Chapter 7

Reproduction Biology and Embryonic Development

PAUL JIVOFF, ANSON H. HINES, AND L. SCOTT QUACKENBUSH

INTRODUCTION

Reproduction in the blue crab *Callinectes sapidus* is a complex process requiring precise coordination of physiological, behavioral, and ecological processes to ensure reproductive success. Mating is timed to the female's maturity molt, which occurs once in the female's life (Van Engel 1958). It involves intricate interactions between males and females, and between competing males before, during, and after mating (Teytaud 1971; Gleeson 1980; Jivoff 1997a; Jivoff and Hines 1998b). Environmental conditions, such as temperature and salinity, can modify aspects of blue crab mating (and other aspects of reproduction) because they influence the timing of molting, as well as the structure of local populations, including the spatial and temporal distribution of crabs (Hines et al. 1987; Steele and Bert 1994). In blue crabs, and a variety of other species, the structure of local populations, such as the number of males and females that are ready to mate (operational sex ratio), influences an individual's ability to find and compete for receptive mates (Emlen and Oring 1977; Borgia 1979). The evidence from other commercially important crab species suggests that fishing pressure influences reproduction in complex and profound ways (McMullen and Yoshihara 1971; Nizyaev and Fedoseev 1989; Sainte-Marie et al. 1995; Jamieson et al. 1998) although how the blue crab fishery influences reproduction is still unclear. Effects could occur in a variety of ways such as changes in population structure that reduce the reproductive success of individuals as well as removal of individuals before they have had a chance to reproduce. The blue crab reproductive cycle of molting, maturation, mating, and brood production differs from other fished crabs such that blue crab reproduction may respond differently to intense fishing pressure. Developing a better understanding of blue crab reproduction will not only lead to improved management of harvested populations but can also provide a good model for the evolution of life history strategies and mating systems.

In this chapter, we review what is known about the reproductive biology of the blue crab and discuss potentially important aspects that are known in other crustaceans but still unknown in this species. The chapter is organized around five major topics including (1) sexual maturity, (2) reproductive systems, including internal structures and external anatomy, (3) mating and insemination, (4) fertilization and brood production, and (5) embryonic development.

SEXUAL MATURITY

Sexual Dimorphism

Blue crabs are sexually dimorphic. The most obvious difference in external anatomy between males and females is the shape and color of the abdomen (Figs. 1A and B). The abdomen is long and slender throughout the life of the male. In contrast,

juvenile females have a triangular-shaped abdomen, which changes to a semi-circular shape at the terminal (pubertal) molt to maturity. In some other species of portunids, sexually mature males have triangular-shaped abdomens, similar to that of juvenile female blue crabs (Williams 1984).

The color of the abdomen is white throughout the life of the male whereas pre-pubertal and adult females exhibit coloration on the abdomen. As pre-pubertal females progress towards the terminal molt, the abdomen changes from faint shades of blue and red to dark blue or purple that eventually cover the entire abdomen; the perimeter of the abdomen is often red (Fig. 2). In adult females, the semi-circular abdomen may be greenish-blue or brown. Unlike some other families of crabs, including spider crabs (Majidae) and fiddler crabs (Ocypodidae), blue crabs do not exhibit marked sexually dimorphic chelae, except for differences in color. The inner and outer surfaces of the chelae and the dactyls are blue and may be tipped with a reddish or purplish color in males, whereas the dactyls on the chelae of mature females are orange (Williams 1984). Two bisexual individuals have been reported from different areas

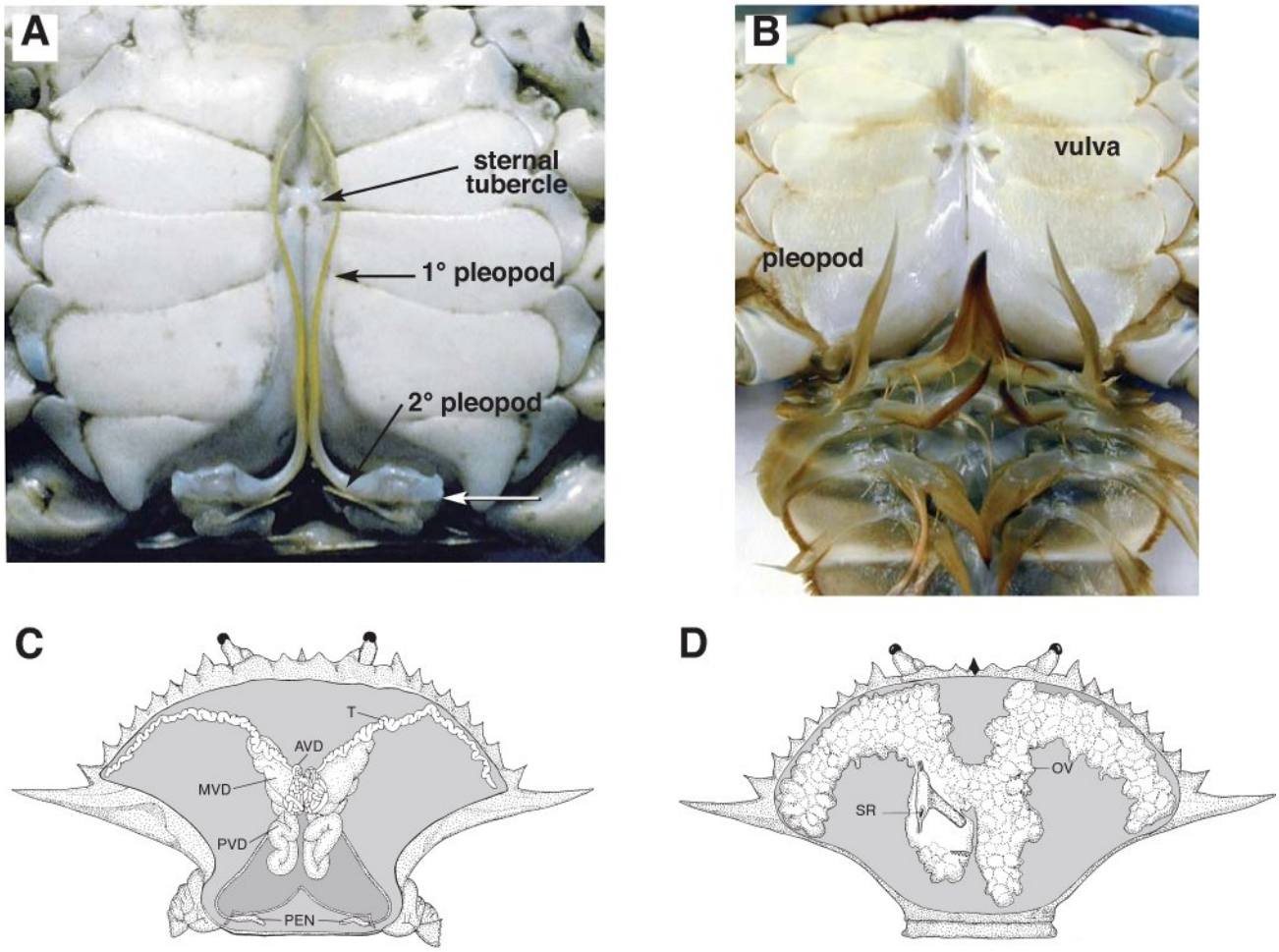

Figure 1. (A) External anatomy of male reproductive system, sternal tubercle, primary [1°] pleopod, and secondary [2°] pleopod (removed from primary pleopod). White arrow shows approximate insertion point of secondary pleopod into primary pleopod. (B) External anatomy of female reproductive system. (C) Internal anatomy of male reproductive system – testis [T], penes [PEN], anterior vasa deferentia [AVD], middle vasa deferentia [MVD], posterior vasa deferentia [PVD]. (D) Internal anatomy of female reproductive system – ovary [OV], seminal receptacle [SR] or spermatheca. Photos (A) and (B) by P.R. Jivoff; (C) and (D) redrawn from Pyle and Cronin (1950).

of Chesapeake Bay (Cargo 1980; Johnson and Otto 1981). Both individuals exhibited bilateral division of external and internal characteristics, with normal male characteristics on the right side and normal female characteristics on the left side.

MALES

Size at Maturity

Male blue crabs reach sexual maturity at the 18th or 19th juvenile instar (18 or 19 post-larval molts), and do not have a terminal molt at maturity (Van Engel 1958). Sexual maturity is associated with size (Millikin and Williams 1980); therefore the time required to reach sexual maturity is influenced by factors affecting growth rates (e.g., water temperature; see also Smith and Chang, Chapter 6). In Chesapeake Bay, the size range (all measurements reported are carapace width between tips of the lateral spines) of sexually mature males is approximately 82 to 227 mm (Williams 1984), with 50% of males at 107 mm showing full sexual maturity (Van Engel 1990). Unlike some other portunids (Haefner 1985; Choy 1988; Haefner 1990; González-Gurriáran and Freire 1994; Pinheiro and Fransozo 1998), male blue crabs do not exhibit appreciable changes in external morphology at the pubertal instar (Newcombe et al. 1949b;Van Engel 1958). In other species from different families, various methods have been used for estimating the minimum size-at-maturity of males in

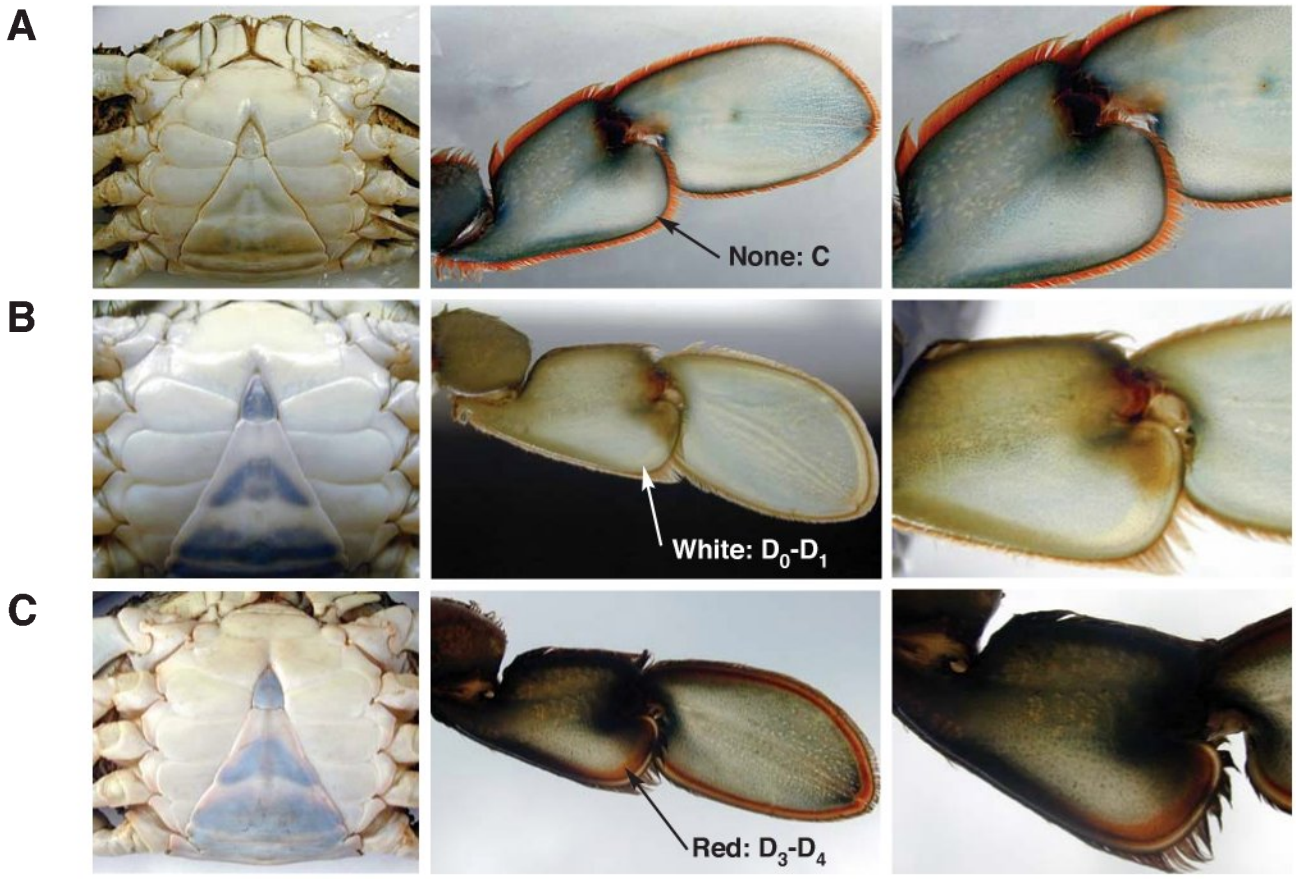

Figure 2. External anatomy of pre-pubertal female progressing through the pubertal molt, including coloration of abdomen and epidermal retraction, and coloration of second-to-last segment of the swimming appendage. (A) Intermolt female (molt stage C). (B) Early molt stage female [D_0-D_1]. (C) Late molt stage female [D_3-D_4]. Photos by A. Young-Williams.

the absence of distinct external morphological changes at sexual maturity, including the presence of "mating scars" on the chelae or carapace that show only after mating (Butler 1960; Ahl et al. 1996; Knuckey 1996), the initial appearance of spermatophores in the reproductive tract (Pinheiro and Fransozo 1998), the ability of males to inseminate females (Paul and Paul 1989a), and the diameter of the aperture of the intromittent organ (Kwei 1978). Gray and Newcombe (1938) approximated the minimum size at which male blue crabs attain sexual maturity as 89 mm (approximately the 17th juvenile instar), because their growth rate increases at that size. Van Engel (1990) estimated a minimum size-at-maturity of 82 mm using the appearance of traits required to accomplish copulation, namely that the penes are inserted in the secondary pleopods, the secondary pleopods are inserted in the primary pleopods (also known as gonopods or intromittent organs), and there are spermatophores in the gonads.

In some portunid, cancrid, and majid crabs, males exhibit increased development of the gonads, positive allometric growth in pleopod length and chelae size, and appreciable changes in chelae morphology at the pre-pubertal or pubertal instars or both (Hartnoll 1974; Pinheiro and Fransozo 1998). In blue crabs, one measure of chelae size (total length) in males exhibits an allometric relationship with carapace width (Jivoff 1997b) but it is lower in magnitude as compared with similar measures in some other species (Hartnoll 1974). The changes in chelae size and form enhance the ability of males to compete for mates or physically control females during mating in blue crabs (Jivoff 1997b) and in many other species, including other portunids (Fielder and Eales 1972; Hartnoll 1974; Berrill and Arsenault 1982; Choy 1988; González-Gurriáran and Freire 1994), cancrids (Edwards 1964), majids (Orensanz and Gallucci 1988; Donaldson and Adams 1989; Homola et al. 1991; Claxton et al. 1994), ocypodids (Henmi et al. 1993), and xanthids (Knuckey 1996).

Characteristics of the Sexually Mature Male Reproductive System

The internal male reproductive system is bi-lateral, generally "H" shaped, and consists of paired testes (sperm production) and vasa deferentia that are composed of three main sections: (1) anterior (spermatophore production); (2) middle (seminal fluid production); and (3) posterior (transports ejaculate to the penes) (Cronin 1947; Johnson 1980) (Fig. 1C). The ejaculate of blue crabs consists of spermatophores (each containing many sperm) and seminal fluid. In sexually mature males, the testes are white and contain sperm (in all developmental stages), the anterior vasa deferentia are white and contain spermatophores, the middle vasa deferentia contain pink seminal fluid, and the posterior vasa deferentia are translucent and contain a greenish, viscous secretory fluid that may aid in the transport of ejaculate (Fig. 3) (Cronin 1947; Johnson 1980).

The external portion of the male reproductive system is located beneath the abdomen and consists of three sets of paired structures for transferring ejaculate to the female: the penes, the secondary pleopods, and the primary pleopods (Fig. 1A). In immature males, the abdomen is held tightly against the sternum by the sternal tubercles, a pair of "snap-fastener-like" structures (Van Engel 1958). In sexually mature males (>115 mm), the abdomen is free of the sternal tubercles and can easily be pulled away from the sternum (Van Engel 1990). This movement is necessary during copulation because the male holds his abdomen away from his sternum (thus exposing the primary pleopods that are inserted into the external reproductive openings of the female) and delivers spermatophores and seminal fluid to each of her sperm storage organs.

In many species of crabs, differences may occur among the sizes at which males are physiologically mature (produce sperm), morphologically (or morphometrically) mature (fully express secondary sexual characters), and functionally mature (actually mate) (Comeau and Conan 1992; Paul and Paul 1995; Pinheiro and Fransozo 1998). To pass ejaculate to the female, a male blue crab must (1) pull his abdomen away from his sternum, (2) insert his penes into the secondary pleopods, and (3) insert the secondary pleopods into the primary pleopods. The ability to perform these actions is achieved approximately one molt after spermatophores appear in the (anterior) vasa deferentia (Van Engel 1990). In a sample of males from the lower Chesapeake Bay, the

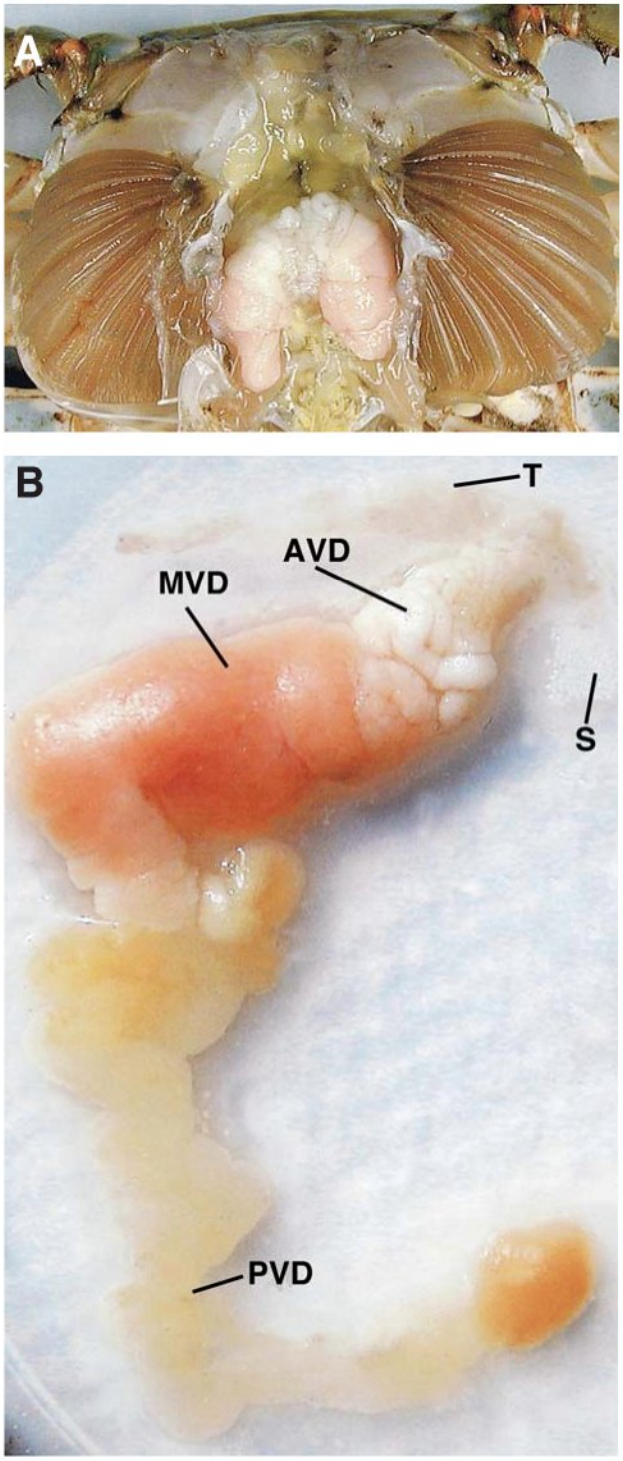

Figure 3. Internal anatomy of sexually mature male reproductive system. (A) Within the body cavity. (B) Removed from body cavity – testis [T], anterior vasa deferentia [AVD], middle vasa deferentia [MVD], posterior vasa deferentia [PVD], spermatophores [S]. Photo (A) by A.Young-Williams and (B) by P.R. Jivoff.

percentage of males showing all of these characteristics was about 8% of 80 mm males, 50% of 107 mm males, and more than 80% of 117 mm males; these data provide an estimate for the minimum size for complete sexual maturity (Van Engel 1990). In captivity, the smallest males Van Engel (1990) observed mating were 82 mm, suggesting that males may attempt to mate before they have attained full sexual maturity. The smallest males captured in free-ranging mating pairs during 1991 to 1994 in the Rhode River, a sub-estuary in the upper-third of Chesapeake Bay, were 105 to 110 mm (Jivoff 1997b). All of these males had abdomens free from the sternum and most (92.8%, 1991; 100%, 1992; 100%, 1993; 99.4%, 1994) had the secondary pleopods inserted into the primary pleopods (Jivoff unpubl. data), confirming that males must attain the full suite of sexually mature features to mate successfully in the field.

The pattern of maturation whereby males must be both physiologically and morphologically mature before they can become functionally mature occurs in many other species, including some cancrids and ocypodids, but differs from others such as in some majids, including *Chionoecetes* sp. and *Libinia* sp. (Dawe et al. 1991; Ahl and Laufer 1996). In *Chionoecetes* sp., two sperm-producing male morphs exist that differ primarily in morphology such that morphometrically immature males have relatively small claws but morphometrically mature males have relatively large claws (Comeau and Conan 1992; Stevens et al. 1993). Morphometrically mature males are predominantly found in mating pairs (Sainte-Marie and Hazel 1992; Stevens et al. 1993; Comeau et al. 1998) but so many large, morphometrically mature males are removed by intense fishing pressure that morphometrically immature males, otherwise competitively excluded from mating, have opportunities to mate (Sainte-Marie and Hazel 1992; Sainte-Marie and Lovrich 1994).

Timing and Control of Sexual Maturity

Environmental Factors

Sexual maturity is closely tied to body size. Therefore, environmental factors that influence

growth or molting, such as temperature, salinity (Leffler 1972; Cadman and Weinstein 1988), and the quantity and quality of food (Newcombe et al. 1949b; Millikin et al. 1980) also influence the timing of sexual maturity for males (see also Smith and Chang, Chapter 6). Environmental variables also influence the onset of reproductive readiness such that the condition of both the internal (Johnson 1980) and external (Van Engel 1990) reproductive system varies seasonally. In the late autumn and winter, the internal reproductive system is inactive, as evidenced by arrested sperm production in the testis and lack of seminal fluid in the middle vasa deferentia (Johnson 1980). In another portunid *Callinectes ornatus*, a tropical species, males exhibit a continuous cycle of gonad maturation (Mantelatto and Fransozo 1999). In addition, otherwise sexually mature male blue crabs often do not have the penes inserted in the secondary pleopods or the secondary pleopods inserted in the primary pleopods in the spring, before significant mating activity has begun (Van Engel 1990; Jivoff unpubl. data).

Hormonal Factors

In decapod crustaceans, only males have an androgenic gland, which determines sexual differentiation and is responsible for primary and secondary sexual characters of males (Adiyodi and Adiyodi 1970; Charniaux-Cotton and Payen 1985). Little work has examined the hormonal controls of the timing of sexual maturity specifically in male blue crabs. In another portunid *Carcinus maenas*, the androgenic gland produces farnesylacetone, a hormone similar to the juvenile hormone in insects, which stimulates protein synthesis but not spermiogenesis in the testes (Berreur-Bonnenfant and Lawrence 1984). In other crustaceans, the activity of the androgenic gland varies seasonally, producing seasonal changes in the testes, vasa deferentia, and external reproductive morphology (Adiyodi and Adiyodi 1970; Dudley and Jegla 1978). In the blue crab, evidence suggests that the androgenic gland regulates the courtship behavior of males (see below) (Gleeson et al. 1987). In other crab species, such as the spider crab *Libinia emarginata* (Laufer et al. 1987), male sexual maturity may be regulated by methyl farnesoate, a juvenile-hormone-like hormone produced by the mandibular organ, because increased levels of this hormone correlate with large male size, well developed vasa deferentia, and the appearance of the mature chelae allometry (Homola et al. 1991; Sagi et al. 1994; Laufer and Ahl 1995; Ahl and Laufer 1996). Methyl farnesoate occurs in the mandibular gland of blue crabs (Laufer et al. 1984), but its influence on sexual maturity in male blue crabs has not been investigated.

FEMALES

Size at Maturity

Unlike males, female blue crabs reach sexual maturity after a terminal (pubertal) molt, which typically occurs between 90 to 100 mm (after approximately 18-20 post-larval instars) (Newcombe et al. 1949a; Van Engel 1958). In Chesapeake Bay, the size range of mature females is 52 to 207 mm (Williams 1984), with 50% of females at 132 mm being mature (Uphoff 1998). The size range of pre-pubertal females is about 70 to 140 mm (Jivoff unpubl. data). The smallest recorded adult female blue crab (52 mm) was captured near Cape Hatteras, North Carolina (Fischler 1959). Also in contrast to males, adult females are easily distinguished from juveniles (see below).

The terminal nature of the pubertal molt is well accepted because few records of molting in adult females exist (see also Smith and Chang, Chapter 6) (Abbe 1974; Olmi 1984). However, in Chesapeake Bay, a small percentage (11%) of adult females have regenerating limb buds, suggesting the potential for an additional molt (Havens and McConaugha 1990). One mechanism for the control of terminal anecdysis (lack of molt) in other crabs (especially the Majidae) is the degeneration of the Y-organ, which produces the ecdysteroids responsible for initiating molting (Carlisle 1957; Skinner et al. 1985). Adult female blue crabs have very low concentrations of ecdysteroids in the blood after the terminal molt but higher concentrations in the ovaries during vitello-

genesis, suggesting that there is a physiological link between the terminal molt and ovarian development (Adiyodi and Adiyodi 1970; Soumoff and Skinner 1983). The other mechanism for the control of terminal anecdysis is the production by the X-organ of a molt-inhibiting hormone that acts on the Y-organ to inhibit the production of ecdysteroids (Carlisle 1957; Skinner et al. 1985). The X-organ is located in the eyestalks, and adult females have been induced to molt by ablation of the eyestalks, leading to the hypothesis that some adult females enter a diapause stage as opposed to terminal anecdysis (Havens and McConaugha 1990).

Characteristics of the Sexually Mature Female Reproductive System

At the maturation (terminal) molt, a conspicuous change transforms the shape of the female abdomen from triangular to semi-circular shape (Newcombe et al. 1949b; see also Kennedy and Cronin, Chapter 3), providing a larger surface area for brooding eggs (Fig. 1B). As compared to males of the same instar, females at the terminal molt grow larger in carapace width relative to carapace length, producing relatively longer lateral spines (Newcombe et al. 1949b). One advantage of this allometric change may be a greater internal volume in which to store the developing ovary (see below) (Newcombe et al. 1949b; Hines 1982).

The internal reproductive system of females consists of two paired structures, the ovaries and the sperm storage organs (spermathecae) (Fig. 1D). Each spermatheca is connected to a genital pore on the ventral surface of the female sternum via the vagina (Hard 1945; Johnson 1980). During the later stages of the pubertal instar, the spermathecae develop to full size, with the anterior horns of the early stage ovaries attached to their dorsal surface (Hard 1945; Johnson 1980). Copulation occurs immediately after the terminal molt when the ovaries are thin and white, reflecting the lack of yolk (Hard 1945; Johnson 1980). In contrast, the spermathecae are distended with ejaculate, which contains the easily visible pink seminal fluid, capped with a dense accumulation of white spermatophores (Fig. 4B, D) (Hard 1945; Johnson 1980). Over approximately a 2-month period, the ovaries increase in size (with a concomitant shrinking of the spermathecae) and develop the typical orange coloration as the eggs mature and yolk is formed (Fig. 4A, C) (Hard 1945).

Timing and Control of Sexual Maturity

Environmental Factors

In females, sexual maturity is linked to body size and is established at the terminal molt. Thus, environmental factors that influence growth or molting, such as temperature and salinity (Leffler 1972; Cadman and Weinstein 1988; Fisher 1999) and the quantity and quality of food (Newcombe et al. 1949b; Millikin et al. 1980), influence the timing of sexual maturity. In addition, seasonal and spatial (among and within estuaries) variation in the sizes of mature female blue crabs (Haefner and Shuster 1964; Olmi and Bishop 1983; Hines et al. 1987; Havens and McConaugha 1990; Fisher 1999) and a variety of other crab species (Blau 1989; Hines 1989; Dumbauld et al. 1996) suggests that environmental factors influence the timing of sexual maturity.

Hormonal Evidence

Little work has examined the influence of hormones on the timing of sexual maturity specifically in female blue crabs. However, because sexual maturity is linked to the terminal molt, hormones that regulate molting also, in part, regulate sexual maturity in blue crabs and other crab species (Cheung 1969; Adiyodi and Adiyodi 1970; Soumoff and Skinner 1983; Quackenbush 1986). The X-organ produces gonad-inhibiting hormone as well as molt-inhibiting hormone, so that ablating the eyestalks of adult females induces molting in blue crabs (Havens and McConaugha 1990), but induces either molting or spawning (depending on the season) in other species (Cheung 1969; Adiyodi and Adiyodi 1970; Fingerman 1987). Ecdysteroids from the Y-organ and other tissues that regulate molting may influ-

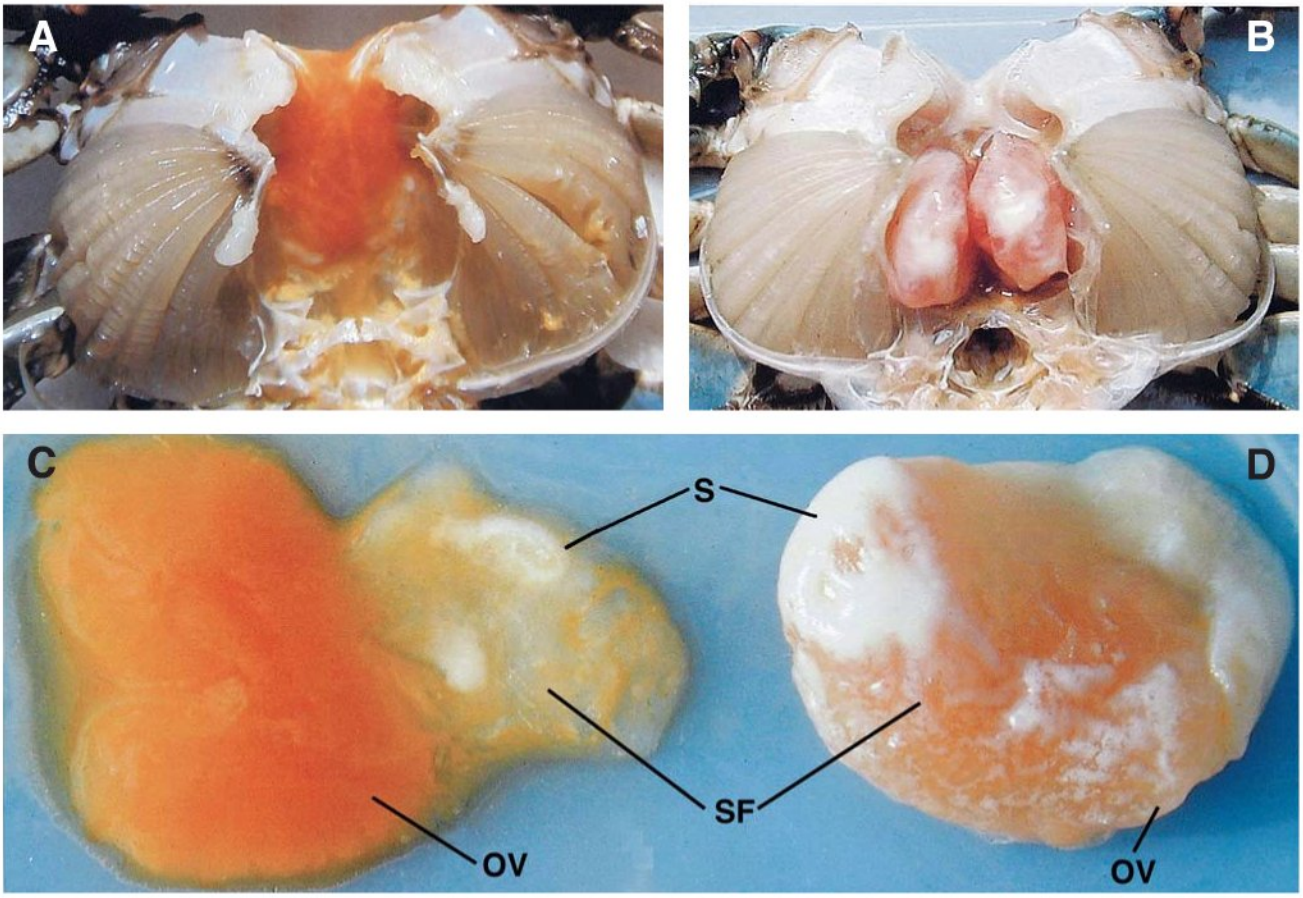

Figure 4. Anatomy of adult female reproductive structures (A and B) within the body cavity and (C and D) removed from body cavity. Structures from a recently mated female (B and D) and a female about 2 months after mating (A and C) include spermatophores [S], seminal fluid [SF], and ovary [OV]. Photos by P.R. Jivoff.

ence the timing of sexual maturity because in some species they are found in the gonads and stimulate vitellogenesis (Adiyodi 1985; Quackenbush 1986). As in a variety of species, adult female blue crabs have low concentrations of ecdysteroids in the hemolymph but begin sequestering these hormones in reproductively active ovaries where they also promote vitellogenesis and embryonic development (Adiyodi and Adiyodi 1970; Soumoff and Skinner 1983). As ovarian development progresses, levels of ecdysteroids increase in the ovary, while a concomitant decrease occurs in the spermathecae (Soumoff and Skinner 1983), but it is not known whether the spermathecae act as a source of ecdysteroids.

REPRODUCTIVE SYSTEMS

Male Internal Structures

As noted earlier, the internal portion of the male reproductive system is bilateral, generally "H" shaped, and consists of paired testes and vasa deferentia that are composed of three main sections: (1) anterior, (2) middle, and (3) posterior (Figure 3B) (Cronin 1947; Johnson 1980). Cronin (1947) also identified the vasa efferentia, a small tissue connecting the testes to the anterior vasa deferentia, that Johnson (1980) considered as a portion of the anterior vasa deferentia.

The anatomy and histology of the male reproductive system have been described in detail by the excellent work of Cronin (1947) and Johnson (1980); therefore, only a summary of their observations will be presented here. The testes are tubular organs consisting of a central seminiferous duct surrounded by the testicular lobes. Spermiogenesis takes place within the lobes, which contain spermatogonia, spermatocytes, spermatids, and mature sperm. Mature sperm are typically found in the center of the testicular lobes. An epithelium encloses the seminiferous duct except where it faces the testicular lobes, which open broadly into the ducts allowing passage of mature sperm to the ducts. Mature sperm begin to appear in the testicular lobes of males as small as 65 mm (Johnson 1980). Only mature sperm are found in the seminiferous duct, which gradually becomes a short, muscular structure (Cronin's vasa efferentia) delivering sperm to the anterior vasa deferentia (AVD) (Johnson 1980).

The AVD are highly coiled tubules with blood vessels, blood sinuses, and connective tissue between the tubules. They receive mature sperm from the testes, encapsulate groups of sperm (about 2.25×10^4 sperm per spermatophore; Hines et al. [2003]), into ovoid-shaped spermatophores (from 200 × 150 μm to 500 × 300 μm in size), and transport the spermatophores to the middle vasa deferentia (MVD). The MVD are the largest portions of the male reproductive system and are composed of many large coils, with blood vessels, blood sinuses, and connective tissue between them; there are numerous lateral out-pockets from the coils. Each coil contains a large lumen that is typically filled with a granular, pink secretion (seminal fluid). The posterior vasa deferentia (PVD) are long, complex tubes also containing many lateral out-pockets. The posterior portion of the PVD ("ductus ejaculatoris"; Cronin [1947]) is more muscular and appears secretory because the epithelium bears a "brush" border composed of what Cronin (1947) called cilia but that are more likely microvilli (Johnson 1980). The PVD transport ejaculate to the external penes.

Ejaculate Contents

The ejaculate of blue crabs consists of seminal fluid and spermatophores (which contain sperm). In another portunid *Portunus sanguinolentus*, the contents of the ejaculate are passed to the female in succession such that the translucent secretion from the posterior vasa deferentia comes first, then the seminal fluid with some spermatophores, and finally the majority of spermatophores (Ryan 1967a). In the spermathecae, the ejaculate contents occur in the reverse order in which they are passed, with most of the spermatophores in the dorsal section of the spermathecae (some are found within the seminal fluid matrix) and the seminal fluid in the ventral section (Ryan 1967b), as occurs in blue crabs (Johnson 1980; Jivoff 1997b). This reversal of ejaculate contents in the spermathecae suggests that males insert their pleopods deeply into the spermathecae so that individual ejaculate components are flushed ventrally by successive components. In other crab species, the layering of ejaculate contents in the spermathecae dictates how (Diesel 1988) or when (Sainte-Marie and Sainte-Marie 1999b) the sperm are used by the female. In blue crabs (Johnson 1980) and many other crab species including other portunids (Ryan 1967b; Bawab and El-Sherief 1989; Norman and Jones 1993), cancrids (Bigford 1979; Elner et al. 1980; Orensanz et al. 1995; Jensen et al. 1996), and some majids (Diesel 1990), the seminal fluid is viscous during copulation but eventually (about a week for *C. sapidus*) hardens in the spermathecae into a tough, wax-like matrix. In contrast, the ejaculate of other species of crabs, such as some xanthids (Jeyalectumie and Subramoniam 1987), contains relatively little seminal fluid and does not harden once passed to the female.

In a variety of taxonomic groups, male seminal fluid plays an important role in male, and sometimes female, mating success (Boggs and Gilbert 1979; Markow and Ankney 1984; Eberhard and Cordero 1995). In blue crabs and other crab species, little is known about the function of the seminal fluid even though males may pass a considerable volume to females. However, researchers have observed that

the hardened seminal fluid "disappears" over a period of time (see below) after copulation (see Fig. 4C, D) (Hard 1945; Ryan 1967b; Sainte-Marie 1993). The loss of seminal fluid may be accomplished by materials secreted from the walls of the spermathecae (Ryan 1967b; Diesel 1989; Beninger et al. 1993) or by metabolic activity during sperm storage (Jeyalectumie and Subramoniam 1987; Anilkumar et al. 1996). Although not analyzed in blue crabs, the seminal fluid in other crab species contains proteins, carbohydrates, and lipids (Jeyalectumie and Subramoniam 1987, 1991; Anilkumar et al. 1996), and thus it has been suggested that the seminal fluid acts as a nutritive source for the stored sperm (Subramoniam 1991). It has also been suggested that the seminal fluid allows for the maturation of sperm in the spermathecae (Sainte-Marie and Sainte-Marie 1999a), prevents the loss of sperm from the spermathecae (Ryan 1967b; Johnson 1980), stops the entrance of bacteria (Beninger and Larocque 1998; Jayasankar and Subramoniam 1999), or blocks additional males from mating with the female (Jensen et al. 1996; Jivoff 1997a; Beninger and Larocque 1998). In blue crabs, this latter function of blocking other males seems most likely to be the major adaptive advantage (Jivoff, 1997a) because the seminal fluid rapidly "disappears" during storage, so that it is essentially gone within 4 to 6 weeks after copulation, even though sperm are stored within the spermathecae before fertilization for 6 to 12 months in Chesapeake Bay and 2 to 12 months in Florida (Hines et al. 2003; Hopkins 2002).

In most species of crabs, many individual sperm are packaged in spermatophores that are then passed to females (Subramoniam 1991, 1993). As in other decapod crustaceans (Felgenhauer and Abele 1991; Medina 1994; Guinot et al. 1998), the mature sperm of blue crabs lack flagella and consist of a spherical acrosome covered by an apical cap and embedded in a nuclear cup with eight radial arms (Brown 1966) (Fig. 5). In two other portunids and one raninid crab, the spermatophore wall or pellicle consists of two layers (Uma and Subramoniam 1979; Babu et al. 1988; Minagawa et al. 1994): an inner, pliable proteinaceous layer (Uma and Subramoniam 1979; Babu et al. 1988) and an outer, rigid layer made of either protein, e.g., keratin (Babu et al. 1988) or chitin (Uma and Subramoniam 1979). The pellicle is resistant to acidic, alkaline, and salt solutions (Uma and Subramoniam 1979) and thus may protect the sperm during insemination (Subramoniam 1991),

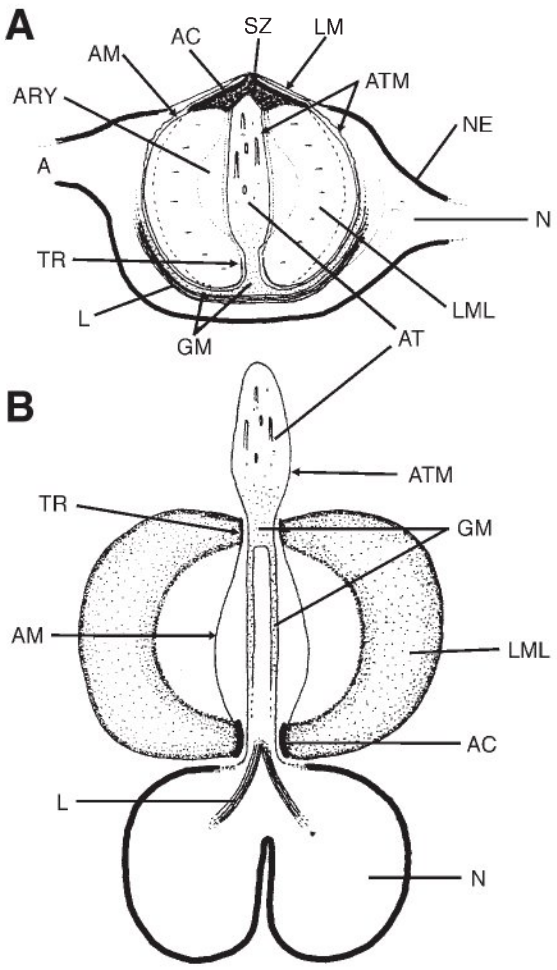

Figure 5. Diagram of blue crab sperm. (A) Mature, unreacted sperm. (B) Reacted sperm (acrosomal reaction). Radial arms of nucleus [A], apical cap [AC], acrosomal membrane [AM], acrosomal rays [ARY], acrosomal tubule [AT], acrosomal tubule membrane [ATM], granular material [GM] of acrosomal tubule, lamella [L] or central region, limiting membrane [LM], large "microtubular" layer [LML] of the acrosomal vesicle, nucleus [N] or nuclear cup, nuclear envelope [NE], subcap zone [SZ], thickened ring [TR]. From Brown (1966).

although it is permeable to low molecular weight substances, which could allow sperm release via spermatophore dehiscence (Uma and Subramoniam 1979; Beninger et al. 1993). In a variety of species, spermatophores contain carbohydrates, proteins, and lipids in a composition that is distinct from seminal fluid (Jeyalectumie and Subramoniam 1987, 1991; Subramoniam 1991) and that could be metabolized by sperm during long periods of storage within the female (Subramoniam 1991). By the time of fertilization and extrusion through the spermathecae, the spermatophores break down and sperm are free individually (Johnson 1980; Hopkins 2002).

Accessory Structures

In males of a variety of crab species, including other portunids, majids, and cancrids, the primary pleopods contain gonopod tegumental glands that communicate directly with the ejaculatory duct (Charniaux-Cotton and Payen 1985; Diesel 1989; Beninger and Larocque 1998). Cronin (1947) first observed these glands in blue crabs, calling them "rosette glands," but did not speculate on their function. In other portunids (*Carcinus maenas, Portunus sebae*, and *Ovalipes ocellatus*), the glands secrete materials that are passed to the female in the ejaculate, which may harden the ejaculate once inside the spermathecae, and materials that are not passed to the female, which may act as a lubricant (Beninger and Larocque 1998).

Male External Structures

The external portion of the male reproductive system is located beneath the abdomen and consists of three paired structures: the penes, the secondary pleopods, and the primary pleopods (Fig. 1A). As outlined in a previous section, seminal fluid and spermatophores are transported from the penes to the secondary pleopods, and then to the primary pleopods, which are inserted into the external openings of the female reproductive tract during copulation and which pass ejaculate to the female's spermathecae (Cronin 1947; Hartnoll 1968). The penes are short, muscular ducts with an internal epithelium lined with cilia and an external covering of cuticle (Cronin 1947). At the point that the penes enter the secondary pleopods, they lose their musculature and the internal epithelium is replaced by invaginated cuticle (Cronin 1947). The secondary and primary pleopods consist of an internal cavity, or ejaculatory duct, surrounded by a hard, external cuticulum (Cronin 1947). Muscles are present at the base of each pleopod, but are absent in the distal sections (Cronin 1947).

Female Internal Structures

The internal reproductive system of female blue crabs consists of two paired structures: the ovaries and the spermathecae (Fig. 1D) (Hard 1945; Johnson 1980). The anatomy and histology of the female reproductive system has been described in detail by the excellent work of Hard (1945) and Johnson (1980); therefore, only a summary of their observations will be presented here. Before the pubertal molt and at copulation, the ovaries are undeveloped, contain only small immature eggs, and appear as thin white strands of tissue connected to the dorsal surface of the spermathecae (Hard 1945). This pattern of ovary development differs from that of other crab species, for example, some majids (Sainte-Marie and Hazel 1992; Bryant and Hartnoll 1995) in which the ovaries are fully developed at copulation and ovulation occurs soon after mating. In blue crabs, the ovary is enclosed by a thin layer of connective tissue, separating it from the hemocoel. During the two or three months after copulation (e.g., October to December in Chesapeake Bay), vitellogenesis occurs and yolk is formed; thus, the ovary increases in size and develops an orange color. The developing ovary contains two types of cells: oocytes (in various stages of development) and accessory cells (also known as "nurse cells" or "follicle cells") (Johnson 1980). In the portunid *Portunus sanguinolentus*, some accessory cells form a single layer around each oocyte and eventually comprise the chorionic membrane of the mature eggs, whereas others are arranged, several layers thick, as septa that divide the ovary into compartments, each containing several oocytes (Ryan 1967b).

In Chesapeake Bay, some female blue crabs are

able to copulate and spawn within the same season; however, most females overwinter after copulation and spawn the following spring and summer (Hard 1945; Van Engel 1958). During the winter and early spring, the ovary continues to thicken and elongate while the spermathecae continues to shrink. Before spawning, in late spring or early summer, the ovary is very large and orange because many of the eggs are mature and full of yolk. After the first spawning, the ovary contains numerous eggs with smaller amounts of yolk that will develop into a subsequent brood, and the area from which eggs were discharged is full of a globular material (Hard 1945). In Chesapeake Bay, although never quantified, estimates indicate that during a 4 to 6 month spawning season, female blue crabs may produce two to three broods of eggs (McConaugha et al. 1983). Measures of brood production in Florida indicate that females can produce as many as eight successive broods in a 4 to 6 month period, with as little as 10 to 14 d between the release of larvae in one brood and the production of a subsequent brood (Hines et al. 2003).

As in most brachyurans, the spermatheca of blue crabs is a hybrid structure. The dorsal portion, connected to the ovary, is derived from the oviduct but the ventral portion, connected to the external opening of the reproductive tract by the vagina (Hartnoll 1974; Johnson 1980), is derived from the vagina (Bauer 1986). The spermathecae store sperm and seminal fluid and are considered the site of fertilization in blue crabs as eggs move from the ovary to the ventral surface of the female (Hard 1945). In blue crabs and other portunids, the ovary is connected to the dorsal surface of the spermathecae via the oviduct (Ryan 1967b; Johnson 1980), a broad opening that in *Portunus sanguinolentus* allows the passage of four oocytes at one time (Ryan 1967b). In contrast, the ovary is connected to the ventral surface of the spermathecae in other species, including some majids (Hartnoll 1968; Diesel 1989). The topographical arrangement of the connection between the oviduct and spermathecae has important implications for how the sperm, which in some species may come from different males, are used for fertilization (see below) (Diesel 1991; Urbani et al. 1997).

In a variety of crabs, including other portunids, majids, and cancrids, the spermathecae are complex organs and their structure and activity can vary with the age or sexual maturity of the female, her reproductive state, and the quantity of stored ejaculate (Ryan 1967b; Hartnoll 1968; Diesel 1991; Beninger et al. 1993; Jensen et al. 1996; Sainte-Marie and Sainte-Marie 1998). The spermathecae are essentially large sacs surrounded by connective tissue, with an inner epithelium that is lined with cuticle only in the ventral portion of the spermathecae. As indicated by Hard (1945), the overall appearance of the spermathecae of blue crabs changes dramatically between copulation and fertilization. At the time of the pubertal molt and copulation, the wall of the spermathecae is thick and well developed but by the time the seminal fluid disappears (4-6 weeks after copulation), the spermathecal wall becomes thin, translucent, and delicate (Fig. 4 C, D) (Hines et al. 2003). This transformation in the spermathecae may be the result of changes in the cellular structure of the epithelium, which differs between pre-pubertal and mature females and between the dorsal and ventral portions of the spermathecae (Johnson 1980). In mature females, the epithelium of the dorsal section of the spermathecae becomes highly modified and localized, occurring only immediately above the ventral cuticle-lined portion of the spermathecae (Johnson 1980). The modified epithelium with a border of many long microvilli appears to be secretory because the cells contain material that streams off the surface of the tissue into the lumen of the spermathecae (Johnson 1980). The secretion may dissolve the hard, seminal fluid matrix of the ejaculate or prevent bacteria from entering the spermathecae (Johnson 1980).

Female External Structures

At the terminal molt, the shape of the female abdomen changes from triangular (Fig. 2) to semicircular (Fig. 1B) (Newcombe et al. 1949b). In addition, the four pairs of pleopods, or swimmerets, on the abdomen of the adult female contain many fine

setae in contrast to those of the immature female (Van Engel 1958). The change in the shape of the abdomen provides a larger surface area for brooding eggs and the addition of numerous setae provides structures to which the extruded fertilized eggs are attached (Van Engel 1958).

MATING AND INSEMINATION

Mating in the blue crab is timed to the female's pubertal molt which occurs once in the female's life (Van Engel 1958). As a result, mating involves intricate interactions between males and females, and among competing males before, during, and after mating (Teytaud 1971; Gleeson 1980; Jivoff 1997a; Jivoff and Hines 1998b). These interactions influence blue crab mating behavior and the structure of the mating system.

Pre-mating Interactions and Pair Formation

Both male and female blue crabs play an active role in pre-mating interactions and pair formation (Teytaud 1971; Gleeson 1980; Jivoff 1997b; Jivoff and Hines 1998b). As in a variety of crustaceans (Hartnoll 1969; Ridley and Thompson 1985; Christy 1987), female blue crabs mate immediately after molting, and males search for and defend pre-pubertal females approaching their pubertal molt. Male blue crabs ensure access to receptive females by using pre-copulatory mate guarding, or precopula (Parker 1974; Ridley 1983), by physically carrying females beneath them for as long as 5 to 7 d before copulation (Fig. 6B) (Jivoff and Hines 1998b). In blue crabs, pre-pubertal females release a urinary-borne pheromone several days before the pubertal molt, which attracts and elicits courtship behavior in males (Teytaud 1971; Gleeson 1980). Recent evidence suggests that non-urine based chemical signals from females and males may also be important in courtship (Bushmann 1999). The female pheromone is not crustecdysone (Gleeson et al. 1984), which is the molting hormone that may also act as a sex pheromone in some crustaceans (Dunham 1978). Males detect the female pheromone using chemosensory structures on the antennules (first antennae) (Gleeson 1982) and respond with courtship behavior (Fig. 6A) (Teytaud 1971; Gleeson 1980).

Courtship in blue crabs has been described from laboratory observations (Teytaud 1971; Gleeson 1980). More recently, courtship was described (Table 1) and the importance of courtship in pair formation, the factors that regulate differences in courtship behavior among males, and the relative control of each sex in determining pair formation were assessed in large field enclosures (Jivoff and Hines 1998a, b). Courtship behavior, including the outcome of courtship, is influenced by the molt stage of females (Fig. 7), but in general, males respond to the female pheromone by searching for the female, often while in the courtship stance (Fig. 6A). This stance consists of the male raised on the tips of his walking legs, the chelae laterally extended (not shown in Fig. 6A), and the swimming legs (or paddles) raised above the carapace and waved in a circular motion (Jivoff and Hines 1998b). When the male locates the female he attempts to pair with her, but her response, which is influenced by her molt stage, determines if pair formation is achieved. Pre-pubertal females early in the molt cycle (D_0-D_1) resist males by threatening and moving away, whereas pre-pubertal females late in the molt cycle (D_3-D_4) (Fig. 2) initiate mate guarding by positioning themselves underneath males (Jivoff and Hines 1998a, b). As in other crustaceans, female blue crabs may avoid prolonged pre-copulatory mate guarding due to the potential costs of being guarded such as reduced opportunities to feed (Robinson and Doyle 1985; Donaldson and Adams 1989; Perez and Bellwood 1989; Jormalainen 1998). As a result, the ability to establish and maintain physical control of females, including actively subduing resistant females, is critical to male pairing success.

In some ways, courtship behavior in blue crabs is similar to that of other crustaceans, particularly other portunids (Ryan 1966; Fielder and Eales 1972; Berrill and Arsenault 1982; Campbell 1982). For example, male blue crabs use their chelae to control or to manipulate the female before copulation, as seen in other crabs (Edwards 1964; Bigford 1979;

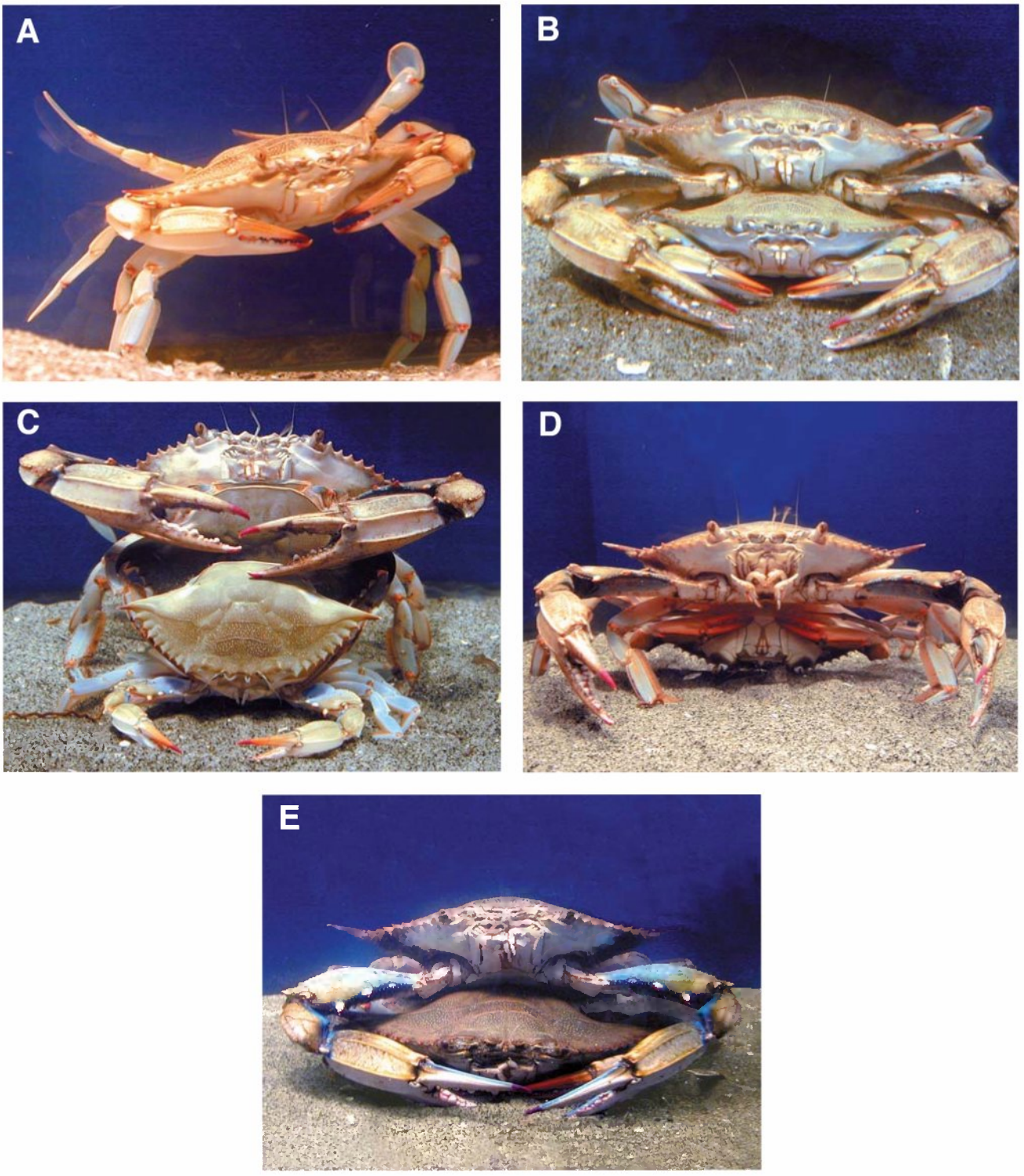

Figure 6. (A) Male mating display. (B) Pre-copulatory mate guarding. (C) Female undergoing terminal maturation molt. (D) Copulation. (E) Post-copulatory mate guarding. Photos by A. Young-Williams.

Elner et al. 1987; Donaldson and Adams 1989; Perez and Bellwood 1989; Claxton et al. 1994), shrimps (Seibt and Wickler 1979; Nakashima 1995), lobsters (Lipcius et al. 1983; Atema 1986; Waddy and Aiken 1991), and crayfish (Mason 1970; Ingle and Thomas 1974; Stein 1976; Snedden 1990). As part of the courtship stance, males spread their chelae laterally thus exposing the bright blue inner-surfaces of the chelae to the female. Blue crabs can distinguish blue from other colors (Bursey 1984), suggesting that the lateral chelae spread may be a visual display. However, the importance of the courtship stance as a visual display has recently been questioned because when either males or females are experimentally blinded, courtship behavior and subsequent pair formation are unaffected (Bushmann 1999). In contrast, when males are unable to perceive chemical signals from the female, then both male courtship behavior and the initiation of pair formation are reduced. These observations suggest that chemical signals are more important than visual signals in the pre-mating interactions between males and females, and that chemical signals influence the outcome of these interactions (Bushmann 1999).

A unique aspect of blue crab courtship behavior, compared with that of other non-swimming crabs (Hartnoll 1969) and some other portunids (Fielder and Eales 1972; Eales 1974; Campbell 1982), is the rotation of the swimming legs or paddles ("paddling") during courtship. Paddling has been considered a visual display (Teytaud 1971) but it also produces a strong current that is directed towards the female due to the position of the male's body and his lateral chelae display (pers. obs.; Bushmann unpubl. data). Males may also produce urine- (Gleeson 1991) or non-urine- (Bushmann 1999) based chemicals that attract females. Thus paddling may also contain tactile or chemical information carried in the strong directional currents produced, as seen in other species (Atema 1986; Cowan 1991). The types of signals involved in blue crab courtship are still not entirely clear, but evidence suggests that chemical (both urine- and non-urine-based) signals may be of primary importance whereas visual information from both sexes may be of secondary importance (Teytaud 1971; Gleeson 1991; Bushmann 1999).

FACTORS INFLUENCING PAIR FORMATION

Population Characteristics

As in a variety of crustaceans (Seibt and Wickler 1979; Ridley and Thompson 1985; Forbes et al. 1992; Jormalainen 1998), pre-copulatory mate guarding in the blue crab is a male response to high levels of competition for access to receptive females that are limited numerically, temporally, or spatially (Jivoff and Hines 1998b). In a variety of taxonomic groups, pre-mating interactions and pair formation are influenced by local population characteristics, such as the number of males and females that are ready to mate (operational sex ratio), that dictate the abundance and the temporal and spatial availability of receptive females (Trivers 1972; Emlen and Oring 1977; Borgia 1979). In blue crabs, as the operational sex ratio becomes male-biased, males initiate courtship more readily and try harder to capture resistant females (Jivoff and Hines 1998a, b). Alternatively, pre-pubertal females that are late in the molt cycle reduce their rate of courtship towards males, presumably because they have access to a greater number of potential mates (Jivoff and Hines 1998b). These behavioral responses by both males and females to variation in local population structure influence the timing of pair formation and the individuals that successfully form pairs (Carver 2001).

Male Characteristics

In numerous taxonomic groups, there are a variety of male characteristics that enhance male pairing or mating success, including body size, health and physical condition, and the quality of secondary sexual characteristics (Andersson 1994). Large male blue crabs have advantages in competing for access to receptive females, as in a variety of other crabs (Salmon 1983; Adams et al. 1985; Reid et al. 1994; Koga and Murai 1997; Sainte-Marie et al. 1999). For example, large male blue crabs have proportionately

Table 1. Description of blue crab courtship behaviors by each sex-based on observations in field enclosures.

Behavior	Performer	Description
Approach	Both sexes	Crab elevated on walking legs, moves towards another crab. Often combined with chelae spread and paddle (Fig. 6A).
*Chelae Spread	Both sexes	Crab lifts and fully extends chelae laterally with dactyls closed. Often combined with approach and paddle.
*Paddle/Paddle-up	Both sexes	Crab's paddles (swimming legs) held above dorsal carapace and waved in circular motion (not so in paddle-up). Waving rate increases as the paddler approaches other crab. Often combined with approach and chelae spread (Fig. 6A).
*Jump-back	Male	While raised on the walking legs and paddling, male may vigorously thrust his posterior down and back.
Corral	Male	Male physically encloses female between chelae and positions her beneath him so both crabs face in the same direction.
*Pre-copulatory embrace (Guard: mate guarding)	Male	Once male is on top of female, he wraps first pair of walking legs under her and carries her with his sternum against her dorsal carapace until just before copulation (Fig. 6B).
*Bat	Male	Once male is on top of female, she may raise and wave her chelae. The male deflects her chelae with his own.
Let Go/Drop	Male	Once male is on top of female, he may release her temporarily (let go), often in response to female resistance; then he either reassumes mate guarding or abandons the female (drop).
*Courtship embrace	Male	Once female has molted, male flips her onto her dorsal carapace with his chelae so that his abdomen rests on hers, his walking legs cradle her, and they face in the same direction (Fig. 6D).
Backing	Female	Female turns away from the male and moves beneath him into the pre-copulatory position.
Follow/chase	Both sexes	Crab pursues another crab while both are walking. A chase ensues when both crabs are rapidly swimming.
Grab/Hold	Male	After chasing a female, the male may capture her with his chelae (grab) and restrain her (hold).
*Threat	Both sexes	Crab lifts and laterally spreads chelae towards another crab, usually with dactyls open.
Move away	Both sexes	Crab walks in the opposite direction of other crab, often combined with threat.
Flee	Both sexes	Crab rapidly swims (at least 1 m) in the opposite direction of another crab, often combined with threat, follow, or chase.
Block/Push	Both sexes	Crab lifts and extends chela to obstruct other crab (block). If other crab touches first crab, it may thrust chela to move other crab (push).
Poke/Stab	Both sexes	Crab thrusts chela to contact other crab (poke). Crab may thrust both chelae and forcefully lunge at other crab (stab).

* Indicates behaviors previously described by Teytaud (1971).

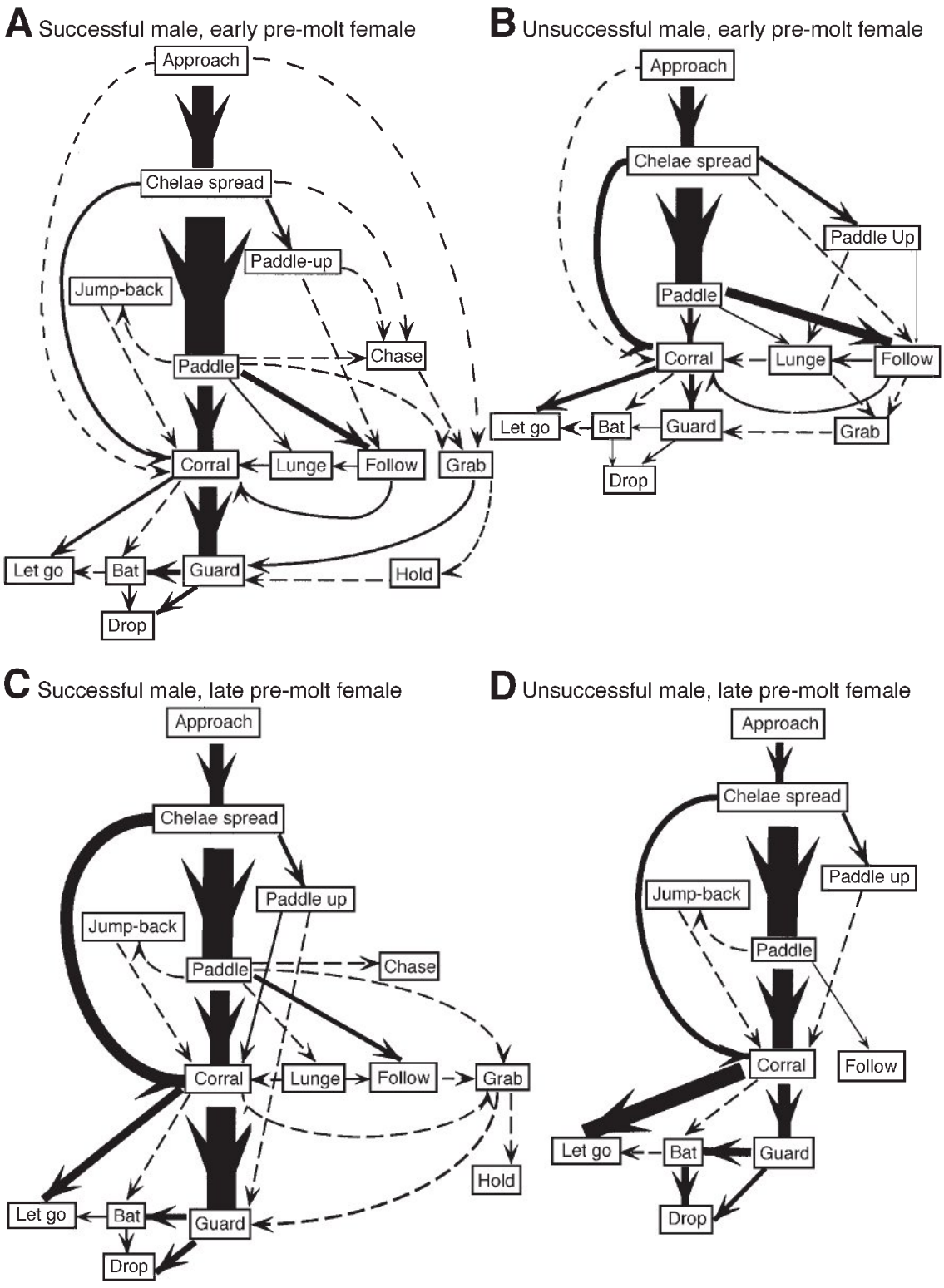

Figure 7. The effect of female molt stage on the sequence of male courtship behaviors that occurred in field enclosures by (A) successful males and (B) unsuccessful males towards pre-pubertal females early in the pre-molt cycle and by (C) successful males and (D) unsuccessful males towards pre-pubertal females late in the pre-molt cycle. Successful males paired with a female whereas unsuccessful males did not. Width of each continuous line and the size of its arrow are proportional to the mean rate of the behavioral sequence represented; dashed lines are sequences performed at low rates by not more than two different males. See Table 1 for description of each behavior. From Jivoff and Hines (1998b).

longer chelae than small males (Jivoff 1997b). This attribute in other species provides a distinct advantage during aggressive interactions for females (Stein 1976; Berrill and Arsenault 1984; Lee and Seed 1992; Claxton et al. 1994), as well as in physically controlling females (Arnqvist 1989; Snedden 1990; Lee 1995). Large male blue crabs more often displace smaller guarding males and can prevent displacement in competitive interactions for females (Fig. 8) (Jivoff 1997b). In the field, large males have a pairing advantage over smaller males in that they are more often paired (Fig. 9) and mate with larger, more fecund females (Jivoff 1997b). As in many other crustaceans, male blue crabs mate almost exclusively in the intermolt stage (C), suggesting that molting and mating are incompatible (Lipcius and Herrnkind 1982; Lipcius 1985; Sainte-Marie and Hazel 1992; Paul et al. 1995). Molting frequency decreases with crab size (Tagatz 1968b; Millikin and Williams 1980); therefore, large males spend more time in the intermolt stage and can dedicate more time to sexual competition and mating than small males can (Fig. 9) (Jivoff 1995).

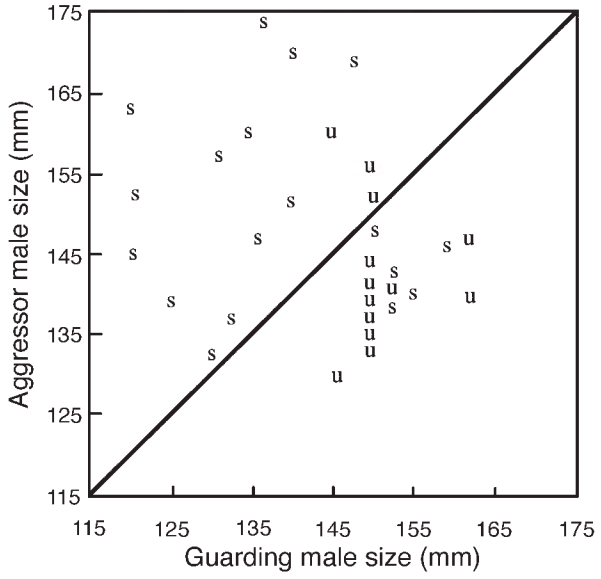

Figure 8. Distribution of successful (s) and unsuccessful (u) takeover attempts according to the sizes of the guarding male and the unpaired aggressor occurring in field enclosures. Successful takeovers resulted in the displacement of the guarding male; unsuccessful attempts did not. The diagonal line shows where the two types of males are the same size. From Jivoff and Hines (1998a).

Male health and physical condition may also be important factors influencing male mating success (Zahavi 1977; Kodric-Brown and Brown 1984; Brown 1997). In blue crabs, males spend considerable time and energy in mating activities; thus a male's physical condition may influence his degree of sexual receptivity and his ability to compete for access to females and to maintain mate guarding relationships. There are a variety of factors that may influence the physical condition or overall health of male blue crabs, including limb loss (autotomy), disease and parasite infection (see also Shields and Overstreet, Chapter 8), and male mating history (frequency of previous mating, especially time since last ejaculation). Males use their chelae during courtship to physically capture and control females and in aggressive interactions for females with other males. Thus, the loss of one chela is a significant handicap to male mating success in blue crabs (Smith 1992) and in other crab species (Sekkelsten 1988; Abello et al. 1994; Paul and Paul 1996).

In a variety of species, males with elevated parasite loads have reduced mating success resulting from decreased resistance to disease (Hauton et al. 1997), reduced competitive ability (Ward 1986; Nakashima 1995; Zohar and Holmes 1998), or poor quality of secondary sexual characteristics (Johnson et al. 1993; Kavaliers and Colwell 1995; Thompson et al. 1997). Blue crabs can be infected by a variety of parasites, viruses, and diseases that lead to poor physical condition (Millikin and Williams 1980; Couch and Martin 1982; Overstreet 1982) and diminished reproductive potential (Millikin and Williams 1980; O'Brien and Van Wyk 1985; Shields and Wood 1993) (see also Shields and Overstreet, Chapter 8) but in most cases, little is known about their effect on male mating success. However, the parasitic rhizocephalan barnacle *Loxothylacus texanus* has a marked effect on the mating success of male *C. sapidus* because the parasite castrates or feminizes its host and replaces the host's reproductive output with its own (O'Brien and Van Wyk 1985) and it is host-

specific even in the presence of closely related species (e.g., *C. similis, C. danae, C. rathbunae*) (Hsueh et al. 1993; Lazaro-Chavez et al. 1996).

In some species, sperm stores or the ability to pass large ejaculates to females influence male mating success (Markow et al. 1978; Eady 1995; Gage and Barnard 1996). Male blue crabs pass, on average, about 47% of their stored ejaculate contents to females (Jivoff 1997b) and they require between 9 to 12 d to fully recover their ejaculate stores (Jivoff 1997b; Kendall and Wolcott 1999). Recently mated males are as equally competitive for access to females as are virgin males (Kendall and Wolcott 1999), but they may forgo additional mating opportunities by ignoring pre-pubertal females or may delay mating by exchanging pre-pubertal females late in the molt cycle for females early in the molt cycle (Jivoff unpubl. data).

Female Characteristics

There are a variety of female characteristics that may influence pair formation and mating success in blue crabs, including body size and proximity to the pre-pubertal molt. As in many other species of crabs, the fecundity of female blue crabs increases with their size (Hines 1982,1988,1991). Thus, the larger females may be more attractive to males due to their higher reproductive value. However, as compared with other species (Hines 1982), the relationship between fecundity and female size is highly variable in the blue crab: (Hines 1982, $\log_{10}$ egg number = [1.022] $\log_{10}$ body weight + 4.57, n = 12, r^2 = 0.511; Prager et al. 1990, egg number $\times 10^6$ = [0.38] carapace width – 2.25, n = 134, r^2 = 0.39), so that factors in addition to body size may influence pair formation in this species (Jivoff 1997b; Jivoff and

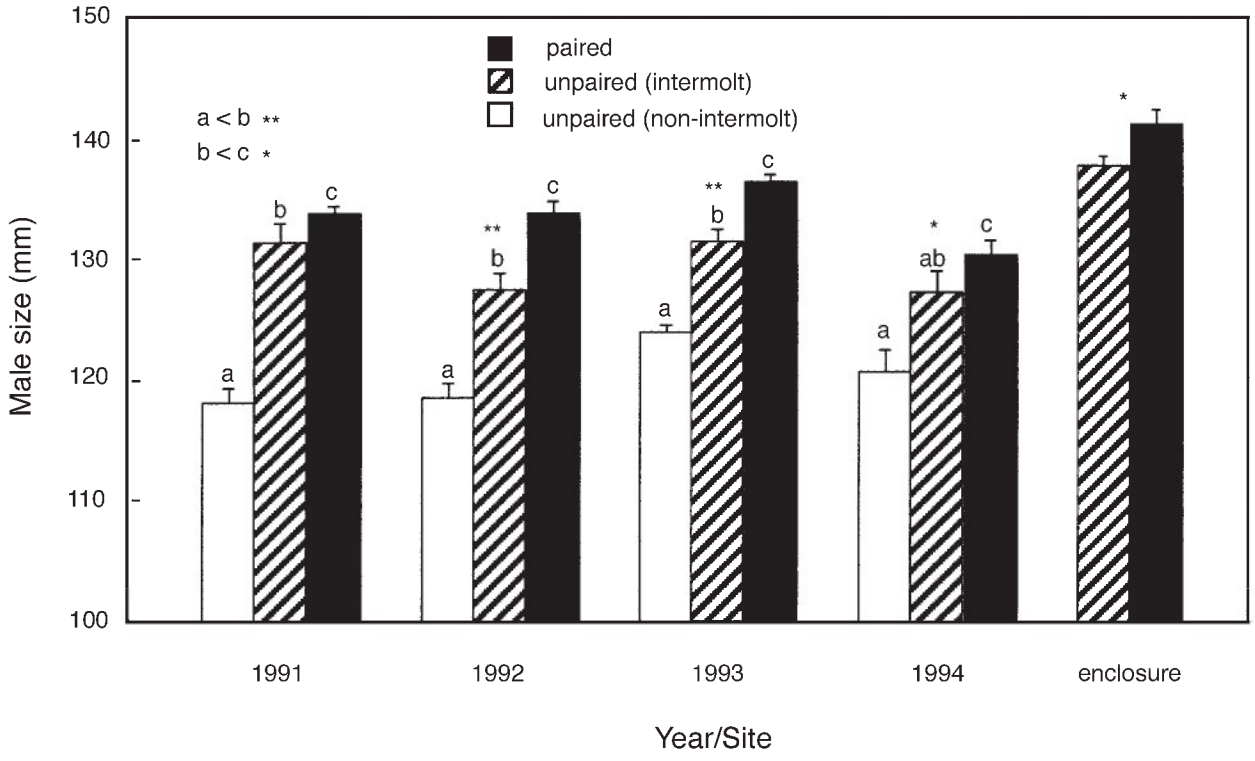

Figure 9. Mean carapace width (+1SE) of pre-copulatory mate-guarding males (filled bars), unpaired males in intermolt stage (hatched bars), and unpaired males in non-intermolt stages (open bars) captured in the field between 1991 and 1994 near the Rhode River, Maryland. Within each year, bars sharing the same letter are not significantly different. **=P<0.01, *=P<0.05.

Hines 1998b). In other mate-guarding species, male mating success is influenced by the amount of time a male spends with each female (Parker 1974, 1978). Male blue crabs may increase their reproductive success by balancing the trade-offs related to female size and molt stage, such that males may pair with (1) larger females, which have higher fecundity but may require longer mate guarding, (2) smaller females, which may require shorter mate guarding but have lower fecundity, or (3) pre-pubertal females late in the molt cycle, which require shorter pre-copulatory mate guarding and less effort during pair formation because they are less resistant to mate guarding than are pre-pubertal females early in the molt cycle (Jivoff and Hines 1998a, b).

Environmental Factors

Environmental factors, particularly temperature and salinity, can influence blue crab mating because they affect molting behavior (Shirley et al. 1990; Wolcott and Hines 1990; Fisher 1999), which dictates sexual maturity and the timing of mating. In temperate areas, mating typically occurs during the warm summer months (Van Engel 1958) but can begin much earlier in sub-tropical areas (Steele and Bert 1994; Fisher 1999). Molting does not occur below about 9°C (see Smith and Chang, Chapter 6), creating temporal variation in the abundance (both absolute and relative to the number of males) and distribution of pre-pubertal females. For example, in late spring there is an abundance of pre-pubertal females ready for the pubertal molt in the warmer waters of lower Chesapeake Bay, whereas further up the bay there are very few receptive females due to colder water temperatures (Hines et al. 1987; Gibbs 1996). As a result, there are two periods of mating activity in the lower bay (in the spring and late summer to early fall) versus a single peak in mating in the mid and upper bay (mid to late summer). Differences in local population structure, particularly sex ratio, during the two periods of mating in the lower bay may lead to significant variation in the mating success of males and females that mate during those periods. For example, during the spring, more females may go unmated or receive less sperm and seminal fluid at mating because males, especially of large size or that have not mated recently, are less abundant as compared with during the late summer (Hines et al. 2003).

Salinity also influences the temporal and spatial distribution of sexually receptive crabs (Hines et al. 1987; Steele and Bert 1994), dictating the temporal and spatial distribution of mating opportunities. In the Rhode River, a sub-estuary of Chesapeake Bay, low salinity areas are used during the summer for molting, predominantly by pre-pubertal males, whereas brackish areas are used for mating and thus are dominated by intermolt males and pre-pubertal females (Hines et al. 1987).

Hormonal Control

Different hormones, including ecdysteroids, chromatophorotropins, and terpenoids, may contribute to sexual receptivity in some species of crabs (Quackenbush 1986) and thus influence pair formation and mating success. Ecdysteroids are involved in gonad maturation, which may be an important factor determining the sexual receptivity of individuals. Chromatophorotropins, released from the eyestalk neuroendocrine system, regulate color patterns (Quackenbush 1986) that in some species, such as *Uca musica* (Ocypodidae), may indicate reproductive readiness or competence (Zucker 1984). Terpenoid hormones, such as juvenile hormones in insects, also stimulate gonad maturation in some species (Quackenbush 1986). For example, in the portunid *Carcinus maenas*, the androgenic gland releases farnesylacetone, which stimulates protein synthesis in the testes (Berreur-Bonnenfant and Lawrence 1984) but not spermiogenesis (Ferezou et al. 1977). In the blue crab, and other species such as the spider crab *Libinia emarginata*, the mandibular organ may also produce terpenoid hormones (Laufer et al. 1984). In *L. emarginata*, male sexual receptivity may be regulated by the terpenoid hormone methyl farnesoate because increased levels of this hormone occur in adult males in the intermolt stage that have well developed vasa deferentia and mature chelae allometry (Homola et al. 1991; Sagi et al. 1994; Laufer and Ahl 1995; Ahl and Laufer 1996). In blue crabs, the role

of hormones in regulating male sexual receptivity is still unclear despite evidence that there is considerable variation in the response of males to pre-pubertal females (Teytaud 1971; Gleeson et al. 1987; Jivoff and Hines 1998b; Bushmann 1999).

INSEMINATION AND POST-MATING INTERACTIONS

In blue crabs, copulation occurs shortly after the female completes her terminal molt (Van Engel 1958). When the female begins the molting process, the male loosens the pre-copulatory embrace, and may even assist the female out of her old carapace. Within minutes of her completing ecdysis, the male turns the female upside-down beneath him, such that their ventral surfaces meet and both face in the same direction (Fig. 6D). Copulation commences when both sexes lower their abdomens, allowing the male to insert the primary pleopods into the external openings of the female reproductive tract, and may last for 5 to 12 h. After copulation, the male turns the female right-side up beneath him in the post-copulatory mate guarding embrace, which may last for 4 to 5 d (Van Engel 1958; Jivoff 1997a). Males may mate several times (the number is undetermined) within a mating season, and may survive through at least two mating seasons (Van Engel 1958; Fischler 1965). However, recent evidence based on the condition of male vasa deferentia suggests that males indeed mate more than once during the mating season (Kendall and Wolcott 1999; Kendall et al. 2001).

In contrast, female blue crabs have a single opportunity to mate, immediately after the pubertal molt, and it has been assumed that they mate with only one male at that time (Van Engel 1958; Millikin and Williams 1980). However, recent experimental and field evidence indicates that about 12% of females mate with more than one male during the pubertal molt, storing both ejaculates such that both males' sperm have access to the unfertilized eggs (Fig. 10) (Jivoff 1997a). In many species from a variety of taxonomic groups, females mate with more than one male, which results in competition among the different males' sperm for egg fertilizations (sperm competition) and influences the way in which post-copulatory mate guarding occurs (Smith 1984).

In crabs, post-copulatory mate guarding occurs when females mate immediately after molting, when their carapace is soft and they are extremely vulnerable to predation (Hartnoll 1969; Salmon 1983). In blue crabs, unpaired pre-pubertal females suffer higher mortality rates during the pubertal molt than do paired females (Shirley et al. 1990; Jivoff 1997a), indicating that mate guarding protects females during the pubertal molt. In addition, male blue crabs guard longer in the presence of predators than in their absence (Jivoff 1997a), which is also true for the stone crab *Menippe mercenaria* (Xanthidae), another species that mates when the female is soft and vulnerable (Wilber 1989). Moreover, in the presence of other males, and thus an increased risk of sperm competition, male blue crabs guard longer and pass larger ejaculates to females, which may prevent additional males from mating with the female (Jivoff 1997a). Furthermore, the longest post-copulatory mate-guarding durations in the field correspond to those produced by an increased risk of sperm competition (Jivoff 1997a). Thus, varying levels of sexual competition (for example, because of local population sex ratios) influence male blue crab reproductive investment in terms of mate guarding time and the volume of ejaculate passed to females.

Female blue crabs have a single opportunity to mate, so it is critical that they copulate at that time and that they obtain enough ejaculate to ensure their full reproductive potential. Although insemination of most adult female blue crabs has been documented in a variety of estuaries (e.g., Maryland [Jivoff 1997b; Hines et al. 2003], South Carolina [Wenner 1989], North Carolina [T. Wolcott et al., North Carolina State University, unpubl. data], Florida [Hines et al. unpubl. data]), the amount of ejaculate they store varies temporally (e.g., among months) and spatially (e.g., within and among estuaries) (Jivoff 1997b, Hines et al. 2003) (Fig. 11). That amount is influenced by the size and mating history of their mate (Jivoff 1997b; Kendall and Wolcott 1999; Kendall et al. 2001, 2002), copulation duration

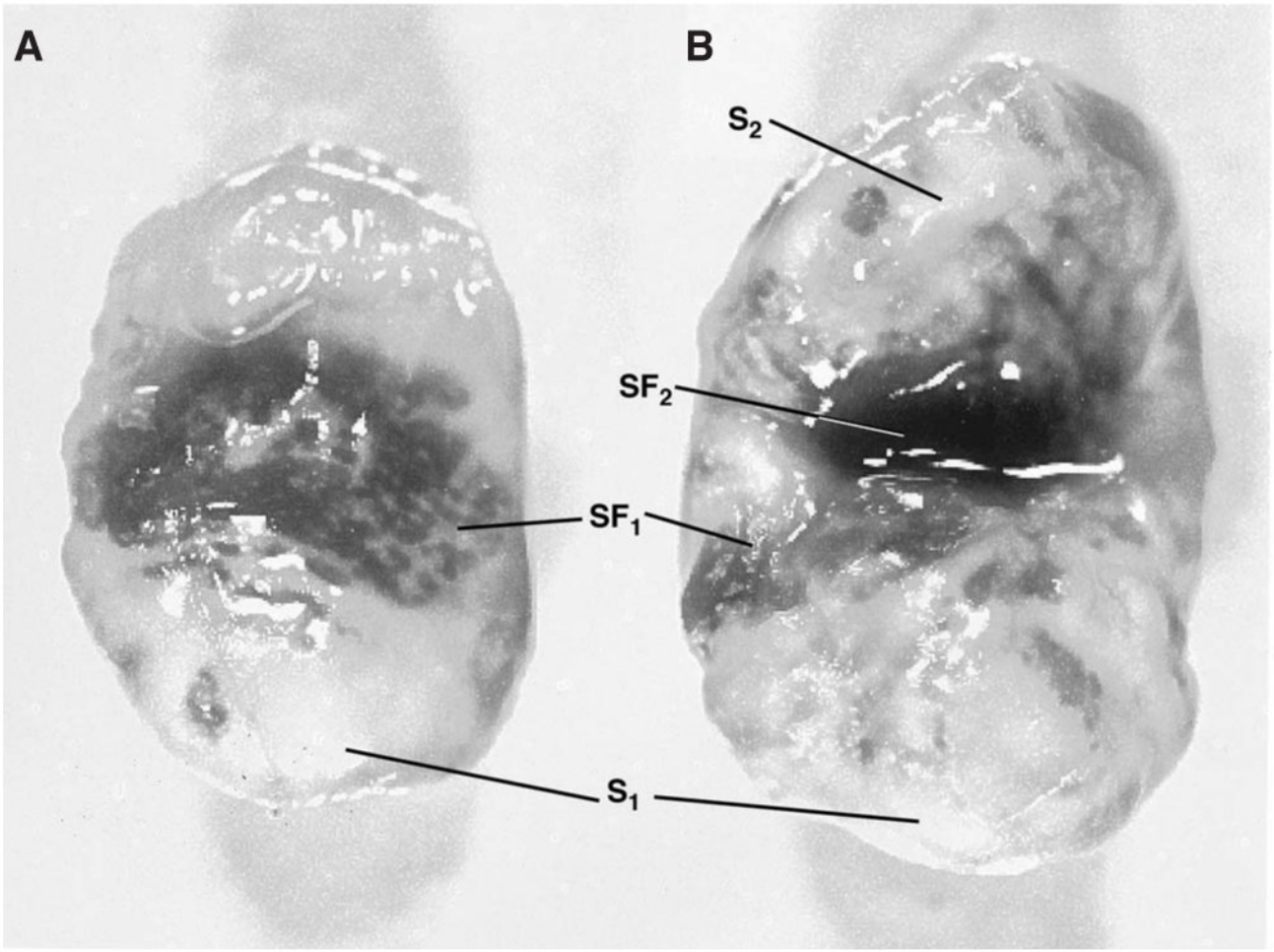

Figure 10. Condition of adult female spermatheca (A) mated with one male and (B) mated with two males including spermatophores of ejaculate one [S_1], spermatophores of ejaculate two [S_2], seminal fluid of ejaculate one [SF_1], seminal fluid of ejaculate two [SF_2]. Photo by P.R. Jivoff.

(Jivoff 1997b), and local sex ratio (Jivoff 1997a). Evidence from other crab species indicates that the amount of sperm females have available for egg fertilization influences their reproductive output (Powell et al. 1974; Nizyaev and Fedoseev 1989; Paul and Paul 1989a; Norman 1996). Preliminary evidence indicates that the amount of ejaculate female blue crabs have stored in the spermathecae also influences the number and the fertility of broods produced (Hines et al. 2003) (Fig. 12). Sperm are lost from the spermathecae during storage, but factors that affect the rate of loss are poorly understood (Hopkins 2002).The only direct study of the loss of sperm was done in warm months (Hopkins 2002), so that effects of storage during cold winter months in Chesapeake Bay are unknown.

Potential Fisheries Implications

Concern has increased in recent years that intense fishing pressure is disrupting mating and reproduction in blue crabs (e.g., Cole 1998; Uphoff 1998; Carver 2001; Kendall et al. 2001, 2002; Hopkins 2002; Hines et al. 2003) and other commercially important crab species (Caddy 1989; Jamieson 1993; Sainte-Marie and Lovrich 1994). Crustacean fisheries differ from those of other groups because they typically concentrate on large, sexually mature males that often are removed at the highest rates

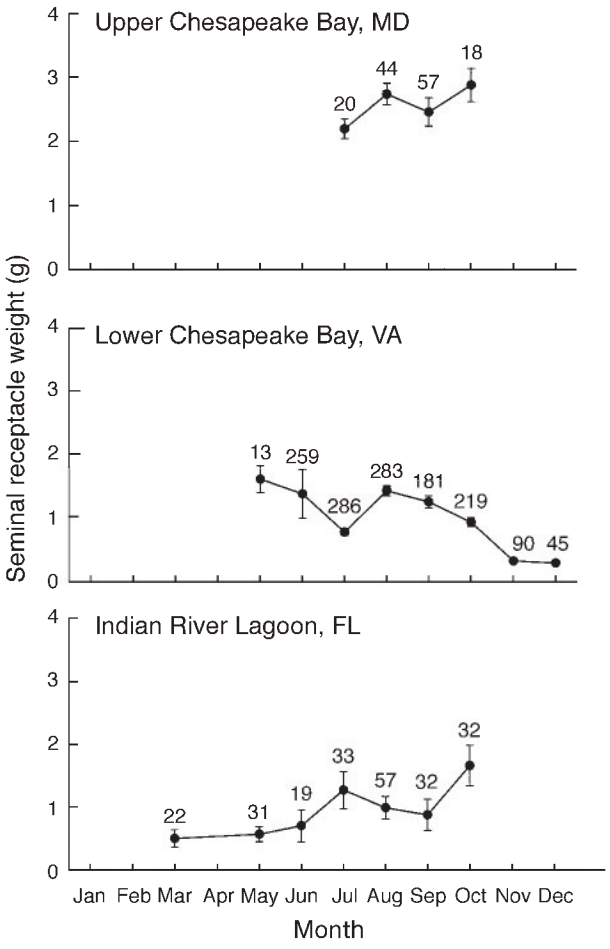

Figure 11. Seasonal variation in mean weight (± 1SE) of seminal receptacles of female blue crabs from upper and lower Chesapeake Bay and Indian River Lagoon, Florida during 1996. Number of mature females are indicated for each month. From Hines et al. (2003).

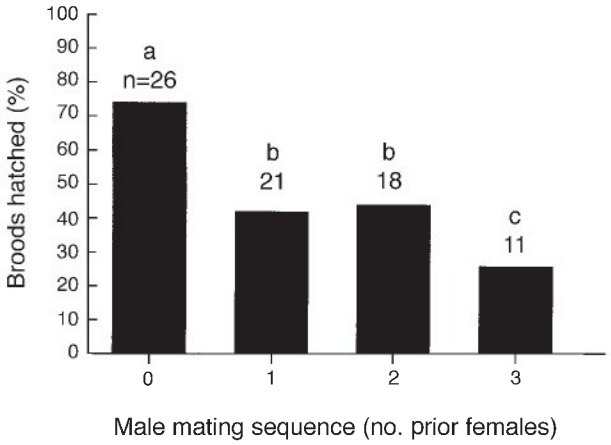

Figure 12. Relationship between brood hatching success and male mating history for female blue crabs in laboratory mating experiments in Indian River Lagoon, Florida. Histogram bars indicate percent of first broods hatching as a function of the number (no.) of prior females mated in sequence to males. Sample sizes (n) indicate number of females in each group. Bars sharing the same letter are not significantly different. From Hines et al. (2003).

during the reproductive season (Cobb and Caddy 1989). Analyses of blue crab populations along the U.S. east coast indicate that fishing effort is increasing; catch per unit effort is decreasing; and the average size of legal-sized males is decreasing in Maryland (Abbe and Stagg 1996; Uphoff 1998), Louisiana (Guillory and Perret 1998), and Texas (Hammerschmidt et al. 1998). In blue crabs (Abbe and Stagg 1996) and other crustaceans (Ennis et al. 1990; Smith and Jamieson 1991; Donaldson and Donaldson 1992), evidence suggests that intense removal of large males alters local population structure by reducing both the ratio of sexually active males:females, and the size-structure of a population. In other commercially important crabs, small, less competitive, males may have increased opportunities to mate as a result of fishing presssure (see Jamieson et al. 1998) and females may have difficulty finding a male or may mate with a male that provides a limited amount of ejaculate (Paul and Paul 1989a; Smith and Jamieson 1991; Sainte-Marie et al. 1995; Hankin et al. 1997). In blue crabs, such changes in population structure have important consequences on the way mating takes place, including providing small males with increased access to females and more frequent matings (Jivoff and Hines 1998a, b) and reducing the investments males make (mate guarding time, quantity of ejaculate) in mating and reproduction (Jivoff 1997a, b; Kendall and Wolcott 1999). These changes in blue crab mating may contribute to reduced female reproductive output (see below).

FERTILIZATION AND BROOD PRODUCTION

Fertilization

As in many other crab species, fertilization in the blue crab is thought to occur in the spermathecae (Hard 1945; Johnson 1980). In a variety of species (Villavaso 1975; Eberhard and Cordero 1995; Arthur et al. 1998; Ward 1998), including other species of crabs (Jensen et al. 1996; Sainte-Marie and Sainte-Marie 1998, 1999a), the processes that occur within the female spermathecae to accomplish egg fertilization are just as complex as those seen to accomplish insemination. Despite large changes that occur in the spermathecae between insemination and oviposition in blue crabs (Hard 1945; Johnson 1980), relatively little is known about how those changes occur or how they are regulated.

In temperate areas, insemination occurs during the summer months although most females do not produce their first brood of eggs until the following spring or summer, using sperm stored for "at least" 1 year or more, depending on the longevity of the female (Hard 1945; Van Engel 1958; Hines et al. 2003). During the 2 months after insemination, the hardened seminal fluid softens and "dissolves," which eventually allows the unfertilized eggs to move through the spermathecae for fertilization (see Fig. 4) (Hard 1945). It is not clear how the dissolution of the seminal fluid takes place, although secretions from the epithelium of the spermathecae have been implicated in blue crabs (Johnson 1980) and other crab species (Ryan 1967b; Diesel 1989; Beninger et al. 1993; Sainte-Marie and Sainte-Marie 1998). Concomitant with seminal fluid dissolution is the process of spermatophore dehiscence, whereby sperm from at least some of the spermatophores are released into the spermathecae (Johnson 1980; Hopkins 2002). In other crab species, secretions from the epithelium of the spermathecae may weaken the resistant pellicle of the spermatophores (Ryan 1967b; Diesel 1989; Beninger et al. 1993), then a combination of water absorption or physical disturbance may break the spermatophore and allow sperm to be released (Uma and Subramoniam 1979; Beninger et al. 1993). The unfertilized eggs move from the ovary into the spermathecae for fertilization, but in blue crabs it is not clear what triggers or controls this egg movement. In other species, it was suggested that muscular contractions assist in the evacuation of eggs from the ovary (Ryan 1967b; Bawab and El-Sherief 1989; Beninger et al. 1993) because as many as 2 to 6 million eggs may travel through the spermathecae in approximately 1 h (Ryan 1967b) to 2 h (Van Engel 1958). It is thought that eggs are fertilized in the spermathecae before being extruded onto the four pairs of pleopods on the female abdomen.

As noted on page 264, the mature sperm of blue crabs lack flagella. Each consists of an acrosome, apical cap, and eight radial arms (Brown 1966) (see Fig. 5). The radial arms attach to the unfertilized egg and the apical cap unites with the outer egg membrane or chorion (Brown 1966). The acrosome elongates through the apical cap and penetrates the egg. A complex series of changes in the shape of the sperm occurs during attachment to the egg, culminating in an acrosomal reaction that "injects" the sperm through the chorion (Brown 1966). In addition, the radial arms of the sperm consistently attach to the egg in the same orientation and subsequently release from the egg before the acrosomal reaction, suggesting that a chemically driven "attach-and-release mechanism" may modulate the injection of the sperm into the egg (Brown 1966). The acrosome reaction can be induced by the addition of seawater, or by osmotic or physical pressure, and occurs in the presence of unfertilized eggs (Brown 1966). Several hundred reacted sperm were observed with the acrosomal region everted through the chorion of a single egg (Brown 1966), suggesting that sperm-to-egg ratios required for successful fertilization may far exceed 1:1, as seen in other species (e.g., 70:1, see Sainte-Marie and Carriere 1995). In the snow crab *Chionoecetes opilio*, females will not extrude eggs if the sperm-to-egg ratio in the spermathecae is less than 7:1 (Sainte-Marie and Carriere 1995).

In Chesapeake Bay and other estuaries, there is temporal and spatial variation in the amount of

sperm female blue crabs have stored (Hines et al. 2003) (Fig. 13). On average, the number of sperm stored by recently mated females in the Rhode River is 6×10^8 (Hines et al. 2003). Given that the average number of eggs per brood is approximately 3×10^6 and that females may produce three broods per spawning season, the sperm-to-egg ratio is 66:1. If females are capable of producing more broods over their lifetime (see below) (Hines et al. 2003), then sperm-to-egg ratios may become limiting. Although it is not known whether the presence or quantity of sperm in the spermathecae dictates egg extrusion, preliminary evidence indicates that the quantity of material in the spermathecae influences the number and/or fertility of broods produced (see below and Fig. 12) (Hines et al. 2003).

Brood Production

In the blue crab, relatively little is known about the factors governing brood production, a complicated process involving the temporal and spatial coordination of female physiology with particular environmental conditions. Previous work suggests that female blue crabs in temperate areas produce one to three broods of eggs (Hard 1945; Van Engel 1958; Prager et al. 1990; Hines et al. 2003). In subtropical waters of Florida, blue crabs produced as many as 8 broods per season, which extrapolates to 16 broods per lifetime if females live for two years after mating (Hines et al. 2003). However, the number of broods and size of each brood spawned by females is influenced by a variety of factors, including environmental conditions (e.g., temperature and salinity) and female characteristics, (e.g., size). As in other species of crabs (Hartnoll 1985), broods are produced using sperm stored for long periods (e.g., 8 to 12 months in blue crabs), which can affect sperm viability at the time of fertilization (Morgan et al. 1983; Paul 1984; Sainte-Marie 1993). In blue crabs, nothing is known about the factors that influence sperm viability during storage in the female but preliminary evidence suggests there may be considerable variation among females in the viability of their stored sperm (Hopkins 2002). As in other crabs (Powell et al. 1974; Paul and Paul 1992,1997), recent evidence in blue crabs suggests that the characteristics of the female's sexual partner (e.g., size, mating history) may also influence her reproductive output (Hines et al. 2003).

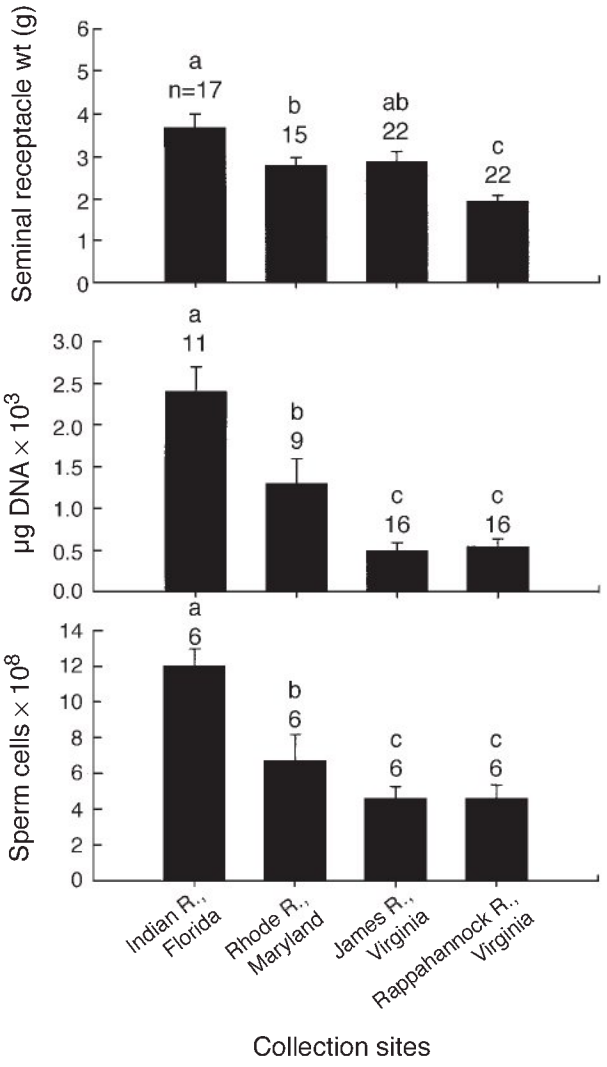

Figure 13. Geographic variation in seminal receptacle weight (wt), weight of DNA, and number of sperm cells in seminal receptacles of female blue crabs. Means (± 1SE) and sample sizes (n) are plotted for samples from Indian River Lagoon, Florida; Rhode River, upper Chesapeake Bay, Maryland; James River and Rappahannock River, Virginia, in lower Chesapeake Bay. Within each panel, bars sharing the same letter are not significantly different. From Hines et al. (2003).

TIMING OF BROOD PRODUCTION

In the blue crab, there is temporal and spatial variation in the timing and duration of the spawning season. The timing of brood production is influenced by environmental conditions, and spawning is initiated earlier in the spring at lower latitudes (Millikin and Williams 1980). Spawning occurs from June to August in New Jersey (Jivoff unpubl. data), May to September in Chesapeake Bay (Van Engel 1958; McConaugha et al. 1983), March to September in North and South Carolina (Williams 1971), and February to October in Florida (Tagatz 1968a). In Chesapeake Bay and other estuaries, mating occurs throughout much of the estuary whereas spawning occurs in high salinity regions in the lower estuary (Van Engel 1958; Schaffner and Diaz 1988). Thus, sometime after mating, adult females migrate from their mating area to particular regions in the lower estuary for brood production and spawning.

Migration from the mating area to spawning regions occurs in two phases (Tankersley et al. 1998). In phase I, inseminated females move to the lower estuary, where they subsequently produce and incubate broods; in phase II, ovigerous females migrate near or out of the mouth of the estuary to hatch their eggs, releasing larvae into the water column. In upper Chesapeake Bay, post-copulatory females remain in the mating areas to feed, recover from molting, and begin to accumulate nutritional stores during summer and early fall. They undergo phase I migration in late September to November, when environmental conditions (probably colder water temperature or changing photoperiod) trigger movement to the lower bay (Turner 2000; Turner et al. 2003; Aguilar et al. 2005). During phase I migration in Chesapeake Bay, females move as much as 200 km (although many move much shorter distances) along the deep channel of the mainstem of the bay rather than along routes in the shallow shoulders or nearshore areas (Aguilar et al. 2005). Upon reaching the mid- to lower estuary when temperatures drop below about 10°C, the females cease movement and bury into the sediment over winter and do not begin brood production until the following late spring and summer (Hines et al. 2003; Aguilar et al. 2005). In phase II migration, females with broods in advanced developmental stage move further towards and/or into the ocean to hatch their eggs, and use particular behaviors cued to photoperiod and tidal and lunar rhythms (see Larval Release below).

BROOD CARE

While not traditionally considered providers of parental care, female blue crabs do perform a variety of behaviors that enhance the survival of their offspring. For example, egg development and hatching success are promoted by salinities of at least 20[1] (Davis 1965). In addition, larval development occurs in offshore waters above the continental shelf (Provenzano et al. 1983; Epifanio et al. 1984). Therefore, the down-estuary migration of females to high salinity water enhances the development and hatching success of eggs and the dispersal of larvae. Blue crabs are excellent swimmers, capable of moving considerable distances relatively quickly (Wolcott and Hines 1989; Hines et al. 1995), but the down-estuary migration of adult females (as long as 200 km in Chesapeake Bay) may be facilitated by vertical movements into ebb-tide currents (selective tidal-stream transport; see Tankersley and Forward, Chapter 10). The selective use of these currents may minimize energy expenditures during migration, thus saving energy for further egg development or for maintaining the female during over-wintering. However, initial evidence from Chesapeake females equipped with data logging tags for depth, salinity, and temperature indicates that most crabs move along the bottom during Phase I migration (T. Wolcott, unpubl. data). At the spawning grounds, females prefer areas dominated by sediments of sand

[1] Salinity is presented as a pure ratio with no dimensions or units, according to the Practical Salinity Scale (UNESCO 1985).

or a mixture of sand and silt in which to bury for the winter (Schaffner and Diaz 1988). In spring when the eggs are extruded, these sediment types allow the adherence of fertilized eggs to the pleopods by promoting the formation of the egg membranes and attachment strands to the pleopods, which is critical for successful egg development (see Ryan 1967b; Kuris 1991). It is not known how sediments promote this process, but in laboratory studies in the absence of sediment, newly extruded eggs do not attach to the pleopods (Sulkin et al. 1976; Jivoff unpubl. data). Females carry the developing eggs on their abdomen for 14 to 17 d and during that time they may flex their abdomens or stroke the eggs with their walking legs in order to aerate or remove inviable eggs or parasites, as seen in other species (Kuris 1991; Levi et al. 1999; Oh and Hartnoll 1999).

FECUNDITY

There are three main factors that can contribute to the total number of eggs produced by female blue crabs: (1) the number of eggs per brood, (2) the viability of eggs in each brood, and (3) the number of broods produced per season and per lifetime. Much of the previous work on blue crab fecundity has examined the number of eggs produced in the first brood. However, females are capable of producing two or more broods per spawning season (Van Engel 1958) and we have a poor understanding of the factors that dictate the reproductive potential of female blue crabs beyond the first brood.

Female blue crabs are highly fecund, producing between 0.7 and 6×10^6 eggs in their first brood (mean, $3.2 \times 10^6 \pm 1.6 \times 10^6$ SD; Van Engel 1958; Prager et al. 1990) weighing an average of about 30 g (range, 24–98 g wet weight; Tagatz 1965; Roberts and Leggett 1980). One factor contributing to the very high fecundity is that blue crabs have relatively small eggs (251 μm diameter; see also Davis 1965) compared with other crab species (range among 20 species, 251–731 μm), including other portunids, majids, cancrids, and xanthids (Hines 1982). As in other species (Hines 1982, 1988, 1991; Reid and Corey 1991; Siddiqui and Ahmed 1992), the number of eggs produced increases linearly with female size (Hines 1982; Prager et al. 1990). The volume of the body cavity available for the developing ovary constrains brood size (Hines 1982), suggesting that the relatively large increase in carapace width of females (due to growth of the lateral spines) at the pubertal molt (Newcombe et al. 1949b) may increase the available space for the developing ovary. Blue crabs are more fecund than other crab species, but the female size-fecundity relationship is also more variable, suggesting that factors in addition to female size are also important (Hines 1982). In other species, fecundity can vary temporally and spatially (Davidson et al. 1985; Shields 1991; Kennelly and Watkins 1994), and with the availability of energy stores for ovary development (Kennish 1997). In addition, trade-offs between egg number and egg size (Sainte-Marie 1993) or between energy for somatic growth (e.g., limb regeneration) and reproduction (Norman and Jones 1993) also influence female fecundity. Little is known of the factors that contribute to the variation in fecundity of the first brood, and the few observations available indicate that subsequent broods are smaller and contain a greater percentage of inviable eggs (Darsono 1992; Hines et al. 2003).

Van Engel (1958) noted that "many" eggs in a brood do not hatch, indicating that egg infertility reduces fecundity between oviposition and larval release and contributes to the variation in the female size-fecundity relationship. In a variety of species, numerous factors result in egg losses between oviposition and larval release (see below). The loss of eggs may occur more often in the later stages of egg development (Oh and Hartnoll 1999) and may be size-related (Kuris 1991; Norman and Jones 1993), suggesting that fecundity within one brood can vary over time. In other crab species, characteristics of a female's sexual partner, including his size and frequency of mating in the recent past (mating history), influence egg fertility (Powell et al. 1974; Paul and Paul 1989b,1997), which suggests that the quantity or quality of sperm available for fertilization affects egg fertility rates. For example, long periods of sperm storage in the female (Paul 1984; Hopkins

2002) or the male (Leung-Trujillo and Lawrence 1987) of other species may limit the number of viable sperm available for fertilization. Preliminary evidence (Hines et al. 2003) suggests that egg fertility, especially in broods subsequent to the first, decreases perhaps as a result of reduced sperm stores in the female spermathecae.

POTENTIAL FISHERIES EFFECTS

A major concern for the management of blue crabs (see Cole 1998; Uphoff 1998), as well as other commercially important species, is the maintenance of an abundant spawning stock to ensure reproduction and sustained levels of recruitment (Caddy 1989; Lipcius and Van Engel 1990). Although male blue crabs are the primary target of the fishery (large males being of greater economic value), adult females are also taken and represent an increasing percentage of the catch as a result of a decreasing supply of males in Maryland (Rugolo et al. 1998; Uphoff 1998) and Delaware (Cole 1998). Therefore, fishing pressure results in direct losses in female egg production because females are removed before spawning, either during their down-estuary migration to the spawning grounds or during overwintering (Jordan 1998). However, there is increasing concern that changes in population structure due to intense fishing pressure on blue crabs and other commercially important species (Jamieson et al. 1998) can indirectly reduce female reproductive output in complex ways. For example, compared with non-fished crab species, commercially important species show greater losses of eggs to nemertean brood parasites as a result of changes in host-population structure from intense fishing pressure (Wickham 1986).

Reduced female egg production may also stem from intense fishing pressure on males (McMullen and Yoshihara 1971; Nizyaev and Fedoseev 1989; Norman and Jones 1993). In a wide array of species, female reproductive output is enhanced by the quantity or quality of ejaculate received from males (Nakatsuru and Kramer 1982; Gwynne 1984; Rutowski et al. 1987). Thus, intense removal of males, especially large males with greater sperm stores, may prevent females from finding a male altogether or a male that can provide enough ejaculate for females to achieve their full reproductive potential (McMullen and Yoshihara 1971; Nizyaev and Fedoseev 1989; Smith and Jamieson 1991; Sainte-Marie et al. 1995). An analysis of red king crab *Paralithodes camtschaticus* fisheries suggests that reduced fishing pressure on breeding males may provide more stable and sustainable yields and maintain reproductive potential (Schmidt and Pengilly 1989). *Paralithodes* species are particularly vulnerable to reduced female reproductive potential via fishery depletion of males because females are unable to store sperm. In blue crabs, intense removal of large males may lead to small males mating more frequently than otherwise expected, resulting in females receiving reduced quantities of ejaculate (Jivoff 1997b; Kendall and Wolcott 1999). Receiving adequate sperm supplies may be especially important for female blue crabs because most females use stored sperm from a single male to fertilize their lifetime supply of eggs (Van Engel 1958; Jivoff 1997a). Preliminary results indicate that adult females with reduced ejaculate stores produce infertile eggs more quickly, suggesting that female reproductive potential may be limited by the quantity of material available for fertilization (see Fig. 12) (Hines et al. 2003).

EMBRYONIC DEVELOPMENT

Embryonic development (Fig. 14) occurs externally on the underside of the female abdomen and is influenced by environmental conditions. Newly extruded embryos are relatively small (273 × 263 μm) but increase in volume by about 18% by the time of hatching (320 × 278 μm; Davis 1965). Development takes 12 to 15 d at 28°C and salinity 30; (Darsono 1992) but takes longer at colder temperatures (14 to 17 d at 26°C; Costlow and Bookhout 1959). The major steps in embryonic development include a granular appearance of successive cleavage stages (day 1), development of a transparent area that marks the development of endodermal cells and the beginning of gastrulation (day 2), separation of embryos from the lipid-rich

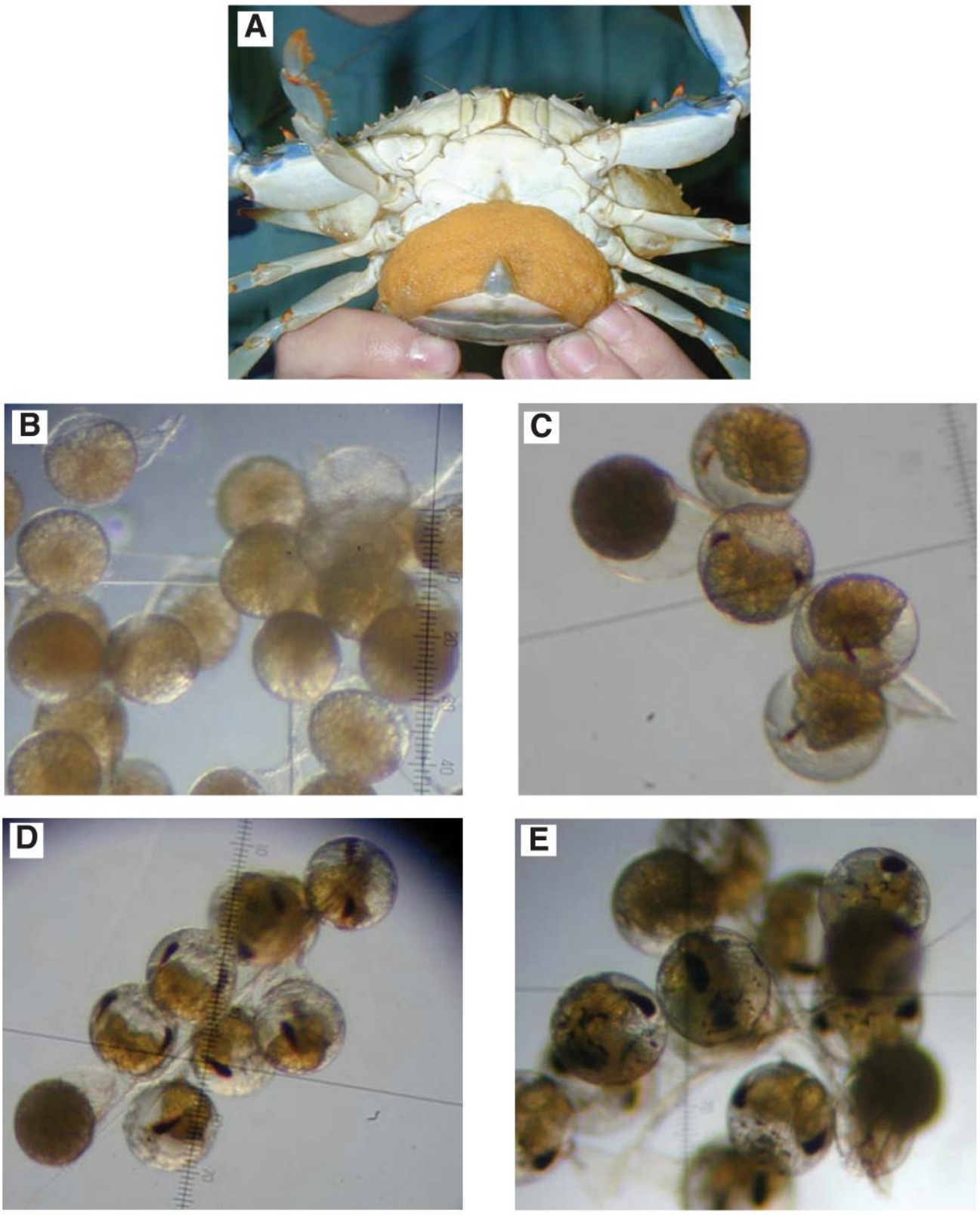

Figure 14. Embryonic development of blue crab eggs during incubation. (A) Female with newly extruded brood of eggs, or sponge. (B) 5-day-old embryos with egg attachment stalks evident. (C) 9-day-old embryos with eye pigments forming. (D) 11-day-old embryos with eyes clearly visible. (E) 12-day-old embryos ready to hatch as zoeas. Photos by A. Young-Williams.

yolk (days 4-5), the appearance of eye pigments (day 8), and appearance of zoeal appendages as the yolk is reduced to small patches (day 11) (Darsono 1992). During development, the color of the entire brood changes, appearing yellow to orange 1 to 7 d after extrusion and brown to black 8 to 15 d after extrusion (Bland and Amerson 1974; Millikin and Williams 1980).

Embryo Loss during Development

Embryo loss during development is common among crustaceans, with one study finding about 30% of species exhibiting decreases in brood size during development (Kuris 1991). The extent of embryo loss per brood varies among species but can be significant, ranging from 0 to 69% among crayfish (Corey 1991) and from 0 to 100% in other crustaceans (Wickham 1986). Numerous factors result in the loss of embryos during development including lack of embryo adhesion to the pleopods, mechanical losses, embryo predation, disease, and parasites (see also Shields and Overstreet, Chapter 8) (Perkins 1971; Otto et al. 1989; Corey 1991; Kuris 1991). Relatively little is known about the incidence and extent of embryo loss that occurs during development in blue crabs. Blue crab embryos are susceptible to fungal infection, especially by the marine phycomycete *Lagenidium callinectes,* which eventually destroys the infected embryos (Bland and Amerson 1974). Temporal and spatial variation occurs in both the incidence of infection (as high as 95%) and the degree of infestation (33-50% of the brood), especially in late stage embryos (Bland and Amerson 1974). In addition, the nemertean egg predator *Carcinonemertes carcinophila* may infest the embryo masses of blue crabs, with the incidence of infection among females ranging from 0 to 100% (Overstreet 1982). Infestation rates correlate with high salinities and the peak of spawning (Millikin and Williams 1980; Overstreet 1982), but little work has examined the relative effect of this predator on female reproductive output. Nemertean egg predators are an important source of egg loss in other crabs, particularly in commercially important species because intense fishing pressure leads to changes in host-population structures that result in a higher prevalence or intensity of infestation (Wickham 1986).

Larval Release

Blue crab larvae develop in the offshore waters above the continental shelf (see Epifanio, Chapter 12; McConaugha et al. 1983; Epifanio et al. 1984). Evidence indicates that just before larval release, females carrying embryos in the later stages of development migrate from the spawning grounds to the ocean (Tagatz 1968a) by vertically swimming into nocturnal, ebb-tide currents (selective tidal-stream transport; Tankersley et al. 1998; Tankersley et al. in review). In a variety of crab species, larval release is synchronized to light:dark, tidal phase, and tidal amplitude cycles such that larval release occurs during nocturnal high tides of the largest amplitudes (Forward 1986; Morgan and Christy 1994; Morgan 1996). In blue crabs, larval release is apparently synchronized by two coupled endogenous oscillators, one with circatidal periodicity and one with circadian periodicity (Ziegler et al. in review). Salinity and light (photoperiod) serve as cues for the two oscillators, and expression of the circatidal rhythm in hatching is influenced by the circadian clock such that larvae are released and transported seaward during morning ebb tides (Tankersley et al. 1998; Tankersley et al. in review; Ziegler et al. in review). This synchrony reduces predation on the newly released larvae by rapidly transporting them in strong ebb-tides to deeper waters, away from planktivorous predators in the near-shore zone (Morgan and Christy 1995, 1997).

Hatching begins with the uptake of water into the embryo, which is promoted by salinities of at least 18 (Costlow and Bookhout 1959; Davis 1965). Osmotic swelling of the inner embryonic membrane initiates hatching by rupturing the outer embryonic membrane (chorion), then larval movements rupture the inner embryonic membrane, releasing the prezoeae (about 14-20 min after chorion rupture; Davis 1965). The prezoeae molt to the first zoeal stage within 3 min of release (Davis 1965), which may explain why they were not

observed in earlier studies (Costlow and Bookhout 1959) (see Kennedy, Chapter 2). Both the inner and outer embryonic membranes remain attached to the pleopod setae of the female for a few days after larval release, and thus are an excellent indicator that the female has recently spawned, although they do not indicate the frequency of spawning (Hard 1945). In an ocypodid *Uca pugilator*, a xanthid *Neopanope sayi*, and several grapsid crabs *(Sesarma haematocheir, S. pictum, S. dehaani, S. cinereum*, and *Hemigrapsus sanguineus)*, the embryos contain a proteinase ("oviger-ous-hair stripping substance") that removes the embryonic remnants from the pleopod setae after larval release and thus prepares the setae for the subsequent brood (DeVries and Forward 1991; Saigusa 1996; Saigusa and Iwasaki 1999).

Summary and Areas of Future Research

Blue crab reproduction is complex and interesting from a variety of perspectives. Many factors influence the way mating and reproduction take place, including environmental conditions (e.g., temperature, salinity), local population characteristics (e.g., sex ratio, size structure), physiology (e.g., hormones, pheromones), and the characteristics of males (e.g., size, physical condition) and females (e.g., size, molt stage). Together, these factors produce a complicated mating system with physiological changes and behaviors that are often highly variable and that differ from those of many other crabs, including other portunids. As a result, studying blue crab reproduction is challenging and a number of questions about mating and reproduction remain.

- What processes regulate sexual maturity and receptivity, particularly of males? In other species, hormones (e.g., methyl farnesoate) play an important role but relatively little is known about these in blue crabs. In a variety of species, a male's parasite load, mating history, and future mating prospects also influence sexual receptivity but little information exists for blue crabs.

- How do sexually receptive males and females come together for mating and what role does each sex play in finding a mate? Visual and chemical signals (from different sources) from both sexes seem to be important in pair formation, but the source and identity of these chemicals and how, in females, they are linked to the pubertal molt are still unknown.

- What role do males play in determining the reproductive potential of females? In blue crabs and other species, males make considerable investments (e.g., mate guarding time, ejaculate volume) in their mates. In other species, the quantity or quality of the ejaculate passed to females enhances their reproductive success, and we are beginning to understand that the same may also occur in blue crabs. This avenue of research is interesting from an evolutionary perspective because it addresses the selective forces behind these investments, and, from a more practical perspective, because it examines factors that influence the quality of the spawning stock.

The blue crab supports one of the most important commercial and recreational fisheries along the east and Gulf coasts of the United States, including Chesapeake Bay (Rugolo et al. 1998), North Carolina (Henry and McKenna 1998), Georgia (Evans 1998), Florida (Steele and Bert 1998), Louisiana (Guillory and Perret 1998), and Texas (Hammerschmidt et al. 1998) A major concern for fisheries managers of this and other species is how to conserve the spawning stock to insure sustainable recruitment levels. To do so effectively requires information on the factors that influence spawning and reproductive output; however, we know relatively little about these in blue crabs. This paradox was eloquently stated by the late Eugene Cronin during a blue crab symposium at the 88th Annual National Shellfisheries Association Meeting: "A most crucial problem is that of determining the

effect of spawning stock on recruitment. Most of our management is directed toward the vague hope of protecting an 'adequate' or 'prudent' spawning stock — and we don't know what they would be." (Cronin 1998). Discouragingly, based on our current understanding of reproduction in the blue crab and information from other commercially important crab species, we can expect that increasing fishing pressure will negatively influence reproduction in complex ways (Lipcius and Stockhausen 2002). Therefore, an important area for future research is determining the reproductive potential (seasonal and lifetime) of females, and the factors that allow females to reach their full reproductive potential, including environmental conditions, physiological constraints, and the characteristics of the female and her sexual partner. Specifically, little is known about the processes that occur within the female between insemination and larval release, including the viability of sperm during storage, the dissolution of the seminal fluid, egg fertilization, and the viability or loss of embryos during development. This kind of information will provide a better understanding of reproduction and how the reproductive biology of this species is influenced by fishing pressure, an understanding that is critical for maintaining a viable fishery.

ACKNOWLEDGMENTS

We thank Midge Kramer, Laura Nye, and Karen Metcalf for assistance in processing samples and managing data. Many students at VIMS and SERC assisted with crab collections and dissections. Alicia Young-Williams assisted in preparing some of the photographs and Rob Andrews and Deborah Kennedy assisted in preparing some of the figures. We thank two anonymous reviewers for constructive and helpful comments on earlier drafts of the manuscript. Funded by: NSF OCE-9711843 to A.H.H. and P.R.J.; Smithsonian Environmental Sciences Program to A.H.H.; Disney Wildlife Conservation Fund to A.H.H.; NSF RTG in the Biology of Small Populations Postdoctoral Fellowship to P.R.J.; and NOAA Chesapeake Bay Fisheries funding through the BCARC to A.H.H.

REFERENCES

Abbe, G.R. 1974. Second terminal molt in an adult female blue crab, *Callinectes sapidus*. Transactions of the American Fisheries Society 103:643-644.

Abbe, G.R. and C. Stagg. 1996. Trends in blue crab (*Callinectes sapidus* Rathbun) catches near Calvert Cliffs, Maryland, from 1968 to 1995 and their relationship to the Maryland commercial fishery. Journal of Shellfish Research 15:751-758.

Abello, P., C.G. Warman, D.G. Reid and E. Naylor. 1994. Chela loss in the shore crab *Carcinus maenas* (Crustacea:Brachyura) and its effect on mating success. Marine Biology 121:247-252.

Adams, J., A.J. Edwards and H. Emberton. 1985. Sexual size dimorphism and assortative mating in the obligate coral commensal *Trapezia ferruginea* Latrelle (Decapoda, Xanthidae). Crustaceana 48:188-194.

Adiyodi, K.G. and R.G. Adiyodi. 1970. Endocrine control of reproduction in Decapod Crustacea. Biological Reviews 45:121-165.

Adiyodi, R.G. 1985. Reproduction and its control. Pages 147-216 in D.E. Bliss and L.H. Mantel (eds.). The Biology of Crustacea, Volume 9. Academic Press, New York.

Aguilar, R., A.H. Hines, T.G. Wolcott, D.L. Wolcott, M.A. Kramer, and R.N. Lipcius. 2005. The timing and route of movement and migration of post-copulatory female blue crabs, *Callinectes sapidus* Rathbun, from the upper Chesapeake Bay. Journal of Expermental Marine Biology and Ecology 319:117-128.

Ahl, J.S.B. and H. Laufer. 1996. The pubertal molt in Crustacea revisited. Invertebrate Reproduction and Development 30:177-180.

Ahl, J.S.B., H. Laufer, A.J. Ahl and P. Takac. 1996. Exoskeletal abrasion as an indicator of reproductive readiness in the spider crab *Libinia emarginata*. Journal of Crustacean Biology 16:443-447.

Andersson, M. 1994. Sexual Selection. Princeton University Press, Princeton, New Jersey. 599 p.

Anilkumar, G., K. Sudha, E. Anitha and T. Subramoniam. 1996. Aspects of sperm metabolism in the spermatheca of the brachyuran crab *Metopograpsus messor* (Forskal). Journal of Crustacean Biology 16:310-314.

Arnqvist, G. 1989. Sexual selection in a water strider: the function, mechanism of selection and heritability of a male grasping apparatus. Oikos 56:344-350.

Arthur, B.I., Jr., E. Hauschteck-Jungen, R. Nothiger and

P.I. Ward. 1998. A female nervous system is necessary for normal sperm storage in *Drosophila melanogaster*: a masculinized nervous system is as good as none. Proceedings of the Royal Society of London B 265:1749-1753.

Atema, J. 1986. Review of sexual selection and chemical communication in the lobster, *Homarus americanus*. Canadian Journal of Fisheries and Aquatic Sciences 43:2283-2390.

Babu, T., K. Shyamasundari and K.H. Rao. 1988. Cytochemical nature of spermatophore layers in the edible crab, *Portunus sanguinolentus* (Herbst) (Portunidae). Proceedings of the Indian National Sciences Academy B54:129-132.

Bauer, R.T. 1986. Phylogenetic trends in sperm transfer and storage complexity in Decapod Crustaceans. Journal of Crustacean Biology 6:313-325.

Bawab, F.M. and S.S. El-Sherief. 1989. Contributions to the study of the origin, nature and formation of the plug in the spermathecae of the female crab *Portunus pelagicus* (Linnaeus, 1766) (Decapoda, Brachyura). Crustaceana 57:9-24.

Beninger, P.G., C. Lanteigne and R.W. Elner. 1993. Reproductive processes revealed by spermatophore dehiscence experiments and by histology, ultrastructure, and histochemistry of the female reproductive system in the snow crab *Chionoecetes opilio* (O. Fabricius). Journal of Crustacean Biology 13:1-17.

Beninger, P.G. and R. Larocque. 1998. Gonopod tegumental glands: A new accessory sex gland in the Brachyura. Marine Biology 132:435-444.

Berreur-Bonnenfant, J. and F. Lawrence. 1984. Comparative effect of farnesylacetone on macromolecular synthesis in gonads of crustaceans. General and Comparative Endocrinology 54:462-468.

Berrill, M. and M. Arsenault. 1982. Mating behavior of the green shore crab *Carcinus maenas*. Bulletin of Marine Science 32:632-638.

Berrill, M. and M. Arsenault. 1984. The breeding behaviour of a northern temperate orconectid crayfish, *Orconectes rusticus*. Animal Behaviour 32:333-339.

Bigford, T.E. 1979. Synopsis of biological data on the rock crab, *Cancer irroratus* Say. FAO Synopsis 123 N.O.A.A. Technical Report N.M.F.S. Circular 426, Washington, D.C. 25 p.

Bland, C.E. and H.V. Amerson. 1974. Occurrence and distribution in North Carolina waters of *Lagenidium callinectes* Couch, a fungal parasite of blue crab ova. Chesapeake Science 15:232-235.

Blau, S.F. 1989. Size at maturity of female red king crabs (*Paralithodes camtschatica*) in the Adak Management area, Alaska. Pages 105-116 in A.S.G.C. Program (ed.). International Symposium on King and Tanner Crabs. Alaska Sea Grant, Anchorage, Alaska.

Boggs, C.L. and L.E. Gilbert. 1979. Male contribution to egg production in butterflies: Evidence for transfer of nutrients at mating. Science 206:83-84.

Borgia, G. 1979. Sexual selection and the evolution of mating systems. Pages 19-80 in M. Blum and A. Blum (eds.). Sexual Selection and Reproductive Competition in Insects. Academic Press, New York.

Brown, G.G. 1966. Ultrastructural studies of sperm morphology and sperm-egg interaction in the decapod *Callinectes sapidus*. Journal of Ultrastructure Research 14:425-440.

Brown, J.L. 1997. A theory of mate choice based on heterozygosity. Behavioral Ecology 8:60-65.

Bryant, A.D. and R.G. Hartnoll. 1995. Reproductive investment in two spider crabs with different breeding strategies. Journal of Experimental Marine Biology and Ecology 188:261-275.

Bursey, C.R. 1984. Color recognition by the blue crab, *Callinectes sapidus* Rathbun (Decapoda, Brachyura). Crustaceana 47:278-284.

Bushmann, P.J. 1999. Concurrent signals and behavioral plasticity in blue crab (*Callinectes sapidus* Rathbun) courtship. Biological Bulletin 197:63-71.

Butler, T.H. 1960. Maturity and breeding of the Pacific edible crab, *Cancer magister* Dana. Journal of the Fisheries Research Board of Canada 17:641-646.

Caddy, J.F. 1989. Marine Invertebrate Fisheries: Their Assessment and Management. John Wiley & Sons, New York. 752 p.

Cadman, L.R. and M.P. Weinstein. 1988. Effects of temperature and salinity on the growth of laboratory-reared juvenile blue crabs *Callinectes sapidus* Rathbun. Journal of Experimental Marine Biology and Ecology 121:193-208.

Campbell, G.R. 1982. A comparative study of adult sexual behaviour and larval ecology of three commercially important portunid crabs from the Moreton Bay region of Queensland, Australia. PhD Dissertation. University of Queensland, Brisbane. 253 p.

Cargo, D.G. 1980. A bisexual blue crab, *Callinectes sapidus*

Rathbun, from the Chesapeake Bay. American Midland Naturalist 104:378-382.

Carlisle, D.B. 1957. On the hormonal inhibition of moulting in Decapod Crustacea II. The terminal anecdysis in crabs. Journal of the Marine Biological Association of the United Kingdom 36:291-307.

Carver, A.M. 2001. Selective fishing pressure on large male blue crabs negatively affects male size, sex ratio, and population reproductive potential in the upper Chesapeake Bay. M.S. thesis. Department of Marine, Earth and Atmospheric Sciences, North Carolina State University, Raleigh. 38 p.

Charniaux-Cotton, H. and G. Payen. 1985. Sexual differentiation. Pages 217-299 in D.E. Bliss and L.H. Mantel (eds.). The Biology of Crustacea, Volume 9. Academic Press, New York.

Cheung, T.S. 1969. The environmental and hormonal control of growth and reproduction in the adult female stone crab, *Menippe mercenaria* (Say). Biological Bulletin 136:327-346.

Choy, S.C. 1988. Reproductive biology of *Liocarcinus puber* and *L. holsatus* (Decapoda, Brachyura, Protunidae) from the Gower Peninsula, South Wales. Marine Ecology 9:227-241.

Christy, J.H. 1987. Competitive mating, mate choice and mating associations of brachyuran crabs. Bulletin of Marine Science 41:177-191.

Claxton, W.T., C.K. Govind and R.W. Elner. 1994. Chela function, morphometric maturity, and the mating embrace in male snow crab, *Chionoecetes opilio*. Canadian Journal of Fisheries and Aquatic Sciences 51:1110-1118.

Cobb, J.S. and J.F. Caddy. 1989. The population biology of decapods. Pages 327-374 in J.F. Caddy (ed.). Marine Invertebrate Fisheries: Their Assessment and Management. John Wiley & Sons, New York.

Cole, R.W. 1998. Changes in harvest patterns and assessment of possible long-term impacts on yield in the Delaware commercial blue crab fishery. Journal of Shellfish Research 17:469-474.

Comeau, M. and G.Y. Conan. 1992. Morphometry and gonad maturity of male snow crab, *Chionoecetes opilio*. Canadian Journal of Fisheries and Aquatic Sciences 49:2460-2468.

Comeau, M., G. Robichaud, M. Starr, J.C. Therriault and G.Y. Conan. 1998. Mating of snow crab *Chionoecetes opilio* (O. Fabricius, 1788) (Decapoda, Majidae) in the fjord of Bonne Bay, Newfoundland. Crustaceana 71:925-941.

Corey, S. 1991. Comparative potential reproduction and actual production in several species of North American crayfish. Pages 69-76 in A. Wenner and A. Kuris (eds.). Crustacean Issues 7: Crustacean Egg Production. A.A. Balkema, Rotterdam.

Costlow, J.D. and C.G. Bookhout. 1959. The larval development of *Callinectes sapidus* Rathbun reared in the laboratory. Biological Bulletin 116:373-396.

Couch, J.A. and S. Martin. 1982. Protozoan symbionts and related diseases of the blue crab, *Callinectes sapidus* Rathbun from the Atlantic and Gulf coasts of the United States. Pages 71-80 in H.M. Perry and W.A. Van Engel (eds.). Proceedings of the Blue Crab Colloquium, October 16-19, 1979. Gulf States Marine Fisheries Commission Publication 7. Ocean Springs, Mississippi.

Cowan, D.F. 1991. The role of olfaction in courtship behavior of the American lobster, *Homarus americanus*. Biological Bulletin 181:402-407.

Cronin, L.E. 1947. Anatomy and histology of the male reproductive system of *Callinectes sapidus* Rathbun. Journal of Morphology 81:209-239.

Cronin, L.E. 1998. Reactions to the blue crab symposium. Journal of Shellfish Research 17:587.

Darsono, P. 1992. Investigations on mating and fertilization success in the blue crab, *Callinectes sapidus* Rathbun (Decapoda, Portunidae). Masters Thesis. University of Charleston, Charleston, South Carolina. 61 p.

Davidson, K., J.C. Roff and R.W. Elner. 1985. Morphological, electrophoretic, and fecundity characterisitics of Atlantic Snow Crab, *Chionoecetes opilio*, and implications for fisheries management. Canadian Journal of Fisheries and Aquatic Sciences 42:474-482.

Davis, C.C. 1965. A study of the hatching process in aquatic invertebrates: XX. The blue crab, *Callinectes sapidus*, Rathbun, XXI. The nemertean, *Carcinonemertes carcinophila* (Kölliker). Chesapeake Science 6:201-208.

Dawe, E.G., D.M. Taylor, J.M. Hoenig, W.G. Warren, G.P. Ennis, R.G. Hooper, W.E. Donaldson, A.J. Paul and J.M. Paul. 1991. A critical look at the idea of terminal molt in male snow crab (*Chionoecetes opilio*). Canadian Journal of Fisheries and Aquatic Sciences 48:2266-2275.

DeVries, M.C. and R.B. Forward, Jr. 1991. Mechanisms of

crustacean egg hatching: evidence for enzyme release by crab embryos. Marine Biology 110:281-291.

Diesel, R. 1988. Discrete storage of multiple mating sperm in the spider crab *Inachus phalangium*. Naturwissenschaften 75:148-149.

Diesel, R. 1989. Structure and function of the reproductive system of the symbiotic spider crab *Inachus phalangium* (Decapoda: Majidae): observations on sperm transfer, sperm storage, and spawning. Journal of Crustacean Biology 9:266-277.

Diesel, R. 1990. Sperm competition and reproductive success in the decapod *Inachus phalangium* (Majidae): a male ghost spider crab that seals off rivals' sperm. Journal of Zoology 220:213-223.

Diesel, R. 1991. Sperm competition and the evolution of mating behavior in Brachyura, with special reference to spider crabs (Decapoda, Majidae). Pages 145-163 in R. Bauer and J.W. Martin (eds.). Crustacean Sexual Biology. Columbia University Press, New York.

Donaldson, W.E. and A.A. Adams. 1989. Ethogram of behavior with emphasis on mating for the Tanner crab, *Chionoecetes bairdi* Rathbun. Journal of Crustacean Biology 9:37-51.

Donaldson, W.E. and W.K. Donaldson. 1992. A review of the history and justification for size limits in Alaskan king, Tanner and snow crab fisheries. Alaska Department of Fish and Game Fisheries Research Bulletin 92-02. Alaska Department of Fish and Game, Fairbanks. 22 p.

Dudley, H.G. and T.C. Jegla. 1978. Control of reproductive form in male crayfish. General and Comparative Endocrinology 34:108(Abstract).

Dumbauld, B.R., D.A. Armstrong and K.L. Feldman. 1996. Life-history characteristics of two sympatric Thalassinidean shrimps, *Neotrypaea californiensis* and *Upogebia pugettensis*, with implications for oyster culture. Journal of Crustacean Biology 16:689-708.

Dunham, P.J. 1978. Sex pheromones in Crustacea. Biological Reviews 53:555-583.

Eady, P.E. 1995. Why do male *Callosobruchus maculatus* beetles inseminate so many sperm? Behavioral Ecology and Sociobiology 36:25-32.

Eales, A.J. 1974. Sex pheromone in the shore crab *Carcinus maenas*, and the site of its release from females. Marine Behaviour and Physiology 2:345-355.

Eberhard, W.G. and C. Cordero. 1995. Sexual selection by cryptic female choice on male seminal products - a new bridge between sexual selection and reproductive physiology. Trends in Ecology and Evolution 10:493-495.

Edwards, E. 1964. Mating behavior in the European edible crab (*Cancer pagurus* L.). Crustaceana 10:23-30.

Elner, R.W., C.A. Gass and A. Campbell. 1980. Mating behavior of the jonah crab, *Cancer borealis* Stimpson (Decapoda, Brachyura). Crustaceana 48:34-38.

Elner, R.W., S. Koshio and G.V. Hurley. 1987. Mating behavior of the deep-sea red crab, *Geryon quinquedens* Smith (Decapoda, Brachyura, Geryonidae). Crustaceana 52:194-201.

Emlen, S.T. and L.W. Oring. 1977. Ecology, sexual selection and the evolution of mating systems. Science 197:215-223.

Ennis, G.P., R.G. Hooper and D.M. Taylor. 1990. Changes in the composition of snow crab (*Chionoecetes opilio*) participating in the annual breeding migration in Bonne Bay, Newfoundland. Canadian Journal of Fisheries and Aquatic Sciences 47:2242-2249.

Epifanio, C.E., C.C. Valenti and A.E. Pembroke. 1984. Dispersal and recruitment of blue crab larvae in Delaware Bay, U.S.A. Estuarine, Coastal and Shelf Science 18:1-12.

Evans, C. 1998. Conservation and management of the blue crab fishery in Georgia. Journal of Shellfish Research 17:451-458.

Felgenhauer, B.E. and L.G. Abele. 1991. Morphological diversity of decapod spermatozoa. Pages 322-341 in R. Bauer and J.W. Martin (eds.). Crustacean Sexual Biology. Columbia University Press, New York.

Ferezou, J.P., J. Berreur-Bonnenfant, A. Tekitek, M. Rojas, M. Barbier, M. Suchy, H.K. Wipf and J.J. Meusy. 1977. Biologically-active lipids from the androgenic gland of the crab, *Carcinus maenas*. Pages 361-366 in D.J. Faulkner and W.H. Fenical (eds.). Marine Natural Products Chemistry. Plenum Press, New York.

Fielder, D.R. and A.J. Eales. 1972. Observations on courtship, mating and sexual maturity in *Portunus pelagicus* (L., 1766) (Crustacea, Portunidae). Journal of Natural History 6:273-277.

Fingerman, M. 1987. Endocrine mechanisms in Crustaceans. Journal of Crustacean Biology 7:1-24.

Fischler, K.J. 1959. Occurrence of extremely small ovigerous crabs (*Callinectes* sp.) in coastal North Carolina. Ecology 40:720.

Fischler, K.J. 1965. The use of catch-effort, catch-sampling, and tagging data to estimate a population of

blue crabs. Transactions of the American Fisheries Society 94:287-310.

Fisher, M.R. 1999. Effect of temperature and salinity on size at maturity of female blue crabs. Transactions of the American Fisheries Society 128:499-506.

Forbes, M.R.L., H. Pagola and R.L. Baker. 1992. Causes of non-random pairing by size in the brine shrimp, *Artemia salina* (Crustacea: Anostraca). Oecologia 91:214-219.

Forward, R.B., Jr. 1986. Larval release rhythms of decapod crustaceans: An overview. Bulletin of Marine Science 41:23-28.

Gage, A.R. and C.J. Barnard. 1996. Male crickets increase sperm number in relation to competition and female size. Behavioral Ecology and Sociobiology 38:349-353.

Gibbs, D.S., III. 1996. Field and laboratory evidence of pheromone mediated mating behavior in the blue crab, *Callinectes sapidus*. Masters Thesis. The College of William and Mary. Williamsburg, Virginia. 100 p.

Gleeson, R.A. 1980. Pheromone communication in the reproductive behavior of the blue crab, *Callinectes sapidus*. Marine Behaviour and Physiology 7:119-134.

Gleeson, R.A. 1982. Morphological and behavioral identification of the sensory structures mediating pheromone reception in the blue crab, *Callinectes sapidus*. Biological Bulletin 163:162-171.

Gleeson, R.A. 1991. Intrinsic factors mediating pheromone communication in the blue crab, *Callinectes sapidus*. Pages 17-32 in R. Bauer and J.W. Martin (eds.). Crustacean Sexual Biology. Columbia University Press, New York.

Gleeson, R.A., M.A. Adams and A.B.I. Smith. 1984. Characterization of a sex pheromone in the blue crab, *Callinectes sapidus*: crustecdysone studies. Journal of Chemical Ecology 10:913-921.

Gleeson, R.A., M.A. Adams and A.B.I. Smith. 1987. Hormonal modulation of pheromone-mediated behavior in a crustacean. Biological Bulletin 172:1-9.

González-Gurriáran, E. and J. Freire. 1994. Sexual maturity in the velvet swimming crab *Necora puber* (Brachyura, Portunidae): morphometric and reproductive analyses. ICES Journal of Marine Science 51:133-145.

Gray, E.H. and C.L. Newcombe. 1938. The relative growth of parts in the blue crab *Callinectes sapidus* Rathbun. Growth 2:235-246.

Guillory, V. and W.S. Perret. 1998. History, management, status, and trends in the Louisiana blue crab fishery. Journal of Shellfish Research 17:413-424.

Guinot, D., G.M. Jamieson, B. Richer de Forges and C.C. Tudge. 1998. Comparative spermatozoal ultrastructure of the three Dromiacean families exemplified by *Homolodromia kai* (Homolodromiidae), *Sphaerodromia lamellata* (Dromiidae), and *Dynomene tanensis* (Dynomenidae) (Podotremata: Brachyura). Journal of Crustacean Biology 18:78-94.

Gwynne, D.T. 1984. Courtship feeding increases female reproductive success in bushcrickets. Nature 307:361-363.

Haefner, P.A., Jr. 1985. Morphometry, reproduction, diet, and epizoites of *Ovalipes stephensoni* Williams, 1976 (Decapoda, Brachyura). Journal of Crustacean Biology 5:658-672.

Haefner, P.A., Jr. 1990. Morphometry and size at maturity of *Callinectes ornatus* (Brachyura, Portunidae) in Bermuda. Bulletin of Marine Science 46:274-286.

Haefner, P.A., Jr. and C.N. Shuster, Jr. 1964. Length increments during terminal molt of the female blue crab, *Callinectes sapidus*, in different salinity environments. Chesapeake Science 5:114-118.

Hammerschmidt, P., T. Wagner and G. Lewis. 1998. Status and trends in the Texas blue crab (*Callinectes sapidus*) fishery. Journal of Shellfish Research 17:405-412.

Hankin, D.G., T.H. Butler, P.W. Wild and Q.-L. Xue. 1997. Does intense fishing on males impair mating success of female Dungeness crabs? Canadian Journal of Fisheries and Aquatic Sciences 54:655-669.

Hard, W.L. 1945. Ovarian growth and ovulation in the mature blue crab, *Callinectes sapidus* Rathbun. Chesapeake Biological Laboratory Contribution 46. Solomons, Maryland. 17 p.

Hartnoll, R.G. 1968. Morphology of the genital ducts in female crabs. Journal of the Linnean Society of London 47:279-301.

Hartnoll, R.G. 1969. Mating in the Brachyura. Crustaceana 16:162-181.

Hartnoll, R.G. 1974. Variation in growth patterns between some secondary sexual characteristics in crabs (Decapoda Brachyura). Crustaceana 27:131-136.

Hartnoll, R.G. 1985. Growth, sexual maturity and reproductive output. Pages 101-128 in A.M. Wenner (ed.). Crustacean Issues 3: Factors in Adult Growth. A.A. Balkema, Boston.

Hauton, C., J.A. Williams and L.E. Hawkins. 1997. The effects of a live in vivo pathogenic infection on aspects of the immunocompetence of the common

shore crab, *Carcinus maenas* (L.). Journal of Experimental Marine Biology and Ecology 211:115-128.

Havens, K.J. and J.R. McConaugha. 1990. Molting in the mature female blue crab, *Callinectes sapidus* Rathbun. Bulletin of Marine Science 46:37-47.

Henmi, Y., T. Koga and M. Murai. 1993. Mating behavior of the sand bubbler crab *Scopimera globosa*. Journal of Crustacean Biology 13:736-744.

Henry, L.T. and S. McKenna 1998. Status and management of the blue crab fishery in North Carolina. Journal of Shellfish Research 17:465-468.

Hines, A.H. 1982. Allometric constraints and variables of reproductive effort in Brachyuran crabs. Marine Biology 69:309-320.

Hines, A.H. 1988. Fecundity and reproductive output in two species of deep-sea crabs, *Geryon fenneri* and *G. quinquedens* (Decapoda: Brachyura). Journal of Crustacean Biology 8:557-562.

Hines, A.H. 1989. Geographic variation in size at maturity in Brachyuran crabs. Bulletin of Marine Science 45:356-368.

Hines, A.H. 1991. Fecundity and reproductive output in nine species of *Cancer* crabs (Crustacea, Brachyura, Cancridae). Canadian Journal of Fisheries and Aquatic Sciences 48:267-275.

Hines, A.H., P.R. Jivoff, P.J. Bushmann, J. van Montfrans, S.A. Reed, D.L. Wolcott and T.G. Wolcott. 2003. Evidence for sperm limitation in the blue crab, *Callinectes sapidus*. Bulletin of Marine Science 72:287-310.

Hines, A.H., R.N. Lipcius and A.M. Haddon. 1987. Population dynamics and habitat partitioning by size, sex, and molt stage of blue crabs *Callinectes sapidus* in a subestuary of central Chesapeake Bay. Marine Ecology Progress Series 36:55-64.

Hines, A.H., T.G. Wolcott, E. González-Gurriáran, J.L. González-Escalante and J. Freire. 1995. Movement patterns and migrations in crabs: telemetry of juvenile and adult behaviour in *Callinectes sapidus* and *Maja squinado*. Journal of the Marine Biological Association of the United Kingdom 75:27-42.

Homola, E., A. Sagi and H. Laufer. 1991. Relationship of claw form and exoskeleton condition to reproductive system size and methyl farnesoate in the male spider crab, *Libinia emarginata*. Invertebrate Reproduction and Development 20:219-225.

Hopkins, W.C. Bost. 2002. Number and viability of stored sperm in the female blue crab *Callinectes sapidus*. M.S. thesis. Department of Marine, Earth & Atmospheric Sciences. North Carolina State University, Raleigh. 47 p.

Hsueh, P.-W., J.B. McClintock and T.S. Hopkins. 1993. Population dynamics and life history characteristics of the blue crabs *Callinectes similis* and *C. sapidus* in bay environments of the northern Gulf of Mexico. Marine Ecology 14:239-257.

Ingle, R.W. and W. Thomas. 1974. Mating and spawning of the crayfish *Austropotamobius pallipes* (Crustacea: Astacidae). Journal of Zoology 173:525-538.

Jamieson, G.S. 1993. Marine invertebrate conservation: evaluation of fisheries over-exploitation concerns. American Zoologist 33:551-567.

Jamieson, G.S., A. Phillips and B.D. Smith. 1998. Implications of selective harvests in Dungeness crab (*Cancer magister*) fisheries. Pages 309-321 in G.S. Jamieson and A. Campbell (eds.). North Pacific Symposium on Invertebrate Stock Assessment and Management. Canadian Special Publication of Fisheries and Aquatic Sciences 125.

Jayasankar, V. and T. Subramoniam. 1999. Antibacterial activity of seminal plasma of the mud crab *Scylla serrata* (Forskal). Journal of Experimental Marine Biology and Ecology 236:253-259.

Jensen, P.C., J.M. Orensanz and D.A. Armstrong. 1996. Structure of the female reproductive tract in the Dungeness crab (*Cancer magister*) and implications for the mating system. Biological Bulletin 190:336-349.

Jeyalectumie, C. and T. Subramoniam. 1987. Biochemical composition of seminal secretions with special reference to LDH activity in the reproductive tissues of the field crab, *Paratelphusa hydrodromous*. Experimental Biology 46:231-236.

Jeyalectumie, C. and T. Subramoniam. 1991. Biochemistry of seminal secretions of the crab *Scylla serrata* with reference to sperm metabolism and storage in the female. Molecular Reproduction and Development 30:44-55.

Jivoff, P. 1995. The role of mate guarding, male size and male investment on individual reproductive success in the blue crab, *Callinectes sapidus*. Ph.D. Dissertation. University of Maryland, College Park. 158 p.

Jivoff, P. 1997a. The relative roles of predation and sperm competition on the duration of the post-copulatory association between the sexes in the blue crab, *Callinectes sapidus*. Behavioral Ecology and Sociobiology 40:175-185.

Jivoff, P. 1997b. Sexual competition among male blue crab, *Callinectes sapidus*. Biological Bulletin 193:368-380.

Jivoff, P. and A.H. Hines. 1998a. Effect of female molt stage and sex ratio on courtship behavior of the

blue crab *Callinectes sapidus*. Marine Biology 131: 533-542.

Jivoff, P. and A.H. Hines. 1998b. Female behaviour, sexual competition and mate guarding in the blue crab, *Callinectes sapidus*. Animal Behaviour 55:589-603.

Johnson, K., R. Thornhill, L.J.David and M. Zuk. 1993. The direction of mother's and daughter's preferences and the heritability of male ornaments in red jungle fowl (*Gallus gallus*). Behavioral Ecology 4:254-259.

Johnson, P.T. 1980. Histology of the Blue Crab (*Callinectes sapidus*): A Model for the Decapoda. Praeger Scientific, New York. 440 p.

Johnson, P.T. and S.V. Otto. 1981. Histology of a bilateral gynandromorph of the blue crab, *Callinectes sapidus* Rathbun (Decapoda: Portunidae). Biological Bulletin 161:236-245.

Jordan, S.J. 1998. The Blue Crab Fisheries of North America: Research, Conservation, and Management. Journal of Shellfish Research 17:367-587.

Jormalainen, V. 1998. Precopulatory mate guarding in crustaceans: male competitive strategy and intersexual conflict. Quarterly Review of Biology 73:275-304.

Kavaliers, M. and D.D. Colwell. 1995. Odours of parasitized males induce aversive responses in female mice. Animal Behaviour 50:1161-1169.

Kendall, M.S., D.L. Wolcott, T.G. Wolcott and A.H. Hines. 2001. Reproductive potential of individual male blue crabs, *Callinectes sapidus*, in a fished population: depletion and recovery of sperm number and seminal fluid. Canadian Journal of Fisheries and Aquatic Sciences 58:1168-1177.

Kendall, M.S., D.L. Wolcott, T.G. Wolcott, and A.H. Hines. 2002. Influence of male size and mating history on sperm content of ejaculates of the blue crab *Callinectes sapidus*. Marine Ecology Progress Series 230: 235-240.

Kendall, M.S. and T.G. Wolcott. 1999. The influence of male mating history on male-male competition and female choice in mating associations in the blue crab, *Callinectes sapidus* (Rathbun). Journal of Experimental Marine Biology and Ecology 239:23-32.

Kennelly, S.J. and D. Watkins. 1994. Fecundity and reproductive period, and their relationship to catch rates of spanner crabs, *Ranina ranina*, off the east coast of Australia. Journal of Crustacean Biology 14:146-150.

Kennish, R. 1997. Seasonal patterns of food availability: influences on the reproductive output and body condition of the herbivorous crab *Grapsus albolineatus*. Oecologia 109:209-218.

Knuckey, I.A. 1996. Maturity in male mud crabs, *Scylla serrata*, and the use of mating scars as a functional indicator. Journal of Crustacean Biology 16:487-495.

Kodric-Brown, A. and J.H. Brown. 1984. Truth in advertising: The kinds of traits favored by sexual selection. American Naturalist 124:309-323.

Koga, T. and M. Murai. 1997. Size-dependent mating behaviours of male sand-bubbler crab, *Scopimera globosa*: alternative tactics in the life history. Ethology 103:578-587.

Kuris, A.M. 1991. A review of patterns and causes of crustacean brood mortality. Pages 117-141 in A. Wenner and A. Kuris (eds.). Crustacean Issues 7: Crustacean Egg Production. A.A. Balkema, Rotterdam.

Kwei, E.A. 1978. Size composition, growth and sexual maturity of *Callinectes latimanus* (Rathbun) in two Ghanaian lagoons. Zoological Journal of the Linnean Society 64:151-175.

Laufer, H. and J.S.B. Ahl. 1995. Mating behavior and methyl farnesoate levels in male morphotypes of the spider crab, *Libinia emarginata* (Leach). Journal of Experimental Marine Biology and Ecology 193:15-20.

Laufer, H., D. Borst, F.C. Baker, C. Carrasco, M. Sinkus, C.C. Reuter, L.W. Tsai and D.S. Schooley. 1987. Identification of a juvenile hormone-like compound in a crustacean. Science 235:202-205.

Laufer, H., D.W. Borst, C. Carrasco, F.C. Baker and D.A. Schooley. 1984. The detection of juvenile hormone in Crustacea. American Zoologist 24:33(Abstract).

Lazaro-Chavez, E., F. Alvarez and C. Rosas. 1996. Records of *Loxothylacus texanus* (Cirripedia: Rhizocephala) parasitizing the blue crab *Callinectes sapidus* in Tamiahua Lagoon, Mexico. Journal of Crustacean Biology 16:105-110.

Lee, S.Y. 1995. Cheliped size and structure: the evolution of a multi-functional decapod organ. Journal of Experimental Marine Biology and Ecology 193:161-176.

Lee, S.Y. and R. Seed. 1992. Ecological implications of cheliped size in crabs: some data from *Carcinus maenas* and *Liocarcinus holsatus*. Marine Ecology Progress Series 84:151-160.

Leffler, C.W. 1972. Some effects of temperature on the growth and metabolic rate of juvenile blue crabs,

Callinectes sapidus, in the laboratory. Marine Biology 14:104-110.

Leung-Trujillo, J.R. and A.L. Lawrence. 1987. Observations on the decline in sperm quality of *Penaeus setiferus* under laboratory conditions. Aquaculture 65:363-370.

Levi, T., A. Barki, G. Hulata and I. Karplus. 1999. Mother-offspring relationships in the red-claw crayfish *Cherax quadricarinatus*. Journal of Crustacean Biology 19:477-484.

Lipcius, R.N. 1985. Size-dependent reproduction and molting in spiny lobsters and other long-lived decapods. Pages 129-148 in A.M. Wenner (ed.). Crustacean Issues 3: Factors in Adult Growth. A.A. Balkema, Boston.

Lipcius, R.N., M.L. Edwards, W.F. Herrnkind and S.A. Waterman. 1983. In situ mating behavior of the spiny lobster *Panulirus argus*. Journal of Crustacean Biology 3:217-222.

Lipcius, R.N. and W.F. Herrnkind. 1982. Molt cycle alterations in behavior, feeding and diel rhythms of a decapod crustacean, the spiny lobster *Panulirus argus*. Marine Biology 68:241-252.

Lipcius, R.N. and W. Stockhausen. 2002. Concurrent decline of the spawning stock, recruitment, larval abundance and size of the blue crab in Chesapeake Bay. Marine Ecology Progress Series 226:45-61.

Lipcius, R.N. and W.A. Van Engel. 1990. Blue crab population dynamics in Chesapeake Bay: Variation in abundance (York River, 1972-1988) and stock-recruit functions. Bulletin of Marine Science 46:180-194.

Mantelatto, F.L.M. and A. Fransozo. 1999. Reproductive biology and moulting cycle of the crab *Callinectes ornatus* (Decapoda, Portunidae) from the Ubatuba region, Sao Paulo, Brazil. Crustaceana 72:63-76.

Markow, T.A. and P.F. Ankney. 1984. *Drosophila* males contribute to oogenesis in a multiple mating species. Science 224:302-303.

Markow, T.A., M. Quaid and S. Kerr. 1978. Male mating experience and competitive courtship success in *Drosophila melanogaster*. Nature 276:821-822.

Mason, J.C. 1970. Copulatory behavior of the crayfish, *Pacifastacus trowbridgii* (Stimpson). Canadian Journal of Zoology 48:969-976.

McConaugha, J.R., D.F. Johnson, A.J. Provenzano and R.C. Maris. 1983. Seasonal distribution of larvae of *Callinectes sapidus* (Crustacea: Decapoda) in the waters adjacent to Chesapeake Bay. Journal of Crustacean Biology 3:582-591.

McMullen, J.C. and H.T. Yoshihara. 1971. Deposition of mature eggs in unmated king crabs, *Paralithodes camtschatica* (Tilesius). Transactions of the American Fisheries Society 100:583-584.

Medina, A. 1994. Spermiogenesis and sperm structure in the shrimp *Parapenaeus longirostris* (Crustacea: Dendrobranchiata): comparative aspects among decapods. Marine Biology 119:449-460.

Millikin, M.R., G.N. Biddle, T.C. Siewicki, A.R. Fortner and P.H. Fair. 1980. Effects of various levels of dietary protein on survival, molting frequency and growth of juvenile blue crabs (*Callinectes sapidus*). Aquaculture 19:149-161.

Millikin, M.R. and A.B. Williams. 1980. Synopsis of biological data on the blue crab, *Callinectes sapidus* Rathbun. FAO Fisheries Synopsis 138, N.O.A.A. Technical Report NMFS 1. Washington, District of Columbia. 39 p.

Minagawa, M., J.-R. Chiu, M. Kudo and F. Takashima. 1994. Male reproductive biology of the red frog crab, *Ranina ranina*, off Hachijojima, Izu Islands, Japan. Marine Biology 118:393-401.

Morgan, S.G. 1996. Influence of tidal variation on reproductive timing. Journal of Experimental Marine Biology and Ecology 206:237-251.

Morgan, S.G. and J.H. Christy. 1994. Plasticity, constraint, and optimality in reproductive timing. Ecology 75:2185-2203.

Morgan, S.G. and J.H. Christy. 1995. Adaptive significance of the timing of larval release by crabs. American Naturalist 145:457-479.

Morgan, S.G. and J.H. Christy. 1997. Planktivorous fishes as selective agents for reproductive synchrony. Journal of Experimental Marine Biology and Ecology 209:89-101.

Morgan, S.G., J.W. Goy and J.D. Costlow. 1983. Multiple ovipositions from single matings in the mud crab *Rhithropanopeus harrisii*. Journal of Crustacean Biology 3:542-547.

Nakashima, Y. 1995. Can small male shrimps achieve copulation in the presence of larger ones? Journal of Ethology 13:9-16.

Nakatsuru, K. and D.L. Kramer. 1982. Is sperm cheap? Limited male fertility and female choice in the lemon tetra (Pisces, Characidae). Science 216:753-755.

Newcombe, C.L., F. Campbell and A.M. Eckstine. 1949a. A study of the form and growth of the blue crab *Callinectes sapidus* Rathbun. Growth 13:71-96.

Newcombe, C.L., M.D. Sandoz and R. Talbert-Rogers. 1949b. Differential growth and moulting characteristics of the blue crab, *Callinectes sapidus* Rathbun. Journal of Experimental Zoology 110:113-152.

Nizyaev, S.A. and V.Y. Fedoseev. 1989. Disorders of the reproductive cycle in crab females of the genus *Paralithodes*. Pages 91-93 in A.S.G.C. Program (ed.). International Symposium on King and Tanner Crabs. Alaska Sea Grant. Anchorage, Alaska.

Norman, C.P. 1996. Reproductive biology and evidence for hard-female mating in the Brachyuran crab *Thalamita sima* (Portunidae). Journal of Crustacean Biology 16:656-662.

Norman, C.P. and M.B. Jones. 1993. Reproductive ecology of the velvet swimming crab, *Necora puber* (Brachyura: Portunidae), at Plymouth. Journal of the Marine Biological Association of the United Kingdom 73:379-389.

O'Brien, J. and P. Van Wyk. 1985. Effects of crustacean parasitic castrators (epicaridean isopods and rhizocephalan barnacles) on growth of crustacean hosts. Pages 191-218 in A.M. Wenner (ed.). Crustacean Issues 3: Factors in Adult Growth. A.A. Balkema, Boston.

Oh, C.-W. and R.G. Hartnoll. 1999. Brood loss during incubation in *Philocheras trispinosus* (Decapoda) in Port Erin Bay, Isle of Man. Journal of Crustacean Biology 19:467-476.

Olmi, E.J.I. 1984. An adult female blue crab, *Callinectes sapidus* Rathbun (Decapoda, Portunidae) in proecdysis. Crustaceana 46:107-109.

Olmi, E.J.I. and J.M. Bishop. 1983. Variations in total width-weight relationships of blue crabs, *Callinectes sapidus*, in relation to sex, maturity, molt stage, and carapace form. Journal of Crustacean Biology 3:575-581.

Orensanz, J.M. and V.F. Gallucci. 1988. Comparative study of postlarval life-history schedules in four sympatric species of *Cancer* (Decapoda: Brachyura: Cancridae). Journal of Crustacean Biology 8:187-220

Orensanz, J.M., A.M. Parma, D.A. Armstrong, J. Armstrong and P. Wardrup. 1995. The breeding ecology of *Cancer gracilis* (Crustacea: Decapoda: Cancridae) and the mating systems of cancrid crabs. Journal of Zoology 235:411-417.

Otto, R.S., R.A. MacIntosh and P.A. Cummiskey. 1989. Fecundity and other reproductive parameters of female red king crab (*Paralithodes camtschatica*) in Bristol Bay and Norton Sound, Alaska. Pages 65-90 in A.S.G.C. Program (ed.). International Symposium on King and Tanner Crabs. Alaska Sea Grant. Anchorage, Alaska.

Overstreet, R.M. 1982. Metazoan symbionts of the blue crab. Pages 81-87 in H.M. Perry and W.A. Van Engel (eds.). Proceedings of the Blue Crab Colloquium, October 16-19, 1979. Gulf States Marine Fisheries Commission Publication 7. Ocean Springs, Mississippi.

Parker, G.A. 1974. Courtship persistence and female-guarding as male time investment strategies. Behaviour 48:157-184.

Parker, G.A. 1978. Searching for mates. Pages 214-244 in J.R. Krebs and N.B. Davies (eds.). Behavioural Ecology, An Evolutionary Approach. Sinauer Associates. Sunderland, Massachusetts.

Paul, A.J. 1984. Mating frequency and viability of stored sperm in the Tanner crab *Chionoecetes bairdi* (Decapoda, Majidae). Journal of Crustacean Biology 4:205-211.

Paul, J.M. and A.J. Paul. 1989a. Reproductive success of sublegal size male red king crab with access to multiple mates. Pages 37-50 in A.S.G.C. Program (ed.). International Symposium on King and Tanner Crabs, Alaska Sea Grant, Anchorage, Alaska.

Paul, A.J. and J.M. Paul. 1989b. The size at the onset of maturity in male *Chionoecetes bairdi* (Decapoda, Majidae). Pages 95-103 in A.S.G.C. Program (ed.). International Symposium on King and Tanner Crabs. Alaska Sea Grant. Anchorage, Alaska.

Paul, A.J. and J.M. Paul. 1992. Second clutch viability of *Chionoecetes bairdi* Rathbun (Decapoda, Majidae) inseminated only at the maturity molt. Journal of Crustacean Biology 12:438-441.

Paul, A.J. and J.M. Paul. 1995. Molting of functionally mature male *Chionoecetes bairdi* Rathbun (Decapoda: Majidae) and changes in carapace and chela measurements. Journal of Crustacean Biology 15:686-692.

Paul, A.J. and J.M. Paul. 1996. Observations on mating of multiparous *Chionoecetes bairdi* Rathbun (Decapoda:

Majidae) held with different sizes of males and one-clawed males. Journal of Crustacean Biology 16:295-299.

Paul, A.J. and J.M. Paul. 1997. Breeding success of large male red king crab *Paralithodes camtschaticus* with multiparous mates. Journal of Shellfish Research 16:379-381

Paul, A.J., J.M. Paul and W.E. Donaldson. 1995. Shell condition and breeding success in Tanner crabs. Journal of Crustacean Biology 15:476-480.

Perez, O.S. and D.R. Bellwood. 1989. Observations on the mating behaviour of the Indo-Pacific sandy shore crab *Matuta lunaris* (Forskal) with notes on the reproductive behaviour of the Matutinae (Decapoda, Brachyura, Calappidae). Crustaceana 57:1-9.

Perkins, H.C. 1971. Egg loss during incubation from offshore northern lobsters (Decapoda: Homaridae). Fishery Bulletin 69:451-453.

Pinheiro, M.A.A. and A. Fransozo. 1998. Sexual maturity of the speckled swimming crab *Arenaeus cribrarius* (Lamark, 1818) (Decapoda, Brachyura, Portunidae), in the Ubatuba littoral, Sao Paulo State, Brazil. Crustaceana 71:434-452.

Powell, G.C., K.E. James and C.L. Hurd. 1974. Ability of male king crab, *Paralithodes camtschatica*, to mate repeatedly, Kodiak, Alaska, 1973. Fishery Bulletin 72:171-179.

Prager, M.H., J.R. McConaugha, C.M. Jones and P.J. Geer. 1990. Fecundity of blue crab, *Callinectes sapidus*, in Chesapeake Bay: Biological, statistical and management considerations. Bulletin of Marine Science 46:170-179.

Provenzano, A.J., Jr., J.R. McConaugha, K.B. Philips, D.F. Johnson and J. Clark. 1983. Vertical distribution of first stage larvae of the blue crab, *Callinectes sapidus*, at the mouth of Chesapeake Bay. Estuarine, Coastal and Shelf Science 16:489-499.

Pyle, R. and E. Cronin. 1950. The general anatomy of the blue crab *Callinectes sapidus* Rathbun. Chesapeake Biological Laboratory Publication 87. Solomons Island, Maryland. 40 p.

Quackenbush, L.S. 1986. Crustacean endocrinology: A review. Canadian Journal of Fisheries and Aquatic Sciences 43:2271-2282.

Reid, D.G., P. Abello, C.G. Warman and E. Naylor. 1994. Size-related mating success in the shore crab *Carcinus maenas* (Crustacea: Brachyura). Journal of Zoology 232:397-407.

Reid, D.M. and S. Corey. 1991. Comparative fecundity of decapod crustaceans, II: The fecundity of fifteen species of anomuran and brachyuran crabs. Crustaceana 61:175-189.

Ridley, M. 1983. The Explanation of Organic Diversity: The Comparative Method and Adaptations for Mating. Clarendon Press, Oxford. 272 p.

Ridley, M. and D.J. Thompson. 1985. Sexual selection of population dynamics in aquatic crustacea. Pages 409-422 in R.M. Sibly and R.H. Smith (eds.). Behavioural Ecology: Ecological Consequences of Adaptive Behaviour. Blackwell Scientific Publications, Oxford.

Roberts, M.H., Jr. and A.T. Leggett, Jr. 1980. Egg extrusion as a kepone-clearance route in the blue crab, *Callinectes sapidius*. Estuaries 3:192-199.

Robinson, B.W. and R.W. Doyle. 1985. Trade-off between male reproduction (amplexus) and growth in the amphipod *Gammarus lawrencianus*. Biological Bulletin 168:482-488.

Rugolo, L.J., K.S. Knotts and A.M. Lange. 1998. Historical profile of the Chesapeake Bay blue crab (*Callinectes sapidus* Rathbun) fishery. Journal of Shellfish Research 17:383-394.

Rutowski, R.L., G.W. Gilchrist and B. Terkanian. 1987. Female butterflies mated with recently mated males show reduced reproductive output. Behavioral Ecology and Sociobiology 20:319-322.

Ryan, E.P. 1966. Pheromone: evidence in a decapod crustacean. Science 151:340-341.

Ryan, E.P. 1967a. Structure and function of the reproductive system of the crab *Portunus sanguinolentus* (Herbst) (Brachyura: Portunidae) I. The male system. Pages 506-521 in Proceedings of the Symposium on Crustacea, Marine Biological Association of India.

Ryan, E.P. 1967b. Structure and function of the reproductive system of the crab *Portunus sanguinolentus* (Herbst) (Brachyura: Portunidae) II. The female system. Pages 522-544 in Proceedings of the Symposium on Crustacea, Marine Biological Association of India.

Sagi, A., J.S.B. Ahl, H. Danaee and H. Laufer. 1994. Methyl farnesoate levels on male spider crabs exhibiting active reproductive behavior. Hormones and Behavior 28:261-272.

Saigusa, M. 1996. Two kinds of active factor in crab hatch

water — ovigerous-hair stripping substance (OHSS) and a proteinase. Biological Bulletin 191:234-240.

Saigusa, M. and H. Iwasaki. 1999. Ovigerous-hair stripping substance (OHSS) in an estuarine crab: purification, preliminary characterization, and appearance of the activity in the developing embryos. Biological Bulletin 197:174-187.

Sainte-Marie, B. 1993. Reproductive cycle and fecundity of primiparous and multiparous female snow crab, *Chionoecetes opilio*, in the northwest Gulf of Saint Lawrence. Canadian Journal of Fisheries and Aquatic Sciences 50:2147-2156.

Sainte-Marie, B. and C. Carriere. 1995. Fertilization of the second clutch of eggs of snow crab, *Chionoecetes opilio*, from females mated once or twice after their molt to maturity. Fishery Bulletin 93:759-764.

Sainte-Marie, B. and F. Hazel. 1992. Moulting and mating of snow crabs, *Chionoecetes opilio* (O. Fabricius), in shallow waters of the northwestern Gulf of Saint Lawrence. Canadian Journal of Fisheries and Aquatic Sciences 49:1282-1293.

Sainte-Marie, B. and G.A. Lovrich. 1994. Delivery and storage of sperm at first mating of female *Chionoecetes opilio* (Brachyura: Majidae) in relation to size and morphometric maturity of male parent. Journal of Crustacean Biology 14:508-521.

Sainte-Marie, B., R. Raymond and J.-C. Brethes. 1995. Growth and maturation of the benthic stages of male snow crab, *Chionoecetes opilio* (Brachyura:Majidae). Canadian Journal of Fisheries and Aquatic Sciences 52:903-924.

Sainte-Marie, B., N. Urbani, J.-M. Sevigny, F. Hazel and U. Kuhnlein. 1999. Multiple choice criteria and the dynamics of assortative mating during the first breeding season of female snow crab *Chionoecetes opilio* (Brachyura, Majidae). Marine Ecology Progress Series 181:141-153.

Sainte-Marie, G. and B. Sainte-Marie. 1998. Morphology of the spermatheca, oviduct, intermediate chamber, and vagina of the adult snow crab (*Chionoecetes opilio*). Canadian Journal of Zoology 76:1589-1604.

Sainte-Marie, G. and B. Sainte-Marie. 1999a. Reproductive products in the adult snow crab (*Chionoecetes opilio*). I. Observations on spermiogenesis and spermatophore formation in the vas deferens. Canadian Journal of Zoology 77:440-450.

Sainte-Marie, G. and B. Sainte-Marie. 1999b. Reproductive products in the adult snow crab (*Chionoecetes opilio*). II. Multiple types of sperm cells and of spermatophores in the spermathecae of mated females. Canadian Journal of Zoology 77:451-462.

Salmon, M. 1983. Courtship, mating systems, and sexual selection in decapods. Pages 143-169 in S. Rebach and D.W. Dunham (eds.). Studies in Adaptation: the Behavior of Higher Crustacea. Wiley and Sons, New York.

Schaffner, L.C. and R.J. Diaz. 1988. Distribution and abundance of overwintering blue crabs, *Callinectes sapidus*, in the lower Chesapeake Bay. Estuaries 11:68-72.

Schmidt, D. and D. Pengilly. 1989. Alternative red king crab fishery management practices: modelling the effects of varying size-sex restrictions and harvest rates. Pages 551-565 in A.S.G.C. Program (ed.). International Symposium on King and Tanner Crabs. Alaska Sea Grant. Anchorage, Alaska.

Seibt, U. and W. Wickler. 1979. The biological significance of the pair-bond in the shrimp *Hymenocera picta*. Zier Tierpsychology 50:166-179.

Sekkelsten, G.I. 1988. Effect of handicap on mating success in male shore crabs *Carcinus maenas*. Oikos 51:131-134.

Shields, J.D. 1991. The reproductive ecology and fecundity of *Cancer* crabs. Pages 193-213 in A. Wenner and A. Kuris (eds.). Crustacean Issues 7: Crustacean Egg Production. A.A. Balkema, Rotterdam.

Shields, J.D. and F.E.I. Wood. 1993. Impact of parasites on the reproduction and fecundity of the blue sand crab *Portunus pelagicus* from Moreton Bay, Australia. Marine Ecology Progress Series 92:159-170.

Shirley, M.A., A.H. Hines and T.G. Wolcott. 1990. Adaptive significance of habitat selection by molting adult blue crabs *Callinectes sapidus* (Rathbun) within a subestuary of central Chesapeake Bay. Journal of Experimental Marine Biology and Ecology 140:107-119.

Siddiqui, G. and M. Ahmed. 1992. Fecundities of some marine brachyuran crabs from Karachi (Pakistan). Pakistan Journal of Zoology 24:43-45.

Skinner, D.M., D.E. Graham, C.A. Holland, D.L. Mykles, C. Soumoff and L.H. Yamaoka. 1985. Control of molting in crustacea. Pages 3-14 in A.M. Wenner (ed.). Crustacean Issues 3: Factors in Adult Growth. A.A. Balkema, Boston.

Smith, B.D. and G.S. Jamieson. 1991. Possible consequences of intensive fishing for males on the mating

opportunities of Dungeness crabs. Transactions of the American Fisheries Society 120:650-653.

Smith, L.D. 1992. The impact of limb autotomy on mate competition in blue crabs, *Callinectes sapidus* Rathbun. Oecologia 89:494-501.

Smith, R.L. 1984. Sperm Competition and the Evolution of Animal Mating Systems. Academic Press, New York. 661 p.

Snedden, W.A. 1990. Determinants of male mating success in the temperate crayfish *Orconectes rusticus*: chela size and sperm competition. Behaviour 115:100-113.

Soumoff, C. and D.M. Skinner. 1983. Ecdysteroid titers during the molt cycle of the blue crab resemble those of other crustacea. Biological Bulletin 165: 321-329.

Steele, P. and T.M. Bert. 1994. Population ecology of the blue crab, *Callinectes sapidus* Rathbun, in a subtropical estuary: Population structure, aspects of reproduction, and habitat partitioning. Florida Marine Research Institute Publication 51. St. Petersburg, Florida. 24 p.

Stein, R.A. 1976. Sexual dimorphism in crayfish chelae: functional significance linked to reproductive activities. Canadian Journal of Zoology 54:220-227.

Stevens, B., W.E. Donaldson, J.A. Haaga and J.E. Munk. 1993. Morphometry and maturity of paired Tanner crabs, *Chionoecetes bairdi*, from shallow- and deepwater environments. Canadian Journal of Fisheries and Aquatic Sciences 50:1504-1516.

Subramoniam, T. 1991. Chemical composition of spermatophores in decapod crustaceans. Pages 308-321 in R. Bauer and J.W. Martin (eds.). Crustacean Sexual Biology. Columbia University Press, New York.

Subramoniam, T. 1993. Spermatophores and sperm transfer in marine crustaceans. Advances in Marine Biology 29:129-201.

Sulkin, S.D., E.S. Branscomb and R.E. Miller. 1976. Induced winter spawning and culture of larvae of the blue crab, *Callinectes sapidus* Rathbun. Aquaculture 8:103-113.

Tagatz, M.E. 1965. The fishery for blue crabs in the St. Johns River, Florida, with special reference to fluctuation in yield between 1961 and 1962. U.S. Fish and Wildlife Service Special Scientific Report No. 501. St. Petersburg, Florida. 11 p.

Tagatz, M.E. 1968a. Biology of the blue crab, *Callinectes sapidus* Rathbun, in the St. Johns River, Florida. Fishery Bulletin 67:17-33.

Tagatz, M.E. 1968b. Growth of juvenile blue crabs, *Callinectes sapidus* Rathbun, in the St. Johns River, Florida. Fishery Bulletin 67:281-288.

Tankersley, R.A., M.G. Wieber, M.A. Sigala and K.A. Kachurak. 1998. Migratory behavior of ovigerous blue crabs *Callinectes sapidus* — evidence for selective tidal-stream transport. Biological Bulletin 195:168-173.

Tankersley, R.A., T.A. Ziegler and K. Butler. In review. Spawning behavior of the blue crab *Callinectes sapidus*: Patterns of migration and timing of larval release. Marine Ecology Progress Series.

Teytaud, A.R. 1971. The laboratory studies of sex recognition in the blue crab *Callinectes sapidus* Rathbun. Sea Grant Technical Bulletin No. 15. University of Miami Sea Grant. Miami, Florida. 63 p.

Thompson, C.W., N. Hillgarth, M. Leu and H.E. McClure. 1997. High parasite load in house finches (*Carpodacus mexicanus*) is correlated with reduced expression of a sexually selected trait. American Naturalist 149:270-294.

Trivers, R.L. 1972. Parental investment and sexual selection. Pages 136-179 in B. Campbell (ed.). Sexual Selection and the Descent of Man, 1871-1971. Aldine Press, Chicago, Illinois.

Turner, H.V. 2000. Behavior and growth in post-copulatory female blue crabs. M.S. thesis. Department of Marine, Earth and Atmospheric Sciences. North Carolina State University, Raleigh. 88p.

Turner, H.V., D.L. Wolcott, T.G. Wolcott and A.H. Hines. 2003. Post-mating behavior, intramolt growth, and onset of migration to Chesapeake Bay spawning grounds by adult female blue crabs, *Callinectes sapidus* Rathbun. Journal of Experimental Marine Biology and Ecology 295: 107-130.

Uma, K. and T. Subramoniam. 1979. Histochemical characteristics of spermatophore layers of *Scylla serrata* (Forksal) (Decapoda: Portunidae). International Journal of Invertebrate Reproduction 1:31-40.

UNESCO 1985. The International System of Units (SI) in Oceanography. Technical Paper in Marine Science 45. 124 p.

Uphoff, J.H. 1998. Stability of the blue crab stock in Maryland's portion of Chesapeake Bay. Journal of Shellfish Research 17:519-528.

Urbani, N., B. Sainte-Marie, J.-M. Sevigny, D. Zadmorny and U. Kuhnlein. 1997. Sperm competition and paternity assurance during the first breeding period

of female snow crab (*Chionoecetes opilio*) (Brachyura: Majidae). Canadian Journal of Fisheries and Aquatic Sciences 55:1104-1113.

Van Engel, W.A. 1958. The blue crab and its fishery in Chesapeake Bay: reproduction, early development, growth and migration. Commercial Fisheries Review 20(6):6-17.

Van Engel, W.A. 1990. Development of the reproductively functional form in the male blue crab, *Callinectes sapidus*. Bulletin of Marine Science 46:13-22.

Villavaso, E.J. 1975. Functions of the spermathecal muscle of the boll weevil, *Anthonomus grandis*. Journal of Insect Physiology 21:1275-1278.

Waddy, S.L. and D.E. Aiken. 1991. Mating and insemination in the American lobster, *Homarus americanus*. Pages 126-144 in R.T. Bauer and J.W. Martin (eds.). Crustacean Sexual Biology. Columbia University Press, New York.

Ward, P.I. 1986. A comparative field study of the breeding behaviour of a stream and a pond population of *Gammarus pulex* (Amphipoda). Oikos 46:29-36.

Ward, P.I. 1998. A possible explanation for cryptic female choice in the yellow dung fly, *Scathophaga stercoraria* (L.). Ethology 104:97-110.

Wenner, E.L. 1989. Incidence of insemination in female blue crabs, *Callinectes sapidus*. Journal of Crustacean Biology 9:587-594.

Wickham, D.E. 1986. Epizootic infestations by nemertean brood parasites on commercially important crustaceans. Canadian Journal of Fisheries and Aquatic Sciences 43:2295-2302.

Wilber, D.H. 1989. The influence of sexual selection and predation on the mating and post-copulatory guarding behavior of stone crabs (Xanthidae, Menippe). Behavioral Ecology and Sociobiology 24:445-451.

Williams, A.B. 1971. A ten-year study of meroplankton in North Carolina estuaries: Annual occurrence of some brachyuran developmental stages. Chesapeake Science 12:53-61.

Williams, A.B. 1984. Shrimps, Lobsters, and Crabs of the Atlantic Coast of the Eastern United States, Maine to Florida. Smithsonian Institution Press. Washington, District of Columbia. 550 p.

Wolcott, T.G. and A.H. Hines. 1989. Ultrasonic biotelemetry of muscle activity from free-ranging marine animals: A new method for studying foraging by blue crabs (*Callinectes sapidus*). Biological Bulletin 176:50-56.

Wolcott, T.G. and A.H. Hines. 1990. Ultrasonic telemetry of small-scale movements and microhabitat selection by molting blue crabs (*Callinectes sapidus*). Bulletin of Marine Science 46:83-94.

Zahavi, A. 1977. The cost of honesty (further remarks on the Handicap Principle). Journal of Theoretical Biology 67:603-605.

Ziegler, T.A., P.N. Pochelon and R.A. Tankersley. In review. Entrainment of the larval release rhythm of the blue crab *Callinectes sapidus* by step changes in salinity and the light:dark cycle. Marine Ecology Progress Series.

Zohar, S. and J.C. Holmes. 1998. Pairing success of male *Gammarus lacustris* infected by two acanthocephalans: a comparative study. Behavioral Ecology 9:206-211.

Zucker, N. 1984. Delayed courtship in the fiddler crab *Uca musica terpsichores*. Animal Behaviour 32:735-742.