Growth per Molt of Male Snow Crab *Chionoecetes opilio* from Conception and Bonavista Bays, Newfoundland

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Abstract.– Over 6000 male snow crabs were tagged during a 6-year period in Conception Bay, Newfoundland, in order to estimate the increase in size at the time of molting. Ninety-two animals were recaptured which had usable information on growth increments. Based on the amount of growth, we hypothesized that 20 of these had molted once while the remainder molted twice. Two lines of evidence support this interpretation. First, animals in the group presumed to have molted twice were at liberty on average twice as long as those presumed to have molted once. Second, a regression line fitted to data on single-molters predicted the size after two molts in close agreement with a regression line fitted to data on double-molters. A nonlinear regression model was developed to estimate the parameters of the relationship between post- and pre-molt sizes using the combined data set for single and double molters. The method was also generalized to account for a quadratic relationship between post- and pre-molt size. For crabs in the size range 80–110 mm carapace width, the predicted size after molting in mm is equal to 7.398 + 1.038 × premolt size. A similar study conducted in Bonavista Bay, Newfoundland, yielded growth information for 18 animals. The molt increments appear similar to those observed from Conception Bay.

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The snow crab *Chionoecetes opilio* has supported extensive commercial fisheries on both the Atlantic and Pacific coasts of North America since the 1960s (Elner and Bailey 1986). Snow crabs are also commercially exploited in Japan. Only the males are harvested in North America because females never attain commercially acceptable sizes. Efforts to manage the resources have been hampered by a lack of detailed life-history information. This is because the crabs are found in deep water (50–700 m) and are thus difficult to study.

Information on growth of snow crabs is required for effective management for at least three reasons: (1) for incorporation in a yield-per-recruit model, (2) to forecast the biomass available to the fishery from size-specific, pre-season biomass estimates, and (3) to interpret size-frequency distributions. Although growth can be studied in the laboratory, there is no guarantee that the observed growth will reflect what happens in free-living populations. Consequently, there is a need to estimate growth parameters from field data.

There have been some tagging studies of snow crab growth, but the reported results were either of a preliminary nature or were unsatisfactory due to tag retention problems (McBride 1982, Taylor 1982, Bailey and Dufour 1987). Improvements in tagging methods (Hurley et al. In press) have made field studies feasible.

Growth of crustacea is often estimated by studying two components: the increase in size at the time of molting (molt increment) and the timing of molting (either the intermolt period or the proportion molting in a given season). Recent work by Moriyasu and Mallet (1986) and O'Halloran and O'Dor (1988) has provided a method for estimating the proportion of the population that will molt in a given time period. In this paper, we concentrate on the problem of estimating the size-specific molt increment of snow crabs in Conception and Bonavista Bays, Newfoundland, from mark-recapture data consisting of the size at the time of tagging, the size at recapture, and the time at liberty.

Conception and Bonavista Bays are deepwater bays on the Northeast coast of Newfoundland (maximum depth 295 m in Conception Bay; 412 m in Bonavista Bay). Commercial fishing grounds for crabs exist at depths exceeding 180 m. The bottom type in these areas is predominantly mud or muddy sand with mean bottom temperatures ranging from −1.3 to 0.5°C. Since the mid 1970s both areas have experienced high levels of commercial crab fishing effort (Taylor and O'Keefe 1987). While aggregations of crabs may be found at depths <180 m, the deeper commercial fishing grounds appear to have the soft substrate necessary for snow crab molting.

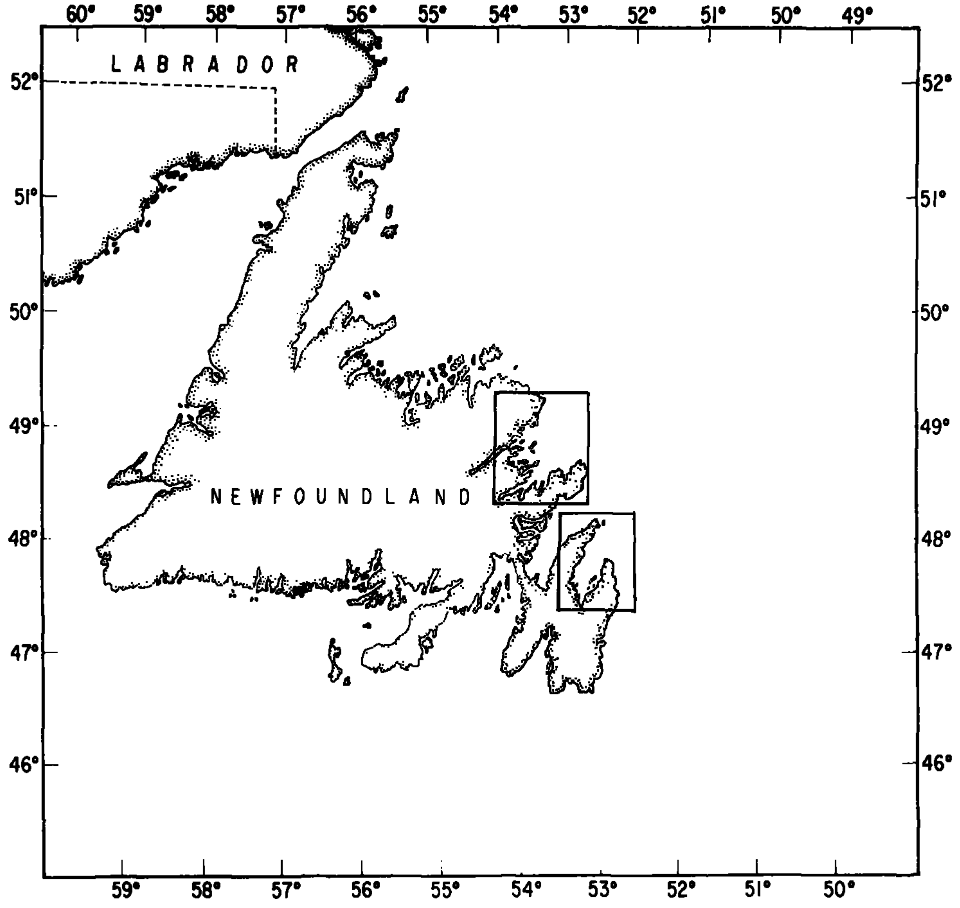

Figure 1
Map of Newfoundland, Canada, showing the location of Conception Bay (lower box) and Bonavista Bay (upper box).

Materials and methods

From 1979 to 1984, nine research cruises were made to Conception Bay, Newfoundland, Canada (47°30'N, 53°W, Fig. 1), to tag 6296 male snow crabs, size range 56–135 mm carapace width (CW). An additional 2253 male crabs, size range 45–125 mm CW, were tagged during four cruises to Bonavista Bay, Newfoundland (48°50'N, 53°20'W), from 1979 to 1984.

Crabs were captured using Japanese-style conical traps baited with squid *Illex illecebrosus* and set in longlines of twelve traps at depths ranging from 110 to 285 m. Traps were hauled after soaking for 24 hours.

Tagging was conducted in a manner designed to minimize mortality. Traps were spaced approximately 40 m apart, which allowed us to tag crabs from the trap on deck while the other traps remained in the water. Before tagging, we examined each animal and discarded any that appeared injured. Carapace width was measured to the nearest millimeter using vernier calipers. Animals were tagged with a T-bar tag (Floy Tag Mfg. Co., Inc., Seattle, WA 98105) and immediately released on location. Details of the tagging procedure are described in Hurley et al. (In press). Tags were inserted in the posterior ecdysial suture (epimeral line) which was made visible by applying gentle upward pressure to the carapace. The tagging location was 2–6 mm from the right coxopodite of the last walking leg. Before releasing the crab, the end of the tag was given a gentle tug. If the tag appeared loose, it was removed and the animal was discarded. To determine measurement errors, one biologist measured 90 animals three times in blind trials. The animals ranged in size from 63 to 124 mm. Recaptured animals were obtained mostly from commercial fishermen. Only animals that were examined by a staff biologist were used in the analysis.

Results and discussion

Repeated measurements by a biologist of a group of crabs were always within 1 mm of the mean for each animal. Workers studying other species of large crustacea have suggested that measurements can be

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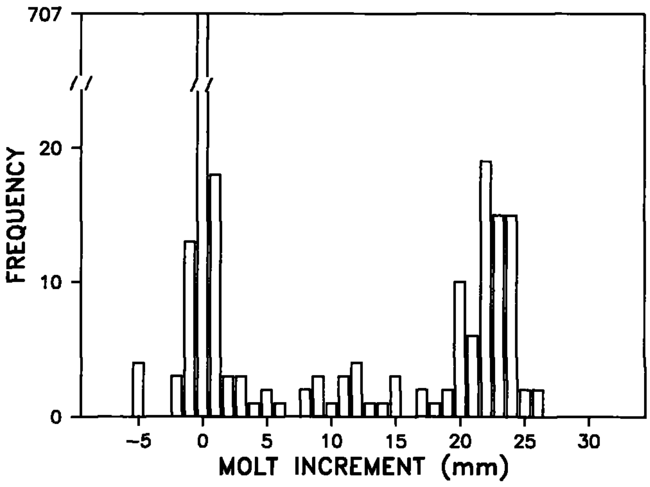

Figure 2

Frequency of occurrence of growth increments for recaptures of *Chionoecetes opilio* from Conception Bay.

precise to within 3 mm (Restrepo 1989, Hunt and Lyons 1986, Little 1972). If measurement errors occur at both the time of tagging and the time of recapture, then errors as large as 5 or 6 mm might be encountered.

Conception Bay

We recovered 850 tagged animals from Conception Bay. Of these, 751 had measured increases in size of 3 mm or less; three had increases of 4–5 mm; the remaining 93 animals had increases of at least 6 mm (Fig. 2). None of the three animals with molt increments of 4 or 5 mm were particularly small (premolt sizes: 92, 96, 99 mm). Consequently, these animals would not be expected to have particularly small increments. Their times at liberty were 325, 187, and 157 days, respectively. We assume that the 93 animals with increments of 6 mm or more molted at least once, and none of the other animals molted. The average time at liberty for animals which did not molt is under a year ($\bar{x}$ 322 days, median 251 days, range 6–1598 days; Fig. 3).

The size at recapture of Conception Bay crabs which molted was plotted against the size at tagging, and two distinct linear clouds of points were apparent (Fig. 4). The line indicating a 17% increase in size appears to separate the two clouds nicely. A reasonable working hypothesis is that the lower cloud consists of animals which molted once, while the upper cloud consists of animals which molted twice. One animal in the two-molt group was at liberty for only 29 days and was tagged and recaptured in a hard-shelled condition. Animals remain soft-shelled for 2–3 months after molting, and soft-shelled animals cannot molt (Taylor et al. 1989). For this reason, this animal was eliminated from further consideration.

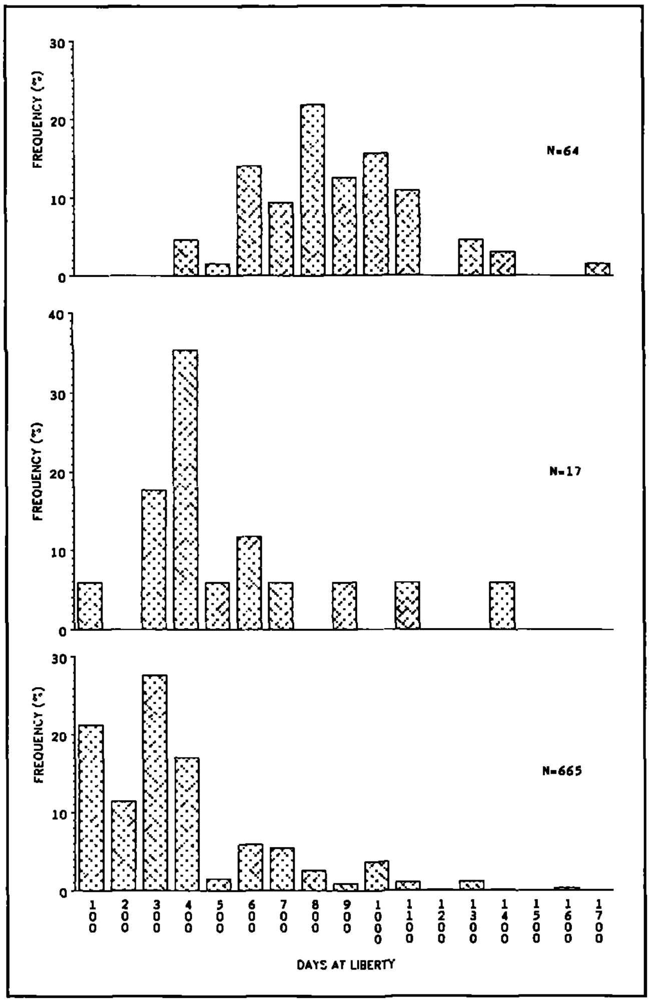

Figure 3

Histograms of times at liberty for Conception Bay *Chionoecetes opilio*. Upper figure corresponds to the upper cloud of points in Figure 4, i.e., to animals believed to have molted twice. Middle figure corresponds to the lower cloud in Figure 4. Lower figure corresponds to recaptured animals which had not molted while at liberty.

The times at liberty for 81 of the 92 Conception Bay animals which molted ranged from 18 to 1618 days. (Exact times at liberty could not be determined for 11 animals.) However, the mean time at liberty for the hypothesized two-molter group was approximately twice as long as for the single-molter group (828 vs. 468 days) and there was little overlap in the distributions of time at liberty for the two groups (Fig. 3). Animals which did not molt were at liberty for an average of 322 days. Although there is little information in the literature on intermolt periods for snow crabs, it is believed that crabs approaching commercial size molt once per year (Robichaud et al. 1989) and

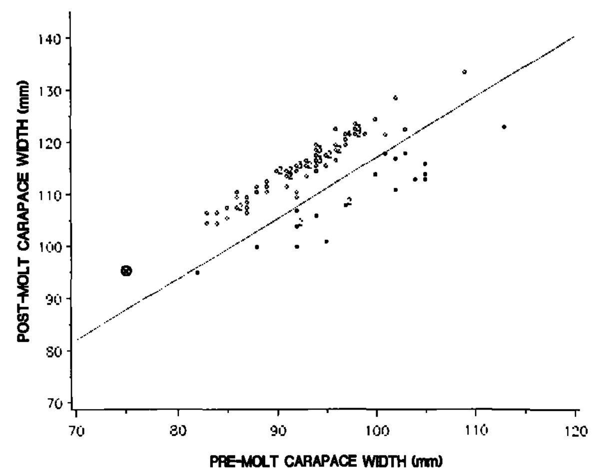

Figure 4

Plot of size at recapture vs. size at tagging for recaptures of *Chionoecetes opilio* from Conception Bay. The solid line, which indicates a 17% increase in size while at liberty, seems to separate the data into two clouds of points. Solid symbols represent animals believed to have molted once; open symbols represent animals which molted twice. Bulls-eye symbol represents one animal which was reportedly at liberty for only 29 days and which consequently was excluded from analysis.

Table 1

Regressions of length at recapture vs. length at tagging for the two groups of *Chionoecetes opilio* from Conception Bay shown in Figure 4. Lower cloud animals are presumed to have molted once; upper cloud, twice. Parameter estimates a and b pertain to equations (1) and (2) in the text.

Attribute	Lower cloud	Upper cloud
Number of observations	20	72
Adjusted r^2	0.85	0.92
Intercept (standard error)	17.250 (8.935)	12.667 (3.640)
Slope (standard error)	0.941 (0.091)	1.104 (0.039)
Interpretation of intercept	a	$a(1+b)$
Interpretation of slope	b	b^2
a	17.250	6.179
b	0.941	1.051

that the largest crabs may skip a year between molts. Thus, the information on time at liberty supports the hypothesis that animals in the lower group of Figure 4 molted once while those in the upper group molted twice.

The data in the lower group in Figure 4 appear to be well described by a linear relationship:

$$\text{Recapture size} = a + b\,(\text{size at tagging}) + e \qquad (1)$$

where e is a random error term. Suppose that equation (1) describes the size after one molt. Then the size after two molts would be given by the recursive formula (Kurata 1962):

$$\text{Size after two molts} = a + b\,(a + b\,(\text{size at tagging})) + e. \qquad (2)$$

Application of equation (2) to the size at tagging should provide a good prediction of the size at recapture for animals in the upper group if the assumption is correct that equation (1) describes the size after one molt.

We fitted lines to the two clouds of points in Figure 4 by ordinary least squares (Table 1). The results are consistent with the hypothesis of one and two molts for the two groups. For example, the fitted equation (1) (with parameters estimated from the lower cloud of points) predicts that an animal 80 mm in size will be 92.53 mm after one molt. Inserting this estimate of 92.53 mm into equation (1) gives a predicted size of 104.32 mm after another molt. In contrast, a linear regression fitted to the upper cloud of points predicts that an animal 80 mm in size will be 100.91 mm after two molts, i.e., 3.41 mm smaller than the estimate from equation (1). Similarly, the size after two molts predicted by equation (1) for a 110-mm CW animal is 130.89 mm, whereas the size predicted by the regression for the upper cloud is 134.00 mm, i.e., 3.11 mm larger. Over the range of sizes for which we have data, results from the two equations agree closely. In fact, approximate confidence bands for the size after two molts, as determined from the lower regression line, enclose the confidence bands for the upper regression line over the entire range of the data (Fig. 5; see Appendix A for derivation of approximate confidence bands). We therefore conclude that animals in the lower cloud of points molted once, while those in the upper cloud molted twice.

The regressions in Table 1 are based on 20 and 72 animals. Since the sample sizes are small, it would be useful to use the combined molting data from all 92 animals to derive a best estimate of the parameters a and b. This can be accomplished by combining equations (1) and (2) into a single equation in the form of a nonlinear regression model. Let Y be the observed size at the time of recovery, X be the size at tagging, and let Z be an indicator variable for whether an animal molted once or twice, i.e., let

$$Z = \begin{cases} 0, & \text{animal molted once} \\ 1, & \text{animal molted twice.} \end{cases}$$

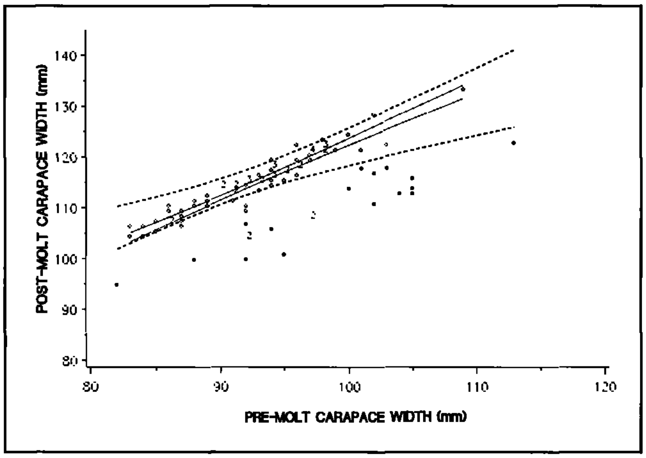

Figure 5

Recapture data for *Chionoecetes opilio* from Conception Bay. Solid symbols represent animals presumed to have molted once; open symbols represent animals which molted twice. Solid lines show the 95% confidence band obtained from the linear regression fitted to the open circle data. Dashed lines give an approximate 95% confidence band for the size after two molts based on the regression for the presumed single-molters (solid symbols). (See Appendix A for method of constructing the confidence band.) The dashed lines enclose the solid lines, indicating that the two predictions of size after two molts are not significantly different. This supports the idea that the two clouds in Figure 3 represent single- and double-molters.

Table 2

Estimates of the parameters a and b in the nonlinear regression model relating size at recapture (Y) of Conception Bay *Chionoecetes opilio* to size at tagging (X) for animals molting once or twice. The model is: $Y = a + abZ + bX + b(b - 1)ZX + e$, where e is the error term and $Z = 0$ if the animal molted once, and 1 if the animal molted twice.

Parameter	Estimate	Standard error	
a	7.398	2.074	correlation
b	1.038	0.021	−0.998

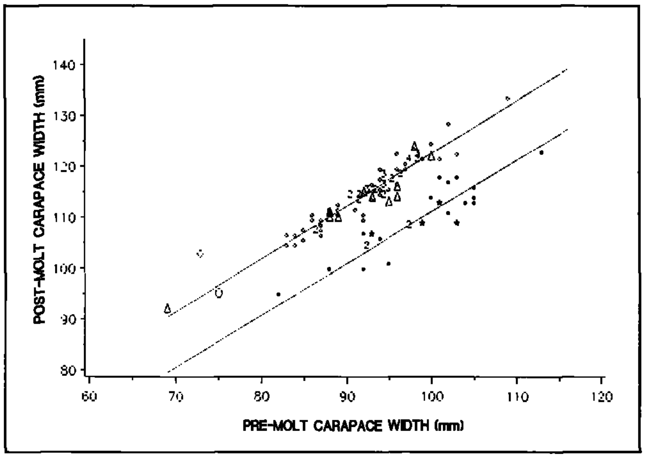

Figure 6

Plot of size at recapture vs. size at tagging for recaptures of *Chionoecetes opilio* from Conception Bay (circles) and Bonavista Bay (triangles and stars). Solid circles and stars represent animals believed to have molted once; open triangles and circles represent animals which molted twice. Diamond represents an animal from Bonavista Bay at liberty for ~1000 days which was presumed to have molted three or more times. Large circle represents an animal which normally would be assumed to have molted twice; however, it was reportedly at liberty for only 29 days and consequently was excluded from analysis. Regression lines were determined using equation (3) from all data on single and double molters from both bays.

Then the growth parameters a and b can be estimated by regressing Y on X and Z in the regression model

$$Y = a + abZ + bX + b(b - 1)ZX + e \qquad (3)$$

where e is a random error term. Equation (3) reduces to (1) when $Z = 0$ and to (2) when $Z = 1$. The model is generalized in Appendix B to account for a quadratic relationship between post- and pre-molt size. The predicted sizes from the fitted equation (3) (Table 2) are very similar to the results obtained using equations (1) and (2) separately.

Bonavista Bay

Molt information was obtained from 18 animals recaptured in Bonavista Bay. Of these, four animals appeared to have molted once; 13 animals appeared to have molted twice; and one animal at liberty for approximately 1000 days appeared to have molted three or more times (Fig. 6). This interpretation is supported by the fact that the animals presumed to have molted once were at liberty for an average of 198 days, while the animals presumed to have molted twice were at liberty for an average of 698 days.

The molt increments appeared very similar to those from Conception Bay. Since there is not much information from Bonavista Bay, we computed a regression to predict molt increments for Bonavista Bay crabs using the combined recapture data on single and double molters from Bonavista and Conception Bays. The predicted size after molting is given by

$$\text{Predicted size} = 9.21 + 1.02\,(\text{pre-molt size}).$$

Other populations

The predicted molt increments from equation (3) for Conception Bay crabs (Table 2) were very close to a constant (10.5 – 11.7 mm) over the size range of animals we studied (82–113 mm CW). These estimates are consistent with the limited information from a tagging study in the Gulf of Alaska. McBride (1982) reported the mean growth increment of six tagged snow crabs at liberty for up to 1 year was 14.7 mm. McBride's animals were somewhat larger than those in our study ($\bar{x}$ 113.8 mm, range 108–124 mm CW at tagging) and would, on the basis of our regression, be predicted to have slightly larger molt increments.

Laboratory studies of snow crab growth are also consistent with our findings. O'Halloran (1985) reported an average molt increment of 11.6 mm for eight animals. However, five of the eight animals had their eyestalks ablated bilaterally and these animals died during ecdysis. Consequently, these estimates are not very reliable. Miller and Watson (1976) and R.J. Miller (Dep. Fish. Oceans, Halifax, Nova Scotia, Canada 83J 2S7, pers. commun., June 1989) observed a mean molt increment of 15.5 mm for 18 crabs ranging in pre-molt size from 59.3 to 101.1 mm CW ($\bar{x}$ 80.5 mm). G. Hurley (Hurley Fish. Consulting, 45 Alderney Dr., Dartmouth, Nova Scotia, Canada B2Y 2N6, pers. commun., June 1989) observed a mean increment of 13.9 mm for 47 crabs, size range 60.7–83.4 mm CW ($\bar{x}$ 66.1 mm). In these studies, crabs were fed *ad libitum*. In another laboratory study, Moriyasu et al. (1987) reported a regression line that indicates that animals in the size range we studied (82–113 mm CW) have predicted molt increments of 14–16 mm CW.

Molt increments have also been estimated by size-frequency analysis for Japanese populations of snow crabs. Kon et al. (1968) reported estimates for small individuals. Ito (1970) suggested that 81-mm CW individuals molt to 97 mm, then to 111 mm and 121 mm (i.e., molt increments of 16, 14, and 10 mm). Kon (1980) suggested that 80-mm CW individuals molt to 93.4 mm, then to 105.6 and 116.7 mm (molt increments of 13.4, 12.2, and 11.1 mm). These estimates are similar to the ones we derived from the tagging data. Robichaud et al. (1989) analyzed size-frequency distributions of snow crabs from the Gulf of St. Lawrence. Their samples consisted of small animals, so their results are not comparable to the results presented here.

Effect of possible terminal molt

Some workers believe that male snow crabs undergo a "terminal" or final molt which is associated with a change in allometry. Although this idea is controversial (see Jamieson and McKone 1988 for reviews), it is worth examining whether the two groups evident in Figure 4 might reasonably be interpreted as those molting to the terminal state (e.g., lower group) and those molting but not to the terminal state (upper group). To accept this hypothesis implies that all of the following are accepted:

(1) males do, in fact, undergo a terminal molt;

(2) the size increment at the terminal molt is considerably different (presumably smaller) than the penultimate molt increment;

(3) it is a coincidence that the animals in the upper group were at liberty twice as long as those in the lower group (828 vs. 468 days on average), and that the animals which did not molt were at liberty for less than a year on average ($\bar{x}$ 322 days);

(4) it is a coincidence that the size predicted after two molts by the regression fitted to the lower cloud of points is in close agreement to the size after two molts predicted by the regression fitted to the upper cloud of points;

(5) there must be an as yet unidentified reason why a third cloud of points, corresponding to animals which molted twice, is not evident in Figure 4.

Even if males undergo a terminal molt, there is no evidence to suggest that the final molt increment is distinctly smaller than the penultimate molt increment. In an aquarium study, Moriyasu et al. (1987) found, for male snow crabs in the size range 60–70 mm CW, that animals molting to the large-clawed state have molt increments about 3 mm smaller than those molting to a small-clawed state. This small difference in molt increments is not sufficient to account for the two clouds we identified in the field observations. Ennis et al. (1988) have shown that males can become functionally mature before attaining the morphometry associated with the terminal molt. Hence, the terminal molt is not necessarily associated with a diversion of energy from growth to reproductive processes, and the terminal molt increment need not be small. We conclude that if animals undergo a terminal molt, the molt increment at this time is similar to the penultimate molt increment. We do not rule out the possibility that some of the scatter about the regressions through the two clouds of points is due to mixing terminal and non-terminal molt data.

In summary, our interpretation of the tagging data is supported by two lines of evidence. Animals presumed to have molted twice were at liberty twice as long on average as animals presumed to have molted once. Also, the predicted size after two molts, as estimated from data on animals presumed to have molted once, agrees closely with the predicted size estimated from data on animals presumed to have molted twice. We conclude that male snow crabs in the size range 75–115 mm have molt increments of around 11 mm. Our results are consistent with the limited information about snow crab growth in the literature.

Acknowledgments

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Appendix A
Derivation of Confidence Bands

The predicted size after one molt can be obtained by regressing the size at recapture on the size at tagging for those animals which molted once (text equation 1). Thus,

$$\text{predicted recapture size} = a + bX \qquad \text{(A.1)}$$

where a and b are parameter estimates and X is the size at tagging. Estimates of the variances and covariances (i.e., V(a), V(b), Cov(a,b)) are easily obtained in the standard way.

The predicted size after two molts is obtained from A.1 as

$$\begin{aligned} Y &= \text{predicted size after two months} \\ &= a + b(a + bX) = a + ab + b^2X. \end{aligned}$$

An approximate (asymptotic) estimate of the variance of the size after two months, V(Y), is found by the Taylor's series or delta method to be

$$\begin{aligned} V(Y) \doteq {} & \left(\frac{\partial Y}{\partial a}\right)^2 V\,(a) + \left(\frac{\partial Y}{\partial b}\right)^2 V(b) \\ & + 2\left(\frac{\partial Y}{\partial a}\right)\left(\frac{\partial Y}{\partial b}\right) \mathrm{Cov}(a,b) \end{aligned}$$

where the derivatives are evaluated at the parameter estimates. Thus.

$$\begin{aligned} V(Y) = {} & (1 + b)^2\, V(a) + (a + 2bx)^2\, V(b) \\ & 2(1 + b)(a + 2bx)\, \mathrm{Cov}(a,b). \end{aligned}$$

An approximate 95% confidence band is thus obtained as

$$Y \pm 2\sqrt{V(Y)}.$$

Appendix B Estimating molt increments for a quadratic model

Over the size range of animals we studied, the relationship between post- and pre-molt size appeared linear. However, when a wide range of pre-molt sizes is considered, it is common to find a curvilinear relationship which may be modeled satisfactorily by a quadratic equation. The non-linear regression model (equation 3) in the text can be generalized to allow estimation for the quadratic model.

Let the size at tagging be denoted by X, and assume the size after one molt is given by

$$\text{size after one molt} = a + bX + cX^2. \qquad \text{(B.1)}$$

Then the size after two molts is given by

$$\begin{aligned} \text{size after 2 molts} = {} & a + b(a + bX + cX^2) \\ & + c(a + bX + cX^2)^2. \qquad \text{(B.2)} \end{aligned}$$

As before, let Y be the size at recapture (for animals molting once or twice), and define Z to be an indicator variable for whether an animal molted once or twice, i.e., let

$$Z = \begin{cases} 0, & \text{animal molted once} \\ 1, & \text{animal molted twice} \end{cases}$$

Then equations (B.1) and (B.2) can be combined in a single non-linear regression as

$$\begin{aligned} Y = {} & a + (ab + a^2c)Z + bX + b(b - 1 + 2ac)ZX \\ & + c^2X + c(b + 2ac + b^2 - 1)ZX^2 \\ & + 2bc^2ZX^3 + c^3ZX^4 + e \qquad \text{(B.3)} \end{aligned}$$

where e is the random error term. Equation (B.3) reduces to (B.1) when $Z = 0$ and to (B.2) when $Z = 1$.