A REVIEW OF MALE MATING SUCCESS IN THE BLUE CRAB, *CALLINECTES SAPIDUS,* IN REFERENCE TO THE POTENTIAL FOR FISHERIES-INDUCED SPERM LIMITATION

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ABSTRACT

This paper reviews information learned on reproduction and mating system structure of the blue crab since the last Blue Crab Symposium in relation to the potential for fisheries-induced effects on reproduction. Male size influences male mating success through its effect on male-male interactions, and the investments males make in the duration of mate guarding and the amount of ejaculate they pass to females. As compared with small males, large males are more often paired with larger females, win at aggressive interactions with rivals, guard longer, store more ejaculate contents before and after copulation, and pass larger ejaculates to females. The time a male spends guarding influences the female's survival, his access to her and, combined with his ejaculate output, to her unfertilized eggs. Mate guarding time and ejaculate size increase at high male : female ratios but ejaculate size decreases when males mate frequently, with short inter-mating intervals. Intense, size-biased fishing on males may alter the male size structure and sex ratio of local populations. These changes increase mating opportunities for small males and reduce the advantages to males of providing long periods of mate guarding and large ejaculates to females, thereby creating conditions that diminish the amount of ejaculate females receive. Female blue crabs use stored sperm to fertilize their lifetime production of eggs, and reduced amounts of stored sperm may limit the total number of eggs they produce.

The determinants of male mating success have been the subject of much theoretical and empirical work because the mating success of males is typically more variable than that of females (see Bateman, 1948; Andersson, 1994). The variance in male mating success is often explained by the outcome of sexual competition among males, female preferences for certain males, or both (Trivers, 1972). These processes are influenced by the structure of local populations including the sex ratio of reproductive individuals and the size or age composition (Trivers, 1972; Emlen and Oring, 1977). In a variety of species, there are many characteristics of males that enhance their ability to compete aggressively for access to females, including large body size (Salmon, 1983; Christy, 1987), the condition of specialized traits used in fighting (Borowsky, 1985; Lee and Seed, 1992; Juanes and Smith, 1995) and their overall health and physiological condition (Huntingford et al., 1995; Vye et al., 1997). Females mate differentially with males based on a number of features including male body size (Shuster, 1990; Fukui, 1995), courtship display (Cowan, 1991; Watson and Lighton, 1994), or the quality of resources males provide that enhance female reproductive output, including protection (Sih et al., 1990; Mathis and Hoback, 1997), nutritional supplements (Thornhill, 1983; Marden, 1989; Choe, 1995; Snedden, 1996), and ejaculate contents (Eberhard and Cordero, 1995).

In many species, males influence the ability of females to achieve their full reproductive potential by the quantity and quality of ejaculate they pass to females (Ridley, 1989; Keller and Reeve, 1995; Reynolds, 1996). In some species with extended sperm storage in the female, the amount and/or quality of sperm females receive influences the number of sperm available for egg fertilization, because sperm viability decreases with time (Nakatsuru and Kramer, 1982; Morgan et al., 1983; Paul, 1984). The duration and conditions of sperm storage in the female may contribute to sperm limitation, reducing the number and/or viability of fer-

tilized eggs females produce (Austin, 1975; Kirkendall, 1990; Sainte-Marie, 1993). In a variety of species, the amount of ejaculate males pass to females increases with male size (Svard and Wiklund, 1989; MacDiarmid and Butler, 1999; Parker and Simmons, 2000), decreases with the mating frequency of males (Woodhead, 1985; Svard and Wiklund, 1986; Paul and Paul, 1989; Cook and Gage, 1995), and males require time to replenish their supply of sperm and seminal products between matings (Ryan, 1967; Simmons et al., 1992; Pitnick and Markow, 1994). Thus, females may enhance their reproductive potential by mating with males that provide a full complement of sperm and seminal products (Markow et al., 1978; Gwynne, 1984; MacDiarmid and Butler, 1999).

As seen in exploited finfish populations (Trippel, 1995; Rochet, 1998), there is increasing concern over the negative effects of fishing on reproduction in exploited crustaceans (Wickham, 1986; Daniel et al., 1989; Ennis et al., 1990; Jamieson, 1993; Hankin et al., 1997). Many crustacean fisheries concentrate on large, sexually mature males and removal rates are often highest during the reproductive season (see Caddy, 1989). Concentrated removal of large males may alter the sex ratio of the population or the size structure of reproductive males (Smith and Jamieson, 1991; Sainte-Marie et al., 1995a). Heavily exploited populations may contain an insufficient number of males available for mating (Powell et al., 1973; Courchamp et al., 1999; Adams et al., 2000), a larger proportion of sexually immature males unable to mate, or an abundance of smaller adult males with increased opportunities to mate (Powell et al., 1974; Ennis et al., 1990; Donaldson and Donaldson, 1992). As in other species, these changes in population structure may alter the way mating occurs (Borgia, 1979; Christy, 1987), such that females may have difficulty finding a mate or receiving a full complement of sperm from available males (McMullen and Yoshihara, 1971; Norman and Jones, 1993). Reduced reproductive potential of females in heavily exploited populations of snow crab, *Chionoecetes opilio* (Sainte-Marie et al., 1995b), and king crab, *Paralithodes camtschatica* (McMullen and Yoshihara, 1971) indicates that the loss of males is diminishing female reproduction, because females are immune to fishing pressure.

Male blue crabs are the primary target of the largest fishery in Chesapeake Bay (Rugolo et al., 1998) and are under increasing fishing pressure along the east coast of the United States (Jordan, 1998). In some areas of Chesapeake Bay, fishing pressure has contributed to reductions in the size structure of adult males and the ratio of males to females (Abbe and Stagg, 1996; Uphoff, 1998). Recent work on the blue crab mating system indicates that the size structure and sex ratio of local populations influence aspects of male mating success that may affect the reproductive potential of females (see Hines et al., this volume). The interaction between the fishery and the blue crab mating system may create conditions that lead to sperm limitation. This paper reviews the determinants of male mating success in blue crabs, including (1) the importance of male behavior during pre-mating interactions with females, (2) the influence of male size on (a) the outcome of male-male interactions, (b) the duration of mate guarding, and (c) the amount of ejaculate males pass to females, and (3) how local sex ratios influence (a) the duration of mate guarding, and (b) the amount of ejaculate females receive, and discusses the potential for fisheries-induced sperm limitation.

MATERIALS AND METHODS

Much of this research was carried out at the Smithsonian Environmental Research Center on the Rhode River, a sub-estuary of Chesapeake Bay, in Maryland (38°51′N, 76°32′W) from mid-June through late September 1991–1994. Methods of field collection and the variables taken from field

collected crabs for evidence of a male size effect on mating (Jivoff, 1997b; Jivoff and Hines, 1998b), and variation in the amount of sperm and seminal fluid stored by both sexes (Jivoff, 1997b) are described elsewhere. The methods for the experimental manipulations, including those that tested the importance of male behavior during pre-mating interactions with females (Jivoff and Hines, 1998b; Jivoff and Hines, 1998a), the influence of male size on male-male interactions, the duration of mate guarding, and the amount of ejaculate males pass to females (Jivoff, 1997a; Jivoff, 1997b; Jivoff and Hines, 1998b), and how local sex ratio influences the duration of mate guarding, and the amount of ejaculate females receive (Jivoff, 1997a; Jivoff, 1997b) are described elsewhere.

RESULTS

MALE-FEMALE INTERACTIONS.—Female blue crabs have a single opportunity to mate, immediately after their final (pubertal) molt to maturity (Van Engel, 1958). Males pair with females (i.e., establish physical control over them) and physically carry them for several days before (i.e., pre-copulatory mate guarding) and after (i.e., post-copulatory mate guarding) the pubertal molt. Earlier work suggested that both males and females use chemical signals during courtship and pair formation (Gleeson, 1991), and more recent evidence supports that view (Bushmann, 1999). The outcome of pre-mating interactions between males and pre-pubertal females is modified by female molt stage, which influences the way females respond to males (Jivoff and Hines, 1998a; Jivoff and Hines, 1998b). Females early in the pubertal molt cycle resist male mate guarding attempts, but females late in the cycle initiate mate guarding with males. As a result, males often fail to establish physical control of early pre-pubertal females on their first attempt and must pursue them to successfully pair with them, but more easily establish physical control of late pre-pubertal females. Females do not appear to choose certain males based on male physical characteristics or courtship behavior during pre-mating interactions (Smith, 1992; Jivoff and Hines, 1998b; Bushmann, 1999). Males that successfully pair with females, more often establish and maintain physical control of them until copulation, whereas males that are unsuccessful at pairing more often lose control of females before mating can occur (Fig. 1). Some males that maintain physical control of a female do not ultimately mate with her (Fig. 1), which may be the result of male-male interactions (see below).

MALE SIZE AND PAIRING SUCCESS.—In the field, large males are more often paired with large pre-pubertal females (Fig. 2), suggesting that large males have a pairing advantage. In two of the four years examined, large males were more often paired with large adult females in post-copulatory mate guarding pairs (Jivoff, 1997b). Paired males are typically larger than pre-pubertal females but smaller than their adult female partners (Fig. 2). However, male size explained very little (2–14%) of the variation in the size of paired pre-pubertal or adult females (Fig. 2), suggesting that factors in addition to body size (e.g., female molt stage) influence which individuals pair.

Male blue crabs mate almost exclusively in the intermolt stage (Jivoff, 1995), which increases in duration as crabs get larger (Newcombe et al., 1949; Tagatz, 1968). In the field, paired males were significantly larger than unpaired males in non-intermolt stages (Fig. 3), suggesting that large males have a reproductive advantage over small males because they spend more time in the reproductive molt stage. Paired males were significantly larger than unpaired males that were also in the intermolt stage (except in 1994 when no significant difference was found) (Fig. 3), suggesting that large males have a pairing advantage over smaller males. Large males have proportionately longer chelae as compared with smaller males (Jivoff, 1997b). Male blue crabs use their chelae extensively during aggressive interactions with rivals for females and to physically control females, thus males that are missing one or both chelae or that have relatively small chelae
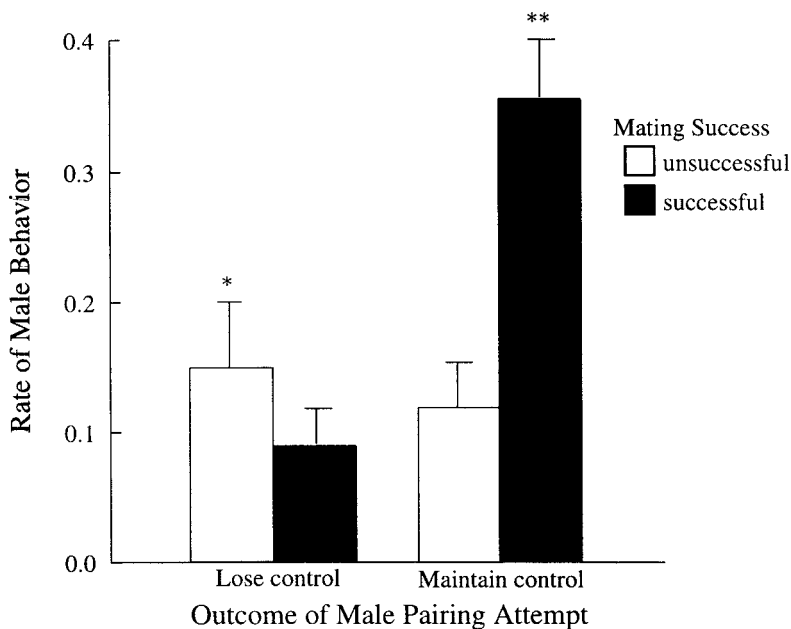
Figure 1. Rate of two male behavioral sequences, lose control and maintain control of female, performed by unsuccessful (□) and successful (■) males in experimental field enclosures. Vertical lines are +1 SE. * $P < 0.025$, ** $P < 0.001$. From Jivoff and Hines, 1998b.

are at a disadvantage during mating (Smith, 1992; Jivoff, 1997b). Indeed, during aggressive male-male interactions that occurred in field enclosures, large males were better able to displace smaller males from females and to prevent displacement (Fig. 4).

MALE SIZE AND MATE GUARDING DURATION.—Post-copulatory mate guarding protects female blue crabs from predation during their final soft phase, and reduces the chance that other males will subsequently mate with her (Jivoff, 1997a). Extended periods (>96 hours) of post-copulatory mate guarding prevent additional males from passing a larger ejaculate than that of the guarding male's, thereby enhancing the guarding male's fertilization rate even if the female mates again (Jivoff, 1997a). Large males provide longer periods of post-copulatory mate guarding than do small males, suggesting that large males have an advantage in the competition that occurs for egg fertilizations if the female remates (sperm competition) (Jivoff, 1997a).

MALE SIZE AND EJACULATE SIZE.—Male blue crabs store seminal fluid and spermatophores (which contain sperm) in the vasa deferentia and pass these ejaculate contents to the spermathecae (sperm storage organs) of females (Hard, 1945; Cronin, 1947). The amount of seminal fluid and spermatophores stored in the vasa deferentia both before and after one mating increases with male size (Fig. 5). The size-related increase in the weight of seminal products stored before mating is greater than that after mating (the difference is a measure of ejaculate weight), and the weight of female spermathecal contents (a direct measure of ejaculate weight) also increases with male size (Jivoff, 1997b). Large males pass larger ejaculates to females compared with small males, irrespective of mating history.

When males are provided the opportunity to mate with a number of females in succession, both male size (Jivoff, 1997b) and the number of his previous mates
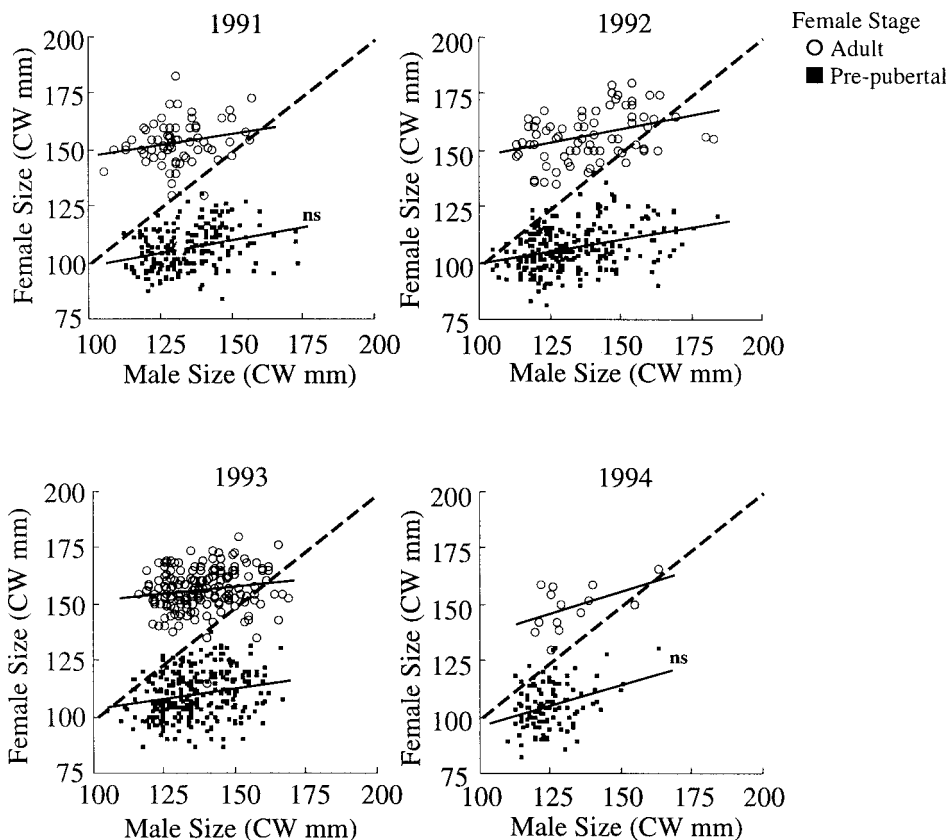
Figure 2. Relationship between guarding male carapace width (CW in mm) and pre-pubertal (■) and adult (○) female carapace width in mate guarding pairs captured in the field between 1991–1994. The dashed line in each graph indicates where the male and female sizes are equal. The regression lines for pre-copulatory mate guarding pairs are as follows: 1991; $Y = 74.44 + 0.24X$, $r^2 = 0.099$, $P < 0.001$, n = 200, 1992; $Y = 77.11 + 0.22X$, $r^2 = 0.123$, $P < 0.001$, n = 272, 1993; $Y = 82.31 + 0.20X$, $r^2 = 0.064$, $P < 0.001$, n = 283, 1994; $Y = 59.46 + 0.36X$, $r^2 = 0.104$, $P < 0.001$, n = 114. The regression lines for post-copulatory mate guarding pairs are as follows: 1991; not significant, 1992; $Y = 121.88 + 0.25X$, $r^2 = 0.142$, $P = 0.001$, n = 73, 1993; $Y = 139.24 + 0.12X$, $r^2 = 0.026$, $P = 0.035$, n = 174, 1994; not significant. From Jivoff, 1997b.

(male mating history) influence the amount of ejaculate passed to females (Jivoff, 1997b). Large males pass more ejaculate to each of their mates than do small males, and more ejaculate to their second mate than do medium-sized males (Fig. 6). Overall, the weights of female spermathecal contents decreased across all three matings; however, within male size classes, only large males showed a significant decrease in ejaculate weight across all three matings (Fig. 6). With increased time between the first and second matings, males pass ejaculates to their second female that are equivalent in weight to those passed to the first female (Jivoff, 1997b), suggesting that males need time to replenish their ejaculate supplies to pass similar sized ejaculates to each of their mates. Recent experimental evidence indicates that males require at least nine days to fully recover their ejaculate supplies (Kendall and Wolcott, 1999).

During a single reproductive season, many males, especially in the smaller size classes, have reduced ejaculate stores, and females do not appear to differentially
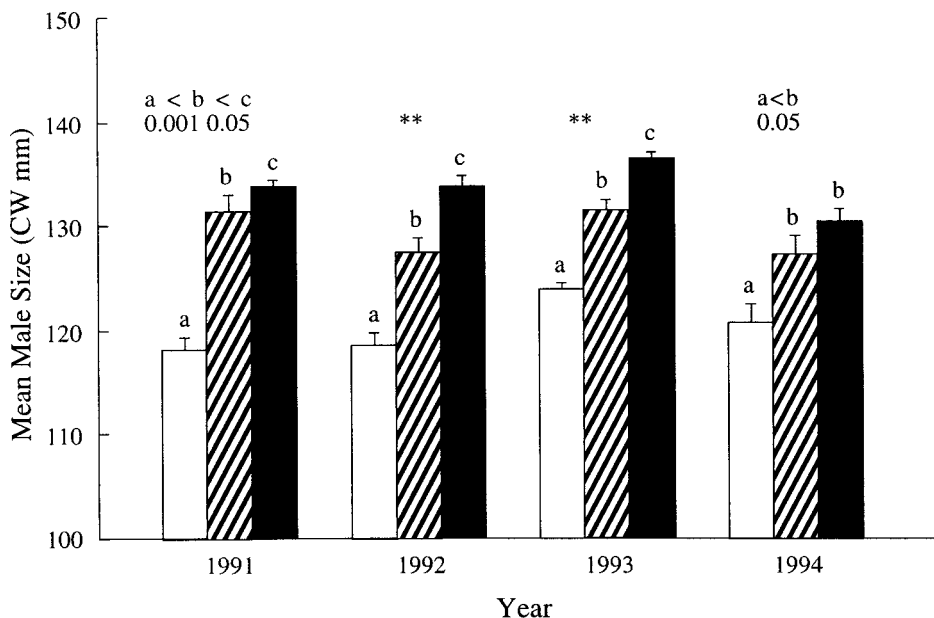
Figure 3. Mean carapace width of pre-copulatory mate guarding males (■) , unpaired males in the intermolt stage (▨), and unpaired males in non-intermolt stages (□) captured in the field between 1991–1994. Within each year, bars sharing the same letter are not significantly different. ** all differences $P < 0.001$. Vertical lines are +1 SE.
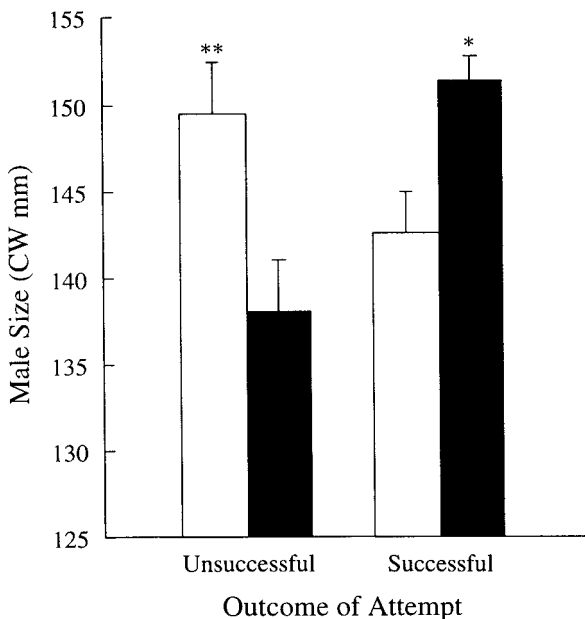

Figure 4. The mean carapace width of guarding (□) and unpaired aggressor (■) males in successful and unsuccessful takeover attempts occurring in experimental enclosures. Successful takeovers, resulting in the displacement of the guarding male, occurred when the unpaired male was larger (paired $t = 2.62$, df $= 17$, $P = 0.018$). Unsuccessful attempts, not resulting in displacement, occurred when the paired male was larger (paired $t = 3.12$, df $= 12$, $P = 0.009$).
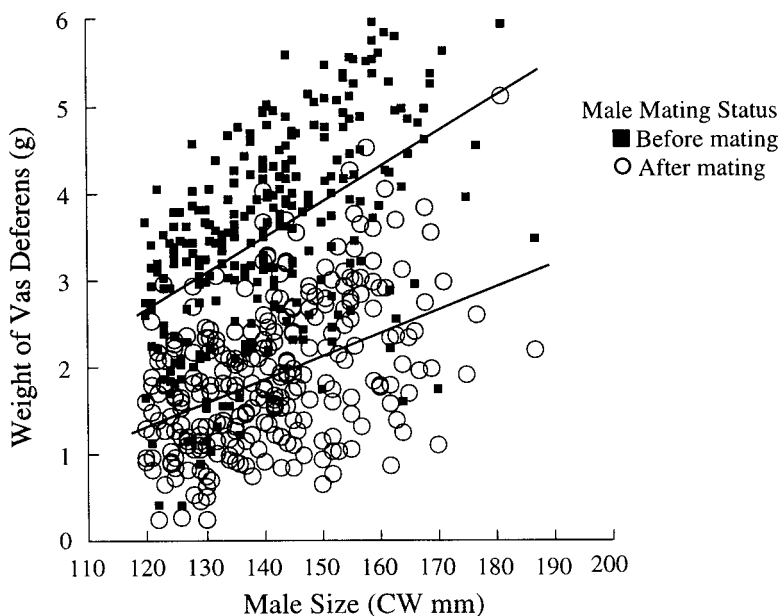
Figure 5. Relationship between male carapace width and the weight of ejaculate stored in the vas deferentia before (■) and after (○) one mating. Males had one pleopod removed before mating. Ejaculate stored before mating was the weight of the unmated (full) vasa deferentia. Ejaculate stored after mating was the weight of the mated (spent) vasa deferentia. The equation for the regression lines are as follows: $Y = -2.40 + 0.04X$, $r^2 = 0.263$, $P < 0.001$, n = 335 (before mating) and $Y = -1.92 + 0.03X$, $r^2 = 0.202$, $P < 0.001$, n = 335 (after mating). The before-mating slope is larger than the after-mating slope ($t = 3.12$, df = 669, $P < 0.002$). From Jivoff, 1997b.

mate with males that will provide them with larger ejaculates (Kendall and Wolcott, 1999). If small males, with diminutive ejaculate stores, are allowed increased opportunities to mate, females may receive reduced supplies of ejaculate. In the field, the weight of female spermathecal contents was greatest when the average size of paired males was largest (Fig. 7). In a number of heavily fished populations along the east coast (Maryland—Abbe and Stagg, 1996; Uphoff, 1998, Delaware—Cole, 1998, Louisiana—Guillory and Perret, 1998) the average size of legal sized males is decreasing, suggesting that these populations may offer excellent models for assessing the relationship between the supply of large males and that of female spermathecal contents.

SEX RATIO AND EJACULATE SIZE.—Male blue crabs alter the degree of reproductive investment they make in females based, in part, on the local sex ratio. Males pass a significantly larger percentage of their ejaculate to females in the presence of competitors than in their absence, and the duration of post-copulatory mate guarding is longest in the presence of competitors (Jivoff, 1997a). Thus, males invest more time and ejaculate in each female as the number of competitors, and thus the level of sexual competition for females increases.

DISCUSSION

As in many crustaceans, including other exploited species, the mating success of male blue crabs is influenced by the outcome of competitive interactions between males for females, and pre-mating interactions between males and females (Salmon, 1983; Christy, 1987). Local population structure moderates these inter-
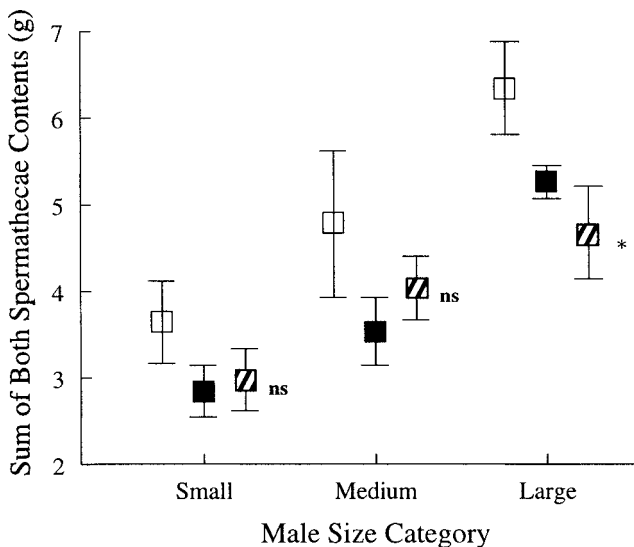
Figure 6. Sum of the weight of both spermathecae contents from the first (□), second (■) and third (▨) females mated in succession by males in three size categories. The following are the results of Tukey comparison tests between male size categories for the first mating; large vs. small ($P = 0.009$), large vs. medium ($P = 0.182$), medium vs. small ($P = 0.338$); second mating, large vs. small ($P = 0.0002$), large vs. medium ($P = 0.003$), medium vs. small ($P = 0.272$); and third mating, large vs. small ($P = 0.036$), large vs. medium ($P = 0.359$), and medium vs. small ($P = 0.084$). Only large males showed a significant decrease in successive ejaculate weight (Repeated Measures ANOVA, $F_{2,10} = 5.28$, $P = 0.034$), as indicated by *. Vertical lines are ± 1 SE.

actions, thereby dictating how mating occurs and the traits males develop for successful mating (Emlen and Oring, 1977). In blue crabs and other species, males must establish and maintain physical control of females to mate successfully (Berrill and Arsenault, 1982; Berrill and Arsenault, 1984; Donaldson and Adams, 1989; Perez and Bellwood, 1989). After pair formation, males may lose control of females because of female resistance towards males (see Donaldson and Adams, 1989). As in other species (Adams et al., 1985; Stevens et al., 1993; Reid et al., 1994), large male blue crabs are paired more often with larger females, and can guard longer than small males, suggesting that large size is an advantage in pairing and controlling females. Mate guarding pairs are also aggressively disrupted by unpaired competitors (Berrill and Arsenault, 1982; Laufer and Ahl, 1995; Orensanz et al., 1995). Large male blue crabs displace smaller guarding males and prevent displacement by smaller rivals, thus excluding smaller males from mating opportunities. In blue crabs and other crustaceans, males mate during the intermolt stage, which gets longer with body size (Tagatz, 1968; Lipcius, 1985; Freeman et al., 1987), therefore large males potentially have more time to dedicate to mating than small males. This is particularly important in mate guarding species like the blue crab, because male mating success is dictated by the amount of time males invest in mating (Parker, 1970; Parker, 1974).

As in other species of crabs (Diesel, 1990; Koga et al., 1993; Sevigny and Sainte-Marie, 1996), female blue crabs may mate with more than one male (during her terminal molt) (Jivoff, 1997a). In contrast to other species, female blue crabs store ejaculate such that both male's sperm compete for the unfertilized eggs (i.e., sperm competition) (Jivoff, 1997a). The level of sperm competition is moderated by the local sex ratio or the density of males and it influences the degree to which
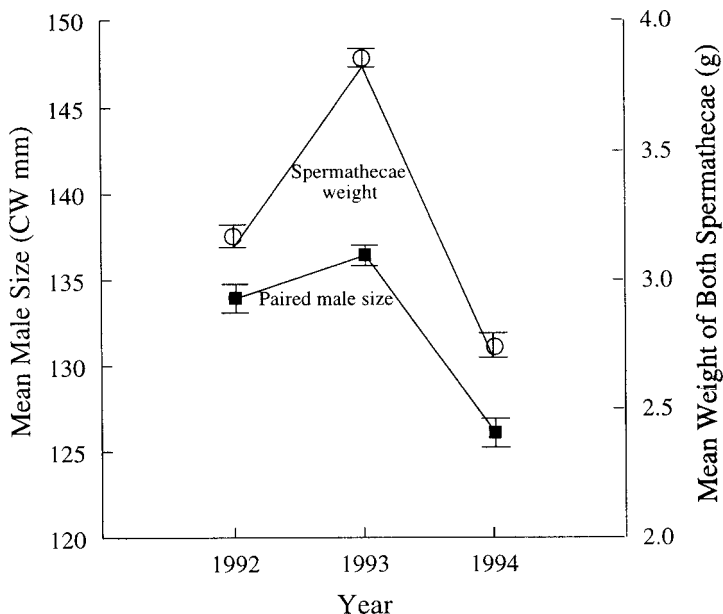
Figure 7. Mean carapace width of males paired with females (■), and mean weight of female spermathecae contents (○) between 1992–1994. Results of Tukey comparison tests for differences between years are: for males; 1993 > 1992 ($P = 0.007$), 1993 > 1994 ($P < 0.001$) and 1992 > 1994 ($P < 0.001$), and for spermathecae contents: 1993 > 1992 ($P < 0.001$), 1993 > 1994 ($P < 0.001$) and 1992 > 1994 ($P = 0.005$). Vertical lines are ±1 SE.

males invest reproductively in females (Parker, 1984; Smith, 1984). Male blue crabs respond to an increased number of competitors with longer post-copulatory mate guarding times and larger ejaculates. A male's ability to respond to sexual competition is related to his size, such that large males can guard longer, and pass larger ejaculates, because of greater stores of ejaculate contents (as seen in other species, e.g., Kwei, 1978; Wilber, 1987). The ability to pass large ejaculates is also related to male mating history such that males with relatively long times between previous matings to replenish ejaculate supplies may pass larger ejaculates to each of their mates (Ryan, 1967; Jivoff, 1997b; Kendall and Wolcott, 1999). In some species, the amount of time and ejaculate that males devote to females enhances the male's fertilization rate (even if his female mates with another male (Johnson, 1982; Smith, 1984)). The female's reproductive potential may also be enhanced because the amount of sperm she has stored for egg fertilization may influence her total egg production (Paul, 1984; Sainte-Marie, 1993). This may be especially true for blue crabs in Chesapeake Bay because of the potential for diminished quantity and quality of sperm available for fertilization (see Hines et al., this volume). Females have a single opportunity to mate, an extended period of sperm storage (9–12 months) that occurs during harsh environmental conditions, and they use stored sperm for their lifetime production of eggs.

The blue crab mating system involves sexual competition among males and sexual conflict between males and females, both of which favor large males, but intense fishing pressure may alter the way mating takes place. In blue crabs and other species, many males, especially in the larger size classes, may be removed prior to mating (Powell et al., 1973; Ennis et al., 1990; Smith and Jamieson,

1991; Norman and Jones, 1993). In some areas of Chesapeake Bay, both the mean size and the number of legal-size males relative to that of females has decreased (Abbe and Stagg, 1996; Uphoff, 1998). These changes in population structure may influence mating in two important and interrelated ways that may lead to sperm limitation and diminished reproductive output in females: (1) reducing female access to males that can provide large ejaculates, and (2) reducing the advantages to males of investing heavily in females.

The relative absence of large males in a local population may enhance the mating opportunities of small males that are less competitive and have a reduced ability to invest time and ejaculate in females (Butler, 1960; Smith and Jamieson, 1991; Paul and Paul, 1995). In the blue crab (Jivoff, 1997b) and Dungeness crab (*Cancer magister*) (Hankin et al., 1997), small males are able to mate with females of various sizes, such that, even in heavily exploited populations, the majority of females are inseminated (Wenner, 1989; Jivoff, 1995; Hankin et al., 1997). However, the amount of ejaculate female blue crabs have stored varies spatially (among and within estuaries), and temporally (among and within years) (Jivoff, 1997b; Hines et al., this volume). One source of the annual variation in female spermathecal contents may be the variation in the size of mating males, such that when a high proportion of small males mate, females receive less ejaculate (Jivoff, 1997b). If small male blue crabs mate frequently, with short inter-mating intervals, this may lead to further reductions in the amount of ejaculate females receive, because males will be unable to replenish their ejaculate supplies between matings (Jivoff, 1997b; Kendall and Wolcott, 1999). Recent evidence indicates that female egg production may be determined by the amount of ejaculate she has stored (see Hines et al., this volume). Thus, female reproductive potential may be compromised simply by reduced access to males that provide large amounts of ejaculate.

The relaxation of sexual competition also reduces the advantages to males of providing large amounts of mate guarding and ejaculate to females (Dewsbury, 1982; Parker, 1984). In many species, the reproductive investments males make in females allows males to succeed at sexual competition (Parker, 1970; Borgia, 1979). In blue crabs (Jivoff, 1997a) and some other mate guarding species, when sexual competition is less intense due to reductions in the number or changes in the type of competitors, males diminish their investments in the duration of mate guarding (Manning, 1980; Iribarne et al., 1995) and the amount of ejaculate passed to females (Parker, 1984; Gage, 1991). Thus, fisheries-induced changes in local population structure may exacerbate the diminished ejaculates females receive from small males by also reducing the incentives for those males to invest heavily in females. Furthermore, if males spend less time with each female they may be able to mate more frequently (Parker, 1974; Clutton-Brock and Parker, 1992), thus further aggravating their ability to replenish their ejaculate supplies.

Traditionally, resource managers have been concerned with maintaining exploitation rates that ensure an adequate supply of reproductive females (Jones et al., 1990; Lipcius and van Engel, 1990; Rugolo et al., 1998). However, even when females are immune to fishing pressure, some exploited crustaceans show signs that reproduction may be detrimentally influenced in complex ways (McMullen and Yoshihara, 1971; Smith and Jamieson, 1991; Sainte-Marie et al., 1995a). Information presented here on the blue crab mating system indicates many similarities between blue crabs and other exploited species, and the potential for an alternative mechanism by which fisheries exploitation may reduce reproduction in blue crabs.

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