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

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Abstract: New criteria for determining the early-premolt stage (D_0) of the snow crab *Chionoecetes opilio* are described, based on histological observations. Identifying the early-premolt stage in snow crabs on the basis of observations of setagenesis poses difficulties for inexperienced observers. At the start of the premolt phase, numerous actively secreting cells beneath the epithelium and Leydig cells in the connective tissue can be observed using histological techniques. A semitransparent substance observed between the membranous layer and epithelium by histological means was further subjected to transmission electron microscope observations, which suggested that this was the molting fluid whose presence represents the beginning of the process of deposition of the epicuticle. At the time when the molting fluid is secreted in snow crabs, no morphological characteristics of premolt stage D1 are discernible, therefore these features can be used to identify D0. Using this technique, the molt stages of adolescent male crabs in the southern Gulf of St. Lawrence were examined, revealing the existence of two different types of molters that enter into the molting process in different times of the year. The majority of adolescent males go through the premolt stages in August–December and start to molt in March–April of the following year; another group of adolescent males with more epibionts on the carapace in the spring (adolescents that did not molt in the previous spring) are in the premolt stages in May–July and probably start to molt in December–January. The present study reveals that the molting patterns of snow crabs are far more flexible than the previous literature had suggested. The implications for long-term stock management are quite important, and further study on the structure and dynamics of molters is needed.

Résumé : On trouvera ici la description de nouveaux critères basés sur des observations histologiques pour déterminer le début du stade de pré-mue (D_0) chez le crabe des neiges *Chionoecetes opilio*. La détermination du début de la pré-mue chez le crabe des neiges est basée sur l'observation de la morphologie des soies et peut comporter certaines difficultés pour l'observateur inexpérimenté. Au début de la phase de pré-mue, un examen histologique révélera la présence d'un grand nombre de cellules sécrétrices actives dans l'épithélium et de cellules de Leydig dans le tissue conjonctif. Une substance semi-transparente entre la couche membraneuse et l'épithélium a été observée sur les coupes histologiques. L'examen au microscope électronique à transmission a révélé que cette substance est probablement le fluide de mue, marquant le début du processus de formation de la nouvelle épicuticule. Au moment de la sécrétion de ce fluide, aucune caractéristique morphologique du stade D1 n'est encore perceptible chez le crabe des neiges. Par conséquent, ces caractéristiques peuvent être utilisées comme indices du début du stade D0. Les stades de mue ont été examinés au moyen de cette technique chez des crabes mâles adolescents du sud du golfe du Saint-Laurent, ce qui a révélé l'existence de deux groupes qui entreprennent le processus de leur mue à des moments différents de l'année. La majorité des crabes mâles adolescents subissent les stades de pré-mue d'août à décembre et commence à muer en mars–avril de l'année suivante, tandis que le groupe des adolescents qui portent plus d'épibiontes sur leur carapace au printemps (ceux qui n'ont pas mué au printemps précédent) subissent les stades de pré-mue durant l'été (mai–juillet) et probablement commence à muer en décembre–janvier. Ces résultats démontrent que la mue du crabe des neiges est beaucoup plus flexible que ne le permettaient de croire les publications antérieures. L'impact de ces résultats en gestion de stocks à long terme est important et d'autres études sur la structure et la dynamique des individus en mue s'imposent.

Introduction

Techniques for identifying molt stages in crustaceans on the basis of integumental changes and setal development have been established by Drach (1939, 1944) and Drach and Tchernigovtzeff (1967) and adapted for a variety of crustacean species by numerous authors (for reviews see Skinner 1985; Stevenson 1985).

For the snow crab *Chionoecetes opilio*, the most commercially important crab species in eastern Canada, refining of the technique for identifying molt stages has been needed since Conan and Comeau's (1986) finding of the terminal molt in males. Moriyasu and Mallet (1986) first described a rapid technique for identifying three molt periods (premolt, postmolt, and intermolt), based on setagenesis on the maxilla. O'Halloran and O'Dor (1988) applied the same technique to the maxilliped and compared the results with detailed external and behavioral observations. Conan and Comeau (1986) and

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Table 1. Classification of adolescent male snow crabs in the southern Gulf of St. Lawrence, based on carapace condition in May–July, with corresponding molt stages and estimated molting periods.

	Carapace condition[a]	Molt stage in May–July[b]	Estimated molting period
Type I	Brightly colored, some irridescent, soft, no epibionts, chelae easily bent, durometer reading <68	$A–C_3$ (type I′)	Current spring
	Brightly colored, irridescent, may have epibionts, chelae not easily bent, durometer reading <72	C_4 (type I″)	Previous winter
Type II	Dull brown dorsally and yellow–brown ventrally, no irridescence, epibionts present, chelae relatively hard, durometer reading <72	$C_4–D_0$	Spring of previous year

[a]Type I and II males were classified according to carapace condition in May–July (color, epibiont coverage, and carapace rigidity).
[b]Type I males were further subdivided into two types, I′ and I″, based on histological observations of the integument.

Yamasaki and Kuwahara (1991) used this technique to verify the existence of the terminal molt in male snow crabs. Based on this technique and observations of molting of animals in aquaria, Conan et al. (1988) suggested that the molting season of male crabs occurs between March and April in the southern Gulf of St. Lawrence.

However, Dawe et al. (1992) reported difficulty in objectively identifying the early-premolt stage (D_0) on the basis of the retraction of the epidermis observed on the maxilla or maxilliped. Sainte-Marie et al. (1995) concluded that setagenesis was not an appropriate technique for determining D_0 in the snow crab because the formation of new shell preceded changes in the mouthparts. Hoenig et al. (1994) then proposed using the exterior color change as an indicator of premolt. However, this technique is efficient only for crabs that are about to molt (D_3 and later stages), for which setagenesis can also be used to accurately identify molt stages.

Between 1991 and 1993, monthly trawl surveys were conducted in Baie des Chaleurs in the southern Gulf of St. Lawrence to obtain information on the population structure and dynamics of snow crabs. During the survey, an extensive assessment of the molt cycle was also made by means of histological observations of the integument. The objective of this study is to provide a technique for recognizing molting animals at the earliest possible stage with maximum sensitivity. Although various other techniques are available, such as measuring the epidermal DNA concentration (Stevenson 1972), we chose histological examination of the integument, which is traditionally used in our laboratory for assessing the intermolt cycle in this species. As a case study, this technique was applied to a sample of males from the southern Gulf of St. Lawrence.

Materials and methods

Sample collection

Male snow crabs (*Chionoecetes opilio*) were collected by a Bay of Biscay "Bigouden" *Nephrops* otter trawl (Conan et al. 1994) on board the Department of Fisheries and Oceans Canada research vessel C.S.S. *Opilio* in Baie des Chaleurs (Fig. 1) between June and November 1990, May and November 1991, and June and November 1992. Subsamples of 4005 male crabs (990 adults and 3015 adolescents) with carapace width (CW) ranging from 40 to 134 mm were examined for the present study. All crabs were brought to the laboratory and the following measurements were taken: CW, chela height (CH), carapace rigidity measured with a durometer (Foyle et al. 1989), and carapace condition (color and degree of epibiont coverage). Maturity status was determined according to a modified discriminant function (Conan and Comeau 1986) applied to data sets of logarithms of CH against logarithms of CW. Terminology for the maturity phases of males used herein follows Sainte-Marie et al. (1995). Although adolescent males have been generally considered to molt every spring (Conan and Comeau 1986), afterwards bearing a new/soft carapace (type I), a certain percentage of harder shell adolescent males with evidently more epibionts on the carapace was observed (type II). These crabs apparently did not molt in the previous spring. Therefore, adolescent males were further divided into these two types (Table 1). The percentages of premolt individuals amongst the two types of males in June–November were compared by χ^2 test. The results were deemed significant at the $P < 0.05$ level.

Histological observations of the integument and observations of setagenesis on the endite of the first maxilliped (Moriyasu and Mallet 1986) were made on all 4005 males caught. From the individuals classified as type II males, 30 animals were selected for additional histochemical and transmission electron microscope (TEM) observations.

Histological and histochemical observations

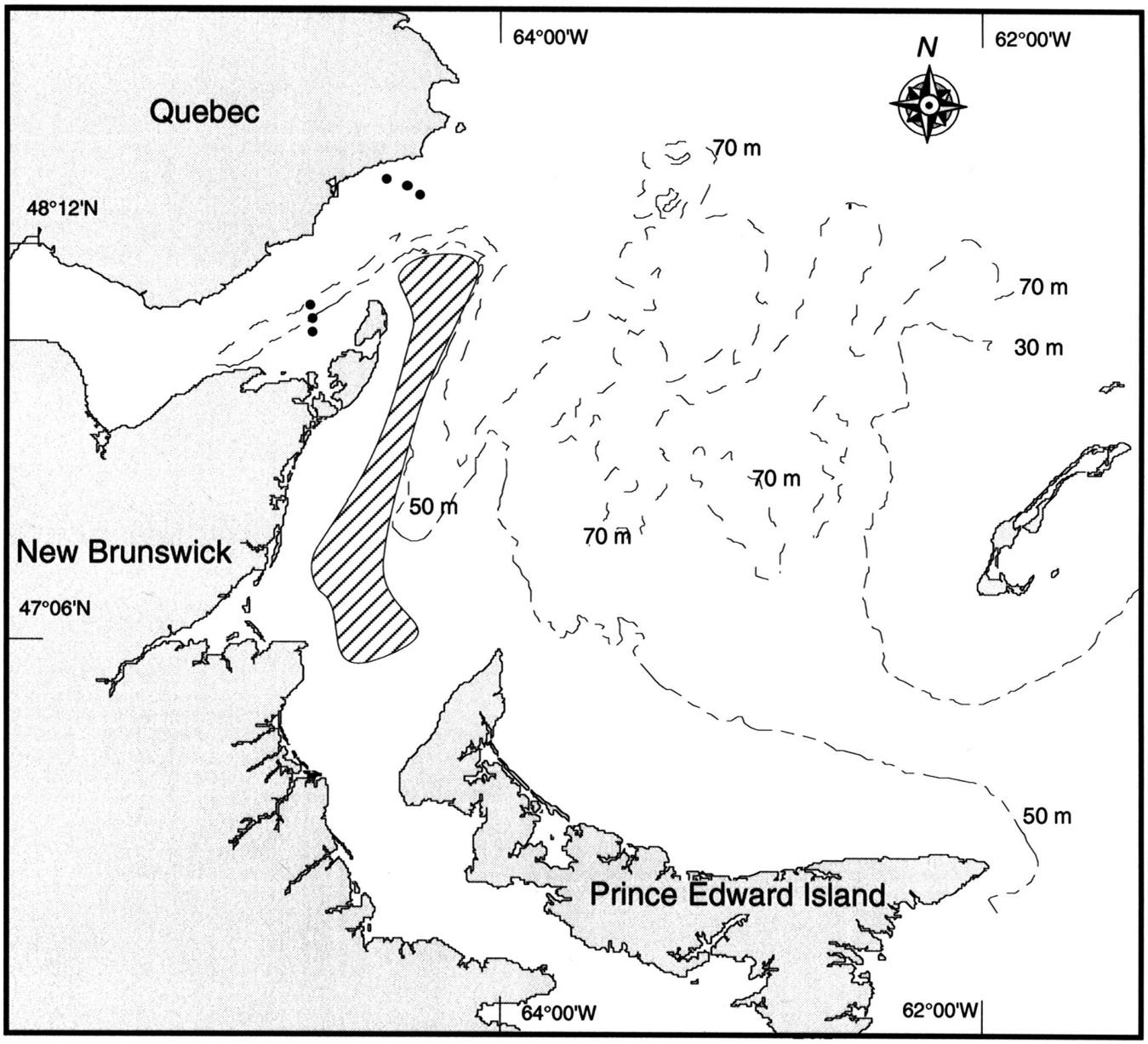
For light microscope observations, a cuticle sample approximately 10 mm in length was dissected from the propodus of the right fourth pereopod and preserved in Bouin's solution for 48 h. The fixed tissue was dehydrated in a series of aqueous ethanol solutions, cleared in xylene, and then embedded in paraffin wax in a vacuum chamber. Blocks were sectioned serially at 5–7 μm on a rotary microtome. Serial sections were mounted on glass slides and stained with modified Masson's trichrome, using ethanol and xylene as the dehydration and clearing agent, respectively. Final mounts were made with glass cover slips, with Paramount as the mounting resin.

For histochemical observations, the periodic acid – Schiff (PAS) technique of Hotchkiss–McManus–Lillie (Martoja and Martoja-Pierson 1967) and the Alcian Blue technique (Pearse 1985) were used to observe carbohydrates and acidic mucopolysaccharides, respectively. Light microscope examination was performed with a Leitz Dialux 20 compound light microscope equipped with an Olympus automatic 35-mm camera and sections were photographed using bright-field optics.

TEM observations

For TEM observations, the cuticle samples removed from animals were cut into small pieces about 1 mm^2 in area. Tissues were fixed at 4°C with 5% glutaraldehyde in 0.1 M cacodylate buffer at pH 7.2 for 1 h and rinsed in cold 0.175 M cacodylate buffer at pH 7.2. Specimens were postfixed with 2% osmium tetroxide in 0.31 M cacodylate buffer at pH 7.2 for 1 h and rinsed in the buffer mentioned above, and then dehydrated for 5–15 min through a graded ethanol series. Embedding procedures followed general preparation for TEM in Epon 812 resin, but a longer impregnation time was required because the cuticle samples were not decalcified. Polymerization occurred in a vacuum chamber at 60°C. Survey sections 1 μm thick were obtained using glass knives on a LKB ultramicrotome, mounted on a glass slide, stained with 0.1% toluidine blue in borax, and examined under a light microscope. Ultrathin sections made with a diamond knife on

Fig. 1. Geographic locations of snow crabs (*Chionoecetes opilio*), sampling sites (solid circles) and the area of the 1991 December herring survey during which molting male crabs were captured (diagonal lines).



a LKB ultramicrotome were mounted on a copper grid, stained with uranyl acetate and bismuth subnitrate, and viewed with a Philips EM400T electron microscope.

Results

Integument structure

During the intermolt stage (C_4), the cuticle usually comprises four layers: epicuticle, exocuticle, endocuticle, and the membranous layer (Fig. 2A). The epicuticle consists of two layers: an outer thin membrane that stains red with fuchsin–ponceau and an inner, thicker layer. The exocuticle and endocuticle appeared to be composed of fibrous laminae lying parallel to the surface (Fig. 2A).

The exocuticle and endocuticle stained blue with the aniline in Masson's trichrome, the former darker than the latter. Formation of the cuticle through the postmolt period (A–C_3) was complete when secretion of the innermost layer (the membranous layer) was over, then the period of intermolt (C_4) began (Fig. 2A). At this stage the epithelium consisted of single layer of cells, which were extremely long and attenuated and fibrillar in nature. The relatively large nuclei were situated near the internal cell walls. The cytoplasm was hyaline, with few granules, and generally colorless. Under the epithelium was a layer of fibrous, loose, spongy connective tissue.

The early-premolt stage (D_0) is generally recognized from the degree of development of the epithelium. The first sign of premolt activity was seen in the epithelial cells, which stained more darkly than during the intermolt stage (C_4). At this stage, the cuticle was separated from the epithelium. A layer of

Fig. 2. Morphological observations of the cuticle of a snow crab (*Chionoecetes opilio*) by light microscopy. (A) Transverse section through the cuticle, showing the four layers formed in intermolt stage C_4: epicuticle (Ep), exocuticle (Ex), endocuticle (En), and membranous layer (Ml). *ep*, fibrillar epithelium; *ct*, connective tissue. (B) Early phase of stage D_0, showing the epithelium with the nuclei (Nu) in an apical position and short microvilli (*mv*), pear-shaped secretory cells (Sc) in the epithelium, and an ovoid Leydig cell (Ld) underneath the epithelium. (C) Intermediate phase of stage D_0, showing the newly deposited molting fluid (Nf) forming a layer above the epithelium. (D) Advanced phase of stage D_0, showing a thicker layer of deposited molting fluid and the beginning of dissolution of the membranous layer. (E) Premolt stage D_2; formation of the new epicuticle (Epn) and exocuticle (Exn) is complete and they are supported by tonofibrillae (Tf). (F) Late-premolt stage D_4, showing the old epicuticle (Epo) and exocuticle (Exo) and the newly formed epicuticle (Epn) and exocuticle (Exn) supported by tonofibrillae (Tf).

Table 2. Mean carapace widths, sample sizes, and percentages of premolt individuals amongst adult and type I (types I′ and I″) and type II adolescent males observed in the southwestern Gulf of St. Lawrence between 1990 and 1992.

	1990			1991			1992		
	Adult	Type I	Type II	Adult	Type I	Type II	Adult	Type I	Type II
Sample number	224	858	71	209	523	679	557	575	309
CW (mm)[a]	100.2±1.1	82.7±0.5	96.2±1.8	96.7±1.1	96.7±1.1	84.6±0.3	103.7±0.3	87.0±0.4	83.7±0.7
Premolt (%)									
May–Aug.	0	4.7	21.1	0	2.0	19.4	0	0.3	20.1
Sept.–Dec.	0	28.5	32.4	0	8.4	74.7	0	3.7	57.6
Total	0	33.2	53.5	0	10.4	94.1	0	4.0	77.7

[a]Mean ± SE.

columnar epithelial cells became greatly elongated and their nuclei were enlarged. The epithelial cells sent their cytoplasmic extensions or short microvilli into the space between the cuticle and the epithelium (Fig. 2B).

Ultrathin sections revealed that the epithelial cells were elongated and the nucleus was situated more or less in a central position (Fig. 3A). The outer epithelial cells were tall and columnar. In the apical cytoplasm, the inclusions stained light red with fuchsin acid. The cuticle-secreting cells were pear-shaped, lay beneath the epithelial cells, and stained positively with Alcian Blue and toluidine blue, indicating the presence of mucopolysaccharide acid (Figs. 2B, 2C). TEM observations revealed the presence of electron-lucent secretion globules in the secretory cells (Fig. 3B). The material in the globules stained bright red with PAS. This type of inclusion suggests that this is a glandular zone, which probably consists of protein crystalloids (Fig. 3A). Dark cells were also present in the epithelium (Fig. 3A). Much of the apical cytoplasm was occupied by large membrane-bound vesicles containing loose-textured fibrous material very similar in appearance to the molting fluid. The endoplasmic reticulum appeared in the apical cytoplasm just under the vesicles (Fig. 3C). Underneath the epithelium, large oval cells described as "protein cells" or Leydig cells (Cuénot 1893) (Figs. 2B, 3D) contained a large number of spherical or oval electron-dense secretion droplets. Collagen-like fibers were found throughout the connective tissue. A large number of hemocyte cells occupied the blood spaces. These hemocyte cells aggregate underneath the epithelium and then progressively lose their characteristics when the molting fluid is secreted. The space between the old cuticle and the surface of the epithelial cells is occupied by a very thin, birefringent, transparent fluid (Fig. 2C). The newly deposited fibrils accumulate and form a layer immediately above the epithelium (Fig. 2D). At this time, neither resorption of the membranous layer (Fig. 2D) nor signs of setal organization on the maxilliped were observed.

The epithelium appears to be thickest at the stage of active secretion (Figs. 2C, 2D), and decreases to less than half this thickness after the retraction of the epithelium. When the epithelium retracts, the fibers appear to rise towards the apical pole of the epithelium. Premolt stage D_2 starts when the developing layers of the new cuticle are embedded in the fibrous network and the inner surface is covered with a thick, denser mesh-like material (Figs. 2D, 2E). The external part of this layer becomes slightly thinner and appears to be composed of thin, fine fibrous material that has staining properties similar to the epicuticle (Fig. 2E). At the end of this formation process, the basal ends of some of the epithelial cells become elongated and extend from the new cuticle to the connective tissue (Figs. 2E, 2F). This structure, called the tonofibrillae, is made up of parallel collagen-like fibers that traverse the length of the epithelial cells. This new structure probably supports the newly formed cuticle (Fig. 2F).

Molting-stage observations and molting season

Of the 3015 adolescent males, 2112 were of type I and 903 individuals of type II (Table 2). Amongst the type I males, two subgroups of postmolt individuals were identified between May and July, based on histological observations of the integument: type I′ males with a soft shell (durometer reading below 68) and in postmolt stages A–C_3) and type I″ males with a relatively hard shell (durometer reading between 68 and 72 and in intermolt (C_4) (Table 1). No distinction between these two subgroups could be made on the basis of histological observations of the integument after July, because the majority of type I′ males also reached the intermolt stage (C_4) at the end of July. The proportion of type I″ individuals amongst type I males observed in May–July varied from year to year (27, 2, and 57% in 1990, 1991, and 1992, respectively). The proportion of type II individuals in the total number of adolescent males also varied from year to year (8, 56, and 35% in 1990, 1991, and 1992, respectively).

The monthly percentage of adolescent males in the premolt period (D_0 and later stages) varied from 1% in June 1992 to 66% in November 1992 (Fig. 4). The percentage of premolt individuals amongst type II males was significantly higher, at

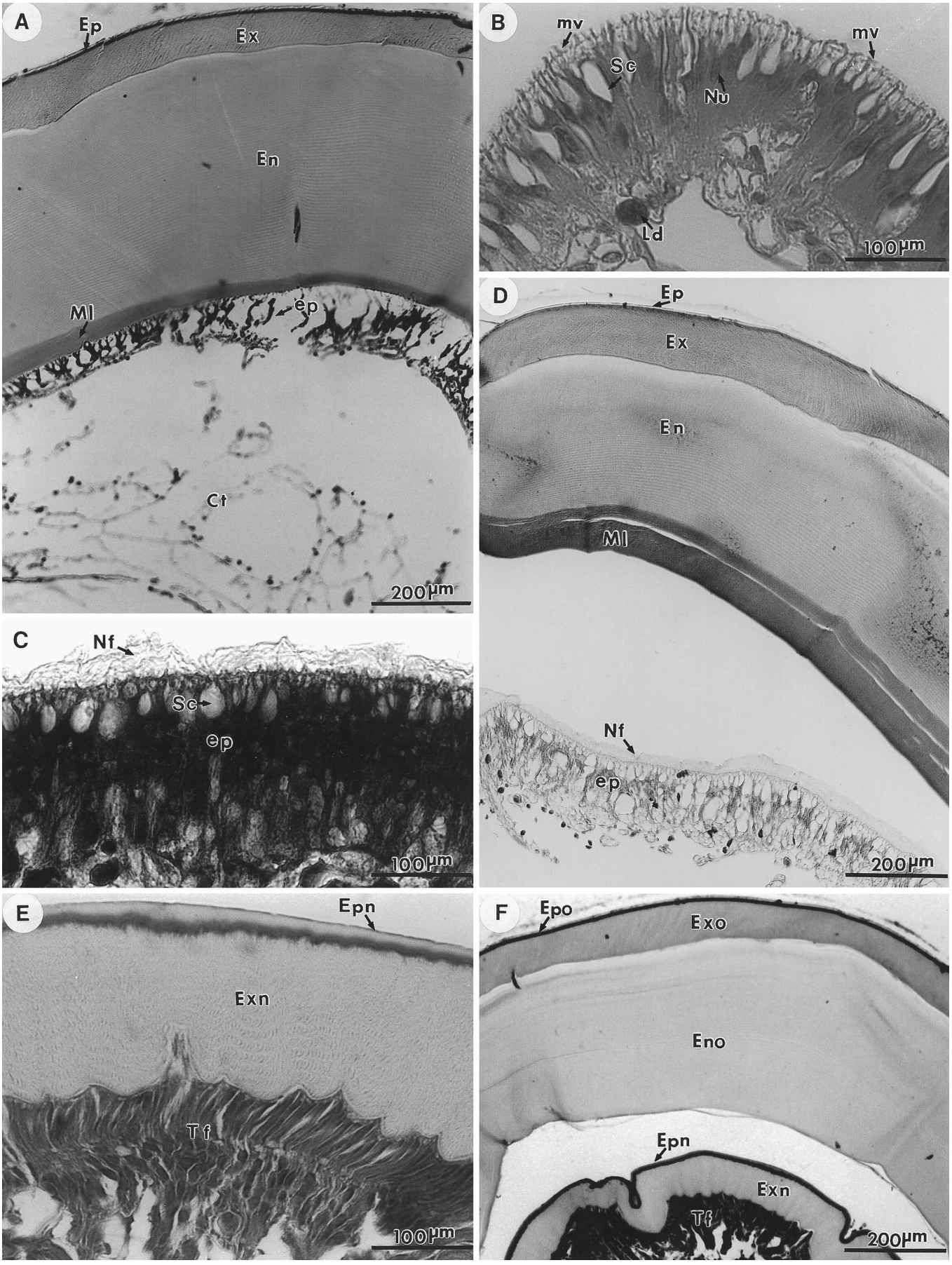
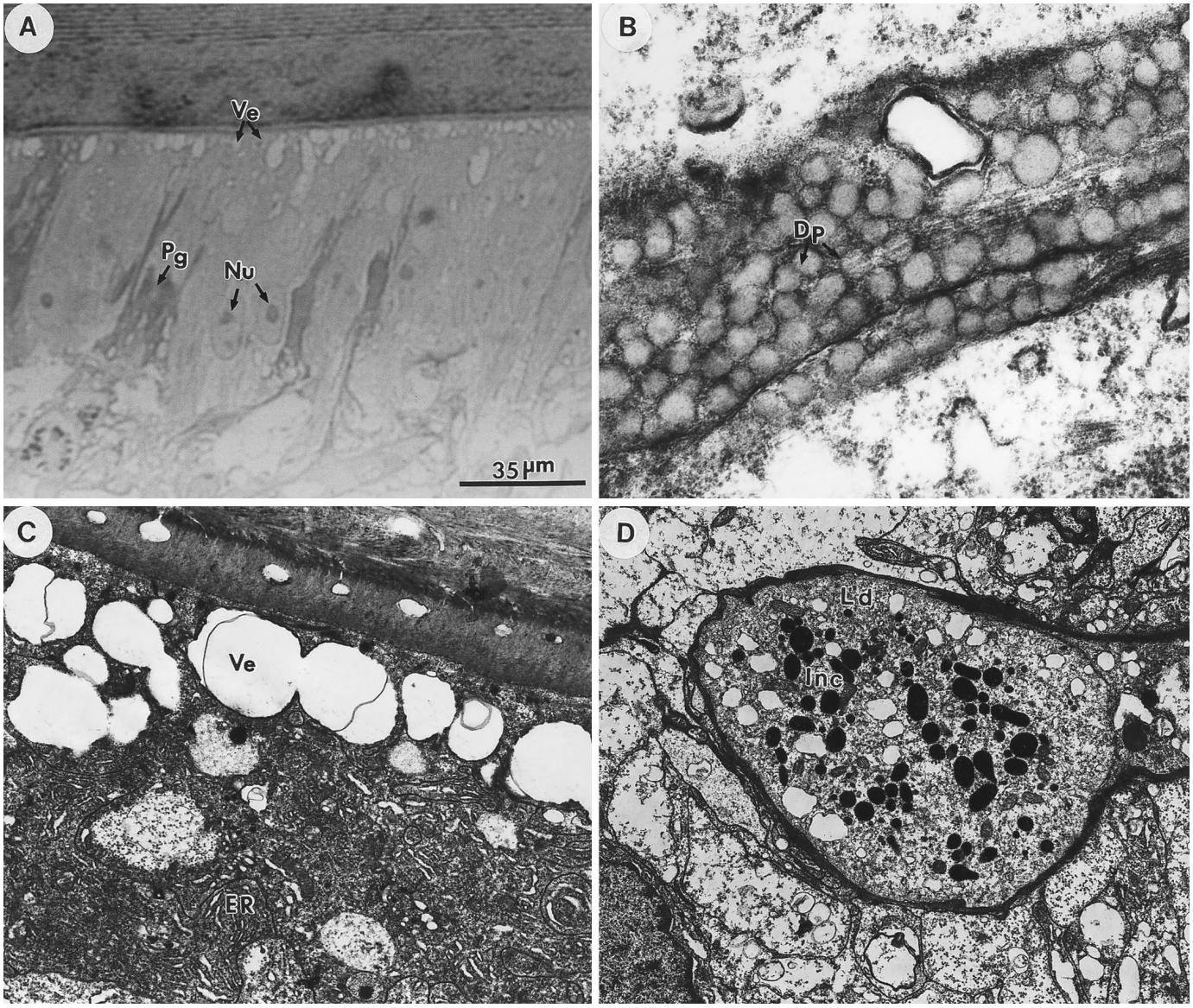


Fig. 3. (A) Survey section from a crab at the early phase of stage D_0, showing the epithelium with dark pigment cells (Pg), nuclei (Nu), and apical cytoplasm occupied by vesicles (Ve). (B) Electron micrograph showing pear-shaped cells containing numerous oval or spherical secretion droplets (Dp). × 40 500. (C) Electron micrograph showing large membrane-bounded vesicles (Ve) containing loose-textured fibrous material and tubular endoplasmic reticulum (Er). ×5400. (D) Electron micrograph showing ovoid Leydig cells (Ld) containing electron-dense inclusions (Inc). ×4200.



the $P = 0.01$ level, than that amongst type I males between June and November ($\chi^2 = 6.86$, $P = 0.008$, $\chi^2 = 166.06$, $P < 0.0001$, and $\chi^2 = 211.11$, $P < 0.0001$, for 1990, 1991, and 1992 respectively). Of type II molters, individuals in the premolt stages were observed as early as May and the percentage of individuals in the premolt stage increased rapidly afterwards, while premolt type I males appeared later (August).

No adolescent males in the advanced premolt stages (D_3 and later) were observed in the area surveyed. None of the 990 adult males were in the premolt stages, regardless of the season and their size.

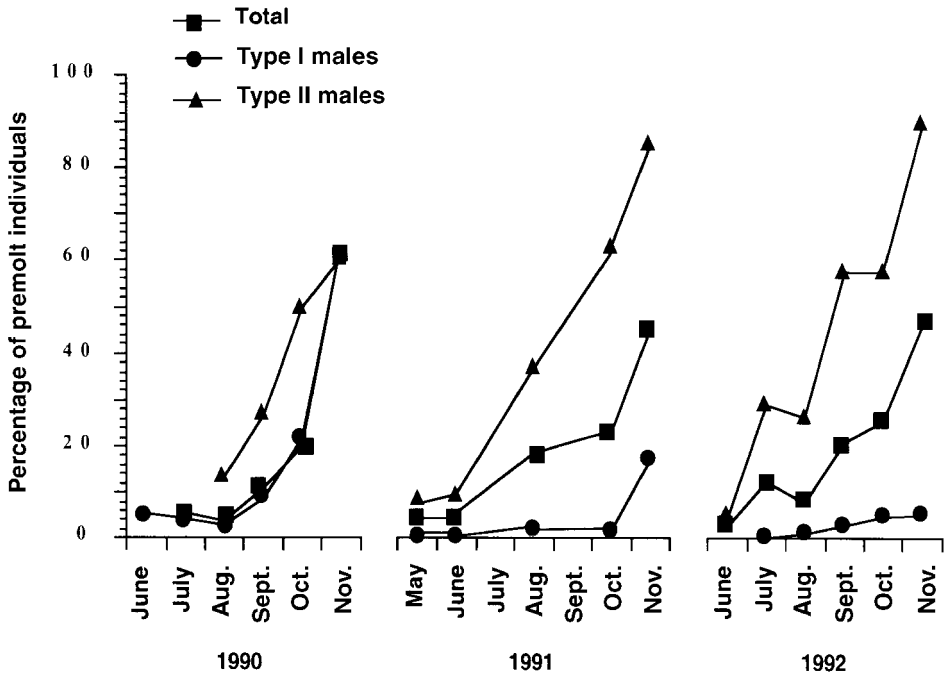
Amongst the individuals identified as early stage D_0 in May–July by means of histological examination (54), 22 (41%) were also discernible from setagenesis on the endite of the first maxilliped. For the remaining 32 individuals, no sign of apolysis was discernible from setagenesis, despite the fact that molting fluid was observed in the same individuals by means of histology. The presence of a double carapace was not observed in individuals identified as premolt stages (D_0–D_1') by means of histology and from setagenesis.

Discussion

Techniques for identifying the early-premolt stage

The molt stages universally used for various crustacean species were established by Drach (1939): A and B (postmolt), C (intermolt), and D (premolt). Further division of each stage into substages requires detailed histological observations of

Fig. 4. Monthly percentages of adolescent male snow crabs (*Chionoecetes opilio*) during the premolt period (stage D_0 or later), based on histological observations of the integument. (The total number of type II males in June and July 1990 was less than 5 and the percentages of premolt invividuals are not shown in this figure.)



the formation of each cuticle layer. The technique of predicting molt 2–3 months in advance (late-premolt stages) can be used for snow crabs by checking for the presence of a double carapace, i.e., the formation of new cuticle (Hoenig et al. 1994; Sainte-Marie et al. 1995), when the animal can be sacrificed. However, this method often leads to misclassification, owing to the presence of a membrane detached from the carapace of intermolt animals. Newly formed carapace and the detached membrane both appear red, and this can result in discordance between visual observations and histological examination of the integument (Dawe et al. 1992). Observation of setagenesis in any transparent appendages, as defined by Drach (1939, 1944) and Drach and Tchernigovtzeff (1967), is the most appropriate technique for identifying the premolt stages and substages in the snow crab (Moriyasu and Mallet 1986; O'Halloran and O'Dor 1988). However, Dawe et al. (1992) reported that identifying D_0 in snow crabs on the basis of observations of setagenesis poses some technical difficulties. Saint-Marie et al. (1995) also reported difficulty in using setagenesis to detect D_0, which led to their conclusion that formation of the new shell preceded changes in the mouthparts. However, formation of the new shell (i.e., the presence of double carapace) cannot be detected before the D_1'' stage, during which clear changes in setal morphology (the formation of a setal invagination) can easily be observed (Skinner 1985; Stevenson 1985).

According to Drach (1939), premolt stage D_0 can only be identified by apolysis (retraction of the membranous layer from the epidermis) and cannot be observed by histological examination of the integument. Identifying apolysis in histological sections is possible but not reliable, owing to the presence of artifacts caused when the hypodermis separates from the cuticle. TEM observations revealed that the secretion of fibrous material, also observed in histological sections, corresponds to the beginning of formation of a new epicuticular layer. During this phase, numerous actively secreting cells are present beneath the epithelium and Leydig cells in the connective tissue, and the secretion of molting fluid (Roer and Dillaman 1993) accelerates. It is, therefore, appropriate to use the presence of molting fluid as the key criterion for identifying D_0 in snow crabs, since this stage preceded any sign of D_1, i.e., resorption of the membranous layer (Skinner 1985) or setal organization on the maxilliped (Reaka 1975).

Identifying D_0 by histological means is a more sensitive technique than observing setagenesis. Although the present technique requires time-consuming histological treatment, it may provide a tool for increasing our understanding of the molt cycle in this species. When a high degree of sensitivity in identifying D_0 is not required, observation of setagenesis provides a rapid, less expensive, and reliable method of assessing pre-ecdysial events in snow crabs.

Molting dynamics of male snow crabs

The growth mechanism of snow crabs has become increasingly enigmatic since the finding of the terminal molt in male crabs by Conan and Comeau (1986). Two types of molt are known in snow crabs: terminal and nonterminal (Conan and Comeau 1986). Once the crabs become terminally molted, they do not seem to molt again (Conan and Comeau 1986; Yamasaki and Kuwahara 1991; Sainte-Marie and Hazel 1992). Not all adolescent males molt each spring, contrary to the findings of Conan and Comeau (1986) and Conan et al. (1988). Conan and Comeau (1986) reported the occurrence of adolescent males in D_0 in October–November in the southern Gulf of St. Lawrence, based on observation of setagenesis on the maxilliped (Moriyasu and Mallet 1986). These individuals

advanced slowly though the molting process and reached ecdysis in March–April (5–6 months later). The length of the period from premolt to ecdysis concurs with what has been reported by Moriyasu and Mallet (1986) and O'Halloran and O'Dor (1988). This molt pattern corresponds to that of the type I′ males described in this study.

The histological feature of the cuticle that was confirmed by TEM observations, i.e., the presence of molting fluid between the membranous layer and the epithelium, revealed that type II males had already entered D_0 as early as May. Based on the length of premolt stages from D_0 to ecdysis (Moriyasu and Mallet 1986; O'Halloran and O'Dor 1988), individuals preparing for molting in May–July should normally reach ecdysis in December–January. During a herring (*Clupea harengus harengus*) survey in the Shediac Valley, southern Gulf of St. Lawrence (Fig. 1), by-catches of molting males of sublegal and legal sizes were observed in December 1991 (Dr. H. Dupuis, Department of Fisheries and Oceans Canada, Moncton, N.B., personal communication). Although morphometric measurements are not available for these individuals, the males may correspond to the individuals that were observed in D_0 in May–July. Molting of type II males in aquaria was also observed from early December (M. Moriyasu, unpublished data). If this is the case, the intermolt cycle for type II molters may last approximately 21 months. The external features and molting pattern of type II males correspond to those of the crabs described by Chiasson et al. (1991) and Comeau and Conan (1992), which are commonly called skip-molters.

Amongst type I males, individuals that appeared to have molted before the current spring were discernible (i.e., had reached intermolt stage C_4) in May–July by means of histological examination of the integument (type I″ males). These crabs had probably skipped one molt in March–April of the previous year (type II males in spring of the previous year) and molted in December–January. Although they are difficult to follow after both types (I' and I") of males have reached intermolt stage C_4 in August, the percentage of type I″ in the total number of type I males in May–July in a given year seems to correspond to that of type II individuals in the total number of adolescent males in March–April of the previous year. In fact, the percentages of type I″ in the total number of type I males in 1991 (2%) and 1992 (57%) correspond to those of type II individuals in the total number of adolescent males in 1990 (8%) and 1991 (56%).

The characteristics of each type of adolescent male observed in May–July in the southern Gulf of St. Lawrence can be summarized as follows: (*i*) type I′ males are the individuals that molted in March–April of the current year, on a 12-month cycle. This has been thought to be the species' only molting schedule (Conan and Comeau 1986); (*ii*) type I″ males are the individuals that molted in the previous December–January, which could be the result of two different molting schedules, i.e., molting of type I″ males on a 12-month cycle and molting of type II individuals on a 21-month cycle that skipped one spring molting season in the previous year (skip-molters). The existence of a 12-month winter molting cycle could not be confirmed in this study. The factor that affects skip-molting is still unknown.

The duration of the molting season depends on the abundance of each type of male in the adolescent crab population on a different molting schedule. The percentage of type II males observed in the southern Gulf of St. Lawrence during the spring commercial fishing season varied from 13 to 28% (Hébert et al. 1992; Chiasson et al. 1995). In addition, the durometer readings from newly molted males during the fishing season (May–July) in the southern Gulf of St. Lawrence also showed a very wide range, from a completely soft shell to a relatively hard shell, in certain years (M. Hébert, personal observation), which suggests interannual variation in molting pattern. A scarcity of individuals in the advanced premolt stages in November–December (especially amongst type II molters) in the current study area suggests the occurrence of a molting migration to outside the study area.

Based on the present observations, it is reasonable to think that the molting season of snow crabs in the southern Gulf of St. Lawrence is far more complex and variable than has been reported (Conan et al. 1988). The interannual variation in molting pattern may result from recruitment of individuals from areas where molting patterns differ or from genetically different groups. Density-dependent factors may also influence the annual molting patterns of adolescent males. The variable molting patterns of male snow crabs have quite important implications for long-term stock management. Further study on the structure and dynamics of molters, especially the plasticity of molting patterns over years, is needed.

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