The Reproductive Biology of Snow Crab, *Chionoecetes opilio*: A Synthesis of Recent Contributions[1]

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SYNOPSIS. The existing literature concerning reproduction of snow crab (*Chionoecetes opilio*) is critically reviewed and discussed in the context of recent conceptual paradigms and ongoing research. The functional anatomy of the male and female reproductive systems is presented and interpreted in terms of the various mating pathways available to this species. Hypotheses to account for immediate and delayed fertilization are presented. The possible adaptive values of spermatophore storage and a novel mechanism for ensuring last male precedence are explored. In addition to critical gaps in our understanding of reproduction in snow crab and other brachyurans, ambiguities in current concepts and terminology are highlighted. Directions for future research which addresses central problems of snow crab reproductive biology are suggested.

INTRODUCTION

Snow crab, *Chionoecetes opilio* (Brachyura, Majidae), are common on deep mud bottoms in the Northwest Atlantic, the Bering Sea and Sea of Japan. The size and abundance of the species has made it a target for intensive commercial exploitation and, consequently, scientific scrutiny (Bailey and Elner, 1989). Over the past 10 years, appreciation of snow crab biology has changed markedly. In particular, there have been fundamental re-appraisals of reproduction and growth (see Conan *et al.,* 1990 for review). However, rather than clarifying snow crab life history and facilitating fisheries management, the implications of the

new insights remain both controversial and enigmatic (Elner and Beninger, 1989).

There is no single crab species whose reproduction is sufficiently well-understood to serve as a comprehensive model for crabs in general. Moreover, the fact that re-examination of the tenets of snow crab biology has revealed many discrepancies suggests that scrutiny of other species would also uncover problems. We suggest that snow crab, by virtue of ongoing research and its multiplicity of reproductive pathways common to the biology of a wide variety of crabs, could become a "model" for the Brachyura. Here we take a multidisciplinary approach to describing the reproductive system and fertilization in snow crab in an attempt to both provide the bigger picture, and add depth to the various individual studies. In doing so, we identify gaps in knowledge of snow crab reproduction. We hope that this review will serve to stimulate experimental studies to further understanding of reproduction in *C. opilio.*

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THE SYSTEMS

Male reproductive system

As is the rule for higher brachyurans, the internal reproductive system of male snow crab comprises paired testes, located above the stomach, with each testis joining into a vas deferens (Fig. 1A). Each vas deferens is divided into three functionally distinct regions (anterior, mid- and posterior) and leads into a small fleshy penis located externally at the base of the fifth pereiopod. The penes and their respective gonopods (modified first and second pleopods) are two complete insemination units. The first gonopod is tubulated and forms a canal for the transmission of seminal fluids from the penis into the spermatheca of the female. The shorter second gonopod is normally inserted within the first gonopod. Abdominal flexing at copulation causes piston-like movements of the second gonopod which drive seminal fluids down the canal (Hartnoll, 1969). The internal reproductive organs are well described for both *C. opilio* (Sapelkin and Fedoseev, 1981; Beninger *et al.*, 1988) and other crab species (*e.g., Callinectes sapidus* by Johnson, 1980). The structure and ultrastructure of mature spermatozoa and spermatophores of *C. opilio* have also been reported (Beninger *et al.*, 1988). In addition, a mechanism for spermatophore dehiscence and facilitation of spermatozoa devagination has been proposed, based on the hydration of the spermatophore upon contact with a medium diluted with seawater (Beninger *et al.*, 1988). A brief description of the first gonopod of a majid crab, *Inachus phalagium*, was presented by Diesel (1989). Recently, a detailed investigation of the external and internal anatomy of the first and second gonopods of *C. opilio* was made by Beninger *et al.* (1991). Both of the latter studies reported on rosette glands in the first gonopod and reasoned that the secretions contribute to the seminal fluids during copulation.

Criteria to distinguish reproductive capability and indices of size at maturity for male *C. opilio* are not well established (Somerton, 1981; Elner and Beninger, 1989). Watson (1970) made observations on gonad development, presence of spermatophores and chela allometry for male *C. opilio* from the Gulf of St. Lawrence. The smallest mature male (on the basis of gonad state and subtle morphometric differentiation of the chelae) out of a sample of 194 was 51 mm CW; all males above 72 mm CW appeared mature and 50% maturity was estimated at approximately 57 mm CW. Regional variability in size at maturity has been shown for male *C. opilio* from the Bering Sea, with overall 50% maturity (chela morphometrics) being estimated at 65 mm CW. Maturity estimates by both of these latter authors are influenced by their belief that males continue to molt after achieving maturity. However, recent evidence strongly indicates that for *C. opilio* of the Northwest Atlantic, at least, the pubertal molt (at which the chelae undergo a change in allometry) is a terminal molt (O'Halloran, 1985; Conan and Comeau, 1986; Conan *et al.*, 1990). Hence, the implications [as for other majid crabs, Hartnoll (1965)] are that males can cease growing over a wide size range, between approximately 50–150 mm CW, and that males without differentiated chelae are not fully "mature." Nonetheless, morphometrically immature males can have fully formed spermatophores in their vas deferens (Beninger *et al.*, 1988). Ramifications of the recent findings (Jamieson and McKone, 1988) and the terminology used to define maturity (Conan *et al.*, 1990; Elner and Beninger, 1989) are being debated.

Female reproductive system

The female reproductive system in *C. opilio* resembles that of other crabs, comprising a pair of ovaries and oviducts which lead to paired spermathecae or seminal receptacles. These in turn are linked to the external medium via a short vagina terminating in a gonopore (Fig. 1B). Although the histological picture is relatively complete for *Callinectes sapidus* (Johnson, 1980) and *C. opilio* (Beninger *et al.*, 1988; Beninger *et al.*, 1992), fundamental questions have yet to be answered on the functioning of the female reproductive system in general, and the spermatheca (Fig. 1C) in particular. Histological studies show that the inner lining of the spermatheca is a secretory epithelium (Johnson, 1980; Diesel, 1989; Beninger *et*
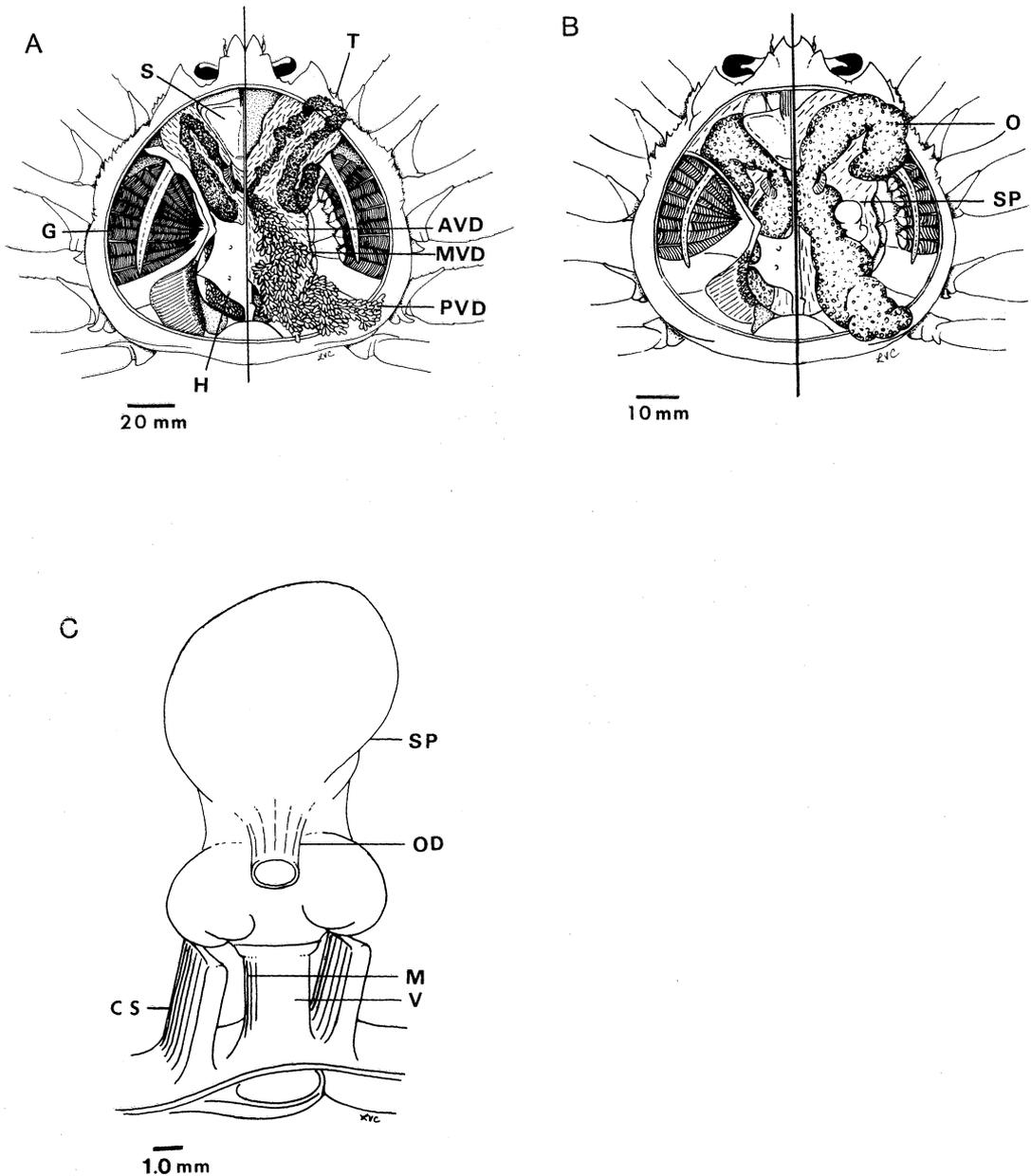
FIG. 1. Reproductive system in *Chionoecetes opilio*. A, B. Internal morphology of mature male and female. A. Dorsal view of male. Right side shown with heart and stomach removed. Anterior vas deferens (AVD), gills (G), heart (H), mid-vas deferens (MVD), stomach (S), testis (T), posterior vas deferens (PVD). B. Dorsal view of female. Right side shown with heart removed and spermatheca evident. Ovary (O), spermatheca (SP). C. External anatomy of spermatheca. Cuticular septum (CS), oblique muscles (M), attached to inner wall of vagina, sectioned oviduct (OD), concave (inner) wall of cuticular vagina (V). (Adapted from Beninger *et al.*, 1988.)

al., 1992); however, the chemical nature of the secretions is still being investigated. The secretory, and indeed squamous, nature of this epithelium is at variance with the pres- ence of either cilia (virtually unknown in the Arthropoda) or microvilli (which signify absorption) as suggested by Johnson (1980). A secretory epithelium appears also to be

incompatible with the mechanism of dehydration of the spermathecal matrix for spermatophore storage as proposed by Beninger *et al.* (1988). Ongoing histochemical and ultrastructural studies have demonstrated the presence of a dense, morphologically homogeneous population of bacteria, dominated by rods, inside the spermatheca of many females (Beninger *et al.,* 1992). We hypothesize that these bacteria are cultivated by secretions from the spermatheca lining, the end products of their metabolism serving to lower the pH in the spermathecal lumen. The system, somewhat analogous to the vagina in mammals, may act to inhibit attack by opportunistic bacteria on spermatophores retained in the spermatheca. An alternative, although not mutually exclusive hypothesis, is that the end products could be metabolized by the stored spermatozoa.

Female *C. opilio* are acknowledged to attain terminal molt status at maturity (Watson, 1970; but see Ito and Kobayashi [1967] and Hooper [1986] for exceptions). At terminal ecdysis the abdomen undergoes a large allometric shift in growth, relative to carapace size, which facilitates egg brooding (Hartnoll, 1969). The carapace sizes of pre- and post-puberal females overlap but the size range attained at terminal molt (approximately 47–95 mm CW) is less than that for males. In females, in contrast to males, reproductive capability can be readily ascertained from the presence of eggs under the abdomen.

The fecundity of *C. opilio* has been studied over most of its geographical range (see Elner and Robichaud, 1983 for review). Estimates of the number of eggs carried by females from the Northwest Atlantic range from approximately 12,000 to 128,000 (Elner and Robichaud, 1983) and are generally higher, for a given CW, than for conspecifics from the Bering Sea (Haynes *et al.,* 1976; Davidson *et al.,* 1985). Most workers have found significant relationships between fecundity and CW. However, total egg number is reported to decrease by approximately 50% between the time of extrusion and hatching (Brunel, 1962; Kon, 1974). Further, Kon (1974) demonstrated a progressive decline in both the intercept and slope of the fecundity : CW relationship through

the brooding period for females from the Japan Sea, suggesting that egg losses are proportionately greater for larger, more fecund, females. A similar differential loss rate is indicated for females from the Northwest Atlantic (Elner and Gass, 1984). Presumably eggs are lost due to factors such as predation, parasitism, abrasion and decay of unfertilized eggs. Free-living nematodes, *Oncholaimus* sp., and turbellarian, *Ectocotyla* sp., egg capsules are common in *C. opilio* broods from Cape Breton Island (Elner and Gass, 1984; Brattey *et al.,* 1985).

Variability in fecundity patterns may be partly attributable to a longer egg development period and relatively lower fecundity for primiparous, as compared to multiparous, females. Sampling of females off Cape Breton Island in November, 1983 revealed a mixture of newly oviposited and older eggs (Elner and Gass, 1984), suggesting that Atlantic *C. opilio* may be similar to conspecifics from the Japan Sea in having two spawning cycles. Ito (1967), Kon (1974, 1980) and Sinoda and Kobayashi (1982) determined that primiparous females from the Japan Sea require 18 mo to brood their eggs whereas multiparous females take only 12 mo. Furthermore, Atlantic snow crab females with hatching and freshly extruded eggs are most common from late April to June (Watson, 1969) during the multiparous mating period (Taylor *et al.,* 1985), whereas primiparous mating and egg extrusion occur from February to early March (Watson, 1970, 1972). Somerton and Meyers (1983) demonstrated that primiparous Tanner crab, *Chionoecetes bairdi,* from the Bering Sea are only approximately 70% as fecund as equivalent-sized multiparous females. Similar relationships between fecundity and primi- *vs.* multiparous spawners are suggested for *C. opilio* (Elner and Robichaud, 1983; Elner and Gass, 1984) but remain to be tested. Since primiparous females have recently molted and multiparous females do not molt, the lesser fecundity of primiparous individuals could be related to either the energetic cost of molting or their relatively smaller internal volume for ovarian tissue at the premolt size. These factors underscore the importance of distin-

guishing between primi- and multiparous females when reporting fecundity data.

Mating pathways

Copulations involving both soft-shelled primiparous females (Watson, 1970, 1972) and hard-shelled multiparous females (Taylor et al., 1985) have been observed, but male crabs can only copulate in the hard-shelled state (Hartnoll, 1969). Although male C. opilio attain a molt to morphometric maturity which involves acquisition of the secondary sexual characteristics of enlarged and modified chelae (probably facilitating prolonged grasping of the female during multiparous mating), males with morphometrically immature chelae may copulate with soft-shelled females (Conan et al., 1990) and some hard-shelled, multiparous females (Ennis et al., 1989). Primiparous copulation has only been observed in February and March (Watson, 1970, 1972) and is probably spatially and temporally separated from multiparous copulation in April and May (Taylor et al., 1985; Hooper, 1986).

The behavioral sequences of primiparous mating, in the laboratory, are described by Watson (1970, 1972). During the week-long precopulatory embrace, the hard-shelled, morphometrically mature male holds the female and drives away intruding males. Before a 45 min copulation period, the male assists the female in ecdysis. The male continues to embrace the female for approximately 8 hr after copulation. Egg extrusion usually occurs within 24 hr of mating. Watson (1972) also demonstrated that males can be polygamous and copulate at a relatively small size. A 98 mm CW male mated with six females in a 1-month period and successful mating occurred between a 61 mm CW male and a female which increased, after molting, from 64 mm to 74 mm CW. In examining the possibility that in areas of heavy fishing, males could be reduced to such low density that some females might not be fertilized immediately after molting to maturity, Watson (1972) noted that three females copulated successfully 27, 53 and 95 hr after ecdysis.

Although Watson (1972) reported that hard-shelled mature females were incapable of copulation, others speculated that such behaviour could occur. Hartnoll (1969) noted that females of the Majidae, specifically Hyas coarctatus, sometimes mate in the hard-shelled condition. Paul (1982) reported that 98% of multiparous female C. bairdi from off Kodiak, Alaska, had grasping marks from males as result of hard-shelled mating. Supporting evidence for re-mating in C. bairdi was provided by laboratory and field observations (Somerton, 1981; Adams, 1982). In a study of ontogenetic migration patterns, Somerton (1981, 1982) suggested that bipartite breeding occurs in C. opilio elongatus, C. tanneri and C. bairdi. Essentially, he proposed that mating occurs amongst two distinct life history groups: a) primiparous females and recently-mature males, and b) multiparous females and large mature males. Finally, definitive evidence for multiparous mating in Atlantic C. opilio came from observations of an annual spring breeding migration to shallow water in Bonne Bay, Newfoundland (Taylor et al., 1985; Conan and Comeau, 1986; Hooper, 1986). The multiparous mating process may last up to approximately 2 mo (Taylor et al., 1985; Hooper, 1986). During the precopulatory period the male clasps the ovigerous female near the base of the walking legs and carries her for several weeks. Male competition for females is intense and many females lose limbs in the process (Hooper, 1986; R. W. Elner, personal observations). Copulation occurs shortly after the female releases her clutch of larvae, and the pair separates soon afterwards. Egg extrusion presumably occurs shortly after copulation although the interval has not been reported in the literature. Ennis et al. (1988) suggest that the incidence of unfertilized clutches is low. Accounts in Hooper (1986) on multiparous females releasing larvae and then molting are perplexing given the consensus on female terminal molt to maturity. Although there are no published reports of multiparous mating outside of Bonne Bay, the patterns of grasping marks on most multiparous females captured in the Northwest Atlantic (R. W. Elner, unpublished data) indicate that the phenomenon is common. Males in multiparous pairs sampled by Taylor et al. (1985) and Hooper (1986) were

invariably larger than their partners and above the commercial minimum size of 95 mm CW. Conan and Comeau (1986) argued from their own observations that only morphometrically mature males larger than 95 mm CW could effectively mate with multiparous females; however, surveys in subsequent years at the same site indicate that smaller males increase participation in mating activity when competition from larger males is reduced (Ennis *et al.,* 1988, 1989; but see also Elner and Beninger, 1989). Moriyasu and Conan (1988) reported, on the basis of aquarium observations, that mating success increases with male CW, with 50% success at 80–84 mm CW, without competition, and 90–94 mm CW under competitive conditions.

Female *C. opilio,* without access to males, are able to fertilize their ova using spermatophores stored from the primiparous copulation at least one year earlier (Watson, 1970, 1972). However, information is lacking on the length of time stored sperm remains viable, the number of egg extrusions that can occur from a single mating and the relative occurrence of this reproductive pathway. Females of the majid *I. phalangium* can store sperm from successive copulations and one female kept isolated from males produced six successive broods (Diesel, 1986). Ninety-six of ninety-eight ovigerous female *C. opilio* collected from Cape Breton in November 1983 by Elner and Gass (1984) had stored spermatophores, suggesting that they would have been capable of extruding at least one further brood without remating. In contrast, only one out of 16 females (old-shell, see Ennis *et al.,* 1989) sampled from the same area in August 1984 had spermatophores (Beninger *et al.,* 1988). Similarly, Watson (1970) collected *C. opilio* females from the Gulf of St. Lawrence from May to September 1969 and found that all 25 mature females with new shells had stored spermatophores whereas only 37 of 46 mature females with old shells had them. None of nine immature females examined had spermatophores. Thus, there may be an inverse relationship between time since primiparous copulation and the incidence of spermatophore storage, perhaps indicating that

spermatophore storage is relatively less frequent at multiparous copulation.

Adams and Paul (1983) studied relationships between male parent size, the number of eggs produced and the number of sperm remaining after egg extrusion for *C. bairdi.* They found that all sizes of mature males examined produced an excess of sperm at copulation and that following egg extrusion 93% of females had enough stored sperm to fertilize additional egg clutches. Adams (1982), in documenting the reproductive behaviour of *C. bairdi,* observed that: 1) very small males grasped newly molted females and mated precociously without subsequent production of viable zygotes; and 2) primiparous females, which had been isolated from males, could extrude unfertilized eggs of the normal orange colour. However, the eggs produced by some unmated primiparous females were resorbed rather than extruded.

FERTILIZATION

The precise events leading to fertilization in *C. opilio* are presently uncertain, largely because they take place within the "black box" of the spermatheca. However, given the available observations on reproductive behaviour, morphology and physiology, likely scenarios can be hypothesized. Intuitively, spermatophores introduced at the primiparous mating are partitioned; one fraction bursts and fertilizes the initial egg batch and the second fraction remains intact and in storage within the spermatheca. The mechanism for such a partitioning remains unknown. Indeed, Watson (1970, 1972) did not observe whether or not the male's gonopods were actually inserted into the female's gonopores during primiparous copulation.

Observations by Watson (1970, 1972) on spermatophores issuing from the male gonopods indicate that the spermatophore transfer process is "leaky." Following from this, Beninger *et al.* (1988) argued that spermatophores are likely to come into contact with seawater during copulation and suggested that the greatly folded pellicle of the spermatophore inhibits premature rupturing by allowing rapid swelling due to osmosis or hydration. Further, Beninger *et al.*

(1988) determined that while some spermatophores, from the posterior vas deferens of morphometrically mature males, ruptured in less than one minute when exposed to seawater, others were still intact after 2 hr. Such differential resistance to bursting could be part of the mechanism by which spermatophores are partitioned into the two fractions. Recent testing (Beninger and Elner, in preparation) has shown that, while spermatophores from the PVD can be highly resistant to bursting, stored spermatophores from the spermatheca burst rapidly, with little swelling, when agitated in seawater. Thus, the susceptibility of spermatophores to rupture changes markedly upon storage. The latter observation appears adaptive in that stored spermatophores are not subject to the threat of premature bursting during copulation but, rather, must burst rapidly when the spermatheca is (presumably) flooded with seawater during egg extrusion without multiparous copulation. The mechanical trigger required for bursting is probably supplied by muscular contractions of the ventral region of the spermathecal wall (Beninger et al., 1988), which also serve to mix the ova and sperm together for fertilization prior to egg extrusion.

The extent to which fertilization from stored sperm contributes to reproductive output is unknown. Multiparous females observed in the Bonne Bay breeding migration are invariably paired with males (R. W. Elner, personal observations). Conceivably, multiparous females that do not participate in a breeding migration may fail to locate a mate and can rely on stored spermatophores. Alternatively, stored sperm may be used to fertilize a new clutch when the original clutch is lost. Kuris et al. (1991) found that egg predation by symbiotic nemerteans results in substantial reduction, even complete loss, of clutches in red king crab, *Paralithodes camtschatica* (for review of egg predators on brachyurans, see Kuris and Wickham, 1987). Egg loss appears to occur commonly in *C. opilio* and could be induced by factors such as parasitism (Brattey et al., 1985), predation, disease or insufficient vitelline reserves (Elner and Gass, 1984). Elner (unpublished) removed all the

eggs from an ovigerous female *C. opilio,* held in the laboratory in the absence of males, and noted that a new brood was extruded within 6 wk. Further experimentation on egg re-extrusion in the absence of males is underway.

Stored spermatophores appear unlikely to be utilized at multiparous mating. The recurved tip and arrangement of setae at the end of the first gonopod suggest that males may be capable of evacuating at least the ventral most (i.e., most recent) stored products from previous matings before depositing their own ejaculate (Beninger et al., 1991). If so, mixing and competition between sperm from rival males would be limited and only the last male to copulate before egg extrusion would achieve reproductive success. The pre-copulatory removal of spermathecal contents would constitute a previously unsuspected mechanism of reducing sperm competition which would not depend on last male precedence of "layered" ejaculate (Diesel, 1991). The multiparous mating system in *C. opilio* appears analogous to that described by Snedden (1990) for the crayfish *Orconectes rusticus* and arguments similar to Snedden's can be developed to account for intermale conflict after copulation (see also, Christy, 1987).

CONCLUSION

Our review presents recent progress as well as major gaps in understanding of the various mechanisms involved in snow crab reproduction. Currently, there is need for more precise data and experimentation on copulatory behaviour, spermatophore transfer, spermatophore storage, fertilization and subsequent egg extrusion. In all observations and testing we should accurately characterize the reproductive status of the crabs under investigation. Hitherto, key factors such as the morphometric maturity status of males and the primi-or-multiparous status of females has either been ignored entirely or possibly misinterpreted (Elner and Beninger, 1989). Similarly, to definitively assess reproductive success, egg extrusion must be observed and the fertility and size of the brood ascertained. As the complexity of reproductive events in *C. opi-*

lio has become evident so has the need for accurate sub-definitions of the term "maturity." Clearly, there are ambiguities with current terminology; for example, a male may possess fully-formed spermatophores, copulate successfully with some types of females under specific conditions and yet be termed either morphometrically immature or juvenile (Conan *et al.,* 1990; Paul and Paul, 1990). For males, at least, maturity has physiological, morphological, behavioral and ecological components; while individuals with only some of these components may have less potential to express their genes than "fully" mature males, they should nevertheless be considered "potentially" mature. A continuing question is the relative reproductive success of morphometrically mature *versus* morphometrically immature males and the reproductive status of the females they fertilize. To properly address this, it is important to identify the partners and success of males and females through the various life history stages. The success of morphometrically mature males relative to their size is also of interest given the high incidence of "pygmy" males in terminal molt status (Bailey and Elner, 1989; Safran *et al.,* 1990).

Much of the research and many of the problems on snow crab have been generated by the fisheries. A low incidence of barren mature females and a high incidence of females with stored spermatophores suggests that the population fecundity of *C. opilio* is being maintained at a high level (Elner and Robichaud, 1983; Elner and Gass, 1984; Ennis *et al.,* 1988). However, high egg production has not either translated into high recruitment levels into the fishery (Elner and Beninger, 1989) or ensured stock stability (Bailey and Elner, 1989). We recommend that comprehensive, sustained sampling schemes in tandem with multidisciplinary experimentation are now required to elucidate snow crab reproductive biology.

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