Fecundity and duration of egg incubation for multiparous female snow crabs (*Chionoecetes opilio*) in the fjord of Bonne Bay, Newfoundland

Michel Comeau, Michel Starr, Gérard Y. Conan, Guy Robichaud, and Jean-Claude Therriault

Abstract: Multiparous female snow crabs (*Chionoecetes opilio*) were collected by trap and *Nephrops* trawl in the fjord of Bonne Bay, Newfoundland, between April 1988 and August 1992 to study the fecundity and embryonic development. A relationship was established between the color of the egg mass and embryonic development. Fecundity was positively correlated with carapace width. A female of 67 mm carapace width can produce up to about 54 000 eggs. Egg mortality over the incubation period could reach 21%, being greater in larger females. Based on the bimodal distributions of embryonic developmental stages observed in the study, the female reproductive cycle was determined as 2 years and females probably only hatch two broods in their lifetime. Eggs hatch mainly in May and June.

Résumé : Des femelles multipares du crabe des neiges (*Chionoecetes opilio*) ont été capturées à l'aide de casiers et un chalut *Nephrops* dans le fjord de Bonne Bay, Terre-Neuve, entre avril 1988 et septembre 1992 afin d'étudier la fécondité et le développement embryonnaire. Une relation a été trouvée entre la couleur de la masse d'oeuf et le développement embryonnaire. La fécondité est positivement corrélées avec la largeur de la carapace. Une femelle d'une taille de 67 mm largeur de la carapace peut produire 54 000 oeufs. La mortalité des oeufs au cours de l'incubation pourrait atteindre 21%; étant plus élevée pour les femelles de grande taille. Basé sur les distributions bimodales des stages de développement embryonnaire observés dans l'étude, le cycle reproducteur des femelles est approximativement de deux ans et les femelles ne libèrent probablement que deux portées au cours de leur vie. L'éclosion des oeufs a lieu surtout en mai et juin.

Introduction

In the past, the egg incubation period for snow crab (*Chionoecetes opilio*) was believed to be about 1 year (Ito 1963; Watson 1969) or 1.5 years (Kon 1974*b*). However, recent studies conducted in Japan (Kanno 1987) and in the Gulf of St. Lawrence (Mallet et al. 1993; Sainte-Marie 1993) suggested that the female reproductive cycle may be 2 years. Furthermore, the reproductive cycle may be 1 year in one area and 2 years in another area due to temperature and (or) other environmental parameters (Mallet et al. 1993; Sainte-Marie 1993). This reproductive cycle could influence the reproductive potential of different stocks.

Gaining a better understanding of the snow crab reproductive cycle is important for this fishery. Maturity is reached for both male and female snow crabs after a terminal molt over a wide range of ages and sizes (Yoshida 1941; Ito 1963; Watson 1970; Conan and Comeau 1986; Comeau and Conan 1992; Sainte-Marie and Hazel 1992). Females mate for the first time shortly after their terminal molt while the carapace is still soft (Watson 1969) and the next mating occurs shortly before or immediately after the hatching of the eggs (Conan and Comeau 1986). Female snow crabs may also produce more than one viable brood from spermatophores stored in their spermatheca (Sainte-Marie and Carrière 1995) without mating. Females extruding eggs for the first time immediately after molting and repeat spawners with hard-shell carapace are termed primiparous and multiparous, respectively.

A male-directed fishery can affect the reproductive potential of females (McMullen and Yoshihara 1971; Smith and Jamieson 1991). As fewer mature males become available for mating due to fishing, multiparous females would have to rely on old stored ejaculates in their spermathecae for egg fertilization. Laboratory studies on Tanner crab (*Chionoecetes bairdi*) showed that females using old stored spermatophores to fertilize their eggs have a lower fecundity than females that have recently mated (Paul 1984). For *C. opilio*, Sainte-Marie and Carrière (1995) found that fe-

Received August 28, 1998. Accepted February 10, 1999. J14772

M. Comeau[1] **and G. Robichaud.** Department of Fisheries and Oceans, Science Branch, Gulf Fisheries Centre, P.O. Box 5030, Moncton, NB E1C 9B6, Canada.
M. Starr and J.-C. Therriault. Ministère des Pêches et des Océans, Région Laurentienne, Institut Maurice-Lamontagne, Division de la Productivité des Océans, C.P. 1000, Mont-Joli, QC G5H 3Z4, Canada.
G.Y. Conan.[2] Department of Fisheries and Oceans, Marine Biology Research Laboratory, Université de Moncton, Moncton, NB E1A 3E9, Canada.

[1]Author to whom all correspondence should be addressed. e-mail: comeaum@mar.dfo-mpo.gc.ca
[2]Present address: 5 Halifax Street, St. John's, NF E1A 2P6, Canada.

males can effectively fertilize a second clutch of eggs from stored ejaculate but warned that their laboratory findings cannot be indiscriminately extrapolated to the field, due firstly to the importance of interannual sperm storage and secondly to a 2-year reproductive cycle instead of the 1-year cycle from their experiment. Thus, fishing could reduce the fecundity of females and (or) increase egg mortality by reducing the number of mature males.

The objectives of the present study are to examine the reproductive cycle and fecundity of multiparous female snow crabs from an unexploited stock located in the fjord of Bonne Bay, northeast Gulf of St. Lawrence, and to compare these results with published data from exploited stocks in the northwest and southwest Gulf of St. Lawrence.

Materials and methods

Study site and field sampling

Female snow crabs were sampled during spring and summer between April 1988 and August 1992 in the fjord of Bonne Bay, Newfoundland (49°32′N, 57°56′W). Detailed information on the study site is provided in Comeau et al. (1998). An important feature of the fjord is the shallow sill at its entrance that appears to restrict adult movements in or out, and there is no known concentration of snow crabs in the Gulf near Bonne Bay. Furthermore, during the time of the study, snow crabs were not commercially exploited in Bonne Bay, and thus may show characteristics of a stock in its pristine state, prior to any commercial fishing. Small conical traps (base diameter 115 cm, height 62 cm, opening 51 cm) covered with a 2.0-cm-mesh net were used to collect females at depths ranging from 90 to 130 m on the steep slope and the flat muddy bottom. A Bay of Biscay *Nephrops* 25-m headrope otter trawl with 2.5-cm-mesh codend was also used to collect females on the flat muddy bottom. The trawl has a heavy chain footrope and is designed to capture crustaceans semiburied in the mud.

Biological parameters

The following characteristics of all mature females collected were recorded from live specimens prior to preservation: carapace width (CW), exoskeleton condition, color of the eggs under the abdomen, and presence of new and (or) old grasping marks on the pereiopods (as an index of mating embrace). CW measurements were made to the nearest 0. 1 mm using a caliper. The average color and condition of the egg mass were divided into six categories: bright orange, orange, brown (developing eyed eggs), black (eyed eggs), empty eggshells mixed or not with black eggs, and degenerating eggs. The color standardization was done on fresh egg samples using the Pantone® Color Formula Guide 1000 (Pantone, Inc., Carlstadt, NJ 07072-3098, U.S.A.). Criteria used to describe the exoskeleton condition are detailed in Comeau et al. (1998). In this study, newly molted primiparous (first spawners) females, characterized by a clean soft-shell or clean hard-shell condition and newly spawned eggs under the abdomen, were not considered. These females were excluded from this study because of the uncertainty of their time of spawning, which is probably before multiparous (repeat spawners) females in Bonne Bay (Comeau et al. 1991). Also, the larger size of their eggs (Sainte-Marie 1993), which could influence embryo development, could have biased our estimation of the duration of egg development.

Subsamples of eggs, still attached to the abdomen of females, were fixed in 4% buffered formalin in seawater and were used to determine the embryonic developmental stage as described by Kon (1974*b*). Eggs from inside the brood were detached and placed in a dye solution (green light at 1% dilution) to enhance details of the embryo for stereomicroscopic observations at 16 and 40× magnification. Empty eggshells were classified as Stage 7, as they were often associated with eyed eggs. Degenerated eggs, associated with dirty soft (senile) females, were discarded.

To establish the fecundity of multiparous females, 70 clutches of eggs were randomly selected from the trawling survey done on September 10, 1991. At the laboratory, the preserved clutches of eggs were separated based on embryonic developmental stage, dried for 48 h at 80°C, and weighed to the nearest 10^{-5} g. For each brood, a subsample of 250 eggs was dried for 48 h at 80°C and weighed to the nearest 10^{-5} g. Fecundity was determined as the ratio of the total dry weight of the brood to the dry weight of the 250-egg subsamples.

Statistical methods

The squared residual of the regression lines of the number of eggs and the CW was tested for homogeneity (F test). Because of heterogeneity ($p < 0.05$), the comparison of regression lines was done graphically using the ellipses of joint confidence limits for slopes and elevations (y-intercept). In this comparison, the regression lines are significantly different ($p < 0.05$) if the ellipses do not intersect.

Results

Seasonal changes in color of the egg mass

A total of 6868 mature females, with a mean size of 67 mm CW (ranging from 37 to 90 mm CW) were sampled from April 1988 to August 1992 (Table 1). Orange eggs were observed in all samples (Fig. 1). Females with orange eggs were observed simultaneously with females having well-developed eggs, females with empty eggshells and (or) remains of a previous brood, and females with bright orange eggs in the spring samples from March to June (Fig. 1). The presence of bright orange eggs was observed in May 1991 and June of every year except for 1992, which is probably due to the low number of females sampled in that particular year (Fig. 1). Females observed in May 1991 with bright orange eggs, sometimes with eggs not yet attached to the pleopods, were only observed on two occasions (May 29 and 31, 1991). Consequently, spawning (extrusion of a new brood) of multiparous females in Bonne Bay probably occurs between the end of May and mid-June. Thereafter, no females with either bright orange eggs, black eggs, or empty eggshells were observed. Brown eggs were only observed in late summer in September 1991 and August 1992 concurrently with females carrying orange eggs (Fig. 1).

Description and seasonal changes in embryonic development

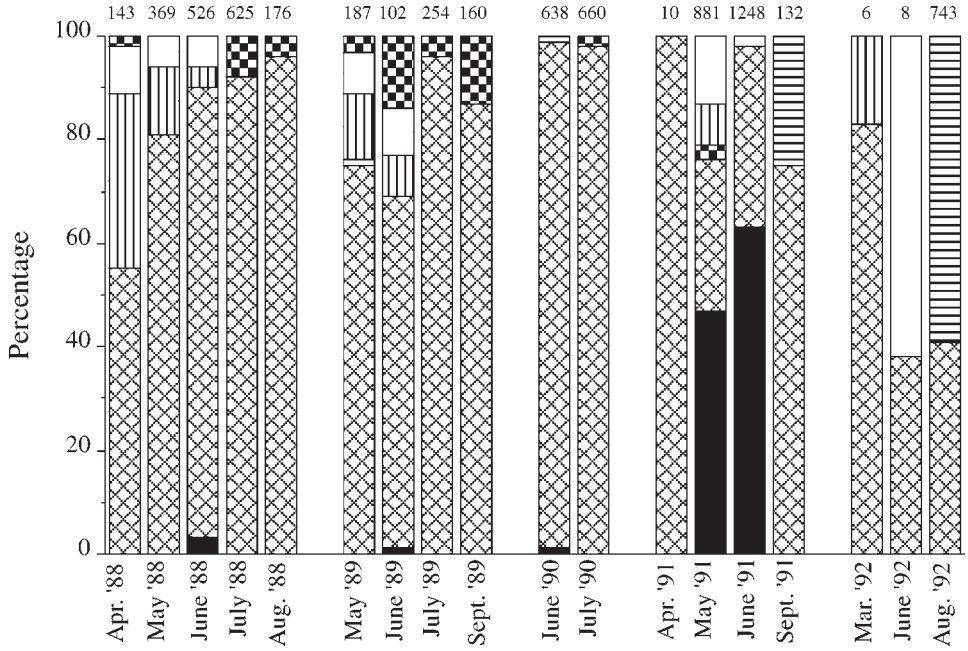
A total of 912 mature females with eggs were examined to determine the embryonic development of the eggs. All the developmental stages described by Kon (1974*b*) were observed in Bonne Bay with the exception of Stage 5, which was too difficult to distinguish from late Stage 4.

A strong relationship was observed between embryonic development and the color of the eggs (Table 2). The bright orange color of the eggs is observed in early Stage 1 (cell cleavage stage) immediately after fertilization. At late Stage 1, the color of the eggs becomes orange and remains that color until early Stage 4. By late Stage 4, the color of the eggs gradually changes to brown and the abdomen bulges as the brood increases in volume and is easily visible from the

Table 1. Number of mature multiparous snow crab females sampled by traps and trawls between 1988 and 1992 in Bonne Bay.

Year	Gear used	March	April	May	June	July	Aug.	Sept.
1988	Trap		143	369	526	474	176	
	Trawl					151		
1989	Trap			187	102	18		160
	Trawl					236		
1990	Trap					5		
	Trawl				638	655		
1991	Trap		10	215	62			
	Trawl			666	1186			132
1992	Trap	6			8			
	Trawl						743	

Fig. 1. Percentage of multiparous snow crab females with eggs at different embryonic developmental stages in Bonne Bay from April 1988 to August 1992. The total number of females sampled appears above the bars. Solid, bright orange eggs; cross-hatching, orange eggs; horizontal hatching, brown eggs; vertical hatching, black eggs; open, empty eggshells mixed or not with black eggs; checkered, degenerating eggs.



side. In Stage 6, the eggs are dark in color (black), due mainly to the pigmentation of the eyes and the chromatophores. Stage 7 is the hatching stage: the egg is black and a well-formed larva can be observed inside the eggshell.

On the basis of embryonic development, two groups of females can be distinguished at any given time between March and September (Table 3). Between March and June, females with embryonic developmental Stage 7 (hatching) and Stage 1 (eggs being spawned) were observed simultaneously with females in Stage 3 (nauplius stage) and early Stage 4. During July and August, females in Stage 4 and Stage 1 were observed simultaneously. In September, females in embryonic developmental early Stage 2 (gastrula) were observed with females in late Stage 4 (metanauplius).

In 1991, the percentage of females in their second year of egg development was about 26%, as the orange eggs (Stage 3 and early Stage 4) observed in spring developed to brown eggs (late Stage 4) by September (Tables 3 and 4). In 1991, 83% (1129/1362) had mated or were involved in a mating courtship embrace, as identified by the new grasping mark in the spring of either black (late Stage 7), hatched, or bright orange (early Stage 1) eggs.

Size–fecundity relationship

Fecundity was positively correlated with carapace size (Fig. 2*a*). A significant difference ($p < 0.05$) was observed between the size–fecundity relationships of orange (Stage 2) and brown eggs (late Stage 4), as determined from the non-intersection of the ellipses of joint confidence limits for slopes and elevations (*y*-intercept). The difference was greater for larger females.

Discussion

Reproductive cycle

Based on egg color observations and embryonic develop-

Table 2. Relationship between Kon's (1974*b*) embryonic developmental stages and egg color for snow crab females collected in Bonne Bay.

Embryonic developmental stage	Egg color[a]	Observations
Early 1	Bright orange (021C)	Egg cleavage stage; immediately after fertilization of the egg to about the 64- or 128-cell stage of the cell division; at the earliest stage the eggs are not yet attached with a stem on the pleopods; abdomen covers the entire brood
Late 1	Orange (151C)	Egg cleavage stage; no appearance of a blastopore; abdomen covers the entire brood
2	Orange (151C)	Gastrula stage; abdomen covers the entire brood
3	Orange (151C)	Nauplius stage; abdomen covers the entire brood
Early 4	Orange (151C)	Volume of the brood increased; some eggs are visible on the front
Late 4	Brown (144C)	Formation of the metanauplius; abdomen is bulged and the eggs are visible on the side
5	—	Not observed in the Bonne Bay samples
6	Black	Eggs dark; pigmentation of the compound eyes and chromatophores can be observed
7	Black	Eggs dark; hatching stage; well-formed larvae can be observed

[a]Color standardization using the Pantone® Color Formula Guide 1000 (Pantone, Inc., Carlstadt, NJ 07072-3098, U.S.A.).

Table 3. Percentage of multiparous snow crab females with eggs at different embryonic developmental stages in Bonne Bay from April 1988 to August 1992.

			Embryonic developmental stage								
Year	Month	Number	Early 1	Late 1	2	3	Early 4	Late 4	5	6	7
1988	April	55				66				29	5
	May	57		16		40	28				16
	June	73	14	21		27	26				12
	July	114		43		13	44				
	August	43		22	24		54				
1989	May	63		51		24					25
	June	27		37		33					30
	July	20		90	10						
	September	25			100						
1990	June	106		41		53					6
	July	61		31	16	15	38				
1991	April	10				100					
	May	55	46	18		22					14
	June	60	50	25		25					
	September	70			76			24			
1992	March	6					83				17
	June	8					38				62
	August	59			34		17	49			

Note: A description of the embryonic developmental stages is outlined in Table 2.

ment, our study suggests that multiparous female snow crabs in Bonne Bay have a 2-year reproductive cycle. Females with recently fertilized eggs (early Stage 1), hatching eggs (late Stage 7), and middevelopment eggs (early Stage 3) were observed simultaneously in the spring. By September, the newly extruded eggs (Stage 1) developed to the gastrula stage (Stage 2) and the middevelopment eggs (Stage 3) developed to brown eggs (late Stage 4). The observation of bimodal distributions of the embryonic developmental stage suggests that the incubation period of multiparous female eggs in Bonne Bay is 2 years.

Data from recent studies carried out on heavily exploited stocks in the Gulf of St. Lawrence and in Japan corroborate our findings of a 2-year reproductive cycle for multiparous females. In the southwestern Okhotsk Sea (Japan), Kanno (1987) reported that female snow crabs have a reproductive cycle of 2 years based on a gonad index showing bimodal distribution. In a study conducted at various locations in the southwestern Gulf of St. Lawrence, Mallet et al. (1993) suggested a 2-year reproductive cycle for female snow crabs based on the histology of the gonads, the development of the embryo, and the color of the eggs. Sainte-Marie (1993) also indicated that female snow crabs from Baie Sainte-Marguerite located on the northwestern Gulf of St. Lawrence had a 2-year reproductive cycle based on ovarian condition and weight, color of the eggs, and quantitative analyses of spermathecal contents. Furthermore, Sainte-Marie (1993) estimated that the maturation of the ovaries and brood lasted 27 months for primiparous and 24 months for multiparous females. These results and ours therefore suggest that a 2-year reproductive cycle is characteristic of the female snow crab life cycle and is not related to fishing pressure.

In Japan, Kon (1974*b*) estimated a 1-year duration of embryonic development based on laboratory rearing at temperatures ranging from 4.5 to 5.5°C. He estimated the duration

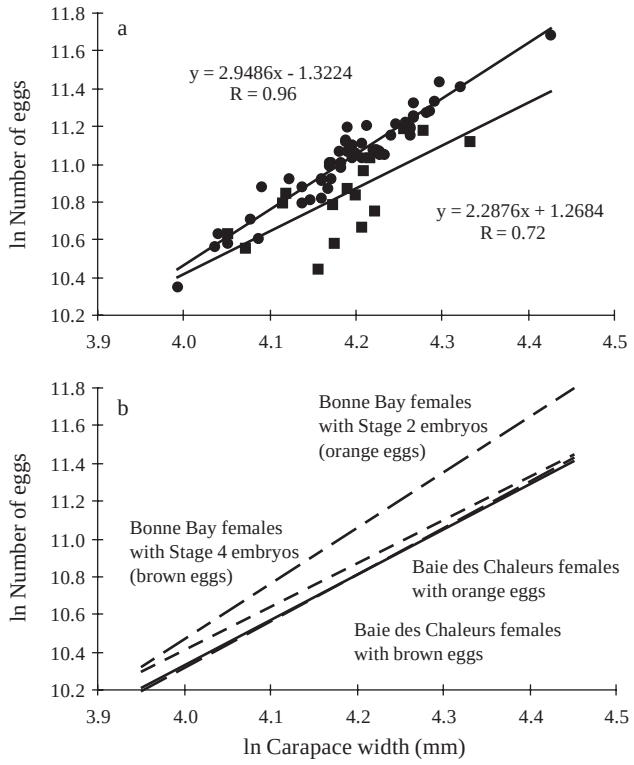
Table 4. Percentages of multiparous snow crab females collected by trawl in Bonne Bay in spring (May–June) and September 1991 with new grasping marks on the walking legs, indicating possible mating, in relation to the color of the eggs.

	Total no. females examined	Eggs		Females with new grasping marks (%)
		Color	%	
Spring (May–June)	1852	Bright orange	63	89
		Orange	26	29
		Brown	<1	0
		Black	3	27
		Empty eggshell	7	60
		Degenerated	<1	0
September	132	Orange	75	85
		Brown	25	36

of the first stage of development at 28 days and the second and third stages at 74 and 27 days, respectively. Stages 4–7 were estimated to take a total of 194 days. Our observations from the wild in Bonne Bay suggest a 2-year cycle at temperatures ranging from –1 to 1°C (Starr et al. 1994). Our estimates are about twice that calculated by Kon (1974*b*) for Stages 4–7 and three times that for Stages 1–3. As will be discussed later, temperature and other environmental factors observed in a natural environment, often not reproducible in the laboratory, are important controlling factors for the incubation period of the eggs and may explain the differences observed between aquarium and field studies. For example, a major difference in the duration of egg development between Kon's (1974*b*) aquarium estimates and ours is the slowing down of the embryonic development at very early stages, especially at the gastrula stage (Stage 2). Such a diapause early in the incubation period has already been reported by Sainte-Marie (1993) and for other brachyurans by Wear (1974) (*Hyas coarcticus* and *Corystes cassivelaunus*) and Peterson (1995) (*Hyas araneus*). Compared with other spider crabs, which have incubation periods varying between 3 and 11 months (Hartnoll 1963; Wear 1974), female snow crabs have possibly one of the longest reproductive cycles currently known for majid crabs.

The 2-year reproductive cycle and the diapause observed for female snow crabs may be related to the low temperature regime found in the natural habitat. Mallet et al. (1993) mentioned that the 2-year cycle that they observed in the southwestern Gulf of St. Lawrence may only be valid for that location, as females remain year-round in a water layer with temperatures ranging from –1 to +1°C. They also suggested that egg development may benefit from a higher temperature regime as females move up to shallower waters in certain locations such as Bonne Bay (Conan and Comeau 1986; Hooper 1986; Comeau et al. 1991; Comeau and Conan 1992) and Baie Sainte-Marguerite (Sainte-Marie and Hazel 1992) and shorten the incubation period of the eggs from 2 years to 1 year. Mallet et al. (1993) based this assumption on the fact that females from the Gulf of St. Lawrence, with a reproductive cycle of 2 years in nature, could complete their egg development in 1 year if they were placed in a temperature above 2°C. A similar temperature-dependent egg incubation period has also been observed by

Fig. 2. Linear relationship between the natural logarithm (ln) of the number of eggs and the CW of multiparous snow crab females. Predictive regression equations were fitted to multiparous females with orange and brown eggs from (*a*) Bonne Bay in 1991 (circles, orange eggs (n = 53); squares, brown eggs (n = 17)) and (*b*) Bonne Bay and Baie des Chaleurs (data from Baie des Chaleurs were taken from Conan et al. 1989).



Sainte-Marie and Carrière (1995) and a related cold-water majid crab (*H. araneus*) (Petersen 1995) from laboratory studies. Although a 1-year reproductive cycle was observed in aquarium studies, females in nature do not seem to take advantage of a higher temperature regime as they move up to shallow waters in the spring during mating (Sainte-Marie's 1993; this study). In Bonne Bay, for instance, females observed in shallow waters, where water temperature may occasionally reach 5°C in early June, are almost exclusively females in the mating courtship embrace (precopulatory embrace, Conan and Comeau 1986) with hatching eggs (Stage 7) or early Stage 1 eggs (Comeau et al. 1991). Solitary females are seldom observed at temperatures above 1°C (Comeau et al. 1991). Females that were sampled on the slope for this study were captured at a depth of 90 m and more, where temperatures ranged from –1 to 0°C year-round (Comeau et al. 1991; Starr et al. 1994). However, Sainte-Marie and Gilbert (1998) proposed that a warming trend in the cold intermediate layer over the entire snow crab habitat would shorten the incubation time from 2 years to 1 year, as observed in 1996–1997 in Baie Sainte-Marguerite. Although temperature may be an important environmental factor influencing the incubation period of the eggs, other factors such as dissolved oxygen may also play a role in the development of the embryos.

The color of the eggs was found to be as good an indicator of embryonic development as the system proposed by Kon (1974*b*) (Table 2). Although the color of the eggs is less accurate, especially in the summer (July–August) when late Stage 1 and Stage 3 (both characterized by orange eggs) are found simultaneously, it can be used as an alternative to Kon's (1974*b*) egg staging by stereomicroscope.

Indication of mating

Grasping marks identify multiparous females that were potentially participating in spring mating. Grasping marks are left when the male grasps the pereiopods of the female with his propodite during the mating courtship embrace (Comeau and Conan 1992). During the 1991 spring trawl survey, 83% of females with old eggs (Stage 7) or newly extruded eggs (Stage 1) had new grasping marks compared with 29% for females with Stage 3 and early Stage 4 eggs, indicating that a large number of females with old (hatching) or newly extruded eggs were involved in the act of mating. Although 29% of females with Stage 3 and early Stage 4 eggs (middevelopment) had grasping marks, they should not be considered as involved in mating, as they will not spawn for another year. Thus, the percentage of multiparous females involved in the act of mating could be determined by the presence of new grasping marks in spring and the color of the eggs (bright orange or hatching eggs) and (or) the embryonic development of the embryo (either Stage 1 or Stage 7). The fact that not all gravid multiparous females appear to have mated recently may be due to the use of stored spermatophores in their spermatheca to inseminate the new brood (Watson 1970, 1972; Sainte-Marie 1993; Sainte-Marie and Carrière 1995). Alternatively, it may indicate that some females mated without injury (Donaldson and Adams 1989).

Fecundity

In Bonne Bay, females with well-developed eggs have fewer eggs than those with newly extruded eggs. Our results indicate that egg mortality over the incubation period could reach 21% for large females (75 mm CW). Similarly, Kon (1974*a*) in Japan, Conan et al. (1989) in the southern Gulf of St. Lawrence, and Elner and Gass (1984) in Cape Breton suggested egg loss during incubation. These results contrast with those reported by Sainte-Marie (1993) in Baie Sainte-Marguerite, northwestern Gulf of St. Lawrence, who indicated no significant egg mortality over time for primiparous and multiparous females.

Because the egg developmental stage has a significant effect on the estimates of fecundity, it must be taken into consideration when establishing a size–fecundity relationship. In Baie des Chaleurs, Conan et al. (1989) indicated that the number of eggs for multiparous females (size ranging from 55 to 85 mm CW) ranged between 31 000 and 90 500 for orange eggs and between 31 000 and 88 800 for brown eggs (Fig. 2*b*). The results of the present study show that the number of orange eggs (Stage 2) of large females (85 mm CW) is actually higher (116 000) for the females from Bonne Bay, indicating a higher fecundity for newly extruded eggs. However, this higher fecundity for large females in Bonne Bay seems to be balanced by a higher egg mortality, which may result from a variety of processes such as predation, parasitism (Brattey et al. 1985), abrasion, unfertilized eggs, or developmental failure (Elner and Beninger 1995). Thus, our final estimate (88 500) for females with brown eggs is comparable with what was found by Conan et al. (1989). The number of eggs of smaller females (55 mm CW) from Bonne Bay (31 500) is comparable with what was estimated by Conan et al. (1989) in Baie des Chaleurs. Egg loss for smaller females was not observed in Bonne Bay, suggesting that egg loss is proportionately greater for large females. A similar relationship has been reported by Kon (1974*a*) and Elner and Gass (1984). Comparison with other published results is difficult, as many did not differentiate the egg developmental stage (Watson 1969; Haynes et al. 1976; Thompson 1979; Davidson et al. 1985) or had poor fecundity relationships due to low correlation coefficients (Elner and Gass 1984).

Implication to the fishery

For management and industry, one of the most important questions is the impact of the fishery on the population reproductive potential. Since females are protected from harvesting, the reproductive potential of the resource has been hypothesized to be unaffected by the commercial removal of males only. However, McMullen and Yoshihara (1971) and Smith and Jamieson (1991) indicated that a reduction in fecundity could result from a reduction in the availability of suitable mates in crustacean populations subjected to high male fishing mortality. For snow crab, a reduction of suitable males, either by natural or fishing mortality, can be counteracted by an increased reliance of females on stored spermatophores (Sainte-Marie 1993; Elner and Beninger 1995; Sainte-Marie and Carrière 1995). Long-term monitoring of exploited and unexploited populations is necessary to evaluate the impact of a fishery on the populations' reproductive potential. To date, our data indicate no major impact of fishery on female snow crab fecundity.

A 2-year reproductive cycle has important implications for management of this recruitment-based fishery. Based on isotopic aging techniques, the life expectancy of female snow crabs in Bonne Bay is about 5 years (Comeau et al. 1991; G.Y. Conan, unpublished data) after their terminal molt. Consequently, as mentioned by Sainte-Marie (1993), a female can probably only hatch two broods in its lifetime. Assuming that the fecundity of primiparous females is about 20% less than that of multiparous females (Sainte-Marie 1993), the lifetime fecundity of an average female of 67 mm CW from Bonne Bay would be a little less than 100 000 eggs. This estimate is at least half of what was previously estimated. In terms of fishery management, females would only participate twice in the recruitment process and not every year for 4–5 years as was originally thought. Thus, to trace the fluctuations in recruitment back to parental stocks and to develop a sound yield per recruit model, it is important to identify the timing of egg production and the reproductive cycle of both primiparous and multiparous females. In view of these new findings, statements based on a 1-year female reproductive cycle that 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) have to be reassessed.

Further studies on the effect of the percentage of male removals (exploitation level) on the potential of egg produc-

tion would be needed in order to achieve a better understanding of stock fluctuation in relation to female fecundity.

Acknowledgments

The authors wish to thank R. Bannister, B. Comeau, A. Jones, G. Paulin, M. Wen, and the crew of the CSS *Opilio* for technical assistance in the field. Special thanks to Y. Chiasson, K.G. Davidson, and Drs. M. Chadwick, M. Moriyasu, and T.W. Sephton for critically reviewing the manuscript. Logistic and financial support of M. Starr was provided by the Gulf and Québec regions, now renamed the Maritimes and Laurentien regions, respectively, of the Department of Fisheries and Oceans through the NSERC/DFO visiting fellowship program.

References

Bailey, R.F.J., and Elner, R.W. 1989. Northwest Atlantic snow crab fisheries: lessons in research and management. *In* Scientific approaches to management of shellfish resources. *Edited by* J.F. Caddy. John Wiley & Sons, New York. pp. 261–280.

Brattey, J., Elner, R.W., Uhazy, L.S., and Bagnall, A.E. 1985. Metazoan parasites and commensals of five crab (Brachyura) species from eastern Canada. Can. J. Zool. **63**: 2224–2229.

Comeau, M., and Conan, G.Y. 1992. Morphometry and gonad maturity of male snow crab, *Chionoecetes opilio*. Can. J. Fish. Aquat. Sci. **49**: 2460–2468.

Comeau, M., Conan, G.Y., Robichaud, G., and Jones, A. 1991. Life history patterns and population fluctuations of snow crab (*Chionoecetes opilio*) in the fjord of Bonne Bay on the west coast of Newfoundland, Canada — from 1983 to 1990. Can. Tech. Rep. Fish. Aquat. Sci. No. 1817.

Comeau, M., Conan, G.Y., Maynou, F., Robichaud, G., Therriault, J.-C., and Starr, M. 1998. Growth, spatial distribution and abundance of the benthic stages of the snow crab *Chionoecetes opilio* in Bonne Bay, Newfoundland, Canada. Can. J. Fish. Aquat. Sci. **55**: 262–279.

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

Conan, G.Y., Moriyasu, M., Maynard, D.R., and Chiasson, Y. 1989. Factors influencing egg production in decapod Crustacea with two case studies: *Chionoecetes opilio* and *Homarus americanus* in the Gulf of St. Lawrence. Int. Counc. Explor. Sea C.M. 1989/Mini 04.

Davidson, K., Roff, J.C., and Elner, R.W. 1985. Morphological, electrophoretic and fecundity characteristics of Atlantic snow crab, *Chionoecetes opilio*, and implications for fisheries management. Can. J. Fish. Aquat. Sci. **42**: 474–482.

Donaldson, W.E., and Adams, A.E. 1989. Ethogram of behavior with emphasis on mating for the Tanner crab *Chionoecetes bairdi* Rathbun. J. Crustacean Biol. **9**: 37–53.

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

Elner, R.W., and Beninger, P.G. 1995. Multiple reproductive strategies in snow crab, *Chionoecetes opilio*: physiological pathways and behavioral plasticity. J. Exp. Mar. Biol. Ecol. **193**: 94–112.

Elner, R.W., and Gass, C. 1984. Observations on the reproduction condition of female snow crabs from N.W. Cape Breton Island, November 1983. Can. Atl. Fish. Sci. Adv. Comm. Res. Doc. 84/14.

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

Haynes, E., Karinen, J.F., Watson, J., and Hopson, D.J. 1976. Relation of number of eggs and length to carapace width in the brachyuran crabs *Chionoecetes bairdi* and *C. opilio* from the southwestern Bering Sea and *C. opilio* from the Gulf of St. Lawrence. J. Fish. Res. Board Can. **33**: 2592–2595.

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.

Ito, K. 1963. A few studies on the ripeness of eggs of Zuwai-gani, *Chionoecetes opilio*. Bull. Jpn. Sea Reg. Fish. Res. Lab. **11**: 65–76. (Translated from Japanese; Fish. Res. Board Can. Transl. Ser. 1117.)

Kanno, Y. 1987. Reproductive ecology of tanner crab in the southwestern Okhotsk Sea. Nihon Suisan Gakkaishi, **53**: 733–738.

Kon, T. 1974*a*. Fisheries biology of the Japanese Tanner crab — VI. On the number of ovarian eggs and eggs held on the pleopods. Bull. Jpn. Soc. Sci. Fish. **40**: 465–469.

Kon, T. 1974*b*. Fisheries biology of the Tanner crab, *Chionoecetes opilio* — VII. Changes of the external morphogenesis in the process of the embryonic development. Aquaculture, **23**: 103–110.

Mallet, P., Conan, G.Y., and Moriyasu, M. 1993. Periodicity of spawning and duration of incubation time for *Chionoecetes opilio* in the Gulf of St. Lawrence. Int. Counc. Explor. Sea C.M. 1993/K:26.

McMullen, J.C., and Yoshihara, H.T. 1971. Deposition of unfertilized eggs in unmated king crabs, *Paralithodes camtschatica* (Tilesius). Trans. Am. Fish. Soc. **100**: 583–584.

Paul, A.J. 1984. Mating frequency and viability of stored sperm in the tanner crab *Chionoecetes bairdi* (Decapoda, Majidae). J. Crustacean Biol. **4**: 375–381.

Petersen, S. 1995. The embryonic development of *Hyas araneus* L. (Decapoda, Majidae): effects of temperature. Sarsia, **80**: 193–198.

Sainte-Marie, B. 1993. Reproductive cycle and fecundity of primiparous and multiparous female snow crab, *Chionoecetes opilio*, in the northwest Gulf of St. Lawrence. Can. J. Fish. Aquat. Sci. **50**: 2147–2156.

Sainte-Marie, B., and Carrière, C. 1995. Fertilization of the second clutch of eggs of snow crab, *Chionoecetes opilio*, from females mated once or twice after their molt to maturity. Fish. Bull. U.S. **93**: 759–764.

Sainte-Marie, B., and Gilbert, G. 1998. Possible effects of changes in CIL temperature and thickness on population dynamics of snow crab, *Chionoecetes opilio*, in the Gulf of Saint Lawrence. DFO Can. Stock Assess. Sect. Res. Doc. 98/38.

Sainte-Marie, B., and Hazel, F. 1992. Moulting and mating of snow crab, *Chionoecetes opilio* (O. Fabricius), in shallow waters of the northwestern Gulf of Saint Lawrence. Can. J. Fish. Aquat. Sci. **49**: 1282–1293.

Smith, B.D., and Jamieson, G.S. 1991. Possible consequences of intensive fishing for males on the mating opportunities of Dungeness crabs. Trans. Am. Fish. Soc. **120**: 650–653.

Starr, M., Therriault, J.-C., Conan, G.Y., Comeau, M., and Robichaud, G. 1994. Larval release in a sub-euphotic zone invertebrate triggered by sinking phytoplankton particles. J. Plankton Res. **16**: 1137–1147.

Thompson, R.J. 1979. Fecundity and reproductive effort in the blue mussel (*Mytilus edulis*), the sea urchin (*Strongylocentrotus droebachiensis*), and the snow crab (*Chionoecetes opilio*) from populations in Nova Scotia and Newfoundland. J. Fish. Res. Board Can. **36**: 955–964.

Watson, J. 1969. Biological investigations on the spider crab *Chionoecetes opilio*. Can. Fish. Rep. **13**: 24–47.

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.
Wear, R.G. 1974. Incubation in British decapod Crustacea, and the effects of temperature on the rate of success of embryonic development. J. Mar. Biol. Assoc. U.K. **54**: 745–762.
Yoshida, H. 1941. On the reproduction of useful crabs in North Korea. Suisan Kenkyushi, **36**: 116–123.