BRILL

Moulting and Growth of Male Snow Crab, Chionoecetes opilio (O. Fabricius, 1788) (Decapoda, Majidae), in the Southern Gulf of St. Lawrence

Author(s): M. Hébert, K. Benhalima, G. Miron and M. Moriyasu

Source: *Crustaceana*, May, 2002, Vol. 75, No. 5 (May, 2002), pp. 671-702

Published by: Brill

Stable URL: https://www.jstor.org/stable/20105447

Brill is collaborating with JSTOR to digitize, preserve and extend access to *Crustaceana*

MOULTING AND GROWTH OF MALE SNOW CRAB, CHIONOECETES OPILIO (O. FABRICIUS, 1788) (DECAPODA, MAJIDAE), IN THE SOUTHERN GULF OF ST. LAWRENCE

BY

M. HÉBERT[1,3]), K. BENHALIMA[1]), G. MIRON[2]) and M. MORIYASU[1])

[1]) Department of Fisheries and Oceans, Gulf Region, Science Branch, Gulf Fisheries Centre, P.O. Box 5030, Moncton, New Brunswick E1C 9B6, Canada

[2]) Département de Biologie, Université de Moncton, Moncton, New Brunswick E1A 3E9, Canada

ABSTRACT

Laboratory and field experiments were conducted from 1988 to 1992 to determine moult and growth characteristics of male snow crab in the southern Gulf of St. Lawrence. Eleven moult stages were identified, based on histological observations of the exoskeleton (Postmoult: A_1, A_2, B_{1-2}, C_{1-2}, C_3; Intermoult C_4; and Premoult: D_0, D_1, D_2 ($D_{2'}$, $D_{2''}$), D_3, D_4). The mean total duration for a postmoult crab to reach intermoult stage C_4, observed in the laboratory, was 70.1 ± 11.6 days. The carapace hardening process continued up to 8-9 months after ecdysis. Two distinct periods of moulting were observed in the laboratory. Moulting of type I males (normal moulters) occurred in January-May (peaked in March). Moulting of type II males (skip moulters) occurred in December-March (peaked in January). Our results showed that the size-weight relationship of male crabs differs significantly in relation to moult stage and morphometric maturity. We also found that a reduction of carapace moult increment occurred for type I males, from the immature to adolescent phase, and from the adolescent to adult phase. No significant difference in carapace moult increment was found for type II males moulting to the adolescent or adult phase. Carapace growth comparison between types I and II males showed no significant difference in the mean percentage of moult increment for those moulting within the adolescent phase but a significantly higher moult increment for type II males moulting from the adolescent to adult phase. The present study revealed that the moulting and growth patterns of male snow crab were more complex than the previous literature had suggested. The implications for long-term stock management are important and further studies on growth parameters and moulting pattern of male snow crab are needed to develop an optimal harvesting strategy in the southern Gulf of St. Lawrence snow crab fisheries.

RÉSUMÉ

Des expériences en laboratoire et en milieu naturel ont été effectuées entre 1988 et 1992 pour déterminer les caractéristiques de la mue et de la croissance du crabe des neiges mâle dans le sud du golfe du Saint-Laurent. Des observations histologiques de l'exosquelette nous ont permis d'identifier

---

[3]) e-mail: hebertm@dfo-mpo.gc.ca

onze stades de mue (Postmue: A_1, A_2, B_{1-2}, C_{1-2}, C_3; Intermue C_4; et Prémue: D_0, D_1, D_2 ($D_{2'}$, $D_{2''}$), D_3, D_4). Le temps moyen pour q'un crabe en postmue atteigne l'intermue C_4 en laboratoire a été de $70,1 \pm 11,6$ jours. Le processus de durcissement de la carapace se continue jusqu'à 8-9 mois après l'ecdysis. Deux périodes distinctes de mue ont été observées en laboratoire. La mue chez les mâles de type I (mue normale) a eu lieu en janvier-mai (sommet en mars) tandis que la mue chez les mâles de type II (saut de mue) a eu lieu en décembre-mars (sommet en janvier). Nos résultats ont démontré que la relation taille-poids des mâles diffère significativement selon le stade de mue et la maturité morphométrique. Une réduction significative de l'accroissement de la carapace à la mue n'a été observée chez les mâles de type I lors du passage de la phase immature à la phase adolescente, et de la phase adolescente à la phase adulte. Aucune différence significative de l'accroissement de la carapace à la mue n'a été observée chez les mâles de type II muant à la phase adolescente ou adulte. La comparaison de l'accroissement de la carapace entre les crabes mâles de types I et II n'a indiqué aucune différence significative du pourcentage moyen de l'accroissement pour ceux qui ont mué à la phase adolescente, mais un accroissement significativement plus élevé pour les mâles de type II qui ont mué de la phase adolescente à la phase adulte. Cette étude a démontré que les modalités de la mue et de la croissance du crabe des neiges mâle sont beaucoup plus complexes que ne le suggéraient les études antérieures. Les implications pour la gestion de stocks à long terme sont importantes et des études approfondies sur les paramètres de croissance et du patron de mue du crabe des neiges mâle sont nécessaires pour développer une stratégie d'exploitation optimale pour les pêcheries du sud du golfe du Saint-Laurent.

INTRODUCTION

The snow crab, *Chionoecetes opilio* (O. Fabricius, 1788), fishery in the southern Gulf of St. Lawrence (Area 12, fig. 1) is one of the most valuable fisheries in Atlantic Canada (Hébert et al., 2000). In the southern Gulf of St. Lawrence, moulting takes place in late winter-early spring, i.e., February-April (Watson, 1972; Conan et al., 1988) prior to the fishing season. Immature and adolescent males normally moult every year until they reach a terminal moult at sizes ranging approximately between 40 and 150 mm of carapace width (Conan & Comeau, 1986; Sainte-Marie & Hazel, 1992; Sainte-Marie et al., 1995). After moulting, the crab has a soft shell and its content is mostly water for a period of time. Soft-shelled adult males that cannot mate during their postmoult period, will be able to participate in reproduction in the spring of the following year, just before the fishing season (Moriyasu & Conan, 1988). In addition, adult soft-shelled crabs of legal size (carapace width $\geqslant$ 95 mm) will be recruited to the fishery as commercial-quality crabs the following season (Hébert et al., 2000).

The snow crab fishery is extremely sensitive to the fluctuation of recruitment into the fishery due to an intensive harvesting of adult hard-shelled crabs $\geqslant$ 95 mm CW. In 1990, the fishing season was closed early due to a high incidence of soft-shelled crab and a rapid decline in catch rate (Hébert et al., 1992). Conan & Comeau (1986) stressed the importance of minimizing the catch of soft-shelled crabs during fishing activities in order to protect the reproductive potential
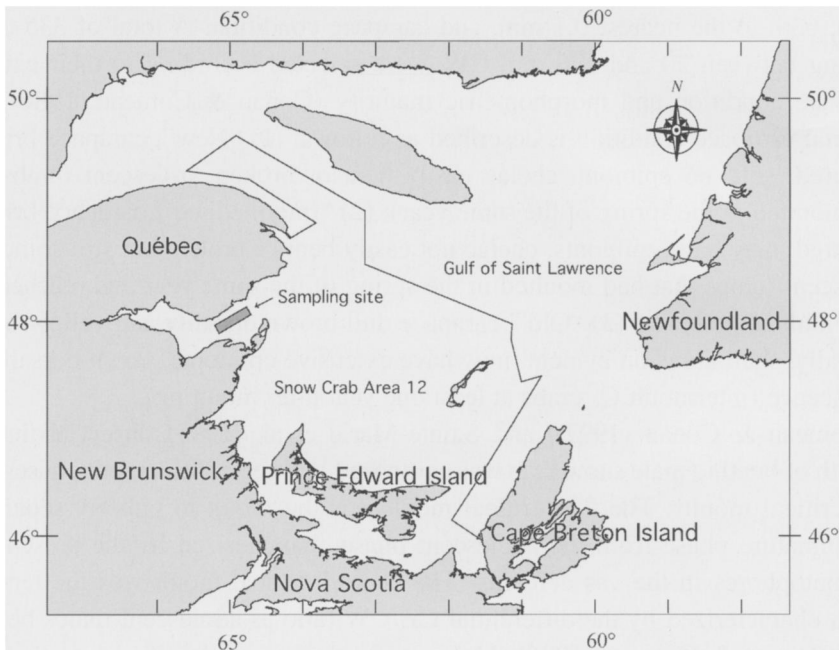
Fig. 1. Location of sampling area in the southern Gulf of St. Lawrence.

of the stock and to achieve maximum yield per recruit. Soft-shelled crabs have a low commercial value due to their low meat content (Elner & Bailey, 1986) and are, therefore, discarded at sea by fishermen, which may lead to high mortality for these crabs (Dufour et al., 1997). A detailed knowledge of the snow crab moult cycle, e.g., identification of moult stages, moulting pattern and schedule, and growth increment per moult, could provide a tool for enhancing predictive capability of population fluctuation and thereon improving sound stock management strategies.

The purpose of this study is to: (1) describe moult stages throughout the male moult cycle; (2) determine the duration of each moult stage during the postmoult period; (3) establish size-weight relationships in relation to moult stage and morphometric maturity, and (4) determine growth and moulting period based on aquarium observations.

MATERIALS AND METHODS

Moult stage determination and duration

Male snow crabs were collected with a *Nephrops* trawl in the Baie des Chaleurs (fig. 1) between July and November 1984 and between July and October 1986. The following basic measurements were taken: carapace width (CW), chela height

(CH), both to the nearest 0.1 mm, and carapace condition. A total of 335 crabs, ranging between 20 and 120 mm CW, were selected according to their external carapace condition and morphometric maturity (Conan & Comeau, 1986). The external carapace condition is described as follows: (1) "New", carapace brightly coloured, soft, no epibiont, chelae easily bent or broken, iridescent (crabs that had moulted in the spring of the same year); (2) "Intermediate", carapace brightly coloured, may have epibionts, chelae not easily bent or broken but still somewhat iridescent (crabs that had moulted in the spring of the same year and reached late postmoult stages); and (3) "Old", carapace dull brown dorsally and yellow-brown ventrally, shell abrasion evident, may have extensive epibionts grown dorsally, no iridescence (intermoult C_4 crabs at least one year after moulting).

Comeau & Conan (1992), and Sainte-Marie et al. (1995) observed that the growth of benthic male snow crab was composed of three development phases with two critical moults. The first critical moult was the moult to puberty separating the immature phase from the adolescent phase characterized by the presence of spermatophores in the vas deferens. The second critical moult was the terminal moult characterized by the differential CH/CW ratio as adolescent males become adult (Conan & Comeau, 1986). Males were, therefore, classified into the three morphometric maturity phases (immature, adolescent, and adult) based on the CH-CW relationships described by Conan & Comeau (1986) and Comeau & Conan (1992).

Once immature and adolescent males (potential moulters) were identified, they were kept in a 540 l re-circulating sea water tank at a temperature and salinity of 0 to 7°C and 28.5 to 31‰, respectively. The sea water temperature remained at 0-4°C throughout the experiment except for several incidences of the water chilling system malfunction, which resulted in an increased water temperature up to 7°C. Crabs were fed once a week with pink shrimp, *Pandalus borealis* Krøyer, 1838, and rainbow smelt, *Osmerus mordax* (Mitchill, 1815). Each crab was identified by a numbered plastic tag around the right chela. The development of the crab's integument was monitored throughout premoult and postmoult periods by dissecting a piece (approximately 5 × 5 mm) of the posterolateral margin of the carapace. Successful ecdysis was observed for 190 crabs. Date and time of the day of ecdysis were recorded. The dissection of a piece of the carapace from postmoult males was made at variable intervals (1 hr to 15 days) after the ecdysis. The frequency of sampling was limited to the maximum of 5 times per individual throughout the experiment for reducing the potential negative effect on the growth and survival rates.

To evaluate postmoult duration from crabs in the wild, male snow crabs were collected from a monthly trawl survey conducted in the Baie des Chaleurs (fig. 1) between June and October, from 1990 to 1992. In addition to the basic

measurements (CW, CH, and carapace condition), the carapace hardness (Foyle et al., 1989) was measured with a durometer (durometer readings from 0 to 100 units with a precision of 1 unit) using a 7-lb (approx. 3-kg) gauge (Pacific Transducer Corp., California, U.S.A.). A piece of the carapace was dissected from 2,555 recently moulted male crabs ("New" and "Intermediate" categories) for histological observations.

Moult stage determination of samples collected from the wild and in the aquarium was carried out by light microscopic observations of exoskeleton structures. The tissue was fixed in Bouin's solution for 48 h. Fixed samples were washed in 70% ethanol, progressively dehydrated using a series of increasing ethanol solution, then cleared with xylene. A longer embedding time in paraffin was necessary since cuticle pieces were not decalcified. Serial sections were cut at 5-7 μm thickness, stained with Masson's trichrome (variant Goldner) according to Martoja & Martoja-Pierson (1967). The tissue sections were observed under a compound microscope and moult stages determined according to the method described by Drach & Tchernigovtzeff (1967). At least two individuals were examined for each stage.

Size-weight relationship

Nephrops trawl and trap (1.8 × 1.8 m rectangular crab traps) surveys were conducted in the Baie des Chaleurs (fig. 1) in June-July and September-October 1989. Male snow crabs were brought to the laboratory where CW and CH were measured to the nearest 0.1 mm. Wet weight was measured using a digital scale with a precision of 0.1 g. The external carapace condition of each crab was recorded as "New", "Intermediate", or "Old". Crabs with intact claws and less than 3 missing legs were chosen for the analysis (a total of 490 crabs). Crabs were further divided by morphometric maturity (adolescent and adult). Carapace width-weight relationship was established for five groups of males: (1) "New-adult" (N-Adu); (2) "New-adolescent" (N-Ado); (3) "Intermediate-adult" (I-Adu); (4) "Intermediate-adolescent" (I-Ado); and (5) "Old-adult" (O-Adu). The size-weight relationship was expressed by the following equation:

$$\ln W = a \cdot \ln CW + b$$

where W is the total wet weight in g, CW the carapace width in mm, *a* the slope and *b* the elevation.

A predictive linear regression was fitted by least squares for each set of paired log-transformed data. Slopes and, where applicable, elevations of regressions for carapace width-body weight were compared by ANCOVA (Sokal & Rohlf, 1995). A 95% level of significance was used in all analyses.

Growth at moult and moulting period

Male snow crabs were collected with a *Nephrops* trawl in the Baie des Chaleurs (fig. 1) between July and November 1984, July and October 1986, and June and October from 1990 to 1992. CW, CH, both to the nearest 0.1 mm, and carapace condition (New, Intermediate, and Old) were noted for each individual. Only immature and adolescent male crabs, CW ranging from 18 to 120 mm, were immediately brought to the laboratory. Immature and adolescent males were classified into two groups based on the moulting schedule during the previous moulting season as described by Benhalima et al. (1998). Males with a clean and soft carapace ("New" and "Intermediate" categories) that had moulted in the spring of the same year were considered as type I (normal moulters), and those with a hard and dirty carapace ("Old" category) that had not moulted in the previous moulting season were considered as type II (skip moulters). After measurements, a numbered plastic tag was placed around the right chela for identification. A total of 1,615 immature and adolescent males (the number of individuals used varied from 272 to 423 per year) were kept individually in floating cages in two 750 l recirculating sea water tanks with water conditions as described for the experiment of moult stage determination. Crabs were fed pink shrimp and rainbow smelt once a week. Mortality and moulting were monitored once a day. Successful ecdysis was observed in 1,350 crabs. Date and time of the day of ecdysis for each crab were recorded and postmoult measurements (CW and CH) made at postmoult stage C_{1-2}.

Growth at moult for male crabs moulting to the immature, adolescent, and adult phases (Comeau & Conan, 1992; Sainte-Marie et al., 1995; Comeau et al., 1998) was estimated by linear regression using Hiatt's growth model (Hiatt, 1948; Kurata, 1962):

$$L_{t+1} = aL_t + b$$

where L_{t+1} is the postmoult CW, L_t the premoult CW, a the slope and b the elevation. Slopes and, where applicable, regression elevations for different male groups were compared by ANCOVA (Sokal & Rohlf, 1995).

The relationship between the percentage of growth increment (PGI) and premoult CW (L_t) was also analysed:

$$PGI = aL_t + b$$

where PGI is the percentage of growth increment expressed by

$$[(L_{t+1} - L_t)/L_t] \cdot 100.$$

L_{t+1} is the postmoult CW, L_t the premoult CW, a the slope and b the elevation. Mean percentages of growth increment (MPGI) were compared within and between moult types (Type I and II), and moulting phases (immature, adolescent,

and adult) with a Mann-Whitney's test (U-test). The monthly moulting frequencies between type I and II males were compared using the Kolmogorov-Smirnov two-sample test. A 95% level of significance was used in all analyses.

## RESULTS

Moult stage determination

Eleven moult stages (stage D_2 was further divided into two sub-stages) were identified based on the histological observations of the exoskeleton (Postmoult: A_1, A_2, B_{1-2}, C_{1-2}, C_3; Intermoult C_4; and Premoult: D_0, D_1, D_2 ($D_{2'}$, $D_{2''}$), D_3, D_4):

Stage A_1 (fig. 2A). — This stage began immediately after ecdysis. The exoskeleton consisted of three different layers (epicuticle, exocuticle, and epithelium). The epicuticle appeared as a dense layer coloured in red with acid fuchsin, while the exocuticle consisted of several stratified layers coloured in blue with aniline in Masson's trichrome. The epithelium was composed of well-defined elongated cells. The cells continued to increase in height throughout this stage reaching their maximal height. The cytoplasm of the cell was basophilic and the nuclei were oval and situated in the middle of the cell. Layers of connective tissue of varying thickness lay beneath the epithelium. The connective tissue consisted of a collagenous fibre layer, haemolymph spaces, and ovoidal reserve cells containing large multilobular nuclei. A layer of basal lamina was visible immediately under the connective tissue.

Stage A_2 (fig. 2B). — This stage was characterized by the completion of two layers: epicuticle and exocuticle. The epicuticle was composed of two distinctive laminae, the outer lamina being much thinner than the inner lamina. The exocuticle was composed of thick, stratified layers. The epithelial cells began to transform into tonofibrils. As the number of tonofibrils increased, the nucleus was displaced to the periphery of the cell. This stage was deemed to end when a thin layer of the endocuticle started to develop. The border between the exocuticle and endocuticle appeared irregular. The epithelial cells, at their maximum length, started to reduce in length. The tonofibrils inserted into the basal surface of the developing endocuticule.

Stage B_{1-2} (fig. 2C). — At this stage, three cuticular layers (epicuticle, exocuticle, and endocuticle) and epithelium with lacunar connective tissue were observed. The epicuticle was bilaminate consisting of two layers of a comparable thickness: an outer light and an inner dark layer. During this stage, the development of the endocuticle was observed. The exocuticle and endocuticle appeared to have the same thickness. The border between the exocuticle and endocuticle became regular. The
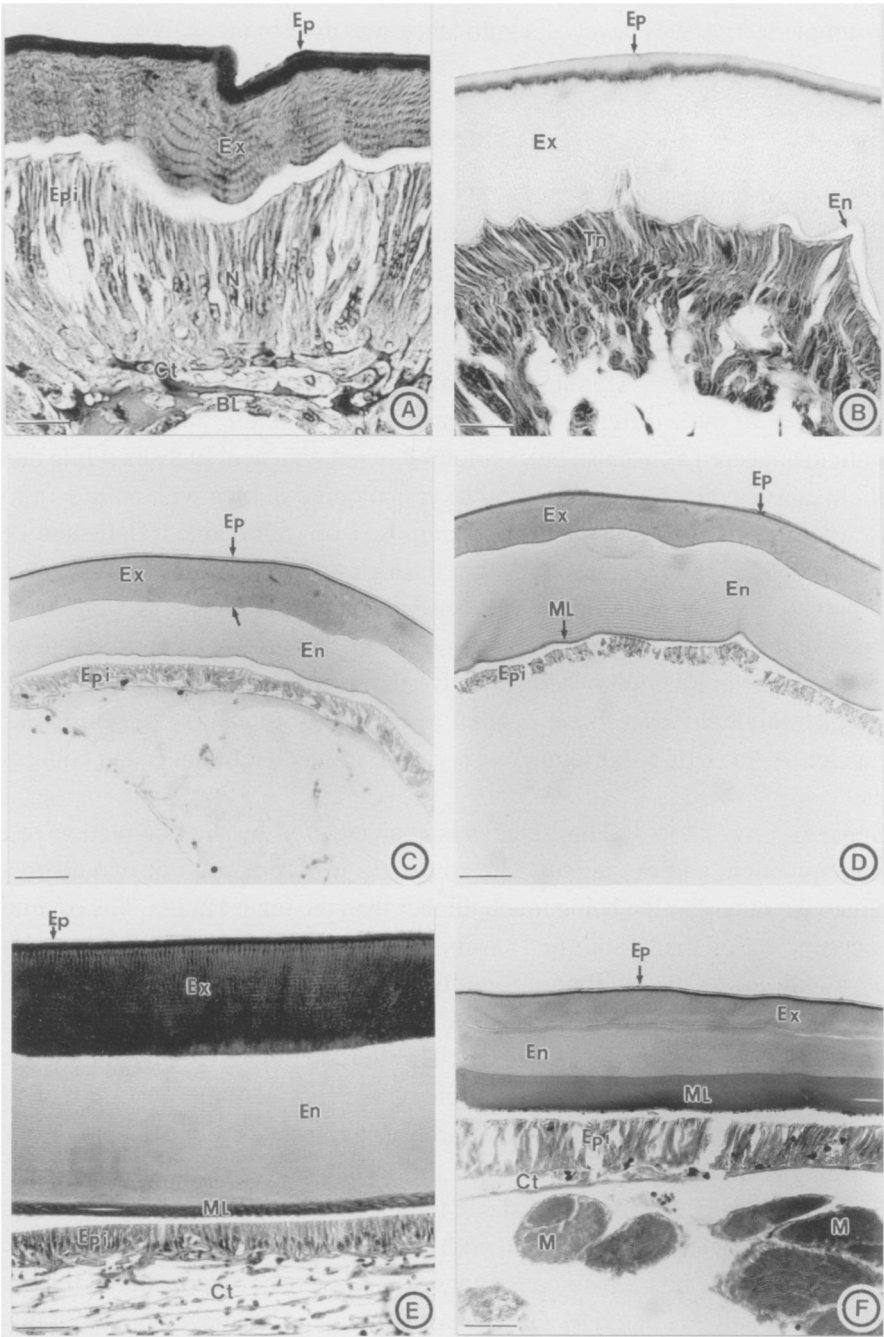
exocuticle appeared in dark blue, while the endocuticle in light blue, both stained with aniline in Masson's trichrome. The epithelium was composed of a single layer of cells with peripheral nuclei. A layer of spongy connective tissue lay below the haemal lacunae.

Stage C_{1-2} (fig. 2D). — This stage was characterized by the growth of the endocuticle layer and this layer became much thicker than the exocuticle. This layer was composed of numerous parallel, fibrous laminae oriented in the plane of the section. The membranous layer started to appear as a thin dark line below the epithelium. The border between the endocuticle and the membranous layer was clearly visible. The epithelial cells were squamous. At the end of this stage, the formation of the endocuticle layer was completed.

Stage C_3 (fig. 2E). — The amorphous zone of the membranous layer continued to develop and appeared as a dark line above the apical surface of the epithelium. The exocuticle was stained darker with blue aniline. The epithelium was composed of simple cuboidal cells containing basally located oval nuclei. The cytoplasm of the cells appeared to be homogeneous. The connective tissue beneath the epithelium contained numerous collagen fibres.

Stage C_4 (fig. 2F). — At this stage, the exoskeleton was fully developed and composed of four distinct layers, epicuticle, exocuticle, endocuticle, and the innermost membranous layer. The thickness of the membranous layer was approximately the same as that of the exocuticle and the endocuticle was the thickest layer. The epithelial cells continued to increase in height. The nuclei of the epithelial cells had distinct nucleoli. Acidophilic granules appeared in the cytoplasm. Through the post-ecdysial period, the epithelial cells continued to decrease in height and reached at this stage their minimum level. The connective tissues and the muscular fibres were fully developed.

Stage D_0 (fig. 3A). — This stage began with the separation of the epithelium from the cuticle. The epithelium was composed of a single layer of the elongated cells. The nuclei were enlarged and situated toward the center. At the apical surface of the cells, the granules in the cytoplasm of the cell secreted amorphous moulting fluid. The presence of this fluid was observed as a thin layer deposited in the space between the cuticle and the epithelium. The membranous layer began to be partially and lightly separated from the cuticle. At this stage, no activity of resorption of the old cuticle was observed.

Fig. 2. Integument structures of post and intermoult periods in the snow crab, *Chionoecetes opilio* (O. Fabricius, 1788). A, stage A_1 (scale bar = 35 μm); B, stage A_2 (scale bar = 45 μm); C, stage B_{1-2} (scale bar = 150 μm); D, stage C_{1-2} (scale bar = 185 μm); E, stage C_3 (scale bar = 65 μm); and F, stage C_4 (scale bar = 200 μm). Epi, epithelium; En, endocuticle; Ep, epicuticle; Ex, exocuticle; ML, membranous layer; Ct, connective tissue; N, nuclei; BL, basal lamina; Tn, tonofibrils; M, muscle fibre.
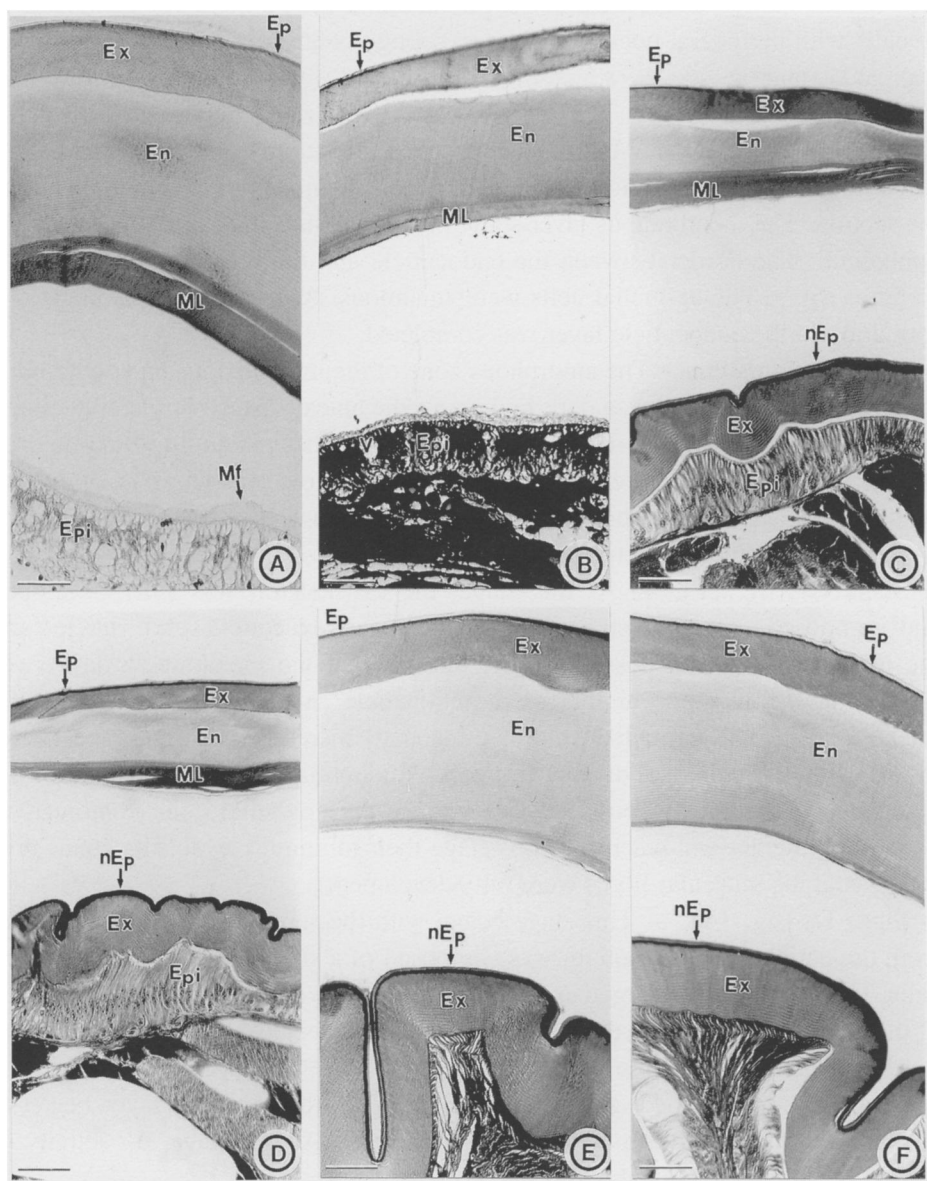
Fig. 3. Integument structures of premoult period in the snow crab, *Chionoecetes opilio* (O. Fabricius, 1788). A, stage D_0 (scale bar = 100 μm); B, stage D_1 (scale bar = 200 μm); C, substage $D_{2'}$ (scale bar = 200 μm); D, substage $D_{2''}$ (scale bar = 200 μm); E, stage D_3 (scale bar = 85 μm); F, stage D_4 (scale bar = 85 μm). Epi, epithelium; En, endocuticle; Ep, epicuticle; Ex, exocuticle; Mf, moulting fluid; ML, membranous layer; nEp, new epicuticle; nEx, new exocuticle.

Stage D_1 (fig. 3B). — This stage was characterized by a complete retraction of the epithelium from the membranous layer with a continuous secretion of moulting fluid. The epithelial cells increased in size. The cytoplasm was acidophilic containing large inclusions and numerous vacuoles appeared toward the apex of the cells. The intense secretion of the moulting fluid continued, showing the accumulation of a thin layer on the apical surface of the epithelial cells. The layer of connective tissue appeared densely stained, and contained abundant granules. At this stage a partial resorption of the membranous layer began. At the end of this stage, the new epicuticle, stained in red, became evident.

Stage D_2 was subdivided into two substages ($D_{2'}$ and $D_{2''}$). Substage $D_{2'}$ (fig. 3C). — This stage was marked by the progressive formation of two new layers of the cuticle underneath the old one. The outer layer, new epicuticle, appeared dark, and the inner layer, new exocuticle, was composed of stratified fibrils. The epithelial cells continued to increase in height. The central nuclei were oval with one or more nucleoli. A thick basal lamina separated the epithelium from the connective tissues and the muscle fibres. The degradation of the old cuticle and the resorption of the membranous layer continued. The resorption of the endocuticle layer also started at this stage.

Substage $D_{2''}$ (fig. 3D). — The new cuticle started to display many small cuticular folds. The new epicuticle and exocuticle layers continued to develop and thicken. The epithelium was composed of high columnar cells with their nucleus located in the centre of the cell. The connective tissues were filled with haemolymphatic lacunae. A progressive degradation of the old cuticle continued. The secretion of epicuticle and exocuticle was completed at the end of this stage.

Stage D_3 (fig. 3E). — During this stage, many compact, U-shape folds of the newly formed cuticle appeared under the old exoskeleton. The new exocuticle continued to increase in thickness while the membranous layer had almost disappeared. The epithelial cells became narrower and elongated. The thickness of the new cuticle was approximately one-third of that of the old cuticle.

Stage D_4 (fig. 3F). — This stage was the preparatory phase for exuviation. The membranous layer completely disappeared. The epithelial cells reached their maximum length to support the newly formed layer of cuticle.

Moult stage duration

No significant difference (Student's *t*-test, $P > 0.05$) was found in the duration of each postmoult stage between the adolescent and adult males (table I). The mean duration in day $\pm$ standard deviation (SD) of each postmoult stage from ecdysis to intermoult C_4 for male snow crabs moulted in the aquarium was 0.79 ± 0.58 in stage A_1, 6.66 ± 6.78 in stage A_2, 16.78 ± 5.51 in stage B_{1-2}, 45.37 ± 12.96 in stage C_{1-2}, 63.79 ± 12.68 in stage C_3 and 70.06 ± 11.60 in intermoult stage C_4 (table I).

M. HÉBERT ET AL.

TABLE I

Mean duration in day $\pm$ standard deviation of each postmoult stage (A_1, A_2, B_{1-2}, C_{1-2}, C_3) and intermoult stage C_4 for adolescent and adult male snow crabs, *Chionoecetes opilio* (O. Fabricius, 1788), moulted in the aquarium and comparisons of the mean duration between adolescent, and adult at each moulting stage by Student's *t*-test

Stage	Adolescent (in days)	Number of observations	Adult (in days)	Number of observations	Student's *t*-value	Student's *P*-value	Mean duration (in days)
A_1	0.80 ± 0.63	10	0.75 ± 0.50	4	0.140^{NS}	0.891	0.79 ± 0.58
A_2	4.67 ± 2.50	15	8.41 ± 8.75	17	-1.598^{NS}	0.121	6.66 ± 6.78
B_{1-2}	17.26 ± 5.42	86	15.98 ± 5.63	51	1.312^{NS}	0.192	16.78 ± 5.51
C_{1-2}	44.54 ± 12.73	101	46.91 ± 13.37	54	-1.082^{NS}	0.281	45.37 ± 12.96
C_3	63.07 ± 13.30	53	64.94 ± 11.70	33	-0.661^{NS}	0.510	63.79 ± 12.68
C_4	68.04 ± 11.82	25	75.10 ± 9.81	10	-1.669^{NS}	0.105	70.06 ± 11.60

Statistical comparison between group, $*$ = significance at $P = 0.05$, NS = non-significant.
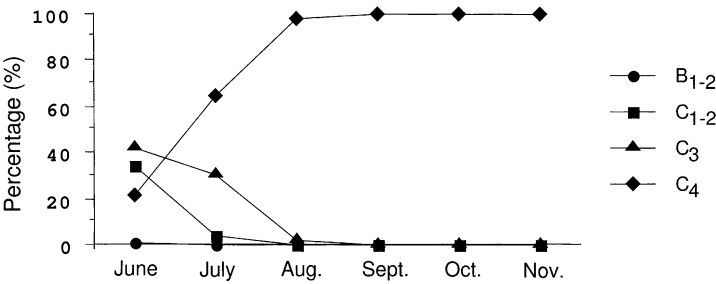

Fig. 4. Percentages of male snow crab, *Chionoecetes opilio* (O. Fabricius, 1788), per moult stages caught during the monthly trawl survey between 1990 and 1992 in the southern Gulf of St. Lawrence.

The percentage of postmoult male crabs per moult stage caught during the monthly trawl surveys from 1990 to 1992 showed that postmoult male crabs in stage B_{1-2} in June were at 1.1% and almost all postmoult crabs (97.5%) reached intermoult C_4 by August (fig. 4). The percentage of postmoult crabs in moult stages C_{1-2} and C_3 was more important in June (34.0 and 42.7%, respectively). The percentage of these two categories fell to 0 and 2.5% in August. The mean carapace hardness increased from June to November in each moult stage for postmoult adolescent and adult male crabs (fig. 5). The mean carapace hardness for postmoult adult crabs reaching intermoult C_4 was continuously increasing from 60 to 85 units between June and November, while the mean carapace hardness for adolescent in intermoult C_4 reached a plateau in June at values between 60 to 65 units. No significant difference (Student's *t*-test, $P = 0.748$) in the mean carapace hardness was observed between adolescent and adult postmoult males in stage B_{1-2}. The mean carapace hardness between adolescents and adults was significantly different (Student's *t*-test, $P < 0.05$) in stages from C_{1-2} to intermoult C_4 (table II). The
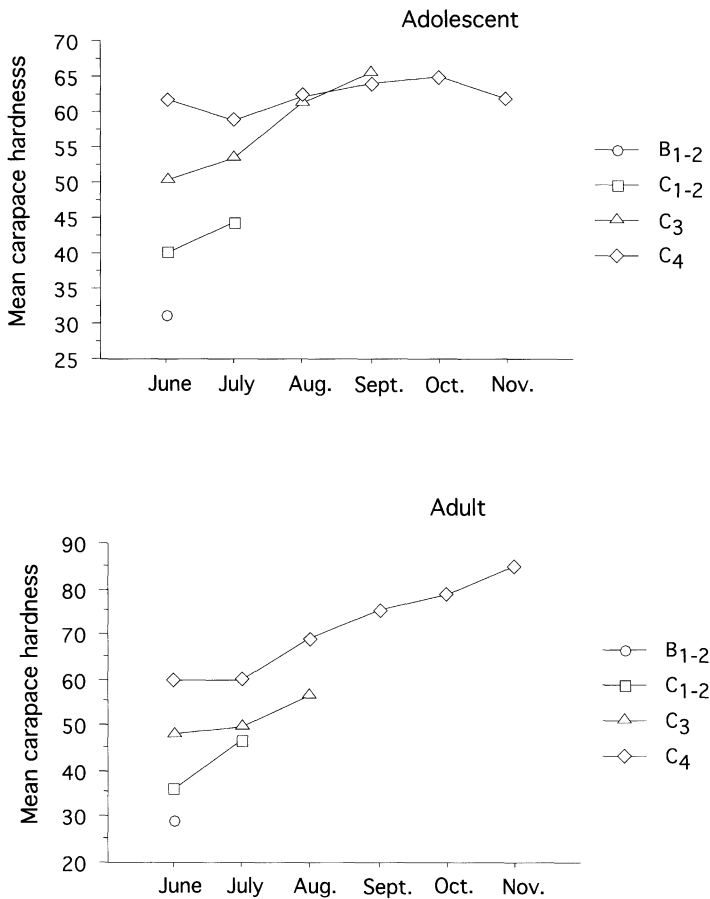
Adolescent

Adult

Fig. 5. Mean carapace hardness at each moult stage for adolescent and adult male snow crab, *Chionoecetes opilio* (O. Fabricius, 1788), caught during the monthly trawl survey between 1990 and 1992 in the southern Gulf of St. Lawrence.

mean carapace hardness was significantly higher in adolescent than in adult males in postmoult stages C_{1-2} ($P < 0.011$) and C_3 ($P < 0.0001$), but at intermoult stage C_4, the mean carapace hardness was significantly higher ($P < 0.0001$) in adult than in adolescent males (table II).

Size-weight relationship

The comparison of regressions between adolescents and adults of the "New" category (table III, fig. 6) showed that the slopes were not significantly different (F = 0.728, $P > 0.05$) but elevations were significantly different (F = 35.931, $P < 0.05$). Both N-Ado (mean weight at 95 mm CW, $W_{95} = 317.9$ g) and N-Adu ($W_{95} = 305.5$ g) were significantly heavier than the other groups (table III, fig. 6). Comparison of regressions between adolescents ($W_{95} = 267.9$ g) and adults

TABLE II

Mean carapace hardness (mean ± standard deviation) at each postmoult (B_{1-2}, C_{1-2}, C_3) and intermoult (C_4) stages, for adolescent and adult snow crabs, *Chionoecetes opilio* (O. Fabricius, 1788), caught during the monthly trawl survey between 1990 and 1992 in the southern Gulf of St. Lawrence and comparisons of the mean carapace hardness between adolescent, and adult at each moult stage by Student's *t*-test

Stage	Adolescent (unit)	Number of observations	Adult (unit)	Number of observations	Student's *t*-value	Student's *P*-value
B_{1-2}	31.25 ± 10.81	4	29.00 ± 3.61	3	0.339[NS]	0.748
C_{1-2}	40.27 ± 8.09	159	37.06 ± 9.96	69	2.563*	0.011
C_3	51.88 ± 6.25	287	48.91 ± 7.05	124	4.24*	<0.0001
C_4	62.55 ± 7.12	1436	71.73 ± 13.32	473	−19.133*	<0.0001

Statistical comparison between group, * = significance at $P = 0.05$, NS = non-significant.

TABLE III

Comparisons of size-weight relationships regression equations by ANCOVA between "New-adolescent", "New-adult", "Intermediate-adolescent", "Intermediate-adult", and "Old-adult" groups of *Chionoecetes opilio* (O. Fabricius, 1788)

Groups compared	F-value for slope	df	F-value for elevation	df
New-adolescent vs. New-adult	0.728[NS]	1,145	35.931*	1,146
New-adolescent vs. Intermediate-adolescent	5.549*	1,122	–	–
New-adolescent vs. Intermediate-adult	8.219*	1,116	–	–
New-adolescent vs. Old-adult	6.711*	1,277	–	–
New-adult vs. Intermediate-adolescent	12.860*	1,147	–	–
New-adult vs. Intermediate-adult	6.777*	1,141	–	–
New-adult vs. Old-adult	7.302*	1,302	–	–
Intermediate-adolescent vs. Intermediate-adult	0.904[NS]	1,118	10.795*	1,119
Intermediate-adolescent vs. Old-adult	7.323*	1,279	–	–
Intermediate-adult vs. Old-adult	0.450[NS]	1,273	2.899[NS]	1,274

Statistical regression comparison between groups, *= significance at $P = 0.05$, NS = non-significant.

($W_{95} = 280.7$ g) of the "Intermediate" category did not show significant difference in the slopes (F = 0.904, $P > 0.05$) but showed significant difference in the elevations (F = 10.795, $P < 0.05$). The I-Adu group did not differ significantly from the O-Adu group ($W_{95} = 286.1$ g; table III). However, the I-Ado group was significantly lighter than O-Adu (table III). The relationships of the O-Adu and I-Adu groups were combined, since no significant differences ($P > 0.05$) were found neither in the slopes nor in the elevations (table III, fig. 6).
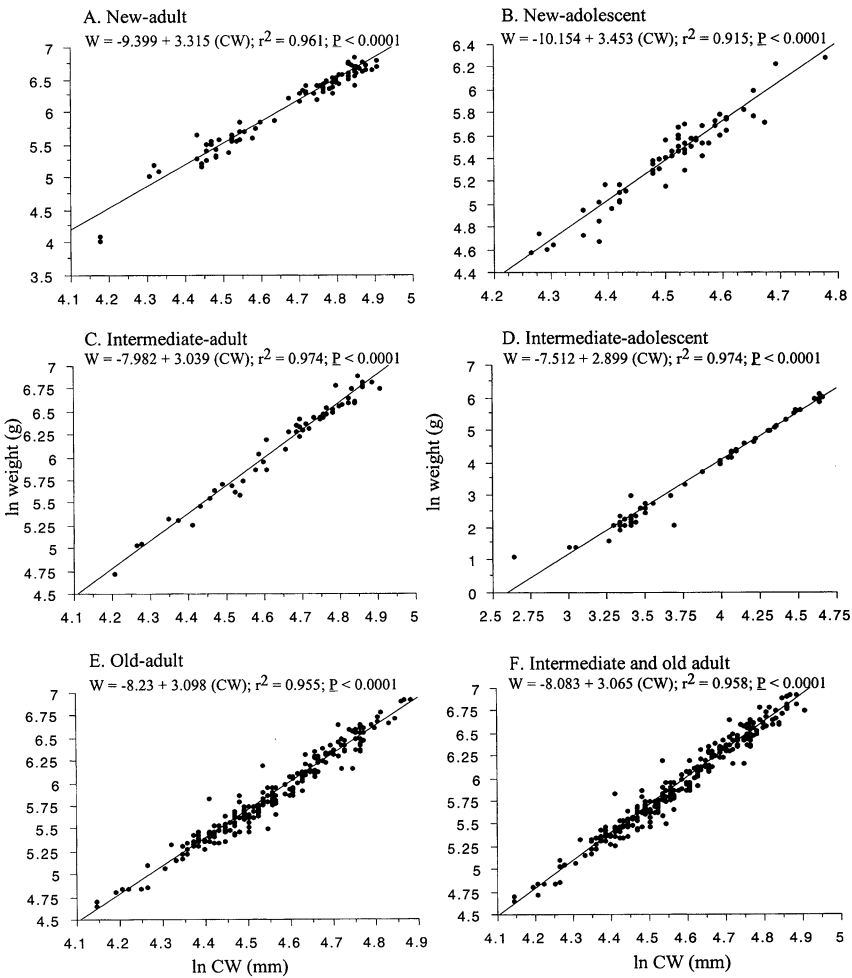
Fig. 6. Regressions between the carapace width (mm) and the total wet-weight (g) for different groups of male snow crab, *Chionoecetes opilio* (O. Fabricius, 1788), in the southern Gulf of St. Lawrence (logarithmic scales).

Moulting period

Direct observations of moulting in the laboratory showed that the moulting activities for immature and adolescent type I males (normal moulters) started in January and ended in May with a peak observed in March. Moulting activity of type II males (skip moulters) started in December peaking in January and ended in March (fig. 7). A significant difference in the monthly moulting frequency was observed between type I and II males (Kolmogorov-Smirnov test, $D = 0.58$, $P < 0.001$).

M. HÉBERT ET AL.

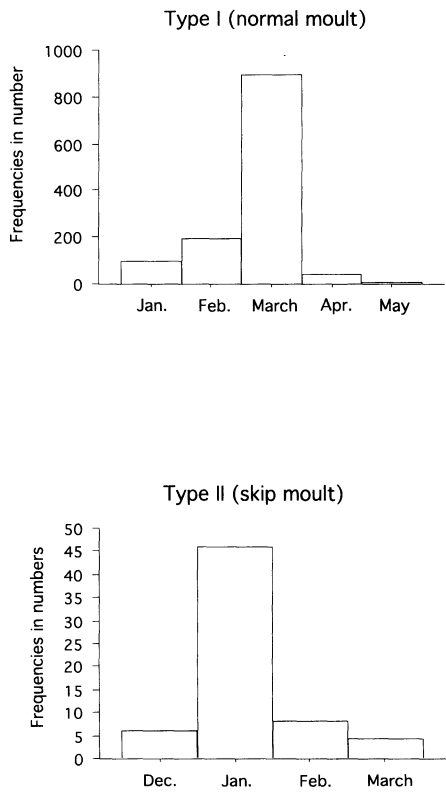Type I (normal moult)

Type II (skip moult)

Fig. 7. Monthly moulting frequency of adolescent male snow crabs, *Chionoecetes opilio* (O. Fabricius, 1788), observed in the aquarium.

Growth at moult

Hiatt's (1948) growth model was fitted to the moulting data (carapace growth per moult) of type I males moulting to the immature, adolescent, and adult phases and for type II males moulting to the adolescent and adult phases (table IV). There were no immature males in type II (skip moulters).

For type I males, a reduction of carapace growth per moult occurred between the immature and adolescent phases, and between the adolescent and adult phases. There was a change in allometry marked by an angular point around 40.5 mm CW at which a reduction of growth occurred (transitional phase between immature and adolescent). The slope of the regression for the immature phase was significantly steeper ($F = 30.73$, $P < 0.05$) than that for the adolescent phase (table V, fig. 8). Comparison of carapace growth at the moult between the adolescent and adult phases showed that the slopes were not significantly different ($F = 0.002$, $P > 0.05$) but the elevations were significant ($F = 115.141$, $P < 0.05$) indicating the second change in growth pattern at the transitional phase from adolescent to adult (table V, fig. 8).

TABLE IV

Hiatt's (1948) growth model and the percentage of growth increment (PGI) and premoult carapace width (L_t) equations for type I males moulting to the immature, adolescent, and adult phases and for type II males of *Chionoecetes opilio* (O. Fabricius, 1788) moulting to the adolescent and adult phases

Male type	Moulting phase	Hiatt's growth model	r^2	P-value	PGI vs. L_t equation	r^2	P-value
Type I	Immature	$L_{t+1} = 1.294L_t + 0.689$*	0.931	<0.0001	$PGI = -0.107L_t + 35.046$NS	0.007	<0.1025
Type I	Adolescent	$L_{t+1} = 1.086L_t + 8.189$*	0.894	<0.0001	$PGI = -0.210L_t + 35.486$*	0.121	<0.0001
Type I	Adult	$L_{t+1} = 1.085L_t + 4.446$*	0.919	<0.0001	$PGI = -0.630L_t + 19.271$*	0.027	<0.0003
Type II	Adolescent	$L_{t+1} = 1.107L_t + 5.485$*	0.931	<0.0001	$PGI = -0.112L_t + 26.449$NS	0.059	<0.4711
Type II	Adult	$L_{t+1} = 1.101L_t + 5.770$*	0.890	<0.0001	$PGI = -0.080L_t + 23.744$NS	0.033	<0.3351

Statistical regression comparison, * = significance at $P = 0.05$, NS = non-significant.
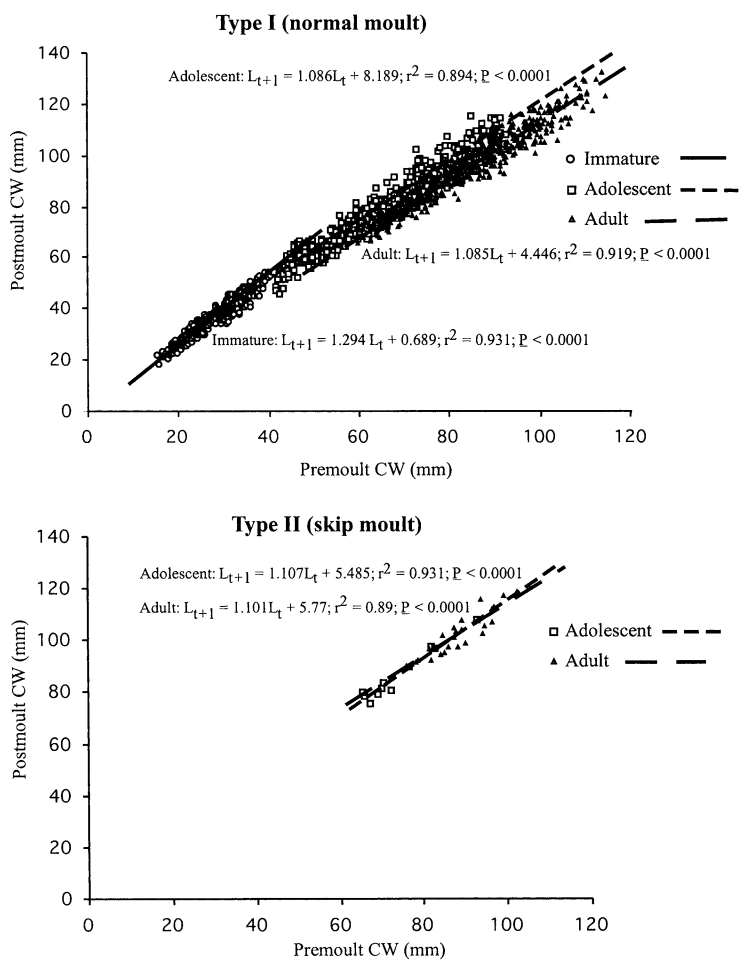
Fig. 8. Growth at moult in carapace width in male snow crabs, *Chionoecetes opilio* (O. Fabricius, 1788), of types I and II observed in the aquarium.

For type II males, comparison of carapace growth at the moult between the adolescent and adult phases showed no significant difference, neither in the slopes (F = 0.002, P > 0.05) nor in the elevations (F = 0.008, P > 0.05), indicating that homogeneous growth pattern throughout the adolescent and adult phases (table V, fig. 8).

Comparison of regressions of the carapace growth at moult for those moulting to the adolescent phase showed no significant difference between type I and II males, neither in the slopes (F = 0.013, P > 0.05) nor in the elevations (F = 0.675, P > 0.05, table V). However, comparison of regressions for those moulting to the adult phase showed no significant difference in the slopes (F = 0.030, P > 0.05) but a significant difference in the elevations (F = 12.939, P < 0.05), indicating

TABLE V

Comparisons of Hiatt's (1948) growth equations by ANCOVA for type I males of *Chionoecetes opilio* (O. Fabricius, 1788) moulting to the immature, adolescent, and adult phases and for type II males moulting to the adolescent, and adult phases

Male types compared	Moulting phase compared	F-value for slope	df	F-value for elevation	df
Within Type I	Immature vs. Adolescent	30.726*	1,867	–	–
Within Type I	Adolescent vs. Adult	0.002[NS]	1,971	115.141*	1,972
Within Type II	Adolescent vs. Adult	0.002[NS]	1,37	0.008[NS]	1,38
Type I vs. Type II	Within Adolescent	0.013[NS]	1,503	0.675[NS]	1,504
Type I vs. Type II	Within Adult	0.030[NS]	1,505	12.939*	1,506

Statistical regression comparison between groups, * = significance at $P = 0.05$, NS = non-significant.

TABLE VI

Means and standard deviations (SD) of the percentage of growth increment for type I males moulting to the immature, adolescent, and adult phases and for type II males moulting to the adolescent and adult phases, of *Chionoecetes opilio* (O. Fabricius, 1788). Comparisons of the mean percentage of growth increment between moulting groups by Mann-Whitney's test (*U*-test) are indicated below

Moulting phase	N	Means	SD
Immature (type I)	375	32.033	7.510
Adolescent (type I)	496	21.674	8.070
Adult (type I)	479	13.942	4.836
Adolescent (type II)	11	16.801	3.608
Adult (type II)	30	18.310	4.151

Male types compared	Moulting phases compared	Z-value	P-Value
Within Type I	Immature vs. Adolescent	−16.581*	<0.0001
Within Type I	Adolescent vs. Adult	−16.053*	<0.0001
Within Type II	Adolescent vs. Adult	−0.912[NS]	0.3617
Type I vs. Type II	Within Adolescent	−1.650[NS]	0.1000
Type I vs. Type II	Within Adult	−3.349*	0.0008

Statistical comparison between groups, * = significance at $P = 0.05$, NS = non-significant.

that type II males have a significantly different growth pattern compared to type I males at moult to the adult phase (table V).

For type I males, the MPGI was significantly higher for individuals moulting to the immature phase than for those moulting to the adolescent phase (*U*-test, $P < 0.0001$; table VI, fig. 9). There was also a significantly higher MPGI for individuals moulting to the adolescent phase than for those moulting to the adult
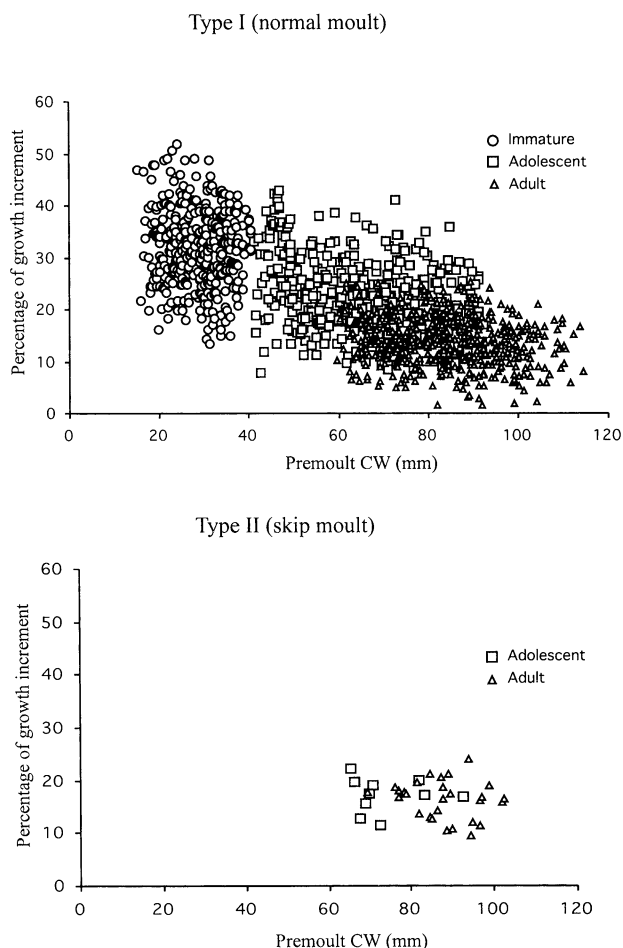
Type I (normal moult)

Type II (skip moult)

Fig. 9. Percentage of growth increment (PGI) versus premoult CW (mm) in male snow crabs, *Chionoecetes opilio* (O. Fabricius, 1788), of types I and II observed in the aquarium.

phase (U-test, $P < 0.0001$; table VI, fig. 9). For type II males, no significant difference in the MPGI was found between individuals moulting to the adolescent or adult phases (U-test, $P = 0.362$; table VI, fig. 9). Between type I and type II males, there was no significant difference in the MPGI for those moulting to the adolescent phase (U-test, $P = 0.1$; table VI, fig. 9) but a significantly higher MPGI was found for those moulting to the adult phase (U-test, $P = 0.0008$) showing a significantly higher moult increment for those that had skipped a moult in the previous moulting season.

No significant linear relationship was found between the PGI and the premoult CW, regardless of the moulting phase (moulting to the immature, adolescent, and adult phases) or male types (type I or II) (table VI, fig. 9).

DISCUSSION

Moult stage determination

Moult stage determination of the snow crab by observations of the exoskeleton morphology confirms Drach's (1939) observations on *Cancer pagurus* Linnaeus, 1758, as well as Skinner's (1962) on *Gecarcinus lateralis* (Fréminville, 1835) and Stevenson's (1968) on *Orconectes sanbornii* (Faxon, 1884). Stage A immediately follows ecdysis and is divided into two stages (A_1 and A_2). During this stage, the exoskeleton is completely soft and the crab displays no feeding activity (Passano, 1960; O'Halloran & O'Dor, 1988) and cannot be caught using conventional traps. Stage B consists of two stages (B_1 and B_2) during which the cuticle seems to thicken faster (Stevenson, 1972). No universal criteria are available for the determination of stages B_1 and B_2 using histological observations of the cuticle (Stevenson, 1968, 1972, 1985; O'Halloran & O'Dor, 1988). Drach & Tchernigovtzeff (1967) discriminated stages B_1 and B_2 by observing the formation of an internal cone in the setae of *Palaemon serratus* (Pennant, 1777), which could not be observed in snow crab (Moriyasu & Mallet, 1986). Some authors used external variation of carapace characteristics, such as rigidity and colour, to distinguish stages B_1 and B_2 (Haefner & Van Engel, 1975; Stevenson, 1985). The latter technique would not be adequate for the snow crab, since its carapace is relatively soft compared to that of other brachyuran species. In general, no evident changes in cuticular morphology can be observed between stages A_2 and B_{1-2}. The only criteria used to distinguish those two stages are the observation of (1) the development of the endocuticle at stage B_{1-2}, (2) an irregular (stage A_2) vs. regular (stage B_{1-2}) border between the exocuticle and endocuticle. The irregularity in this border in stage A_2 may be attributed to the progress in endocuticle development. Stage C is generally divided into four stages (C_1, C_2, C_3, and C_4). It is difficult to identify C_1 and C_2 by either histological techniques (Aiken, 1980) or observation of shell rigidity (O'Halloran & O'Dor, 1988). Moriyasu & Mallet (1986) and O'Halloran & O'Dor (1988) could not discriminate stage C_1 from stage C_2 on the basis of setal morphogenesis. Drach (1939) used the degree of flexibility of the carapace and the pereiopods in *Cancer pagurus* in order to distinguish stage C_1 from C_2. Stevenson (1968) proposed the completion of chemical changes in the pre-ecdysial cuticle as a universal criterion for stage C_1. However, it requires external observation of recognizable modifications correlated with internal chemical changes. These techniques do not apply to the snow crab since no evident modifications in external characteristics were observed. At stage C_4, the integument attains its final stage of rigidity (Stevenson, 1985; O'Halloran & O'Dor, 1988). It is generally agreed that a terminal moult (stage C_4T) occurs in snow crab (Conan & Comeau, 1986) and in other oxyrhynchs

(Skinner, 1985). The membranous layer is secreted last during the integumental development process and is morphologically different in *Pachygrapsus crassipes* (Randall, 1840) between stages C_4 and C_4T (Hiatt, 1948). However, no evident difference was observed in the integumental structure between adolescent (non-terminal moulted) and adult (terminal moulted) crabs at stage C_4.

Stage D is divided into five stages (D_0, D_1, D_2, D_3, and D_4). Dawe et al. (1992) noted the difficulty of objectively identifying the early premoult stages (D_0-D_1) based on setagenesis observations. Benhalima et al. (1998) identified new criteria to determine the early-premoult stage (D_0) in snow crab by histology. This technique relies on histological observations of a semitransparent substance (moulting fluid) secreted from the epithelial cells in the space between the cuticle and the epithelium. Our study confirms that criterion is a useful tool to determine the early premoult stage. Stage D_1 is characterized by the resorption of the membranous layer of the exoskeleton. In contrast to stage D_0, stages D_3 and D_4 are marked by the absence of synthesis of new exoskeleton. Throughout these stages, marked cytological modifications were visible between the hypertrophy of the epithelium (indicating the beginning of the degradation of the old exokeleton) and formation of the new epicuticle and exocuticle.

Histology is an accurate technique to determine the moult stages throughout the moult cycle of snow crab, which may provide indicators to predict the moulting period and timing when soft-shelled crabs enter commercial traps. This information is useful for managers and for the fishing industry to optimize the fishery without causing any damage or mortality on soft-shelled crabs.

Postmoult duration and moulting period

The identification of the moulting period and the duration of each moult stage throughout the moult cycle are important, since the catchability of male snow crab varies in relation to their moult stages. According to O'Halloran & O'Dor (1988), the snow crab in postmoult period enters commercial traps during stages B_{1-2} and C_{1-2}, one to two months after the moult. Until now, the duration of each moult stage for snow crab has not been precisely estimated. For instance, Watson (1971) only observed a single snow crab to estimate the period between moult and intermoult while O'Halloran & O'Dor (1988) observed the duration of each moult stage with a small number of snow crabs without any reference to their morphometric maturity. Our results on moult stage duration of male snow crab observed in the aquarium indicated that postmoult duration was shorter than what was observed earlier by O'Halloran & O'Dor (1988). They estimated from laboratory studies that commercial size males took 12 to 16 weeks to reach the intermoult stage C_4, by examining the changes in carapace hardness throughout the postmoult period. In our study, under the same temperature conditions, males took approximately 11

weeks to reach intermoult stage C_4. However, heterogeneous rearing conditions, especially water temperature, make a comprehensive comparison of output, e.g., the duration of each moult stage, extremely difficult and such comparison should be made with much caution. Although adult male crabs reached stage C_4 later than adolescent males, the duration of each postmoult stage from ecdysis was not significantly different between adolescent and adult crabs. However, observations obtained from the monthly trawl surveys conducted between June and October from 1990 to 1992 suggest that the duration from ecdysis to intermoult C_4 for males was longer than what we observed in the aquarium. According to those survey results, most of the postmoult males reached intermoult C_4 in August while the percentages of postmoult males in stages C_{1-2} and C_3 in June were at 34 and 42.7%, respectively. This suggests that: (1) postmoult duration is 3 to 4 months in the wild (if moulting activity peaks in March, as observed in the aquarium), or (2) moulting activity could probably occur during mid-April and May (later than what was observed in the aquarium).

Our results on moulting activity for male snow crab appear more complex than what Watson (1972) and Conan et al. (1988) observed. These authors showed that the moulting period occurred in February-April in the southern Gulf of St. Lawrence. Inter-annual variations in moulting patterns for adolescent males have been observed by Sainte-Marie et al. (1995) and Benhalima et al. (1998). Sainte-Marie et al. (1995) for instance, observed that the moulting activity shifts from winter to spring for adolescent males > 40 mm CW compared to smaller individuals for which moulting activity peaked in April-May in the northern Gulf of St. Lawrence. According to Benhalima et al. (1998), two distinct patterns of moulting in adolescent males may occur at different times of the year in the southern Gulf of St. Lawrence. They indicated that the majority of adolescent males (type I) moult in March and April, while a small group with more epibionts on the carapace (type II) called skip moulters probably moult in December-January. In our study, two distinct moulting patterns were observed for adolescent male crabs in the aquarium. Moulting of adolescent males of type I started in January, peaked in March and ended in May. Adolescent males that had not moulted in the previous year (type II) moulted earlier in December, peaked in January and ended in March. Inter-annual variations in moulting patterns may be related to environmental factors, genetic variations in crab groups, or intraspecific relationships such as density-dependent factors (Benhalima et al., 1998; Comeau et al., 1998).

The mean carapace hardness for postmoult adult males having reached intermoult stage C_4 continuously increased from June to November indicating that carapace hardening progresses after reaching the intermoult stage C_4. Our results suggest that in nature, a soft-shelled adult male may reach its maximal carapace hardness in about 8 to 9 months after ecdysis. This period is longer than what was observed by Watson (1971) and Taylor et al. (1989) on commercial-size adult males.

Watson (1971) observed that a soft-shelled commercial-size adult male reached a hard-shelled condition in 8 to 12 weeks. Taylor et al. (1989) observed, based on a capture/recapture study in Bonavista Bay (Newfoundland, Canada), that it took about 3-4 months for soft-shelled crabs of commercial size to reach a hard-shelled condition. Contrary to O'Halloran & O'Dor (1988), Mayrand et al. (2000) observed in the aquarium that snow crab held at 3°C began to feed as early as five days after moulting. According to Mayrand et al. (2000), energy expenditure for maintenance metabolism, such as carapace thickening and tissular reorganization, was high during the first weeks after ecdysis (5 to 25 days), while somatic and gonadal production were low. Twenty-five days after ecdysis, energy expenditure is allocated first to gonadal production, then to muscle growth and the accumulation of reserves in the digestive gland. This suggests that snow crabs have the capability to search for food and enter commercial traps as early as late stage B_{1-2} (Passano, 1960; O'Halloran & O'Dor, 1988). In our study, it took about 3 weeks for postmoult males to reach stage B_{1-2}, compared to one month as observed by O'Halloran & O'Dor (1988).

Size-weight relationship

A significantly heavier weight at a given size of "New" category males compared to those in "Intermediate" regardless of their maturity status (adolescent or adult) can be explained by the large amount of water contained in the body of the former compared to the latter. Therefore, size-weight relationships for males in the "New" category should be treated separately from those in other categories. Once crabs reach moult stage C_3 (Intermediate category), the adolescent group should be separated from the adult group, while the Intermediate-adult group is similar to the Old-adult group. However, this does not necessarily mean that males in the Intermediate-adult group have the same meat content as those in the Old-adult group. The meat yield in the fall (Dufour et al., 1997) showed a lower meat percentage in the Intermediate-adult group compared to the Old-adult group. Taylor & Warren (1991) studied the effect of shell condition on weight of legal-sized males off the east coast of Newfoundland from August to October. Conversely to our results, they found that the shell condition of males had little effect on crab weight as the size-weight relationships were not significantly different between soft-shelled, new-hard, and old-hard shelled males.

Growth at moult

Growth increment in carapace size of male snow crab is influenced by sexual (presence of spermatophores in the vas deferens) and morphometric maturity (allometric change in CH/CW relationship). Some authors, however, did not consider sexual or morphometric maturity in their growth models (Kon et al., 1968;

Ito, 1970 for *Chionoecetes opilio elongatus* Rathbun, 1924; Miller & Watson, 1976; Hoenig et al., 1994 for *C. opilio*). Comeau et al. (1998) observed that growth at moult for a normal moult or a terminal moult in adolescent males does not seem to follow a fixed pattern. In contrast, Sainte-Marie et al. (1995) observed that growth at moult seems to be identical for a normal or a terminal moult at a given adolescent male size. The estimated growth at moult by Sainte-Marie et al. (1995) and Comeau et al. (1998) were much higher (about 10-30%) compared to previous laboratory and field studies (Miller & Watson, 1976; Taylor & Hoenig, 1990; Hurley et al., 1990).

In our study, a reduction of carapace growth rate occurred in type I males at the transitional moult from the immature to the adolescent phase (puberty moult). This reduction of carapace growth at the puberty moult was also observed by Comeau & Conan (1992), Sainte-Marie et al. (1995), and Comeau et al. (1998). In crustaceans, the energy allocated for somatic growth is diverted to gonadal development during the puberty phase resulting in a reduction of growth as suggested by Wolff & Soto (1992), Sainte-Marie et al. (1995), and Mayrand et al. (2000). The size at which a reduction of carapace growth at moult occurred from the immature to adolescent phases was at a premoult CW of 40.5 mm, which is higher than the values of 36.6 and 36.7 mm CW observed by Sainte-Marie et al. (1995) and Comeau et al. (1998), respectively.

A reduction of carapace growth also occurred in type I males from adolescent to adult phases (terminal moult). Significantly larger moult increments were observed for individuals moulting to a regular moult (adolescent phase) than for individuals moulting to a terminal moult (adult phase). In contrast, similar carapace growth increments occurred for type II males moulting to the adolescent or adult phases. The carapace growth at moult between type I and II males was comparable for those moulting to the adolescent phase, but higher than growth for type II males moulting to the adult phase. This phase-dependent differential growth increment (skip moult, type II, to terminal moult phase or normal moult, type I, to the terminal moult phase) cannot be explained with the current knowledge on the moulting process in snow crab. Comeau et al. (1998) observed that the moult increments from the adolescent to adult phase did not follow a fixed pattern. It is difficult to establish growth increment at moult for adolescent males in the wild based on the size frequency distributions as their growth process is extremely variable. Adolescent males can moult yearly and stay within the adolescent phase (normal moult), skip a moult for one year (skip moult) or moult to the terminal phase (terminal moult). A highly variable growth pattern and moulting process of adolescent males for any given size makes it particularly difficult to isolate each instar from the extensively overlapping size frequency distributions. Efforts to establish growth model parameters using a length-based population dynamic

model for the snow crab population has recently been undertaken (E. Wade, DFO Moncton, pers. comm.). The method is based on a nonlinear least square optimization approach using post-season trawl survey and fishery data to determine proportions of adolescent males moulting to different moult phases in a particular size-class group, natural mortality, and growth parameters (Zheng et al., 1995). Preliminary results from this study showed a higher size increment for adolescent males undergoing a normal moult than for those moulting to the terminal moult (unpubl. data), which supports our findings.

In our study, carapace moult increments for male snow crab (table VII) are less than those obtained from size-frequency distribution analyses (Robichaud et al., 1989; Sainte-Marie et al., 1995; Comeau et al., 1998). Similar observations in the aquarium for carapace growth at moult by Miller & Watson (1976) and Hurley et al. (1990) showed higher carapace moult increments compared to our results. This may partially be due to the fact that they did not take significant changes (reduction) in growth at puberty phase into account which may then overestimate subsequent growth rate for adolescent males. In this study, carapace increment at moult decreased with increasing crab size at each of the three maturity phases of male snow crab. The mean CW and age of successive instars were estimated (table VII) based on the results of Hiatt's growth model fitted to the three maturity phases and the initial mean CW of instar I at 3.1 mm (Comeau et al., 1998). The PGI for males moulting to the immature phase varied from 51.61 to 32.4% over the first eight postlarval moults, from 35.2 to 17.2% at the adolescent phase (from instars IX to XIV) and from 16.8 to 12.5% at the adult phase (from instars XI to XV). For immature males, we predicted eight consecutive moults (instars) before reaching the puberty moult. This is one moult (instar) more than estimated by Sainte-Marie et al. (1995) and Comeau et al. (1998). Adolescent males should recruit to the commercial size of 95 mm CW as adult crabs at instar XIV. This corresponds to 11 years, or more, after settlement depending on the number of skip moults. Robichaud et al. (1989) predicted that male snow crabs reach the commercial legal size of 95 mm CW at instar XI, 4.5 years after settlement. Sainte-Marie et al. (1995) and Comeau et al. (1998) predicted that male snow crabs recruit to the commercial legal size at instar XII, 8.7-9 years or more after hatching.

Implications for the fishery

A better understanding of growth mechanism and moult cycle in male snow crab is essential for a sound management of the fisheries. Recruitment in snow crabs is highly variable from year to year (Sainte-Marie et al., 1995; Comeau et al., 1998; Moriyasu et al., 1998) depending on environmental and hydrological conditions, nutriments and favourable habitats for settlement. In Atlantic snow crab stocks, biomass of commercial crabs fluctuates in a cyclical manner caused by 3-4 years

TABLE VII

Mean carapace width (CW), percentage of growth increment at moult (PGI), duration, and relative age of successive instars in male snow crab, *Chionoecetes opilio* (O. Fabricius, 1788), based on the results of Hiatt's growth model fitted to type I males moulting to the immature, adolescent, and adult phases

Instar	CW (mm)	PGI	Duration (year)	Age (year)	Moulting phase	CW (mm)	PGI	Duration (year)	Moulting phase
I	3.1[a]		<1 (±6 months)	0[+a]	Immature				
II	4.7	51.6	<1 (±6 months)	1[a]	Immature				
III	6.8	44.0	<1 (±6 months)	1[+a]	Immature				
IV	9.5	39.6	<1 (±6 months)	2[a]	Immature				
V	12.9	36.7	<1 (±6 months)	2[+a]	Immature				
VI	17.4	34.8	1	3[a]	Immature				
VII	23.2	33.3	1	4[a]	Immature				
VIII	30.7	32.4	1	5	Immature				
IX	41.6	35.2	1-2[b]	6	Adolescent				
X	53.3	28.3	1-2[b]	7	Adolescent				
XI	66.1	24.0	1-2[b]	8	Adolescent	62.3[c]	16.8	±5	Adult
XII	80.0	21.0	1-2[b]	9	Adolescent	76.2[c]	15.2	±5	Adult
XIII	95.0	18.8	1-2[b]	10	Adolescent	91.2[c]	14.1	±5	Adult
XIV	111.4	17.2	1-2[b]	11	Adolescent	107.6[c]	13.2	±5	Adult
XV				12	Adolescent	125.3[c]	12.5	±5	Adult

[a] Initial mean CW at 3.1 mm and ages at each instar are based on Comeau et al. (1998); [b] Adolescent males may skip a moult; [c] Terminal moult size.

of high abundance of recruitment to the population followed by a 3-4 years of recruitment trough (Sainte-Marie et al., 1995; Comeau et al., 1998; Moriyasu et al., 1998). The annual recruitment to the fishery appears as commercial-sized soft-shelled males one year prior to harvesting. Since moulting activities in adolescent males peaked in January for type II and in March for type I, most of the postmoult males were potentially catchable as soon as the fishery starts (generally at the end of April in the southern Gulf of St. Lawrence). Soft-shelled crabs in commercial catches were found from late April to August in the southern Gulf of St. Lawrence (Hébert et al., 2000). Soft-shelled crabs are not economically valuable because of their low meat yield and are discarded at sea by fishermen. This practice increases the mortality of discarded crabs as well as the number of crabs with missing legs. Ultimately, this diminishes the reproductive potential of the stock (Dufour et al., 1997; Hébert et al., 2000).

As to the mechanism of moulting to terminal phase, Conan et al. (1988) and Comeau et al. (1998) hypothesized that the moult to terminal phase for a given size group may be density-dependent rather than genetically determined. Comeau et al. (1998) suggested that a high abundance of large mature (adult) males in the population encourages moulting to another larger juvenile (adolescent) instar instead of moulting to the terminal phase and could also inhibit growth resulting in an increase in abundance of skip moulters. In the southern Gulf of St. Lawrence, the percentage of skip moulters caught in commercial traps varies from year to year (e.g., varied from 13% in 1990 to 25% in 1994 and decreased at a level of 7-8% since 1995, Hébert et al., 2000). The annual trawl survey conducted in the southern Gulf of St. Lawrence since 1988 showed a very high (up to 40-45%) skip moulting rate in adolescent males larger than 50 mm CW (Hébert et al., 2000). A high percentage of skip moulters occurring in the high population abundance period may suggest a density-dependent effect on the moulting schedule of larger adolescent males in the southern Gulf of St. Lawrence. This may be a driving factor affecting the strength and delay in the timing of recruitment to the fishery. Waiwood & Elner (1982) hypothesized that the removal of large old crab would release the snow crab population from a "stagnant" to a "dynamic" high-growth phase. Comeau et al. (1998) and Elner & Beninger (1995) suggested that removing large mature (adult) males may enhance the moulting of juvenile (adolescent) males to larger sizes promoting a steady flux of males growing to larger harvestable sizes on the fishing grounds. However, the effect of heavy exploitation of males larger than 95 mm CW may have a negative impact on the future reproductive potential of the stock especially if size at terminal moult is a genetically inherited character (Sainte-Marie & Hazel, 1992; Moriyasu & Comeau, 1996; Comeau et al., 1998; Sainte-Marie et al., 1999).

Further studies on the factors affecting the moulting schedule in male snow crab population are needed for a better understanding of the dynamic growth process of the species and subsequent development and enhancement of optimal harvesting strategies for snow crab fisheries in the southern Gulf of St. Lawrence.

LITERATURE CITED

AIKEN, D. E., 1980. Molting and growth. In: J. S. COBB & B. F. PHILLIPS (eds.), The biology and management of lobsters, **1**, Physiology and behavior: 91-163. (Academic Press, New York).

BENHALIMA, K., M. MORIYASU & M. HÉBERT, 1998. A technique for identifying the early-premolt stage in the male snow crab, *Chionoecetes opilio* (Brachyura: Majidae), in Baie des Chaleurs, southern Gulf of St. Lawrence. Canadian Journ. Zool., **76**: 609-617.

COMEAU, M. & G. Y. CONAN, 1992. Morphometry and gonad maturity of male snow crab (*Chionoecetes opilio*). Canadian Journ. Fish. aquat. Sci., **49**: 2460-2468.

COMEAU, M., G. Y. CONAN, F. MAYNOU, G. ROBICHAUD, J.-C. THERRIAULT & M. STARR, 1998. Growth, spatial distribution, and abundance of benthic stages of the snow crab (*Chionoecetes opilio*). in Bonne Bay, Newfoundland, Canada. Canadian Journ. Fish. aquat. Sci., **55**: 262-279.

CONAN, G. Y. & M. COMEAU, 1986. Functional maturity of male snow crab (*Chionoecetes opilio*). Canadian Journ. Fish. aquat. Sci., **43**: 1710-1719.

CONAN, G. Y., M. MORIYASU, M. COMEAU, P. MALLET, Y. CHIASSON & H. CHIASSON, 1988. Growth and maturation of snow crab (*Chionoecetes opilio*). In: G. JAMIESON & D. MCKONE (eds.), Snow crab biology. Canadian Manuscr. Rep. Fish. aquat. Sci., **2005**: 45-66.

DAWE, E. G., J. M. HOENIG, P. G. O'KEEFE & M. MORIYASU, 1992. Molt indicators and growth per molt for male snow crabs (*Chionoecetes opilio*). International Council for Exploration of the Sea, C.M., **1992/K35**: 1-15.

DRACH, P., 1939. Mue et cycle d'intermue chez les Crustacés Décapodes. Ann. Inst. océanogr. Monaco, **19**: 103-391.

DRACH, P. & C. TCHERNIGOVTZEFF, 1967. Sur la méthode de détermination des stades d'intermue et son application générale aux Crustacés. Vie Milieu, **18**: 595-610.

DUFOUR, R., D. BERNIER & J.-C. BRÊTHES, 1997. Optimization of meat yield and mortality during snow crab (*Chionoecetes opilio* O. Fabricius) fishing operations in eastern Canada. Canadian techn. Rep. Fish. aquat. Sci., **2152**: 1-31.

ELNER, R. W. & R. F. J. BAILEY, 1986. Differential susceptibility of Atlantic snow crab (*Chionoecetes opilio*) stocks to management. Canadian spec. Publ. Fish. aquat. Sci., **92**: 335-346.

ELNER, R. W. & P. G. BENINGER, 1995. Multiple reproductive strategies in snow crab (*Chionoecetes opilio*) physiological pathways and behavioral plasticity. Journ. exp. mar. Biol. Ecol., **193**: 93-112.

FOYLE, T. P., G. V. HURLEY & D. M. TAYLOR, 1989. Field testing shell hardness gages for the snow crab fishery. Canadian Industr. Rep. Fish. aquat. Sci., **193**: 1-38.

HAEFNER, P. A. & W. A. VAN ENGEL, 1975. Aspect of molting, growth and survival of male rock crabs (*Cancer irroratus*) in Chesapeake Bay. Chesapeake Sci., **16**: 253-265.

HÉBERT, M., C. GALLANT, Y. CHIASSON, P. MALLET, P. DEGRÂCE & M. MORIYASU, 1992. Le suivi du pourcentage de crabes mous dans les prises commerciales de crabe des neiges (*Chionoecetes opilio*) dans le sud-ouest du golfe du Saint-Laurent (zone 12) en 1990 et 1991. Canadian techn. Rep. Fish. aquat. Sci., **1886**: 1-18.

HÉBERT, M., A. HÉBERT, E. WADE, T. SURETTE, D. GIARD, P. DEGRÂCE, M. BIRON & M. MORIYASU, 2000. The 1999 assessment of snow crab (*Chionoecetes opilio*) stock in the southwestern Gulf of St. Lawrence (Areas 12-25/26, E and F). Canadian Stock Assessment Secretariat Res. Doc., **2000/14**: 1-57.

HIATT, R. W., 1948. The biology of lined shore crab, *Pachygrapsus crassipes* (Randall). Pacific Sci., **2**: 135-213.

HOENIG, J. M., E. G. DAWE & P. G. O'KEEFE, 1994. Molt indicators and growth per molt for male snow crabs (*Chionoecetes opilio*). Journ. Crust. Biol., **14**: 273-279.

HURLEY, G. V., R. W. ELNER, D. M. TAYLOR & R. F. J. BAILEY, 1990. Evaluation of snow crab tags retainable through molting. American Fish. Soc. Symp., **7**: 84-93.

ITO, K., 1970. Ecological studies on the edible crab (*Chionoecetes opilio* O. Fabricius) in the Japan Sea. III. Age and growth as estimated on the basis of the seasonal changes in the carapace width frequencies and the carapace hardness. Bull. Japanese Sea Reg. Fish. Res. Lab., **22**: 81-116. [Fish. Res. Bd Canada Transl. Ser., **1512**.]

KON, T., M. NIWA & F. YAMAKAWA, 1968. Fisheries biology of the Tanner crab. II. On the frequency of molting. Bull. Japanese Soc. Sci. Fish., **34**: 138-142. [Fish. Res. Bd Canada Transl. Ser., **1129**.]

KURATA, H., 1962. Studies on the age and growth of Crustacea. Bull. Hokkaido Reg. Fish. Res. Lab., **24**: 1-115.

MARTOJA, R. & M. MARTOJA-PIERSON, 1967. Initiation aux techniques de l'histologie animale: 1-345. (Masson et Cie, Paris).

MAYRAND, E., J.-D. DUTIL & H. GUDERLEY, 2000. Changes in muscle of postmoult snow crab (*Chionoecetes opilio* O. Fabricius) fed different rations. Journ. exp. mar. Biol. Ecol., **243**: 95-113.

MILLER, R. J. & J. WATSON, 1976. Growth per molt and limb regeneration in the spider crab (*Chionoecetes opilio*). Journ. Fish. Res. Bd Canada, **33**: 1644-1649.

MORIYASU, M. & M. COMEAU, 1996. Grasping behavior of male snow crab *Chionoecetes opilio* (O. Fabricius, 1788) (Decapoda, Majidae). Crustaceana, **69**: 211-222.

MORIYASU, M. & G. Y. CONAN, 1988. Aquarium observation on mating behaviour of snow crab *Chionoecetes opilio*. International Council for Exploration of the Sea, C.M., **K9**: 1-20.

MORIYASU, M. & P. MALLET, 1986. Molt stages of the snow crab *Chionoecetes opilio* by observation of morphogenesis of setae on the maxilla. Journ. Crust. Biol., **6**: 709-718.

MORIYASU, M., E. WADE, A. SINCLAIR & Y. CHIASSON, 1998. Snow crab, *Chionoecetes opilio*, stock assessment in the southwestern Gulf of St. Lawrence by bottom trawl survey. Canadian spec. Publ. Fish. aquat. Sci., **125**: 29-40.

O'HALLORAN, M. J. & R. K. O'DOR, 1988. Molt cycle of male snow crabs (*Chionoecetes opilio*) from observations of external features, setal changes, and feeding behavior. Journ. Crust. Biol., **8**: 164-176.

PASSANO, L. M., 1960. Molting and its control. In: T. H. WATERMAN (ed.), The physiology of Crustacea, **1**: 473-536. (Academic Press, New York).

ROBICHAUD, D. A., R. J. F. BAILEY & R. W. ELNER, 1989. Growth and distribution of snow crab (*Chionoecetes opilio*) in the southeastern Gulf of Saint Lawrence. Journ. Shellfish Res., **8**: 13-23.

SAINTE-MARIE, B. & F. HAZEL, 1992. Moulting and mating of snow crabs, *Chionoecetes opilio* (O. Fabricius), in shallow waters of the northwestern Gulf of Saint Lawrence. Canadian Journ. Fish. aquat. Sci., **49**: 1282-1293.

SAINTE-MARIE, B., S. RAYMOND & J.-C. BRÊTHES, 1995. Growth and maturation of the benthic stages of male snow crab, *Chionoecetes opilio* (Brachyura, Majidae). Canadian Journ. Fish. aquat. Sci., **52**: 903-924.

SAINTE-MARIE, B., N. URBANI, J. M. SÉVIGNY, F. HAZEL & U. KUHNLEIN, 1999. Multiple choice criteria and the dynamics of assortative mating during the first breeding season of female snow crab *Chionoecetes opilio* (Brachyura, Majidae). Mar. Ecol. Progr. Ser., **181**: 141-153.

SKINNER, D. M., 1962. The structure and metabolism of a crustacean integumentary tissue during a molt cycle. Biol. Bull., Woods Hole, **123**: 635-647.

— —, 1985. Molting and regeneration. In: D. E. BLISS & L. H. MANTEL (eds.), The biology of Crustacea, **9**: 43-146. (Academic Press, Orlando).

SOKAL, R. R. & F. J. ROHLF, 1995. Biometry (3rd ed.): 1-887. (W. H. Freeman and Cy, New York).

STEVENSON, J. R., 1968. Metaecdysial molt staging and changes in the cuticle in the crawfish, *Orconectes sanborni* (Faxon). Crustaceana, **14**: 169-177.

— —, 1972. Changing activities of the crustacean epidermis during the molting cycle. American Zool., **12**: 373-380.

— —, 1985. Dynamics of the integument. In: D. E. BLISS & L. H. MANTEL (eds.), The biology of Crustacea, **9**: 1-42. (Academic Press, Orlando).

TAYLOR, D. M. & J. M. HOENIG, 1990. Growth per molt of male snow crab (*Chionoecetes opilio*) from Conception and Bonavista Bays, Newfoundland. Fish. Bull. U.S., **88**: 753-760.

TAYLOR, D. M., G. W. MARSHALL & P. G. O'KEEFE, 1989. Shell hardening in snow crab (*Chionoecetes opilio*) tagged in soft-shelled condition. North American Journ. Fish. Managem., **9**: 504-508.

TAYLOR, D. M. & W. G. WARREN, 1991. Male snow crab, *Chionoecetes opilio* (Fabricius, 1788), weight-width relationships: an exercise in multi-source regression. Journ. Shellfish Res., **10**: 165-168.

WAIWOOD, K. & R. W. ELNER, 1982. Cod predation of snow crab (*Chionoecetes opilio*) in the Gulf of St. Lawrence. In: B. MELTEFF (ed.), Proceedings of the International Symposium on the Genus *Chionoecetes*. Lowell Wakefield Fisheries Symposia Series, University of Alaska, Alaska Sea Grant Rep., **82-10**: 63-78.

WATSON, J., 1971. Ecdysis of the snow crab (*Chionoecetes opilio*). Canadian Journ. Zool., **49**: 1025-1027.

— —, 1972. Mating behavior in the spider crab (*Chionoecetes opilio*). Journ. Fish. Res. Bd Canada, **29**: 447-449.

WOLFF, M. & M. SOTO, 1992. Population dynamics of *Cancer polyodon* in La Herradura Bay, northern Chile. Mar. Ecol. Progr. Ser., **85**: 69-81.

M. HÉBERT ET AL.

ZHENG, J., M. C. MURPHY & G. H. KRUSE, 1995. A length-based population model and stock-recruitment relationships for red king crab (*Paralithodes camtschaticus*) in Bristol Bay, Alaska. Canadian Journ. Fish. aquat. Sci., **52**: 1229-1246.