Fertilization of the second clutch of eggs of snow crab, *Chionoecetes opilio,* from females mated once or twice after their molt to maturity

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Females of the commercially important genus *Chionoecetes* (Brachyura: Majidae) copulate and extrude eggs for the first time soon after a terminal molt to maturity (Watson, 1972; Adams, 1982). Females preparing for the molt to maturity are termed "pubescent," those bearing a first clutch are "primiparous," and those bearing a second or subsequent clutch are "multiparous." Spermathecae allow females to store sperm that is not expended at spawning (Watson, 1970; Adams and Paul, 1983; Beninger et al., 1988).

The importance of sperm stored from the first mating to reproductive output is partially documented for the Tanner crab, *Chionoecetes bairdi* (Adams and Paul, 1983; Paul and Paul, 1992), but remains largely unknown for the snow crab, *Chionoecetes opilio* (Elner and Beninger, 1992). Watson (1970) observed that some female *C. opilio* hatched a clutch and then extruded a new clutch of fertilized eggs without remating. Assuming that copulation occurs only at the molt to maturity, he concluded that female *C. opilio* can produce more than one batch of fertile eggs from a single mating (also see Watson, 1972). Subsequently, field and laboratory studies have shown that multiparous females of *C. opilio* and of *C. bairdi* can, and often do, mate before extruding a new clutch (Adams, 1982; Paul, 1984; Taylor et al., 1985; Conan and Comeau, 1986; Hooper, 1986; Claxton et al., 1994; Moriyasu and Conan[1]). Because the female *C. opilio* that Watson observed spawning were of unknown reproductive history (i.e. number of matings and clutches), the conclusion that one mating is sufficient to produce more than one viable clutch is suspect and warrants further investigation.

In *C. bairdi*, the viability of stored sperm apparently decreases over time, and some multiparous females may fail to spawn or may extrude unfertilized eggs when isolated from males for more than one breeding season (Paul, 1984). Furthermore, in laboratory experiments with *C. bairdi*, Paul and Paul (1992) found that 10 out of 11 females did not receive enough sperm at the first mating to fertilize more than one clutch. These investigators suggested that this may also be the case for *C. opilio*. However, Sainte-Marie and Lovrich (1994) estimated that primiparous *C. opilio* usually have enough stored sperm to fertilize at least one additional clutch. Therefore, we compared the size of the second clutch and the proportion of divided (i.e. fertilized) eggs for female *C. opilio* mated only at the molt to maturity with those values obtained for females with access to males at a second spawning.

Materials and methods

Males and pubescent females were collected in Baie Sainte-Marguerite (ca. 50°06'N, 66°35'W), northwest Gulf of Saint Lawrence, from September through October 1991, and in March 1992. Carapace width (CW) of females and males, and right chela height (CH) of males, were measured to the nearest 0.1 mm as described in Sainte-Marie and Hazel (1992). Males >40 mm CW were classified on the basis of chela allometry into either of two sperm-producing forms (Comeau and Conan, 1992), designated adolescent or adult following terminology in Sainte-Marie et al. (in press). (Other investigators have used the terms "small-clawed," "morphometrically immature," or "juvenile" to designate adolescent males, and "large-clawed" or "morphometrically mature" to designate adult males.) Classification was initially done by visual comparison of individual male measurements with scatterplots of CH on CW for a large sample of males from the source site, and verified a posteriori by using a site-appropriate discriminant function from Sainte-Marie and Hazel (1992).

Crabs were segregated by sex in tanks of either 1,400 or 2,000 L with flowing seawater. The mean temperature of seawater over the year following the first mating of females was 1.5°C, and monthly

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[1] Moriyasu, M., and G. Y. Conan. 1988. Aquarium observation on mating behavior of snow crab, *Chionoecetes opilio*. Int. Counc. Explor. Sea C.M. (Council meeting) 1988/k:9, 14 p.

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means ranged from a low of 0.1°C in March 1992 to a high of 3.0°C in August 1992 (daily records: low of −0.3°C and high of 6.5°C). Photoperiod was controlled to correspond to natural light rhythms. Individual crabs were identified by a plastic tag tied around the basipodite of one of the fourth or fifth pereiopods. Crabs were fed frozen shrimp (*Pandalus borealis*) semiweekly. Beginning in January 1992, tanks were checked twice daily for molting individuals.

Less than 12 hours after molting to maturity, each female was placed in a 120-L tank that was either empty or contained one male. Male mates were hard-shelled adult crabs in either of three size categories, 40–60, 80–100, and 120–140 mm CW, or hard-shelled adolescent crabs of 80–100 mm CW. Actual size ranges were 48.6–59.8, 82–99.4, and 120.3–138.3 mm CW for adult males, and 80.1–99.8 mm CW for adolescent males. The female was left in the tank until either eggs were extruded or 24 hours had elapsed. The female was then allowed to harden her shell for 5–6 days in isolation and was monitored daily to detect delayed egg extrusion. Finally, the female was retagged and transferred to a communal holding tank for females. Males were used once only and then held in communal tanks for up to 14 months after mating, to determine whether they would moult.

Egg color of each primiparous female was monitored at least every 2–3 months in order to evaluate development of the clutch. About one month before the anticipated period of hatching, i.e. May to June 1993, females bearing ripe eggs were isolated in either 90- or 120-L tanks with flowing seawater. One hard-shelled adult male of 78.8–119.5 mm CW was introduced into the tanks of randomly selected females in each of two groups, representing those females that had initially mated either with adolescent (3 females remated) or with adult (17 females remated) males. The tanks were monitored once a day to detect the onset of hatching and, where appropriate, mating behavior.

Ten to 12 weeks after the second clutch was extruded, a sample of at least 25 eggs was taken at the base of each of the eight pleopods of 58 females. Pleopods on the right-hand side were assigned numbers 1 to 4, and those on the left-hand side were assigned numbers 5 to 8, from front to rear. During sampling, females did not shed or lose more than ≈50 eggs in excess of those removed by the observer. Samples of eggs from each pleopod were fixed and stained to reveal nuclear DNA by means of a technique adapted from Dubé et al. (1985) and Dufresne et al. (1988). Eggs were fixed for one hour in a solution of 97% glucamine-acetate (GA) buffer, 2% formaldehyde, and 1% Triton, and then rinsed in GA buffer. The GA buffer was composed of 250 mM N-methyl glucamine, 250 mM potassium gluconate, 50 mM Hepes, and 10 mM EGTA, adjusted to pH 7.4 with glacial acetic acid. Eggs were then stained for one hour in a solution of 0.5 µg Hoescht dye per mL of GA buffer and were then rinsed twice and preserved in GA buffer at 4°C. The numbers of divided and undivided eggs in each pleopod sample were determined by epifluorescent microscopy.

Females were examined to evaluate clutch size one week after eggs were sampled from second clutches. Female abdomens were indexed for repleteness with eggs on a scale of 0 (empty) to 4 (very full). The index of clutch size is similar to the more refined percent clutch statistic, where actual clutch size is rated as a percentage of the largest clutch a female decapod of a given size can hold (Blau, 1986). The egg repleteness index and the percent clutch statistic both correlate significantly with the actual number of eggs held by a female decapod (Shields et al., 1990; Sainte-Marie, unpubl. data).

Results and discussion

Females molted to maturity from 8 January to 12 April 1992 and ranged in size from 49.7 to 74.4 mm postmolt CW. Only females that survived until August 1993 were analyzed in this study. Overall mortality of females from time of maturity molt until August 1993 was 50.3% (of 155) but was unrelated to mating status (mated or unmated) or to the mate's identity (maturity, CW). Of the 11 adolescent males that were mated, eight molted 3–57 days ($\bar{x}$=30 d) after mating, one molted 384 days after mating, and two died within 14 months of mating. No adult male molted over the 14-month period, consistent with the hypothesis that adult males are in anecdysis (O'Halloran, 1985; Conan and Comeau, 1986).

Of the nine females that were initially unmated, only four extruded a first clutch (Table 1) four or more days after their molt to maturity. All of the 68 females that initially mated extruded a first clutch: 56 did so while in the presence of their mate and 12 extruded later, i.e. 1–5 days after separation from their mate. First clutches did not develop and hatch on the four females that were unmated and on the 12 females that were mated but slow to spawn. Sainte-Marie and Lovrich (1994) reported that delayed spawning occurred in *C. opilio* when few or no sperm were delivered to females at mating. These authors hypothesized that females can gauge the contents of their spermathecae and, when insufficiently inseminated, postpone extrusion in expectation of a more fecund mate. By comparison, only two females that extruded eggs while in the presence of their mate failed to hatch their first clutch. Clutches

Table 1

Mating and spawning history of female snow crab, *Chionoecetes opilio*, that were not paired with a male after their molt to maturity or that were paired with a male but lost their first clutch. Male mates were adolescent or adult. Median and range (in parentheses) for clutch size and percentage of divided eggs are given for the second clutch. Clutch size is based on a 0 (empty) to 4 (very full) scale for abdomen repleteness with eggs. Calculation of median clutch size includes females with no eggs (scored as 0). The percentage of divided eggs is followed by the number of clutches examined, in superscript.

Male after molt	Total number of females	Females with first clutch	Male at second spawning	Females with second clutch	Second clutch	
					Size	% Divided eggs
No	9	4	No	2	0.0 (0–3)	—
Adolescent	3	3	No	2	2.5 (1–4)	$0.0^{n=1}$
			Adult	1	2.0	$97.5^{n=1}$
Adult	11	11	No	6	1.0 (0–4)	$4.2\ (0–56.7)^{n=4}$

carried by the 18 unsuccessful primiparous females started to show signs of degradation about 2–4 months after spawning as many or all eggs changed from bright to pale orange and eventually became almost white, and clutches were sloughed or lost within 8–10 months of spawning. The relatively high, 20.6%, incidence of first clutch loss recorded for mated females may be a laboratory artifact resulting from the 24-hour time limit for mating and noncompetitive mating context.

We examined 516–1,769 eggs from each second clutch of six females that lost their first clutch and of 52 females that hatched their first clutch, for a combined total of 54,808 eggs. Divided eggs were at the 128- or 256-cell stage. In 24 out of 55 females that carried at least some divided eggs, the ratio of divided eggs to total number of eggs in the pleopod sample was not independent of pleopod position (χ^2 test, $P<0.05$). One female had 89.5–100% divided eggs on pleopods 1–7, but no egg was divided on pleopod 8. Eggs from this female were sampled a second time to confirm the observation. The heterogeneous distribution of divided eggs in some clutches was not expected and to our knowledge has not yet been documented. Most previous studies contain little or no information on methods for sampling and determining viability of eggs. The reason for the contagious distribution of divided eggs is unknown. Perhaps attachment of eggs to individual pleopods is orderly and follows an extrusion hierarchy, and sperm in the fertilization chamber is temporarily or permanently depleted during extrusion. Nevertheless, our finding underscores the importance of sampling eggs from throughout the clutch when assessing fertilization success. We estimated the overall proportion of divided eggs in a clutch as the mean of proportions of divided eggs on each of the eight pleopods.

Among females that lost their first clutch, 38.9% did not spawn a second time (Table 1), and the remainder extruded second clutches from February to March 1993. In the latter group, second clutches contained 0–56.7% divided eggs when females had no access to males or 97.5% divided eggs in the case of one female that was paired with a male at the second spawning (Table 1).

Most females that were initially mated with adult males and then hatched a first clutch of eggs produced a large second clutch with a high percentage of divided eggs without remating (Fig. 1; Table 2). Of the 34 successful primiparous females that mated only at the molt to maturity, only two (5.9%) did not spawn a second time, whereas two others produced second clutches with <60% divided eggs (Fig. 1). There was no significant difference in the size of the second clutch (Kruskal-Wallis test, H=4.60, P=0.10) or in the percentage of divided eggs in the second clutch (H=2.50, P=0.29) among groups of females mated only at the molt to maturity by adult males with CW's of 40–60 mm (median clutch size: 3.0, median percentage divided eggs: 88.9%, n=13), 80–100 mm (4.0, 96.0%, n=8), or 120–140 mm (3.0, 94.6%, n=8). These data are consistent with the number of sperm cells stored by female *Chionoecetes* after the first spawning being unrelated to male CW (Adams and Paul, 1983; Sainte-Marie and Lovrich, 1994). Similarly, our data, although limited, indicate that stored sperm from adolescent males also resulted in the production of a large second clutch containing a high proportion of divided eggs, and was as effective as stored sperm from adult males (Fig. 1; Table 2). Although virgin females mated with adolescent males store as many sperm as those mated with adult males, Sainte-Marie and Lovrich (1994) speculated that the longevity of adolescent sperm might be less than that of adult sperm because of a higher sperm-cell to seminal-plasma ratio in ejaculate. However, this was not apparent after one year of storage.

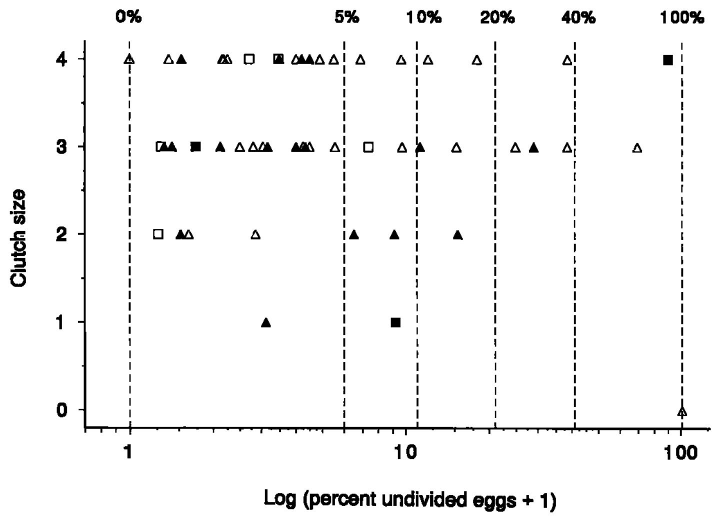

Figure 1

Scattergram of clutch size and percentage undivided eggs for second clutches of female snow crab, *Chionoecetes opilio*, that hatched their first clutch. Females were mated either with adolescent (squares) or adult (triangles) males after their molt to maturity and were subsequently prevented (open symbols) or allowed (solid symbols) to mate with an adult male at second spawning. The open triangle in the lower right corner of the scattergram represents two females with no clutch.

Among successful primiparous females, there was no significant difference in the size of the second clutch (Kruskal-Wallis test, H=2.45, P=0.12) or in the percentage of divided eggs (H=0.44, P=0.51) between those with (median clutch size: 3.0, median percentage divided eggs: 96.9%, n=20) and those without (3.0, 96.3%, n=34) access to males at second spawning (also see Table 2). It is likely that remating occurred in a majority of females with access to males at second spawning because we observed precopulatory embraces in 18 of 20 pairs and copulation in five pairs. Although the proportion of divided eggs in second clutches was high for females isolated from males, one might have expected an even higher proportion in females paired with males owing to the potential for acquiring additional, fresh sperm. However, it was hypothesized for *C. opilio* that stored sperm can be evacuated from the spermathecae by the second mate using his gonopods (Beninger et al., 1991; Elner and Beninger, 1992). If this or any other mechanism to prevent a rival's sperm from fertilizing eggs (see for example Diesel, 1990) exists in *C. opilio*, then successive matings would not contribute additively to the pool of sperm available to fertilize a new clutch. Nevertheless, our results indicate that the viability and number of sperm remaining in spermathecae after one year of storage were not limiting for the fertilization of a second clutch in females mated only at the molt to maturity.

The success of female *C. opilio* in fertilizing a second clutch of eggs with stored sperm and the contrasting failure of female *C. bairdi* (Paul and Paul, 1992) can probably be explained by the ≈10-fold greater number of sperm cells stored after the first spawning by *C. opilio* (Sainte-Marie and Lovrich, 1994). Moreover, mean size and fecundity of females are less in *C. opilio* than in *C. bairdi* (Haynes et al., 1976); therefore, fewer sperm cells are mobilized to fertilize a clutch in the former species.

Table 2

Median and range (in parentheses) of clutch size and percentage of divided eggs for second clutches of female snow crab, *Chionoecetes opilio*, that were paired with a male after their molt to maturity and that hatched their first clutch. First male mates were adolescent or adult; all second male mates were adult. Clutch size is based on a 0 (empty) to 4 (very full) scale for abdomen repleteness with eggs. Calculation of median clutch size includes females with no eggs (scored as 0). The Kruskal-Wallis test was used to compare clutch size and percentage of divided eggs for females in different experimental treatments: H-statistic and probability level (P) are shown.

Male after molt	Adult male at second spawning	n	Second clutch: Size	Second clutch: % Divided eggs
Adolescent	No	5	3.0 (2–4)	98.3 (93.6–99.7)
	Yes	3	3.0 (1–4)	91.8 (11.2–99.3)
Adult	No	29	3.0 (0–4)	95.5 (0.0–100.0)
	Yes	17	3.0 (1–4)	97.0 (72.1–99.7)
			H = 2.50	H = 5.15
			P = 0.48	P = 0.16

Although our laboratory findings suggest that sperm stored at the first mating is effective for fertilizing the second clutch in *C. opilio*, these findings cannot be indiscriminately extrapolated to the field, for at least two reasons. First, the importance of sperm stores in wild *Chionoecetes* females might fluctuate interannually (Beninger et al., 1988; Paul and Paul, 1992). In the northwest Gulf of Saint Lawrence, the intensity of recruitment to the first benthic instar of *C. opilio* varies among years in an apparently recurrent pattern: five consecutive, moderate-to-strong year classes alternate with three consecutive, weak year classes (Sainte-Marie et al., in press, and unpubl. data). Given that adult snow crab are anecdysic and that there exist marked differences between the sexes in size and age at adulthood, recruitment pulses cause adult sex ratios and characteristics of breeding males to change considerably over time (Ennis et al., 1990; Comeau et al., 1991; Sainte-Marie et al., in press). Thus, in some years, the number or quality, or both, of males available for mating with pubescent females might be limiting and this could conceivably result in a decrease in the proportion of primiparous females having received enough sperm to fertilize a second clutch. Second, our laboratory experiments pertain only to a one-year reproductive cycle. However, under some natural conditions female *C. opilio* incubate their eggs for 24–27 months (Kanno, 1987; Mallet et al.[2], 1993; Sainte-Marie, 1993), instead of the ≈12-month duration observed in our laboratory and inferred for many wild populations (e.g. Ito, 1967; Watson, 1969; Kon, 1980). Mallet et al.[2] suggested that this difference is due to temperature: in the Gulf of Saint Lawrence, egg development would take two years for females in their usual deep-water habitat (–1° to 1°C year-round), but only one year for females that stayed for some time in warmer shallow waters. In the former case, effective fertilization of the second clutch in which stored sperm was used would thus depend on sperm surviving in sufficiently high numbers over a 2-year period. Clearly, a better understanding of the interrelations between population and reproductive dynamics, sperm delivery, sperm longevity (viability), and the duration of sperm storage is necessary before any general statement can be made about the importance of stored sperm to reproductive output in *C. opilio*.

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