Growth and maturation of the benthic stages of male snow crab, *Chionoecetes opilio* (Brachyura: Majidae)

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Abstract: Growth and maturation of postlarval male snow crab (*Chionoecetes opilio*) in an exploited Gulf of Saint Lawrence population were elucidated using size distributions in beam trawl samples taken bimonthly from April 1991 to May 1992, moult and maturity indices, and measures of growth per moult. Males develop in three stages: immature, without spermatophores; adolescent, with spermatophores but undifferentiated chelae; and adult, with spermatophores and differentiated chelae. Males change from immature to adolescent after a puberty moult, and from adolescent to adult after a terminal moult producing a final carapace width (CW) >40 mm. The slope of the regression relating post- to pre-moult CW decreases after puberty. Carapace moult increments are the same at pre-terminal and terminal moults, for a constant premoult CW. Males recruit to the legal size of 95-mm CW at instar XII, ≈8.7 years or more after settlement. The slope of the regression of gonad weight on CW is less for adult than for adolescent males owing to the formers' participation in reproduction and to greater depletion of sperm stores in large than in small adult males. Gonad weight increases with time since moult, but for large adults, did not reach levels recorded in prefishery times or in an unfished population.

Résumé : La croissance et la maturation des stades postlarvaires du mâle du crabe des neiges (*Chionoecetes opilio*) dans une population exploitée du golfe du Saint-Laurent ont été élucidées à l'aide de distributions des tailles dans des échantillons bimestriels prélevés à l'aide d'un chalut à perche d'avril 1991 à mai 1992, d'indices de mue et de maturité et de mesures d'accroissement de la taille à la mue. Le mâle se développe en trois étapes: immature, sans spermatophores; adolescent, avec spermatophores mais à pinces non différenciées; adulte, avec spermatophores et pinces différenciées. Le mâle immature devient adolescent après une mue de puberté et l'adolescent devient adulte après une mue terminale résultant en une largeur de carapace (LC) finale >40 mm. La pente de la régression entre les LC post- et prémue décroît après la puberté. L'accroissement de la carapace à la mue est pareil aux mues pré-terminale et terminale, pour une même LC prémue. Les mâles recrutent à la taille légale de 95 mm de LC au stade XII, ≈8,7 ans ou plus après l'établissement. La pente de la régression du poids des gonades sur la LC est plus faible chez les mâles adultes que chez les mâles adolescents, parce que les premiers participent à la reproduction et que les réserves de sperme sont plus entamées chez les gros que chez les petits mâles adultes. Le poids des gonades croît en fonction du temps écoulé depuis la mue, mais n'atteignait pas chez les gros mâles adultes les niveaux enregistrés avant l'essor de la pêche ou dans une population vierge.

Introduction

The snow crab *Chionoecetes opilio* supports major fisheries in the Northwest Atlantic and North Pacific (FAO

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1990). In eastern Canada, localized exploitation started in the early 1960s, but the fishery did not expand into a large-scale operation until the mid-1970s (Elner 1982; Hare and Dunn 1993). The *C. opilio* fishery is regulated mainly by quota, by a limitation of the number of traps allowed per permit, by season, and by a minimum legal size of 95 mm carapace width (CW), which effectively prevents the harvest of females (Bailey and Elner 1989). The condition of catches is also taken into account: the fishery is closed when the percentage of soft-shelled crab surpasses 20% of cumulative catch for two consecutive weeks (Hébert et al. 1992). This is done to reduce resource wastage, because soft-shelled crab have little market value and may

suffer high mortality when rejected at sea (Miller 1977; Ke et al. 1981; Hardy et al. 1994).

A clear understanding of maturation and growth processes is essential for proper management of the snow crab resource (e.g., Elner and Robichaud 1983; Jamieson and McKone 1988; Conan et al. 1988b; Bailey and Elner 1989; Comeau and Conan 1992). To date, development of male primary and secondary sexual characters is well documented. Notably, Comeau and Conan (1992) showed that males fully mature after completing three developmental stages that are separated by two critical moults. Immature males undergo a first critical moult they called the juvenile moult, which marks the onset of sperm production and is followed by a subtle but significant increase in the growth rate of chelae relative to CW. Some time and a variable number of moults later, juvenile males perform a second critical moult they called the moult to morphometric maturity or terminal moult (see below), during which the chelae enlarge disproportionately to carapace. Males having completed this second critical moult were called morphometrically mature. Other investigators have used the terms small clawed and large clawed to designate juvenile and morphometrically mature males, respectively.

As far as growth is concerned, however, little is known for snow crab in eastern Canada. Moulting of males >40 mm CW occurs annually between late winter and early summer (e.g., Moriyasu et al. 1987; Conan et al. 1988b; O'Halloran and O'Dor, 1988; Comeau et al. 1991; Sainte-Marie and Hazel 1992; Hoenig et al. 1994), but information on the frequency and time of moulting of smaller males is scarce (Brêthes et al. 1987; Robichaud et al. 1989). Moriyasu et al. (1987) measured carapace moult increments for laboratory-held C. opilio. They related post- to pre-moult CW by linear regression, for males of 22–108 mm premoult CW, and concluded that carapace moult increments were relatively greater for males growing through a regular moult (i.e., any moult except the moult to morphometric maturity) than for males undergoing a moult to morphometric maturity. Moriyasu et al. (1987) did not estimate instar or age at the legal size limit of 95 mm CW. Robichaud et al. (1989) collected C. opilio by beam trawl off northwest Cape Breton in May 1981 and in May, July, and September 1982. They inferred the number of instars, the moulting frequency and carapace moult increments from CW frequency distributions, extrapolating values for several missing instars. Robichaud et al. (1989) suggested that males reach the legal size of 95 mm CW at instar XI within 4.5 years of hatching. By contrast, Watson's (1969) growth model predicted that males attain 95-mm CW at instar XIII and at a post-hatching age of 9.5 years. Watson provided moult increment data for snow crab of 10–35 mm CW, but moult increments for larger crab and the duration of intermoult were hypothetical or came from the Japanese literature.

The implications of the juvenile and morphometric maturity moults for male growth are unclear and (or) controversial. Robichaud et al. (1989) inferred the size of large instars missing in their field collections by extrapolating carapace moult increments from a single growth function developed for instars III–VII. Similarly, Moriyasu et al.

(1987) used a single regression model to describe growth for males of 20–68 mm CW that underwent a regular moult, but discussed the possibility of a reduction in growth after the juvenile moult owing to gonad development. A reduction of growth at sexual maturity has been demonstrated for a variety of crustaceans (e.g., Kurata 1962; Hartnoll 1985). For C. opilio, specifically, Miller and Watson (1976) found that the slopes of regressions of moult increment on pre-moult CW differed significantly between males that were assumed, on the basis of body size, to be immature (<57 mm CW) and those that were assumed to be producing spermatophores (>57 mm CW). For the Gulf of Alaska population of Tanner crab, Chionoecetes bairdi, Donaldson et al. (1981) found that the slope of the regression relating post- to pre-moult CW was significantly greater in males <45 mm CW than in larger males. They tentatively attributed this to a change in lifestyle, but Wolff and Soto (1992) reinterpreted their results and suggested that this change in slope reflected the onset of gonad development. Similarly, Somerton (1981a) detected a reduction of growth at 59 mm CW for C. bairdi in the Bering Sea, but was unable to relate this change to maturity, which he defined according to chela allometry.

O'Halloran (1985) and Conan and Comeau (1986) hypothesized that the moult to morphometric maturity is a terminal moult, but this hypothesis and (or) the supporting evidence were challenged and debated (Conan et al. 1988a, 1988b, 1990; Donaldson 1988; Donaldson and Johnson 1988; Jamieson and McKone 1988; Dawe et al. 1991). Sainte-Marie and Hazel (1992) observed moulting of male C. opilio in nature and provided direct evidence for the terminal moult hypothesis. In four consecutive years of field observations during the late winter moulting period, they observed for hard-shelled males that 23% of juveniles larger than the minimum size for morphometric maturity (i.e., 40-mm CW) were moulting. This contrasted with a mere 0.3% for males classified as morphometrically mature. Confirmation of a terminal moult for males may have numerous and important implications for Chionoecetes fisheries (e.g., Conan and Comeau 1986; Conan et al. 1988b; Sainte-Marie and Hazel 1992; Stevens et al. 1993).

Reviews of growth in C. opilio have stressed that development of a general growth model is compromised by lack of information on moult periods and growth per moult (Conan et al. 1988b) or have presented growth models that did not integrate the moult to morphometric maturity (Adams 1979; Kon and Sinoda 1992). In this paper, growth and maturation processes are elucidated to produce a comprehensive growth model for male C. opilio. Our model is based on analyses of (i) gonad development, (ii) chela allometry, (iii) size distributions and moulting record for males in beam trawl samples taken bimonthly over a 14-month period, and (iv) moult increments determined from size-frequency data and measured directly in the field and laboratory. The study site was a small bay in the northwest Gulf of Saint Lawrence, where C. opilio have been exploited since 1977, and which in recent years has sustained some of the highest fishery yields per unit area in the northern Gulf (Sainte-Marie 1993).

Fig. 1. Map of Baie Sainte-Marguerite and the Gulf of Saint Lawrence (inset) showing locations of beam trawl samples.
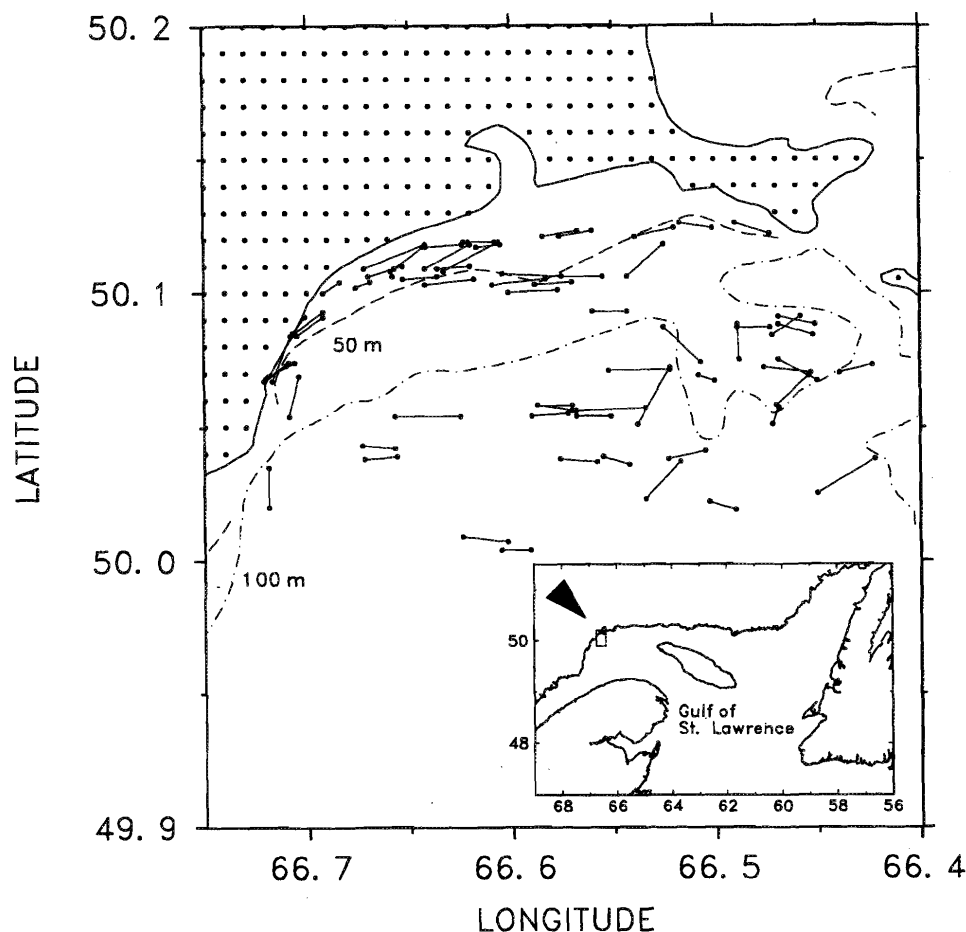
Materials and methods

Terminology

Some of the terms used in the literature to describe the critical moults and developmental stages for male *C. opilio* are misleading. We have amended Comeau and Conan's (1992) terminology as follows: "immature male" remains, "puberty moult" replaces "juvenile moult", "adolescent male" replaces "juvenile male", "terminal moult" remains, and "adult male" replaces "morphometrically mature male". The term puberty moult clearly indicates that generative organs become functional, so that after this moult the male (once hard shelled) has the potential to mate successfully, at least with virgin soft-shelled females. Indeed, Sainte-Marie and Lovrich (1994) demonstrated that hard-shelled adolescent males were as effective as hard-shelled adult males at inseminating and inducing egg extrusion for virgin females in a noncompetitive aquarium setting. Moriyasu and Conan (1988) showed that virgin females after copulating with adolescent males extruded eggs that underwent division and were thus presumably viable. The terms adolescent and adult are more self-explanatory: the former indicates that the male has reached puberty and is approaching the adult stage; the latter clearly reflects the fact that growth and maturation processes are complete. The term

juvenile as it is used by Comeau and Conan (1992) is incompatible with previous usages. Websters' dictionaries, for example, define a juvenile as an individual that is "physiologically immature or undeveloped." In crustaceans, the term juvenile is often used to designate all physiologically immature stages or specifically, in decapods, the megalopa and early benthic stages (e.g., Schram 1986).

Study site and sampling

Baie Sainte-Marguerite is located in the Gulf of Saint Lawrence (Fig. 1). The Bay is 21.9 km wide by 6 km long and weakly indents the coastline of the north coast of the Gulf of Saint Lawrence. Bottom temperature in the Bay is cold year-round, and ranged in 1991–1992 from −1.5 to 3°C at 50 m and from −1 to 0.8°C at 100 m (Raymond 1995).

Chionoecetes opilio were collected with a 3-m beam trawl fitted with heavy tickler chains to dislodge buried animals. The 25-mm netting was doubled in the codend with 15-mm netting and retained *C. opilio* with CWs exceeding ≈15 mm. However, rapid occlusion of the mesh by other fauna and sediment also resulted in the retention of many smaller *C. opilio* (Raymond 1995). Sampling was conducted during 11–15 April, 19–24 June, 22–29 August, 23–29 October, and 11–12 December 1991, and 19–21 March

and 12–14 May 1992. A fraction of the *C. opilio* population in Baie Sainte-Marguerite, and elsewhere in the northern Gulf, moves into very shallow waters during winter and spring (Taylor et al. 1985; Hooper 1986; Sainte-Marie et al. 1988; Comeau et al. 1991; Sainte-Marie and Hazel 1992). Therefore, during each field mission we sampled at least three randomly selected locations in each of three bottom depth strata: 0 to ≤20 m, >20 to ≤80 m and >80 to 140 m (Fig. 1). This enabled us to obtain samples that were representative of the whole population in the Bay. Tows lasted 15–20 min at a ship speed of 1.3–1.5 m·s⁻¹.

Characterization of *C. opilio*

Trawl contents were sorted on board on a 5-mm sieve. Sex, exoskeleton condition, and the number and position of missing limbs were determined for *C. opilio*. Sex was determined by the shape of the abdomen. However, the sex of *C. opilio* <6 mm CW could not be determined by visual inspection alone, because the abdomens of males and females are not well differentiated at these sizes. Exoskeleton condition was rated 1 (clean soft), 2 (clean hard), 3 (intermediate), 4 (dirty hard), or 5 (dirty soft) according to criteria in Sainte-Marie (1993). This scale reflects gradual changes in the appearance of the exoskeleton with time elapsed since the previous moult: conditions 1 and 5 indicate that individuals moulted ≈0–5 months and ≈4–6 years ago, respectively (Sainte-Marie and Dufour 1994; B. Sainte-Marie, unpublished data). Males in the dirty-soft condition are irreversibly deteriorated: i.e., they die but never moult (Sainte-Marie and Hazel 1992, unpublished data). Occasionally, male *C. opilio* that were moulting and male exuviae were also collected. Moulting males had swollen pericardial sacs that lifted the old shell, thereby exposing the new soft shell as described by Watson (1971).

The maximum width of the carapace of intact male exuviae and of live male and unsexed *C. opilio* was measured, excluding spines, to the nearest 0.1 mm using a nonmodified vernier caliper. For all males exceeding 40 mm CW, and for some smaller males, the height of the propodus of the right chela excluding spines (CH) was also measured to the nearest 0.1 mm as described in Sainte-Marie and Hazel (1992). The propodus of the left chela was measured if the right chela was missing or diminutive, the latter case indicating incomplete regeneration (Sainte-Marie and Hazel 1992). Males were classified as adolescent or adult based on their individual CH and CW measurements and a site-appropriate discriminant function (see below).

To determine the maturity and weight of gonads, adolescent and adult males were fixed by injection of, and immersion in, 4% buffered formalin in seawater. Our objective on each field mission from April 1991 to March 1992 was to sample 10 males per 20 mm CW size class, starting at 20 mm CW for immature-adolescent and 40 mm CW for adult males. However, this objective was never achieved owing to a paucity of males of intermediate size (see below). In the laboratory, the preserved males were dissected and the genital tract, including testes and vasa deferentia, was extracted and its blotted wet weight determined to the nearest 10⁻³ g. For a few males, testes and vasa deferentia were weighed separately to provide an estimate of their relative contributions to total weight of the genital tract. Maturity of male gonads was determined by microscopic examination of vasa deferentia smears following the method of Watson (1970). Males that were physiologically mature were those with smears that contained spermatophores, i.e., sperm-loaded spheres of about 60–100 μm diameter (Beninger et al. 1988; Chiba et al. 1992).

Additionnally, we also determined gonad weights for adult males with dirty-hard exoskeletons that were collected in the Saguenay Fjord in July 1992. The Fjord opens into the Saint Lawrence Estuary, west of our study site, and harbours a small, commercially unexploited population of *C. opilio* (Sainte-Marie et al. 1992).

The periods of moulting were derived from field data using four different indicators. The first was temporal change in CW frequency distributions, which proved to be particularly useful for small males. A second indicator was temporal change in the frequency of occurrence of moulting males, of exuviae and of soft-shelled males. The third indicator was the presence of males with a new shell underlying the old shell. Dissection to detect an underlying shell was used by Dawe et al. (1991) and Sainte-Marie and Hazel (1992) to estimate moulting frequency of adolescent and adult males, and by Ito (1970) and Hoenig et al. (1994) to predict moulting activity. Finally, the fourth indicator of moulting was moult stage determination by microscopic examination of male maxillae, following the method of Moriyasu and Mallet (1986). Maxillae were removed from live males and preserved in 4°C seawater for ≤36 h until they were read. In principle, all males in D₀ to D₄ stages are committed to moult. We were quite aware, however, of the difficulty in discerning the early D₀ stage from the intermoult C stage (e.g., Dawe et al. 1991; Hoenig et al. 1994). Males selected for dissection and moult-staging were hard-shelled, and we attempted to examine equal numbers per 20-mm CW size class in the range of 40–100 mm CW for adolescent males and 40–120 mm CW for adult males. Examined males were in the intermediate or dirty-hard condition, except in June, August, and October when a few clean-hard males also occurred in samples.

Direct measurements of CW and CH increments at moult were obtained from the laboratory and field. Moult increments from laboratory-held *C. opilio* were taken from individuals kept in captivity for up to 5 months. Males were segregated by size and maturity, and held in tanks with density not exceeding ≈10 crab·m⁻². Other holding conditions are described in Sainte-Marie and Lovrich (1994). Tanks were checked at least daily to detect moulting activity. Males that had started to moult were isolated in a 1-m² chamber. Field measurements of moult increments were taken from 19 to 29 March 1992 in Baie Sainte-Marguerite. SCUBA divers collected moulting males at depths of 6–31 m and then transferred them to 500-L shipboard holding tanks with running fresh seawater. Mortality was nil and males finished moulting within 6–8 h of capture. In the laboratory and field, CW and CH of the exuvium and live crab were measured a few days after the moult was completed.

Analysis of data

Chela allometry was determined by linear regression (Sokal and Rohlf 1981) of CH on CW, after data were transformed to their natural logarithm (ln). Regression was performed separately for immature and adolescent males. Slopes and, where appropriate, elevations of regressions were then compared by analysis of variance (ANOVA) and analysis of covariance (ANCOVA), respectively (Sokal and Rohlf 1981). The abscissa value for the point of intersection (I) between lines with significantly different slopes was calculated as $I = (b_2 - b_1)/(a_1 - a_2)$, where a_1 and a_2 are the slopes and b_1 and b_2 the Y-intercepts of the two lines.

A size–frequency histogram was used to represent distribution of CWs for unsexed and male *C. opilio* from all beam trawl samples. Modal structure in the histogram was analyzed using the MacDonald and Pitcher (1979) method. Size–frequency distributions for unsexed and male *C. opilio* <40 mm CW from each sampling period were analyzed sequentially to detect seasonal changes in modal composition. Modes were interpreted as instars and a marked decline of one mode and concomitant increase of the adjacent larger mode was interpreted as a moult from one instar to the next (Hartnoll 1982).

Although a variety of models have been proposed to describe size increase for Crustacea, none has received unanimous support (e.g., Somerton 1980; Botsford 1985; Easton and Misra 1988; Wainwright and Armstrong 1993). The Hiatt growth model (Hiatt 1948; Kurata 1962) relates some linear measure of body size in post- (L_{T+1}) and premoult (L_T) conditions by simple linear regression as $L_{T+1} = aL_T + b$. The Hiatt model was used to model carapace and chela growth per moult. Crabs missing three or more limbs in the premoult condition were excluded from analyses because they had smaller moult increments, unless they underwent a terminal moult. In many brachyuran species, growth per moult is reduced for individuals regenerating limbs (e.g., Hartnoll 1982; Smith 1990). The methods of analysis and of comparison of Hiatt models for different groups of males were the same as those used above for chela allometry.

For males >40 mm CW, gonad weight (GW) was related to CW by linear regression for each combination of male maturity (adolescent or adult) and exoskeleton condition (1–5), after logarithmic transformation of data. Using ANCOVA, GWs were adjusted for a standard CW for those groups of males which had regressions with significant and homogeneous slopes. Adjusted GW was used instead of a gonadosomatic index, because it is independent of exoskeleton fouling and injuries (Sainte-Marie 1993).

Results

Maturity and chela allometry

Spermatophores were detected in vasa deferentia smears of all males >39.2 mm CW, but none was seen in smears from males <36.9 mm CW. The size transition from 100% immature gonads to 100% mature gonads was consequently abrupt, and 50% of males had mature gonads at 38.5 mm CW (Fig. 2A).

For males exceeding 40 mm CW, two clouds of points were easily resolved in scattergrams of ln(CH) on ln(CW)

Fig. 2. Percentage of male *C. opilio* classified (A) physiologically mature (with spermatophores) or (B) adult, by 5-mm carapace width size classes. Males were collected from April 1991 to March 1992 in Baie Sainte-Marguerite. The equation in Fig. 2A is for the logistic curve fitted to the data, while the vertical broken line shows the carapace width of crab of which 50% have mature gonads. Solid circles and lines represent percentage; open circles represent sample size.
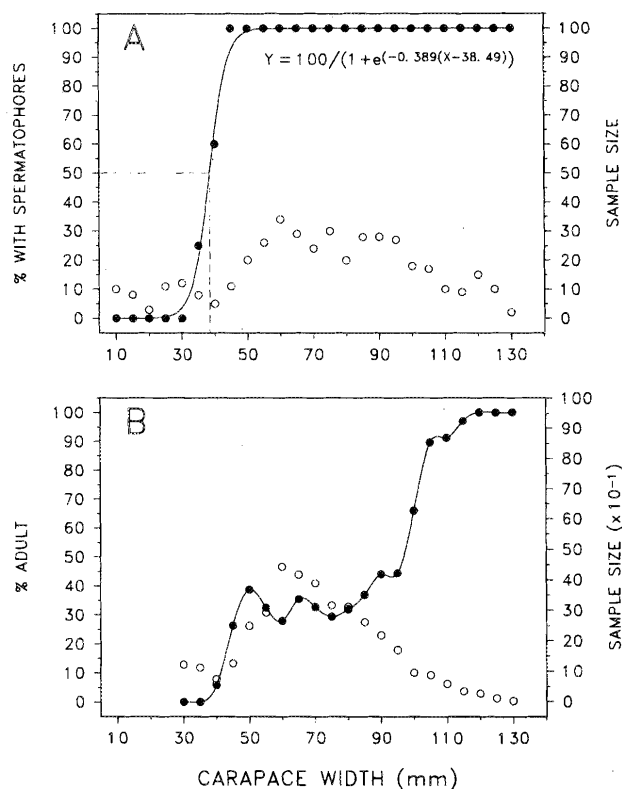
(Fig. 3). The lower and upper clouds represent adolescent and adult males, respectively. The two clouds of points were not quite parallel and gradually diverged at larger CWs. The bivariate discriminant function used by Sainte-Marie and Hazel (1992) to classify adolescent and adult males from Baie Sainte-Marguerite in 1990 also separated the present data (Fig. 3). The equation of that discriminant function is ln(CH) = 1.2209ln(CW) − 2.6077. The smallest adult male had a CW of 40.8 mm and the largest adolescent male was 113.2 mm CW. Four small males of 31.4–37.1 mm CW had relatively large chelae (Fig. 3), but we attribute these to measurement error or chela deformity. The size transition from 0 to 100% adult males was irregular and occurred over a very broad range of CWs (Fig. 2B). The proportion of adult males relative to the total number of males per 5-mm CW size class rose sharply from 0% at 35 mm to 35% at 50 mm, varied around 35% from 50 to 85 mm, and then increased to reach 100% at 120 mm.

The slopes of regressions of ln(CH) on ln(CW) differed significantly between immature and adolescent males (Fig. 4). The slope of the regression for immature males did not differ significantly from one ($t = 1.94$, $P > 0.05$),

Fig. 3. Scattergram of ln(chela height) versus ln(carapace width) for male *C. opilio* collected in Baie Sainte-Marguerite from April 1991 to May 1992. Chela height was measured for all males ≥40 mm CW (i.e., ≥3.69 ln units), but only for some smaller males. $N = 4839$. The line separating the two clouds of points is the discriminant function from Sainte-Marie and Hazel (1992).
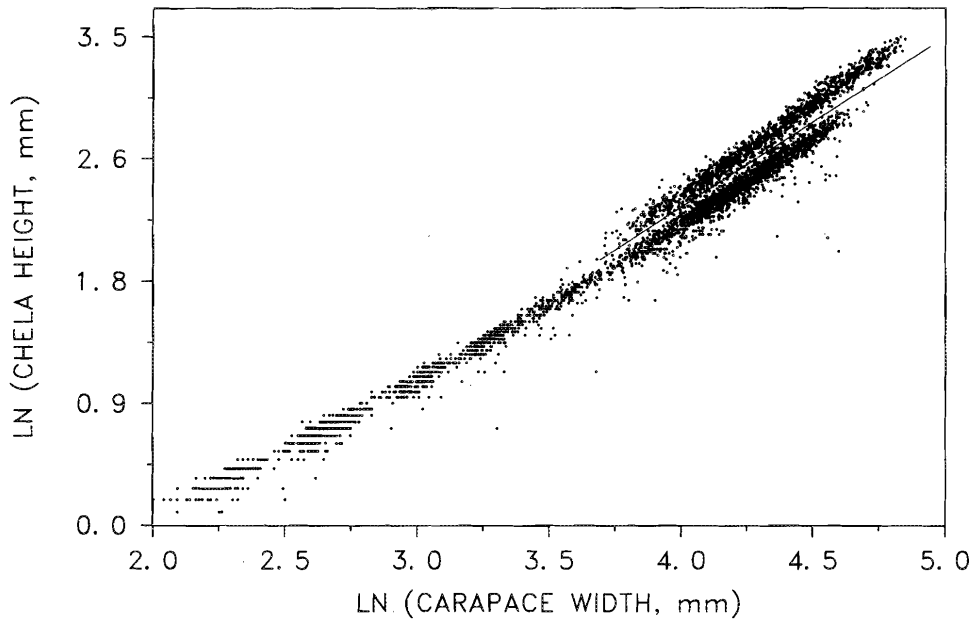

Fig. 4. Scattergram of ln(chela height) on ln(carapace width) for samples of immature, adolescent and adult male *C. opilio* taken in Baie Sainte-Marguerite from April 1991 to May 1992 for determinations of gonad maturity (same individuals as in Fig. 2A). Maturity of males was based on spermatophore absence (immature), spermatophore presence associated with undifferentiated chelae (adolescent), or spermatophore presence associated with differentiated chelae (adult). Equations of regressions are $\ln(\text{CH}) = 1.028$ $\ln(\text{CW}) - 2.044$ for immature males (oblique broken line, $N = 59$, $r^2 = 0.99$, $P < 0.001$) and $\ln(\text{CH}) = 1.226 \ln(\text{CW}) - 2.754$ for adolescent males (solid line, $N = 175$, $r^2 = 0.97$, $P < 0.001$). The two slopes differ significantly according to an ANOVA ($F = 85.11$, $P < 0.001$). The vertical dashed line indicates the abscissa value at which the two regressions intersect (I).
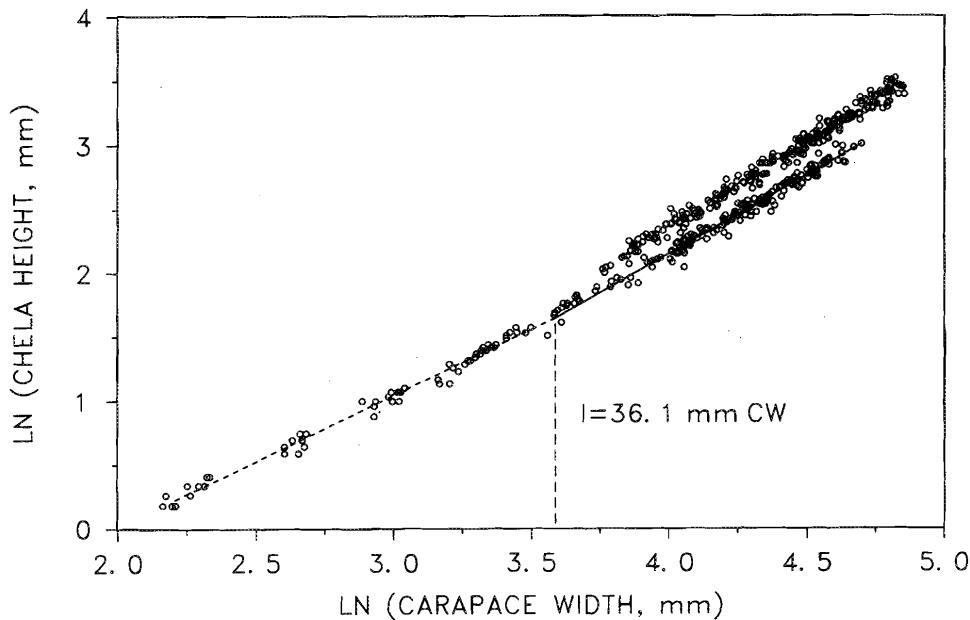
Fig. 5. Size–frequency distribution for beam-trawled males and unsexed *C. opilio* in Baie Sainte-Marguerite from April 1991 to May 1992. Snow crab are grouped by logarithmic size classes of 0.02 units and classified as immature/adolescent (solid bars) or adult (open bars) males. Note the relative scarcity of males in the 3.4–4.0 range on abscissa scale. Instars I–VIII are identified. Frequencies were stacked when adolescent and adult males were represented in the same size class. The first and second broken vertical reference lines indicate 40 and 95 mm carapace width, respectively. $N = 24\ 823$.
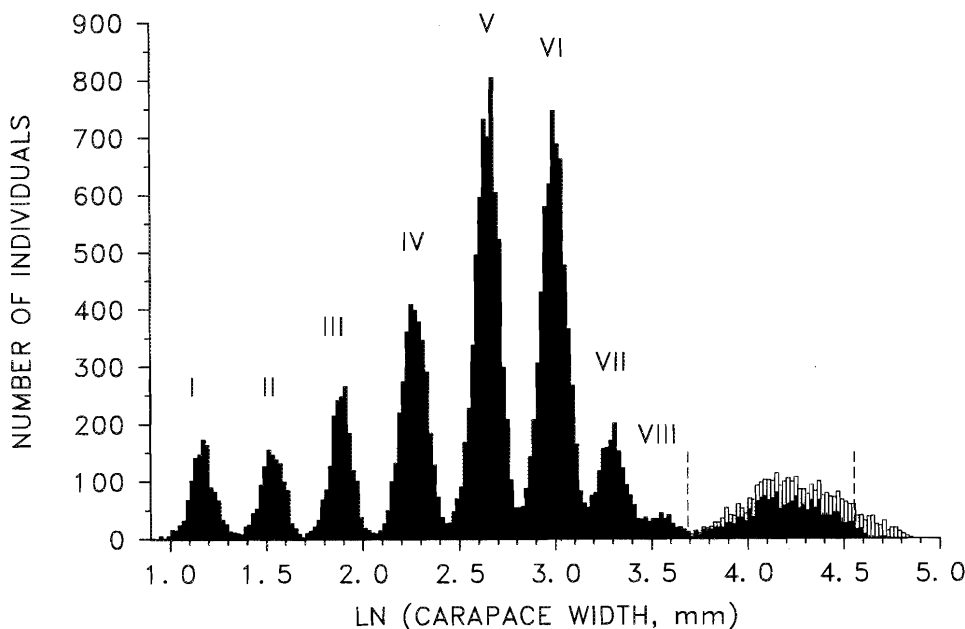
indicating isometric growth of chelae relative to carapace. However, the slope of the regression for adolescent males was significantly greater than one ($t = 15.04$, $P < 0.001$), indicating positive growth allometry of chela relative to carapace. The regression lines for immature and adolescent males intersected at 36.1 mm CW.

Size frequency distributions

A total of 24 823 live male and unsexed *C. opilio* was collected in 65 beam trawl samples. Overall size–frequency distributions showed a paucity of immature and adolescent males in the ≈32- to 55-mm CW size range (Figs. 5 and 6). Considering this discontinuity and the lack of modal structure or seasonal change in the size frequency distributions of males larger than ≈40 mm CW, we focused attention on male *C. opilio* ≤40 mm CW. Within this size range, seven modes were outstanding and an eighth could be discerned: these were designated instars I–VIII (Figs. 5 and 6, Table 1).

There were obvious shifts between months in the relative importance of the first seven instars (Fig. 6). Instar I was not found in August samples; was scarcely represented in April, May, and June samples; but was very well represented in October, December, and March samples. The seven other instars were present year-round. Instar II was best represented from March to June, excepting the May sample, and was rare from August to December. Instar III was scarce from April to June, but common from August to March. Instar IV was relatively uncommon from June to

December but generally abundant from March to April. Instar V was strongly represented from May to October but relatively less abundant from December to April. Many representatives of instar VI were found from December to May but they were rather scarce in other months. Instar VII was generally uncommon from April to December 1991, but was better represented in March and May 1992 samples. Instar VIII was extremely scarce and showed no clear temporal pattern of abundance. The approximate periods of peak moulting that can be inferred from shifts in the size-frequency distributions (Fig. 6) are the following: March for *C. opilio* moulting from instar I to II and from instar III to IV, May–June for instar IV to V, August for instar II to III, and December for instar V to VI. The time periods for moulting of instars VI and VII could not be inferred from the size–frequency data.

Moulting activity

Observations of moulting or soft-shelled *C. opilio* provided direct evidence for moulting activity (Table 2) and corroborated the moulting schedule inferred for instars I–V from size–frequency distributions. Peak moulting activity was recorded in April for instars I and IV, in August for instar II, in December for instars III, V, VI, and VII (Table 2). However, instars II–VI had protracted moulting periods that spanned 8–10 months. The scant data for instar VIII suggest moulting in May (Table 2).

For hard-shelled adolescent males >40 mm CW, our data indicated a clear annual moult cycle with peak moulting

Fig. 6. Size frequency distributions by sampling period for beam-trawled males and unsexed *C. opilio* <40 mm carapace width. Instars I–VIII are identified in the upper left summary histogram for all samples combined. Roman italic numbers above the modes in histograms for individual sampling periods highlight the appearance or a marked increase in the relative abundance of a given instar.
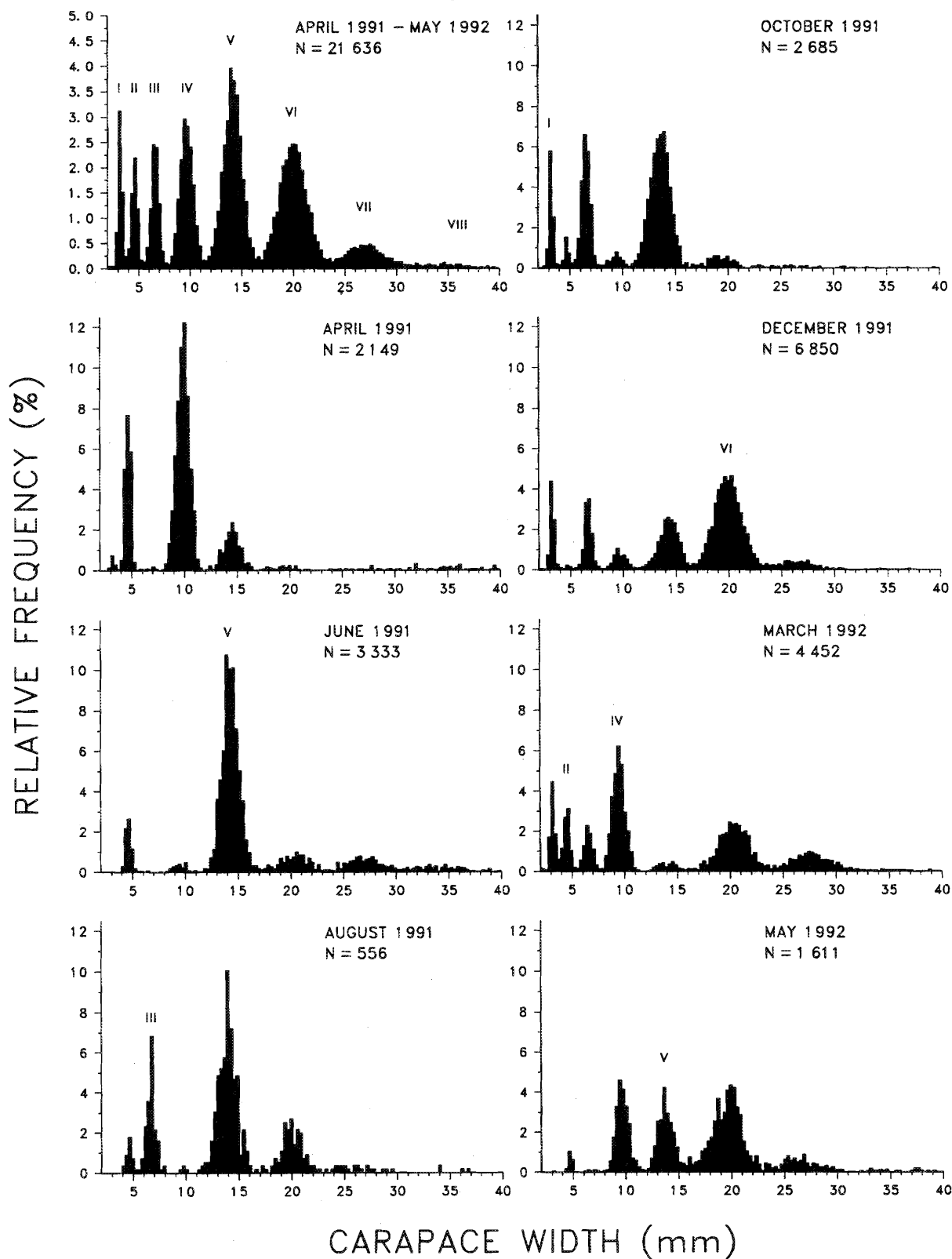
occurring in April or May. Indeed, intact male exuviae ≥40 mm CW were found only from March to June, with the highest numbers recorded in May, while moulting adolescent males were collected only in April and May (Table 3). Soft-shelled adolescent males were found only from March to August, with a peak occurrence in June (Table 3). Using the criterion of moult stage estimated from the maxillae, we found that adolescent males were in intermoult (C stage) in August and October, and that the highest proportions ($\approx$40–70%) of premoulters (D_1–D_4 stages) occurred in March and April (Fig. 7). Accordingly, adolescent males in postmoult stages A–B were detected only in April and June (Fig. 7). Using the criterion of number of shells, we found that all adolescent males were intermoult (single shell) in June, while the highest proportion ($\approx$85%) of premoulters (double shell) occurred in December (Fig. 7).

In contrast to the extensive moulting activity recorded for adolescent males, only one live male classified as adult showed any sign of moulting. Over the 14-month sampling period, no adult male among 1349 sampled was moulting, while all moult-staged adult males were determined to be intermoult (C stage) and only one dissected adult male had a double shell (Fig. 7). This last male had a CW of 93.3 mm and a CH of 22.3 mm, which placed it well above (0.175 ln units) the splitting line for separation of adolescent and adult males. Only 1 of 48 exuviae was attributed to an adult male. This exuvium had a CW of 59.9 mm and a CH of 13.9 mm, which placed it above the splitting line by 0.243 ln units. However, measurement error cannot be excluded as these exceptional males were not initially recognized and double checked in the field.

The occurrence of adolescent males with double shells in August and October, before preparation for moulting could be detected by reading maxillae, indicates that formation of the new shell precedes changes in the mouthparts, as concluded by Hoenig et al. (1994). This is also supported by the fact that 65.5% of adolescent males with double shells were determined to be intermoult (C stage) by the maxilla method (Table 4).

Carapace growth per moult

A total of 75 males of 3.2–90.8 mm premoult CW moulted in the laboratory (Fig. 8). Moreover, divers collected 17 moulting adolescent males, ranging in size from 43.2 to 81.0 mm premoult CW, which moulted on board the research ship within hours of capture (Fig. 8). For analyses of carapace growth per moult, unsexed and male *C. opilio* were separated a priori into immature and adolescent categories on the basis of CW, chela allometry, and preceding analyses of gonad maturity.

Hiatt models for immature males were highly significant for moult increment data obtained from the laboratory ($N = 27$, $r^2 = 0.998$, $P < 0.001$) and derived from size–frequency analyses of crab <40 mm CW collected in the field ($N = 6$, $r^2 = 0.998$, $P < 0.001$; data from Table 1). There was no significant difference in the slopes ($F = 0.27$, $P = 0.605$) or Y-intercepts ($F = 0.67$, $P = 0.420$) of the Hiatt models derived from these two data sets. Therefore, a common Hiatt model was adjusted to the two data sets (Table 5, Fig. 8).

Table 1. Carapace width (CW) and age at moult for postlarval male *C. opilio* in Baie Sainte-Marguerite.

Instar	CW_{obs}	SD_{obs}	CW_{pre}	%	Age at moult
I	3.19	0.25	3.19		
II	4.63	0.29	5.12	60.5	5–7 months
III	6.60	0.38	7.65	49.4	12 months
IV	9.66	0.64	10.97	43.4	17 months
V	14.10	0.92	15.32	39.7	22 months
VI	19.96	1.33	21.02	37.2	28 months
VII	26.88	1.90	28.48	35.5	3.3 years
VIII	34.47[a]	2.71[a]	38.25	34.3	4.3 years
IX			50.73	32.6	5.7 years
X			64.53	27.2	6.7 years
XI			79.79	23.6	7.7 years
XII			96.67	21.2	8.7 years
XIII			115.34	19.3	9.7 years
XIV			135.99	17.9	10.7 years

Note: Observed mean and standard deviation of CW (CW_{obs} and SD_{obs}) were derived from size–frequency analyses of field data. Predicted CW (CW_{pre}) and percent growth increment (%) were derived from the immature and adolescent growth equations in Table 5 using a starting value of 3.19 mm CW.

[a]Values uncertain due to small sample size.

Significant Hiatt models were obtained from field moult increment data for adolescent males performing regular ($N = 10$, $r^2 = 0.977$, $P < 0.001$) or terminal ($N = 7$, $r^2 = 0.963$, $P < 0.001$) moults. Hiatt models were also significant for laboratory moult increment data obtained for adolescent males performing regular ($N = 20$, $r^2 = 0.993$, $P < 0.001$) or terminal ($N = 15$, $r^2 = 0.957$, $P < 0.001$) moults. A comparison of the four Hiatt models showed no significant difference in slopes (ANOVA, $F = 1.37$, $P = 0.265$) or Y-intercepts (ANCOVA, $F = 0.70$, $P = 0.560$), so a common Hiatt model was adjusted to the four data sets (Table 5, Fig. 8).

The transition from immature to adolescent was marked by a change in growth. Indeed, the slope of the Hiatt growth model was significantly steeper ($P < 0.001$) for immature (slope ± SE: 1.310 ± 0.010) than for adolescent (1.106 ± 0.018) males (Table 5). The two Hiatt models intercepted at an abscissa value of 36.6 mm CW. Using the Hiatt growth models for immature and adolescent males in Table 5 and the observed 3.19 mm CW for instar I as a starting value, we predicted the mean CW for 14 successive instars in Table 1. Predicted percentage growth increments decreased in two steps, from 60.5 to 34.3% over the first seven postlarval moults, and then from 32.6 to 17.9% over the next six postlarval moults.

Chela growth per moult

Growth increments of chelae at regular or terminal moults were obtained for males of 22.7–90.8 mm CW (Fig. 9). Data were available for only eight immature males (i.e., <36.9 mm CW), corresponding to premoult chela heights of <5 mm. For this reason, a single Hiatt model was used to describe chela growth per moult for immature and

Table 2. Percentage of moulting activity for unsexed and male *C. opilio* in the first eight postlarval instars in Baie Sainte-Marguerite from April 1991 to May 1992.

Date	Percentage moulting activity							
	I→II	II→III	III→IV	IV→V	V→VI	VI→VII	VII→VIII	VIII→IX
April 1991	<u>4.1</u>	0.0	0.2	<u>5.9</u>	0.0	0.0	0.0	4.8
	(465)	(432)	(1284)	(1571)	(339)	(68)	(90)	(62)
June 1991	1.4	0.9	0.0	1.2	0.6	1.0	0.0	0.0
	(218)	(225)	(87)	(2321)	(2585)	(671)	(489)	(161)
August 1991	0.0	<u>4.8</u>	0.0	0.3	1.2	0.0	0.0	0.0
	(22)	(124)	(108)	(304)	(406)	(130)	(26)	(4)
October 1991	0.0	0.6	0.1	0.0	0.1	0.5	0.0	0.0
	(348)	(727)	(740)	(1549)	(1610)	(194)	(41)	(8)
December 1991	0.0	3.4	<u>8.9</u>	2.8	<u>14.6</u>	<u>7.2</u>	<u>5.1</u>	0.0
	(600)	(790)	(1091)	(1738)	(4888)	(3919)	(455)	(34)
March 1992	1.6	0.3	1.8	0.8	0.9	1.3	1.0	0.0
	(771)	(728)	(1656)	(1459)	(1379)	(1807)	(668)	(87)
May 1992	0.0	0.0	1.4	<u>5.2</u>	0.6	2.5	0.0	<u>12.5</u>
	(31)	(38)	(358)	(725)	(1077)	(845)	(167)	(24)

Note: The percentage of molting activity for instars I through VII is the sum of the number of moulting individuals in one instar and of the number of soft-shelled individuals in the following instar, expressed as a percentage of the total number (in parentheses) of snow crab in both instars. For instar VIII, only the percentage of moulting individuals relative to total number of snow crab in that instar is given. Maximum values for moulting activity by each instar are underlined.

Table 3. Male *C. opilio* of >40 mm carapace width in Baie Sainte-Marguerite from April 1991 to May 1992.

Date	No. of exuviae	Clean-soft (%)		Moulting (%)
		Adolescent	Adult	Adolescent
April 1991	6	25.8 (503)	5.0 (199)	4.2 (373)
June 1991	2	56.8 (384)	37.7 (255)	0.0 (166)
August 1991	0	4.9 (285)	8.3 (144)	0.0 (271)
October 1991	0	0.0 (116)	0.7 (142)	0.0 (116)
December 1991	0	0.0 (229)	0.0 (248)	0.0 (229)
March 1992	1	1.7 (180)	0.5 (188)	0.0 (177)
May 1992	39[a]	35.3 (156)	7.5 (173)	28.6 (101)

Note: Number of intact exuviae, percentage with a clean soft shell relative to total number of adolescent or adult males (in parentheses), and percentage of moulting relative to total number of hard-shelled adolescent males (in parentheses). All exuviae except one were attributed to adolescent males; no moulting adult male was found.

[a]One exuvium was attributed to an adult male

adolescent males performing regular moults. However, the few data available for immature males lay very close to the resulting line (Fig. 9), suggesting that there is no change in the chela growth function after the onset of gonad maturity. Therefore, the change from isometric to positive allometric chela growth at the puberty moult (Fig. 4 and see above) might simply reflect a reduction in growth of carapace. As shown by Moriyasu et al. (1987) and seen in Fig. 9, relative chela growth was generally much greater at terminal (≈55%) than at regular (≈30%) moults for males with a premoult CH of 10–15 mm (Fig. 9). Moreover, the difference in percentage chela growth between regular and terminal moulters increased with CW, thereby explaining the divergence of clouds of points representing adolescent and adult males in CH–CW scatterplots (Fig. 3).

Gonad weight

Virtually no adolescent males in the dirty-hard or dirty-soft conditions were collected in the field, and adult males in the clean-hard and dirty-soft conditions were scarce. Regressions between ln(GW) and ln(CW) were highly significant for males in all remaining combinations of maturity and exoskeleton condition (Table 6, Fig. 10). Note, however, that CW explained a much greater proportion of the

Fig. 7. Changes in moult stage and number of shells for samples of hard-shelled adolescent and adult male *C. opilio* ≥ 40 mm carapace width from Baie Sainte-Marguerite from April 1991 to May 1992. The moult stages identified (AB, C, D_0, D_1, D_3 for D_{3-4}) were determined by reading maxillae using the Moriyasu and Mallet (1986) method. The number of shells (1S for 1 shell; 2S for 2 shells) was determined by dissection. Sample size appears above each bar.
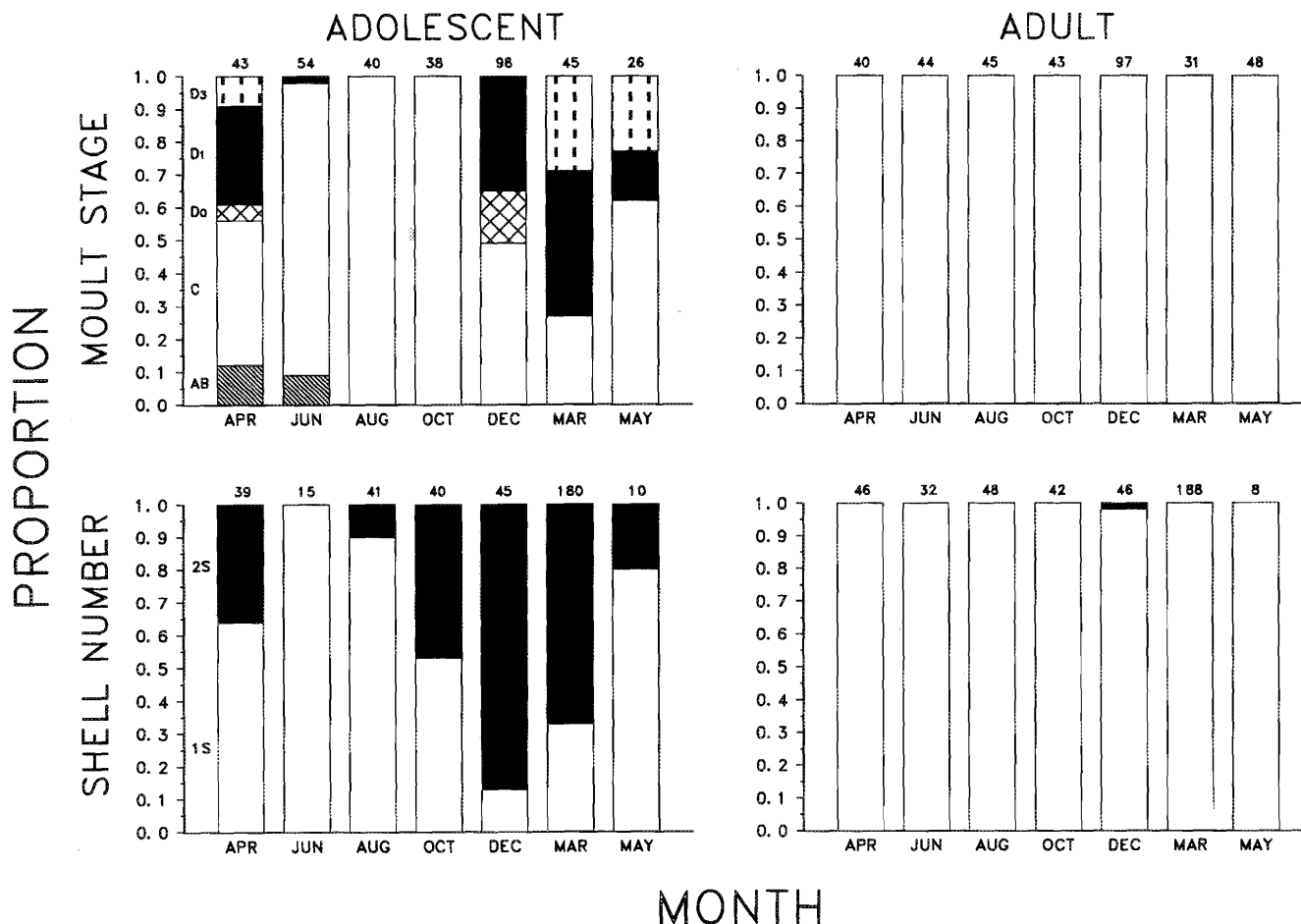
variation in GW of adolescent ($r^2 = 0.80$–0.88) than of adult ($r^2 = 0.25$–0.56) males (Table 6).

Comparison of regressions of $\ln(GW)$ on $\ln(CW)$ by ANOVA distinguished three groups of males with homogeneous slopes (Table 6, Fig. 10). Adolescent males in the clean-soft, clean-hard, and intermediate conditions formed the first group, with an adjusted common slope value of 2.96. The second group consisted of adult males in the intermediate and dirty-hard conditions, which were characterized by a small adjusted slope value of 0.74. Finally, the third group comprised adult males in the clean-soft condition, which had an intermediate slope value of 1.79. An ANCOVA on the first and second groups of males indicated significant differences in elevation (Table 6). Adjusted $\ln(GW)$ was significantly greater for adolescent males in the intermediate condition (-0.290 ± 0.029) than for adolescent males in the clean-hard (-0.641 ± 0.096) or clean-soft (-0.700 ± 0.053) conditions. Adult males in the dirty-hard condition had significantly heavier gonads ($1.535 \pm$

0.026) than adult males in the intermediate condition (1.246 ± 0.025). The general trends derived from visual examination of the adjusted regression lines in Fig. 10 are increasing GW with increasing age of exoskeleton for a given male developmental stage and greater GW for adult than for adolescent males in the intermediate condition. These same trends were also seen, and generally were significant, at each sampling period.

We determined the relative contribution of testes and vasa deferentia to total GW in a subsample of 22 males representing various combinations of maturity and exoskeleton condition. Testes accounted for 5.7–13.3% of total GW, and their relative contribution appeared to decrease as exoskeletons aged.

Gonads of large adult males with dirty-hard exoskeletons were conspicuously heavier in the Saguenay than in Baie Sainte-Marguerite (Fig. 10). Moreover, the slope of the regression of $\ln(GW)$ on $\ln(CW)$ for adult males with dirty-hard exoskeletons was significantly steeper for Saguenay

Table 4. Distribution by moult stage (% of sample size, N) of a sample of adolescent and adult male *C. opilio* from Baie Sainte-Marguerite with second shells.

Moult stage	Adolescent	Adult
A–B (%)	0.0	0.0
C (%)	65.5	100.0
D_0 (%)	8.6	0.0
D_1 (%)	24.2	0.0
D_{3-4} (%)	1.7	0.0
N	58	1

Note: Moult stage was determined by reading maxillae using the Moriyasu and Mallet (1986) method. The presence of a second shell was determined by dissection.

than for Baie Sainte-Marguerite males (1.47 vs. 0.78, $F = 13.15$, $P < 0.001$).

Discussion

The extensive observations presented here provide for the first time the information necessary to derive a comprehensive model for growth and maturation of the benthic stages of male *C. opilio*. Although field work was conducted in a restricted geographical area, our model probably can be generalized to other Gulf of Saint Lawrence populations, at least, where *C. opilio* habitat (notably temperature) is quite uniform. Growth/maturation processes for Pacific *C. opilio*, whose relationship to Atlantic *C. opilio* remains uncertain (Squires 1990), might be different owing to geographical isolation and habitat differences.

Puberty and terminal moult

As is the case for many majids (e.g., Teissier 1935, 1960; Vernet-Cornubert 1958; Hartnoll 1963, 1965; Aldrich 1974), the postlarval life of male *C. opilio* is marked by two critical moults that determine three developmental stages with different physiological, behavioural, and morphological features. The first critical moult for male *C. opilio* in Baie Sainte-Marguerite in 1991–1992 was the seventh (instar VII to VIII), when males changed from immature to adolescent. The size transition from 0 to 100% gonad maturity occurred over a very narrow range of CWs (36.9–39.2 mm) and 50% gonad maturity was achieved at 38.5 mm CW. Moreover, in the same years, Angers et al. (1994) detected major biochemical changes in males from Baie Sainte-Marguerite at instar VIII and suggested that these were related to the onset of spermatogenesis and the development of reproductive and (or) migratory behaviours. The pivotal role for the eighth instar is also seen in the change in chela allometry (Fig. 4).

There is some regional and (or) temporal variation in size at puberty for male *C. opilio*. Our work and that of Comeau and Conan (1992) showing that 50% of males had mature gonads at 38.5 and 34 mm CW, respectively,

contrast with pioneering studies in the Gulf of Saint Lawrence, which indicated a transition from immature to adolescent at larger sizes. Watson (1970) reported that all males <50 mm CW had immature gonads and evaluated that 50% gonad maturity occurred at 57 mm CW. Powles (1968) found one physiologically immature male of ≈82 mm CW and evaluated that 50% gonad maturity occurred at about 50 mm CW. For the distant Japan Sea, Kon and Honma (1970) reported that most male *C. opilio* had mature gonads at instar IX (i.e., 49.2 mm CW).

The second critical moult marks the complete development of male secondary sexual characters, most conspicuously the differentiation of chelae (Conan and Comeau 1986). Our data clearly show that this second critical moult is also a terminal moult, as hypothesized by O'Halloran (1985) and Conan and Comeau (1986). Indeed, the present field observations extend by another year Sainte-Marie and Hazel's (1992) 4-year spring moulting record for hard-shelled adolescent and adult males in Baie Sainte-Marguerite, confirming that moulting frequency for adult males over several consecutive years is virtually nil. Among hard-shelled males >40 mm CW sampled from March to May of 1988–1992, 25.3% of 910 adolescents but only 0.3% of 743 adults were moulting. Moreover, we have provided evidence, as have Yamasaki and Kuwahara (1991), that moulting activity for adult males is virtually nil year-round, in sharp contrast to the high, seasonal levels of moulting activity recorded for adolescent males (Table 3, Fig. 7). These direct field observations complement the growing body of evidence supporting the terminal moult hypothesis: (*i*) extreme exoskeleton ageing, which leads to an irreversible deterioration, is seen almost exclusively in adult males (herein; Sainte-Marie and Hazel 1992; unpublished data); (*ii*) serum protein concentration is less in adult than in adolescent males (Cormier et al. 1993); (*iii*) no limb budding occurs on adult males that are missing pereiopods (Conan et al. 1988b; Halcrow and Steel 1992); (*iv*) Y-organs of adult males degenerate as exoskeletons age (Bataller 1992); (*v*) adult males have low to very low ecdysteroid titers in comparison with adolescent males (Cormier et al. 1992; Halcrow and Steel 1992); (*vi*) exuviae records of moulting activity indicate that adult males rarely moult (Ennis et al. 1990; Comeau et al. 1991; Sainte-Marie and Hazel 1992; herein); (*vii*) wild adult males in early premoult stages are scarce (herein; Conan and Comeau 1986; Conan et al. 1988a, 1990); and (*viii*) adult males may die but seldom moult in captivity (Conan and Comeau 1986; Moriyasu et al. 1987; O'Halloran and O'Dor 1988; O'Halloran et al. 1988; Conan et al. 1988a, 1988b, 1990).

Critics of the terminal moult hypothesis have focused on the existence of some (scarce) cases of moulting for *C. opilio* males classified as adult (Donaldson and Johnson 1988; Dawe et al. 1991). We argue, however, that these examples are not irreconcilable with the terminal moult hypothesis, for at least three reasons. First, as with any biological rule, there are exceptions. This is clearly exemplified by two reports of moulting for adult female *C. opilio* (Ito and Kobayashi 1967; Hooper 1986), which nevertheless, have not shaken the consensus that there is a terminal maturation moult for females (Conan et al. 1988b). Second,

Fig. 8. Carapace growth per moult for male *C. opilio* from Baie Sainte-Marguerite. Data
come from laboratory (circles) and field (triangles) observations, and from the mean
carapace width of the first seven postlarval instars (+) as determined by size frequency
analyses (from Table 1). Open symbols indicate a regular moult, solid symbols indicate
a terminal moult. The oblique broken and solid lines are the Hiatt growth models for
immature and adolescent males, respectively. The vertical broken line indicates the
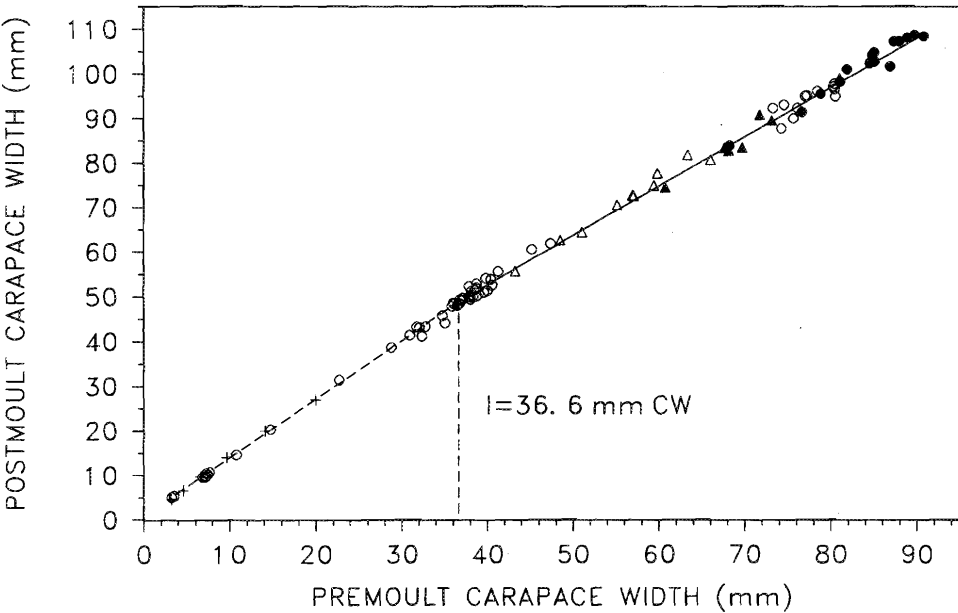abscissa value at which the two regressions intersect (I).

Table 5. Hiatt growth models for immature and adolescent male *C. opilio* in Baie Sainte-
Marguerite.

|	Applicable to instars	Hiatt growth model
Immature	I–VII	$CW_{T+1} = 1.310\ CW_T + 0.946$
Adolescent	VIII–XIII	$CW_{T+1} = 1.106\ CW_T + 8.421$

Note: Instars to which growth models can be applied are based on 1991–1992 observations. Males
might change from immature to adolescent at later instars in other years. CW_{T+1} and CW_T: postmoult
and premoult carapace widths (in mm), respectively.

classification of males into the adolescent and adult
categories is uncertain due to measurement error, lack of
independent criteria for classification (in contrast to
females), and the relatively subtle differentiation of chelae
at the terminal moult, which results in some overlap
between adolescent and adult males in scatterplots of CH
on CW (Conan and Comeau 1986; Conan et al. 1988a;
Sainte-Marie and Hazel 1992; Warren 1994). For the Baie
Sainte-Marguerite population, the probability of misclas-
sifying a male was 0.9% (Sainte-Marie and Hazel 1992)
and this value exceeds the overall moulting frequency
recorded for adult males. Finally, enlarged chelae might
be a symptom rather than a strict condition for terminal
moult status. The shape and size of one chela may also
be modified by other processes, such as injury to it or the
companion chela. Size asymmetry or two diminutive chelae
have been documented for male *C. opilio* and *C. bairdi*
that otherwise were thought to be anecdysic (Sainte-Marie

and Hazel 1992; Stevens et al. 1993). This was attributed
to incomplete regeneration of one or both chelae, consis-
tent with Miller and Watson's (1976) conclusion that males
need four moults to achieve 94% regeneration of a lost
limb. Another possible explanation for size asymmetry,
however, is compensatory growth of one chela following
injury or loss of the companion chela. Indeed, Smith and
Palmer (1994) showed for *Cancer productus* that immo-
bilization of one chela caused the other chela to overgrow,
and speculated that this would happen as well if one chela
was injured or lost.

In contrast to the brusque size transition from the
immature to the adolescent developmental stage, the tran-
sition from adolescent to adult occurred irregularly over
a broad range of CWs (Fig. 2). On one hand, extensive
variation of male CW at terminal moult is documented for
other majids and is attributed to individual differences in
the number of regular moults that precede the terminal

Fig. 9. Chela growth per moult for male *C. opilio* from Baie Sainte-Marguerite. Data from laboratory (circles) and field (triangles) observations. Open symbols indicate a regular moult; solid symbols indicate a terminal moult. Hiatt growth models for males performing regular and terminal moults are represented by a broken line ($CH_{T+1} = 1.217\ CH_T + 0.970$, $r^2 = 0.982$, $P < 0.001$) and a solid line ($CH_{T+1} = 1.565\ CH_T - 0.206$, $r^2 = 0.916$, $P < 0.001$), respectively.
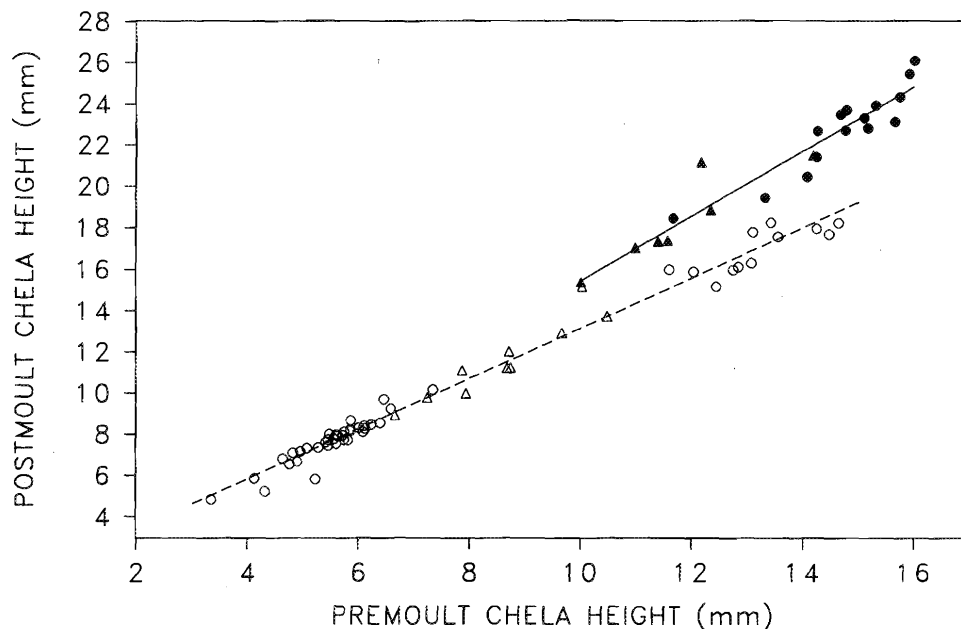
moult, rather than to individual differences in the moult increment for a fixed number of moults (O'Brien 1984; Hines 1989; Hartnoll et al. 1993). On the other hand, the irregular pattern for size transition from adolescent to adult is less well documented and may indicate that there are differences among year-classes in the size at which males undergo their terminal moult. Adults from several different year-classes are likely to be represented in a given size class, particulary in those <95 mm CW owing to lack of fishery mortality. Genetic and density-dependent effects are among the possible factors which might explain year-to-year differences in the instar at which males undergo their terminal moult (Conan and Comeau 1986; Comeau et al. 1991; Hartnoll et al. 1993). An alternative but less likely explanation is that of a two-phase transition from adolescent to adult, with a roughly constant proportion of successive year-classes undergoing the transition at a small CW. Irregular patterns for transition from adolescent to adult are not always so obvious for *Chionoecetes* species (e.g., Somerton 1981b; Yamasaki and Kuwahara 1991), but this may simply reflect different scopes for sampling. Indeed, spatial and (or) bathymetric segregation of males by size and exoskeleton condition have been documented (Miller and O'Keefe 1981; Comeau et al. 1991; Sainte-Marie and Hazel 1992).

Growth per moult and instar identification

The moult increments observed for male *C. opilio* in this study exceed many of those so far published. The mean absolute carapace growth increments from our Hiatt model for males are ≈9–27% greater than those obtained for

similarly sized males in aquarium studies where *C. opilio* were held for many months prior to moulting (Miller and Watson 1976; Moriyasu et al. 1987; Hurley et al. 1990) and ≈9–73% greater than those estimates obtained in mark–recapture studies using external tags (McBride 1982; Taylor and Hoenig 1990; Hurley et al. 1990). However, Dufour and Bailey (1990) in the course of a mark–recapture study using coded wire implants obtained moult increments for seven males that, although approximate owing to measurement imprecision, appear to be very similar to ours. Hoenig et al. (1994) collected premoult males of 45–95 mm CW by trawl and held them in the laboratory until they moulted, for a maximum of up to 3 weeks after capture. Premoult males suffered 20% mortality at or before moulting and moult increments were quite variable, possibly owing to the traumatic collection method, but record relative carapace growth increments of approximately 32% were as great or slightly greater than those observed in the present study for similarly sized males. Previous studies, except the two last, may have underestimated growth per moult for male *C. opilio*. This could be due to negative effects of long-term captivity, as suggested by Hoenig et al. (1994), to unspecified but possibly detrimentally high densities in holding facilities, and to deleterious effects of tags in mark–recapture studies. Regarding this last possibility, however, Hurley et al. (1990) detected no significant difference in moult increments among laboratory-held males with T-bar tags, magnetic tags, or no tag.

The effect of the puberty moult on growth of male *C. opilio* was a reduction of growth (Fig. 8, Tables 1 and 5). Using the Hiatt growth model, we obtained a sig-

Fig. 10. Scattergram of ln(gonad weight) on ln(carapace width) for adolescent (a) and adult (A) male *C. opilio* taken in Baie Sainte-Marguerite from April 1991 to March 1992. Males had clean-soft (1), clean-hard (2), intermediate (3) or dirty-hard (4) exoskeletons. Data for dirty-hard, adult males from the Saguenay Fjord (SA4) are also shown. Lines in graph and equations of regressions were fitted to these data after an ANOVA and an ANCOVA were used to test for differences in slope and elevation (refer to Table 6 for more information).
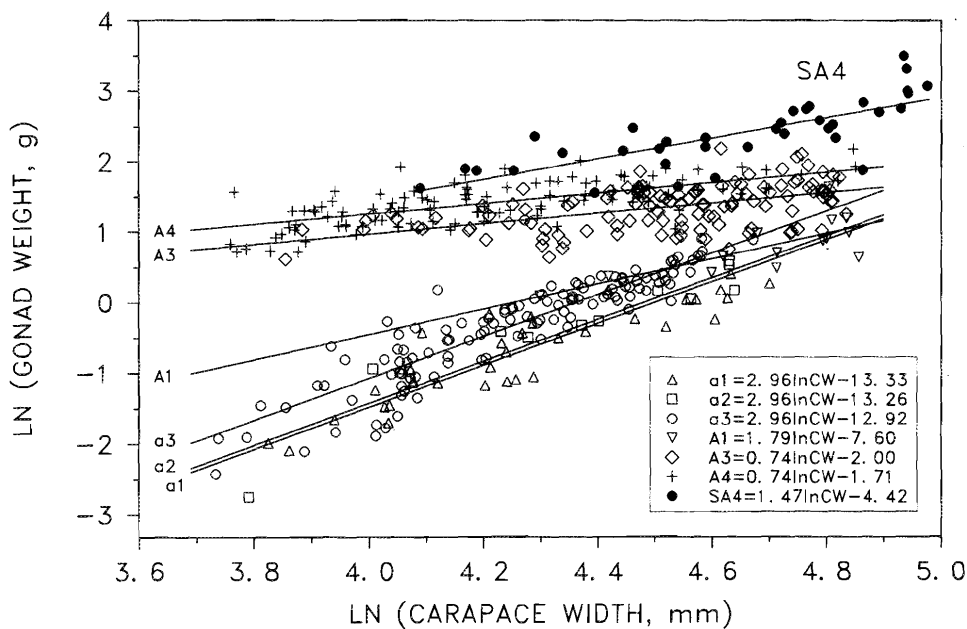
nificantly steeper slope value for immature (1.31) than for adolescent (1.11) males. The likely explanation for this reduction in growth is that some energy is diverted away from somatic growth into germinal growth, as suggested for *C. bairdi* by Wolff and Soto (1992). This hypothesis is possibly supported by Paul and Fuji's (1989) finding that energy allocated to somatic growth is less in physiologically mature than in immature male *C. bairdi*. However, as Paul and Fuji (1989) pointed out, they did not discriminate between males which had undergone a regular moult and those which had undergone a moult to morphometric maturity, which might bias results if there is a terminal moult for *C. bairdi*.

In the present study of *C. opilio* (Fig. 8 and in text above) and in that of Hoenig et al. (1994) there was no evidence of a significant difference in moult increments between similarly sized regular and terminal moulters. In contrast, based on their laboratory study Moriyasu et al. (1987) reported significantly larger moult increments at regular than at terminal moults. While they did not state the magnitude of the difference, examination of their Fig. 1 suggests that it was very small, i.e., <2 mm CW. However, there was a mere 4-mm overlap in CW range for the two groups of male moulters and a constant growth function was assumed to suit immatures and adolescents, and that might have biased statistical analyses. Comeau et al. (1991) also argued that moult increments were less at terminal than at regular moults based on a cursory examination of their CW frequency distributions for *C. opilio* in Bonne Bay, Newfoundland. In support, they contended

that adolescent males in instar D (≈60 mm CW) grew by ≈20 mm CW during a regular moult compared to only ≈14 mm CW during a terminal moult. However, they did not comment on their observation that moult increments inferred for instar E (≈80 mm CW), which was much better represented in samples, were ≈20 mm CW for both regular and terminal moulters. We observed the same for males moulting from instar XI to XII (Table 1). Overall, the data available so far suggest that there is no reduction of moult increments at terminal moult.

Carapace growth per moult for immature males appears to be very uniform over the whole distributional range of *C. opilio*. There are only small differences in the observed and (or) predicted mean carapace widths for instars I–VII from the Japan Sea (Ito 1970; Kon 1980), and southern and northern Gulf of Saint Lawrence (Watson 1969; Robichaud et al. 1989; this study). Also, the Hiatt growth model presented by Kon (1980) for immature males ($CW_{T+1} = 1.31CW_T + 1.01$) is almost identical to ours (Table 5).

Published growth models for adolescent males are much less uniform than those for immature males, and few appear to be reliable. Robichaud et al.'s (1989) conclusion that male *C. opilio* reach the legal size at instar XI is suspect because they extrapolated the number of instars to legal size from a Hiatt model developed for immature males only (i.e., instars III–VII). This model did not incorporate a change in growth at puberty and probably overestimated growth for adolescent males. Watson (1969) proposed a model for male *C. opilio* in eastern Canada, which

Table 6. Relationship between natural logarithm of gonad weight ((lnGW)) measured in g and of carapace width measured in mm (ln(CW)) for male *C. opilio* collected in Baie Sainte-Marguerite from April 1991 to March 1992.

Male developmental stage and condition	Regression	N	r^2	F	P
Adolescent					
a1: Clean-soft	$\ln(GW) = 2.516 \ln(CW) - 11.429$	36	0.80	133.99	<0.001
a2: Clean-hard	$\ln(GW) = 3.144 \ln(CW) - 14.064$	11	0.88	68.83	<0.001
a3: Intermediate	$\ln(GW) = 3.093 \ln(CW) - 13.478$	120	0.82	526.38	<0.001
	Slopes [a1 = a2 = a3]			2.57	0.080
	Elevations [(a1 = a2) < a3]			26.72	<0.001
Adult					
A1: Clean-soft	$\ln(GW) = 1.788 \ln(CW) - 7.605$	14	0.56	15.19	0.002
A3: Intermediate	$\ln(GW) = 0.687 \ln(CW) - 1.751$	117	0.25	37.78	<0.001
A4: Dirty-hard	$\ln(GW) = 0.783 \ln(CW) - 1.883$	108	0.48	98.66	<0.001
	Slopes [A3 = A4]			0.50	0.482
	Elevations [A3 < A4]			54.20	<0.001

Note: An overall ANOVA indicated significant heterogeneity among slopes of regressions ($F = 66.32$, $P < 0.001$). Regressions for groups of males with homogeneous slopes were compared by ANCOVA. The ranking of adjusted elevations is shown.

incorporated a reduction in growth at the onset of physiological maturity. His model predicted that instar XIII is the first to exceed 95 mm CW; however, the component of the model that described growth of physiologically mature (adolescent) males rested on only one datum borrowed from Kon et al. (1968). Growth models developed for adolescent males in the Japan Sea were essentially based on analyses of CW frequency distributions and may, therefore, be plagued with uncertainty (see below). Ito (1970) and Kon (1980) predicted or inferred from size frequency distributions a sequence of instars subject to very small relative moult increments, i.e., decreasing from ≈9–10.5% for their instar XIII (105.6–111.5 mm CW) to ≈4.6–7.2% for their instar XV (126.8–131.5 mm CW). Relative carapace moult increments calculated by Sinoda (1968) for *C. opilio* of 114.9–140.3 mm premoult CW were even smaller and decreased from 3.2 to 1.9%. According to our growth model for adolescent males in the northwest Gulf of Saint Lawrence, moult increments do not decrease below 17% and instar XII is the first to recruit to the legal size of 95 mm CW (Table 1). For the same geographical area, Lafleur et al. (1984) using an extensive data set for CW frequency distributions identified four modes of large males (76, 98, 117, and 132 mm CW) which coincide with CWs predicted by our model for instars XI–XIV.

Identification of instars and derivation of a growth model for adolescent male *C. opilio* using only CW frequency distributions was impossible. This was due in part to a paucity of individuals in the range of 32–55 mm CW, which made it difficult or impossible to resolve mean CW for the eighth and ninth instars. Gaps in CW frequency distributions of males have been reported previously for Pacific (Somerton 1981a) and Atlantic populations. On the north shore of the Gulf of Saint Lawrence, just east of Baie Sainte-Marguerite, a 1982 beam trawl survey

captured very few males in the 15- to 55-mm CW size range (Lafleur et al. 1984; Brêthes et al. 1987). At almost the same time, beam trawl surveys in the southern Gulf of Saint Lawrence indicated that males in the 30- to 70-mm size range were scarce (Coulombe et al. 1985; Robichaud et al. 1989). Reviewing some of these observations, Robichaud et al. (1989) concluded that the gaps in size frequency distributions were genuine, not a bias of sampling. The gap in CW frequencies for immature and adolescent males in Baie Sainte-Marguerite was observed to shift in a gradual and systematic manner from ≈6–32 mm CW in 1989 to ≈55–100 mm CW in 1994 (Sainte-Marie and Dufour 1994; B. Sainte-Marie, unpublished data). It was hypothesized that these gaps reflect recruitment failure at instar I owing to a reduction in the (*i*) number of megalopae settling to the bottom, reflecting changes in the female spawning biomass, and (or) (*ii*) survival of instar I, resulting from space and food limitation exerted by immatures in previously established year-classes (Sainte-Marie and Dufour 1994; B. Sainte-Marie, J.-M. Sévigny, and G.A. Lovrich, unpublished data).

A further difficulty preventing identification of instars for large adolescent and adult males was the lack of discernible modes for CWs exceeding 55 mm. This may be due in part to the small sample size for large males, which are probably able to avoid the beam trawl (Miller 1975; Raymond 1995). However, lack of modal structure in size frequency distributions for adolescent and adult males can occur even when large samples are available (e.g., Kon 1980; Bailey and Elner 1989). Modal structure may become blurred because of the mixing of year-classes with different sizes at moult, owing to skip-moulting (see below) and terminal moult. Differences in CW at a given instar could result from year-to-year variations in size at settlement, in the size at onset of physiological maturity for

a constant carapace growth function, or from year-to-year variations in carapace growth per moult.

Age at moult

The temporal basis to *C. opilio* life history is the following. Females moult to maturity from February to April, then mate and spawn shortly afterwards (Watson 1970; Moriyasu et al. 1987; Sainte-Marie and Hazel 1992; Sainte-Marie 1993). In 1991, eggs of primiparous and multiparous females, which may be incubated for about 24–27 months, hatched from April to June in Baie Sainte-Marguerite (Sainte-Marie 1993). The larvae are planktonic and develop through zoea I, zoea II, and megalopa stages (Watson 1969; Motoh 1973; Lanteigne 1985). Larval development is temperature-dependent (Kon 1970; Davidson and Chin 1991) and in the southern Gulf of Saint Lawrence lasts about 3–5 months at ambient surface temperatures of 8–12°C (Lanteigne 1985). This is consistent with the absence of instar I in June and August but abundant presence in October beam trawl samples (Fig. 6). We, therefore, infer that megalopae settled to the bottom and moulted to instar I in September–October. Male *C. opilio* then required approximately 12 months to develop to instar III, about 10 additional months to reach instar V, and another 6 months to reach instar VI (Table 1). Some uncertainty remains about the exact duration of these first instars, due to the 2- to 3-month gaps between sampling periods. Males would thus attain instar VI about 2.3 years after settlement.

Starting with instar VI, *C. opilio* crab begin to moult annually during the winter to spring period (Table 1). This conclusion is supported by laboratory (Moriyasu et al. 1987) and direct field observations (Table 2; Sainte-Marie et al. 1988; Sainte-Marie and Hazel 1992) of the moulting period for males >20 mm CW, and by the progression of well sampled and distinctive cohorts in a 6-year time series for Baie Sainte-Marguerite (Sainte-Marie and Dufour 1994; B. Sainte-Marie, unpublished data). Comeau et al. (1991), citing G.Y. Conan et al. (unpublished data), reported a 1-year intermoult period for 30- to 40-mm CW males based on carapace ageing by radioelements. From instar VII, the annual moulting period shifts from winter to spring – early summer so that moulting occurs later for large compared with small males (Brunel 1962; Moriyasu et al. 1987; Sainte-Marie and Hazel 1992). Therefore, males that reach the commercial size of 95 mm CW at instar XII have a postsettlement age of 8.7 years (Table 1). Because recently moulted males require up to 2–5 months to harden and develop a high meat yield (Watson 1971; O'Halloran and O'Dor 1988; Taylor et al. 1989), they have little commercial value until the following year, i.e., at the minimum postsettlement age of ≈9.5 year. In fact, some of the males that recruit to the fishery may be even older: the intermoult period for large adolescent males may last up to 2–3 yr (Comeau et al. 1991; B. Sainte-Marie, unpublished data). Our estimate for minimum age at legal size is, thus, considerably longer than the posthatching age of 4.5 year proposed by Robichaud et al. (1989). This difference is due to the much shorter intermoult duration that these authors inferred for instars I–VII and to their assumption that males reach legal size at instar XI.

Gonad development

Relationships between ln(GW) and ln(CW) were distinctly different for adolescent and adult male *C. opilio* (Fig. 10). The adjusted slope value of 2.96 for adolescent males, suggesting a cubic relationship between GW and CW, was significantly greater than slope values for adult males in the clean-soft condition (1.79) or in the intermediate or dirty-hard conditions (0.74). Analogously, Comeau and Conan (1992) found that the vasosomatic index for males in the southern Gulf of Saint Lawrence was independent of CW for adolescent males, and negatively correlated with CW for new- and old-shelled adult males. Two clouds of points are also evident in Watson's (1970) scattergram of $\log_{10}$(vasa deferentia weight) on $\log_{10}$(CW) for males captured in the southern Gulf of Saint Lawrence prior to start of the fishery (his Fig. 5). The lower cloud, which represents immature and undoubtedly adolescent males, can be modeled by a line with a slope value of ≈3. The more scattered upper cloud surely represents adult males and the slope of the line relating maximum values of $\log_{10}$(vasa deferentia weight) to $\log_{10}$(CW) for adult males of 60–100 mm CW is in the range of 1.29–1.74. The greater variability in vasa deferentia weight of adult compared with adolescent males for a constant CW, as seen in Watson's (1970) data set, can be explained by the fact that GW increases with time elapsed since moult (Table 6, Fig. 10 herein) and that there is more time for such increase in (terminally moulted) adult than in intermoult adolescent males. Fedoseyev (1988) showed that spermatogenesis is a continuous process in *C. opilio*, while various investigators have indicated that one function of majid middle and posterior vasa deferentia is the storage of reproductive products (Hinsch and Walker 1974; Beninger et al. 1988; Diesel 1989, 1991). Similarly, in both small- and large-clawed males of the majid *Libinia emarginata*, Homola et al. (1991) found that the weight of the reproductive tract for a constant body size was greater for individuals with abraded (i.e., old) exoskeletons than for those with unabraded (i.e., recent) exoskeletons.

Comeau and Conan (1992) implicitly attributed the change in slope of vasosomatic index on CW at adulthood to the onset of reproductive activity and to relatively greater sperm expenditure by large versus small adult males. This is reasonable considering that (*i*) sperm production appears to be a slow process (Fedoseyev 1988), (*ii*) quantities of reproductive products delivered by a male to a female at copulation can be substantial, up to 0.8 g (Sainte-Marie and Lovrich 1994), and (*iii*) large males apparently participate more often than small males in mating (Conan and Comeau 1986; Moriyasu and Conan 1988; Ennis et al. 1990; Sainte-Marie and Hazel 1992). Moreover, it was hypothesized for exploited populations that fishery mortality would lead to more frequent mating opportunities for surviving large males (Comeau and Conan 1992; Sainte-Marie 1993). This would cause them to expend even more sperm and, thus, prevent accumulation of reproductive products to the extent documented in prefishery times by Watson (1969). Our data support this interpretation. Indeed, adult males in the dirty-hard condition in the unexploited Saguenay population had very large vasa deferentia. More importantly, the slope of the regression of ln(GW) on

ln(CW) (Fig. 10) was significantly steeper for Saguenay males (1.47) than for adult males of similar condition in Baie Sainte-Marguerite (0.74). However, the former value was within the range of the 1.29–1.74 slope values estimated for Watson's (1970) prefishery data for the southern Gulf of Saint Lawrence.

In nature, males may participate in breeding even before they reach adulthood. Indeed, the fact that the slope of the regression relating GW to CW for soft-shelled adult males was intermediate between those slopes obtained for hard-shelled adolescent and adult males seems to suggest that the larger soft-shelled males had already expended some accumulated reproductive products. Because majid males do not copulate while soft shelled (Carlisle 1957; Hartnoll 1969; Donaldson and Adams 1989; Moriyasu and Conan 1988; Conan et al. 1990), which almost surely was the case for these adult males during the April–June mating period for multiparous females, sperm might have been expended before these males underwent their terminal moult, possibly during the February–April mating period for pubescent females. Laboratory observations show that adolescent male *Chionoecetes* can copulate successfully, in some cases less than a few days before they moult (Kon and Nanba 1968; Moriyasu and Conan 1988; Donaldson and Adams 1989; Paul and Paul 1990; Sainte-Marie and Lovrich 1994). Nevertheless, field data in support of the hypothesis that adolescent males participate in the mating of pubescent females are scant. For *C. opilio*, Hooper (1986) on one day found that 8 of 15 sexually paired males were in late premoult stages (thus they were presumably adolescent), while Sainte-Marie and Hazel (1992) reported that 3.3% of males in pubescent–primiparous mating pairs were adolescent. However, field expeditions have sampled only the tail end of the pubescent mating period for *C. opilio*; the possibility that the relative proportions of adolescent and adult males in mating pairs change through the mating period cannot be ruled out. We point out that Laufer et al. (1993) have suggested for the majid *L. emarginata* that blood titers of methyl farnesoate are more important than developmental stage in promoting reproductive behaviour of physiologically mature males. Methyl farnesoate titers apparently increase with time elapsed since moult and equally high levels may be encountered in small- and large-claw males which, however, have different mating strategies.

Implications for the fishery

Our work enables the identification of year-classes from size–frequency distributions and the forecasting of population/fishery trends for *C. opilio* using the relative strength of year-classes. Hence, the gap in CW distributions observed in the north Gulf of Saint Lawrence during a 1982 survey was attributed to three weak year-classes and projected in time to retrospectively explain declines in landings from 1987 to 1989 (Sainte-Marie and Dufour 1994). Moreover, the currently observed gap, which is seen throughout the Saint Lawrence Estuary and northern Gulf (Sainte-Marie and Dufour 1994), was attributed to weak 1985–1987 year-classes and industry has been warned to expect a decline in *C. opilio* catch rates and landings over the 1995–1997 period (Sainte-Marie and Dufour 1994).

Year-to-year fluctuations of year-class strength, in conjunction with marked sexual dimorphism and variability in size and age at terminal moult for females (Alunno-Bruscia 1993) and males (herein), determine dynamic demographic features for *C. opilio* populations. Pulsed recruitment can effectively explain why the size of males participating in multiparous mating pairs changes over the years (Ennis et al. 1990; Comeau et al. 1991). Similarly, one can expect other population features to vary from year to year, e.g., adult sex ratios, proportions of primiparous and multiparous females, proportion of adolescent males over the legal size of 95 mm CW, or participation of adolescent males in reproduction. This means that careful interpretation of all scientific information should precede any general statements made about the efficacy of regulations, for instance those aiming to protect reproductive potential. Variation related to intrinsic and possibly recurrent changes must be identified and separated from long-term fishery effects to properly evaluate the effectiveness of current management practices. A good way to achieve this objective is long-term monitoring of exploited and unexploited populations.

The terminal moult means that there is only a limited time during which adult males are available to the fishery. Indeed, the appearance, catchability, and survival rate of *C. opilio* change after the terminal moult owing to exoskeleton fouling, lesions and limb loss during intra- and inter-specific agonistic interactions, and senescence (Sainte-Marie and Dufour 1994). At present, it is estimated that males do not survive more than 5–6 years after terminal moult (Comeau et al. 1991; Sainte-Marie and Dufour 1994) and that *C. opilio* targeted by the fishery (i.e., clean-hard to intermediate exoskeleton condition) in the spring are mostly 1–3 years of postmoult age (Sainte-Marie and Dufour 1994). Thus, to minimize resource wastage, exploitation must be adjusted to track both qualitative and quantitative changes in populations of legal-sized adult males.

An important conservation issue relating to terminal moult of males is the impact of the fishery on population reproductive potential. With the 95-mm CW legal size, smaller adult males are never harvested and, as the fishery expanded in scale, may be contributing increasingly to overall reproduction on the east coast of Canada. Circumstantial evidence suggests that the minimum and mean size at physiological maturity (Comeau and Conan 1992; this paper) and the minimum size at adulthood (Sainte-Marie and Hazel 1992) have decreased among males in the Gulf of Saint Lawrence over the last 25 years or so. Several workers have argued that if size at terminal moult is an inheritable trait, the fishery might be selecting for precocious maturation (Elner et al. 1986; Conan et al. 1988a; Bailey and Elner 1989; Comeau and Conan 1992; Sainte-Marie and Hazel 1992). The testing of this hypothesis, in conjunction with careful monitoring of size for puberty and adulthood is, therefore, imperative. Conclusions could have a major impact on the fishery, notably by forcing changes in harvest strategies to encourage reproduction of large adult males and to reduce biomass of small adult males. Moreover, any information conducive to an understanding of the factors which determine the

onset of terminal moult could improve our long-term forecasts, by allowing some provision in recruitment models for differential growth to legal size among year-classes.

To maximize yield per recruit, exploitation of adolescent males of legal size should be discouraged (Comeau and Conan 1992). Indeed, adolescent males eventually produce a much higher meat yield, owing to volumetric body growth and differentiation of chelae at terminal moult. An effective way to reduce adolescent fishing mortality, while favouring exploitation of some small adult males, might be to change the basis for minimum legal size from CW to CH or chela length (Elner et al. 1988; Safran et al. 1990; but see Tremblay et al. 1992). Less practical but more effective methods have been proposed, such as a legal size incorporating CH and CW (Comeau and Conan 1992). The possibility of fixing some minimum legal CW while educating fishers to the importance of protecting adolescent males should not be disregarded. Many fishers state that they are committed to comply with this advice and are effectively able to distinguish, by eye alone, most adult from adolescent males.

Acknowledgements

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