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

by

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Abstract

Over 6000 male snow crabs were tagging during a six-year period in Conception Bay, Newfoundland, in order to estimate the increase in size at the time of molting. Ninety-three animals were recaptured which had increased in size. Based on the amount of growth, we hypothesized that 21 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 for 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-molt 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-molt and pre-molt size. For crabs in the size range of 80-100 mm carapace width, the predicted size after molting in mm is equal to 7.398 + 1.038 (pre-molt 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.

Résumé

En six ans, on a étiqueté plus de 6 000 crabes des neiges mâles dans la baie de Conception, à Terre-Neuve, dans le but de déterminer l'accroissement de leur taille lors de la mue. Quatre-vingt trois spécimens recapturés avaient grossi. En se fondant sur l'accroissement de leur taille, on a formulé l'hypothèse que 21 de ces crabes avaient mué une fois et le restant deux fois. Cette hypothèse se fonde sur deux sortes de justification. D'abord les crabes auxquels on a attribué deux mues ont été en liberté en moyenne deux fois plus longtemps que ceux d'une seule mue présumée. Ensuite, la prévision de taille après deux mues établie au moyen d'une ligne de régression ajustée sur les données relatives aux crabes d'une mue correspond étroitement à celle que l'on obtient avec une ligne de régression ajustée en fonction des données sur les crabes de deux mues. On a conçu un modèle de régression non linéaire pour estimer les paramètres du rapport entre les tailles antérieure et postérieure à la mue, en combinant les données sur les crabes d'une et de deux mues. Cette méthode a été généralisée de manière à englober un rapport quadratique entre les tailles antérieure et postérieure à la mue. Pour les crabes dont la largeur de la carapace est de l'ordre de 80 à 100 mm, la taille prévue (en mm) après la mue équivaut à 7 398 + 1 038 (taille préalable à la mue). Une étude semblable réalisée dans la baie de Bonavista, également à Terre-Neuve, a permis d'obtenir des données sur la croissance de 18 crabes, révélant un grossissement du à la mue est comparable à celui que l'on a observé dans la baie de Conception.

INTRODUCTION

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 deep-water 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 180m. The bottom type in these areas is predominantly mud or muddy sand with mean bottom temperatures ranging from -1.3 to 0.5C. Since the mid 1970's 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 <180m, the deeper commercial fishing grounds appear to have the soft substrate necessary for snow crab molting.

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 ranging in size from 56 to 135 mm carapace width (CW). An additional 2253 male crabs, ranging in size from 45 to 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 Manufacturing Company, Inc., P.O. Box 5377, 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

Repeated measurements by a biologist of a group of crabs were always within one mm of the mean for each animal. Workers studying other species of large crustacea have suggested that measurements can be 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; 3 had increases of 4 to 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. 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 size of Conception Bay crabs at recapture was plotted against the size at tagging and two distinct, linear clouds of points were apparent (Fig. 3). 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-molter group was at liberty for only 29 days. It is believed that animals remain soft-shelled for two to three months after molting and that soft-shelled animals cannot molt. For this reason, this animal was eliminated from further consideration.

The times at liberty for 82 of the 92 Conception Bay animals 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. 4). 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 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 molted once while those in the upper group molted twice.

The data in the lower group in Figure 3 appear to be well described by a linear relationship:

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

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)

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

Application of equation (2) to the size at tagging should provide a good prediction of the size at recapture for animals in group two 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 (3) 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, the fitted equation (2) (with parameters estimated from 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 equation (2) is 134.00 mm, i.e. the estimate from equation (2) is 3.11 mm larger. Over the range of sizes for which we have data, results from equation (1) agree closely with results from equation (2) (Figure 5). 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

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

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

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

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 the appendix to account for a quadratic relationship between post-molt 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 also 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 (Figure 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 molt increments are given by

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

DISCUSSION

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 one year was 14.7 mm. McBride's animals were somewhat larger than those in our study (mean 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 Miller (R.J. Miller, Department of Fisheries and Oceans, P.O. Box 550, Halifax, Nova Scotia, Canada B3J 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 (mean 80.5 mm). Hurley (G. Hurley, Hurley Fisheries Consulting, Suite 815, Queens Square, 45 Alderney Drive, Dartmouth, Nova Scotia, Canada B2Y 2N6, pers. commun. June 1989) observed a mean increment of 13.9 mm for 47 crabs ranging in size from 60.7-83.4 mm CW (mean 66.1 mm). In these studies, crabs were fed *ad libitum*. Moriyasu et al. (1987) also studied growth in the laboratory; their regression line predicts a molt increment of 15.1 mm for animals 100 mm cw at the time of molting. These animals developed large claws at the molt.

Molt increments have also been estimated by length 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 length-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.

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 comprehensive reviews), it is worth examining if the two groups evident in Figure 3 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 coincidence that the animals in the upper group were at liberty twice as long as those in the lower group, on average

4) it is 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 3.

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. 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. Moriyasu et al. (1987) studied molting of snow crabs in the laboratory and found that the molt increment at the time of supposed terminal molt is about 4 mm smaller than the normal molt increment for animals around 60 - 70 mm cw. We conclude that, if animals undergo a terminal molt, the molt increment at this time is similar to the penultimate molt increment. Thus, it is possible that some of the scatter about the regressions 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 from 75 to 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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Table 1. Regressions of length at recapture versus length at tagging for the two groups of animals from Conception Bay shown in Figure 3. Group I animals are presumed to have molted once; Group II, twice. Parameter estimates *a* and *b* pertain to equations (1) and (2) in the text.

attribute	Group 1	Group 2
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

Table 2. Estimates of the parameters *a* and *b* in the nonlinear regression model relating size at recapture (Y) of Conception Bay animals 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 is zero if the animal molted once and one if the animal molted twice.

parameter	estimate	standard error	
a	7.398	2.074	correlation
b	1.038	0.021	-.998

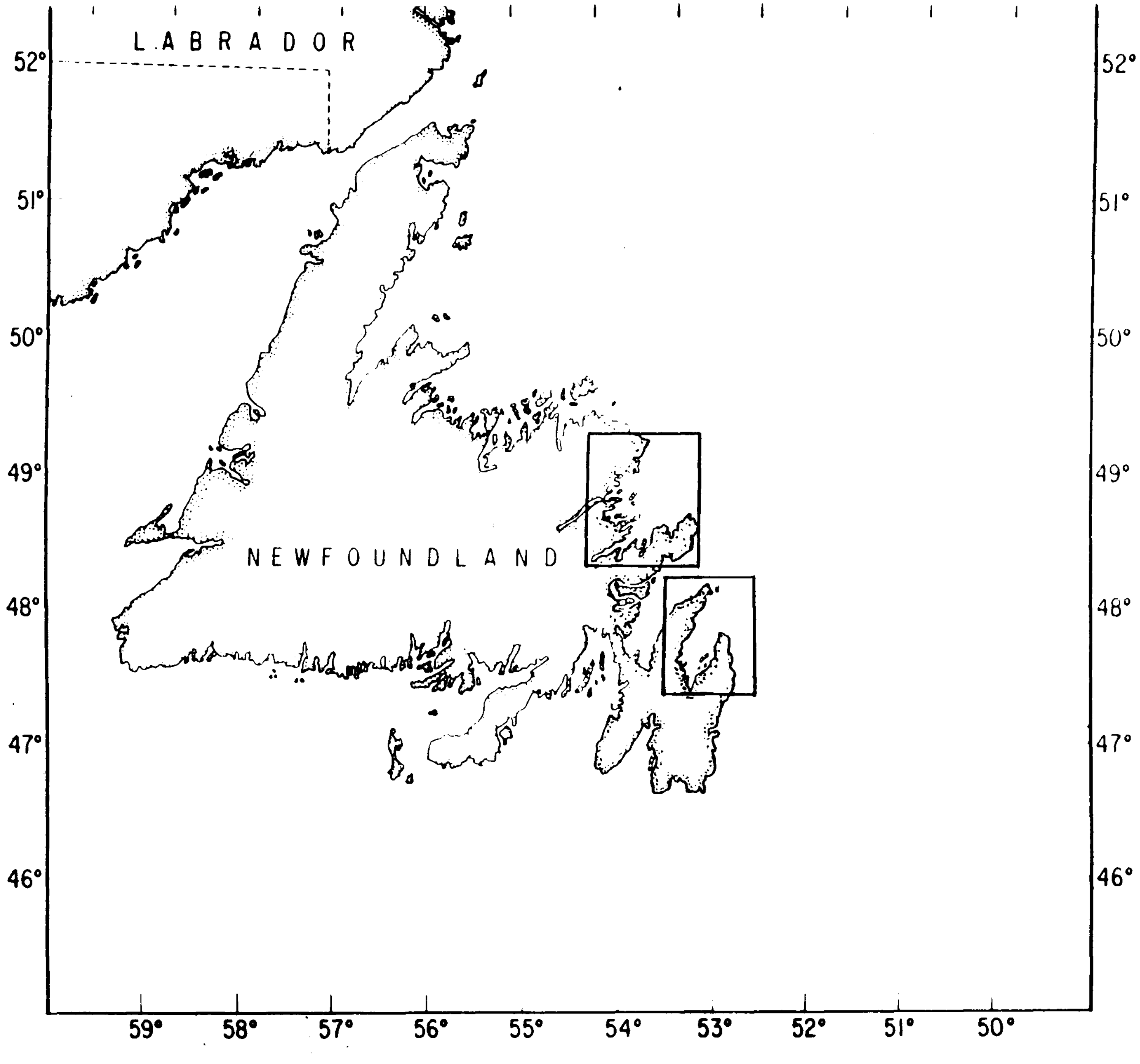


FIGURE 1.-Map of Newfoundland, Canada, showing the location of Conception Bay (lower box) and Bonavista Bay (upper box).

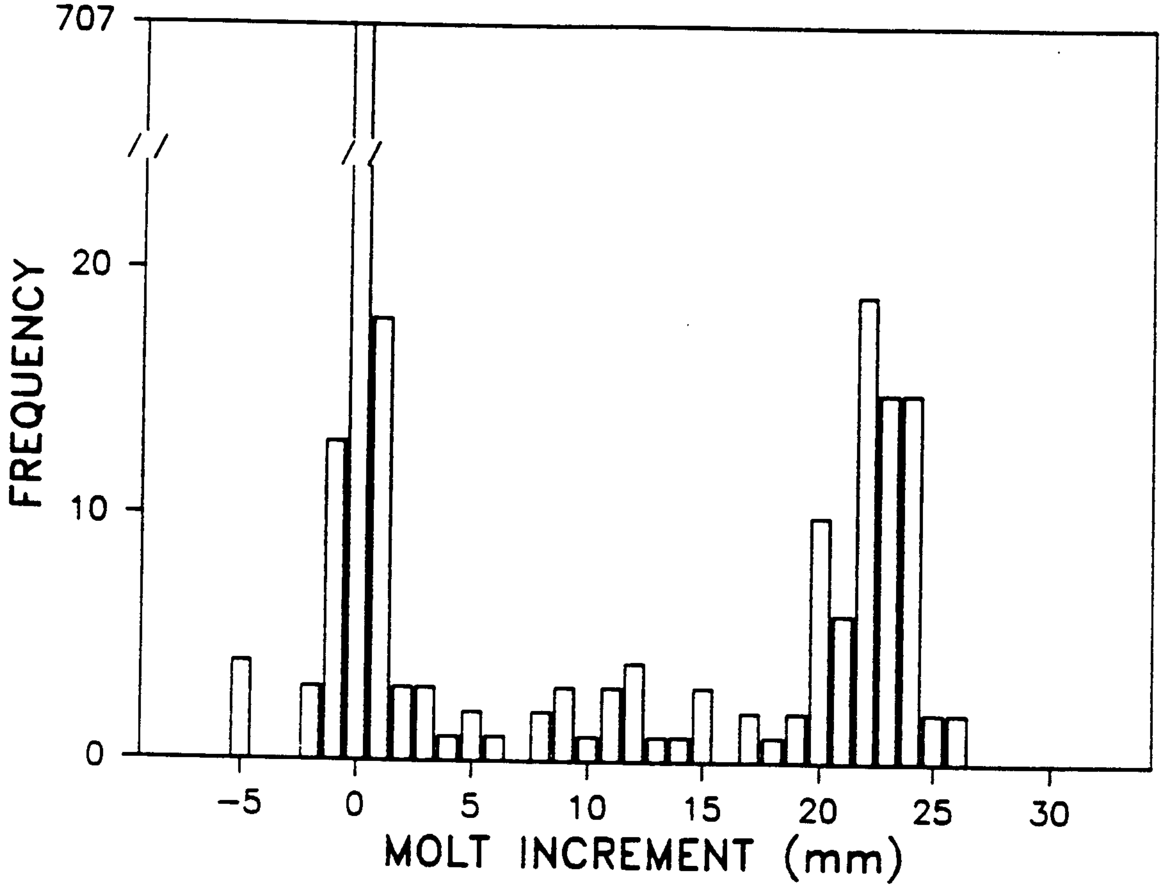


FIGURE 2.-Frequency of occurrence of growth increments for recaptures from Conception Bay.

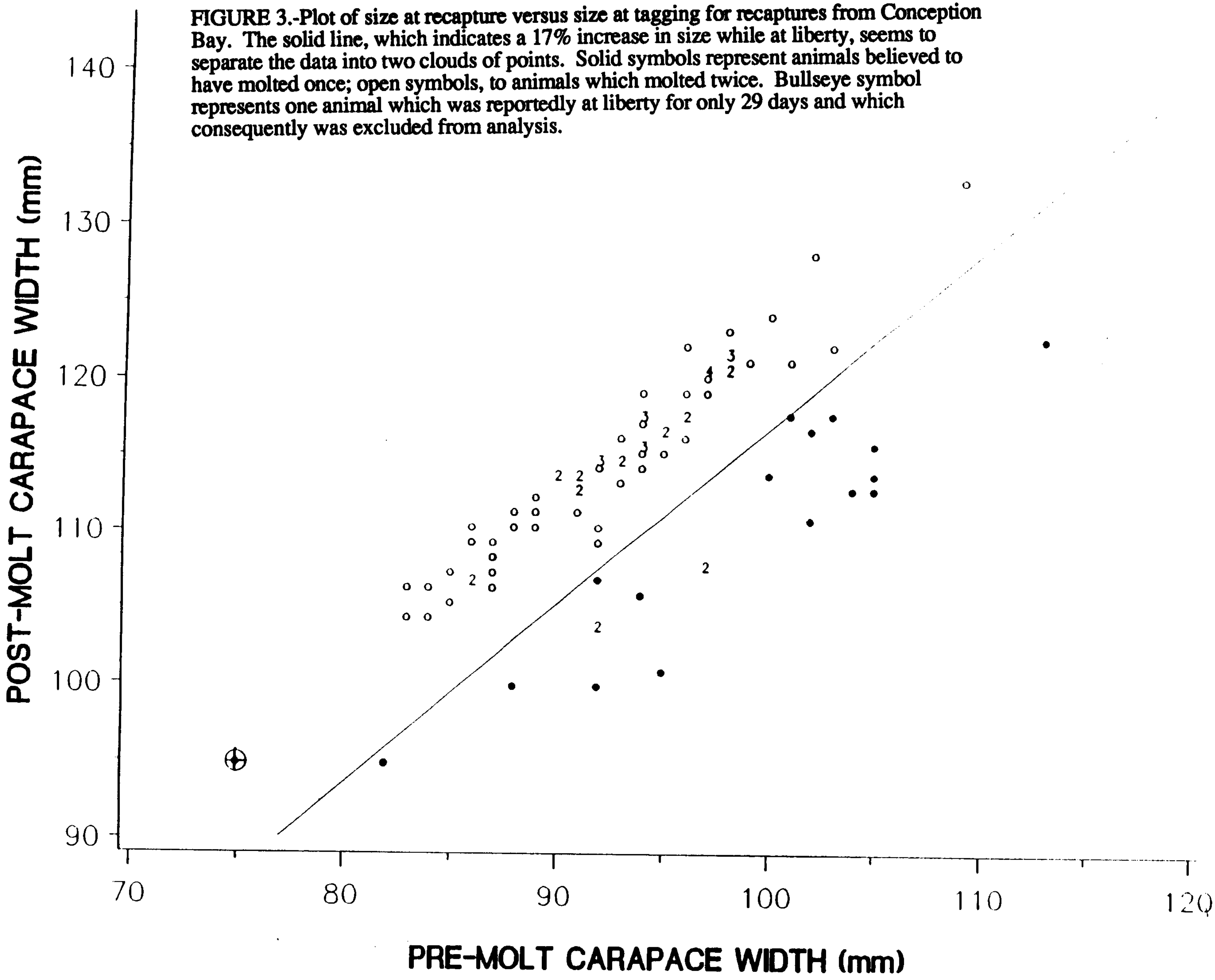
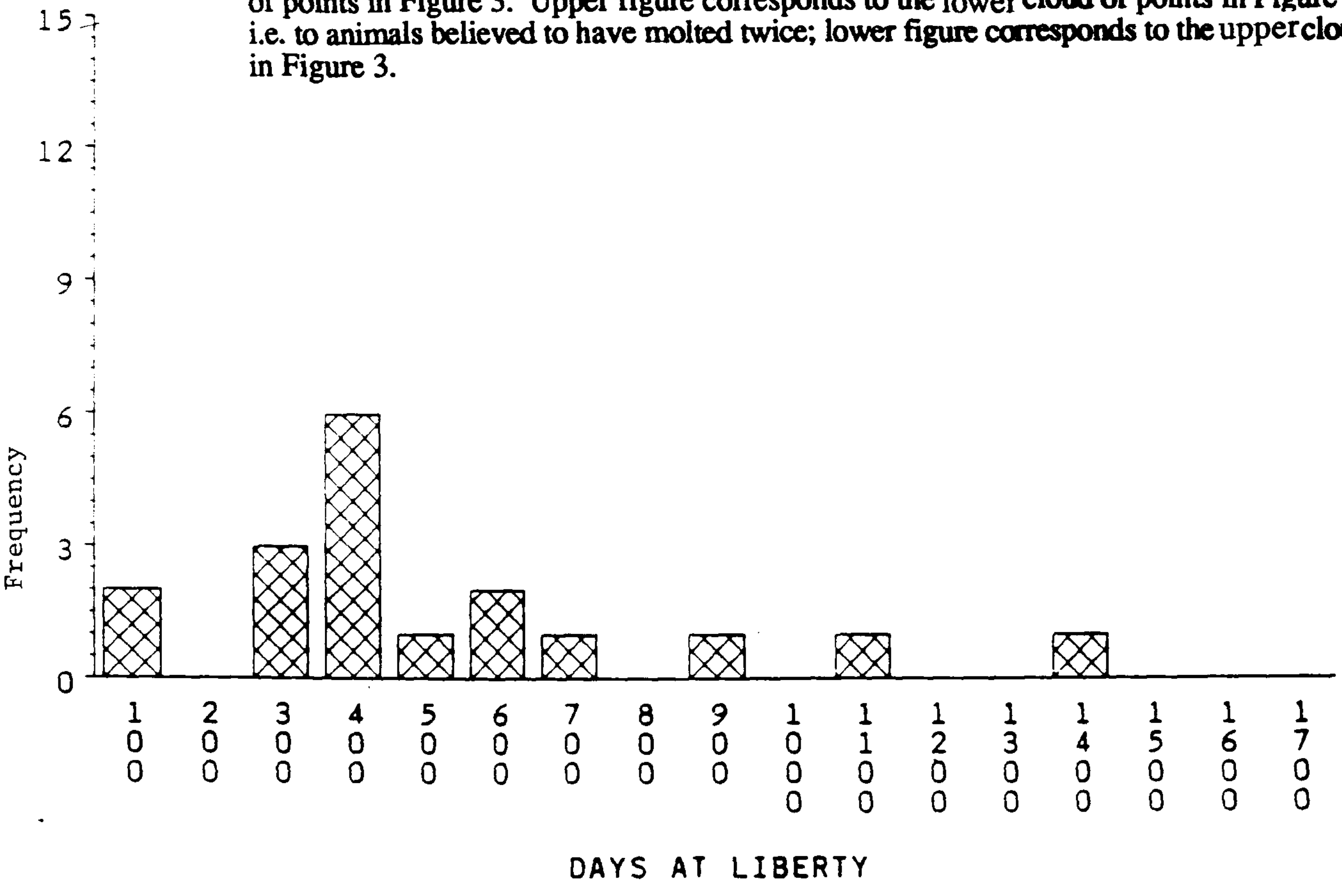


FIGURE 3.-Plot of size at recapture versus size at tagging for recaptures from Conception Bay. The solid line, which indicates a 17% increase in size while at liberty, seems to separate the data into two clouds of points. Solid symbols represent animals believed to have molted once; open symbols, to animals which molted twice. Bullseye symbol represents one animal which was reportedly at liberty for only 29 days and which consequently was excluded from analysis.

FIGURE 4.-Histograms of times at liberty for Conception Bay animals in the two clouds of points in Figure 3. Upper figure corresponds to the lower cloud of points in Figure 3, i.e. to animals believed to have molted twice; lower figure corresponds to the upper cloud in Figure 3.



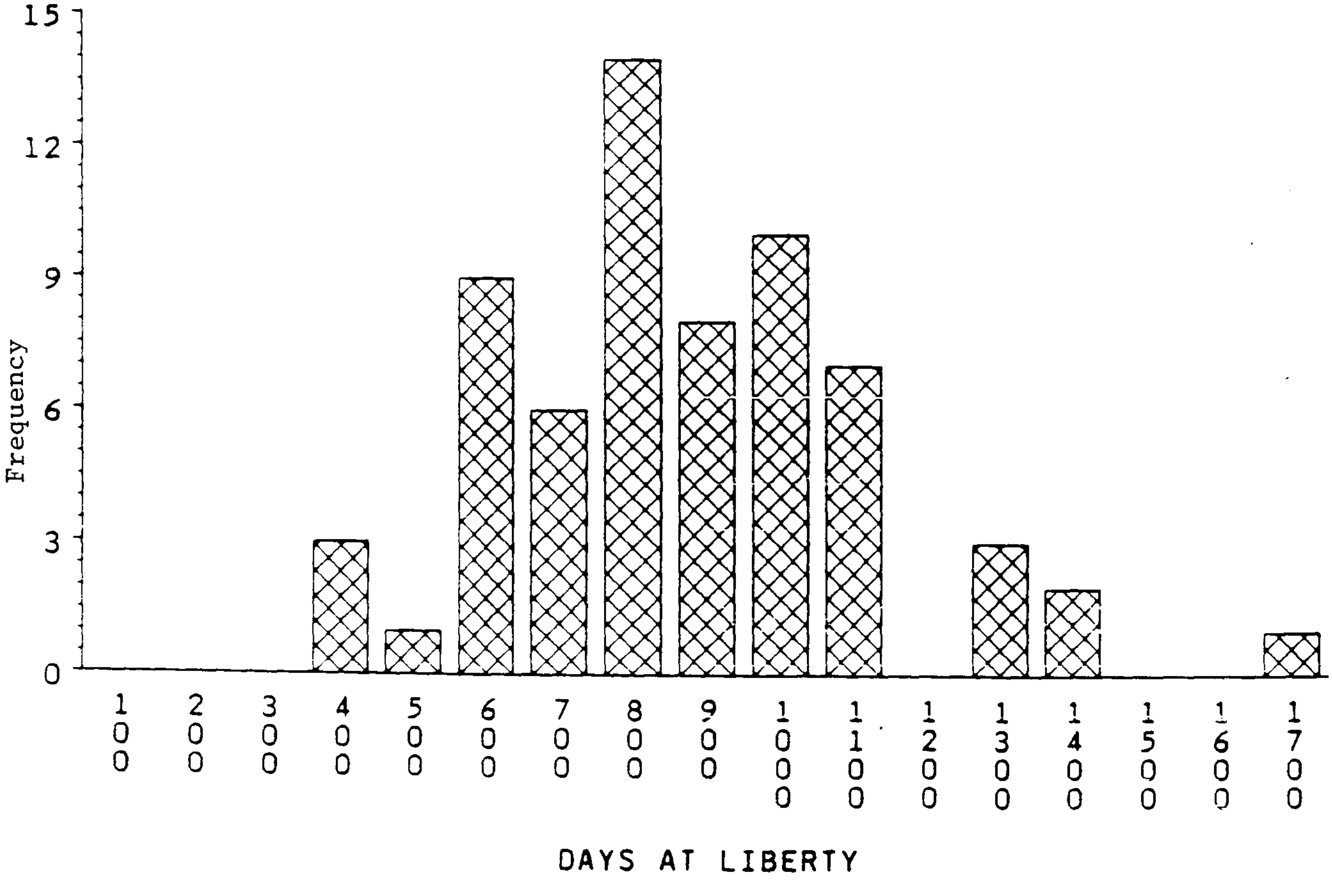


FIGURE 5.- Recapture data from Conception Bay. Solid line in lower part of the figure is the regression line fitted to animals presumed to have molted once; large-dashed line in upper part of the figure gives the predicted size after two molts based on the regression line fitted to single-molters. Solid and dotted lines in the upper part of the figure show the regression line and associated 95% confidence band obtained from animals presumed to have molted twice. The large-dashed line based on presumed single-molters is close to the solid line obtained from presumed double-molters. This supports the idea that the two clouds in Figure 3 represent single- and double-molters.

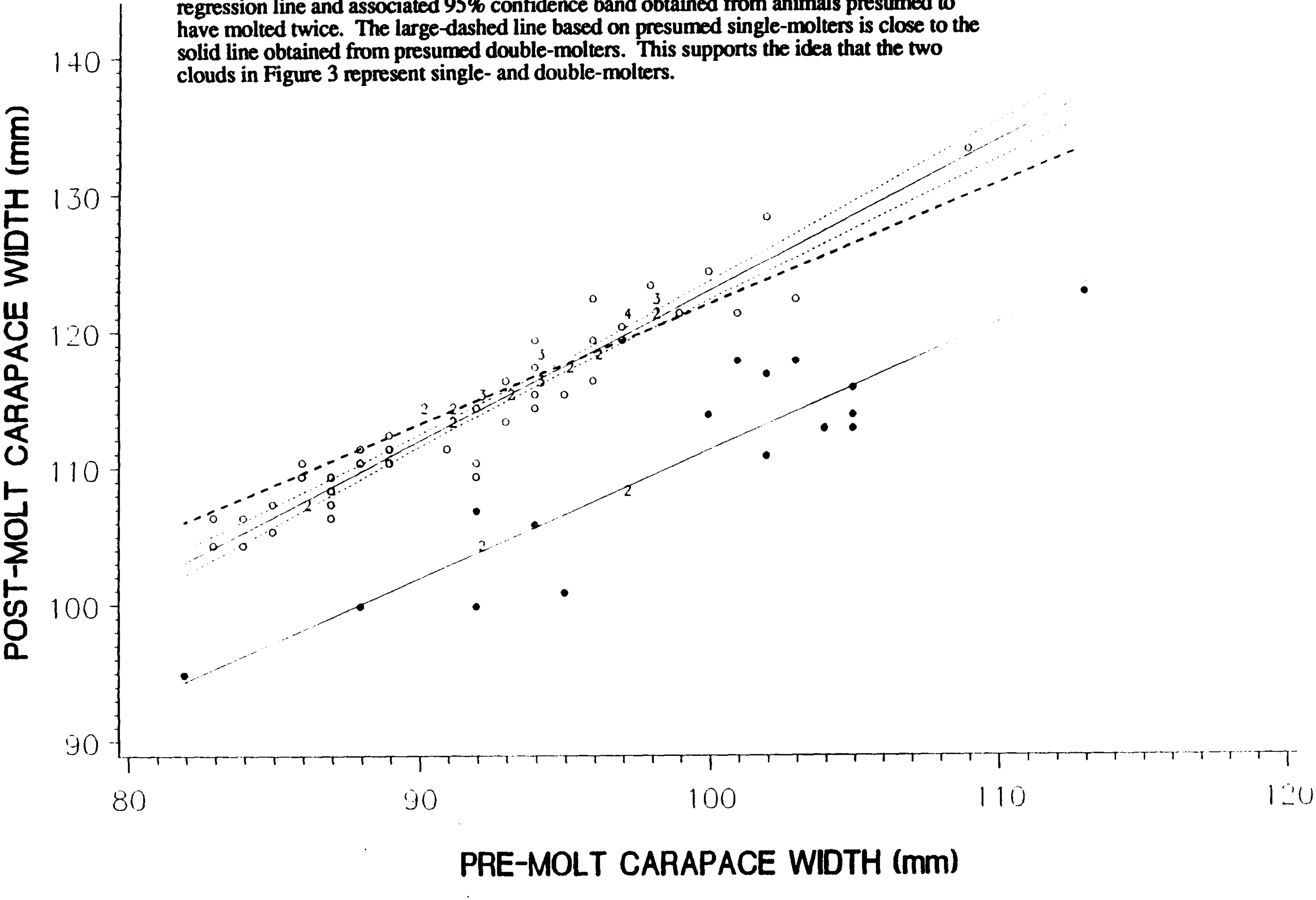
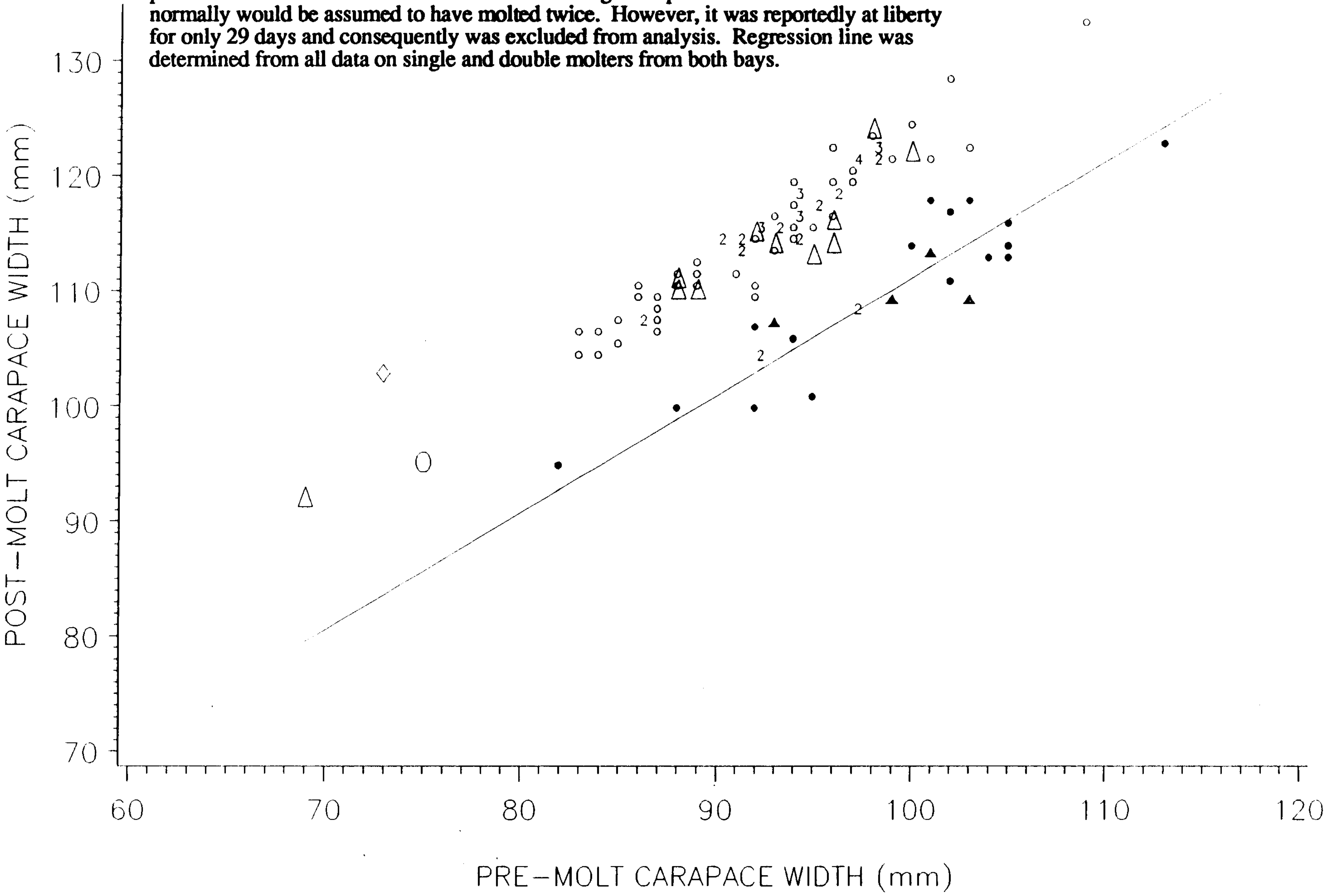


FIGURE 6.-Plot of size at recapture versus size at tagging for recaptures from Conception Bay (circles) and Bonavista Bay (triangles). Solid symbols represent animals believed to have molted once; open triangles and circles, to animals which molted twice. Diamond represents an animal from Bonavista Bay at liberty for approximately 1000 d which was presumed to have molted three or more times. Large O 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 line was determined from all data on single and double molters from both bays.



Appendix. Estimating Molt Increments for a Quadratic Model

Over the size range of animals we studied, the relationship between post-molt 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

$$\text{size after 1 molt} = a + b\mathrm{X} + c\mathrm{X}^2 . \tag{A.1}$$

Then the size after two molts is given by

$$\text{size after 2 molts}$$

$$= a + b(a + b\mathrm{X} + c\mathrm{X}^2) + c(a + b\mathrm{X} + c\mathrm{X}^2)^2 . \tag{A.2}$$

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

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

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

$$\mathrm{Y} = a + (ab + a^2 c)\mathrm{Z} + b\mathrm{X} + b(b - 1 + 2ac)\mathrm{ZX} + c^2\mathrm{X}$$

$$+ c(b + 2ac + b^2 - 1)\mathrm{ZX}^2 + 2bc^2\mathrm{ZX}^3 + c^3\mathrm{ZX}^4 + e \tag{A.3}$$

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