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MOLTING IN THE MATURE FEMALE BLUE CRAB, *CALLINECTES SAPIDUS* RATHBUN

Kirk J. Havens and John R. McConaugha

ABSTRACT

The present study examined the hypothesis that mature female blue crabs, *Callinectes sapidus*, do not enter a terminal anecdysis. Induced molting via eyestalk ablation, size frequency distributions, gonad development and limb regeneration indices from field collected animals are used as indicators of potential post maturity molts. Eyestalk ablation of 15 mature females resulted in ecdysis in 11 individuals approximately 51 days (standard error = 0.64) after ablation, indicating a physiological ability of mature females to complete ecdysis. Analysis of size frequency distributions from catch data indicated two distinct shifts from smaller to larger females, one in early spring and a second in early fall. While migration of larger females into the study area cannot be ruled out, the data suggest molting activity within the sample population. Within the field sample, 11.2% of the animals had regenerating limb buds (R -value = 0.5-5.4). Formation of limb buds is not encountered in species known to have a terminal molt at maturity. These observations suggest that female blue crabs may enter a diapause stage at maturity and some may undergo an additional molt after maturity.

The life history of the blue crab, *Callinectes sapidus* Rathbun, has been the subject of many studies (Hay, 1905; Churchill, 1918; Van Engel, 1958). A female will molt 7-8 times during larval development and 18-20 times as a juvenile (Costlow and Bookout, 1959). The molt from the juvenile to mature stage has historically been considered the "terminal" or final molt for females. Females mate while the cuticle remains soft immediately after this juvenile/adult molt. The present terminal ecdysis theory proposes that this few hour period is the only mating time during the female's 2-4-year life expectancy.

Brachyurans have the ability to regenerate lost limbs at the time of the molt. If a limb is damaged, it is autotomized and the regeneration of a new limb initiated (Adiyodi, 1972; Skinner et al., 1984). Successful culmination of energy allocation to regeneration requires a successful molt.

Molt frequency is likely determined by environmental (e.g., temperature, light, salinity) and physiological (nutrition, regeneration, etc.) states (Passano, 1960b; Chang and Bruce, 1980). The mechanism controlling ecdysis is an antagonistic interaction between molt inhibiting hormone produced in the x-organ sinus gland complex of the eyestalk and the molting hormone ecdysone produced in the y-organ located ventral to the eyestalks (Chang and O'Conner, 1978).

Some decapod crustaceans identified as having a female terminal anecdysis include *Homarus gammarus*, *Maja squinado*, *Libinia emarginata*, *Chionoecetes bairdi* and *C. sapidus* (Passano, 1960a; Hinsch, 1972; Donaldson et al., 1981; Skinner, 1985). Other research is not in agreement and has shown that *Homarus gammarus* may enter a diapause stage when mature and that mature females may molt every other year (Cobb and Phillips, 1980). Some fundamental differences exist between the life histories of *C. sapidus* and other decapods known to exhibit a terminal molt (Table 1). For example, the tanner crab (*Chionoecetes bairdi*) mates while hard and does not regenerate limb buds in the terminal anecdysial stage (Donaldson et al., 1981). Size distribution data for mature female tanner crabs show a range from 80-108 mm resulting in a difference of 35% between smallest and largest (Donaldson et al., 1981). Brachyura that continue to molt

Table 1. A comparison of some characteristics of documented terminal molt species and *Callinectes sapidus*

Terminal molt species	Mature female <i>Callinectes sapidus</i>
Calcification of basal joint	no calcification of basal joint
Hard shell mating	only soft shell mating
No limb regeneration	limb regeneration
Deteriorated carapaces	lack of deteriorated carapaces
Degeneration of y-organ	y-organ remains viable

after maturity show a distinct separation between somatic and reproductive growth (Adiyodi, 1985). Regeneration of limbs is delayed or suppressed as the animal prepares for spawning and energy reserves are directed to ovarian growth. In *C. sapidus*, extremely small ovigerous females have been observed (Fischler, 1959) and mature females undergoing a second molt have been collected (Abbe, 1974; Olmi, 1984; Oesterling, pers. comm., 1987). Within the Chesapeake Bay population, there is a large size difference among mature females (84%), deteriorated carapaces or carapaces with epizoons are usually absent, and limb buds have been found on field collected animals. These observations suggest the possibility of a second molt in mature female blue crabs.

In an effort to examine further the terminal anecdyosis hypothesis versus a possible diapause in molting of mature female blue crabs, the present study examined the size frequency differences over time, gonad index of mature females over time, and the state of limb bud formation in field collected animals. The ability of laboratory held blue crabs to initiate premolt activity following eyestalk removal was also examined.

MATERIALS AND METHODS

Size frequency data were obtained by random samples of 150 mature female *Callinectes sapidus* collected at approximate 2-week intervals, resulting in a total of 2,700 crabs sampled. Crabs were collected by dredging and potting in the lower region of the Chesapeake Bay (Fig. 1). *C. sapidus* were distinguished from *C. similis* based on the number of frontal teeth (Gosner, 1978). Measurements were taken from point to point at the ninth lateral spine and recorded to the nearest millimeter. Crabs were categorized as: small (<136 mm), medium (136–156 mm), or large (>156 mm). Size and number of limb buds were recorded for each animal. In addition, size and number of epizoons (crab barnacle, *Chelonibia patula*) as well as general appearance of the carapace were noted.

R-value is a regeneration index that measures limb development and can be used as an indication of molt readiness. *R*-values were obtained using the following formula: $R = \text{bud length} \times 100 \cdot \text{carapace length}^{-1}$. An *R*-value of over 12 is considered indicative of an impending molt (Bliss, 1956).

Twenty animals were retained from the sample group to test endocrine control of ecdysis. Eyestalk ablation was conducted on 15 mature females and five females were retained as untreated controls. Animals were held in 10-gallon aquarium tanks at 20° to 23° C and fed Purina Catfish Chow. Eyestalks were removed using a scalpel and immediately cauterized. To reduce mortality due to operational stress, one eyestalk was excised at a time with a 2-day recovery period before ablation of the second eyestalk.

Reproductive state was determined by sampling 15 mature females at each bimonthly measurement period. Width, length from point to point, total wet weight, and gonad wet weight measurements were recorded for each animal. Total wet weight was measured on a triple beam balance to the nearest tenth of a gram and gonad wet weight was measured on an analytical balance to the nearest tenth of a gram. A Chi-square statistical test was used to analyze size class frequency distribution.

RESULTS

Size frequency distribution at each sample date is shown in Figure 2. A significant shift from smaller to larger crabs occurred between 1 April and 2 May and between 1 August and 20 September ($P < 0.001$).

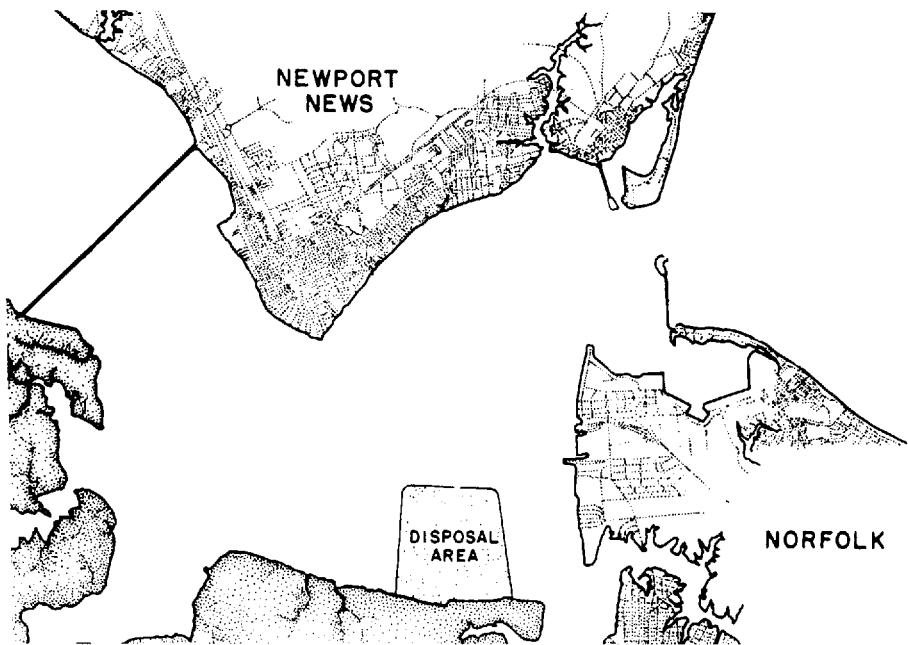


Figure 1. Blue crab sampling location—lower Chesapeake Bay.

Of the 2,700 females sampled during the study, 11.2% displayed limb bud regeneration. Monthly samples averaged as high as 21% (Fig. 3). *R*-values (Regeneration Index) were calculated for the sample set (Fig. 4). The mean *R*-values ranged from 1.5–2.75. The mean *R*-value for the total sample was 2.2 (standard error = 0.05). Of the 11.2% with limb buds, 17% had an *R*-value of 3.0 or greater. The highest observed *R*-value was 5.4 in the 14 March sampling. The 14 March sample also had the highest amount of females with limb buds (25%) with 30% having an *R*-value of 3.0 or greater.

Less than 1% of the total sample had deteriorated or barnacle encrusted carapaces. None of the barnacles exceeded 7 mm in diameter.

Three of the crabs subjected to eyestalk ablation during the study died within the first week, presumably from operational stress and/or infection. All of the remaining females molted within 60 days of eyestalk removal (Table 2). The mean time to ecdysis was 51.6 days (standard error = 0.64). The largest female (125 mm) had the longest intermolt period (54 days) and the smallest female (117 mm) had the shortest intermolt period (47 days).

Spawning activity within the population began in May with a peak period (100% ovigerous) in June to August (Fig. 5). A simultaneous reduction in limb bud production occurred during the peak reproductive period (Fig. 3). As the female prepares for spawning, somatic growth ceases. Energy reserves are used for egg production instead of regeneration. This is typical of decapods that do not exhibit a terminal anecdysial stage (Adiyodi, 1985).

DISCUSSION

Crustaceans with a fixed number of molts prior to reaching maturity subjected to similar environmental conditions should attain similar sizes at maturity. Al-

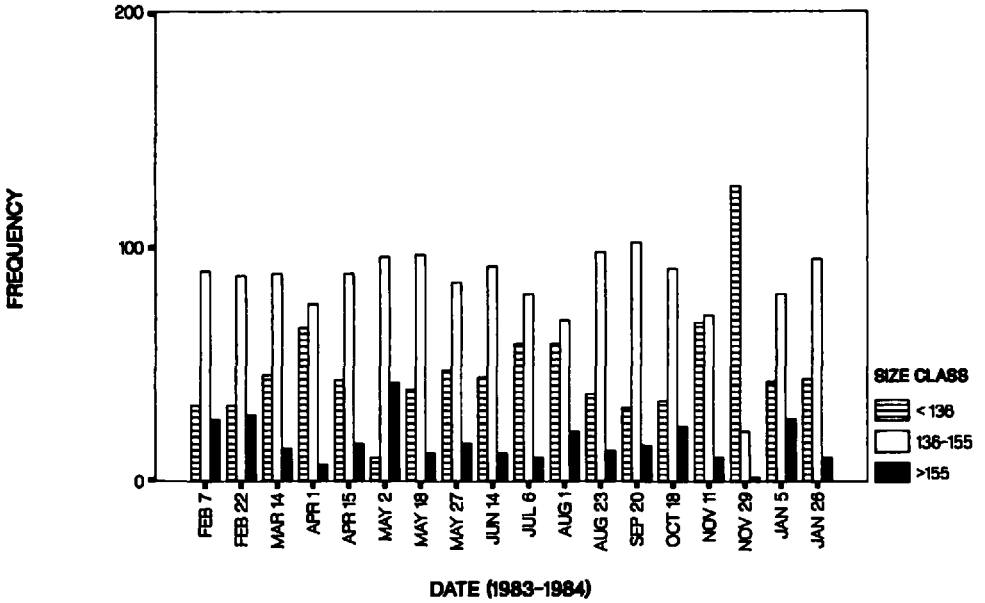


Figure 2. Size frequency distributions per sample date. Carapace width was measured in millimeters from point to point across the ninth lateral spine. Significant size shifts ($P < 0.001$) from small to large crabs occur between the 1 April and 2 May dates and between the 1 August and 20 September dates.

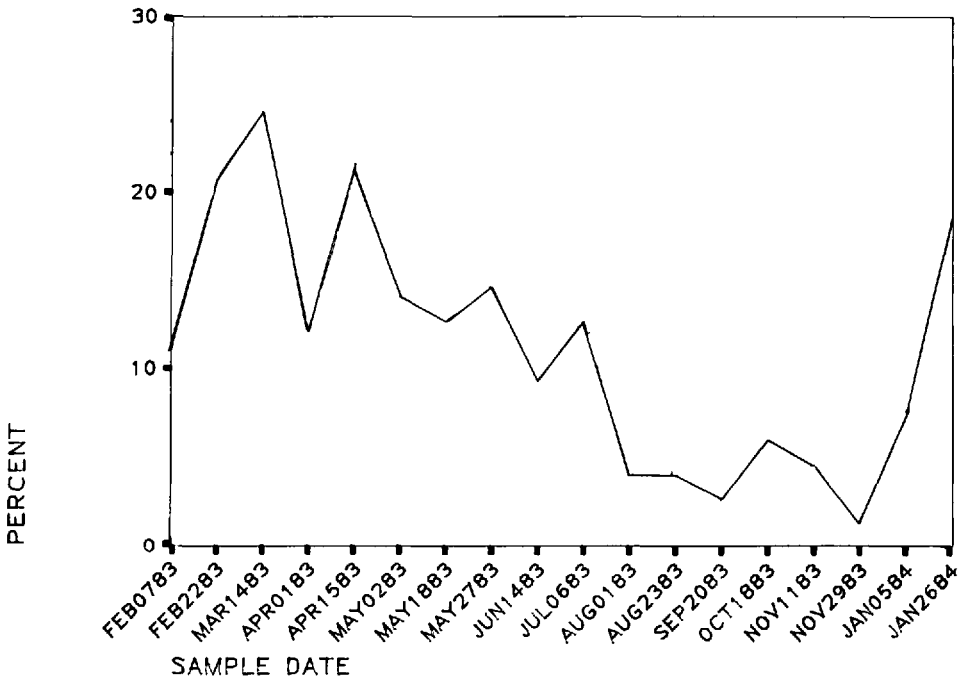


Figure 3. Percent of mature females per sample date displaying limb buds. Limb buds were measured in millimeters. The sample date with the highest percentage of females with limb buds was 14 March with 24.6%.

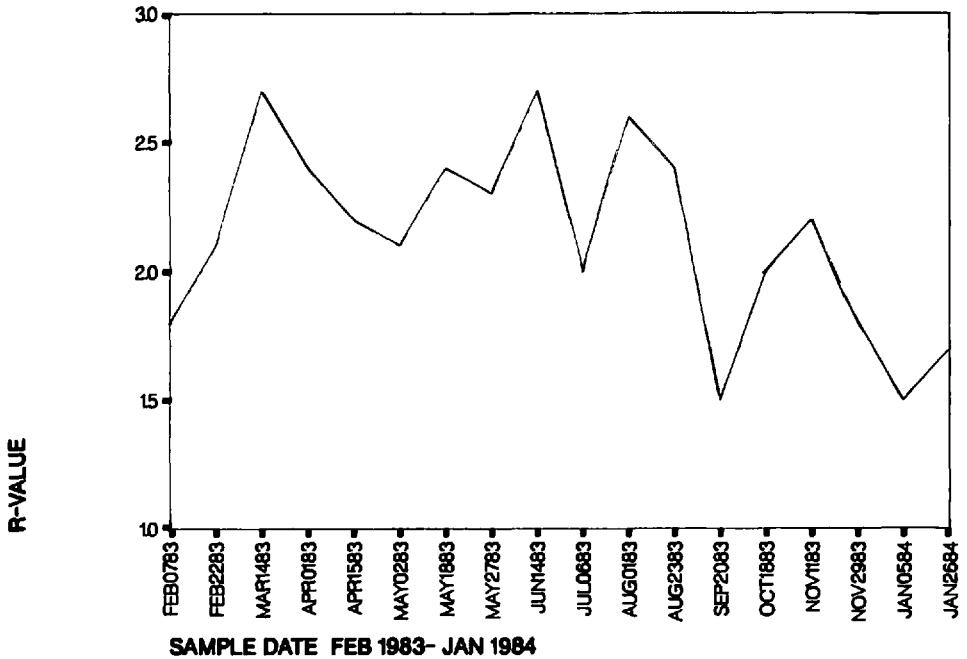


Figure 4. Mean R -values (Regeneration Index) per sample date. R -value is a measure of molt readiness calculated by limb bud $\times 100 \cdot$ carapace width $^{-1}$ from point to point (Bliss and Hopkins, 1974). The highest observed value was 5.4. Mean for the total sample was 2.2 (SE = 0.052).

ternatively, additional molts after maturity would result in a greater size range among adult females. The large size difference among mature female *C. sapidus* indicates either environmental effects or the possibility of additional molts after maturity.

Investigations of the effects of environmental factors on growth have shown mixed results (Ito, 1953; Kurata, 1959; 1962; Haefner and Shuster, 1964; Tagatz, 1968; Leffler, 1972). The effect of salinity on the molt increment in *C. sapidus*

Table 2. Days to molt after eyestalk removal in mature female blue crabs

Carapace width (mm)	Days to molt
120	52
120	54
119	49
117	47
120	50
121	53
119	54
122	52
122	53
121	50
120	52
<u>125</u>	<u>54</u>
\bar{x} 120.5	\bar{x} 51.6
(standard error = 0.57)	(standard error = 0.64)

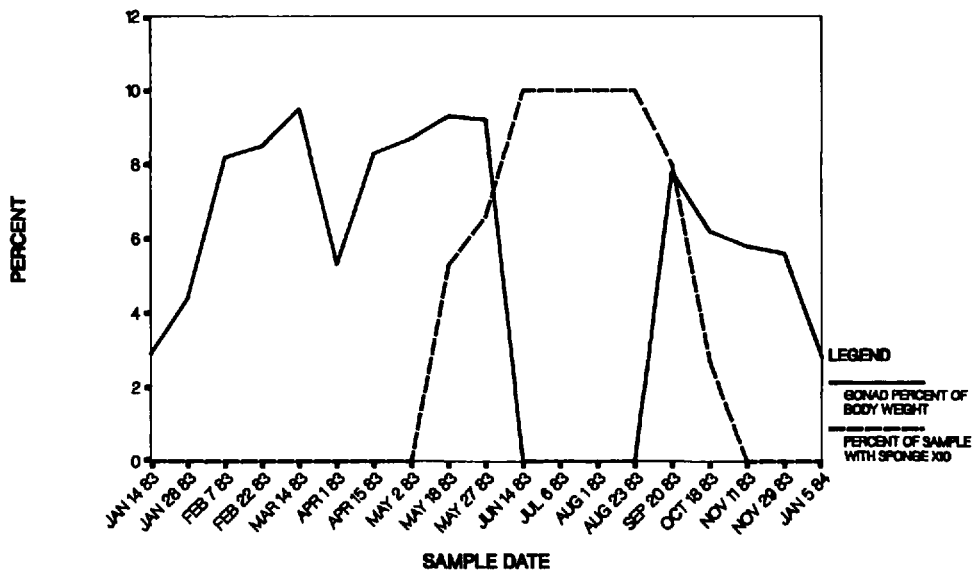


Figure 5. Reproductive state of mature female blue crabs per sample date. Sponge production and gonad percent of body weight. 100% sponge production from June to August.

was found to be minimal in water of less than 1‰ (Tagatz, 1968) and had no effect in salinities from 9–27‰ (Haefner and Shuster, 1964).

Food supply would appear to be the most likely factor that could result in different size increment at molt. A reduction in food supply has been shown to reduce the size increment at molt in the crayfishes *Cambarus clarkii* and *Cambaroides japonicus* (Ito, 1953; Kurata, 1959). However, size increase per molt was unaffected by food level for *Palaemonetes*, *Panulirus longipes* (spiny lobster), and the terminal molt copepods *Cyclops viridis* and *Cyclops vernalis* (Broad, 1957; Heywood, 1970; Knowlton, 1974; Chittleborough, 1975). Millikin et al. (1980) showed an effect of diet on the weight of female blue crabs. However, the effect on carapace width was evident only at extreme diet enhancement or reduction but minimal at the intermediate crude protein levels of 37% and 23%.

Analysis of the data on specific sampling dates (Fig. 2) showed a significant size class shift ($P < 0.001$) between 1 April and 2 May. More small crabs and fewer large crabs than expected were found on 1 April, whereas fewer small and more large crabs were found in May. Generally, the dominant spring molt occurs when temperatures rise into the teens and the moon is full (pers. obs.). Figure 6 shows a sharp temperature rise during this period coincident with a full moon on 27 April. A size increase of 20–30% would place a majority of the small crabs in the large (> 156 mm) class. This shift from small to large females may be the result of a molt of a percentage of the smaller females preceding the peak spawning period of summer and fall. Larger females produce larger egg masses (McConaughy et al., 1987; Prager et al., 1989), thus a molt to a larger size would be advantageous for small females and the population.

A second significant shift ($P < 0.001$) is seen between the 1 August and 20 September sampling dates. More small crabs and fewer medium crabs are found on 1 August and more medium and fewer small crabs on 20 September. This shift from small to medium may coincide with the fall molt and follows the peak spawning period when, generally, molting and regeneration activities are suppressed.

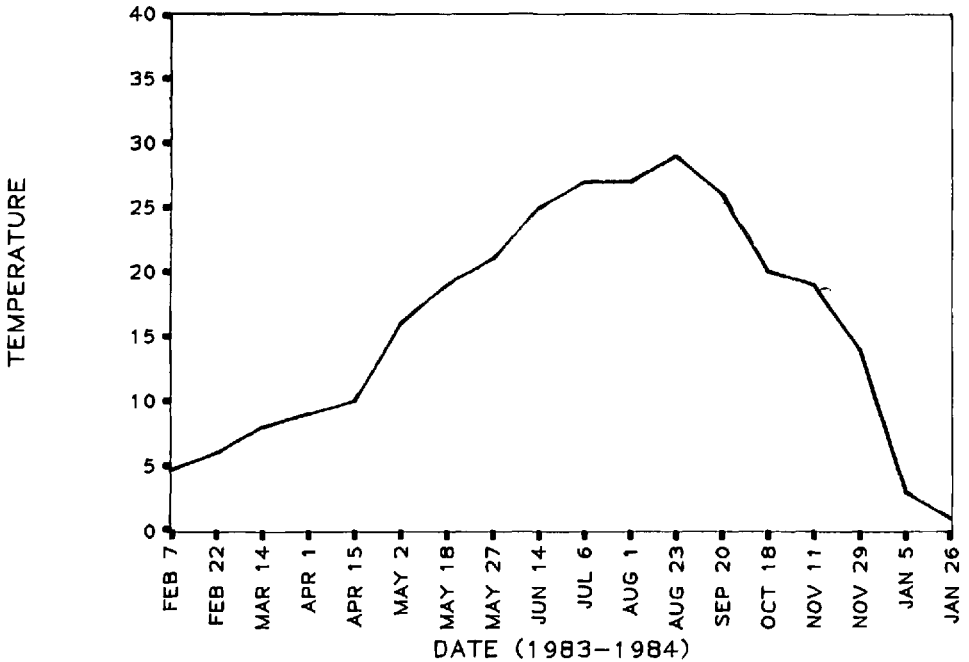


Figure 6. Mean seawater temperature in degrees Celsius as observed in the York River for 1983-1984 (Virginia Institute of Marine Science).

The peak of small females (<136 mm) observed on 29 November sampling date may be the immigration of the previous year-class females as they migrate toward the bay mouth (Jones et al., 1989). These females may overwinter and spawn and/or molt as the temperature rises in the spring.

Data from specific sampling periods suggest a size shift from small to large females during the peak molting times of *C. sapidus*. These brief shifts are masked by the seasonal population dynamics. However this could be a mechanism by which a percentage of smaller and/or virgin females, prompted by temperature and lunar cycle, increase their size and, subsequently, their fecundity.

Calcification of the basal limb joint has been reported in adult spider crabs (*Brachyura*, *Majidae*). This would inhibit the growth of regenerated limb buds and is considered an indicator of terminal anecdyosis (Hartnoll, 1965). The present study revealed no sign of calcification of the basal limb joint in mature female *C. sapidus*. Churchill (1918) cited the lack of limb buds on adult female blue crabs as evidence of terminal anecdyosis. However, data collected in this study conflict with Churchill's statement. Of the 2,700 females sampled, 11.2% displayed limb bud regeneration. Eyestalkless females regenerated limb buds that obtained *R*-values exceeding 14 in all cases before molting. In addition, adult blue crab females with experimentally autotomized chelipeds have been shown to regenerate limb buds (Ary et al., 1985).

The mean *R*-values in this study ranged from 1.5-2.75 with 5.4 the highest recorded value. While *R*-values below 12 are not indicative of imminent molting, they do represent a considerable investment of energy resources (Hodges, 1958; Skinner, 1985; McConaugha, pers. obs., 1989). 11.2% of females in this study diverted energy resources to regeneration. Since the limb will not be fully functional until after the next molt, it would seem to be an inappropriate allocation

of energy for a female to begin limb bud regeneration if the limb will never become functional. In fact, it would seem more efficient for the female to use that energy for egg production.

In large mature crustaceans that molt once a year, such as the land crab, *G. lateralis*, the limb bud may remain small and inactive for as long as 10 months (Skinner, 1962; Holland and Skinner, 1976). At the initiation of the next proecdysial period, growth resumes and proceeds rapidly. The presence of small, inactive limb buds on mature female *C. sapidus* may indicate a diapause stage as seen in *G. lateralis* instead of a terminal anecdyosis stage. This conclusion is supported by the lack of limb bud formation on well-documented terminal anecdyosis animals (Hartnoll, 1965).

Reproduction and molting require substantial energy expenditure and may consume more energy in the adult crustacean life cycle than other activities (Adiyodi, 1985). In order to meet the demands of these events, reproduction and molting are generally separated into distinct seasons (Aiken and Waddy, 1980; Adiyodi, 1985). During reproduction, somatic growth ceases and the energy reserves are used for egg production. In the majority of crustacean species, both males and females continue to molt after maturity (Hinsch, 1972; Adiyodi, 1985).

The major pulse of molting in *C. sapidus* occurs during the spring (Jones et al., 1989), whereas spawning occurs in the summer and fall (Van Engel, 1958; McConaughy et al., 1987).

The percent of each sample with limb buds and the percent of the sample with extruding eggs sacs is shown in Figure 7. Limb bud production was highest in early spring and declined through the summer months. This separation between somatic growth and reproductive growth is consistent with other Brachyura that do not have a terminal molt (Adiyodi, 1985).

In female *C. sapidus*, mating occurs during the postmolt period before the hardening of the exoskeleton. The majority of Brachyura follow this male hard-female soft pattern. However, in some groups such as Majidae, mating can occur in both soft and hard females. In the family Majidae, females that have a terminal molt at maturity can mate in both hard and soft states (Hartnoll, 1965). Thus a terminal molt has little effect on reproductive capability. Because *C. sapidus* females can mate only while soft, the onset of terminal anecdyosis at the pubertal molt would result in only one mating in the female's life cycle.

There is evidence that the y-organ, which produces the molting hormone ecdysone, degenerates in crustaceans that have entered terminal anecdyosis (Skinner, 1985). Carlisle (1957) hypothesized that the juvenile to mature molt was followed by a degeneration of the y-organ. Data from the present study (Table 2) indicates that the y-organ remains functional in mature female blue crabs, *C. sapidus*, further supporting a diapause stage rather than terminal anecdyosis.

Data from this study have shown two distinct size shifts from smaller to larger crabs and a distinct separation between somatic and reproductive growth similar to non-terminal molt brachyurans. In addition, adult females retain the ability to molt and regenerate limbs if the molt inhibiting hormone is removed. Field collected animals displayed limb buds and no calcification of the basal joint was observed. Few individuals had deteriorated carapaces or carapaces with epizoons. Abbe (1974) documented the partial ecdysis of a mature female blue crab and Olmi (1984) reported a mature female in proecdysis. Commercial shedding operators have observed adult females completing ecdysis in holding tanks (Oesterling, pers. comm., 1987). This may be evidence that a percentage of female blue crabs, *C. sapidus*, molt after maturity and enter a diapause stage as opposed to terminal anecdyosis.

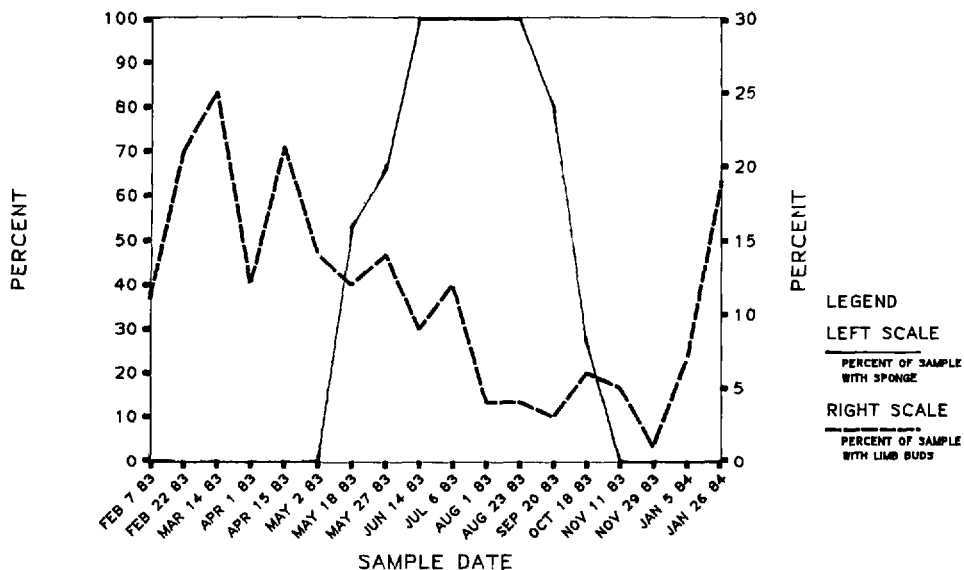


Figure 7. Percent of sample with limb buds and percent of sample with sponge. Egg production increases as limb bud production decreases.

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