Multiple reproductive strategies in snow crab, *Chionoecetes opilio*: Physiological pathways and behavioral plasticity

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Abstract

We review the three major reproductive pathways displayed by snow crab, *Chionoecetes opilio*. Females can copulate in either a soft- or hard-shelled condition and also fertilize eggs with sperm stored in their spermathecae. Spermatophore partitioning and preservation mechanisms in the spermatheca plus postulated spermatophore removal abilities in males play central roles in shaping mating behavior. However, fitness consequences of the various strategies are enigmatic. Fecundity is influenced by both spermatophore source and female characteristics; also, egg production estimates are confounded by high loss rates and uncertainties surrounding brooding period. Males challenge the concept of "maturity" as they copulate both as morphometrically immature (MI) with small chelae and morphometrically mature (MM) with large chelae individuals. Reproductive opportunities for each male morph vary according to long-term population cycles influencing inter-male competition levels. Thus, during phases when MM males are abundant, reproductive opportunities for MI males are probably low; however, the window opens when MM males become scarce. We explore possible mechanisms that control whether males with small chelae either continue to molt and remain MI or attain full sexual maturity and, hence, probable terminal molt-status.

Keywords: Brachyura; Fecundity; Fertilization; Fishery; Growth; Mating; Maturity; Sperm competition

1. Introduction

Snow crab, *Chionoecetes opilio* (Majidae) support major fisheries in the northwest Atlantic, Bering Sea and Sea of Japan (Otto, 1982; Sinoda, 1982; Bailey

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& Elner, 1989). The species occurs on soft bottoms at depths of 60–400 m where temperature remains below 5°C. Commercial interests have drawn much biological attention to snow crab and congeners over the past 25 yr (Jamieson & McKone, 1988; Elner & Beninger, 1992). Although the scrutiny has provided deep insight into life history, population ecology and reproduction of the species, many critical questions remain unresolved (Ennis et al., 1988, 1989; Elner & Beninger, 1989).

Functional morphology of the reproductive system and mating behavior of snow crab are reviewed by Beninger et al. (1988, 1991; 1993) and Elner & Beninger (1992). There is a large size disparity between the sexes. Males can grow to between ≈50 and 160 mm carapace width (CW) and females attain a maximum size of between 47 and 95 mm CW (Conan & Comeau 1986; Conan et al. 1990). Male chelae undergo allometric growth, a disproportionate increase in size relative to CW, at the pubertal molt. An allometric increase in abdominal area, relative to CW, for females at puberty facilitates egg brooding (Hartnoll, 1969). The pubertal molt in both sexes is probably a terminal molt (Conan et al., 1990). Males that have gone through puberty are termed morphologically mature (MM) and readily copulate (Watson, 1970, 1972). However, morphologically immature (MI), or juvenile, males that have not undergone pubertal molt can have fully formed spermatophores in their vas deferens (Beninger et al., 1988). Field studies where morphometrics of male partners in copulating pairs has been recorded indicate that MI males can mate with both primiparous (Saint-Marie & Hazel, 1992) and multiparous females (Ennis et al., 1990).

Primiparous mating of snow crab was first observed in the laboratory by Kon & Nanba (1968) and subsequently described by Watson (1970, 1972) (see schematics, Figs. 1 and 2). The male retains the female in a precopulatory embrace and drives away intruding males for a week prior to her puberty molt. Female ecdysis is assisted by the male. The male copulates with the soft-shelled female for ≈45 min and the pair remain embraced for a further 8 h. At insemination, each of the male's pair of first gonopods are inserted into a vagina of the female; seminal fluid and spermatophores are pumped from the penes through the ejaculatory canal of the first gonopods by piston-like movements of the second gonopods. Fertilized eggs are extruded onto the female's pleopods within 24 h of copulation; also, females can extrude subsequent clutches of eggs fertilized by spermatophores stored in their pair of ventral spermathecae. Watson (1970, 1972) determined that males can be polygamous, mate with larger females and copulate successfully up to 95 h after female ecdysis.

Watson (1972) could not induce males to copulate with multiparous females and, hence, argued that primiparous mating was either the sole or predominate copulatory occasion. However, multiparous snow crab mating was discovered in Bonne Bay, Newfoundland by Taylor et al. (1985) and Hooper (1986). Subsequently, multiparous mating has been studied in the laboratory (Conan & Comeau, 1986; Moriyasu & Conan, 1988; Claxton et al., 1994) and Gulf of Saint Lawrence (Sainte-Marie & Hazel, 1992). Primiparous and multiparous mating of a congener, Tanner crab (*Chionoecetes bairdi*) off Alaska has been documented by
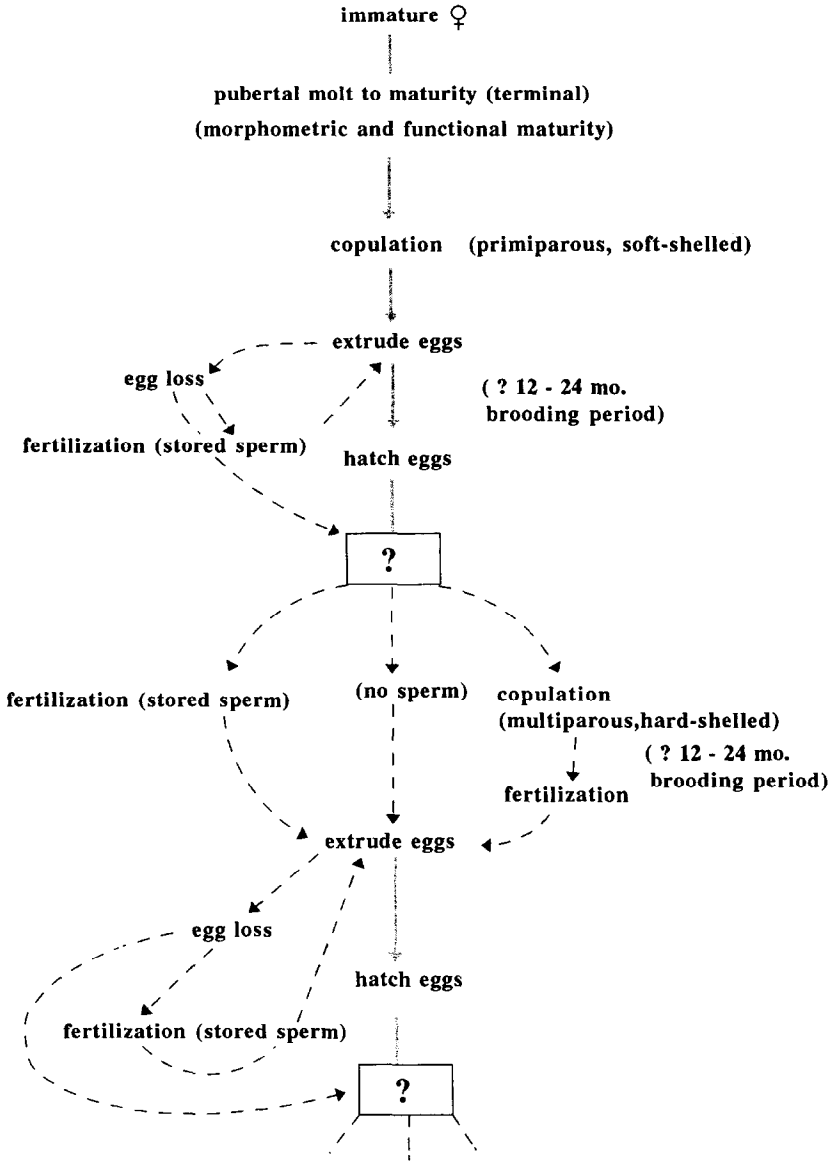
Fig. 1. Schematic illustrating reproductive pathways in female snow crab, *Chionoecetes opilio*; ?'s indicate decision points leading to alternative pathways (– – –).

Stevens et al. (1993, 1994). During multiparous snow crab mating, pairing lasts up to ≈2 months (Taylor et al., 1985; Hooper, 1986). Copulation occurs shortly after the female releases larvae from her old clutch. MM males, but not MI males,
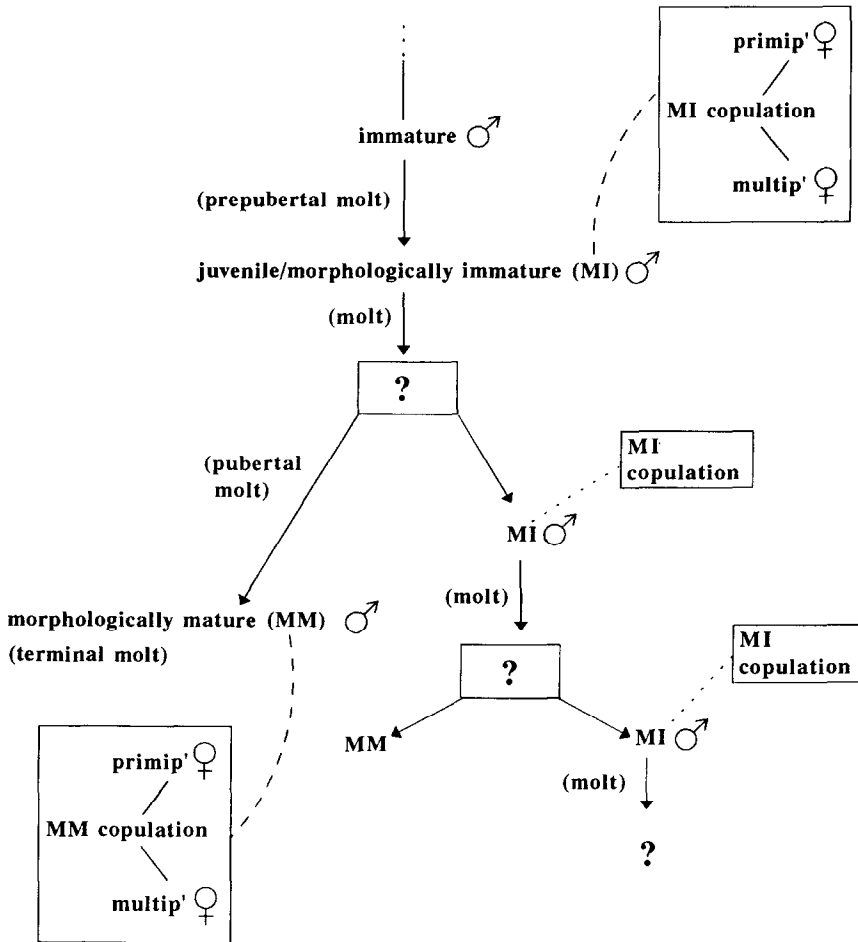
Fig. 2. Schematic illustrating reproductive pathways in male snow crab, *Chionoecetes opilio*; ?'s indicate decision points relating to growth and reproductive status.

usually retain the female until new eggs are extruded, 6 to 24 h after copulation (Claxton et al., 1994). Virtually all mature females sampled at-sea in the northwest Atlantic and Bering Sea (R.W. Elner, pers. obs.) have grasping marks as a result of primiparous and/or multiparous mating (see schematics, Figs. 1 and 2).

Brachyurans, in general, and snow crab, in particular, afford opportunities for gaining broad insight into reproductive processes and strategies. Snow crab are good candidates for laboratory and field studies because of their large size, longevity, international distribution and availability from commercial fisheries. In addition, copulatory transfer of spermatozoa, spermatophore storage and external eggs facilitate experimental manipulation. Here we review recent advances in

snow crab reproduction and linkages between physiology, behavior and population ecology. Further, we expand on hypotheses on reproductive strategy, questions and experimentation suggested in Elner & Beninger (1992).

2. Central role of the spermatheca

2.1. Spermatophore partitioning

Snow crab, as other Majidae, exhibit a complex reproductive biology which includes the possibilities of either immediate (Type I) fertilization at copulation or storage of spermatophores for subsequent autonomous (Type II) fertilization (Fig. 1). Type I and Type II options are established by structural and physiological processes in both the male and female (Beninger et al., 1988, 1991, 1993). Mature spermatozoa are packaged into pellicle-bounded spermatophores (Beninger et al., 1988). Some spermatophores rupture at copulation, while others persist and are stored in the spermathecae. Structural differences in the spermatophore wall (e.g. pellicle thickness or degree of folding) have been postulated to impart differential resistance to dehiscence which partitions the spermatophores into the two categories. Spermatophores from the vas deferens require both mechanical stress and seawater for dehiscence (reflecting conditions at copulation), whereas the initially resistant spermatophores require only seawater addition for dehiscence after storage in the spermatheca (reflecting the conditions of fertilization using stored sperm). Characteristics of spermathecal storage that alter the properties of the spermatophore pellicle are unknown, but erosion due to accumulated products from anaerobic bacterial metabolism is a possible mechanism.

Fertilization success for spermatophores stored in the spermatheca appears to be dependant on their position and age. Probability of fertilization will be greatest for those stored in the ventralmost region, since spermatozoa are non-motile and this is the trajectory of egg extrusion. Also, given the mechanics of copulation, ventralmost spermatophores will be the most recent and, likely, most viable; this may also favour last-male sperm precedence. Indeed, spermatophores stored in the dorsalmost region of the spermatheca are often characterised by degenerate contents (Beninger et al., 1993).

2.2. Performance and maintenance of stored spermatophores

A male may be genetically investing in both the present and future clutches should subsequent fertilization be performed in the absence of males. Thus, egg clutch fertilization capacity and viability of stored sperm cells over their, probable, limited "shelf life" is a concern for both sexes. However, there appear uncertainties over the quantity and longevity of sperm stored by *Chionoecetes* spp. Paul (1984) determined that if males are available, most multiparous female Tanner crab will copulate prior to egg extrusion. In the absence of males, viable

clutches from stored sperm were produced by 97 and 71% of females for 1 and 2 yr, respectively. Although mean numbers of stored sperm appeared adequate to fertilize up to three successive clutches, no female was able to fertilize a third clutch. In comparison, Paul & Paul (1992) found that a single insemination at the maturity molt in female Tanner crab did not typically provide sufficient stored sperm to fertilize a subsequent clutch. Clutches produced with stored sperm were markedly reduced compared to those from females with access to males (but see also, Paul, 1984); however, the maturity status of the males was incompletely documented, and primiparous females had to be used in order to ensure the unique insemination. Subsequently, for snow crab, Sainte-Marie & Lovrich (1994) found that a single mating episode, with either a MI or MM male and a primiparous female, involved multiple copulation and produced sufficient sperm for, in theory, at least four successive clutches; although females were argued to survive only long enough to hatch two clutches (Sainte-Marie, 1993).

Unsubstantiated wisdom is that stored spermatozoa require metabolic subsidy from secretions of the spermatheca (Adiyodi & Adiyodi, 1975). However, low metabolic needs of stored spermatozoa in a 0–5°C environment may well be supplied from the matrix within the spermatophore. Spermatozoa have exclusive access to metabolites in the matrix, and, therefore, avoid competition for such labile resources with microbial fauna of the spermatheca. In addition, should metabolic by-products of the fauna be toxic to spermatozoa, the spermatophore pellicle may present a protective barrier. Another aspect of maintaining spermatozoon integrity may be indirectly met by the spermathecal secretions: protection from opportunistic microbes introduced either at copulation or from the external environment via the gonopore (Beninger et al., 1993). Evidence to-date suggests that protection is accomplished via the incubation of an endogenous, homogeneous bacterial population which excludes potentially harmful microbes (by either competition or accumulation of metabolites). Given limited oxygen within the spermathecal matrix, metabolites of the endogenous bacteria probably include small organic molecules such as lactic acid which may lower the pH of the medium and further serve to exclude opportunistic microbes. In addition, these same substances could be responsible for "conditioning" the spermatophore pellicle, corresponding to the observed dehiscence facilitation of spermatheca-stored spermatophores (Beninger et al., 1993). The male may also participate in protection of his transferred spermatophores by contributing acid mucopolysaccharides, probably produced in the first gonopods. These substances possess bacteriostatic properties (Sasikala & Subramonian, 1987) and are invariably found in the vagina (a non-secreting region) of post-copulated females (Beninger et al., 1993) similar to the situation observed for the mammalian vagina (Hammersen, 1976).

2.3. Advantages of sperm storage

Storage of spermatozoa represents an energetic and physiological investment for both sexes; however, advantages of such storage have yet to be fully explored.

Intuitively, such a strategy would be expected in species which mate only once, yet multiparous mating is common in the snow crab reproductive repertoire. Three advantages have been proposed to accrue from sperm storage in this species: (1) reduction of deleterious effects from grasping encounters with males, (2) "insurance" against total egg clutch loss between matings and (3) maintenance of egg production in the absence of males. First, physical damage to the female which commonly accompanies the highly competitive multiparous mating (Elner & Beninger, 1992) would be reduced if she were able to rely on stored spermatophores for some clutches. Secondly, spermatozoon storage would allow the female to replace a clutch compromised by either predation or parasitism between matings (Fig. 1). Although preliminary experimental data support the latter hypothesis (Elner & Beninger, 1992; Beninger et al., 1993), more studies on "normal" reproductive cycles are needed. The third advantage would be the possibility of using stored spermatophores when there is a dearth of males; there are substantial fluctuations in numbers and morphs of males, as a natural phenomenon (Elner & Bailey, 1986; Comeau & Conan, 1992; Sainte-Marie, 1993).

2.4. Sperm competition

Biological merits of sperm storage, as well as the attendant complexities of sperm competition among successive males, may have first been alluded to by Sir John Harington (1561–1612). Sperm storage and multiple mating by female snow crab provide possibilities for sperm competition. Advantages of fertilization using stored sperm are nullified if the female enters into a mating embrace with a male; a new, intact clutch can be produced, any physical damage will occur regardless of whose sperm she uses, and fresh sperm are probably more viable than stored sperm. Histological observations suggest that in the majid *Inachus phalangium*, male seminal plasma seals in spermatophores from previous copulations, thus ensuring last-male precedence (Diesel, 1991). Such a phenomenon is not seen in snow crab; however, the anatomy of the male first gonopod in snow crab appears consistent with a curetting function to remove spermathecal contents before deposition of fresh spermatophores (Beninger et al., 1991). Although the process has not been observed, both stored and recently deposited sperm might be removed by curetting. Removal of the latter could occur after transfer of a female between competing males. Inter-male competition for females is intense during both types of mating (R.W. Elner, pers. obs.; Sainte-Marie & Hazel, 1992; Claxton et al., 1994). The available interval for curetting is necessarily short given that the female is only receptive to copulation between either molting or egg hatching in primi- and multi-parous mating, respectively, and egg extrusion.   In crab species where curetting is possible, post-copulatory mate guarding should be expected to extend until egg extrusion, or the female is otherwise unreceptive. Claxton et al. (1994) found the former to be the case for most MM, but not MI, male snow crab in multiparous copulations observed in aquaria. In other Brachyura, such as Cancridae, a vaginal sperm plug formed from male ejaculate appears to protect the male investment (Diesel, 1991) and females are released prior to egg

extrusion (Elner et al., 1985). Here curetting, but apparently not multiple copulation, may be prohibited due to the plug. Thus, in Jonah crab, *Cancer borealis*, the tips of the male's first gonopods are smooth and straight (R.W. Elner & J. Stanley, unpubl. obs.) in contrast to the recurved tips and apical setae, seemingly adapted for spermatophore removal, seen in snow crab. We hypothesize that a similar pattern will be repeated throughout the Brachyura, with males in species characterized by sperm plugs having smooth, straight first gonopod tips and apical processes being indicative of species demonstrating spermatophore removal.

Diesel (1991) reviewed mechanisms by which brachyurans might ensure last-male precedence in the event of sperm competition. However, sperm competition in the Brachyura has been only inferred from anatomical disposition. Rigorous controlled mating experiments with either sterile males or genetic markers, as performed with insects (Parker, 1970), are required. Koga et al. (1993) used irradiation to sterilize male sand-bubbler crab, *Scopimera globosa*, and determined that the last male to copulate fertilized over 90% of the eggs. The possibility that rival sperm displacement or removal is similarly incomplete in snow crab, resulting in differential male success rates and multiple paternity cannot be ignored.

3. Reproductive strategies

3.1. Questions of fitness

Fitness, for individual crab may be gauged in terms of Lifetime Reproductive Success (LRS) (Clutton-Brock, 1988). A primary component of LRS is fecundity: thus, for females, the most appropriate strategy should tend to maximise total lifetime number of eggs hatched. In comparison, males should strive to maximise total lifetime number of eggs fertilized. Assessing LRS components for male snow crab is exceedingly complex, given intricate trade-offs exist between growth, size, morphometric maturity status and reproductive opportunity. Further, the outcome of a copulatory episode depends not only on the size and reproductive status of both partners but also subsequent events such as sperm competition and/or removal and egg loss. While forecasting consequences of the former events appears possible, the vagaries of sperm and egg loss are less predictable. Also, for Crustacea in general, a lack of economical, reliable aging techniques for snow crab hinder estimates of both survival and the number of copulatory events in an individuals lifetime. Nevertheless, lifetime fecundity estimates have been attempted for female snow crab based on radioisotopic techniques suggesting maximum longevity after terminal molt is between 4 and 5 yr (Sainte-Marie, 1993).

In Crustacea, where eggs are carried externally and readily quantified, indices of egg production are used to assess both population productivity and individual fitness. However, factors such as differential egg loss, egg quality, variation in development time, the primi- or multi-parous state of the female and, possibly,

spermatophore source may compromise both the utility of the index and comparisons of fecundity data (Elner & Gass, 1984). In Tanner crab at least, stored sperm may yield reduced clutch size (Paul, 1984; Paul & Paul, 1992). Numerous studies on snow crab fecundity (Haynes et al., 1976; Thompson, 1979; Elner & Gass, 1984; Davidson et al., 1985; Sainte-Marie, 1993) have included comparisons between different populations. Davidson et al. (1985) found a high correlation between female CW and number of eggs carried and significant variations in fecundity between four fishing areas of Atlantic Canada (but see Elner & Gass, 1984). The results supported Haynes et al. (1976) in suggesting that Atlantic snow crab have a relatively higher fecundity than conspecifics from the Bering Sea. Nevertheless, all fecundity comparisons to date have either neglected (Davidson et al., 1985) or been unable to standardise (Sainte-Marie, 1993) the various factors known to effect number of eggs extruded and subsequent numbers actually hatched. Somerton & Meyers (1983) demonstrated that primiparous female Tanner crab from the Bering Sea are ≈70% as fecund as multiparous females of the same CW. Subsequently, Sainte-Marie (1993) determined that mean diameter of eggs and mean number of eggs per brood for primiparous snow crab from the Gulf of Saint Lawrence were 1.4–2.7% larger and 16.4–22.7% fewer, respectively, than those for multiparous females. Reduced primiparous fecundity may be due to the energetic cost of somatic growth following ecdysis and/or primiparous females having a smaller ovary volume within their ex-oskeleton at the premolt size.

Snow crab can extrude up to ≈128000 eggs (Elner & Robichaud, 1983). However, number of eggs carried has been reported to decrease progressively by ≈50% from time of extrusion to hatching (Elner & Beninger, 1982); presumably the consequences of predation, non-fertilization, abrasion and developmental failure. Egg loss appears to be proportionately greater for larger, potentially more fecund, females (Elner & Gass, 1984). Monitoring of population fecundity is complicated by the ability of females to extrude unfertilized egg clutches that resemble viable clutches and persist for several weeks before rotting away. In addition, reports of multiparous female snow crab with aged carapaces from Atlantic Canada (Elner & Robichaud, 1986; Saint-Marie, 1993) and the Bering Sea (Incze et al., 1987; R.W. Elner, pers. obs.) being either barren or carrying vestigial broods is suggestive of a reproductive "senility" phenomenon.

There are uncertainties over duration of the reproductive cycle in female snow crab. Originally, both primiparous and multiparous females were assumed to have a 12-month cycle between egg extrusion and hatching because of annual synchrony in these events (Watson, 1969; Adams, 1979). However, the notion became confused as sampling in the Sea of Japan and Atlantic revealed snow crab with eggs in a range of developmental stages, suggesting that primiparous females carry eggs for 18 months whereas multiparous females carry for 12 months (Sinoda, 1970; Elner & Beninger, 1992). Recently, Mallet et al. (1993) and Saint-Marie (1993) assessed gonad and egg development rates for female snow crab sampled from the Gulf of Saint Lawrence over 12- and 21-month periods, respectively. Saint-Marie (1993) determined that ovarian and egg development

periods were phased, with time between egg extrusion and hatching being ≈27 months for primiparous females and 24 months for multiparous females. Mallet et al. (1993) found a similar pattern but estimated a 24 month egg development time for both female types; however, they postulated that egg development could be reduced to 12 months if brooding females were able to remain in shallow, warmer water. Hatching of snow crab eggs appears to be triggered by phytoplankton (Starr et al., 1994), posing another variable in estimating development time. Resolution of fecundity issues will require long-term holding and experimental studies on the number of clutches a female can produce, the effect of utilizing either stored or fresh sperm plus the morphometric maturity status and size of the male donor.

3.2. Defining maturity

Fisheries managers set regulations to ensure most individuals have opportunity to reproduce prior to harvesting. Accordingly, determination of size at maturity for male and female snow crab has been a primary objective since the inception of the Japanese fishery in the 1940s, and the Canadian Atlantic and Bering Sea fisheries in the 1960s (Sinoda, 1970; Watson, 1970; Otto, 1982).

Size of maturity for female crab can be conveniently determined by the presence of extruded eggs. Based on abdomen width, ovary condition and the presence of eggs, Watson (1970) determined that 50% of snow crab females from the Gulf of Saint Lawrence were mature at 50 mm CW, with all females being mature above 60 mm CW. Other studies on Atlantic snow crab are in close agreement (Elner & Robichaud, 1983). However, the occurrence of females up to 95 mm CW casts doubt on one or more assumptions on size at maturity, growth increment and terminal molt. Given all females above 60 mm CW are presumed mature, in terminal molt, and mean growth is 14.8%, then females should attain a maximum size no larger than 69 mm CW (Elner & Robichaud, 1983). The lack of experimental evidence underlying the "fact" that female snow crab enter a terminal molt to maturity is discussed by Conan et al. (1990); nevertheless, only Ito & Kobayashi (1967) have reported a mature female snow crab undergoing ecdysis (but see also, Hooper, 1986).

Watson (1970) reported mature male snow crab as small as 51 mm CW, with 50% maturity at ≈57 mm CW and 100% maturity above 72 mm CW. Determinations were made on the basis of chela allometry and vas deferens condition and were similar to those for previous Canadian and Japanese studies. Given findings on size at maturity, mating observations and economic criteria, a minimum legal size of 95 mm CW has been enforced in the Canadian snow crab fishery since 1973. The intention of the size limit was to base the fishery exclusively on male snow crab that were fully mature and growing (Elner & Bailey, 1986). Mature males were estimated to have 1–4 yr to mate before molting to harvestable size (Elner & Robichaud, 1983). Thus, egg production, and, hence, recruitment, in the various stocks was presumed inviolate to fishing pressure. Although subsequent recruitment patterns proved erratic, continued

high incidence of females carrying eggs have reinforced the premise that the fishery does not impact egg production (Bailey & Elner, 1986; Ennis et al., 1990).

Notwithstanding data in Somerton (1981) and Coulombe (1983) showing MI males above 95 mm CW, it was not until O'Halloran (1985) and Conan & Comeau (1986) that the biological basis to the minimum legal size was challenged. Conan & Comeau (1986) not only showed that the puberty molt to morphometric maturity could occur from 60–120 mm CW but also argued it to be a terminal molt. Further, they proposed, on the basis of aquarium experiments, that only MM males above 96 mm CW could mate effectively with multiparous females (up to 40% of males above 95 mm collected by trawling in the Gulf of Saint Lawrence were determined to be MI). Vigorous debate on reproductive performance and terminal molt has ensued (Donaldson & Johnson, 1988; Ennis et al., 1988, 1990; Jamieson & McKone, 1988). While evidence for male terminal molt appears convincing for snow crab in the Atlantic (Cormier et al., 1992; Saint-Marie & Hazel, 1992) and the concept is now accepted for Japan Sea stocks (Yamasaki & Kuwahara, 1991) resolution is still pending for the Bering Sea (A.J. Paul, B.G. Stevens, pers. comm.).

Much controversy has centred around the definition of male sexual maturity (Donaldson & Johnson 1988; Conan et al., 1988; Ennis et al. 1989). Elner & Beninger (1989) proposed that functional maturity should be assessed as the ability to copulate and transmit ejaculate, as a result of which fertilized eggs are extruded. Also important are roles of morphological, behavioral and physiological sub-components of functional maturity in both sexes; these do not necessarily occur synchronously (Conan et al., 1990). Stevens et al. (1993) from observations of grasping pairs of Tanner crab in the Bering Sea, argued that attainment of morphometric maturity is a prerequisite for functional maturity, defined be-haviorally, as the ability to grasp and mate competitively in wild populations. However, Stevens et al. (1993) used the term functional maturity synonymously with sexual maturity despite not having determined whether copulation had occurred. Given ambiguities, it may be appropriate to introduce the term "Full Sexual Maturity" (FSM) for instances where functional maturity, including all subcomponents, have been ascertained. Definitions in Conan et al. (1990) and Comeau & Conan (1992) for immature, juvenile and morphometrically mature male and female snow crab, based on allometry of secondary sexual features and gonad development, appear useful preliminary standards.

3.3. Expressing maturity

Snow crab in the Gulf of Saint Lawrence are spatially segregated according to maturity and sex (Coulombe et al., 1985; Conan et al., 1992; Sainte-Marie & Hazel, 1992). Similarly, primiparous and multiparous mating is spatially and temporally distinct (Ennis et al., 1988; Sainte-Marie & Hazel, 1992). Conan et al. (1992) discuss evidence for breeding migrations and suggest that the Bonne Bay, Newfoundland, movements are a result of weaker males being displaced towards shallower water during the pair formation process (but see Ennis et al., 1990).

There is strong competition between males on the primiparous (Sainte-Marie & Hazel, 1992) and multiparous (Conan et al., 1992) mating sites discovered to date. Stevens et al. (1993) and Stevens et al. (1994) reported on high density mating aggregations of Tanner crab near Kodiak, Alaska. Aggregations were mainly comprised of multiparous females with mating pairs on the periphery. Primiparous mating was more typically by isolated pairs in shallower water. Stevens et al. (1994) suggested that similar aggregation behavior is likely for snow crab and reviewed the implications of such strategies, including the possibility of female mating pheromones. However, observations on male snow crab paired with either other males or immature, sterile females (Sainte-Marie & Hazel, 1992) and the common occurrence of hybridized *Chionoecetes* spp. in the Bering Sea (R.W. Elner, pers. obs.) tend to confound the pheromone hypothesis.

Experimental (Claxton et al., 1994) and field (Conan et al., 1992) evidence suggest that males are locked in a mating hierarchy, according to morphometric status, shell age and size. Nevertheless, behavior is sufficiently plastic to allow any male with spermatophores, regardless of morphology and size, to take advantage of reproductive opportunities. Large MM males enjoy the highest reproductive success, followed by small MM males, large MI males and small MI males.

Reproductive opportunities of MI males should be viewed in context with population dynamics as their success rate will vary as proportions of primiparous to multiparous females and MI to MM males in the population change over time. There appears a pattern within the either chronic instability (Bailey & Elner, 1986) or cycles (Conan et al., 1992) exhibited by fished snow crab stocks, also common to non-exploited populations (Waiwood & Elner, 1983) (Fig. 3). The pattern is particularly evident in changes in relative abundance and proportions of MI and MM males in the Bonne Bay, Newfoundland, mating population during the mid-1980s to early 1990s (Ennis et al., 1990; Conan et al., 1992). Virgin stocks can be characterized as "stagnant", with low intrinsic rates of growth, and dominated by old-shelled crab, MM males and multiparous females. Recruitment to legal size was so poor off eastern Cape Breton in the early 1980s that fishing resulted in a relic population; most females were either barren or nearing reproductive "senility", with a low incidence of stored spermatophores (Elner & Robichaud, 1986; Beninger et al., 1988). However, eventually the reduction of accumulated virgin biomass reverses with a dramatic surge in juvenile recruitment. During the ensuing "dynamic" phase, stocks are dominated by new-shelled, growing crab with increasing proportions of MI males and primiparous females (Conan & Comeau, 1992). Eventually, as the recruitment wave diminishes, the population enters a "maturing" phase and the relative proportions of MI to MM males and primi- to multi-parous females start to decline. If the majority of crabs in the population enter terminal molt, overall growth slows and the population may be considered in a "climax" phase. In the absence of juvenile recruitment and growth, the population will again become "stagnant". While mechanisms for such boom-and-bust population dynamics in snow crab are uncertain, the consequences are more discernable. We surmise that egg production in the maturing and climax phases will be principally due to MM males and multiparous females (Fig. 3). In the stagnant phase there may be insufficient males to fertilize
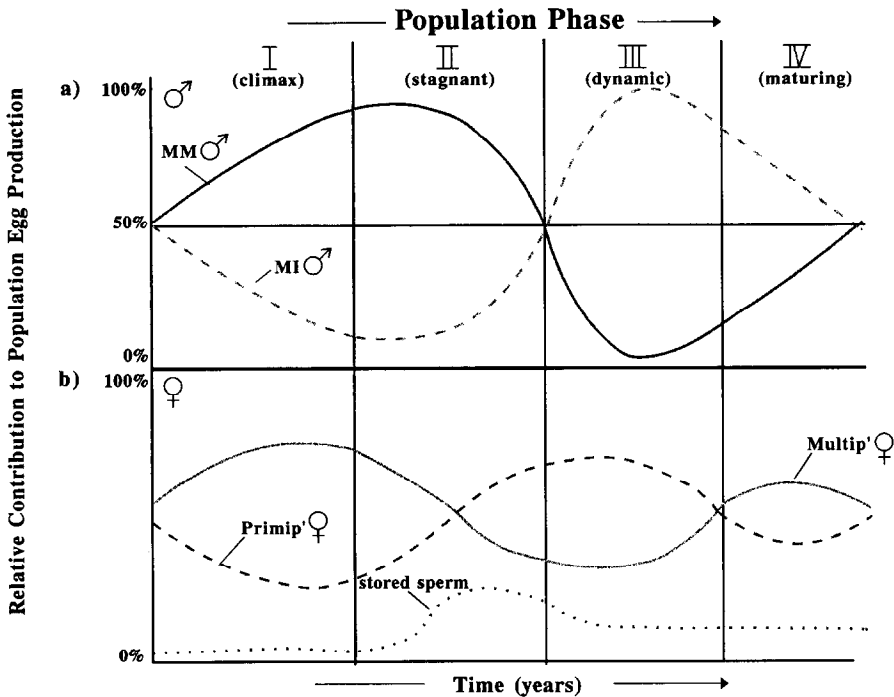
Fig. 3. Schematic postulating relative contributions of, (a) MI and MM males and (b) primiparous and multiparous females to snow crab, *Chionoecetes opilio*, egg production at four population phases (Climax, Stagnant, Dynamic, Maturing); note: in (b), relative contribution of stored sperm (....) applies as a sub-component of multiparous females.

all females and, consequently, a high reliance on stored spermatophores until even that source is exhausted. The dynamic phase necessarily provides favourable opportunity for MI males, in the absence of MM competitors, to fertilize both primiparous and available multiparous females (Ennis et al., 1990).

Assuming non-equality in egg production between primi- and multi-parous females, and possible variations induced by male partner size, morphometric-status and brooding period, total egg production in a snow crab stock may vary according to population phase. Computer simulations by Mohn (1988) of a hypothetical crab population revealed that density dependence and annual variation in reproduction could result in a strong periodicity in abundance. Similarly, a density-dependent fecundity mechanism coupled to environmental forcing has been postulated as responsible for driving a 10-yr cycle in the Dungeness crab, *Cancer magister*, fishery of northern California (Botsford, 1986).

3.4. Mechanisms of maturity

Delayed FSM in male snow crab appears associated with attaining a large body size necessary to retain females in a copulatory embrace in competition against

other males. However, increased size is attained, proportionately, at cost of time in the reproductively disadvantaged MI state and risk of mortality, evidently particularly high at ecdysis (Waiwood & Elner, 1982; Robichaud et al., 1991). These costs are counterbalanced by the finite duration of carapace integrity once terminal molt is attained (Mallet et al., 1993). Yamasaki et al. (1992) estimated that survival rates of male snow crab within a year and more than 1 yr after terminal molt were less than 0.35–0.43 and 0.58–0.71 per annum, respectively.

A key question to the maturity:growth dilemma is identifying the "trigger" that induces MI males to become MM. We offer two, mutually exclusive, hypotheses based on reproductive success at the MI state. Both hypotheses are amenable to experimental testing and assume linkages between the reproductive system and the physiological mechanisms determining growth and morphological-status:

(1) MI copulatory failure triggers MM

The hypothesis advocates that MI males that successfully copulate will opt to remain in the MI state and continue growth after the next molt. In contrast, MI males that fail to copulate will become MM at the next molt. The rationale is that MI males that are copulating are achieving genetic input in a MI state and should risk renewing their carapace and growing to further their reproductive success. MI males that fail to copulate are in a reproductively unfavourable environment and would perhaps be more successful in the MM state. The hypothesized mechanism requires a sub-mechanism to trigger eventual attainment of MM status given that copulatory success is likely to increase with size and MI males are not found above ≈120 mm CW (Comeau & Conan, 1992).

(2) MI copulatory success triggers MM

The antithesis to the above is that MI males that do copulate will become MM at the next molt while MI males that are unsuccessful will continue as MI for at least one more molt. Here the rationale is that reproductively successful MI males are already in a favourable environment and should become MM rapidly rather than risk mortality by continuing to molt. In contrast, unsuccessful MI males are in a competitive reproductive environment and should continue to grow before attaining MM status. Again, a sub-mechanism is required to trigger eventual MM status in unsuccessful MI males above a threshold size.

A third hypothesis, less amenable to testing, is genetic predetermination of terminal size (Bailey & Elner, 1989). Here, a long-term fishery could promote artificial selection in favour of males attaining terminal molt below the legal minimum size limit. While there is no evidence, to-date, of either decreased reproductive output or more males ceasing growth below the minimum legal size, there is ongoing concern over the efficacy of fishing regulations as a result of research findings into reproduction and growth (Elner & Robichaud, 1983; Elner & Beninger, 1989; Sainte-Marie, 1993). Safran et al. (1990) advocated intro-duction of a minimum chela size, as opposed to CW, regulation to allow harvesting of accumulated reservoirs of "pygmy", MM males under 95 mm CW on fishing grounds and protect MI males. However, trial use of a chela gauge in a

Canadian fishery was unsuccessful due to market constraints (Tremblay et al., 1992). Other hypotheses on possible mechanisms controlling male molt to morphometric maturity include either density dependent influences, such as the relative abundance of males and food, or density independent factors, such as temperature.

Selective pressures that have resulted in sexual dimorphism in male snow crab are enigmatic. Unlike many other brachyurans, the shift is subtle and male morphs are not readily distinguishable "by eye"; thus, agonistic display, based on chela size cues, may not be a factor in deciding either inter-male competion or mate choice in snow crab (but see Stevens et al., 1993). Conan & Comeau (1986) suggested that differentiation of the chelae at terminal molt is necessary for clasping and maintaining a female in a mating embrace. Biomechanical analyses of chelae revealed that maximum output force developed by a MM male was several fold greater than that for a MI male of the same CW (Claxton et al., 1994). However, the chela closer muscle, its motor patterns and excitatory neuromuscular synapses are specialized for slow, sustained activity, such as precopulatory clasping, in both MI and MM male snow crab (Govind et al., 1992; Claxton et al., 1994). Overall, observed mechanical differences do not account for why MI males do not readily retain females in a mating embrace.

Modulation of synaptic activity at both the periphery and in the CNS by circulating amines and peptides has been invoked as a neurohormonal mechanism to explain why MI males do not readily retain receptive females (Comeau & Conan, 1992). Claxton et al. (1994) proposed an experiment involving hormonal modification to test the neurohormonal hypothesis; further, they suggested that female choice or inter-male competition during the precopulatory phase has produced strong selective forces for augmented chela size and strength, as observed in MM males. Juvenile hormone, methyl farnesoate, was identified by Homola et al. (1991) in regulating not only chelal differentiation but also reproductive system status in male morphs of another majid, *Libinia emarginata*. Support for a similar trigger to precopulatory clasping in male snow crab comes from measurements revealing elevated methyl farnesoate levels in MM, as compared to MI, male snow crab from the northwest Atlantic and Bering Sea (H. Laufer, pers. communication).

4. Concluding remarks

Commercial interests have provided not only opportunity to routinely sample snow crab but also the prime impetus to explore, debate and revise snow crab biology. Arguably, snow crab and its congeners have become the most studied crabs, second only to American lobster, in the Brachyura, in scope of the research effort. We suggest that snow crab, on account of current understanding and because they display all three major mating pathways, can become an experimental model for the Brachyura.

Development of scientific knowledge on snow crab was largely dictated by the

needs of fisheries managers to establish regulations to protect stocks against overfishing. Biologists had little baseline information on *Chionoecetes* spp. and relied on preliminary observations on maturity, growth and reproduction plus general decapod biology in preparing their advice. However, what should have remained working hypotheses on reproduction and growth evolved into accepted truths (paradigms). Unfortunately, almost all the paradigms (male maturity and growth, reproductive pathways in females and egg brooding period) proved either false, incomplete or variable. Laboratory experiments and field observations should have been major tools in elucidating snow crab life history, growth and reproductive processes but misinterpretation of these findings retarded under-standing (Elner & Beninger, 1989; Conan et al., 1990). The paradigms were and are being challenged with difficulty only after fishery problems forced re-evalua-tion of the fundamental management premises. The controversy has not only produced fresh insight into snow crab but also debate over fundamental aspects of decapod biology.

Many problems, such as definition of maturity in snow crab may appear unique as they have not been encountered elsewhere. Nevertheless, other brachyuran species have not been subjected to the same intensity of debate and we suspect that more terminology, as well as perceptions on growth and reproduction, will likely be problematical on closer scrutiny. Laboratory and field studies of snow crab behavior have often yielded contradictory interpretations of snow crab reproduction (Watson, 1972; Conan et al., 1990; Conan et al., 1992; Ennis et al., 1990). However, given plasticity in crab behavior and the notion that reproductive success may be highly influenced by inter-male competition and female availabili-ty, it is not surprising that behavioral studies alone have not yielded definitive answers. Understanding snow crab reproduction and growth must necessarily be based on a multidisciplinary experimental approach, relating behavioral observa-tions to physiological mechanisms in a long-term population ecology context.

Acknowledgements

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