Embryo development and reproductive cycle in the snow crab, *Chionoecetes opilio* (Crustacea: Majidae), in the southern Gulf of St. Lawrence, Canada

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Abstract: Embryonic stages and egg-incubation durations were compared between female snow crabs, *Chionoecetes opilio*, in captivity and from the wild. In the southern Gulf of St. Lawrence the incubation time is 24–27 months. There are two prolonged periods of embryo development: (1) stages 3 and 4 (cleavage and blastula, gastrula) last for at least 6 months between May and January following egg extrusion, and (2) stages 11 and 12 (eye-pigment formation, chromatophore formation) last for 3–4 months between October and January of the following year. Water temperature plays an important role in determining the egg-development rate. Embryo development takes 12–13.5 months (365–410 days) when females are kept at a higher temperature (1.8–3.8°C) than that of the normal habitat (–1 to +1°C). Ovigerous females usually inhabit depths of 40–100 m, which is the cold intermediate water in the southern Gulf of St. Lawrence (year-round temperature and salinity –1 to +1°C and 32–33‰, respectively). However, ovigerous females are also observed at depths of 100–300 m in the Laurentian Channel, where the year-round water temperature is 3–5°C. For ovigerous females that do not migrate to the deeper, warmer waters, the duration of embryo development is 2 years, whereas females that inhabit deeper waters develop their embryos over a 1-year cycle. The reproductive potential and abundance of females with 1- and 2-year embryo-development cycles in the southern Gulf of St. Lawrence are unknown.

Résumé : Les stades embryonnaires et la durée d'incubation des oeufs du Crabe des neiges, *Chionoecetes opilio*, sont comparés chez des femelles tenues en captivité et d'autres provenant du milieu naturel. La durée d'incubation dans le sud du Golfe du Saint-Laurent semble être d'environ 24–27 mois. Le processus de développement embryonnaire observé dans la nature est prolongé durant deux périodes : (1) les stades 3 et 4 (clivage et de blastula, gastrula) ont une durée d'au moins 6 mois entre mai et janvier après l'émission des oeufs, et (*ii*) les stades 11 et 12 (formation des pigments, formation des chromatophores) ont une durée de 3 à 4 mois entre octobre et janvier de l'année suivante. La température de l'eau joue un rôle très important dans le taux de développement des oeufs. Lorsque les femelles sont gardées à une température supérieure (1,8–3,8°C) à celle de l'habitat normal (–1 à +1°C), le développement embryonnaire dure de 365 à 410 jours. En général, les femelles ovigères habitent à des profondeurs de 40 à 100 m, c.-à.-d. dans la couche intermédiaire dans le sud du Golfe du Saint-Laurent (température et salinité annuelles de –1 à +1°C et de 32 à 33‰, respectivement). Cependant, les femelles ovigères sont également observées à des profondeurs situées entre 100 et 300 m dans le chenal Laurentien, où la température de l'eau varie entre 3 et 5°C. Pour les femelles ovigères qui ne se déplacent pas vers des eaux plus profondes et chaudes, la durée du développement embryonnaire est vraisemblablement de 2 ans. Par contre, les embryons de femelles habitant en eau profonde, se développe probablement plus vite, ce qui résulterait en un cycle de développement embryonnaire de 1 an. Le potentiel reproducteur et l'abondance de femelles avec un cycle de développement embryonnaire de 1 an et de 2 ans dans le sud du Golfe du Saint-Laurent ne sont pas encore connus.

Introduction

The snow crab, *Chionoecetes opilio*, is one of the most important commercially fished species in eastern Canada. Landings in 1995 exceeded 65 000 t, with a value of about $400 million (Canadian). Females are protected from harvesting, and only males ≥95 mm in carapace width are harvested. Despite the high value of this fishery, the biology of females is not well understood, and until very recently they were assumed to produce eggs every year.

Snow crabs exhibit two mating patterns: (1) hard-shelled adult males and multiparous females mate during April–June (Taylor et al. 1985; Conan and Comeau 1986; Hooper 1986; Moriyasu et al. 1987) and (2) adult or adolescent males mate with recently molted virgin females in early February (Watson 1970, 1972; Moriyasu et al. 1987; Moriyasu and Conan 1988; Sainte-Marie and Hazel 1992). Thus, there is a 2- to 3-month difference in the egg-laying period between primiparous and multiparous females.

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In large decapods, various reproductive cycles are known, from a single brood in 2 years (*Homarus americanus*; see Aiken and Waddy 1980) to three or four broods per year (*Panulirus homarus*; see Berry 1971). Jensen and Armstrong (1989) reported that multiparous blue king crabs (*Paralithodes platypus*) in the Pribilof Islands area have a biennial reproductive cycle (1 year for egg incubation followed by a 1-year non-ovigerous period with a 2-year ovarian cycle), while the red king crab (*Paralithodes camtchatica*) has a synchronous annual cycle of ovary maturation and egg incubation (Marukawa 1933; Wallace et al. 1949). According to Berry (1969), nephropid species (such as *Nephrops norvegicus* and *Metanephrops andamanicus*) require 1 year of incubation time with 1 year of synchronous gonad maturation.

For the genus *Chionoecetes*, information on embryo development is available only for *Chionoecetes opilio elongatus* from the Sea of Japan (Kon 1980). The duration of incubation is not known for Atlantic snow crabs. Kon (1980) reported that the incubation time for captive *C. o. elongatus* is about 12 months for multiparous females and 18 months for primiparous females. According to Watson (1970), aquarium observations showed that the incubation time of primiparous *C. opilio* does not exceed 1 year. However, the possibility of longer incubation times is proposed for both *C. o. elongatus* (see Kanno 1987) and *C. opilio* (see Conan et al. 1988; Sainte-Marie and Hazel 1992; Mallet et al. 1993; Sainte-Marie 1993), based on field and aquarium observations of external egg color and gonad maturity.

In this study, the key embryonic stages are described and the duration of embryo development is estimated for Atlantic snow crabs, based on observations of wild and captive animals.

Materials and methods

Sample collection and preparation

Female snow crabs were collected in the Baie des Chaleurs, southern Gulf of St. Lawrence, with a *Nephrops* bottom trawl between May and November of 1991 and 1992. Virgin females were collected in November, prior to the pubescent molt. After carapace width was measured and carapace condition (clean, intermediate, or old), presence or absence of precopulatory embrace marks, and egg color were determined, a numbered plastic tag was attached to the carpus of the left cheliped for individual identification. The animals were kept in an open-circuit aquarium (with filtered seawater continuously pumped in from the bay) with a temperature-control unit and fed weekly with rainbow smelt (*Osmerus mordax*), blue mussel (*Mytilus edulis*), and pink shrimp (*Pandalus borealis*). The temperature and salinity varied between 0.0 and 6.0°C and between 26.0 and 31.0‰, respectively.

Immediately after females molted to maturity, which occurred in February–March, a hard-shelled adult male of 95.0–120.0 mm carapace width was provided to each newly molted female for mating. After mating and egg extrusion, each female was separated from the male and kept in an individual compartment. Multiparous females used in this study were initially brought to the laboratory as ovigerous females from the wild. After hatching their brood in aquaria, they were introduced to hard-shelled adult males for remating. After the copulatory embrace, the next batch of eggs was extruded.

For the observations of females in the wild, multiparous females were identified by carapace condition (accumulation of epibionts on the carapace) and the presence of copulatory marks on the walking legs. Ovigerous females were brought to the laboratory for the observations on a monthly basis from May to November.

Staging and measurements

The relative yolk volume (percent), standard egg color (according to Pantone® Color Formula Guide, Pantone Inc., Carldtadt, NJ 07072-3098, U.S.A.), and embryonic stages were recorded for the eggs of captive and wild females. The eggs were examined with an Olympus SZ stereomicroscope (with a conversion lens 110AL 2×) at a total magnification of 40×. Eggs were immersed in Bouin's (Kon 1980) or fast green solution (T. Kon, Fukui Prefectural Fisheries Experimental Station, Tsuruga, Fukui, Japan, personal communication) for 1–5 min to facilitate observation of the external morphology of the embryos.

For females in captivity, eggs were examined hourly at the beginning of the embryo development period (cell cleavage to the appearance of the blastopore) and then once a month until egg hatching for at least three primiparous and three multiparous females. For the females captured in the wild, the observations and measurements were made immediately after they arrived at the laboratory. Year-round sampling in the wild could not be performed, owing to the presence of water ice. Consequently, the winter observations and measurements were made on individuals caught in November and kept in aquaria until April at water temperatures between 0 and 1°C. The cumulative number of degree-days above 0°C was estimated on the basis of daily average water temperature monitored in the rearing tank for a period of egg incubation.

Measurements of the egg and eye were made using 10–15 eggs from the middle part of the egg mass of wild females on a monthly basis. Fertilized eggs were randomly selected and the diameter was measured from the base of the funiculus. For eyed eggs, the greatest width and length of one eye per embryo were measured to the nearest 1.0 mm on 10–20 individuals with a video measuring system (CUE Micro-200 digital video caliper unit, Olympus Corp., Markham, Ont.) on an Olympus SZ stereomicroscope at a magnification of 40×. All measurements were made on fresh eggs because preliminary observations showed significant swelling of eggs preserved in Bouin's solution.

For comparing the relative duration of each embryonic stage with published results, the proportion (P_{ES}) of the duration of each embryonic stage (D_{ES}) to the total duration of embryo development (D_{TED}) was used:

$$P_{\mathrm{ES}} = \left(D_{\mathrm{ES}}/D_{\mathrm{TED}}\right) \times 100$$

Egg development is a continuous process, but the illustration in this paper shows static morphology of the developing embryo, called stages. Each embryonic stage was determined on the basis of certain key morphological and physiological features that were used as criteria for determining the time course of development. Terminology for embryo development follows Shiino (1950) and Kon (1980).

Results

Embryo-development stages

Embryo development in the snow crab is divided into 14 stages. The egg colors used in this study are clear orange, orange, dark orange, and brown to dark brown, corresponding to Pantone® colors 1514C, 152C, 1595C, and 1685C–440C, respectively. The eggs are clear orange at stages 1–4, orange at stages 5–9, dark orange at stages 10–12, and brown to dark brown at stages 13 and 14 (Table 1). The average diameter of eggs increases by 20% between stages 2 and 14 (Table 1).

The key morphological features of each stage observed in the individuals kept at higher water temperature do not differ

Table 1. Characteristics of each development stage of embryos from wild multiparous female snow crabs (*Chionoecetes opilio*).

Stage	No. of females sampled	No. of eggs sampled	Egg diam. (mean ± SD), μm	% of yolk volume	Color of egg mass
1	—	—	—	100	Clear orange
2	17	242	644.4±21.0	100	Clear orange
3	21	357	649.1±29.4	100	Clear orange
4	20	257	638.7±30.3	98	Clear orange
5	9	89	666.1±27.5	95	Orange
6	7	107	674.9±29.0	88	Orange
7	10	205	673.6±30.0	82	Orange
8	15	292	672.3±29.2	80	Orange
9	7	102	690.9±38.2	75	Orange
10	8	83	716.7±23.4	65	Orange
11	13	125	699.7±23.4	48	Dark orange
12	5	173	756.0±35.0	40	Dark orange
13	9	116	759.4±33.3	20	Brown to dark brown
14	4	85	772.1±31.5	0–5	Brown to dark brown

from those observed in the individuals caught in the wild. The key morphological features of each stage (Fig. 1) are as follows.

Stage 1 (prefuniculus formation)

The egg, filled with yolk, is round and sticky. The funiculus is not formed. The eggs are often lost, especially by primiparous females, when the females are grasped by males for an extended period (2–5 days).

Stage 2 (funiculus formation)

The egg is round and filled with yolk. The funiculus is formed and the eggs are firmly attached to the pleopods.

Stage 3 (cleavage and blastula)

Segmentation of the yolk advances from two cells to the blastula. Between the 16-cell stage and the blastula, the nuclei of the dividing cells become visible as small dots after preservation in fixative.

Stage 4 (gastrula)

The blastopore appears as a disc-shaped structure on the surface of the gastrula. Sometimes the opening of the blastopore can be observed.

Stage 5 (lateral ectodermal band)

The germinal disc with three rudiments appears as a U-shaped structure. From stages 1 to 5 the fresh egg is completely occupied by yolk.

Stage 6 (prenauplius)

The rudiments of larval structure, i.e., optic lobes, antennules, mandibles, antennae, labrum, and thoracic abdomen, appear. The two preoral appendages (antennules and antennae) are present as uniramous outgrowths posterior to the optic lobes and lateral to the labrum. The mandibles are present as tiny buds on each side of the thoracic abdomen. Sometimes a thin anteroposterior line separating the yolk into two parts is observed. After the appearance of recognizable structures (stage 6), a clear area representing the developing embryo is visible. The percentage of yolk diminishes steadily until stage 12 (Table 1). At this stage the cerebrum and mandibular ganglia near the labrum are difficult to identify.

Stage 7 (nauplius)

The antenules and antennae are rod-shaped and separated from the center. The antennae are biramous. The segments forming the upper region are fused. The ramification of the telson appears as a kink-like indentation at the end of the thoracic abdomen.

Stage 8 (maxilliped formation)

The rudiments of the first and second maxillipeds appear. The volume of larval structures seen in the previous stages increases. Crescent-shaped carapace rudiments are present in the anterior part of the thoracic abdomen.

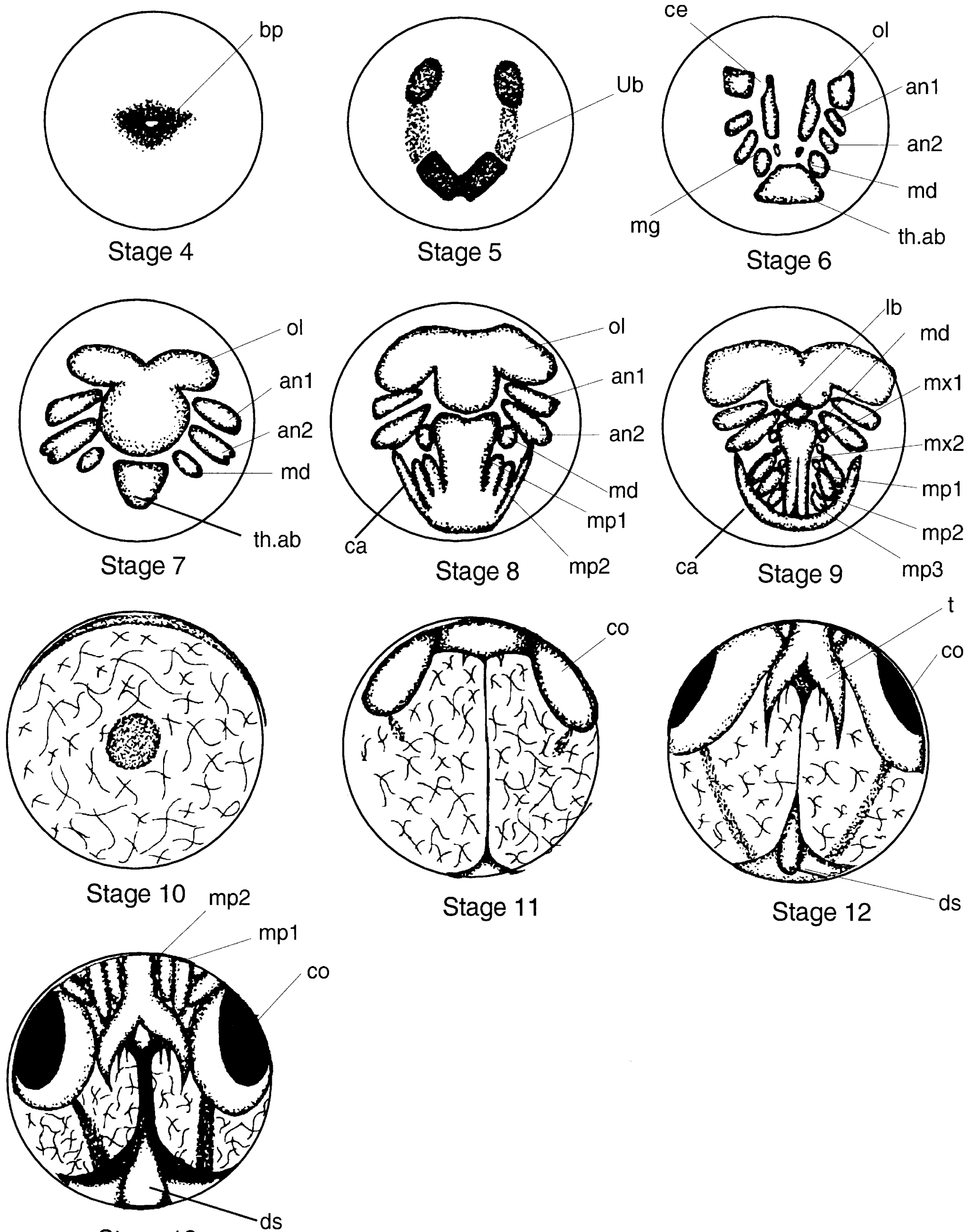
Stage 9 (metanauplius)

The rudiments of the first and second maxillae and the third maxillipeds appear. The antennules and the antennae enlarge and the antennae bear small setae. The labrum is triangular. The mandibles become smaller. The thoracico-abdominal flexure starts to cover the developing post-oral appendages, but only reaches the posterior margin of the labrum. The margins of the thoracic abdomen form and are divided into segments by a transverse groove. The telson is forked and bears seven brush-like setae on each side.

Stage 10 (late metanauplius)

The rudiments of the dorsal spine are recognizable as a disc-shaped structure in the middle of the yolk. The optic lobes are well developed and sometimes a thin pigmented crescent on the antennule side of the compound eyes is visible. The rudiments of the first and second maxillae are covered by the developing maxillipeds and difficult to observe without dissection. The labrum is covered by the developing rudiments of the thoracic abdomen. The developing thoracic abdomen is folded over the labrum, but only reaches the posterior margin of the optic lobes. The antennae are bifurcated, with a short ramus bearing terminal brush-like setae and a spinous process. The antennules are uniramous, with terminal setae. The first and second maxillipeds are bi-

Fig. 1. Schematic representation of the changes in external morphology during embryo development of snow crabs (*C. opilio*). Stages 4–9 and 11–13, ventral view; stage 10, dorsal view. *an*1, antennule; *an*2, antenna; *bp*, blastopore; *ca*, carapace; *ce*, cerebrum; *co*, compound eye; *ds*, dorsal spine; *lb*, labrum; *md*, mandible; *mg*, ganglion of mandible; *mp*1, first maxilliped; *mp*2, second maxilliped; *mp*3, third maxilliped; *mx*1, first maxilla; *mx*2, second maxilla; *ol*, optic lobe; *t*, telson; *th.ab*, thoracic abdomen; Ub, U-shaped lateral ectodermal band.



ramous and bear setae. The third maxillipeds arise from near the base of the thoracic abdomen.

Stage 11 (eye-pigment formation)

All of the larval appendages have formed. The rudiments of the dorsal spine are recognizable as an anteroposterior line separating the yolk into two parts. The developing thoracic abdomen covers the optic lobes. The rudiments of the lateral spines appear to be triangular. The telson is widely forked and the rami are narrow. As development advances, the eye pigments (dot-like and branch-like chromatophores) spread and the yolk volume further diminishes (Table 1). The occurrence of branch-like chromatophores on the maxillipeds of unstained eggs is useful for characterizing the end of this stage.

Stage 12 (chromatophore formation)

The lateral spines elongate and appear as a fine line that separates the yolk into four parts, usually reaching the posterior portion of the embryo. Diminution of the yolk accelerates substantially after this stage (Table 1). The heart starts to beat. The dorsal spine becomes visible. Dot-like chromatophores appear on the maxillipeds. The pigment in the eyes spreads and become teardrop-shaped. The mean eye length and width measured on the fresh samples are 268 ± 11 and 170 ± 7 mm, respectively.

Fig. 2. Monthly progression of embryonic stages in captive female snow crabs. ○, primiparous females in 1991; ●, multiparous females in 1991; □, multiparous females in 1992.

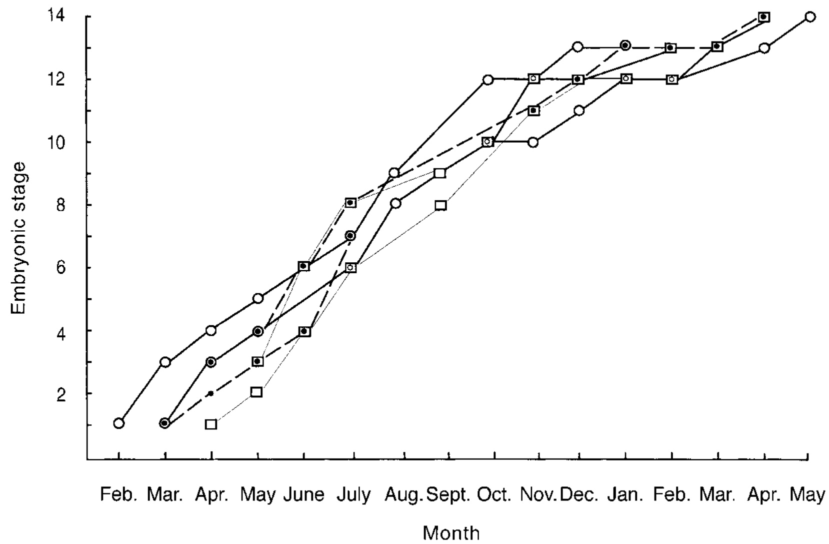


Table 2. Duration of the embryo-development cycle of captive primiparous and multiparous female snow crabs kept at different water temperatures.

Female type	*N*	Spawning period	Hatching period	TID (days)	*T*°C	°C/day
Primiparous	7	March–April 1991	April 1992	380	1196.4	3.15
Primiparous	3	March 1992	May 1993	410	715.9	1.75
Multiparous	2	April 1992	April 1993	365	673.8	1.85

Note: *N*, number of females observed; TID, total incubation duration; *T*°C, cumulative degree-days to egg hatching; °C/day, average daily water temperature required for egg hatching.

Stage 13 (reduced yolk)

Almost no yolk is visible in fresh samples. The rudiments of the dorsal and lateral spines become wider. The yolk is reduced to a small patch between the dorsal and lateral spines. The thoracic abdomen forms six segments including the telson. The amount of yolk decreases and the embryo becomes markedly larger. The yolk is almost completely covered by the rudiments of the carapace. The mean eye length and width measured on the fresh samples are 282 ± 17 and 206 ± 26 mm, respectively.

Stage 14 (prehatching)

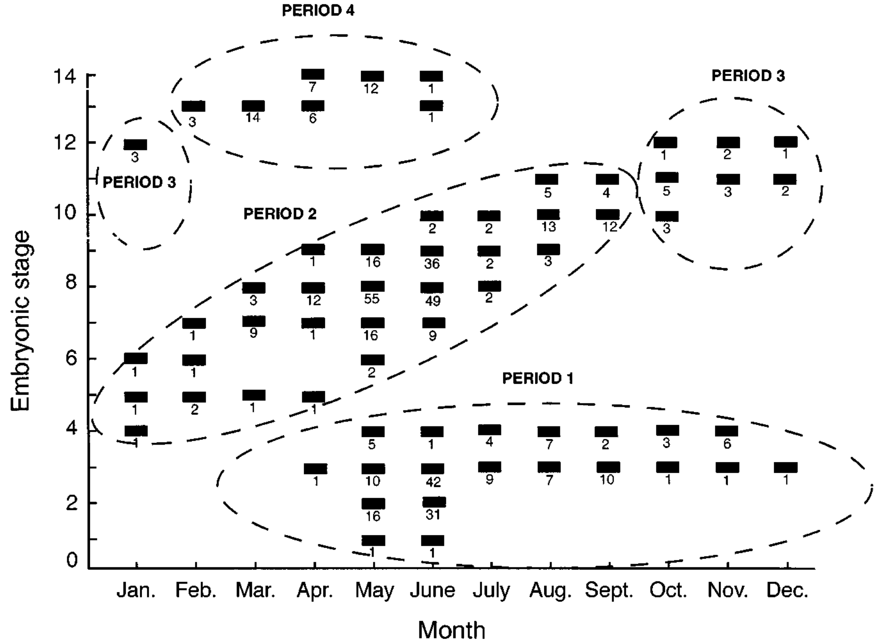
The average egg diameter reaches its maximum (772 ± 32 mm). The eyes are completely pigmented and no yolk is visible. At this stage, if yolk is present it appears to be pale orange with brownish edges in the middle of the egg and is only visible in the fresh samples. The mean eye length and width measured on the fresh samples are 274 ± 19 and 214 ± 18 mm, respectively.

Duration of embryo development

The duration of embryonic development differs in wild and captive females. In aquaria, embryo development is completed in 365 days for multiparous females and in 380–410 days for captive primiparous females (Table 2, Fig. 2). From spawning in March to hatching in June of the following year, egg development is relatively steady with no obvious period of diapause. At an average daily water temperature of 1.75–1.85°C, the duration of egg incubation for primiparous females is 45 days longer than that for multiparous females. At 3.15°C/day (°C/day is the average daily water temperature required for egg hatching), the duration of embryo development for primiparous females is comparable to that for multiparous females reared at 1.85°C/day (365 vs. 380 days) (Table 2). For wild multiparous females, complete embryo development lasts for approximately 2 years. Monthly observations (Fig. 3) showed that the embryonic stages can always be separated into two groups, based on embryo development and egg color. The two groups are at least six stages apart. However, for May and June, when the spawning and hatching seasons overlap, three groups can be encountered: recently extruded eggs (clear orange), intermediate stages (dark orange), and hatching eggs (brown to dark brown).

Development of brood in the wild can be divided into four distinct periods based on season, development speed, egg color, and egg size. Period 1, from spawning in April until December (stages 1–4): the eggs develop no further than the gastrula stage (stage 4) and then enter a period of diapause lasting at least 6 months. This period is characterized by clear orange egg color, yolk is >98% of total egg volume, and mean egg diameter is 644 ± 27 mm. Period 2, from January to September (stages 5–10): the eggs develop steadily from stage 5 to stage 10. The egg color is orange, percentage of yolk is 75–98%, and mean egg diameter is 681 ± 29 mm. Period 3, from October to January (stages 11–12): embryo development slows down between stages 11 and 12. The eggs are dark orange, yolk volume is 40–48%, and mean egg

Fig. 3. Monthly progression of embryonic stages in wild multiparous female snow crabs. The number beside each data point shows the number of individuals observed. For a description of periods see the text.



diameter is 715 ± 27 mm. Period 4, February to June (stages 12–14): development accelerates from stage 12 to final hatching, stage 14. The egg color is brown to black, percentage of yolk is 0–20%, and mean egg diameter is 763 ± 33 mm.

Discussion

Embryo-development stages

This is the first description of the embryo-development stages in the Atlantic snow crab. The results obtained in this study of embryo morphology are generally in concordance with Kon's (1980) descriptions for the snow crab (*C. o. elongatus*) in the Sea of Japan (Table 3). However, Kon (1980) classified the process of embryo development of the snow crab from cleavage to hatching into 7 stages, while the present study describes 14 stages, including two periods of diapause.

Comparison of the proportions of time spent in each stage, P_{ES} (Table 3), between the present study and that of Kon (1980) reveals that in the early embryonic stages, this value is lower in the former (stages 1–9, P_{ES} = 41.55) than in the latter (stages I–IV, P_{ES} = 58.52), while the reverse is observed in the later embryonic stages (stages 10–14, P_{ES} = 58.45 vs. stages V–VII, P_{ES} = 41.48, respectively). This is mainly due to a pronounced difference in P_{ES} values at the gastrula stage (stage 4, P_{ES} = 10.82 vs. stage II, P_{ES} = 22.91) and chromatophore formation / reduced yolk stages (stages 12–13, P_{ES} = 31.39 vs. stage VI, P_{ES} = 18.58).

The egg colors used by many authors (Ito 1963; Elner and Gass 1984; Comeau et al. 1991; Sainte-Marie and Hazel 1992; Mallet et al. 1993; Sainte-Marie 1993) corroborate the four embryo-development periods observed in this study. However, simple observations of the presence or absence of external eggs or observation of the early stages of cleavage cannot be used for evaluating fertilization success. From stages 1 to 3, no clear difference can be observed between a fertilized and an unfertilized egg because unfertilized eggs also develop a funiculus and cleavage-like divisions into unequal numbers and (or) sizes of cells. In addition, unfertilized eggs remain under the abdomen of females for up to 4–6 months. Sainte-Marie and Carrière (1995) also reported the heterogeneous distribution of fertilized and unfertilized eggs on the pleopods and pointed out the importance of sampling eggs throughout the clutch for assessing fertilization success.

Duration of embryo development and reproductive cycle

The embryo-development cycle in snow crabs (*C. opilio* and *C. o. elongatus*) has generally been considered to last 1 year (Watson 1970; Kon 1980) (Fig. 4). However, based on the observations of egg and gonad colors, Comeau et al. (1991) first proposed the existence of a 2-year incubation period for snow crabs in the northern Gulf of St. Lawrence. Indirect evidence of a 2-year embryo-development cycle, from observations of egg color, was provided by Sainte-Marie and Hazel (1992), Mallet et al. (1993), and Sainte-Marie (1993); however, this study provides the first direct evidence. For snow crabs in the Okhotsk Sea, Kanno (1987) suggested that a 2-year reproductive cycle might exist, based on the seasonal change in gonad and egg colors. For the red snow crab (*Chionoecetes japonicus*) on the Yamato Bank in the Sea of Japan, Ito (1976) and Anonymous (1988) suggested an embryo-development cycle lasting 2 years or longer.

As has been shown in the present study, one complete embryo-development cycle lasts approximately 2 years for wild multiparous female snow crabs and includes two periods of diapause: the first occurs at the gastrula stage (stage 4) and lasts for at least 6 months and the second occurs at the eye pigment formation stage (stage 11) and lasts for 3–4 months. This long incubation duration is unique among

Table 3. Comparison of embryonic stages and proportions of time spent in the different stages (P_{ES}) for captive female snow crabs between the present study and Kon's (1980) study.

This study		Kon 1980	
Stage	P_{ES}	Stage	P_{ES}
1. Prefuniculus formation	0.43	I. Cleavage and blastula	8.67
2. Funiculus formation	2.16		
3. Cleavage and blastula	5.19		
4. Gastrula	10.82	II. Gastrula	22.91
5. Lateral ectodermal band formation	3.90	III. Nauplius	8.36
6. Prenauplius	4.98		
7. Nauplius	3.46		
8. Maxilliped formation	4.98	IV. Metanauplius	18.58
9. Metanauplius	5.63		
10. Late metanauplius	9.74	V. Eye pigment formation	10.53
11. Eye pigment formation	7.58		
12. Chromatophore formation	17.32	VI. Chromatophore formation on maxillipeds	18.58
13. Reduced yolk	14.07		
14. Prehatching	9.74	VII. Prehatching	12.38

brachyuran species, which generally have much shorter reproductive cycles of 3–11 months (Hartnoll 1963, 1965; Wear 1974). Although an egg diapause was also reported by Wear (1974) in two other brachyuran species, *Hyas coarctatus* and *Corystes cassivelaunus*, this is, to our knowledge, the first record of the occurrence of two diapause periods within a single reproductive cycle. The difference in the duration of embryo development between the eggs of captive females (12–13.5 months) and wild females (24–27 months) may be explained by the existence of two diapause periods in wild females, apparently because of low water temperature.

The 2-year brooding period has important consequences for estimating lifetime egg production of snow crabs. Mallet et al. (1993) and Sainte-Marie (1993) suggested that the lifespan of females after the terminal molt does not normally exceed 5–6 years. With a 2-year reproductive cycle, a female can, therefore, produce no more than two, or at most three, clutches of eggs in its lifetime. In addition, a longer incubation period may lead to additional mortality of eggs from parasites and physical damage compared with populations with a 1-year reproductive cycle. Consequently, the numbers of larval snow crabs hatched annually may be much lower than was previously thought (Watson 1970).

Influence of water temperature on the reproductive cycle

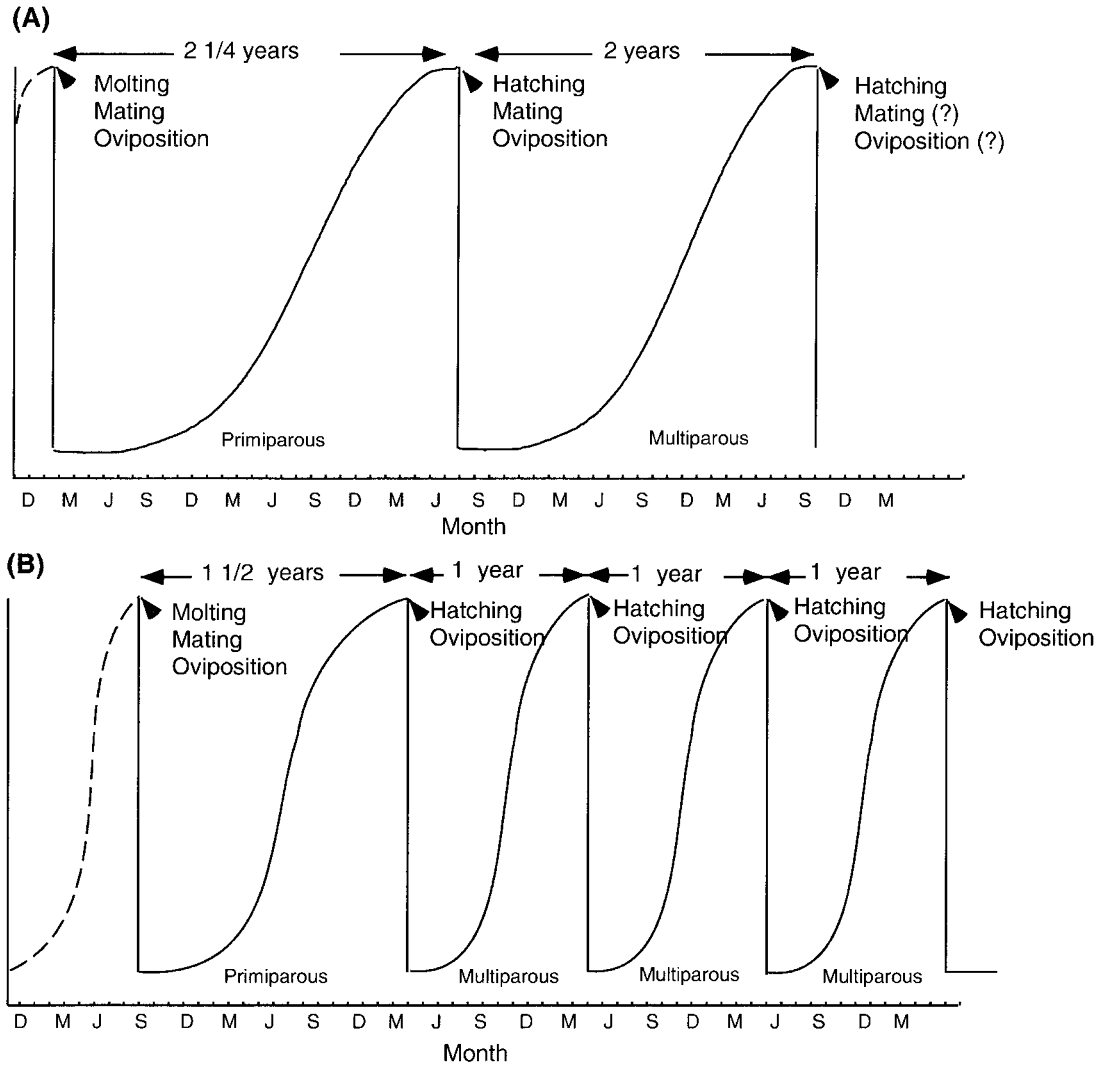
Observations of embryo development in aquaria under different temperature regimes show that water temperature influences the egg-development rate. Furthermore, the total duration of embryo development seems to be largely determined by the duration of the two different diapause periods, which may be controlled by the water-temperature regime.

Comparing embryo-development processes between the present study and Kon (1980) is difficult because the water temperatures are not totally comparable for the two experiments. However, the higher number of cumulative degree-days (1500–1750) estimated for the experiment conducted by Kon (1980) may explain why the embryo-development duration reported, 300–350 days, is shorter than that in our aquarium study, which is 365–410 days, but for fewer cumulative degree-days (674–1196).

For *C. o. elongatus*, Kanno (1987) hypothesized that the reproductive cycle of snow crabs varies considerably depending on the environmental conditions, and that embryo development of snow crabs in the Okhotsk Sea may take two years. The results of the present study support this hypothesis. In Wakasa Bay (Sea of Japan), Kon (1980) reported that the water temperature of the main snow crab habitat (200–400 m) is approximately 0.4–10°C and that the female reproductive cycle lasts 1 year. Snow crabs also inhabit deeper waters (200–600 m) in the same region, and water temperatures range between 0.3 and 0.9°C (Yosho and Hayashi 1994). Therefore, it is possible that Kon (1980) only reported on the reproductive cycle of female snow crabs inhabiting warmer water masses in the Sea of Japan, which lasts for 1 year, whereas female snow crabs inhabiting colder water masses (Yosho and Hayashi 1994) may have a longer reproductive cycle.

We think that the 2-year reproductive cycle of snow crabs in the southern Gulf of St. Lawrence is a consequence of physiological constraints due to low-temperature habitat conditions. When the species encounters more favorable temperature conditions, females can shorten the reproductive cycle to 1 year, as was observed in aquaria with higher water temperatures. In the southern Gulf of St. Lawrence, the year-round bottom water temperature remains between –1 and +1°C in the intermediate cold water layer (50–100 m) and reaches +5°C at depths of 100–300 m (Gilbert and Pettigrew 1997). Trawl surveys conducted in 1994 revealed that there were 1376 – 39 953 ovigerous multiparous females per

Fig. 4. Schematic representation of the reproductive cycle of snow crabs in the southern Gulf of St. Lawrence (A) and Sea of Japan (B) (modified from Kon 1980). D, December; M, March; J, June; S, September.



square kilometre in the deeper water (M. Moriyasu, unpublished data), where the temperature was 1.3–6.3°C. Therefore, if ovigerous females remain in the deeper water for an extended period, their reproductive cycle could become annual. Spring breeding migration to warmer shallows 1–2 months prior to mating (Taylor et al. 1985; Conan and Comeau 1986; Hooper 1986; Ennis et al. 1990; Comeau et al. 1991; Comeau and Conan 1992) does not provide enough cumulative degree-days to shorten the embryo-development process from 2 years to 1 year. Multiparous females seem to be sedentary (Lovrich et al. 1995), and no large-scale seasonal migration of ovigerous females to the shallows has been reported in the Gulf of St. Lawrence. Tremblay (1997) reported that snow crabs near their southern limit on the Scotian Shelf are most abundant where the bottom temperature is <3°C. The annual bottom temperature has shown a declining trend since 1984 that may have resulted in an expansion of snow crab habitats recently. However, the effect of a long-term change in water temperature on female reproductive characteristics is unknown.

The results of the present study are further evidence of the existence of a 2-year embryo-development cycle in snow crabs in the southern Gulf of St. Lawrence (Fig. 4). Further studies are necessary to estimate the abundance of females with shorter and longer reproductive cycles and examine seasonal movement of ovigerous females in relation to depth and water temperature.

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References

Aiken, D.E., and Waddy, S.L. 1980. Reproductive biology. *In* The biology and management of lobsters. Vol. 1. Physiology and behavior. *Edited by* J.S. Cobb and B.F. Phillips. Academic Press, New York. pp. 215–276.

Anonymous. 1988. Research report on the resource and ecology of Benizuwai crab (*Chionoecetes japonicus* Rathbun, 1932). [In Japanese.] Report of the Promotional Project on Regional Development of Important New Technology for 1985–1987, Toyama, Shimane and Tottori Prefectural Fisheries Experimental Stations, Japan.

Berry, P.F. 1969. The biology of *Nephrops andamanicus* Wood-Mason (Decapoda, Reptantia). Oceanogr. Res. Inst. (Durban) Invest. Rep. No. 22.

Berry, P.F. 1971. The biology of the spiny lobster *Panulirus homarus* (Linnaeus) off the east coast of south Africa. Oceanogr. Res. Inst. (Durban) Invest. Rep. No. 31.

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 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.

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., Comeau, M., Mallet, P., Cormier, R., Chiasson, Y., and Chiasson, H. 1988. Growth and maturation of snow crab *Chionoecetes opilio*. Can. Manuscr. Rep. Fish. Aquat. Sci. No. 2005.

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

Ennis, G.P., Hooper, R.G., and Taylor, D.M. 1990. Changes in the composition of snow crab (*Chionoecetes opilio*) participating in the annual breeding migration in Bonne Bay, Newfoundland. Can. J. Fish. Aquat. Sci. **47**: 2242–2249.

Gilbert, D., and Pettigrew, B. 1997. Interannuel variability (1948–1994) of CIL core temperature in the Gulf of St. Lawrence. Can. J. Fish. Aquat. Sci. **54**(Suppl. 1): 57–67.

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

Hartnoll, R.G. 1965. The biology of spider crabs: a comparison of British and Jamaican species. Crustaceana, **9**: 1–16.

Hooper, R.G. 1986. A spring breeding migration of 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.

Ito, K. 1976. Maturation and spawning of Benizuwai crab (*Chionoecetes japonicus*) in Japan Sea — spawning cycle. Bull. Jpn. Sea Reg. Fish. Res. Lab. **27**: 59–74.

Jensen, G.C., and Armstrong, D.A. 1989. Biennial reproductive cycle of blue king crab, *Paralithodes platypus*, at the Pribilof Islands, Alaska and comparison to a congener, *P. camtschatica*. Can. J. Fish. Aquat. Sci. **46**: 932–940.

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

Kon, T. 1980. Studies on the life history of the zuwai crab, *Chionoecetes opilio* (O. Fabricius). Sado Mar. Biol. Stn. Niigata Univ. Spec. Publ. Ser. 2.

Lovrich, G.A., Sainte-Marie, B., and Smith, B.D. 1995. Depth distribution and seasonal movements of *Chionoecetes opilio* (Brachyura: Majidae) in Baie Sainte-Marguerite, Gulf of Saint Lawrence. Can. J. Zool. **73**: 1712–1726.

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. ICES CM/1993: K:26.

Marukawa, H. 1933. Biology and fishery research on Japanese king crab *Paralithodes camtschatica*. J. Imp. Fish. Exp. Stn. Tokyo, **4**: 1–152.

Moriyasu, M., and Conan, G.Y. 1988. Aquarium observation on mating behavior of snow crab (*Chionoecetes opilio*). ICES CM/1988: K:9.

Moriyasu, M., Conan, G.Y., Mallet, P., Chiasson, Y., and Lacroix, H. 1987. Growth at molt, molting season and mating of snow crab (*Chionoecetes opilio*) in relation to functional and morphometric maturity. ICES CM/1987: K:21.

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. **93**: 759–764.

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

Shiino, M.S. 1950. Studies on the embryonic development of *Panulirus japonicus* (von Siebold). J. Fish. Mie Pref. Univ. **1**: 1–168.

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

Tremblay, M.J. 1997. Snow crab (*Chionoecetes opilio*) distribution limits and abundance trends on the Scotian Shelf. J. Northwest Atl. Fish. Sci. **27**: 7–22.

Wallace, M., Pertuit, C.J., and Hvatus, A.R. 1949. Contribution to the biology of the king crab *Paralithodes camtschatica* (Tilesius). U.S. Fish Wildl. Serv. Fish. Leafl. No. 340.

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 effect of temperature on the rate and success of embryonic development. J. Mar. Biol. Assoc. U.K. **54**: 745–762.

Yosho, I., and Hayashi, I. 1994. The bathymetric distribution of *Chionoecetes opilio* and *C. japonicus* (Majidae: Brachyura) in the western and northern areas of the Sea of Japan. Bull. Jpn. Sea Natl. Fish. Res. Inst. **44**: 59–71.