay, 1975; Seiple, 1979a, b, 1981; Seiple and Salmon, 1982, 1987) by closely examining the reproductive ecology of the Gulf populations. However, during other studies treating genetics (Felder and Staton, in prep.) and morphology (Felder and Zimmerman, in prep.), it became apparent that populations endemic to the Gulf are distinctly different from the east coast *S. reticulatum* and should be considered a distinct species. As its closest relative, *S. reticulatum* serves as the best source of background information to supplement what little is known about the Gulf crab.

Collections by one of us (D. L. Felder) indicate that the undescribed Gulf of Mexico form (hereafter referred to as *Sesarma* sp. (nr. *reticulatum*) ranges from Sarasota County, Florida, to Barra del Tordo, Tamaulipas, Mexico, while *Sesarma reticulatum* ranges from Woods Hole, Massachusetts, to Volusia County, Florida (Williams, 1984). *Sesarma reticulatum* inhabits estuarine environments with salinities ranging from less than 2 ppt to 35 ppt (Allen and Curran, 1974), prefers a mean of about 16 ppt (Seiple, 1979a, b), and is found commonly in intertidal areas along stream banks and in well-drained salt marsh habitats above mean tide level (Teal, 1958; Crichton, 1960, 1974; Allen and Curran, 1974; Mulstay, 1975; Seiple, 1979a, b). *Sesarma* sp. (nr. *reticulatum*) lives in similar habitats. It is generally found in areas of relatively low salinities (1–15 ppt) but may also occur in hypersaline habitats. Teal (1958) considered *S. reticulatum* to be an important member of the salt marsh community in Georgia, while *S.* sp. (nr. *reticulatum*) was found to rank as high as fifth among species in terms of both density and biomass in one Florida Gulf coast salt marsh (Subrah-

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manyam *et al.*, 1976). In Gulf coast habitats, *S.* sp. (nr. *reticulatum*) is often found sympatrically with *Sesarma cinereum* (Bosc, 1802), *Eurytium limosum* (Say, 1818), *Panopeus obesus* Smith, 1869, *Rhithropanopeus harrisii* (Gould, 1841), and *Uca* spp. (Subrahmanyam *et al.*, 1976), especially *U. longisignalis* Salmon and Atsaides, 1968, *U. rapax* (Smith, 1870), and *U. spinicarpa* (Rathbun, 1900). The burrows of *S. reticulatum* are important in reworking the soil and often interconnect with those of other species (Crichton, 1960; Allen and Curran, 1974).

Sesarma reticulatum is primarily nocturnal (Crichton, 1960; Palmer, 1967; Mulstay, 1975; Seiple, 1981), and inhabits burrow networks (Crichton, 1960; Allen and Curran, 1974; Seiple and Salmon, 1982), in mean densities as high as 25 crabs/m^2 (Seiple, 1979a, b). Several females (Crichton, 1960; Seiple and Salmon, 1982) and juveniles (Mulstay, 1975) can be found in the network associated with a mature male. During the breeding season, males patrol and defend burrow entrances (Mulstay, 1975). Food reportedly consists primarily of live vegetation such as *Spartina alterniflora* Loisel (Crichton, 1960, 1974; Seiple and Salmon, 1982). *S. reticulatum* has also been observed to feed actively on the marsh surface during overcast days (Teal, 1959). The reproductive season varies depending on latitude (Mulstay, 1975; Seiple 1979a, b), and factors such as temperature and lunar phase influence reproduction (Seiple, 1979a, b).

Sesarma reticulatum, other *Sesarma* species, and many intertidal brachyurans exhibit reproductive periodicities corresponding to lunar and tidal phases (Saigusa and Hidaka, 1978; Seiple, 1979a, b; Saigusa, 1981, 1982, 1988; Christy, 1982; Christy and Stancyk, 1982; Forward, 1987; DeVries and Forward, 1989). Larval release rhythms for *Sesarma* species also coincide with solar day and tidal cycles (Saigusa, 1982; DeVries and Forward, 1989). The onset of the breeding seasons may be cued to temperature (Pillay and Ono, 1978; Seiple, 1979a, b). The synchrony of reproductive cycles is poorly developed in *S. reticulatum* at the beginning and end of the season (Seiple, 1979a, b). The spring asynchrony phenomenon has been recorded for other crabs as well (Wheeler, 1978; Dollard, 1980; Christy, 1982).

Semidiurnal tides have been shown to entrain biological rhythms in many intertidal crabs (Fingerman, 1957; Palmer, 1967; Saigusa, 1982; Decoursey, 1983; Christy, 1986; Forward, 1987), and latitudinal variations in breeding periodicities have been reported for populations of the intertidal grapsid crab *Helice crassa* Dana, 1851, in New Zealand (Jones and Simons, 1983). Also, larval release rhythms for fiddler crabs from the west coast of Florida, which are subject to diurnal tides, differ from those on the Atlantic coast (Christy, 1978). Thus, periodicities in Gulf of Mexico *Sesarma* populations may be expected to vary from those reported from the Atlantic Coast, both because of latitudinal differences and genetic divergence.

In the present study, we investigate aspects of reproductive ecology and life history in *S.* sp. (nr. *reticulatum*), an abundant and previously unstudied inhabitant of the most expansive intertidal estuarine and salt marsh habitats in the conterminous United States. We present information on annual female population changes in reproductive states, such as ovarian activity and growth, and factors that influence female reproductive cycles and molting throughout the year, such as lunar and tidal phases. We also describe details of events that take place during a single female reproductive cycle from mate receptivity, through egg laying and embryonic development, to larval release. The adaptive significance to a low salinity intertidal habitat is discussed.

Materials and Methods

Field samples

Mature-sized female specimens of *Sesarma* sp. (nr. *reticulatum*) were collected (n/collection = 17–44) periodically from 21 March 1989 to 21 March 1990 in coastal Louisiana habitats near Cocodrie, Cypremort Point, Redfish Point, Rockefeller Wildlife Refuge, and Cameron. These areas are all under similar tidal regimes and have salinities under 12 ppt. The majority of samples were collected from a fresh marsh dominated by bulltongue (*Sagittaria lancifolia* L.), *Iris* sp., and deer pea [*Vigna luteola* (Jacq.) Benth.]. Females brought to the lab were chilled on ice, examined, measured, and dissected. An impending molt was noted if a crab's exoskeleton was discolored and brittle with a thickened underlying integument, and a recent molt was noted if the exoskeleton was soft or abnormally thin and clean. Carapace width (CW) was measured ± 0.01 mm. When eggs were present, developmental stage (after Boolootian *et al.*, 1959; Brown and Loveland, 1985) was recorded. Wet weight of the egg mass (if present), body, and ovary were determined to the nearest 0.1 ± 0.03 mg. After weighing, egg masses were preserved in 7% formalin. An analysis of 18 egg masses was used to estimate the number of eggs per gram wet weight of egg mass. Calcification of the genital opercula (after Hartnoll, 1968), presence of spermatozoa in the spermatheca, and maturation stage of the ovary [as determined by color, (after Pillay and Ono, 1978)] were recorded. Spermatozoa were present in the spermatheca of all but the smallest females throughout the sampling period.

Voucher specimens from each field site were archived in the University of Southwestern Louisiana Zoological Collections, USLZ 3484–3493.

Laboratory mesocosms

Laboratory habitats consisted of two fiberglass tanks (0.3 × 1.12 × 2.3 m) each with a permeable partition

separating the tanks into four equal mesocosms. A layer of gravel 5 cm thick was placed under 10 cm of topsoil separated by Weed-X® porous landscaping barrier and nylon window screening, to provide adequate drainage and enable a shallow layer of soil to be used. The area of the tank near the partition was free of soil and gravel and was a source of standing water at low tide periods. Soil was held back from the standing water area by a 10 cm high burlap covered board resting on the edge of the gravel. This enabled crabs to climb down to the water with ease. Topsoil was replaced with soil from the collection site on 6 June 1990, and this was replaced again, on 4 August, with soil from the same site. Four boards (approximately 30 × 40 cm) were placed on top of the soil in each section to provide cover under which crabs could take refuge. Water level was controlled by two (1/70 hp) pumps, one to pump water from storage tanks into the habitat tanks to simulate high tide and the second to reverse the process to simulate low tide. Each pump was controlled by a separate 24-h timer providing a high water period of 4 h per day. These were controlled by a third timer that advanced the high water period by 1 h each day. This tidal regime was for experimental purposes only, as the fluctuating natural tidal cycles could not be duplicated. Salinity was adjusted by mixing full strength seawater with dechlorinated water, and maintained at 5 ppt to represent a salinity value that is intermediate for the coastal Louisiana habitats sampled. Water was changed weekly.

Mesocosms were contained in a light proof room where fluorescent overhead lighting provided a 14 h light:10 h dark cycle. In addition, 1500 watt halogen lights (controlled to turn on and off 1 h after and before the overhead lights) were installed over each tank on 2 July 1990 to simulate the high temperatures characteristic of the natural summer habitat after sunrise. Light intensity reached a maximum of approximately 150 $\mu E\ s^{-1}m^{-2}$, while soil temperature ranged from 23–30°C during the day and dropped to 23°C at night. These temperatures approximated those in the field.

One hundred crabs (80 females and 20 males) of mature size were collected from Cypremort Point on 4 and 9 April 1990. Carapace width was measured, and a numbered plastic tag was glued to the carapace using cyanoacrylamide glue. Twenty-five (20 females and 5 males) crabs were placed in each mesocosm. This did not correspond to the ratio found in the field, but provided adequate breeding interactions and an increased sample size of females. Individual crabs were inspected every few days until crabs began laying eggs, at which time they were checked every 2–3 days for egg laying, developmental stage of the eggs, egg diameter (as an average of ten eggs), larval release, and molting. Crabs were initially fed Tetramin® flake food and Hartz® Shrimp-el-etts® supplemented periodically with lettuce and *Spartina* before the topsoil was replaced with marsh soil and the halogen lights were installed. After this time, the crabs did well without feeding but supplementary food in the form of commercial rabbit and guinea pig pellets was added and seemed to be much preferred over any of the previous foods. To maintain an optimal number of crabs in all of the mesocosms, this initial population of crabs was consolidated into two of the four mesocosms, and new crabs were collected from the same marsh on 7 June 1990, measured, marked, and placed into the empty mesocosms. This consolidation was repeated again on 5 August.

Video observation

To determine timing of genital operculum decalcification, egg laying, and larval release, 90 females were collected in early August, measured, marked, and whenever possible placed individually into 11 cm finger bowls with 1–2 cm of 5 ppt salinity water. Water was changed every day, and crabs were fed commercial rabbit pellets every other day. Crabs were checked daily for softening of the genital opercula by unfolding the abdomen and pressing on the opercula with the tip of a forceps. Very light pressure was needed to depress the opercula after the hinge had softened, and movement could be easily detected. Date and time of detection were recorded, and the crab was then monitored, with a time-lapse video system, for egg laying and subsequent egg hatching. Developmental stage of the eggs was recorded daily and these ovigerous crabs (along with those from the mesocosms with eggs approaching hatching) were placed under video observation. Video observation chambers consisted of four polystyrene boxes (30 × 15 × 8 cm), each spanned at mid-length by a 3 cm wide, 1 cm deep wax trough containing 5 ppt seawater in which larvae could be released and gill water replenished. A plate of glass was placed over the boxes to prevent escape, and an infrared light source was used for night observations. Activity was monitored using a video camera connected to a time-lapse video set to record for 72 h per 120 min VHS tape. The room was kept at a constant 28°C, and a 14:10 h light:dark photoperiod was maintained with overhead fluorescent lights in addition to the constant infrared light source. The larval release of a single crab was videotaped at close range and at real time speed to precisely record the event.

Larval rearing

Larvae from two females were reared in two sets of ten 11 cm finger bowls (initial densities = 20 larvae/bowl) in filtered seawater diluted with deionized water to 25 ppt salinity at 28°C. Larvae were fed newly hatched *Artemia* nauplii daily. These procedures were followed to ensure

maximum survival and to yield results similar to those expected under optimal conditions in the field.

Results

Reproductive and molting peaks

Crabs with newly laid eggs were found in field collections as early as April 14 in 1989, and April 4 in 1990. Sampling throughout 1989 indicated a peak in the percentage of females carrying eggs from late April through late May, followed by another larger peak extending from mid-July through early September. Other ovigerous females were found in late July and from late September to mid-October, and the last egg carrying female of the collection period was taken on October 12. Egg carrying females ranged from a minimum of 11.1 mm to a maximum of 26.9 mm carapace width. A peak in molting for the population began in mid-May and extended to late June and was followed by another peak molt during mid-October. Some crabs also molted in late July and early August. Molting activity was not observed during the winter months, although collections were not made as frequently during this time (Fig. 1).

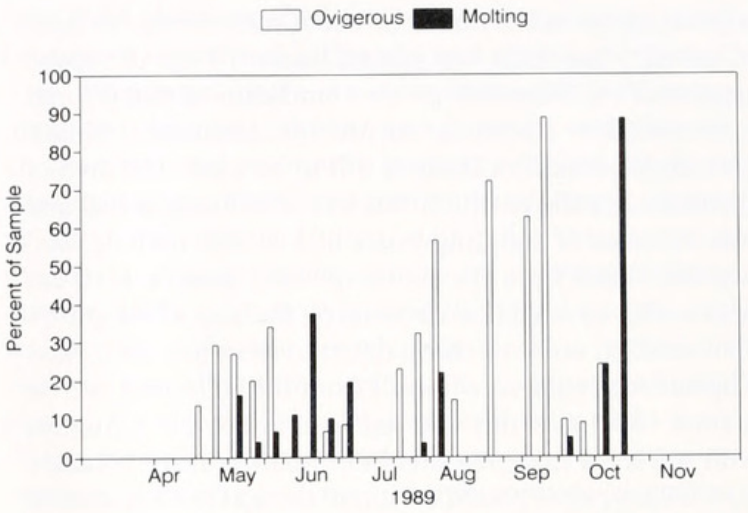

Figure 1. Percentages of ovigerous females (open bars) and females undergoing a molt (solid bars) found in periodic field samples of *Sesarma* sp. (nr. *reticulatum*) taken during 1989. All samples are represented by bars except for those collected during the third week of March, the first week of April, the third week of October and the third week of November, which contained no ovigerous or molting females.

Size differences

Careful examination of peaks in molting and egg-carrying across all size classes sampled indicated that timing of crabs carrying eggs and crabs molting varied between two size cohorts. Crabs smaller than 17.5 mm CW were found carrying eggs only in the latter part of the season from July through September. Larger crabs were found with eggs throughout the reproductive season. Those crabs larger than 23.5 mm CW were found to molt only from late September through October while smaller crabs (≤23.5 mm CW) were found molting during the May–June peak, somewhat during mid-summer, and again in October (Fig. 2).

Reproductive effort

A mean of 20,400.8 (±2469.2 95% CI) eggs per gram wet weight of egg mass was determined from egg counts of 18 individuals. When multiplied by the wet weight of each individual egg mass, this estimated value resulted in average egg numbers ranging from 2,728 for the smallest egg bearing females (11–13 mm CW) to 18,087 for large females (25–27 mm CW). The maximum number of eggs estimated for a single brood was 27,847 found on a crab with a carapace width of 24.5 mm. Estimated numbers of eggs per crab increased with body size in all but the largest size grouping of crabs (Fig. 3).

Seasonal differences

Fecundity data (wet weight of egg mass/carapace width) for spring pre-molt and non-molting ovigerous females collected prior to 1 July (the end of the spring molting period) and summer ovigerous females collected after this date were fitted by linear regression ($y = -0.723 + 0.067\times$, $r^2 = 0.454$ for spring crabs; $y = -0.999 + 0.074\times$, $r^2 = 0.454$ for summer crabs). Weight of the egg mass increased together with female body size in both seasonal sets, and slopes were not significantly different from each other when compared by Student's *t*-test. However, there was a significant difference (Student's $t = 4.21$, $P \geq 0.001$) between the mean weights of egg masses (spring $\bar{X} = 0.719$ g, $n = 44$; summer $\bar{X} = 0.536$ g, $n = 63$) when the two sets were compared (Fig. 4).

Lunar periodicity

Date of egg laying and expected date of larval release for each ovigerous crab collected in the field were back calculated from data obtained by monitoring egg size and development in the laboratory. This was done to determine periodicity of reproductive events in field populations. The mean number of days required for a developmental stage to be reached in the laboratory was subtracted from the date that each ovigerous crab with eggs corresponding to that stage was collected. Expected dates of larval release were then determined by adding the mean number of days remaining from that stage in development to larval release. Extended developmental period caused by lower temperatures, if occurring, should have been reflected in distribution of developmental stages in relation to the dates of the new and full moons. Peak numbers of crabs laying eggs or releasing larvae should also then have been skewed away from the syzygies until increased temperature caused developmental rate in the field to equal

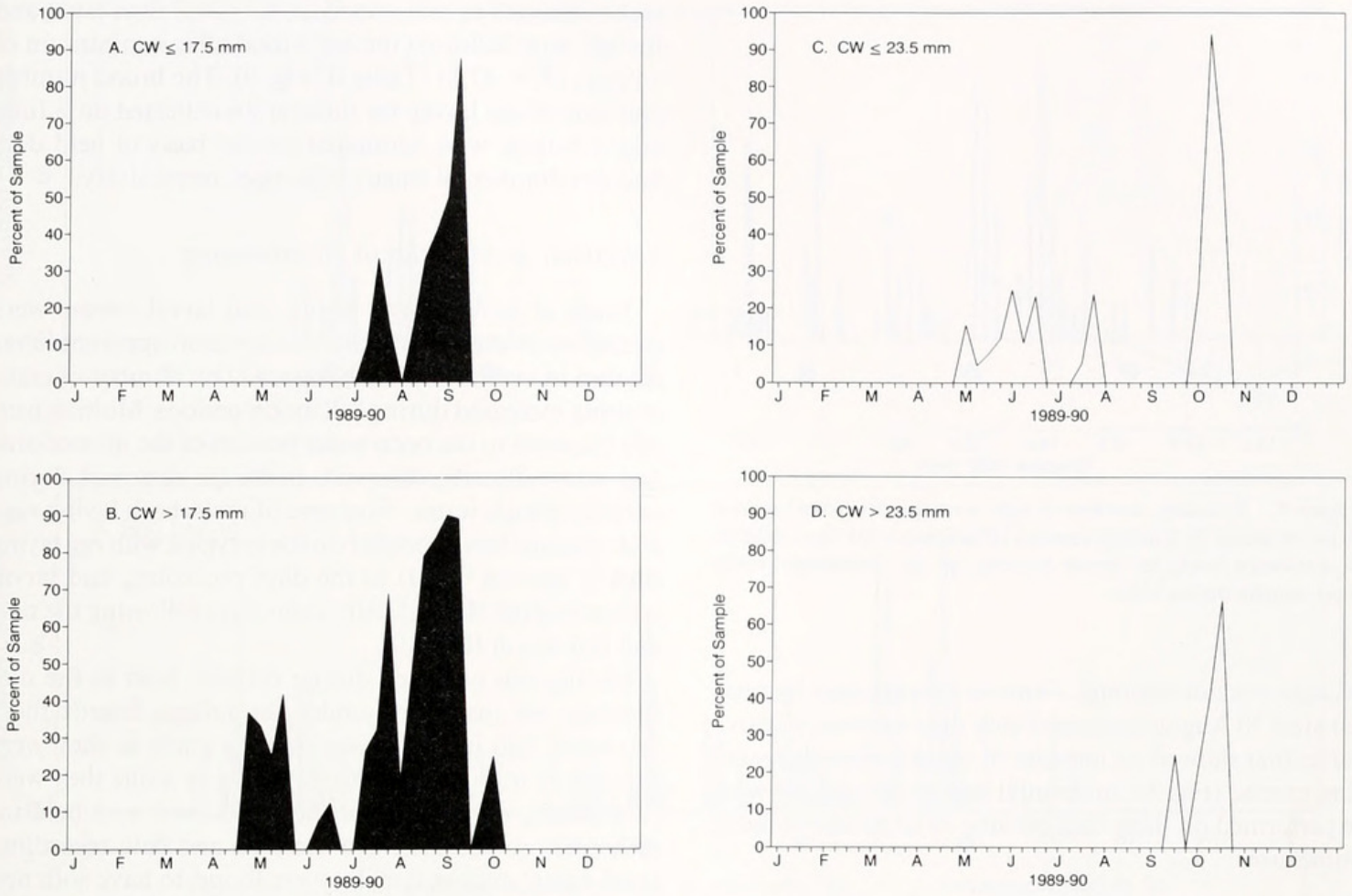

Figure 2. Reproductive and molting cohorts for female *Sesarma* sp. (nr. *reticulatum*) taken in field samples during 1989 and 1990. A. Ovigerous crabs ≤ 17.5 mm carapace width. B. Ovigerous crabs > 17.5 mm carapace width. C. Molting crabs ≤ 23.5 mm carapace width. D. Molting crabs > 23.5 mm carapace width.

that seen in the laboratory. Instead, peaks in egg laying and larval release occurred near dates of new and full moons throughout the reproductive season (Fig. 5).

Ovarian growth

Ovarian wet weights, expressed as an index of grams wet weight ovary per millimeter carapace width, were compared to ovary color; yellow ovaries were the lightest, which suggested inactivity, orange ovaries were slightly heavier, which suggested rebuilding or oogenesis, and red-black ovaries were the most massive because of vitellogenesis (Table I). Vitellogenic ovaries were seen in 37.5% of the sample as early as mid-January, and the numbers of crabs possessing vitellogenic ovaries increased through the reproductive season until August when nearly all female crabs of mature size had reproductively active ovaries. This percentage dropped to near zero in September, after which a slight increase occurred in October before vitellogenesis ended for the season (Fig. 6). Inversely, the percentage of inactive yellow ovaries increased markedly in samples after the cessation of vitellogenesis in September and October. Ovarian rebuilding for the population quickly followed inactivity so that by 22 November 77.8% of the sample possessed orange ovaries.

When only vitellogenic ovaries were considered, intensity of yolk deposition began to increase in late March and April, and to peak in late April. Intensity of yolk deposition declined during the May-early June molting period, and increased to a high level throughout the summer reproductive peak. High values near 0.02 g/mm, which would indicate eggs are ready to be extruded, are absent during the two sampling dates (May 9 and June 1) that fell during peak molting periods (Fig. 7).

Rate of ovarian growth was measured for those crabs carrying eggs by plotting relative ovarian wet weight (g/mm) against developmental stage of the eggs. Early in the season, ovigerous crabs collected before, during, and just after the molting period showed little increase in ovary weight throughout the period that the eggs were carried. After the molt period, during peak reproductive activity, ovarian weight increased throughout the period that car-

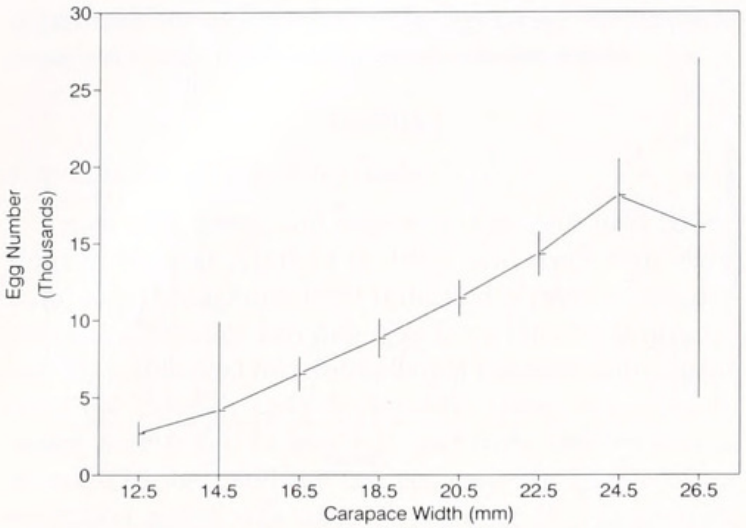

Figure 3. Estimated numbers of eggs per egg mass plotted against crab size as shown by 2-mm increments of carapace width (bars indicate 95% confidence levels) for female *Sesarma* sp. (nr. *reticulatum*) taken in field samples during 1989.

ried eggs were developing. Females bearing eggs (ovigerous) after 30 August possessed very light colored, inactive ovaries that showed no increase in weight while eggs were being carried (Fig. 8). Inferential statistical analyses were not performed on these data because of small and variable sample sizes.

Decalcified opercula

The only day (5 July 1989) in which softened genital opercula were found in a large percentage of the sample (37%) during the study was near full moon. While few ovigerous females (10.5% of females sampled) were found on this date, laboratory data suggested that the cohort with softened genital opercula should have laid eggs within 24 h. Indeed, 31% of the females collected on the following date (6 July 1989) were ovigerous, confirming the laboratory prediction. Because data were plotted at weekly intervals, collections made on these two dates were combined and a value of 23% appears on Figure 1.

Laboratory mesocosms

Crabs held in laboratory mesocosms did not produce a premolt spring brood of eggs possibly because of inadequate substrate or diet. This problem seemed to have been corrected with the substitution of substrate from the natural habitat and the installation of halogen lights. The molting period was also offset from that recorded from field samples by approximately one month. A first brood was produced a minimum of 21 days ($\bar{X}$ = 34 days) following the early season molt. This was followed by a second brood at $\bar{X}$ = 27.7 days later, and a third brood at $\bar{X}$ = 25 days later. A fourth brood was produced by three crabs collected in early April, at $\bar{X}$ = 21.7 days later, and the fall molt followed the last brood after a minimum of 34 days ($\bar{X}$ = 47.8) (Table II; Fig. 9). The brood number and date of egg laying for those crabs collected on 7 June and 5 August were estimated on the basis of field data and developmental stage of the eggs, respectively.

Semilunar periodicities in the laboratory

Dates of molting, egg laying, and larval release were plotted to determine whether there was an apparent lunar rhythm in events in the laboratory. The number of crabs molting increased during full moon periods. Molting usually occurred in the open water portion of the mesocosms, and when directly observed, it always occurred during periods of high water. Numbers of crabs both laying eggs and releasing larvae peaked on the syzygies, with egg laying slightly skewed (right) to the days preceding, and larval release slightly skewed (left) to the days following the new and full moon (Fig. 10).

Mating was observed during the day, both in the mesocosms (by inspecting under the refugia boards there provided) and in containers holding crabs as they were brought in from the field to be tagged or while they were periodically removed from the mesocosms and held together before and after examination and data recording. In all cases, mating females were found to have softened genital opercula, and in two cases the same female was observed mating with more than one male within a few hours time. Usually pairings were between similar sized individuals, but unequal size pairings of both kinds were also seen. In each instance, when tagged crabs from the mesocosms were observed mating (either in the mesocosms or in containers while they were held together dur-

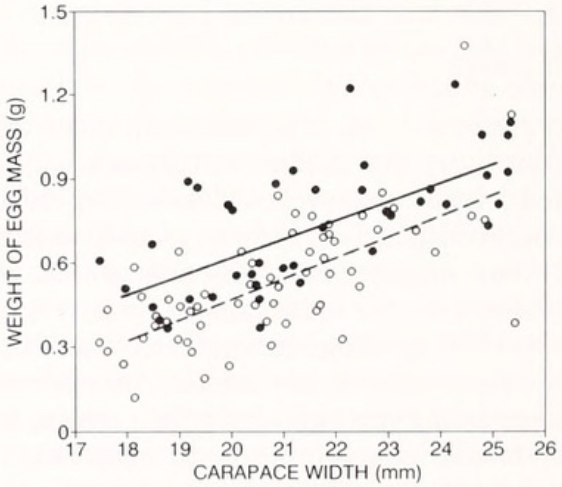

Figure 4. Regression of clutch size (wet wt egg mass) on carapace width (mm) for *Sesarma* sp. (nr. *reticulatum*). Open circles and broken line represent crabs collected before and during the spring molting period (1 July) 1989. Dots and solid line indicate crabs collected in 1989 after this date.

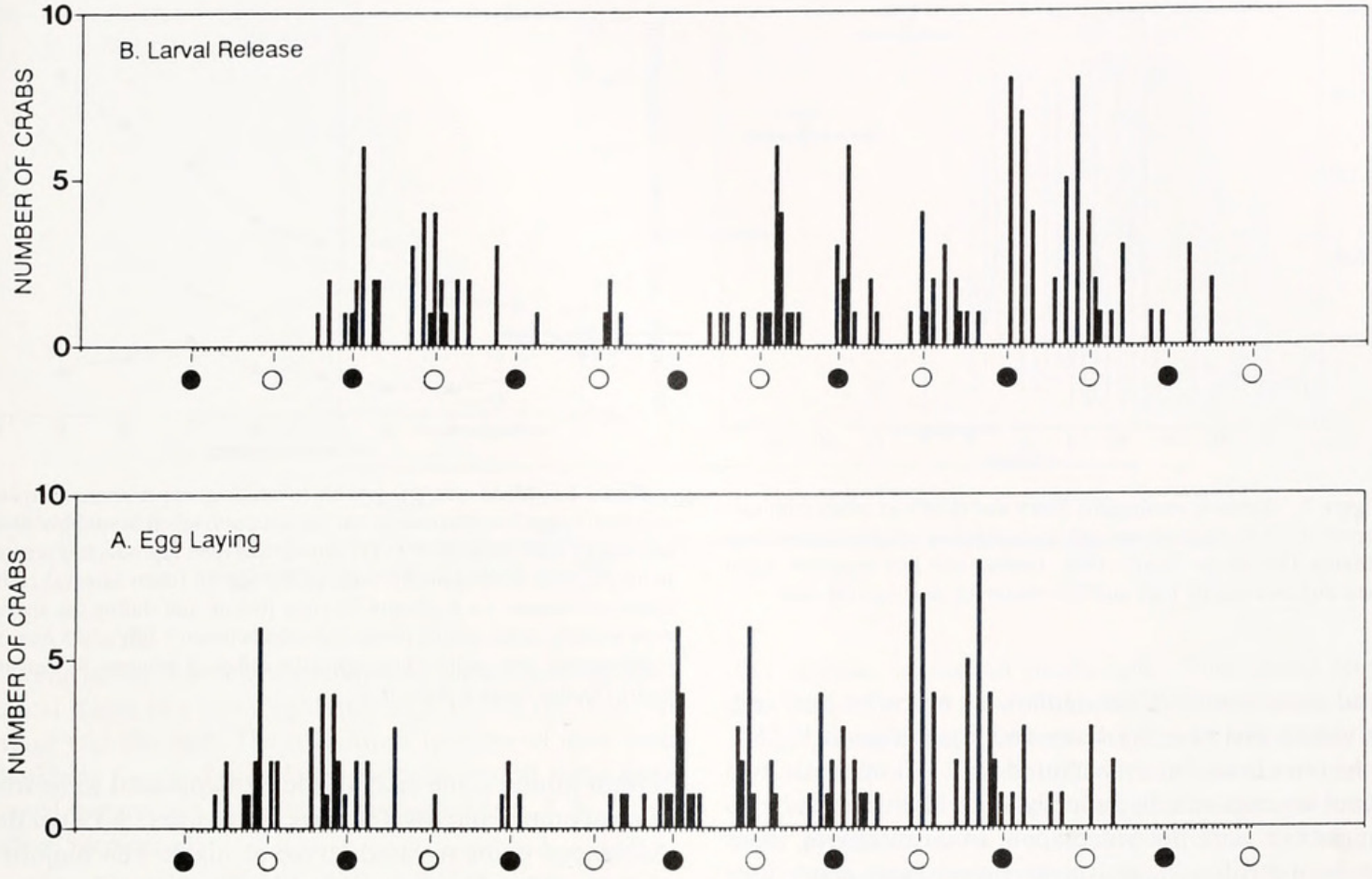

Figure 5. Relationship of lunar cycle to numbers of crabs laying eggs (A), and releasing larvae (B), for *Sesarma* sp. (nr. *reticulatum*) taken in field samples during the 1989 reproductive season. Dates are estimates based on developmental stage of eggs found on each crab. Lunar series begins on 6 April (first filled circle, new moon) and ends on 8 October (last open circle, full moon).

ing data recording), the females were found with eggs within 2–3 days when next captured. Females soft from a molt were never observed mating, and genital opercula, although soft, were not functionally hinged when manipulated under a dissecting scope.

Crabs held individually and checked periodically each day were found with decalcified opercula as early as 1045 h. Six of these crabs were videotaped as they laid eggs out of water between 2051 h of the same day and 0100 h of the following day. Visible light was removed at 2015 h, and the crabs laid eggs out of water after an activity period beginning shortly after darkness that day. Recalcification occurred soon after egg laying, and hard opercula were

Table I

Ovary color, mean wet weight (mg), 95% confidence interval, and number of individual female Sesarma *sp. (nr.* reticulatum*) taken in field collections during 1989 and 1990*

Ovarian color	Mean wet weight (mg)	95% CI	n
Red-black	7.05	0.54	320
Orange	1.98	0.24	126
Yellow	1.50	0.13	142

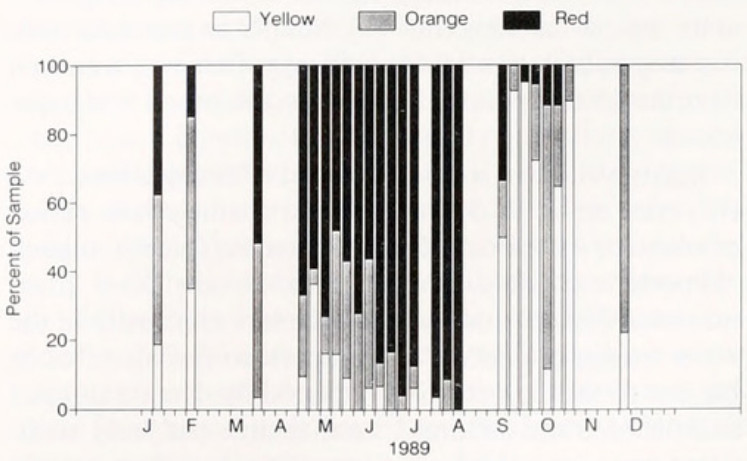

Figure 6. Ovarian activity of *Sesarma* sp. (nr. *reticulatum*) taken in field samples from 21 March 1989 to 21 March 1990 as determined by color. Percentages of crabs in each field sample with inactive (yellow, clear bar), rebuilding (orange, stippled bar), and vitellogenic (red-black, solid bar) ovaries.

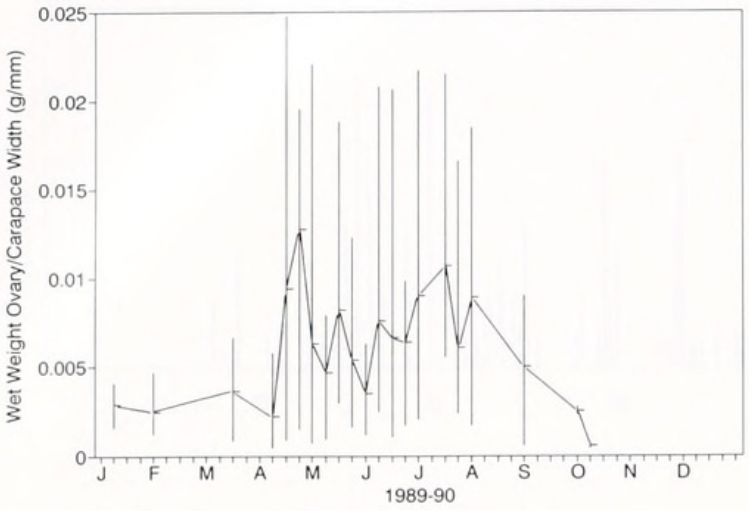

Figure 7. Relative vitellogenic ovary size (g wet wt ovary/mm carapace width) of *Sesarma* sp. (nr. *reticulatum*) taken in field samples from 21 March 1989 to 21 March 1990. Dashes and line represent mean values, and bars signify high and low values for each sample date.

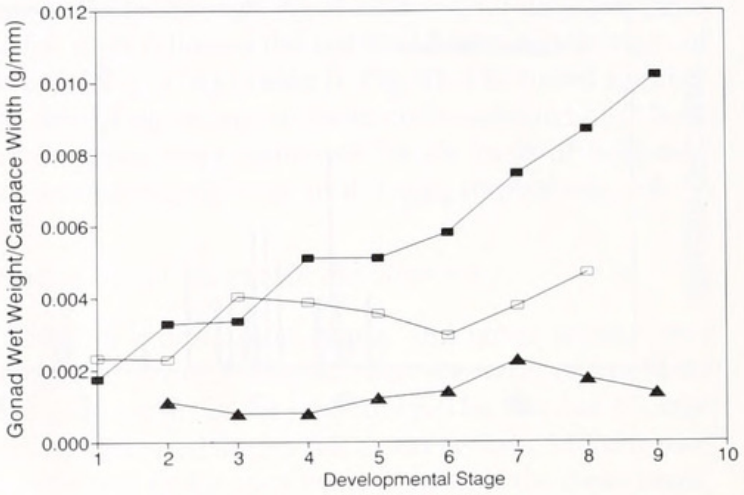

Figure 8. Mean ovarian growth (ovarian g wet wt/mm carapace width) of ovigerous *Sesarma* sp. (nr. *reticulatum*) taken in variably sized samples of each stage (n = 1–17) during the 1989 reproductive season plotted against developmental stage of the egg for (open squares) crabs collected between 14 April and 23 June (before and during the spring molt period), (solid squares) crabs collected between 7 July and 5 August (mid-season), and (solid triangles) crabs collected between 30 August and 3 October (end of season).

found as early as 0800 h the following morning. One crab was videotaped entering water and laying eggs at 1057 h. Of the remaining five crabs found with soft opercula, two did not lay eggs and died shortly after, and three laid eggs at night but were not videotaped. In all instances, these eggs were fertilized with sperm stored from a previous mating.

Development of the embryo within the egg was divided into 10 distinct stages (Table III). The total period of embryo development, which began when the eggs were extruded onto the pleopods, and ended with release of the larvae, averaged 17.3 days (±0.3 95% CI; R = 15–19; n = 47). The first two embryonic stages (Table III; Fig. 11) persisted for approximately one third of the total developmental period. Egg diameter decreased 8% within two days of oviposition. After the fourth day, egg diameter began to increase, reaching 125.7% of the day 4 diameter at the time of hatching (Fig. 11). Neither an initial decrease nor any subsequent increase in egg diameter was seen over the 10-day period that an infertile brood was monitored.

Eighty-two crabs were videotaped releasing larvae. Seventy-nine crabs (96.3%) exhibited a characteristic period of constant increased locomotor activity (herein dubbed "hyperactivity") lasting from 5 to 47 min ($\bar{X}$ = 20.62 min) that ended with release of the larvae (usually in the water trough provided). Close-up video revealed that at the end of the "hyperactivity" period the female stopped and deflexed her abdomen, at that time her body shuddered and a cloud of larvae seemed to abruptly burst out of the egg mass. Not until this initial hatch had occurred and most of the larvae were free did the crab begin to pump her abdomen and pick at the empty egg casings with her chelipeds in an attempt to clear her pleopods. Within minutes, the crab's abdomen appeared to be free of most empty and inviable eggs. Sixty-five (79.3%) of the videotaped crabs released larvae at night. The majority of these released larvae within 1 h after dark (Fig. 12) on nights near or on the new and full moons (Fig. 13). During the latter part of this study, natural darkness fell up to 2 h before laboratory darkness, and increased locomotory activity was observed in the interim, but "hyperactivity" and larval release did not occur until cued by darkness. Seventeen crabs (20.62%) were observed releasing larvae during the day. These releases ranged from 0915 to 1907 h. Only two of these, 1907 h on 5 September and 1818 h on 20 September, occurred after natural sunset. None of the day releases corresponded to either natural or artificial high tide periods, although in the mesocosms, crabs did become more active, and larval release was recorded during periods of daytime high water.

Table II

Mean ($\bar{X}$) and minimum (Min.) number of days separating molting and egg laying events for individuals of Sesarma *sp. (nr.* reticulatum*) held in laboratory mesocosms*

	M to B_1	B_1 to B_2	B_2 to B_3	B_3 to B_4	B_f to M
$\bar{X}$	34.1	27.7	25.0	21.7	47.8
95% CI	2.643	1.515	1.846	1.436	6.061
n	41	41	21	3	18
Min.	21	18	20	21	34

M is date of molt, $B_{1,2,3,4}$ are date of egg laying for the first, second, third, and fourth broods. B_f is the final brood produced by an individual.

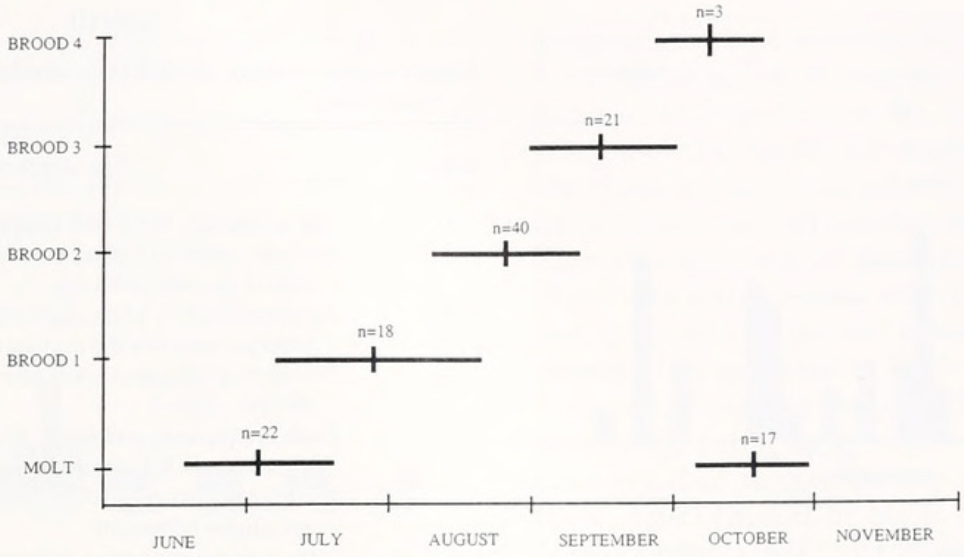

Figure 9. Mean dates and standard deviation of molts and egg laying for individuals of *Sesarma* sp. (nr. *reticulatum*) held in the laboratory in 1990.

The larvae reared in the laboratory passed through three zoeal stages and one megalopal stage before the first crab stage was reached. The minimum number of days from hatching required for a larva to reach second zoeal, third zoeal, megalopal, and first crab stages was 3, 5, 8, and 16 days, respectively.

Discussion

While a variety of factors may be responsible for the onset of the reproductive season for *Sesarma* sp. (nr. *reticulatum*), temperature is often considered to be the single most important factor in determining the beginning of the reproductive season in such temperate marine invertebrates (Geise, 1959). However, the effects of temperature may vary strikingly between populations and between closely related species that are adapted or acclimatized to differing latitudinal regimes (see Vernberg, 1962, for review). The onset of local reproductive seasons may coincide with increased larval food availability (zooplankton) by way of increased primary productivity in coastal waters (Thorson, 1950). Chemical stimulation in relation to diatom blooms has also been suggested as a link to spawning in laboratory-held barnacles (Barnes, 1957).

Populations of *Sesarma reticulatum* in North Carolina begin reproducing at a time when both temperatures and coastal primary productivity increase sharply (Seiple, 1979a, b). In Louisiana, coastal water temperatures are not limiting early in the year, but increases in coastal primary productivity lag behind because of light limitations caused by riverine-influenced turbidity levels (Sklar and Turner, 1981; Madden *et al.*, 1988). Vitellogenesis in *S.* sp. (nr. *reticulatum*) began early in the year with increasing temperatures, but maximum ovary growth, and subsequent egg production did not occur until slightly before the increase in coastal production. This would suggest that some factors other than temperature, such as day length, cue the onset of reproduction in the spring.

The end of the reproductive season occurred in late August to early September when ovaries became inactive after producing their final brood of eggs. At this time, water temperatures are high, but coastal productivity is beginning to decline (Sklar and Turner, 1981; Madden *et al.*, 1988). The majority of crabs held in the laboratory mesocosms produced their final brood of eggs and molted later than most in the field, but within the period recorded for natural populations. However, three crabs did produce a fourth brood of eggs after the end of the reproductive period recorded for field populations. This suggests that the natural seasonal rhythm had been offset.

Endogenous rhythms are cued to environmental events that synchronize free running physiological "clocks," which run either too fast or too slow (DeCoursey, 1983). The endogenous rhythms of some crabs from the mesocosms may have been affected by the lack of appropriate signals. If decreasing day length acts as a zeitgeber for the cessation of reproduction in natural populations, the constant photoperiod in the laboratory could have resulted in the extended reproductive season for these crabs. The length of time that some crabs (all of which were collected early the previous spring) were subjected to laboratory conditions may have contributed to their offset seasonal "clocks." Those crabs collected later in the season may also have been affected by the constant conditions, and their final brood may have been produced later in the season than it would have in the field.

In the field, molting occurred within a short period after release of the first brood of larvae in the spring, and the last brood in the summer. Both of these times were characterized by low or no ovarian growth. In the lab, the

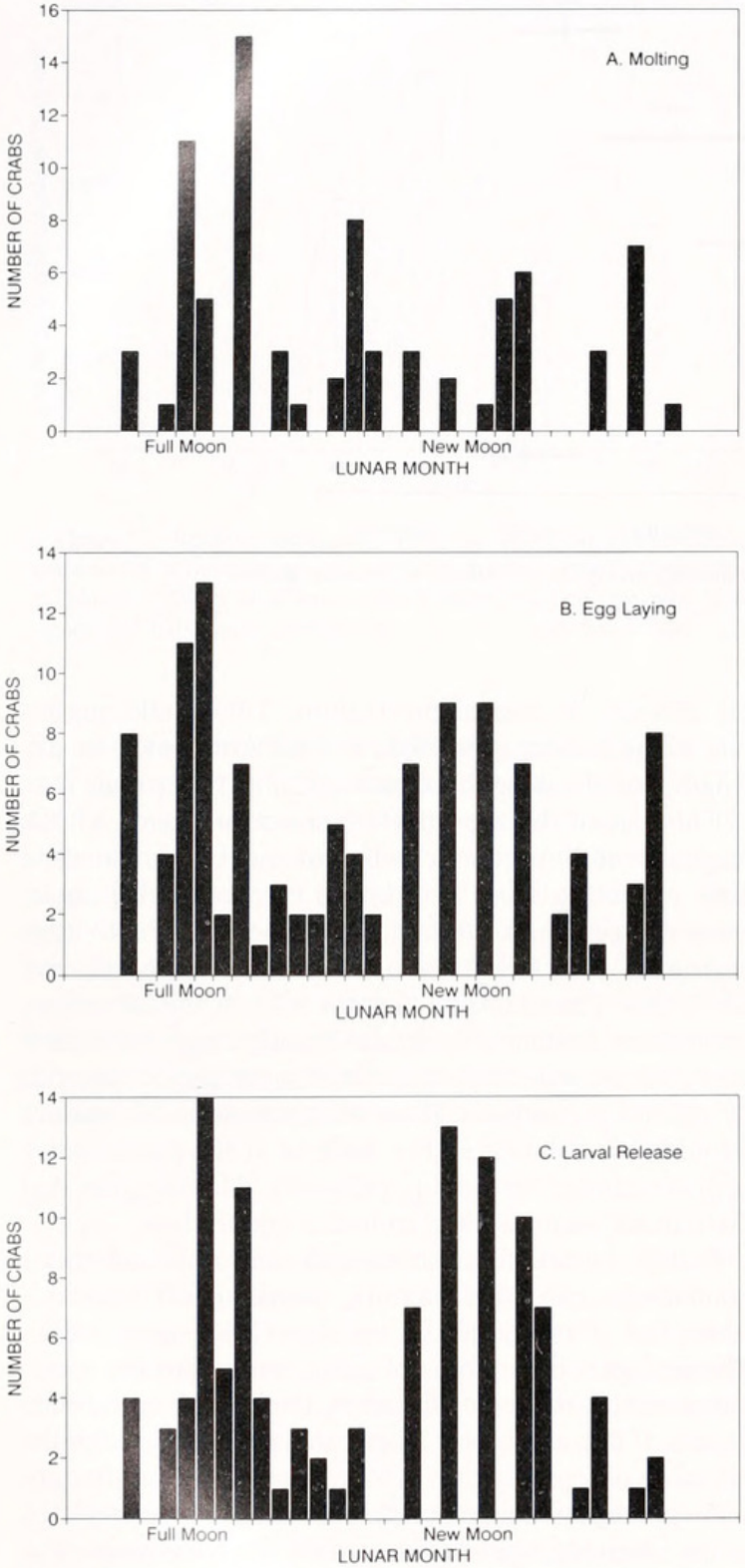

Figure 10. A. Molting, B. egg laying and C. larval release events for *Sesarma* sp. (nr. *reticulatum*) recorded in the laboratory during 1990, plotted by days of the lunar month.

constant regime of physical conditions probably affected the time of molting for those same crabs that had an extended reproductive season. It cannot be determined from this study whether the onset of molting is responsible for inactivation of the ovary in the fall, or whether molting and cessation of reproduction are independently controlled.

Table III

Criteria used for ranking the embryonic development of Sesarma *sp. (nr.* reticulatum*)*

Stage	Egg morphology
1	Egg completely filled with reddish purple yolk droplets.
2	Embryo visible as a small colorless plate of cells on one side of the yolk filled egg.
3	Approximately ⅓ of the egg consists of colorless embryo, yolk fills the remaining ⅔ of the egg.
4	Nearly ½ of the egg consists of colorless embryo, yolk fills the other ½.
5	Dark eye pigment and traces of dark chromatophores present, yolk fills approximately ½ of the egg.
6	Well-pigmented embryo comprises ⅔ of the egg the remainder being yolk.
7	Yolk forming distinctive "four leafed clover" lobed appearance, embryo fills ¾ of the egg.
8	Remaining yolk present as two connected lobes.
9	Traces of yolk remain as two separate patches, each containing a few droplets.
10	Embryo hatches as zoea.

Modified from Boolootian *et al.*, 1959, and Brown and Loveland, 1985.

Decrease in egg number per brood after the spring molting period could be caused by temporal constraints. The period of an individual reproductive cycle may not allow enough nutrients to be taken in or enough yolk to be produced for the maximum number of eggs allowed by body size. Crabs producing eggs in the spring have the advantage of an extended period for vitellogenesis; absence of somatic growth processes that follow a molt may avoid expending nutrients that are instead used to produce yolk. Another possible explanation for the lower fecundity might be an increase in egg mortality in the summer

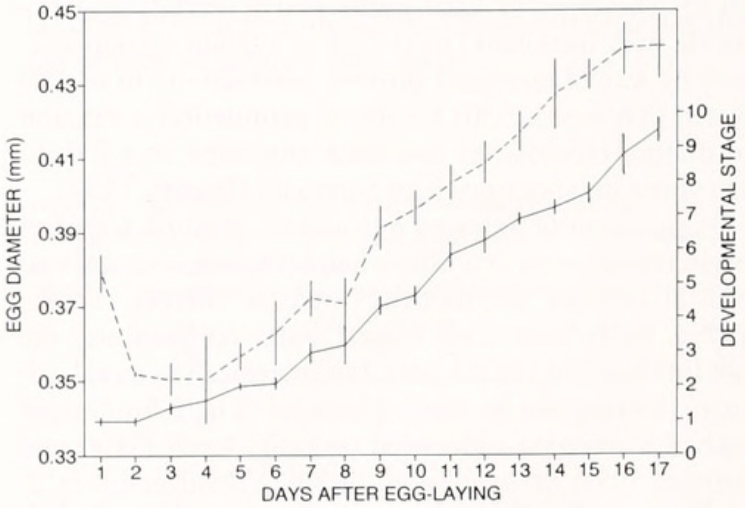

Figure 11. Mean change in egg diameter (broken line) and developmental stage (solid line) of *Sesarma* sp. (nr. *reticulatum*) plotted against the date from egg laying (bars are 95% CI).

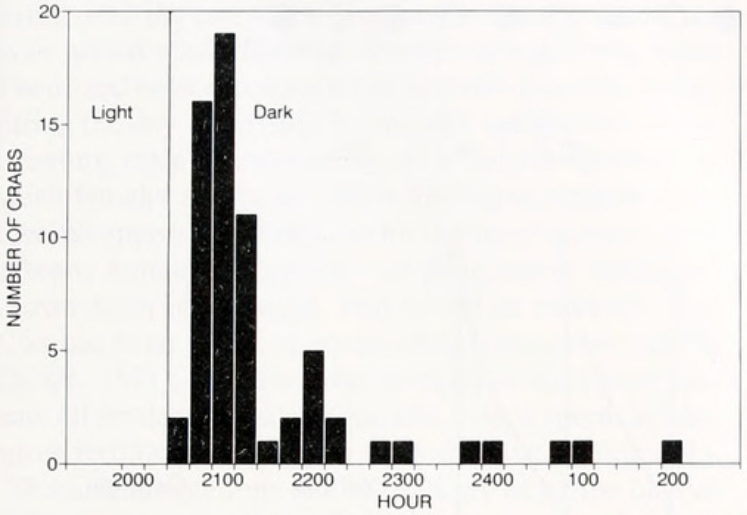

Figure 12. Number of individual *Sesarma* sp. (nr. *reticulatum*) videotaped releasing larvae versus time of release, in videomonitored experiment.

months. Dirty egg masses (often infested with peritrichous ciliates, nematode worms, and the harpacticoid copepod *Cancricola plumipes* Humes, 1941) seemed to be more prevalent in the warmer summer months. Many decapods groom their egg masses, but this behavior is relatively uncommon in brachyuran crabs (see review by Bauer, 1989) and seems to be particularly uncommon in the more terrestrial species such as grapsids and ocypodids.

Cycles within the reproductive season were correlated with the new and full periods (syzygies) of the lunar month. Such semilunar timing of larval release, so as to correspond to spring tides, is hypothesized to be an adaptation that facilitates export of larvae out of estuaries in *Uca* sp. (Sandifer, 1975; Christy and Stancyk, 1982). However, Sandifer (1975) found larvae of *Sesarma reticulatum* concentrated near the bottom, which would facilitate retention within an estuary. Larval release during spring tides in this species, and possibly *S.* sp. (nr. *reticulatum*), would enable females to release larvae under the protection of high tide in upstream areas not strongly affected by tides at other times, and may transport larvae out of marshes, ditches, and tidal creeks, and into deeper water.

For mature larvae to be released coincident with optimal conditions for their survival (*i.e.*, tides at new or full moons), eggs must be produced and laid in adequate advance of some developmental period, the duration of which itself varies according to exogenous factors (*i.e.*, temperature). Thus, selection would most likely favor egg-laying rhythms coincident with lunar phase but modulated to precede new and full moons by a time period that represents the mean period of embryonic development as would occur under typical environmental temperatures during the reproductive season. The period of embryonic development for *S.* sp. (nr. *reticulatum*) in laboratory mesocosms was very consistent (17.3 days, ± 0.3 95% CI, n = 47) for all broods monitored, slightly longer than the mean of 15.2 days (±2.6 SD, n = 10) reported for *S. reticulatum* by Seiple and Salmon (1987). The 17-day embryonic period positions larval release very near actual dates of new and full moons when it is used to project dates of larval release for field-captured ovigerous females (Fig. 5). To accommodate this 17-day developmental period, *S.* sp. (nr. *reticulatum*) populations may become entrained to lay eggs slightly before syzygies.

Species of crabs having reproductive periodicities that are strongly entrained to lunar or tidal cycles such as *S. cinereum*, *Uca pugnax* (Smith, 1870), and *U. pugilator* (Bosc, 1802) [studies by Seiple (1979a, b) and Dollard (1980), Christy (1978), and Wheeler (1978), respectively] may have periodic highs and lows in numbers of ovigerous females over the course of a reproductive season. These fluctuations could be used to estimate the number of days between each brood, or even the number of broods produced by a single crab each season. However, species such as *Sesarma haematochier* (de Haan, 1835) and *S. intermedium* (de Haan, 1835) studied by Saigusa and Hidaka (1978) and *S.* sp. (nr. *reticulatum*), which can be considered moderately entrained by lunar and tidal cycles, may have relatively constant numbers of ovigerous females in a population for long periods. Accurate estimations of time between broods cannot be made from periodic field samples when this situation exists. Long-term observation of some reproductive event such as larval release or mating in the field often yields valuable information about populations that can be used to infer conclusions about individual cycles, especially for *Uca* spp. Other species do not readily lend themselves to observation in nature, and use of an artificially reproduced habitat in the laboratory

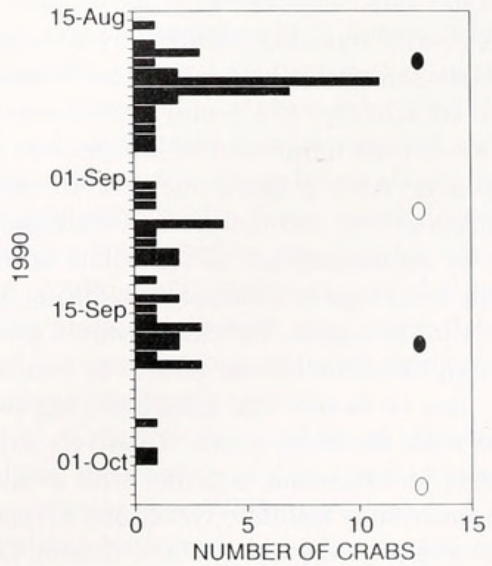

Figure 13. Number of individual *Sesarma* sp. (nr. *reticulatum*) releasing larvae versus date and lunar period, in videomonitored experiments. Solid ovals represent new moons, open ovals represent full moons.

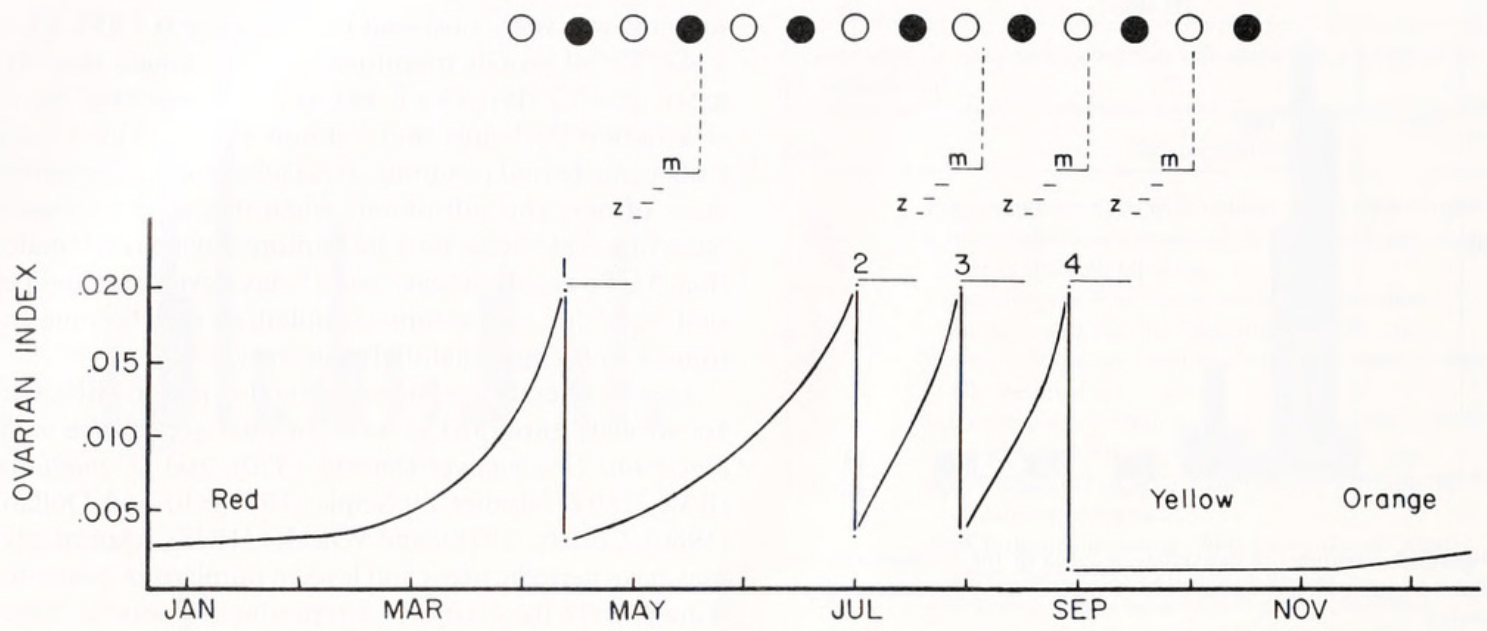

Figure 14. Hypothetical reproductive season for a fully mature female *Sesarma* sp. (nr. *reticulatum*). Base line represents ovarian growth (ovarian wet wt/mm carapace width) over time, peaks indicate egg laying, horizontal lines extending from peaks represent number of days required for embryonic development followed by date of larval release and duration of each larval instar (shorter lines). Vertical dashed lines represent metamorphosis to first crab stage. Molts are indicated, and lunar syzygies are represented by new (solid circles) and full (open circles) moons.

may be the best way to learn about reproduction in these organisms.

At the beginning of the reproductive season, larval release is often out of phase with the lunar cycle (Wheeler, 1978; Dollard, 1980; Christy, 1982). However, evidence of early season synchrony was seen when estimated dates of egg laying and larval release for field samples were compared to dates of new and full moons in the present study. Distinct semilunar peaks were found throughout the reproductive season, although more intensive collecting would have been required to test statistically for rhythmicity.

The previously reported asynchrony of reproductive phase for crabs sampled at higher latitudes (Wheeler, 1978; Dollard, 1980; Christy, 1982) may have been caused by relatively low winter temperatures just prior to the reproductive season. With a sharp increase in temperature cueing ovarian growth and maturation, crabs differentially weakened by winter may not all assimilate nutrients rapidly enough to lay eggs in time to hatch during full or new moons early in the season. Increased ovarian growth rates, together with other metabolic effects of increased temperatures, may be factors that later bring egg production into phase with the lunar cycle. Relatively mild winter temperatures in Louisiana, together with available food early in the year, may facilitate synchrony of reproductive activity even early in the reproductive season. During the latter part of the season, ovarian growth is constrained by the duration of each reproductive cycle, but in the spring ovaries have time to grow to their maximum size. It was at this time that the largest broods of the year were produced.

An overview of the reproductive season for a single crab, based on the evidence gathered in this study (Fig. 14), reveals how reproductive cycles might enable crabs to release larvae under the most favorable conditions for dispersal and survival. The slightly offset semilunar periodicity of egg laying, necessitated by a 17-day embryonic developmental period, would time larval release to take place on or near a full or new moon and thus to coincide with periods of highest tidal amplitude. A combined period of 25 days for oogenesis and vitellogenesis between broods would result in the hatch of a brood approximately one lunar month later. The 16-day larval period would enable a majority of early postlarvae, under optimal conditions, to colonize adult habitats within the marsh during flood tides on or near the dates of full and new moons. Ovarian maturation, decalcification of the genital opercula, and subsequent mating is probably under lunar-influenced hormonal control that corresponds to an offset semilunar rhythm. The minimum period seen between successive broods in the laboratory (21 days) may exemplify an accelerated ovarian maturation in an individual coming into phase synchrony with this rhythm.

Following ovarian maturation in these crabs, the short duration of opercular decalcification and mating receptivity might make it beneficial for females to mate as many times as possible, perhaps without much regard to mate choice. This might be especially advantageous if multiple broods must be fertilized from stored sperm. Delay of egg

laying until the end of the population's early evening activity period would facilitate females encountering males if none had been encountered in burrows or on the surface during the day. Courtship for females appears to involve a mature male's construction of a burrow network in which females are found. While undocumented to date, it would appear advantageous for the male to inseminate as many females as possible and guard them within the burrow from other males. This would be especially true if, as has been found in some other brachyuran species (Diesel, 1991), the last male to copulate displaces and seals off predecessor sperm packets with a sperm gel ensuring fertilization by sperm from the final mating only.

Possible adaptations to a low salinity estuarine habitat in *S.* sp. (nr. *reticulatum*), when compared to *Sesarma cinereum* (a slightly higher salinity and more terrestrial sympatric crab), include an increased duration of embryonic development, increased size of the egg, decreased number of zoeal stages (development of the first zoeal stage within the egg), and decreased period of larval development (Costlow, 1960; Dollard, 1980; Seiple and Salmon, 1987). When compared to development in the majority of grapsid crabs reported in literature to date (most with five zoeal stages), both *S.* sp. (nr. *reticulatum*) and *S. reticulatum* (see Costlow and Bookhout, 1962) would be characterized as having advanced development (Rabalais and Gore, 1985). This adaptation may be advantageous under certain estuarine conditions where low salinity waters bathe the adult habitat and may, as in Louisiana, extend well offshore. Reduction in the number of larval instars from 5 to 2 in certain grapsid crabs has been postulated to serve as an adaptation for freshwater and terrestrial habitats by those species (Hartnoll, 1965), and larval instars may develop profound osmoregulatory ability (Foskett, 1977). Rabalais and Gore (1985), however, are quick to point out that many freshwater and terrestrial crabs, including some grapsids, do not have reduced numbers of larval stages, and they caution making any generalized conclusions about evolutionary trends and adaptive significance of abbreviated development.

Selection for larval release rhythms in *S.* sp. (nr. *reticulatum*) may have occurred because of different pressures than those resulting in rhythms in the more terrestrial *Sesarma* species or those that routinely experience large amplitude lunar tides. The findings of Saigusa and Hidaka (1978) for the Japanese land crabs *Sesarma intermedium* and *S. haematocheir* closely parallel many of the findings of the present study in that all three species were observed to release larvae shortly after dark on days surrounding new and full moons. Although *S. intermedium* and *S. haematocheir* are more terrestrial than *S.* sp. (nr. *reticulatum*), the areas in which these three species released larvae experienced tidal fluctuations in water level that were often greatly affected by other environmental conditions. In particular, the river in which *S. intermedium* and *S. haematocheir* released larvae was influenced by rainfall, and *S.* sp. (nr. *reticulatum*) habitats were influenced by wind. Saigusa (1981) found that *S. dehaani* H. Milne-Edwards, 1853, which lives in rice paddies and river bottoms near the sea, did not exhibit a clear semilunar rhythm of larval release, and the time of larval release was not correlated to times of high tides. The larvae of this species tolerated freshwater better than the larvae of *S. intermedium* and *S. haematocheir.* Saigusa (1982) found that time of larval release for a population of *S. haematocheir* subjected to high amplitude tides was entrained to local daily and tidal cycles; zoea were released during periods of nighttime high tides. But crabs from another population of the same species that experienced low amplitude tides were entrained to a daily rhythm only, and these crabs released larvae soon after dark. In both populations, a semilunar monthly rhythm was retained. Studies in the laboratory show that *S. haematocheir* will retain a natural semilunar rhythm in the absence of moon light, but this rhythm can be phase shifted with an artificial moon light regime (Saigusa, 1980), but not an artificial tidal regime (Saigusa, 1986). However, the time of day that larval release takes place can be entrained by artificial moon light (Saigusa, 1988).

During the present study of *S.* sp. (nr. *reticulatum*), a natural semilunar rhythm was maintained in the laboratory, and entrainment to an artificial tidal cycle was not observed. Entrainment to tidal cycles by moonlight was not addressed in the present study. The moderate and variable tides occurring in the habitat from which *S.* sp. (nr. *reticulatum*) was collected, the intertidal nature of the crab, and the observance of larval release during daytime tidal inundation, would support the hypothesis that *S.* sp. (nr. *reticulatum*) releases larvae whenever conditions insure it would be safest to be exposed, either in the early evening, like in the population of *S. haematocheir* from a low tidal amplitude area, or during tidal inundation. Both tidal inundation and darkness may provide protection for the crab and enable it to be active on the marsh, perhaps with reduced risk of predation during larval release. High tide periods also favor larval dispersal and survival as they are followed by ebbing tides, which carry larvae away. Additionally, high water tends to disperse small planktivorous fish, which may enter the flooded marshes and become less concentrated along shorelines or in tidal creeks during high water.

The control of the exact time of larval release appears to be modulated by behavior of the ovigerous female crab in *S.* sp. (nr. *reticulatum*). While this event may, in turn, be brought about by stimuli from larvae, the nature of such stimuli is unknown. Recent studies of *Sesarma cinereum* and *Uca pugilator* suggest that stereotypic larval release behaviors in these species are not directly mediated

by chemical releases from hatching larvae, such as occurs in some less terrestrially adapted xanthid crabs (see De Vries and Forward, 1989, 1991; De Vries *et al.*, 1991). The period of "hyperactivity" observed to precede *S.* sp. (nr. *reticulatum*) larval release may be linked to this control mechanism, and is likely coupled to behavior in which crabs preparing to release larvae migrate to the marsh edge from burrows that range well into upper intertidal reaches of marshes, stream banks, and other wetland settings.

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