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Longevity and Change in Shell Condition of Adult Male Snow Crab *Chionoecetes opilio* Inferred from Dactyl Wear and Mark–Recapture Data

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Abstract.—Postmolt longevity and changes in the shell condition and body integrity of male snow crab *Chionoecetes opilio* after their terminal molt were assessed through a mark–recapture experiment and population censuses in a commercially unfished locality of eastern Canada. The experiment explored the value of dactyl wear as a quantitative measure and shell condition (SC; measured on a five-stage scale) as a relative index of shell age. Males were recaptured up to 6 years after release. Much of the extensive variation in observed dactyl wear was explained by time at liberty (Δt) and male size, and the extent of change in SC was positively correlated with Δt. The conservative wear-based estimate of male longevity was 7.7 years, a value 1–3 years greater than previously estimated. Dactyl wear and recapture data confirmed that SC is a relative, albeit rough, index of shell age. Shell hardness was positively correlated with male size and peaked in stage 3 about 3.5 years after the terminal molt. The number of missing pereopods increased with shell age and SC stage and overall was negatively correlated with male size. The commercial value of adult males may be highest at 1–4.5 years post–terminal molt and the reproductive value at 2–5.5 years.

Age determination for crustaceans remains difficult and uncertain (e.g., Hartnoll 2001). Methods are needed for estimating the absolute age of crustaceans and in recent years progress toward that goal has been made using neurolipofuscin (e.g., Fonseca and Sheehy 2007). Methods are also needed for measuring shell (exoskeleton) age, which represents the elapsed time between an individual's last molt and the day of examination. Indeed, several key life history features are related to shell age, such as mating success for males (Paul et al. 1995) and total egg production for females that have a terminal maturity molt (Hines et al. 2003).

Information on shell age may be crucial for the management of exploited crustaceans with determinate growth, such as the snow crab *Chionoecetes opilio*, which is fished in the northern Pacific and northwestern Atlantic oceans. In North America, snow crabs are harvested by trap fisheries, subject to regulations that include a minimum legal size (in Canada, 95 mm carapace width [CW]) and the prohibition to land

females. Two male morphs may be represented in catches, and they are distinguished on the basis of chela size relative to CW. Adolescent males have relatively small chelae and can still grow, whereas adult males have relatively large chelae and have terminally molted (reviewed in Sainte-Marie et al. 1995; Conan et al. 1996; Tamone et al. 2005). In Canada, the main season for male terminal molt usually extends from March to June, and adult males can range from 40 to 162 mm in CW (Sainte-Marie et al. 1995, 1996; Conan et al. 1996; Benhalima et al. 1998). The general trajectory of males after terminal molt is known: meat yield and reproductive potential increase for some time, then general condition declines from shell deterioration (i.e., scarring, fouling and decay) and pereopod loss, and death follows (e.g., Sainte-Marie et al. 1995). A balance must be struck between the reduction of economic losses resulting from deterioration and natural mortality of adult males and the maintenance of a male population of sufficient quality and quantity to adequately inseminate females (Elner and Beninger 1995; Sainte-Marie et al. 2002). Achieving this balance requires knowledge of the longevity of males after terminal molt and of the chronology of change in appearance and body integrity.

The external appearance of snow crabs is described by a variety of shell condition (SC) indices (e.g., Otto 1998; Ernst et al. 2005) similar to the one used in the

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TABLE 1.—Shell condition (SC) stages used to rate the external appearance and condition of snow crabs in the northern Gulf of St. Lawrence (modified from Sainte-Marie 1993).

SC stage	Description
1 (clean–soft)	Carapace and chelae iridescent with sharp spines and no epizoites; ventral surface immaculate white; chelae soft or buckle when pressed with thumb
2 (clean–hard)	Carapace and chelae iridescent with sharp spines; no or very few small epizoites (spirorbids, serpulids); ventral surface white; chelae do not buckle when pressed with thumb
3 (intermediate)	Carapace and chelae partially iridescent or dull, spines show some wear; epizoites (sponges, hydroids, bryozoans, spirorbids, serpulids, barnacles) present but of small to intermediate size; ventral surface yellowish or brownish, dull, and scarred; chelae hard
4 (dirty–hard)	Carapace, chelae, and ventral surface yellow or brown, dirty, and scarred; spines eroded; numerous epizoites, often of a large size; chelae hard but pereopods and portions of the carapace generally softened
5 (dirty–soft)	Carapace, chelae, and ventral surface yellow or brown, dirty, and scarred; spines very eroded; numerous epizoites and decaying spirorbid or serpulid shells; carapace and pereopods spongy, chelae likely to buckle when pressed with thumb

northern Gulf of St. Lawrence in eastern Canada (Table 1). Successive stages in the SC index are thought to reflect progression in shell age. There is a consensus that crabs rated SC1 (i.e., postmolt or soft shell) are recently molted and estimates of duration of SC1 based on laboratory and mark–recapture experiments range from about 2–3 months (O'Halloran and O'Dor 1988; Taylor et al. 1989; Otto 1998; Hébert et al. 2002). However, the discreteness and duration of subsequent SC stages 2–5 are not well documented. Nonetheless, the abundance of males with new (SC1 and SC2), intermediate (SC3), and old (SC4 and SC5) shells in population surveys is routinely used to evaluate annual recruitment and exploitation rate for adults and incidence of skip-molting for adolescents (e.g., Caddy et al. 2005). The change in appearance of snow crabs following a molt is accompanied also by a change in shell hardness, which can be measured on the claw propodus with a special gauge called the durometer (Foyle et al. 1989). In Canada, the occurrence in commercial catches of crabs combining SC1 and durometer readings of less than 68 units is monitored in season and when some threshold level is reached fishery closures are imposed to protect recently molted crabs from direct and indirect fishing mortality (e.g., Caddy et al. 2005). Given the importance of the SC index for management of snow crabs, it is imperative to validate it or to implement more quantitative methods for aging shells.

Epibionts on a crustacean may provide an indirect estimate of shell age if their numbers are related to shell age or if the epibionts can be aged (Gili et al. 1993; Dick et al. 1998). For instance, Paul and Paul (1986) determined that barnacles on male Tanner crabs *Chionoecetes bairdi* were mostly 1–2 years old and exceptionally up to 3 years old. However, even when epibionts can be aged accurately, the delay between molting and epibiont settlement on the new shell usually is not known, so inferred shell age is a minimum value. Radiometry has been used to directly estimate shell age (Bennett and Turekian 1984; Gardner et al. 2002). This method derives shell age by measuring the ratio of a naturally occurring maternal radioisotope incorporated into the shell during postmolt calcification to a daughter radioisotope that accumulates over time by radioactive decay. The shells of a few male *Chionoecetes* have been aged using the ^{228}Th : ^{228}Ra pair (which are valid for age ranges of 0–8 years); the oldest were estimated to be 4.9 years among Tanner crabs and 6.8 years among snow crabs (Nevissi et al. 1996; Ernst et al. 2005). Very few crustacean shells have been aged using radiometry, largely because the method is costly and time-consuming (Hartnoll 2001; but see Gardner et al. 2002).

Several studies have reported that parts of the crustacean exoskeleton wear down after a molt, notably spines and dactyls (e.g., Ahl et al. 1996; Nevissi et al. 1996), and the presence of wear is often one of several criteria for determining SC stage (Table 1). While sampling the commercially unexploited population of snow crabs in Saguenay Fjord in eastern Canada, we observed that the dactyls of walking pereopods were variably and often extensively worn (Figure 1). The wear of hard structures such as mandibles or wings in insects and teeth in mammals is routinely used for quantitative aging (Morris 1972; Southwood and Henderson 2000). However, a similar approach has not been implemented for crustaceans.

This study used population censuses and a mark–recapture experiment for snow crab adult males to achieve three interrelated objectives: (1) explore dactyl wear as a quantitative method for measuring shell age, (2) assess the value of SC as an index of shell age, and (3) document natural changes in body appearance and condition after terminal molt. The censuses and experiment were conducted in Saguenay Fjord on a commercially unexploited population of snow crabs, which may most closely represent the virgin population conditions about which little is known.

FIGURE 1.—Right dactyl of the third pereopod pair of two adult male snow crabs from Saguenay Fjord. Note the extensive wear on the lower dactyl. The caliper tips show how dactyl length was measured; the inset shows an enlarged view of the tip of the upper dactyl.

Methods

Field sampling.—Snow crabs were sampled in the Saguenay Fjord of eastern Canada. The Saguenay River and its fjord system open into the St. Lawrence estuary. The fjord (marine) part is divided by sills into three main basins (Figure 2) ranging in maximum depth from about 200 to 260 m. Judging from trap catch rates and photographic surveys, snow crabs are distributed at low densities throughout the western and central basins (Sainte-Marie et al. 1992 and unpublished data). Snow crabs were sampled at five locations annually from 1990 to 1998 for about 1–2 weeks in May or June (Figure 2). In 1990 and 1991 crabs were also sampled in late August. Crabs were collected with Japanese traps baited with herring and soaked for 24–48 h at depths ranging from 30 to 250 m.

Data collection and tagging.—For each male snow crab, various size measurements were taken to the nearest 0.01 mm with a caliper. Carapace width (CW) was measured across the broadest part of the cephalothorax, and right chela height (CH) was measured at the highest part of the propodus; both measurements excluded spines (Sainte-Marie et al. 1995). The length of each of the dactyls of the third pereopod pair in dorsal view (DL_R = right dactyl, DL_L = left dactyl) was determined by flexing the dactyl inward and measuring from the distal tip to the top of the knuckle (Figure 1). The third pereopod pair was selected because it is centrally positioned, is usually the longest of the leg pairs, and with the fourth pereopod pair generates the greatest torque during locomotion (Mitchell and DeMont 2003); thus, it may be more susceptible to wear.

Other information was noted for many male snow crabs. The number of missing pereopods was recorded. Only old pereopod losses, as evidenced by dark or hardened autotomy planes, were noted as missing. Pereopods that were probably lost during trapping, as evidenced by autotomy or jagged breakage zones that were pale and soft (there were very few such cases), were noted separately and discounted in compilations of recapture data. In the absence of commercial fishing, missing pereopods probably reflect natural losses that occur during predator aggressions or sexual competition. Shell hardness was measured (type D Model 307 L durometer; Pacific Transducer Corporation, Los Angeles, California) on the outer part of the chela propodus, halfway between the middle and ventral row of spines. The durometer transfers force to the cuticle via a spring-loaded, rounded indenter of 3.15 mm diameter (7.8 mm^2). The force exerted by the indenter until the cuticle is deflected is linearly related to durometer measurement units, the maximum reading on a scale of 0–100 units corresponding to 44.48 N (Foyle et al. 1989).

Lastly, the SC stage was assigned to males in a haphazard selection of traps from 1990 to 1991 and to every male starting in 1992 following criteria in Table 1. Note that tactile assessment of claw hardness for SC scoring does not discriminate between stages SC2, SC3, and SC4 (they all seem equally hard under the thumb) and that the durometer reading was always taken after SC stage was assigned and on the alternate claw. The SC stage and durometer reading are therefore independent evaluations of crab condition.

Only adult males were considered in this study because they make up the bulk of commercial landings. Male maturity status was determined onboard ship using the equation

$$Y = \log_e CH - [(1.2209 \times \log_e CW) - 2.6077],$$

where $Y \leq 0$ identifies an adolescent and $Y > 1$ identifies an adult (Sainte-Marie and Hazel 1992). Adults of SC2 or greater were marked with a coded spaghetti tag tied around the cephalothorax (Taylor 1992), and along with other crabs they were promptly and carefully returned to the water. Recaptured males, including a haphazard selection of those males tagged and recaptured during the same survey, were remeasured and scored for SC (blind of previous measurements) and returned to the water.

Data analysis.—Data from all males marked, recaptured, and remeasured during the same survey were compared between release and recapture using a paired *t*-test and Pearson's product-moment correlation coefficient. To determine shell age from dactyl wear, paired *t*-tests were used to assess the bilateral symmetry
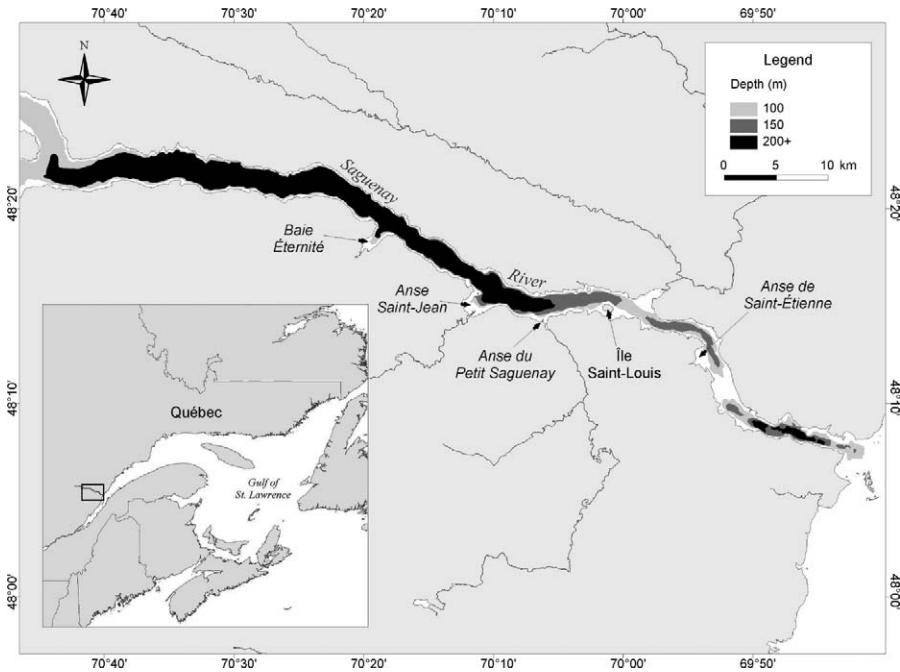
FIGURE 2.—Map of Saguenay Fjord showing the three basins (represented by dark gray or black areas) and five snow crab sampling sites (arrows).

of dactyl length for marked and unmarked males with both pereopods of the third pair. Observed dactyl wear (DW) was determined for marked males as the difference between DL at recapture and that at tagging. All subsequent analyses used the mean of DL_R and DL_L ($DL_{R,L}$) or of DW_R and DW_L ($DW_{R,L}$) by crab because there was no evidence of bilateral asymmetry for either DL or DW. Multiple regression was used to test for effects of time at liberty (Δt) and CW on observed $DW_{R,L}$. To ensure normality, observed $DW_{R,L} + 1$ and CW were $\log_e$ transformed.

Dactyl wear was estimated for unmarked males with no missing pereopods by subtracting their $DL_{R,L}$ from unworn $DL_{R,L}$. This last value was obtained by inputting an individual's CW into a regression of $DL_{R,L}$ against CW, obtained from adult males selected for combining SC1 and pale, needle-sharp dactyl tips. We estimated the age of every adult male with no missing pereopod by rearranging the terms in the regression model developed for observed $DW_{R,L}$.

Data for males tagged and recaptured in different surveys were used to estimate the duration of SC stages in two ways. The progression in successive SC stages from terminal molt to death is conceptually analogous to progression in successive molt stages from one ecdysis to the next. Hankin (2002) proposed a method for determining the duration of unequal molt stages (μ)

that is based on moment-type estimators and uses data from crabs that are captured, molt-staged, and maintained in the laboratory until ecdysis. Hankin's method requires information on mean number of days (D) required to progress from one stage (i) to ecdysis. An explicit and important assumption of the method is that crabs are captured randomly over the full duration of each molt stage, so that they are, on average, halfway through any stage considered. Hankin (2002: 356) provides a system of equations for resolving the duration of individual molt stages (μ_i), which we adapted to snow crabs by replacing molt stages by SC stages as follows:

$$\mu_{SC5} = 2D_{SC5}$$
$$\mu_{SC4} = 2D_{SC4} - 4D_{SC5}$$
$$\mu_{SC3} = 2D_{SC3} - 4D_{SC4} + 4D_{SC5}$$
$$\mu_{SC2} = 2D_{SC2} - 4D_{SC3} + 4D_{SC4} - 4D_{SC5}.$$

We do not know the mean time from any given SC stage to death, but we can approximate it from recapture data if we also assume random sampling of males over the duration of each SC stage. We approximated D_{SC5} as the mean of Δt for males tagged and recaptured in SC5 ($\Delta t_{SC5 \rightarrow SC5}$). We then estimated D_{SC4} as mean Δt for males moving from SC4 to SC5 ($\Delta t_{SC4 \rightarrow SC5} + \Delta t_{SC5 \rightarrow SC5}$), and so on for earlier SC stages ($D_{SC3} = \Delta t_{SC3 \rightarrow SC4} + \Delta t_{SC4 \rightarrow SC5} + \Delta t_{SC5 \rightarrow SC5}$

and $D_{SC2} = \Delta t_{SC2 \to SC3} + \Delta t_{SC3 \to SC4} + \Delta t_{SC4 \to SC5} + \Delta t_{SC5 \to SC5}$). Second, assuming again that males were, on average, halfway through any SC stage at time of tagging, we calculated the duration of SC stages more simply as twice the value of mean Δt for crabs tagged and recaptured in the same SC stage.

The change in claw hardness over time was derived from the difference in hardness between recapture and tagging. Claw hardness did not change perceptibly in two durometer measurements repeated over a few days, and in another study there was no significant difference between a second durometer reading on the right chela and a concurrent first durometer reading on the left chela (Sainte-Marie, unpublished data). The change in claw hardness over time was therefore assumed to reflect only natural change in cuticle strength and it was modeled for crabs tagged in SC2 to SC4 via polynomial or linear regression.

We used linear regression or Spearman's rank correlation coefficient to explore the relationships of claw hardness or number of missing pereopods and CW at each SC stage for all adults. Both variables were expected to vary with CW, based on other studies (Dutil et al. 2000; Sainte-Marie, unpublished data). Analysis of covariance (ANCOVA) was used to test for the homogeneity of slopes and elevations across SC stages for claw hardness. Polynomial or linear regression described changes in mean claw hardness or number of missing pereopods in relation to median age at SC stage.

Results

Capture, Tagging, and Short-Term Recaptures

A total of 7,647 adult male snow crabs ranging from 53.6 to 146.5 mm CW were caught over 9 years. Tagging of males (same CW range) was concentrated in early survey years; cumulative percentages of the total 5,101 tagged males were 6.5% in 1990, 42.1% in 1991, 52.9% in 1992, 70.3% in 1993, 78.0% in 1994, 86.5% in 1995, 95.3% in 1996 and 99.6% in 1997. Excluding males tagged and recaptured within the same survey, 417 males were recaptured on 520 occasions; 50 males were recaptured twice or more, accounting for the excess of 103 recaptures over the number of individual males.

The 27 males that were tagged, recaptured, and remeasured during the same survey were at liberty for only 1–9 d. At recapture, 25 of these 27 males were rated in the same SC category as at tagging. However, two males were regressed one SC stage (SC4 to SC3 and SC3 to SC2) at recapture, and this suggests a misclassification error of about 7.5%. Measurements of male body parts and hardness did not differ significantly between tagging and recapture based on the

paired t-test and Pearson's product-moment correlation coefficient: CW ($t = 1.58$, $P = 0.13$; $r = 0.99$), CH ($t = 0.27$, $P = 0.79$; $r = 0.99$), claw hardness ($t = 1.35$, $P = 0.20$; $r = 0.98$), DL_R ($t = 0.05$, $P = 0.96$; $r = 0.99$), and DL_L ($t = 0.46$, $P = 0.64$; $r = 0.99$). Absolute differences for DL_R and DL_L between tagging and recapture, weighted respectively by mean DL_R (26.15 mm) and mean DL_L (26.19 mm), resulted in an overall average change of 0.27% or 0.07 mm, which may reflect mostly measurement error.

Dactyl Wear for Estimating Shell Age

The wear recorded during the mark–recapture study was symmetrical between dactyls in a pair (paired t-test: $t = 0.13$, $P = 0.79$, $r = 0.94$) and is therefore reported as the mean of wear on both dactyls ($DW_{R,L}$). Observed $DW_{R,L}$ increased and became more scattered with increasing Δt (Figure 3). Dactyls of some males wore extensively, their length decreasing by about 10–15 mm over a period of about 2–6 years at liberty. Six clusters representing observed $DW_{R,L}$ at approximately annual increments of Δt are obvious in Figure 3. The correlation between $\log_e$(observed $DW_{R,L} + 1$) and Δt was weaker for individual values ($r = 0.66$, $P < 0.001$) than for cluster mean values ($r = 0.95$, $P < 0.01$).

Multiple regression determined that Δt and CW were significant ($P < 0.001$ each) sources of variation of observed $DW_{R,L}$:

$$\log_e(DW_{R,L} + 1) = 0.001034(\Delta t) + 0.079185(\log_e CW),$$

for which $R^2 = 0.818$, $P < 0.001$, $N = 398$. Time at liberty accounted for about 56.5% and CW for about 25.3% of the variance in observed $DW_{R,L}$.

Age Based on Dactyl Wear

At each SC stage, the average difference between DL_R and DL_L was small and not significant (paired t-tests by SC stage; $P > 0.11$). Therefore, we used the mean of DL_R and DL_L ($DL_{R,L}$) as a measure for individual males. The regression of $DL_{R,L}$ on CW for SC1 males with needle-sharp dactyls was

$$DL_{R,L} = 0.236CW + 11.925,$$

for which $r^2 = 0.86$, $F_{1,16} = 103.82$, and $P < 0.001$.

This reference line served to calculate unworn $DL_{R,L}$ at any given CW. The 95% confidence interval on estimates of unworn $DL_{R,L}$ was ±2.56 at 53.6 mm CW and ±2.19 mm at 146.5 mm CW. Note that the regression used to derive unworn $DL_{R,L}$, although based on few data, did not differ as to slope from a regression calculated for SC1 adult males from the northern Gulf of St. Lawrence ($P = 0.585$, $N = 64$).
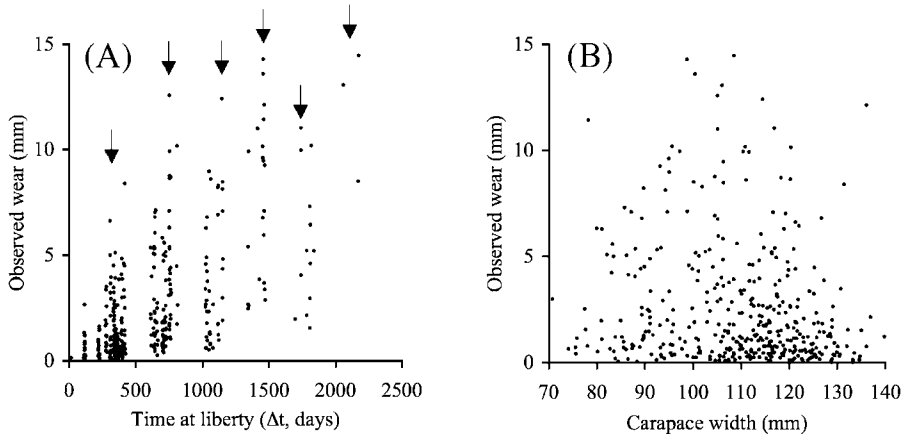
FIGURE 3.—Observed dactyl wear for adult male snow crabs by **(A)** time at liberty and **(B)** carapace width. Wear was determined from 398 crabs tagged and recaptured in Saguenay Fjord that had an intact third pereopod pair. The arrows in panel A point to clusters of recaptures at approximately annual increments of time at liberty.

Figure 4 shows a gradual decline and scattering of observed $DL_{R,L}$ from SC2 to SC5 relative to the reference line. Histograms of estimated $DW_{R,L}$, determined as the difference between observed and unworn $DL_{R,L}$, demonstrate a general progression of estimated $DW_{R,L}$ with increasing SC stage (Figure 4). Median estimated $DW_{R,L}$ was 1.98 mm at SC2, 4.98 mm at SC3, 9.98 mm at SC4, and 15.29 mm at SC5.

We aged males represented in Figure 4 by rearranging the equation derived from the multiple regression describing observed $DW_{R,L}$ (see above) as

$$\Delta t = \frac{-\log_e(DW_{R,L} + 1) + 0.079185(\log_e CW)}{-0.001034}.$$

The estimated $DW_{R,L}$ and measured CW for each male were used as input to the equation. Males with $DW_{R,L}$ equal to or exceeding 0 were coded as having a shell age of 0 years. The median and lower and upper quartiles of age estimates at SC stage are shown in Figure 4. A clear trend of increasing median shell age at SC stage was apparent, the quartile range overlapping for two successive SC stages but not for more distant SC stages. There was considerably more overlap in quartile age ranges between SC2 and SC3 (0.8 years) and SC4 and SC5 (0.9 years) than between SC3 and SC4 (0.2 years). In relative terms, the overlap was greater between SC4 and SC5 (47.4% of the quartile range for SC4 and 60.0% for SC5) than between SC2 and SC3 (36.4% for SC2 and 30.8% for SC3) and was again least between SC3 and SC4 (7.7% for SC3 and 10.5% for SC4).

Duration of Shell Condition Stages

Fewer crabs were tagged in SC2 than in SC3 or SC4, and this reflects the fact that there was little recruitment of adult males to the Saguenay population from 1990 until 1995–1996 (authors' unpublished data). Thus, 53.5% of SC2 males were tagged after 1994 compared with less than 20.1% of males in any of the other SC stages. Overall, 53.1% of males were in the same SC stage at recapture as at release, 34.6% advanced one or more stages, and 7.3% regressed (Table 2). The proportion of males released and recaptured in the same SC stage was not independent of SC stage at tagging ($\chi^2 = 30.32$, df = 3, $P < 0.001$). This heterogeneity reflected smaller same-SC recapture rates for crabs tagged in SC2 (0.7% of 454 tagged) and SC5 (2.3% of 560) than for crabs tagged in SC3 (4.4% of 1,841) and SC4 (5.8% of 2,206). Mean residency time in SC stage was higher for SC3 (1.5 years) and SC4 (1.2 years) than for SC2 (1.0 years) and SC5 (0.8 years). Many males remained in SC3 or SC4 for 3 or more years. Males that advanced one stage in SC were at liberty for longer average periods—from 1.7 (SC4→SC5) to 2.5 (SC3→SC4) years—than males that remained in the same SC stage. Males that advanced two or three stages in SC were at liberty for even longer: 2.6 (SC3→SC5) to 6.0 years (SC2→SC5). Mean Δt and difference in SC stage for each of the entries in Table 2 (excluding males that regressed one SC stage) were positively correlated (Spearman's rank correlation coefficient, $r = 0.95$, $N = 10$).

As was the case with short-term recaptures, some males apparently regressed in SC stage between surveys (Table 2). However, no male regressed from SC2 to SC1 or regressed more than one SC stage. Males that regressed in SC represented 1.0% of all recaptured males tagged in SC3, 10.7% in SC4, and
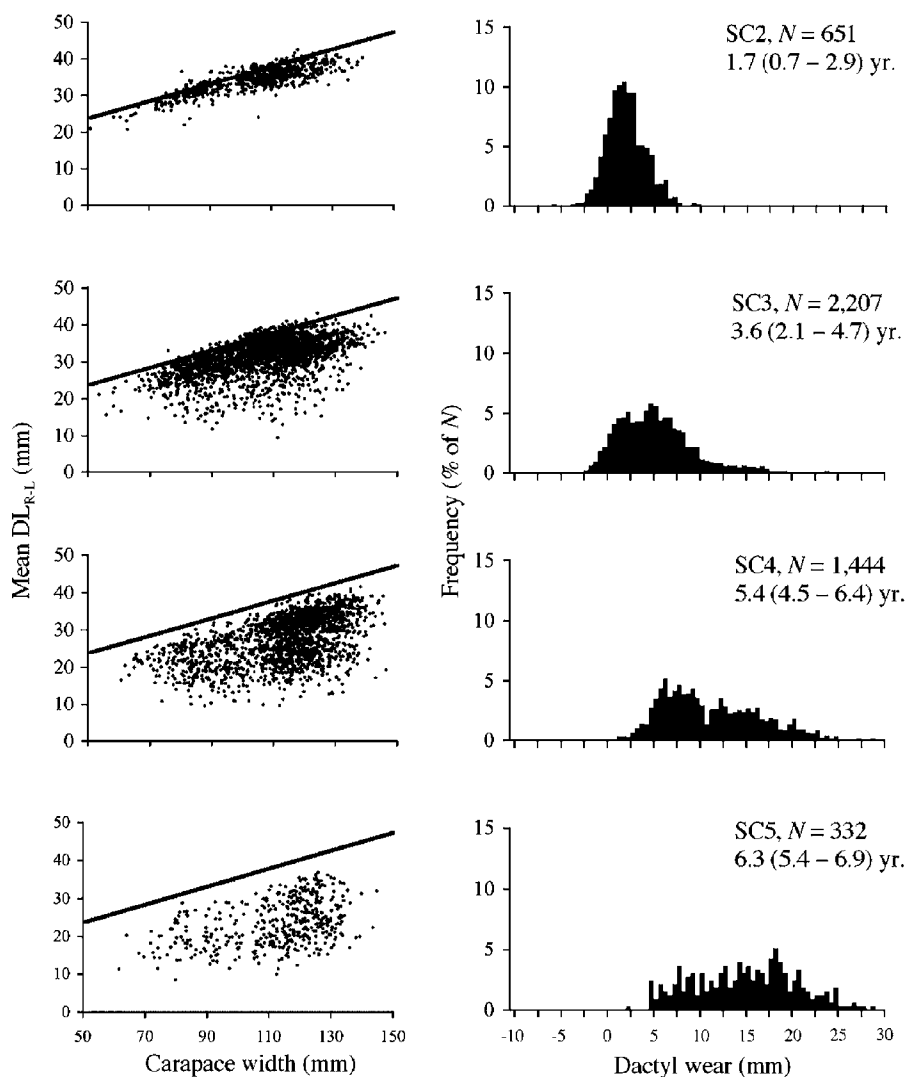
FIGURE 4.—Carapace width (CW; left-hand panels) and dactyl wear (right-hand panels) of adult male snow crabs of shell conditions SC2–SC5 with no pereopods missing collected during population censuses in Saguenay Fjord with respect to right and left dactyl lengths ($DL_{R,L}$) for individuals with the third pereopod pair intact. The reference lines in the left-hand panels represent the mean lengths of unworn dactyls for SC1 adult males. The frequency histograms in the right-hand panels were derived by subtracting the observed values of $DL_{R,L}$ from the estimated unworn values of $DL_{R,L}$ at CW; the numbers given are medians, with the lower and upper quartiles of age at SC stage based on the dactyl wear model (Table 2) in parentheses.

43.5% in SC5. The average Δt for males regressed one SC stage ranged from 0.8 (SC5→SC4) to 1.5 (SC3→SC2) years. Regression of SC stage between surveys could reflect assignment error or an unlikely improvement in crab appearance. Assuming assignment error was the reason, mean Δt for males released and recaptured in the same SC stage would be unchanged if the error was committed only at recapture, but if the error occurred only at tagging, Δt would increase slightly to 1.2 years for SC2, decrease

slightly to 1.4 years for SC3, and remain the same for SC4.

Based on the modified Hankin method (Table 2), if SC1 lasts 0.2 years (see Introduction), then the post–terminal molt shell age at the end of SC stage was 1.4 years for SC2, 4.4 years for SC3, 6.3 years for SC4, and 7.8 years for SC5. With the same assumption for SC1, but using the simple method of 2 × Δt for same SC-stage recaptures, post–terminal molt shell age at the end of SC stage is estimated to be 2.2 years for SC2,

TABLE 2.—Mean ± SD time at liberty (years) for adult male snow crabs tagged and recaptured in Saguenay Fjord by initial shell condition (SC) and degree of change in shell condition. The numbers in parentheses in the column heads are the numbers of crabs tagged; those in parentheses within the table are the numbers of recaptures and the ranges in time at liberty.

Extent of stage change and duration	SC2 (454)	SC3 (1,841)	SC4 (2,206)	SC5 (560)
−1 SC stage		← 1.5 ± 0.7 (2; 1.0–1.9)	← 1.1 ± 0.5 (19; 0.3–2.1)	← 0.8 ± 0.5 (10; 0.3–1.7)
Same SC stage	1.0 ± 0.0 (3; 1.0–1.0)	1.5 ± 0.1 (81; 0.3–3.7)	1.2 ± 0.1 (127; 0.3–4.8)	0.8 ± 0.4 (13; 0.3–1.8)
+1 SC stage	2.1 ± 1.3 (22; 0.3–4.8) →	2.4 ± 1.3 (93; 0.6–5.0) →	1.7 ± 0.9 (31; 0.8–4.0) →	
+2 SC stages	5.3 ± 0.6 (3; 5.0–5.9) →	2.6 ± 1.3 (17; 0.8–5.6) →		
+3 SC stages	6.0 (1) →			
Duration of stage	1.2	3.0	1.9	1.5

5.2 years for SC3, 7.6 years for SC4, and 9.2 years for SC5. By comparison, the dactyl wear method produced median age estimates of 1.7 (SC2), 3.6 (SC3), and 5.4 (SC4) years (Figure 4), which are closer to the modified Hankin method estimates than the $2 \times \Delta t$ estimates. The main difference between the first two methods is that the duration of SC1 + SC2 relative to shell age at SC3 is longer for wear-based (1.7/3.6 = 47.2%) than for modified Hankin (1.4/4.4 = 31.8%) estimates. The 95% quantile of age at SC5 derived by dactyl wear (7.7 years) is similar to the 7.8-year post–terminal molt longevity derived by the modified Hankin method.

Relationships of Claw Hardness and Missing Pereopods to Shell Age

Changes in claw hardness between tagging and recapture in different surveys ranged from −50 to +20 durometer units (Figure 5). For crabs tagged in SC2, the relationship between the change in claw hardness and Δt was best described by a bell-shaped curve (polynomial model: $r^2 = 0.51$ with residuals equally distributed about the estimator; linear model: $r^2 = 0.34$ with residuals unequally distributed) showing initially a slight increase followed by a gradual decline in claw hardness (Figure 5). The Δt to reach maximum hardness estimated with the polynomial model ($\Delta t = -b/2a$, where b is 0.0072 and a is -9×10^{-6}) was 1.1 year. Note that males tagged in SC2 for which changes in claw hardness were available initially had harder claws (mean of 83.2 durometer units, see Figure 5) than the overall average for SC2 males (Figure 6). Negative linear models best described the change in claw hardness over Δt for males tagged in SC3 or SC4, and the slope was steeper for SC4 than SC3 males (Figure 5).

For the overall population of adult males, regressions of claw hardness on CW were significant ($P < 0.001$) for stages SC2 through SC5 but not for SC1 ($P > 0.50$). The slopes of the regressions of claw hardness on CW were not homogeneous for SC2 to

SC5 ($F_{3, 5,430} = 15.57$, $P < 0.001$) owing to a steeper relationship for SC5 ($y = 24.45 + 0.36x$) than for SC2 ($y = 53.30 + 0.22x$), SC3 ($y = 51.71 + 0.29x$) and SC4 ($y = 48.13 + 0.26x$). The slopes of regressions of claw hardness on CW did not differ significantly across SC2 to SC4 ($F_{2, 4,470} = 1.82$, $P = 0.163$) but intercepts did ($F_{2, 4,470} = 269.00$, $P < 0.001$). Mean claw hardness at SC stage was calculated as the arithmetic mean for SC1, hardness adjusted by ANCOVA to a constant CW (111.3 mm) for SC2 to SC4, and a regression-based hardness estimate at 111.3 mm CW for SC5. The relationship of claw hardness to median shell age at SC is bell-shaped (Figure 6), increasing from 55.1 durometer units at SC1 (about 0.1 year post terminal molt) to a peak of 83.4 durometer units at SC3 (3.6 years), and declining to 65.0 durometer units at SC5 (6.3 years). The evidence for shell hardening from SC2 to SC3 and shell softening from SC3 to SC5 is consistent between population censuses and mark–recapture data.

In relation to SC stage, the proportion of adult males with no missing pereopod decreased and the mean number of missing pereopods by male increased (Table 3). At SC4, more than half of all adult males were missing one pereopod, and some missed up to six pereopods. Spearman's rank correlation coefficient indicated an overall negative relationship between number of missing pereopods and CW ($P < 0.001$). The mean number of missing pereopods by SC was positively related to median shell age at SC (Figure 6).

Discussion

Determination of Shell Age by Dactyl Wear

Although it is widely recognized that crab dactyls may wear down between molts or after a terminal molt, to our knowledge this is the first study to quantify dactyl wear and to attempt to implement it as a method for estimating crustacean shell age. In our multiple regression model, Δt explained 56.5% of the variability in observed dactyl wear for male snow crabs. For comparison, r^2 for models relating tooth height or wear
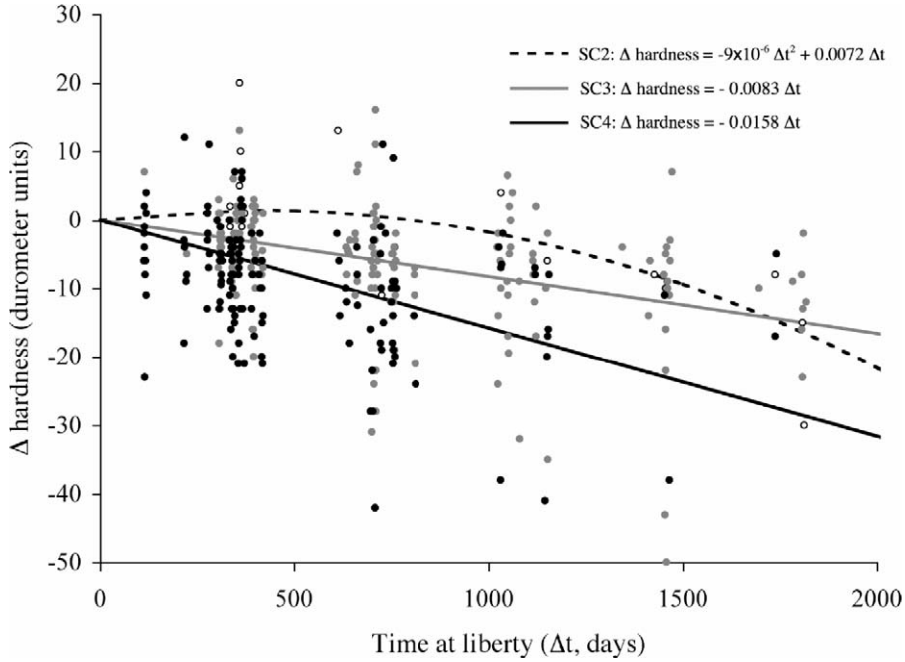
FIGURE 5.—Change in claw hardness with time at liberty for adult male snow crabs tagged and recaptured in Saguenay Fjord. The mean claw hardness at tagging was 83.2 (SD, 8.7) for recaptured crabs released in shell condition 2 (SC2; open circles), 82.7 (SD, 7.0) for those released in SC3 (gray circles), and 79.0 (SD, 8.6) for those released in SC4 (black circles). A polynomial model describes the change for SC2 males ($r^2 = 0.51$, $N = 21$, $P < 0.001$), linear models the changes for SC3 ($r^2 = 0.12$, $N = 184$, $P = 0.010$) and SC4 males ($r^2 = 0.10$, $N = 153$, $P < 0.001$); the models were forced to the origin.
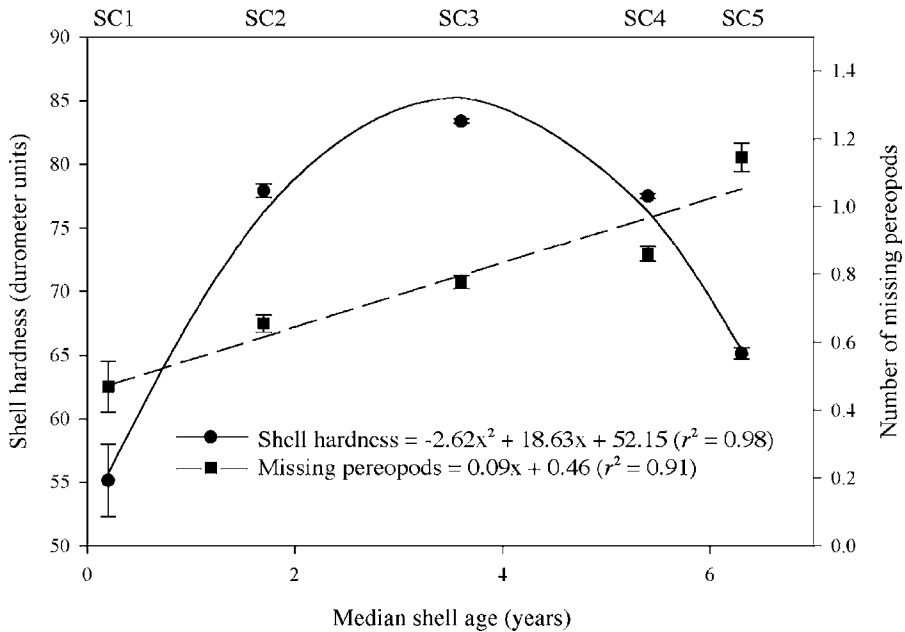

FIGURE 6.—Means and SEs of shell hardness and number of missing pereopods at five shell condition stages (SC1–SC5) for adult male snow crabs from Saguenay Fjord. The regression equations use the median age at SC stage derived from dactyl wear (Figure 4) as a continuous variable.

TABLE 3.—Percentages of adult male snow crabs from Saguenay Fjord missing 0, 1, 2, or 3–6 pereopods, by shell condition stage (SC1 to SC5).

Missing pereopods and n	SC1	SC2	SC3	SC4	SC5
0	71.2	69.4	52.7	48.2	36.3
1	15.9	19.6	27.7	28.8	30.0
2	8.3	7.0	12.3	14.4	21.7
3–6	4.6	4.0	7.3	8.6	12.0
n	131	1,650	2,983	2,379	601

to age in mammals range from 0.33 to 0.66 for roe deer *Capreolus capreolus* (Hewison et al. 1999; Mysterud and Østbye 2006), 0.39 for humans (Mays 2002) and, exceptionally, up to 0.88 for caribou *Rangifer tarandus* (Morrison and Whitridge 1997). Our observations show that the dactyls of male snow crabs wear slowly in the first years after molt and faster in later years. Other analyses we have conducted indicate that wear accelerates once the tip of the dactyl (Figure 1) is worn off. Among crabs in general, the dactyl (or "finger") may be harder than other exoskeleton parts (Bobelmann et al. 2007) and in turn the dactyl tip (representing about 23% of unworn dactyl length in snow crabs) may be harder and tougher than the remainder of the dactyl (Warner 1977; Melnick et al. 1996).

There are other demonstrated or likely sources of variation of dactyl wear in male snow crabs. Carapace width accounted for a substantial portion of variation in observed dactyl wear, and this can probably be explained by increasing dactyl load and amplitude of movement with increasing male size. For instance, Lovrich et al. (1995) reported that larger adult males traveled greater distances than smaller adult males during annual mating runs. Moreover, the rate of dactyl wear may be modulated by substrate abrasiveness (authors' unpublished data), just as tooth wear in mammals can vary between sexes or regions because of differences in diet or food quality and abrasiveness (Loe et al. 2003). It is also conceivable that the rate of dactyl wear varies among male snow crabs in reflection of cuticle quality, just as tooth wear can vary among same-age mammals because of differences in enamel quality (Hewison et al. 1999). Finally, the occasional breakage of a dactyl is likely to introduce some noise in the record of dactyl wear.

Even though snow crab dactyls can be measured very precisely, the derivation of the measure of wear for wild males leads to some uncertainty around shell age estimates. One uncertainty relates to the accuracy of the regression of $DL_{R,L}$ on CW for unworn dactyls, from which $DW_{R,L}$ is estimated. The slope of that regression seems reliable, but any error in the y-intercept will lead to a systematic bias in estimates of $DW_{R,L}$ and shell age. Another uncertainty arises from the fact that the length of unworn dactyls at a given CW is heterogeneous among males. This heterogeneity can be explained by phenotypic variation, as well as incomplete pereopod regeneration following autotomy events before the terminal molt (i.e., 4–5 molts may be needed to fully regenerate a pereopod; Miller and Watson 1976). Uncertainty about estimated $DW_{R,L}$ for individual males could be reduced if unworn DL is better predicted by the length of the propodus (i.e., the leg segment preceding the dactyl) than by CW. Systematic or individual error in DW estimates will be more consequential for estimates of males with little wear than for those with considerable wear. For example, a +2.5-mm difference between estimated and actual $DW_{R,L}$ for a 100-mm-CW male will inflate estimated age by 1.6 years, for an estimated 4.5-mm $DW_{R,L}$ (2.1 versus 3.7 years at 50 mm CW; 1.9 versus 3.5 years at 150 mm CW) compared with only 0.4 years for an estimated 17.5-mm DW (6.5 versus 6.9 years at 50 mm CW; 6.3 versus 6.7 years at 150 mm CW). However, systematic error in the estimation of $DW_{R,L}$ would bias estimates of median age at SC stage, whereas individual errors would not because of the averaging effect in large samples. We are hopeful that modal analysis of wear (i.e., dactyl wear cohorts) may eventually be used to assess male shell age structure, given that molting occurs once annually during a relatively narrow period.

Longevity of Adult Males

The estimates of post–terminal molt longevity (7.7–7.8 years) for adult male snow crabs were consistent between the dactyl wear method and the modified Hankin method. These estimates are greater than the 6 years initially inferred by Sainte-Marie et al. (1995) and references therein, which we derived by summing mean Δt for males passing from SC2 to SC3, SC3 to SC4, and SC4 to SC5 in the Saguenay mark–recapture study up to 1994. Our upper estimates of shell age also exceed other estimates of postmolt longevity for adult males by about 1–3 years. Radiometry produced maximum shell age estimates for adult males of 4–5 years on the west coast of Newfoundland (Conan et al. 1996; Comeau et al. 1998) and 6.8 years in the eastern Bering Sea (Ernst et al. 2005). The greater longevity estimates from our study may be explained by lack of commercial fishing in Saguenay Fjord and the fact that we aged hundreds of times the number of males in the radiometric studies. However, there may also be a methodological issue because radiometry will underestimate shell age when postmolt cuticle calcification is protracted (LeFoll et al. 1989). The shell of male snow

crabs continues to harden for at least 5–9 months after molting (Dutil et al. 2000; Godbout et al. 2002; Hébert et al. 2002), and in our study maximum claw hardness was not reached until SC3 or 2–3 years after terminal molt age. In the warmwater mud crab *Scylla serrata*, the shell thickens and hardens continuously from postmolt (molt stage A) until the end of intermolt (molt stage C_3) through the addition of minerals (mostly calcium carbonate); mineralization occurs over the first 25 d of the 40-d-long molt cycle (Pratoomchat et al. 2002). If mineralization is also responsible for protracted shell-hardening in snow crabs, radiometry will underestimate overall longevity and age at all SC stages. Note that the intriguing stepwise pattern of age at SC stage reported by Ernst et al. (2005) for snow crabs in the Bering Sea (0.2 years at SC1 [$N = 3$], 0.8 years at SC2 [4], 1.0 years at SC3 [3], 5.5 years at SC4 [2], and 4.8 years at SC5 [2]) is not inconsistent with shell rejuvenation up until SC3. The possible impact on radiometric age estimates of shell decay in the last years of post–terminal molt life of male snow crabs, which is evident in the softening of claws through SC4 and SC5 (and which probably implies loss of minerals), has not been discussed.

We are probably still underestimating the maximum longevity of male snow crabs after terminal molt. Trap catchability of adult males increases from SC1 to SC3 and then declines to low values in SC5 as senescing males lose mobility and perhaps appetite (Sainte-Marie and Turcotte 2003). Therefore, our estimates may reflect the average age at ecological death (i.e., when interaction with other crabs and ecosystem components declines) rather than at the actual death of an individual. One large adult male from Saguenay Fjord was recaptured 11 years after tagging, and feeble small adult males with completely butted dactyls and a more degraded appearance than SC5 males from Saguenay Fjord have been captured by trawl in the northern Gulf of St. Lawrence (Sainte-Marie, personal observation).

Value of Shell Condition Index

Our short-term and long-term recapture data demonstrate that even experienced observers may differ in opinion when scoring SC stage or change their opinion when rescoring the same crab. Discrepancies do not exceed one SC stage; the SC3 crabs and especially the older SC4 and SC5 crabs are most likely to be scored differently. Errors in the assignment of SC reflect (1) very gradual change in appearance, (2) subjectivity and difficulty in deciding to score in one stage or the next, and (3) occasionally, the fact that a muddy crab may be scored one SC stage more than it would be if clean. Nevertheless, dactyl wear and tag–recapture data confirm that SC is a rough index of shell age by showing a progression of median wear (age) and number of missing pereopods through successive SC stages and a greater probability of males advancing in SC stage (rather than regressing) with time elapsed since tagging. Although age estimates at SC derived by the dactyl wear and modified Hankin methods are reported to the nearest 0.1 year, their precision may be less because we sampled just once or twice a year (the minimum time step between surveys was 0.3 years). A reasonable explanation for the discrepancy between the two methods in the estimated duration of SC1 + SC2 is that most or all SC2 males tagged during spring surveys were already 1 year or more from terminal molt; therefore, they may have violated the condition of random sampling over the duration of SC stage more severely than at other stages, which would lead to an underestimate of stage duration by the modified Hankin method.

Our findings have two important implications for the assessment of recruitment, mortality, and exploitation rates in snow crabs, based on the abundance of SC stages. First, the SC2 category may include adult males recruited to the population over 2–3 years, depending on aging method, rather than just the current year, as is usually assumed. Thus, annual recruitment is overestimated where and when the combined duration of SC1 and SC2 exceeds 1 year. Second, individual SC stages do not represent discrete age groups, and they differ in duration. It is also possible that the duration of individual SC stages is modified by environment and population density; for instance, the transition from SC1 to SC2 may depend on food availability or accessibility (Godbout et al. 2002), and the process of shell fouling, which is important for assignment of males to SC3–SC5, may vary spatially (Savoie et al. 2007) and probably interannually within regions (Dick et al. 1998). Therefore, inferences about mortality and exploitation rates based on the relative abundance of SC stages are subject to some error. In particular, the uncertain classification and considerable age overlap for males in SC4 and SC5 questions the pertinence of maintaining these two SC stages as two distinct categories (see also Ernst et al. 2005).

Management Implications

The new longevity estimates and chronology of change in SC described for adult male snow crabs are important for understanding population dynamics and productivity and are relevant for management and conservation. First, we confirm Godbout et al.'s (2002) conclusion that legal-size males require a very long period to achieve a good condition after molting, and we can now quantify that timeframe. Dufour et al. (1997) documented for a sample of males with a mean

CW of 103.5 mm that the average yield of cooked meat/mm^3 of body volume increased by 118%, from 0.076 mg at SC1 (hardness <60 durometer units) to 0.166 mg at SC3 (>80 durometer units). In our study, SC3 and peak hardness, associated with peak meat yield, were not reached until about 2–3 years after terminal molt.

Second, from an economic perspective, increasing meat yield may be offset by pereopod loss and deterioration of crab appearance, which result in lower prices. The natural loss of pereopods with increasing shell age (or SC stage) is modest and it is less pronounced in large than in small adult males, probably reflecting the former's dominant status and greater ability to fend off predators (Sainte-Marie et al. 1999; Chabot et al., in press). Each pereopod represents on average about 3% (fifth pereopod) to 17% (first pereopod or cheliped) of total weight of pereopods (Sainte-Marie, unpublished data), where most meat is concentrated, and therefore the average loss of about 0.3 pereopods per male from SC1 to SC3 would not offset the much more substantial gain in meat yield. The deterioration of crab appearance may not become critical economically until SC4, when the cuticle is permanently darkened and epibionts may be too large or encrusted to be scrubbed away, resulting in reduced value for sale as whole live crab or cooked sections. Therefore, the window of opportunity for fishing adult males before they become too deteriorated may extend to about 4.5 years after molting, based on the lower age quartile for SC4 males. Snow crabs are notorious for highly variable and autocorrelated recruitment that occurs as alternating multiyear pulses and troughs (Conan et al. 1996; Sainte-Marie et al. 1996; Zheng and Kruse 2003; Caddy et al. 2005). Our findings indicate that adult male snow crabs can to some extent be "banked" (i.e., conserved for future harvest) by reducing exploitation in the last 1–2 years of a recruitment pulse, which would allow the commercial biomass to accumulate and attenuate the economic effects of transient declines in recruitment.

Third, the peak of reproductive condition and sexual competitiveness of males is reached and maintained from about 2.0 to 5.5 years after the terminal molt, corresponding to the range of the lower age quartile at SC3 to the lower age quartile at SC5. Larger adult males of SC3 and SC4 dominate sexual pairs during the highly competitive pubescent–primiparous mating season (Sainte-Marie et al. 1999). These males have harder shells and greater muscle mass that make them more powerful and less vulnerable to injury than other categories of males. Additionally, sperm reserve of males usually increases from SC1 to SC4 (Sainte-Marie et al. 1995), conferring potential for effective

polygyny (i.e., the ability to inseminate many females during a mating season without allocating too parsimoniously or becoming depleted of sperm; see Sainte-Marie et al. 2002 and references therein). Protection of a quality male spawning biomass implies that some large adult males should be allowed to age to a condition at which they are of lesser or no value to the industry or die naturally, a fate that is regarded by many stakeholders as resource wastage. Acceptance of some level of natural mortality as a necessary component of stock health is perhaps more difficult in the snow crab fishery, compared with vertebrate fisheries, because the process of crab senescence and loss is so conspicuous to stakeholders. To get the highest sustainable yield from snow crab stocks, the economic gains and losses associated with postmolt aging must be balanced against natural and indirect fishing mortality, about which we know very little, and the fecundity benefits of maintaining a minimum ratio of large adult males to receptive females (Zheng and Kruse 2003; Siddeek et al. 2004).

Finally, the extent of adult male longevity revealed by our study implies a potential for long interactions between large adult males and prerecruits in populations. Large adult males may be important for population dynamics in more than just their role as sires. The largest adult males typically recruit en masse to a population toward the end of a recruitment pulse (Sainte-Marie et al. 1996; Comeau et al. 1998) and therefore they can potentially interact with immature crabs from the next recruitment pulse (as with immediate prerecruits of their own recruitment pulse) in a facilitating, competitive, and (or) predatory role. Under intense fishing pressure these interactions are reduced, and this can have a negative impact on future recruitment if large adult males improve the survival of immature crabs and prerecruits; alternatively, it can have a positive impact if large adult males repress the growth or increase the mortality of immature crabs and prerecruits (see discussions in Elner and Beninger 1995; Conan et al. 1996; Sainte-Marie et al. 1996; Lovrich and Sainte-Marie 1997; Comeau et al. 1998; Caddy et al. 2005).

Acknowledgments

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