Chela Function, Morphometric Maturity, and the Mating Embrace in Male Snow Crab, *Chionoecetes opilio*

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Behavior and chela function associated with precopulatory clasping in morphometrically mature (MM) and morphometrically immature (MI) male snow crab, *Chionoecetes opilio*, were compared. MM males clasp receptive females more readily and for a more protracted period than MI males. Moreover, smaller MM males were more successful in initiating and maintaining precopulatory holds than larger MI males. These differences in clasping behavior cannot be attributed to differences in chela function, as the force developed is sufficient for clasping in both cases. The output force of the MM chela is, however, significantly higher than for MI chela because of their higher mechanical advantage and muscle stress and the presence of a larger closer muscle. Nor are differences in clasping behavior due to the fiber composition of the chela closer muscle which is composed of slow fibers in both morphotypes. These fibers are highly differentiated in their sarcomere lengths and enzymatic (ATPase and NADH-diaphorase) profiles which allow them to provide slow, powerful, and sustained contractions suited to precopulatory clasping. Since chela morphology and closer muscle composition appear adapted to precopulatory clasping in both morphotypes, other factors, most likely neurohormonal, may make MM males clasp more readily than their MI conspecifics.

On a comparé le comportement et la fonction des chélipèdes lors de l'étreinte précopulatoire chez des mâles du crabe des neiges, *Chionoecetes opilio*, qui ont atteint leur maturité morphologique (MM) ou non (MI). Les mâles MM étreignent les femelles réceptives plus volontiers et pour plus longtemps que les mâles MI. En outre, les mâles MM de plus petite taille ont plus de succès que les mâles MI plus gros pour prendre et garder les femelles dans une étreinte précopulatoire. Ces différences de comportement d'étreinte ne peuvent pas être attribuées à des différences au niveau du fonctionnement des chélipèdes puisque la force développée est suffisante pour maintenir l'étreinte chez tous les sujets. Toutefois, la force produite par les chélipèdes des MM est significativement supérieure à celle produite par les chélipèdes des MI; cela est attribuable à un avantage mécanique, une plus forte tension musculaire et de plus gros muscles de fermeture des chélipèdes. On ne peut pas, non plus, attribuer les différences dans le comportement d'étreinte à la composition en fibres du muscle de fermeture des chélipèdes, qui est composé de fibres à contraction lente dans les deux types morphologiques. Ces fibres sont très différenciées sur le plan de la longueur des sarcomères et sur le plan des profils enzymatiques (ATPase et NADH-diaphorase), qui rendent possibles des contractions lentes, puissantes et soutenues qui favorisent l'étreinte précopulatoire. Puisque la morphologie et que la composition des muscles de fermeture des chélipèdes paraissent adaptées à l'étreinte précopulatoire chez les deux types morphologiques, d'autres facteurs, fort probablement neurohormonaux, peuvent aider les mâles MM à étreindre plus spontanément les femelles que leurs congénères MI.

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Snow crab, *Chionoecetes opilio* (Brachyura, Majidae), support important fisheries in the Northwest Atlantic, the Bering Sea, and the Sea of Japan (Bailey and Elner 1989). However, fundamental biological criteria to distinguish reproductive capability and maturity for *Chionoecetes* species are not well established (Somerton 1981; Elner and Beninger 1989, 1992). In eastern Canada, the legal minimum size of 95 mm carapace width (CW) was designed to restrict snow crab landings to mature males; females attain a maximum size of only 47–95 mm CW. Early observations on gonad development, presence of spermatophores, and chela allometry suggested that all males attain maturity between 51 and 75 mm CW (Watson 1970). Growth was presumed to continue past maturity; consequently, males were assumed to have at least one opportunity to copulate before being fished (Elner and Bailey 1986). However, reexamination of this premise indicates that for *C. opilio* in the Northwest Atlantic, at least, the molt at which chelae undergo allometric growth is a terminal molt (O'Halloran 1985;

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Conan and Comeau 1986; Conan et al. 1989). As for other majids (Hartnoll 1963), the implications are that male snow crab can cease growth over a wide size range, between approximately 50 and 159 mm CW, and are not fully mature before terminal molt (Elner and Beninger 1992). Nonetheless, males that have not attained terminal molt can have fully formed spermatophores in their vas deferens (Beninger et al. 1988) and may copulate in some circumstances (Conan et al. 1989; Ennis et al. 1990).

Allometric growth of the male chelae at the terminal molt results in subtle changes in chelae shape and relative size (Fig. 1), which, in turn, provide a means to distinguish morphological types. Logarithmic plots of chela size versus CW show separation between regression lines for morphometrically immature (MI) males and morphometrically mature (MM) males in, supposedly, terminal anecdysis (Conan and Comeau 1986). These external changes in chelal dimensions have been surmised to indicate functional changes, allowing a MM male to grip the base of a hard-shelled, multiparous female's walking legs for several weeks prior to copulation, through copulation and subsequent egg extrusion (Conan and Comeau 1986; Elner and Beninger 1992). Laboratory observations (Watson 1970, 1972) and recent field studies (Sainte-Marie and Hazel 1992) indicate that mating of primiparous females also involves protracted male grasping. Govind et al. (1992) determined that the chela closer muscle and its motor patterns and excitatory neuromuscular synapses are specialized for slow, sustained activity, such as an extended precopulatory embrace in both MI and MM male snow crab.

Premises on terminal molt, criteria to determine maturity, and the ramifications for snow crab fisheries management are still being debated (Jamieson and McKone 1988; Elner and Beninger 1989; Safran et al. 1990; Dawe et al. 1991; Sainte-Marie and Hazel 1992). Here we compare aspects of precopulatory behavior, chela mechanics, and muscular properties between MM and MI male snow crab in an effort to resolve aspects of the current controversy.

Materials and Methods

Snow crab were collected near Pinnacle Rock, Bonne Bay, Newfoundland, between May 18 and June 23, 1990. Males for examination of chelal mechanics were captured by either trawl or traps at approximately 90 m depth. These crabs were transported to Nova Scotia and held in running seawater at the Halifax Fisheries Research Laboratory, before being air-freighted to Scarborough College, Ontario. There they were maintained in recirculating seawater at 4°C and used within a month of their arrival. Male and female crabs, for behavioral studies and in vivo force measurements, were taken by SCUBA divers from depths of 4–40 m and kept in seawater at the Memorial University Marine Station, Bonne Bay. They were held for less than 2 wk before being used and were not fed. In these males, the shell condition was noted not only for its hardness but also for the presence of epiphyte growth along the margins of the shell. Only hard-shelled males in intermolt condition C_4 to D_0 (O'Halloran and O'Dor 1988) were used, as mating has not been reported for premolt or early postmolt stages (Watson 1970; Hooper 1986). Also, early postmolt male crabs exhibited poor mobility and little force in dactyl closing, making them poor subjects for experimentation.

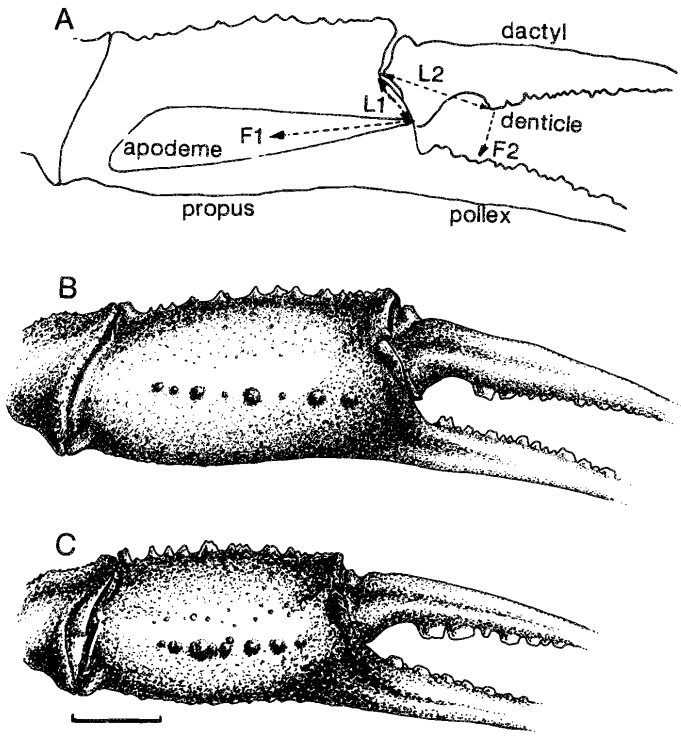

FIG. 1. (A) Chela of male snow crab showing the forces (F) and levers (L) involved in the closing action. (B and C) Representative chela from MM and MI males, respectively; both crabs 88 mm CW. Scale bar: 10 mm.

All crabs were tagged with an identification number and their CW and chela height measured to the nearest millimetre with vernier calipers. Only female carrying eyed-eggs were used, as others were not receptive to males. Males were designated as either MM or MI based on the equation (Conan and Comeau 1986)

$$Y = -0.788931 \ln CW + 0.61448 \ln \text{chela height} + 1.76051.$$

Male crabs of Y greater than zero are MM; crabs are MI when Y is less than zero. The equation is estimated to be 99% effective in distinguishing the two morphs.

Behavior

Two behavioral studies were made of crabs in tanks (90 × 50 × 40 cm) with flowing seawater at ambient temperature (4–5°C) at the Bonne Bay Marine Station. Crabs were used once and then released.

First, observations of individual male/female pairs were made four times daily (08:00, 12:00, 18:00, and 23:00) over 5-min periods. At these times, details of the clasping behavior, if such behavior occurred, were noted such as where the female was held and by which chela. A total of 32 pairs were observed; 17 involved MM males and 15 MI males.

Second, observations were made of competitions between a small (70–85 mm CW) MM male and a large (90–100 mm CW) MI male for a female. Observations were made for 5 min each at the following times: 08:00, 12:00, 18:00, and 23:00. An experiment was terminated when one male maintained the female in an embrace for three consecutive observation periods. A total of 10 competitions were recorded.

TABLE 1. Clasping behavior of MM and MI male snow crab.

	MM	MI
No. observed	17	15
No. initiated clasping	17	8
No. initiated clasping in first observation period (4 h)	17	4
No. maintaining clasp until eggs extruded	16	2
No. copulating	5	0

Functional Morphology

Functional basis to male clasping behavior was examined by analysing chelal mechanics and properties of chela closer muscle for MM and MI males.

Mechanical advantage (MA)

Crustacean chelae are operated by a lever system (Warner and Jones 1976). In a system with frictionless pivots:

$$F1 \times L1 = F2 \times L2$$

where F1 is force applied to the system (i.e., through contraction of the closer muscle) and F2 is force produced (i.e., the closing action). L1 and L2 are the levers along which these forces act and represent the shortest distance between the hinge and lines of action of the respective forces (Fig. 1). Mechanical advantage (MA) is the factor by which the magnitude of the F1 is altered; because the chela hinge has little friction, MA may be estimated by the ratio of lever lengths L1/L2. Thus, F2 increases with MA, although the speed of any movement and distance moved both decrease in proportion. L1 was measured between the hinge and the point of attachment of the apodeme of the closer muscle. L2 is commonly described as the distance between the hinge and the tip of the dactyl. However, as the female's legs are pinched by the large bicuspid first denticle, we considered the effective L2 to be between this latter point and the hinge.

Muscle force and stress

Closing force (F2) was measured in vivo for 25 males. For each, the right chela was immobilized and the central dactyl tooth attached by a short length of nonelastic cord to a linear spring balance. The crab was induced to close its dactyl by stroking the inside of the pollex with a brush. Closing force (F2) was then estimated by pulling vertically upwards on the spring balance until the dactyl began to open. Individual crabs were subjected to three or four such measurements over a 15-min period; only the most forceful measurement for each was retained.

Muscle stress (S), contractile force generated per unit area of the closer muscle, was estimated for each crab from the equation (Alexander 1983)

$$S = F1/A \sin 0.$$

Apodeme area (A), an index of the maximum longitudinal area of the closer muscle, was calculated from tracings of the outlines of apodemes on a computer image analysis system. The angle of pinnation (0) of the closer muscle fibers was measured from tracings of the dorsal surface of the muscle fibers onto the apodeme using a camera lucida.

Muscle composition

A morphological and two histochemical methods were used to characterize fibers from the chela closer muscle. For the morphological method, sarcomere length (SL) of myofibrils was measured; SL is directly related to contractile speed (Atwood 1976). The closer muscle was fixed, in situ, in a relaxed state by holding the dactyl open while Bouin's fluid was injected into the muscle through the exoskeleton. Fixing was continued by immersing the cheliped in Bouin's for 3 d after which it was stored in 70% ethanol. Fibers were sampled by dividing the muscle transversely into proximal, central, and distal sections. Within each section, eight samples were taken: two dorsally, four centrally, and two ventrally. For each sample, three separate measurements were made each consisting of six sarcomeres in series and three A-bands. A-bands are less subject to length changes than myofibrils (Franzini-Armstrong 1970) and served to verify that the sarcomeres were not unduly stretched or contracted. Measurements of SL and A-band lengths were made to the nearest micrometre using phase contrast objectives and an ocular micrometer (Govind et al. 1986). A total of 432 sarcomeres and 216 A-bands were measured for each closer muscle. In total, muscles from four MM males and four MI males were examined.

For the first histochemical method, activity of an enzyme, myofibrillar ATPase, was assessed (Ogonowski and Lang 1979). Differential staining for ATPase reflects differences in specific activity of this enzyme related to contractile speed; fast fibers have a higher specific activity than slow (Hajek et al. 1973). The exoskeleton of the chela was filed down with a hobby drill to expose the hypodermis, before the cheliped was covered with an embedding medium (optimal cutting temperature compound by Tissue Tek) and frozen by immersion in 2-methylbutane cooled in liquid nitrogen. Next, the chela was cut transversely into proximal, central, and distal regions. Cross-sections (20 μm) from each region were obtained by standard techniques (Govind et al. 1986). Sections were air dried on glass coverslips for 15 min before being incubated for 30 min at 4°C in an ATPase medium consisting of 0.05 M glycglycine, buffered at pH 8.0 with KOH, 18 mM $CaCl_2$, 1.5 M MgCl, and 3 M ATP. This was followed by a series of rinses in water and 1% $CaCl_2$ and by an incubation in 2% $CoCl_2$. Next, sections were water rinsed, incubated in 1% ammonium sulphide, and again rinsed in water before being dehydrated in ethanol, cleared in xylene, and mounted on glass slides.

For the second histochemical method, oxidative capacity of muscle fibers was determined by staining frozen cross-sections for NADH-diaphorase, an enzyme located principally in the mitochondria. Sections were incubated in the dark for 2 h, at room temperature, in a 0.05 M phosphate buffer (pH 7.5) containing 0.98 mM nitro-blue tetrazolium and 0.97 mM NADH. After rinsing in water, sections were dehydrated in ethanol, cleared in xylene, and mounted on glass slides. Both histochemical methods were used in each of 30 closer muscles of which 15 muscles were from MM and 15 from MI males.

Results

Behavior

Our observations on clasping or embracing of a female snow crab by a male crab associated with copulation confirm and extend earlier findings (Watson 1970, 1972). The male, using his chelae, initially grasped the female from any angle, at any available site on her appendages or carapace. In the next few minutes, the male manipulated the female into a face-to-face position by grasping her legs on one side with one of his chelae. This position was maintained over the majority of the holding period. Although the general form of the mating embrace appeared similar between MM and MI males, there were differences in clasping behavior between these two morphs (Table 1). Thus, all 17 MM males demonstrated clasping compared with 8 of the 15 MI males, a significant difference ($\chi^2 = 10.15$, df = 1, $p < 0.01$). Moreover, all MM males initiated clasping within the first observation period as compared with four of the eight MI males ($\chi^2 = 19.0$, df = 1, $p < 0.001$). All but one of the 17 MM males retained the female until egg extrusion, in comparison with 2 of 15 MI males. Copulation, defined as insertion of the male's pleopods into the female's genital openings, was observed in 5 of the 17 MM pairings but in none of the 15 MI cases. The interval between copulation and egg extrusion in the five MM males ranged between 6 and 24 h for a mean of 15.6 h.

In 8 of 10 competitive trials, a small MM male gained possession of the female and retained her in the presence of the larger MI male for the entire observation period. The large MI male was successful in 2 of 10 trials. Hence, small MM males were successful more often than their large MI counterparts ($\chi^2 = 7.2$, df = 1, $p < 0.01$). Behavior of MM and MI males differed; upon introduction into the test tank, the small MM male immediately seized the female whereas the large MI male showed sporadic interest in the female by advancing and retreating from her. Also, once clasping had been established by the small MM male, no attempts to break this hold were made by the large MI male. Conversely, the small MM male repeatedly attempted to break clasping by the large MI male.

Functional Morphology

Gross chelal morphology of the two male morphs appears virtually indistinguishable to the casual observer (Fig. 1). The occluding surfaces of the dactyl and pollex are lined by a number by small tubercles. The most prominent amongst these is a single large bicuspid first denticle on the dactyl with a matching socket on the pollex. In a closed chela the occluding surfaces of the first denticle meet.

Mechanical advantage

Mean MA (±SE) values for MM (0.427 ± 0.032; $n = 14$) and MI (0.350 ± 0.032; $n = 15$) males were different ($t = 4.64$, df = 28, $p < 0.05$). Regression of lever length against CW (Fig. 2) shows that L1 is elevated in MM as compared with MI crabs ($t = 7.923$, df = 27, $p < 0.05$). Consequently, a differential increase in L1 at the molt to morphometric maturity is mainly responsible for differences in MA between the two morphs. Paradoxically, however, the regression for L2 was also significantly elevated in MM compared with MI crabs ($t = 3.850$, df = 27, $p < 0.05$) (Fig. 2); here, the higher L2 values would act to lower MA.

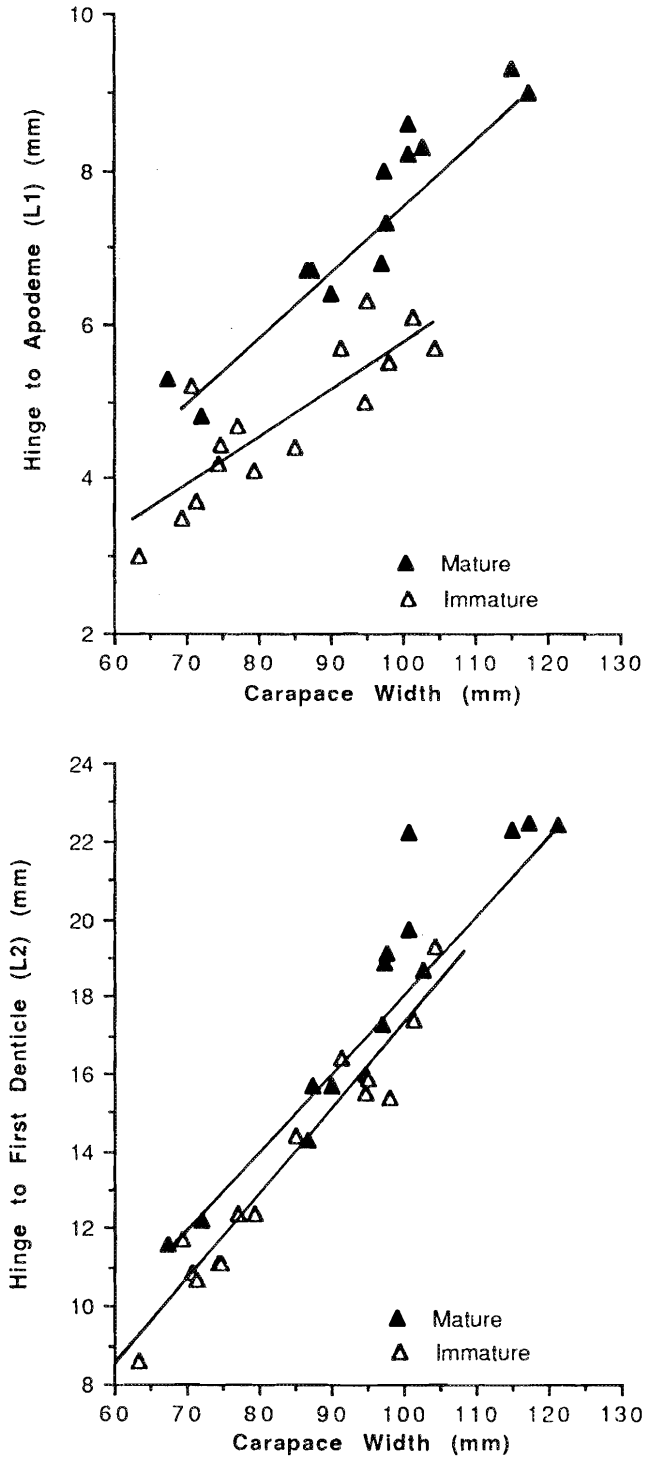

FIG. 2. Relationship between CW and length of levers, L1 (upper) and L2 (lower), in the chela of MM (solid triangles) and MI (open triangles) male snow crab. The relationship between L1 (y) and CW (x) is expressed by the regression line $y = -1.564 + 0.094x$ for MM crabs ($n = 13$) and $y = -0.344 + 0.061x$ for MI crabs ($n = 15$). The regression line for L2 (y) and CW (x) is $y = -3.88 + 0.277x$ for MM crabs ($n = 14$) and $y = -4.92 + 0.227x$ for MI crabs ($n = 31$).

Force and stress

Apodeme area, an index of the closer muscle area, was larger for MM males than for MI males of a given CW ($t = 7.67$, df = 2, $p < 0.05$) (Fig. 3). Because this indicated that MM crabs have allometrically larger chela closer muscles,

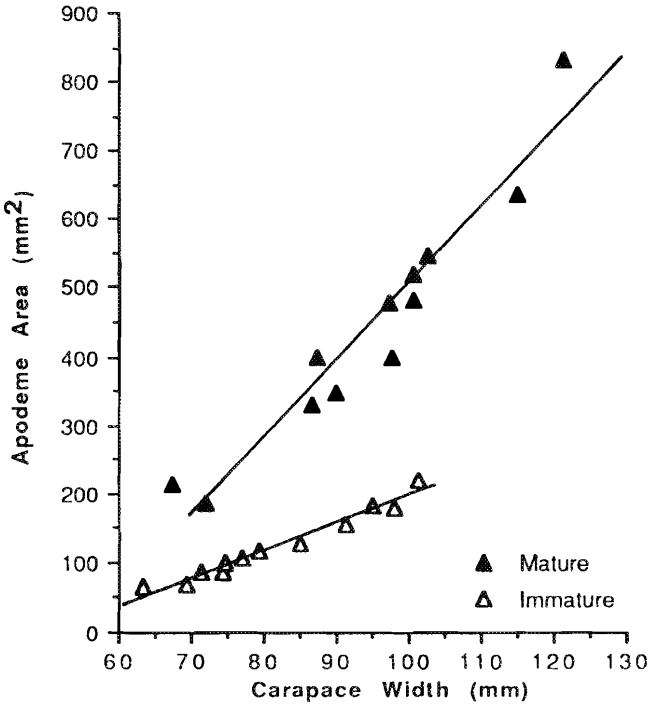

FIG. 3. Relationship between CW and apodeme area of the chela closer muscle in MM (solid triangles) and MI (open triangles) male snow crab. The regression line for apodeme area (y) and CW (x) is $y = -599.96 + 11.029x$ for MM crabs ($n = 12$) and $y = -199.24 + 3.951x$ for MI crabs ($n = 13$).

recorded muscle forces were expressed relative to apodeme area. This allowed a comparison of forces in MM and MI closer muscles of equal size. The maximum force developed by the muscle itself (F1) was greater for MM than MI chela closer muscles ($t = 2.72$, df = 22, $p < 0.05$) (Fig. 4). Likewise, the force of closing of the dactyl (F2) was also greater for MM than for MI males ($t = 4.00$, df = 22, $p < 0.05$) (Fig. 4). This difference between MM and MI males in terms of F2 may be due to superior mechanical advantage of the MM chela. However, bearing in mind that MM males have a much larger closer muscle than their MI counterparts (Fig. 3), the output force (F2) for MM males is severalfold greater than for MI males for crabs with comparable CW.

A further comparison between MM and MI crabs was made in terms of contractile force per unit area of the closer muscle, i.e., stress. The mean maximum stress for MM muscle was 0.552 N/mm^2 ± 0.024 ($n = 12$) and for MI muscle was 0.444 N/mm^2 ± 0.029 ($n = 13$), a significant difference ($t = 2.88$, df = 25, $p < 0.05$).

Muscle composition

SLs of myofibrils were measured from closer muscles of four MM and four MI male snow crab. The pattern of distribution of SLs is essentially similar between the two morphs, as shown by a representative example from each category (Fig. 5). Fibers are of a wide range of SLs, 4–17 μm, and bimodally distributed, with the first mode at 4–6 μm and the second mode at 12–13 μm.

Measurements of A-bands, which are less subject to variations than myofibrils (Franzini-Armstrong 1970), were also made. The A-band data parallel those of the SL, in that they show a wide range from 2 to 9 μm and are bimodal, 3–4 and 7–8 μm (Fig. 5). Thus, the closer muscle is composed of

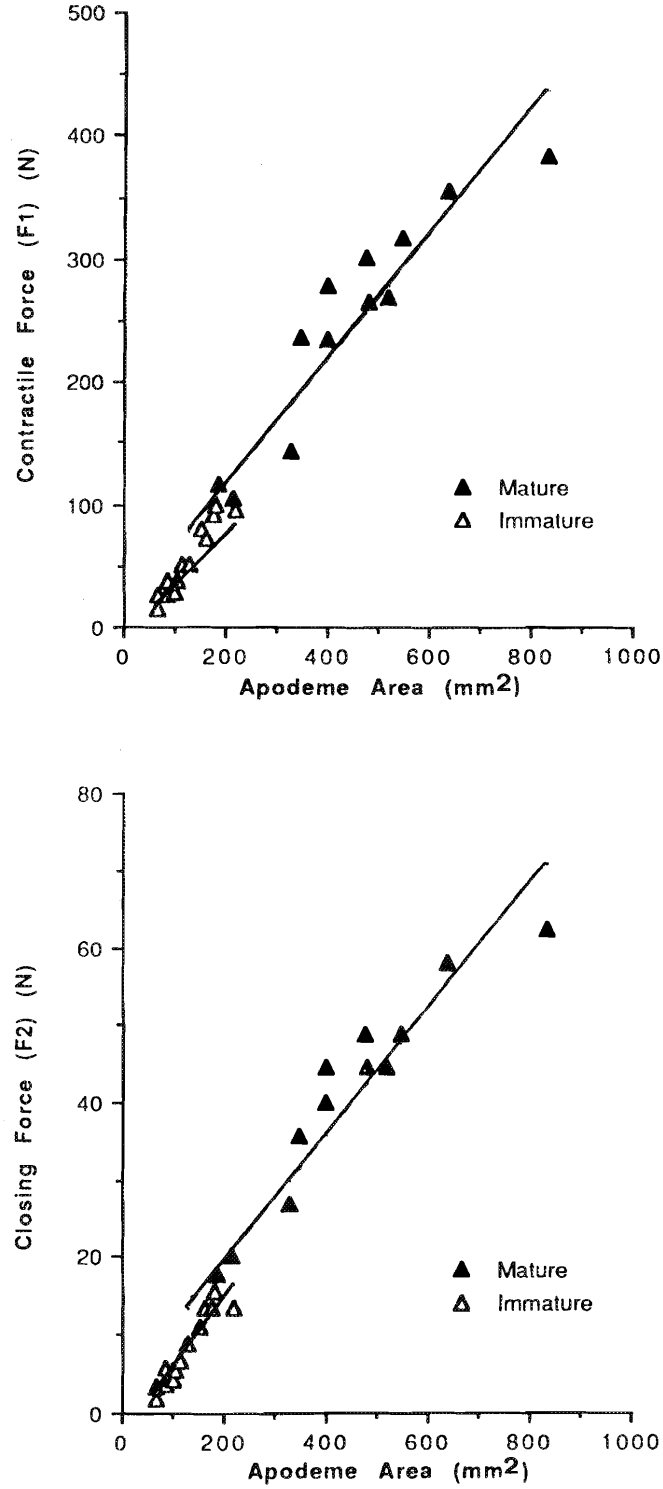

FIG. 4. Relationship between apodeme area of the chela closer muscle and contractile force (F1) (upper) and closing force (F2) (lower) in MM (solid triangles) and MI (open triangles) male snow crab. The regression line for F1 (y) and apodeme area (x) is $y = 43.920 + 0.462x$ for MM crabs ($n = 12$) and $y = -19.167 + 0.586x$ for MI crabs ($n = 13$). The regression line for F2 (y) and apodeme area (x) is $y = 8.22 + 0.073x$ for MM crabs ($n = 12$) and $y = -3.12 + 0.090x$ for MI crabs ($n = 13$).

two populations of fibers differing in SL and, hence, contractile properties. To determine if the populations are distributed in a regional fashion within the muscle, SL data

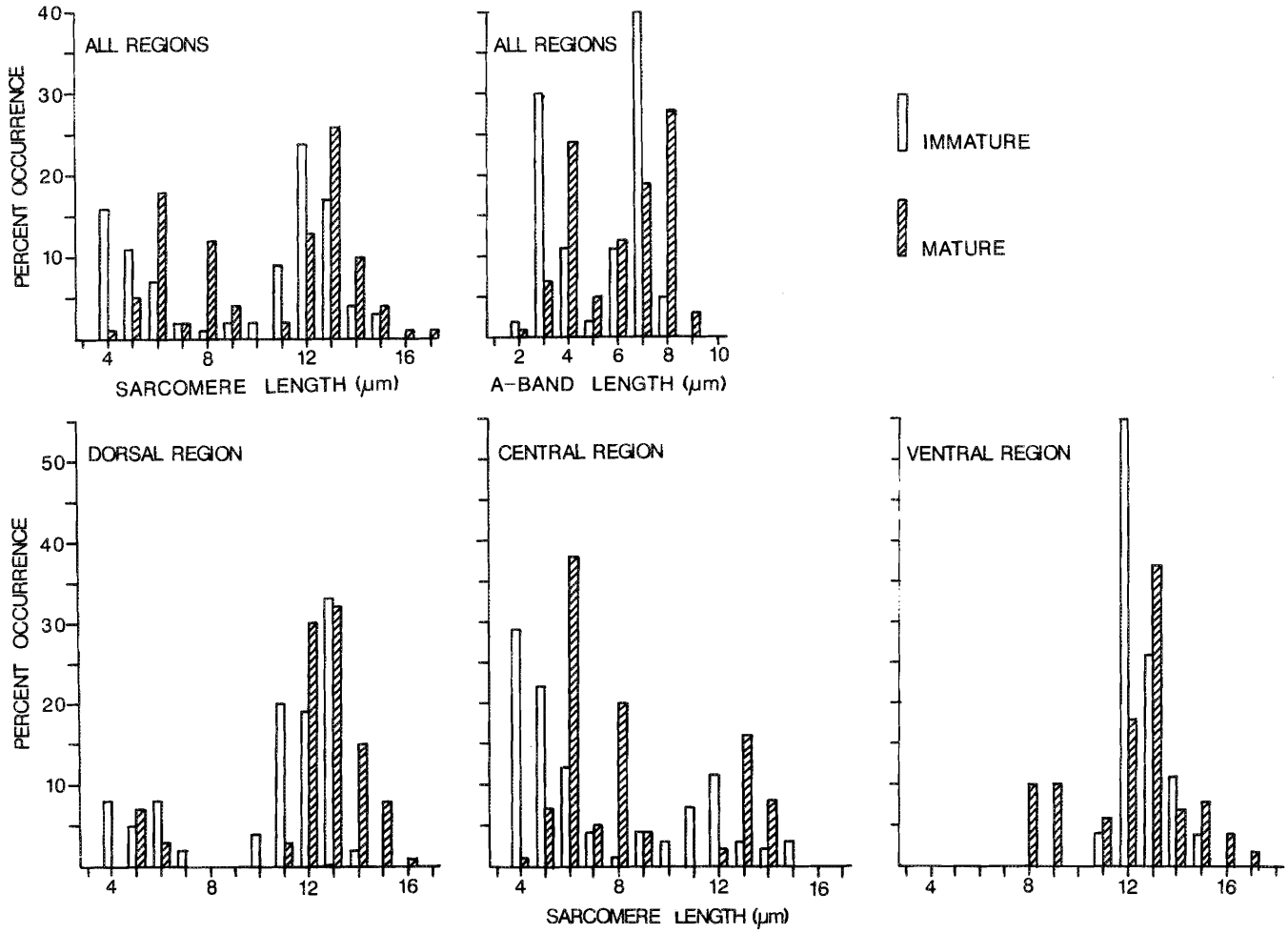

FIG. 5. Frequency histogram of fibers with characteristic sarcomere lengths and A-band lengths in the chela closer muscle of a MI (open bars) and MM (hatched bars) male snow crab shown for the entire muscle (upper) and for different regions (lower); n = 513 sarcomeres (133 dorsal, 239 central, 141 ventral) and 232 A-bands for MI and 481 sarcomeres (122 dorsal, 233 central, 126 ventral) and 283 A-bands for MM.

were analysed based on the area from which the fibers were sampled (i.e., dorsal, central, and ventral region) (Fig. 5). A similar pattern emerged for both MM and MI muscles. The dorsal region contains predominantly long SL fibers, the central region has almost the reverse pattern with mostly short SL fibers and a few long SL ones, and the ventral region has only long SL fibers.

In cross-sections of chelae treated histochemically for detecting myofibrillar ATPase, there was variation in staining intensity between fibers, especially in the proximal and middle regions of the muscle (Fig. 6). Most muscle sections stain in a fairly uniform dark manner, although lighter-staining fibers appear in the dorsal and ventral areas. Fibers in the distal region stain more uniformly. The pattern of staining was similar in both MM and MI males.

Muscle fibers stained either intensely or lightly for NADH-diaphorase and in a distinctly regional manner (Fig. 6). Intensely stained fibers occur as a broad band in the middle of the cross-sections from proximal and middle regions with lightly staining fibers bisecting this band as well as sandwiching it between the dorsal and ventral sides. Fibers in the ventral region appear uniformly lightly stained. Both MM and MI males showed similar staining patterns.

Discussion

Chelae can be considered "ecological templates" in that the life style of a crab species is uniquely reflected in its chelal morphology (Elner 1980). The phenomenon of differentiation of snow crab chelae at the molt to morphometric maturity is seen variously as a key to understanding the terminal molt premise (Conan and Comeau 1986), defining "maturity" (Conan et al. 1989), and a means for regulating the commercial fishery (Safran et al. 1990; Tremblay et al. 1992). Here we assess the functional role of snow crab chelae as a secondary sexual characteristic.

Our behavioral comparisons demonstrate clear differences between the propensities of MI and MM males to clasp and retain multiparous females. These findings support laboratory (Conan and Comeau 1986; Moriyasu and Conan 1988) and field (Taylor et al. 1985; Hooper 1986; Ennis et al. 1988, 1990) observations suggesting that MI males do not usually engage in multiparous mating. Also, recent field surveys in the northwestern Gulf of Saint Lawrence found MI males to be uncommon in sexual pairs with pubescent females (Sainte-Marie and Hazel 1992). We provide data on the interval between copulation and egg extrusion. How-

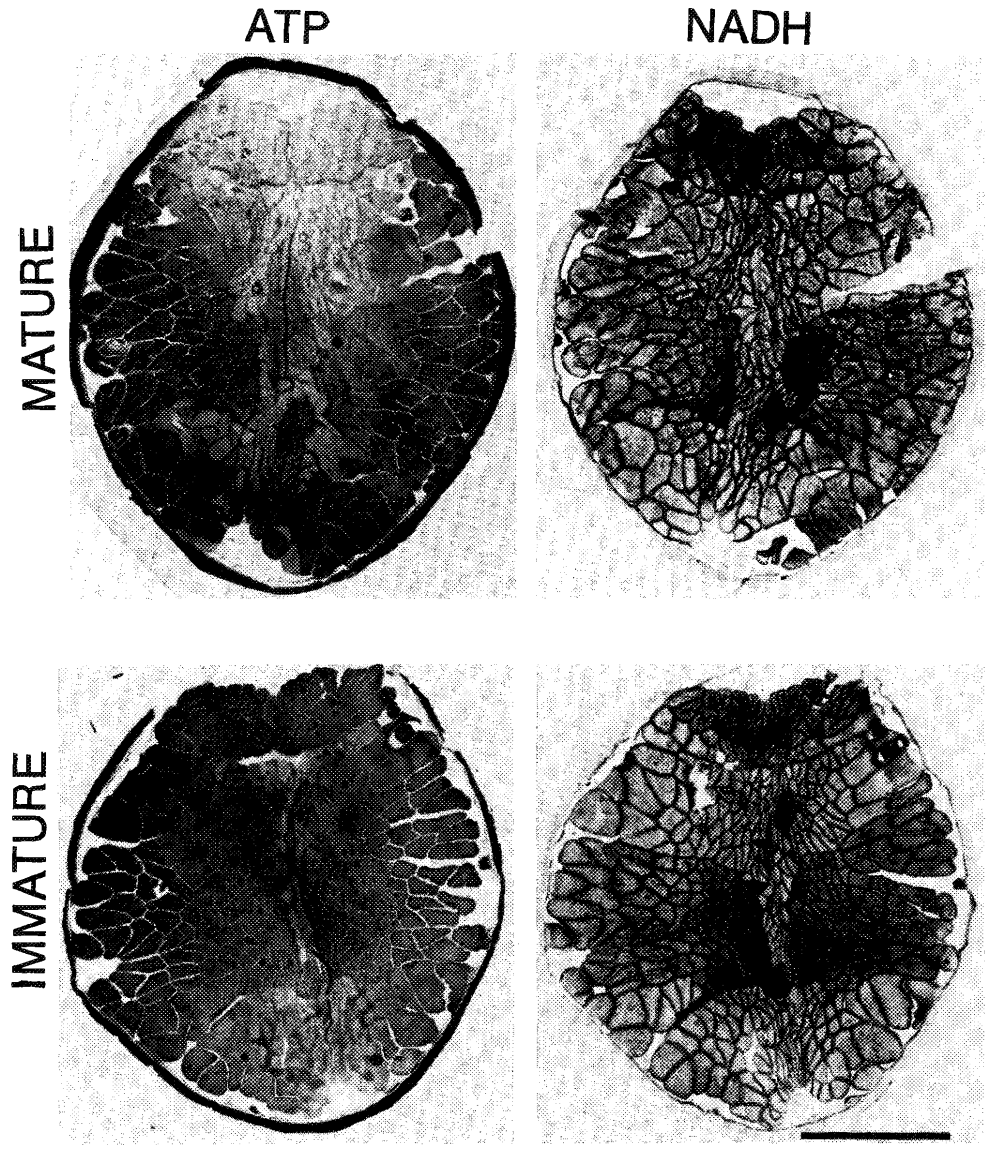

FIG. 6. Adjacent frozen cross-sections stained for myofibrillar ATPase and NADH-diaphorase activity from the midregion of the chela of a MM male and a MI male. The large, bipinnate closer muscle with a tendon down the midline occupies most of the cross-sectional area of the claw, while the small, also bipinnate opener muscle is restricted to the extreme dorsal or upper retion. Scale bar: 5 mm.

ever, although such information has not previously been recorded for multiparous female snow crab, the fertility of the eggs was not ascertained and the possibility that females may have utilized stored sperm remains (Elner and Beninger 1992; Beninger et al. 1993).

We investigated morphological, mechanical, and physiological properties of chelae from both male morphs in an attempt to explain differences in mating behavior. The functional implications of the various allometric and biomechanical differences detected between chelae of the two morphs are uncertain. For example, the chelae of the MM males have a relatively higher mechanical advantage which, coupled with their relatively larger closer muscles and higher stress capabilities, indicates that they can develop bigger output forces than chelae of MI males of comparable CW. However, the output force capabilities of chelae of MI males, although generally only approximately 30% of similar sized MM males, are comparable with estimates for other decapod species (Brown et al. 1979; Elner 1980; Elner and Campbell 1981). Thus, the functional basis to the distinction remains enigmatic. Although there are marked mechanical differences, in terms of relative size, closer muscle stress, and maximum force capability, between the two chela types, these do not appear by themselves to either necessarily preclude MI males from maintaining a mating embrace or explain why they do not. Indeed, other functional aspects of the chelae, such as gross morphology, muscle fiber composition, and motor firing patterns (Claxton 1992; Govind et al. 1992), appear similar in the two morphs. Hence, the original question, "can a MI male hold a multiparous female in a mating embrace?" is modified to "why does a MI male not hold a multiparous female in a mating embrace?"

While differences in F2 are not necessarily a factor in mating ability, muscular composition and innervation are,

but these appear identical between the two morphs. The fiber composition of the closer muscle determines the strength and duration of its contraction (Jahromi and Atwood 1969). Traditionally, crustacean muscle fibers have been classified according to their contractile speed, with mean SL providing a convenient index of speed; fast fibers have short SLs of 2–4 μm and slow fibers have longer SLs of >4 μm (Govind and Atwood 1982). Chela closer muscles from MM and MI male snow crab are strikingly similar in their SLs, which range from 4 to 13 μm, making the muscles essentially slow. However, within this category of slow muscle, there is considerable variation in both MI and MM crabs; about a third are clustered around a SL mode of 4–6 μm and the remaining two thirds around a longer SL mode of 12–13 μm. Overall, evidence from characters investigated suggests that chelae from both MM and MI males can develop slow powerful contractions suitable for clasping. Closer muscles with a similar SL distribution are seen in several other crustaceans, e.g., in the chelae of blue crab (Govind and Blundon 1985), fiddler crab (Rhodes 1986), and crayfish (Govind and Pearce 1985) and in the major chela of American lobster (Lang et al. 1977) and snapping shrimp (Stephens and Mellon 1979). In all these cases, there is a wide range in contractile activity of the slow type. Fast-type contractions are seen in the closer muscle of the minor chela of lobsters in which most of the fibers have SLs of 2–4 μm with the result that closing movements can occur as rapidly as 20 ms.

Differentiation in structural properties of the muscle is complemented by differences in the activities of two enzymes, ATPase and NADH-diaphorase. The former regulates the speed of contraction based on its specific activity and the latter is directly related to muscle fatigability. Histochemical detection of these enzymes revealed several staining intensities for each, demonstrating that there are several different activity levels for these enzymes in the chela closer muscle. Thus, a combination of structural and enzymatic properties endows the closer muscle with considerable versatility in its contractile behavior; but behavior where the emphasis is on slow, forceful, and prolonged contractions, suitable for maintaining a mating embrace, occurs in both MM and MI males.

A hypothesis to explain why otherwise mechanically capable MI males do not readily grasp receptive females invokes modulation of synaptic activity at both the periphery and in the central nervous system by circulating amines and peptides. Neurohormonal regulation of behavior is dramatically seen in the octopamine-regulated alert posture (limbs and abdomen extended) and the serotonin-regulated submissive posture of American lobster (Kravitz 1988). Moreover, behavioral regulation within a molt cycle by blood-borne factors is implicated in the tendency of premolt lobsters to display threat by meral spread (Schwanke et al. 1990). Similar factors at the molt to morphometric maturity in male snow crab may trigger the expression of precopulatory clasping. Support for the hypothesis comes from studies suggesting that juvenile hormone, methyl farnesoate, regulates not only differentiation of chelae but also the state of the reproductive system in different male morphs of another majid, *Libinia emarginata* (Homola et al. 1991).

To account for the allometric growth causing morphological and mechanical differences between chelae of the two male morphs, we hypothesize that female choice and/or intermale competition during the precopulatory phase has produced strong selective forces for the augmented male characteristics, chela size and strength, observed in MM males. A similar argument was advanced for the relatively larger chelae of male, as compared with female, American lobster (Elner and Campbell 1981). If our neurohormonal hypothesis is correct and MI males can be experimentally induced to display MM behavior, the latter hypothesis could be tested by repeating our competition experiments with the addition of MI males modified with MM hormones. If modified MI males were outcompeted by MM males of the same CW, the hypothesis would stand; conversely, the hypothesis could be dismissed should the modified MI males perform as well as their MM conspecifics.

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References

ALEXANDER, R.McN. 1983. Animal mechanics. Sedgewick and Jackson, London. 346 p.

ATWOOD, H.L. 1976. Organization and synaptic physiology of crustacean neuromuscular system. Prog. Neurobiol. 7: 291–391.

BAILEY, R., AND R.W. ELNER. 1989. Northwest Atlantic snow crab fisheries: lessons in research and management, p. 261–280. *In* J.F. Caddy [ed.] Marine invertebrate fisheries: their assessment and management. John Wiley & Sons. Chichester, England.

BENINGER, P.G., R.W. ELNER, T.P. FOYLE, AND P.H. ODENSE. 1988. Functional anatomy of the male reproductive system and the female spermatheca in the snow crab *Chionoecetes opilio* (O. Fabricius) (Decapoda: Majidae) and a hypothesis for fertilization. J. Crustacean Biol. 8: 322–332.

BENINGER, P.G., C. LANTEIGNE, AND R.W. ELNER. 1993. Reproductive processes revealed by spermatophore dehiscence experiments and by histology, ultrastructure, and the histochemistry of the female reproductive system in the snow crab *Chionoecetes opilio* (O. Fabricius). J. Crustacean Biol. 13: 1–16.

BROWN, S.C., S.R. CASUTO, AND R.W. LOOS. 1979. Biomechanics of chelipeds in some decapod crustaceans. J. Zool. Lond. 188: 143–159.

CLAXTON, W.T. 1992. The behavior and chelae physiology associated with precopulatory holding of the female by the male snow crab, *Chionoecetes opilio*. M.Sc. thesis, University of Toronto, Toronto, Ont. 76 p.

CONAN, G.Y., AND M. COMEAU. 1986. Functional maturity and terminal molt of male snow crab, *Chionoecetes opilio*. Can. J. Fish. Aquat. Sci. 43: 1710–1719.

CONAN, G.Y., R.W. ELNER, AND M. MORIYASU. 1989. Review of literature on life histories in the genus *Chionoecetes* in light of recent findings on growth and maturity of *C. opilio* in eastern Canada, p. 163–180. *In* Proc. Intl. Symp. King and Tanner Crabs. Alaska Sea Grant Coll. Program Rep. No. 90-04, Anchorage, Alaska.

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*). Can. J. Fish. Aquat. Sci. 48: 2266–2275.

ELNER, R.W. 1980. The mechanics of predation by the shore crab, *Carcinus maenas* (L.), on the edible mussel *Mytilus edulis* L. Oecologia 36: 333–344.

ELNER, R.W., AND R.F.J. BAILEY. 1986. Differential susceptibility of Atlantic snow crab, *Chionoecetes opilio*, stocks to management. Can. Spec. Publ. Fish. Aquat. Sci. 92: 335–346.

ELNER, R.W., AND P.G. BENINGER. 1989. Comment on functional maturity in small male snow crab (*Chionoecetes opilio*): sizing up the evidence. Can. J. Fish. Aquat. Sci. 46: 2037–2039.

ELNER, R.W., AND P.G. BENINGER. 1992. The reproductive biology of the snow crab, *Chionoecetes opilio*: a synthesis of recent contributions. Am. Zool. 32: 524–533.

ELNER, R.W., AND A. CAMPBELL. 1981. Force, function and mechanical advantage in the chelae of the American lobster *Homarus americanus* (Decapoda: Crustacea). J. Zool. Lond. 193: 269–286.

ENNIS, G.P., R.G. HOOPER, AND D.M. TAYLOR. 1988. Functional maturity in small snow crabs (*Chionoecetes opilio*). Can. J. Fish. Aquat. Sci. 45: 2106–2109.

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. Can. J. Fish. Aquat. Sci. 47: 2443–2449.

FRANZINI-ARMSTRONG, C. 1970. Natural variability in the length of thick and thin filaments in single fibres from a crab, *Portunus depurator*. J. Cell Sci. 6: 559–592.

GOVIND, C.K., AND H.L. ATWOOD. 1982. Organization of neuromuscular systems, p. 63–103. *In* H.L. Atwood and D.C. Sandeman [ed.] The biology of Crustacea. Vol. 3. Neurobiology: structure and function. Academic Press, New York, N.Y.

GOVIND, C.K., AND J.A. BLUNDON. 1985. Form and function of the asymmetric chelae in blue crabs with normal and reversed handedness. Biol. Bull. 168: 321–331.

GOVIND, C.K., K.M. MEAROW, AND A. WONG. 1986. Regeneration of fibre type in paired asymmetric closer muscles of the snapping shrimp, *Alpheus heterochelis*. J. Exp. Biol. 123: 55–69.

GOVIND, C.K., AND J. PEARCE. 1985. Enhanced reappearance of fast fibers in regenerating crayfish claw closer muscles. Dev. Biol. 107: 206–212.

GOVIND, C.K., A.T. READ, W.T. CLAXTON, AND R.W. ELNER. 1992. Neuromuscular analysis of the chela closer muscle associated with precopulatory clasping in male snow crabs, *Chionoecetes opilio*. Can. J. Zool. 70: 2356–2363.

HAJEK, I., N. CHARI, A. BASS, AND E. GUTMANN. 1973. Differences in contractile and some biochemical properties between fast and slow abdominal muscles of the crayfish (*Astacus leptodactylus*). Physiol. Bohemoslov. 22: 603–612.

HARTNOLL, R.G. 1963. The biology of the Manx spider crabs. Proc. Zool. Soc. Lond. 141: 423–496.

HOMOLA, E., A. SAGI, AND H. LAUFER. 1991. Relationship of claw form exoskeleton condition to the reproductive system size and methyl farnesoate in the male spider crab, *Libinia emarginata*. Int. J. Invertebr. Reprod. Dev. 20: 219–255.

HOOPER, R.G. 1986. A spring breeding migration of the snow crab, *Chionoecetes opilio* (O. Fabr.), into shallow water in Newfoundland. Crustaceana 50: 257–264.

JAHROMI, S.S., AND H.L. ATWOOD. 1969. Correlation of structure, speed of contraction, and total tension in fast and slow abdominal muscle fibers of the lobster, *Homarus americanus*. J. Exp. Zool. 171: 25–38.

JAMIESON, G.S., AND W.D. MCKONE. 1988. Proceedings of the International Workshop on Snow Crab Biology, December 8–10, 1987, Montreal, Quebec. Can. MS Rep. Fish. Aquat. Sci. 1880: 1–127.

KRAVITZ, E.A. 1988. Hormonal control of behavior: amines and the biasing of behavioral output. Science (Wash., D.C.) 241: 1775–1781.

LANG, F., W.J. COSTELLO, AND C.K. GOVIND. 1977. Development of the dimorphic claw closer muscles of the lobster *Homarus americanus:* I. Regional distribution of muscle fiber types in adults. Biol. Bull. 152: 75–83.

MORIYASU, M., AND G.Y. CONAN. 1988. Aquarium observation on mating behavior of snow crab, *Chionoecetes opilio*. Int. Counc. Explor. Sea CM 1987/K:21: 14 p.

OGONOWSKI, M.M., AND F. LANG. 1979. Histochemical evidence for enzyme differences in crustacean fast and slow muscle. J. Exp. Zool. 207: 143–151.

O'HALLORAN, M.J. 1985. Moult cycle changes and the control of moult in male snow crab, *Chionoecetes opilio*. M.Sc. thesis, Department of Biology, Dalhousie University, Halifax, N.S. 183 p.

O'HALLORAN, M.J., AND R.K. O'DOR. 1988. Molt cycle of male snow crabs, *Chionoecetes opilio*, from observations of external features, setal changes, and feeding behavior. J. Crustacean Biol. 8: 164–176.

RHODES, W.R. 1986. A comparative study of thoracic and cheliped muscle asymmetry in male fiddler crabs (genus: *Uca*). Biol. Bull. 170: 335–349.

SAFRAN, E.B., T.P. FOYLE, AND R.W. ELNER. 1990. Prospects for distinguishing morphometrically mature and immature crabs: an alternate management strategy for the snow crab fishery. Can. Atl. Fish. Sci. Adv. Comm. Res. Doc. 90/30: 1–22.

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. Can. J. Fish. Aquat. Sci. 49: 1282–1293.

SCHWANKE, M.L., J.S. COBB, AND G. KASS-SIMON. 1990. Synaptic plasticity and humoral modulation of neuromuscular transmission in the lobster claw opener during the molt cycle. Comp. Biochem. Physiol. 97C: 143–149.

SOMERTON, D.A. 1981. Regional variation in the size of maturity of two species of Tanner crab (*Chionoecetes bairdi* and *C. opilio*) in the eastern Bering Sea, and its use in defining management subareas. Can. J. Fish. Aquat. Sci. 38: 183–186.

STEPHENS, P.J., AND DEF. MELLON JR. 1979. Modification of structure and synaptic physiology in transformed shrimp muscle. J. Comp. Physiol. 132: 97–108.

TAYLOR, D.M., R.G. HOOPER, AND G.P. ENNIS. 1985. Biological aspects of the spring breeding migration of snow crabs, *Chionoecetes opilio*, in Bonne Bay, Newfoundland (Canada). Fish. Bull. 83: 707–711.

TREMBLAY, M.J., M. EAGLES, AND R.W. ELNER. 1992. Trial use of a claw gauge as an alternate measure of minimum legal size in the snow crab fishery of eastern Cape Breton (Area 23). Can. Atl. Fish. Sci. Adv. Comm. Res. Doc. 92/94: 1–11.

WARNER, G.F., AND A.R. JONES. 1976. Leverage and muscle fibre type in the crab chelae (Crustacea: Brachyura). J. Zool. Lond. 180: 57–68.

WATSON, J. 1970. Maturity, mating, and egg laying in the spider crab, *Chionoecetes opilio*. J. Fish. Res. Board Can. 27: 1607–1616.

WATSON, J. 1972. Mating behavior in the spider crab, *Chionoecetes opilio*. J. Fish. Res. Board Can. 29: 447–449.