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DEVELOPMENT OF THE REPRODUCTIVELY FUNCTIONAL FORM IN THE MALE BLUE CRAB, *CALLINECTES SAPIDUS*

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ABSTRACT

The progression of the morphological features of the male blue crab reproductive system that culminate in puberty involves one change in the gonad, four combinations of the method and degree of adherence of the abdomen to the sternum, four variations in the positions of the penes, and four variations in the positions of the pleopods. The sequence of development appears to be established: (1) spermatophores must be present in the anterior vasa deferentia; (2) the abdomen must be completely free of the sternum, or, in addition, may be locked by the sternal tubercles; (3) and the penes and second pleopods must be inserted in the first pair of pleopods.

Descriptions of the patterns of growth and reproduction of a brachyuran decapod crustacean should include information on the number of zoeal, megalopal and definitive crab instars, and whether sexual maturity was attained prior to, or at the time of, or after final ecdysis (Hartnoll, 1982; 1985). While Hartnoll's summarizations of the growth and reproductive patterns of sexually mature decapods are extensive, unfortunately, they are almost entirely limited to the patterns of females. Much, or most, of the omission of males in studies is probably due to a preoccupation of interest on the reproductive potential of a stock as measured by female fecundity. Part of the omission must be due to the general acknowledgment that external morphological signs of the transition from the juvenile to the adult stage are usually unknown for males of most decapod species.

Although most morphological features of the blue crab, *Callinectes sapidus,* are established in the early benthic crab stages, some are not fully expressed until sexual maturity. Only a few features of male and female blue crab juvenile external morphology and of the histology and morphology of the gonads have been described (Ordway, 1863; Conn, 1883; Rathbun, 1896; 1930; Hay, 1905; Churchill, 1919; Gray and Newcombe, 1938; 1939; Tagatz, 1968a; Johnson, 1980; Adiyodi, 1985; Charniaux-Cotton and Payen, 1985). Accounts of adult morphology of the gonads, abdomen, sternum, penes and pleopods may be found in Say, 1817; DeKay, 1844; Stimpson, 1860; Ordway, 1863; Brooks, [1882] 1894; Rathbun, 1896; 1900; 1930; Hay, 1905; Churchill, 1919; Cochran, 1935; Snodgrass, 1936; Cronin, 1942; 1947; Hard, 1942; Pyle and Cronin, 1950; Johnson, 1980; Adiyodi, 1985; Charniaux-Cotton and Payen, 1985.

The purpose of this paper is to report on studies of the internal and external morphology of male blue crabs, *Callinectes sapidus,* in the transition from the juvenile to the adult stage. These studies were prompted by the discovery in 1955 that the edges of the abdomen of juvenile females through the penultimate instar, and of the abdomen of small males 25–50 mm carapace width, were sealed to the sternum. In contrast, the abdomen of an adult female and that of a mating male were free from the sternum (Van Engel, 1958).

METHODS

Five collections of male blue crabs were made along the north shore of the York River between Sarah's Creek and Purtan Bay, within 1.6 km downriver of Gloucester Point and 16 km upriver, from

July through November 1956, from June through September 1957, in June and July 1958 and in November 1958. In July 1958, a sixth collection was made in a high-salinity marsh at Oyster, VA, on the ocean side and southern end of the Virginia's eastern shore. Crabs were caught at random by hand, with dipnet, hand pushnet, crab scrape and commercial crab pot. Sites and dates of collections were chosen to provide data that might yield information on differences in morphology between samples separated geographically, seasonally or annually.

Measurements were made of the maximum carapace width across the back between the tips of the longest lateral spines (LCW); 1,127 crabs measuring between 52 and 185 mm LCW were saved for study. The presence or absence of spermatophores in the anterior vasa deferentia (AVDs) and the morphology of the abdomen and the method and degree by which it was attached to the sternum were determined in all crabs; the positions of the penes and 2nd pleopods relative to the 1st pleopods were noted only in the 1957 and 1958 collections. Occasionally, to reduce examination time, when a majority of specimens in a width group showed that the condition of the gonad, abdomen, penes or pleopods was consistent (e.g., when those crabs had spermatophores in the AVDs and none were without spermatophores), the condition of that organ was not examined in the remainder of that width group. All data were pooled in 5-mm width groups.

Mating behavior of some of the males collected in 1956 and on all males collected in 1957 was examined prior to the determination of their internal and external morphological development. Males, 52 mm LCW and larger, and juvenile females in the penultimate instar were caught at frequent intervals and placed in outdoor, concrete-lined pools supplied with a continuous flow of York River water of approximately 20‰ salinity. Pairs of crabs were removed from the pools within hours after they were observed mating. In 1956, carapace width, molt stage, contents of the AVDs, and the condition of the abdomen were determined on the male partner, and the contents of the seminal receptacles examined; in 1957, the positions of the penes and pleopods were also noted. In both years, at 2–3-week intervals, males that had not mated were removed from the pools and their morphological condition was determined.

RESULTS

The inverted T-shape of the abdomen, characteristic of males of the genus *Callinectes*, is superficially divided into five sections, and composed of six segments and a telson. Only the first and second segments and part of the third segment are visible in a dorsal view of the crab, the first overlapped almost completely by the carapace. In all males, the first segment of the abdomen is fused to the second, but the outlines of the first and second segments remain distinct. Movement between these segments is limited to a small angle in Stage B crabs, probably due to the flexibility of the shell, and no movement occurs in Stage C crabs. In some males, the second segment is immovably attached to the third segment, while in others slight movement is possible. The third, fourth and fifth segments are almost completely fused and their outlines are scarcely distinguishable. Both the sixth segment and the telson are freely higher proximally, although movement at the proximal border of the sixth segment can occur. A pair of tubercles on the fifth thoracic sternal segment appose a pair of depressions on the distal end of the sixth abdominal segment, formed by chitinous thickenings of the membrane covering the ventral surface of the abdomen. When the tubercles are seated in the abdominal depressions, the abdomen is locked in position and can be pried free only if force is exerted. This mechanism may keep the abdomen flexed in smaller males, but appears unused in males wider than 115 mm LCW.

Four combinations of the association of the abdomen to the sternum were observed in males between 52 and 125 mm LCW, progressing from positions which physically inhibit the males to those permitting copulation. Group 1. Lateral borders of the third through the sixth segments are sealed to the edges of the sternal groove. Force is needed to pull the abdomen free, and shreds of segments remain on the sternum; Group 2. Lateral borders of the third through the fifth segments are sealed to the edges of the sternal groove. The sixth segment is not sealed to the sternum and may be locked to the sternal tubercles. Force is needed to pull the abdomen free, and the membranous seal tears, leaving shreds of the third to the fifth segments attached to the sternum; Group 3. The sixth segment of the abdomen is hooked over the sternal tubercles, and all other segments are free from the sternum; Group 4. All segments of the male abdomen are completely free from the sternum.

Since the abdomen of a male crab is extended slightly and the intromittent spines of the first pair of pleopods protrude laterally at the narrowing of the sixth segment during copulation, a crab with an abdomen conforming to the description of either Group 3 or 4 should be able to insert its intromittent spines into the ostia of the female. Hence, only Groups 3 and 4 crabs are considered reproductively functional. Locking and partial sealing are presumed to be transitory phases, since relatively few males, approximately 15%, were observed with the sixth segment held to the sternal tubercles (Group 3) or with edges of the fused 3–5th segments partially sealed to the sternum (Group 2).

Four combinations of the positions of the penes and four combinations of the positions of the pleopods were observed, arranged from physically complete conditions to those inhibiting copulation. Pene combinations were designated with odd numbers and pleopod combinations with even numbers. Group 11. Left and right penes are inserted in the bases of the 1st pair of pleopods; Group 31. Left penis is not inserted in the base of the left 1st pleopod; right penis is inserted in the base of the right 1st pleopod; Group 13. Left penis is inserted in the base of the left 1st pleopod; right penis is not inserted in the base of the right 1st pleopod; Group 33. Neither left nor right penis is inserted in a same-side 1st pleopod; Group 22. The intromittent spines of the left and right 2nd pleopods are inserted in the bases of the 1st pleopods; Group 42. The intromittent spine of the left 2nd pleopod is not inserted in the base of the left 1st pleopod; the spine of the right 2nd pleopod is inserted in the base of the right 1st pleopod; Group 24. The intromittent spine of the left 2nd pleopod is inserted in the base of the left 1st pleopod; the spine of the right 2nd pleopod is not inserted in the base of the right 1st pleopod; Group 44. Neither the left nor right intromittent spine is inserted in the base of the same-side 1st pleopod.

In relatively few males, approximately 13%, both penes were not inserted in the 1st pleopods (Groups 31 and 13), and only 2% did not have both spines of the 2nd pleopods inserted in the 1st pleopods (Groups 42 and 24), conditions which suggest that those phases are transitory. In subsequent analyses, only individuals in Groups 11 and 22 were considered physically capable of reproduction, and males in Groups 33 and 44 considered physically incapable; males in other groups were omitted.

All of the collections were combined to simulate a single, random sample of the blue crab population of the Chesapeake Bay and adjacent waters on the ocean side of the Eastern Shore. In the composite, spermatophores first appeared in the AVDs of 3% of the males in the 67-mm width class (65–69 mm LCW range), were present in over 50% of the males of the 82-mm width class, and were found in 95% or more males in the 97-mm and larger width classes (Fig. 1). Percentage occurrence is not shown for width groups >137 mm, since occurrence in all of them ranged from 95–100%. The abdomen was free of the sternum in 3% of the males in the 82-mm width group (Abdomen Group 4), although in some males it was locked to the sternal tubercles, was free in 50–75% of the males of the 102-mm width class, and was completely free in 90% or more males in the 107-mm and larger width classes. Penes and pleopods first appeared in functional positions (Groups 11 and 22) in 5–8% of the males in the 82-mm width class, in approximately 50% of the males in the 107-mm width class, and between 80 and 92% of all males in the 117-mm and larger width classes (Fig. 2).

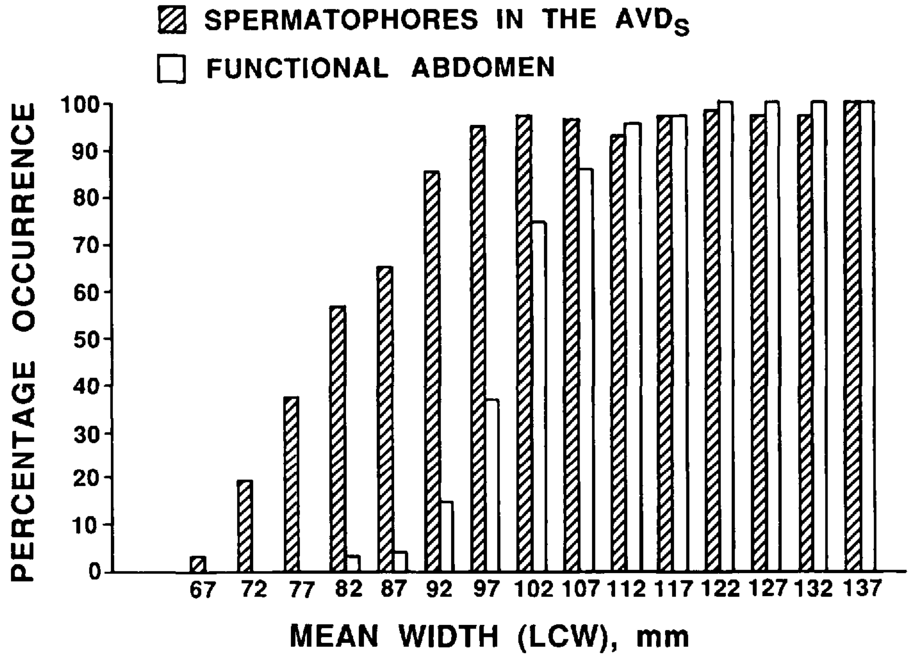

Figure 1. Percentage frequency of occurrence of the total number of male blue crabs for each 5-mm carapace width (LCW) size class, those with spermatophores in the anterior vasa deferentia (AVDs) and those with functional abdomens.

Transition from the juvenile to the stage of being physically capable of copulation can be deduced from the above observations, occurring in about 3% of the individuals in the 82-mm width group, in 50% or more of the composite population in the 107-mm width group and attained by 80% or more at 117 mm.

Estimates of the rate of progression of each morphological feature through the reproductive cycle could be affected by the existence of diverse groups of males in various physiological states within the composite, and the relative number of individuals in each group. Collections that were separated geographically, seasonally or annually, or demonstrated different mating behavior patterns, or consisted of different width ranges were selected for chi-square analyses of the numbers of males with (1) gonads without and with spermatophores, (2) non-functional and functional abdomens, (3) penes not inserted in the 2nd pleopods and those inserted, and (4) 2nd pleopods not inserted in the 1st pleopods and those inserted. Analyses were tests of independence, in fourfold contingency tables, with corrections for continuity (Table 1A–1H).

Highly significant differences in the proportions of males that had functional gonads, abdomens, penes or pleopods occurred between non-mating and mating males in the York River 1957 collection (Table 1A). Since disproportionate numbers of very small or large crabs in any collection could influence estimates of the rate of progression of each morphological feature through the reproductive cycle, the width ranges were made equal and the chi-square tests were repeated: non-mating and mating males remained highly significantly different in their proportions of functional organs (Table 1B).

In the 1956 study of mating behavior, non-mating males were in Stages B, C, and D_0–D_2, ranged in width from 68–142 mm, and represented 28% of all males;

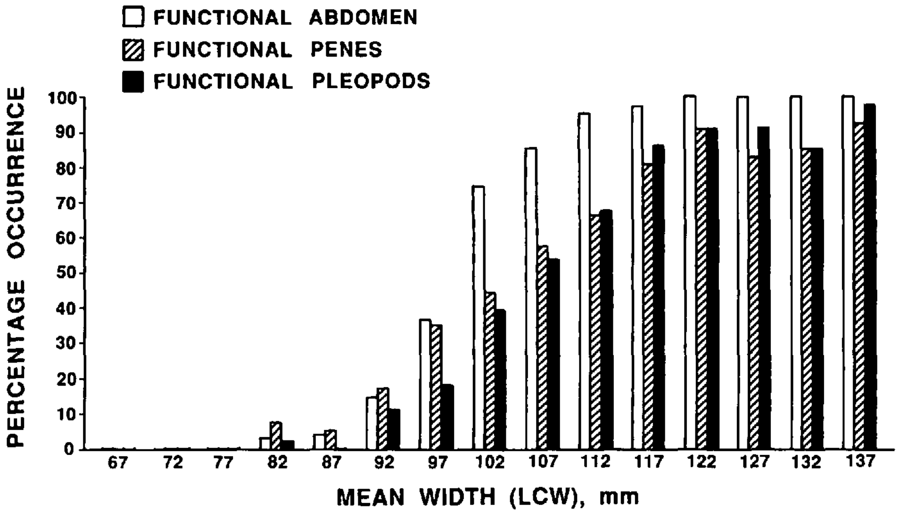

Figure 2. Percentage frequency of occurrence of the total number of male blue crabs for each 5-mm carapace width (LCW) size class, those with functional abdomens, with functional penes and with functional pleopods.

in 1957, among 149 males that ranged in width from 57–132 mm, almost 43% of the males, representing all stages, did not mate. In both years, males that molted did not select mates until they had passed Stage B. Several Stage B males were temporarily marked with tags strapped across the back between the longest lateral spines, and a time lapse of four to six days after the molt was noted before mate selection occurred. In Stage B males, in the interval preceding mate selection, neither the penes nor the spines of the 2nd pleopods were inserted in the 1st pleopods, indicating that the males were physically unable to function sexually. The presence of large Stage B (non-mating) males would incorrectly increase the estimate of the width at which 50% or more of the individuals become physically capable of copulation.

Highly significant differences in the proportions of males that had functional organs occurred in the June–July and November 1958 collections (Table 1C), but after the width ranges were made equal and chi-square tests were repeated, statistical differences occurred only in the condition of the pleopods (Table 1D).

No significant differences in the proportions of males that had functional gonads, abdomens, penes or pleopods were observed between males collected in mid-summer 1958 in the York River and at Oyster, VA, and the absence of differences was not altered by equalizing the width ranges (Table 1E, 1F).

The relative proportions of males with functional gonads in the mid-summer 1956 and 1958 collections from the York River did not differ statistically, but there was a significant difference in the condition of the abdomens (Table 1G). When the width ranges were made equal, statistical differences reversed (Table 1H).

The mean width, 82 mm, at which the abdomen first becomes free from the sternum, is separated from the mean width at first occurrence of spermatophores in the AVDs by approximately 15 mm, a 24% increment (Fig. 1). The abdomen, penes and pleopods become morphologically functional almost simultaneously in a few individuals in the 82–92-mm width ranges, but at larger widths functional positioning of the penes and 2nd pleopods lags behind the development of the

Table 1. Reproductive condition of the male blue crab. G1-2, #1, gonad without spermatophores; #2, gonad with spermatophores; Abdomen Groups 1–4, #1, 3rd to 6th segments sealed to the sternum; #2, 3rd to 5th segments sealed, 6th free; #3, segments not sealed but locked to the sternum; #4, segments not sealed or locked to the sternum; PN, left and right penes not inserted in 1st pleopods; P, left and right penes inserted in 1st pleopods; LN, left and right 2nd pleopods not inserted in 1st pleopods; L, left and right 2nd pleopods inserted in 1st pleopods; NS, N, seminal receptacles without or with spermatophores

Table 1A. Reproductive behavior, with original width ranges

	Gonads		Abdomen		Penes		Pleopods		Seminal receptacles	
	G1	G2	A1 & 2	A3 & 4	NP	P	NL	N	NS	S
York River 1957 Non-mating Width 57–132 mm	13	50	41	22	45	18	54	9	63	
York River 1957 Mating Width 82–132 mm	0.5*	86	19	67	16	70	25	61	56	30

Highly significant differences between non-mating and mating crabs in their proportions of all conditions, $P < 0.005$.
* 0.5 added to permit chi-square calculation.

Table 1B. Reproductive behavior, with width range reduction to 82–132 mm

	G1	G2	A1 & 2	A3 & 4	NP	P	NL	N	NS	S
York River 1957 Non-mating	6	49	33	22	37	18	46	9		
York River 1957 Mating	0.5*	86	19	67	16	70	25	61		

Highly significant differences between non-mating and mating crabs in their proportions of all conditions, $P < 0.005$.
* 0.5 added to permit chi-square calculation.

Table 1C. Seasonal variation with original width ranges

	G1	G2	A1 & 2	A3 & 4	NP	P	NL	N	NS	S
York River 1957 June–July 1958 Width 67–182 mm	50	206	82	174	109	147	108	148		
York River 1957 November 1958 Width 87–172 mm	18	192	18	192	46	164	39	171		

Highly significant differences between summer and fall collections in their proportions of all conditions, $P < 0.005$.

Table 1. Continued

Table 1D. Seasonal variation, with width range reduction to 87–172 mm

York River June–July 1958	9	191	28	172	56	144	55	145
York River November 1958	18	192	18	192	46	164	39	171

No significant differences between summer and fall collections in the proportions of the conditions of gonads, abdomen or penes, $0.25 > P > 0.05$. Significant differences for pleopods, $0.025 > P > 0.01$.

Table 1E. Geographic variation, with original width ranges

	Gonads		Abdomen		Penes		Pleopods	
	G1	G2	A1 & 2	A3 & 4	PN	P	LN	L
York River June–July 1958 Width 67–182 mm	50	206	82	174	109	147	108	148
Oyster, VA July 1958 Width 67–167 mm	43	195	87	151	118	120	110	128

No significant differences between geographically separated collections in their proportions of all conditions of gonads, abdomen, penes or pleopods, $0.75 > P > 0.10$.

Table 1F. Geographic variation, with width range reduction to 67–167 mm

York River June–July 1958	50	203	82	171	109	144	108	145
Oyster, VA July 1958	43	195	87	151	118	120	110	128

No significant differences between geographically separated collections in their proportions of all conditions of organs, $0.75 > P > 0.10$.

Table 1G. Calendar year (year class) variation, with original width ranges

York River June–August 1956 Width 52–132 mm	44	140	101	83
York River June–July 1958 Width 67–182 mm	50	206	82	174

No significant differences between year classes in their proportions of the condition of gonads, $0.25 > P > 0.10$. Highly significant difference in the condition of the abdomens, $P < 0.005$.

Table 1. Continued

Table 1H. Calendar year (year class) variation, with width range reduction to 67–132 mm

York River				
June–August 1956	30	140	87	83
York River				
June–July 1958	50	132	82	100

Significant differences between year classes in their proportions of the condition of the gonads, $0.05 > P$ 0.025. No significant difference in the condition of the abdomens, $0.25 > P > 0.010$.

abdomen (Fig. 2). An estimate of the rate of development of functional abdomens, penes and pleopods in males >92 mm was obtained from width-frequency data from the three 1958 York River and Oyster collections. A difference of 15 mm separated the width at which 50% of the males attained functional abdomens and that at which 50% attained functional penes and pleopods; in that width range, the difference represented a 15–17% increment.

Discussion

The molt of maturity, usually called the pubertal molt, is considered the end of the immature phase in any species (Perez, 1928). In the male blue crab it should be that molt, or molts, at which all the organs attain their reproductively functional forms. The sequence of development of each morphological feature appears to be established: first, spermatophores must be present in the AVDs; second, the abdomen must be completely free of the sternum, or in addition may be locked to the sternum by the sternal tubercles; third, the penes and the 2nd pleopods must be inserted in the 1st pair of pleopods. Puberty is attained by a few males in the 82-mm width range, in 50% or more of the composite population in the 107-mm width group and attained by 80% or more at 117 mm.

Internal anatomical changes precede external morphological modifications, evident from this study and reviewed for decapods extensively by Charniaux-Cotton and Payen (1985).

It is probable that the functional development of the abdomen lags behind the production of spermatophores by one molt, and it is probable that the functional development of the penes and pleopods lags behind the development of the abdomen by a single molt. However, it cannot be determined from these data whether all males attain puberty in the same instar, since considerable variability occurs in individual growth rates, i.e., two individuals of the same instar may have different carapace widths (pers. obs.).

The 24% increment between the mean width of crabs showing the first occurrence of spermatophores (67 mm) and the first appearance of abdomens free of the sternum (82 mm) is in the range of values expected at a molt (Churchill, 1919; Gray and Newcombe, 1939; Tagatz, 1968b; Hartnoll, 1969; 1982). Increments as low as 15–17% were reported by Gray and Newcombe (1939) in males >92 mm LCW: at present that range is the only estimate that has been made of the rate of development between the mean widths at which functional development of the abdomen and of the penes and pleopods are attained.

This study has concentrated on the progression of the morphological features of the male reproductive system that culminate in puberty. Reproductive behavior, leading to copulation and the successful intromission of spermatophores in the female seminal receptacles, has only been briefly studied. For example, still unexplained is the failure of some males to attempt to mate when they were physically capable, or mate selection by some males that were physically incapable of copulation (Table 1A, 1B, for example).

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