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**A Critical Look at the Idea of Terminal Molt in
Male Snow Crabs (*Chionoecetes opilio*)**

by

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ABSTRACT

The question of whether or not male snow crabs undergo a terminal molt, in concert with the development of large chelae, has important implications for stock assessment. We reviewed the available information and conclude that the published evidence in favor of terminal molt is not compelling. Claims concerning degeneration of the Y-organ and failure of large-clawed animals to regenerate limbs appear to be unsubstantiated. There is one report of a large-clawed male snow crab molting while in captivity. We present new data which contradict the idea of a terminal molt including: 1) we recovered two tagged animals which molted while at liberty but which clearly had large claws at the time of tagging, 2) the largest small-clawed animals often do not appear to be large enough or numerous enough to account (through growth attributable to a single molt) for the occurrence of the largest of the large-clawed animals, 3) we found two large-clawed males with well developed second (internal) carapaces indicating impending molts, and 4) we found two large-clawed animals with mouth parts that indicated active premolting status (stage D_1). We find identification and interpretation of the D_0 stage (beginning of premolt) unclear, as do other workers; hence, the occurrence or absence of the D_0 stage does not shed light on the question of terminal molt. We conclude that the evidence does not support the idea of a terminal molt in male snow crabs and that there is some direct evidence against terminal molt. Considerable work is necessary to arrive at a valid quantitative assessment of molting prevalence for large-clawed males.

RESUME

La question de savoir si, chez le crabe-des-neiges mâle, la mue accompagnant la formation de gros chélicèdes est la dernière que subit l'animal revêt une grande importance pour l'évaluation des stocks. Après avoir étudié les documents existant à ce sujet, nous en arrivons à la conclusion que les arguments militant en faveur d'une mue finale ne sont pas probants. Les assertions au sujet de la dégénérescence de l'organe Y et du fait que les animaux à grosses pinces ne régénèrent pas leurs membres ne semblent pas fondées. On a signalé un cas de crabe-des-neiges à grosses pinces qui a mué en captivité. Nous présentons ici des données nouvelles qui contredisent l'hypothèse d'une mue finale : 1) nous avons recapturé deux crabes marqués qui, quoique possédant manifestement leurs grosses pinces au moment du marquage, avaient mué pendant qu'ils étaient en liberté; 2) les plus gros des crabes à petites pinces ne semblent souvent pas assez gros ou pas assez nombreux pour que l'existence des plus gros des crabes à grosses pinces soit imputée à la croissance qui accompagne une seule mue; 3) nous avons découvert deux crabes à grosses pinces munis d'une deuxième carapace (interne) bien développée, révélant une mue imminente; et 4) nous avons également découvert deux crabes à grosses pinces dont les parties buccales révélaient une activité préalable à la mue (stade D_1). Comme d'autres chercheurs, nous estimons que l'identification et l'interprétation du stade D_0 (début de la prémue) restent obscures; par conséquent la présence ou l'absence de stade D_0 ne règle pas la question de la mue finale. Nous concluons donc qu'il n'y a pas de preuve de l'existence d'une mue finale chez les crabes-des-neiges mâles, qu'il y a certaines preuves directes de sa non-existence et que, dans le meilleur cas, la théorie reste à être démontrée. Des travaux considérables seront nécessaires pour en arriver à une évaluation quantitative valable de la fréquence des mues chez les mâles à grosses pinces.

Introduction

The idea that male snow crabs (*Chionoecetes opilio*) undergo a terminal molt, associated with the development of large chelae, was put forth by Conan and Comeau (1986) and defended in Conan et al. (1988a) and Conan et al. (1988b). Donaldson and Johnson (1988) and Donaldson (1988) reviewed the aforementioned works and suggested that male snow crabs do not undergo a terminal molt. An international workshop on snow crab biology obtained a "consensus" that male *C. opilio* "are now considered to have a terminal molt" (Jamieson et al. 1988 p. viii). However, at least seven of the workshop participants remain unconvinced. In the rest of this paper, the term "snow crab" refers to *C. opilio*.

Terminal molt means, according to Conan and Comeau (1986 p. 1718), that large-clawed males "extremely seldom, if ever, molt". We take this to mean that the event rarity is on a par with the rarity of gynandromorphic crabs, albino lobsters, and pug-headed fish. The alternative is that large-clawed males molt commonly although possibly less frequently than small-clawed males. It is generally assumed that intermolt period increases with body size, e.g. the exponential model

$$\text{intermolt period} = a e^{b \cdot \text{body size}} \cdot \epsilon$$

where a and b are positive constants and ϵ is a lognormally distributed error, has sometimes been suggested for crustaceans (Mauchline 1977; Hoenig and Restrepo 1989). Since large-clawed males tend to have larger bodies than small-clawed males, one would expect that large-clawed males have longer intermolt periods than small-clawed males on average. Thus, the accumulation of old-shelled animals among the largest animals in the population does not necessarily imply a terminal molt. A more difficult refinement would be to determine whether or not the intermolt periods of large-clawed males are prolonged beyond that which can be attributed to larger body size. A final point is that, in the above exponential model, the random variability in intermolt period increases with body size. This suggests that a tagging study is likely to find some large-clawed males molting in short periods of time and some failing to molt in large periods of time. Hence, a great deal of effort might be required to get an accurate picture of intermolt periods.

Conan and Comeau (1986) also proposed that reproductive ability is directly related to the development of the large claw. However, Ennis et al. (1989b) have refuted much of their conclusions (see also Elner and Benninger 1989; Ennis et al. 1988, 1989a). Although questions of reproductive ability are important, they are not considered here. We avoid the confusion attributable to use of the terms "morphometrically" and "functionally" mature and immature and use, instead, the terms large-clawed and small-clawed to describe relative claw size of individual males.

The question of whether terminal molt exists has important implications for stock assessment. If only small-clawed animals molt, then a significant proportion of the sub-legal sized population (with large claws) may never reach legal harvest size. Variability in size at terminal molt would then be important for computing yield per recruit and also for determining the expected number of times a male mates during its life.

Lack of definitive results concerning the existence of terminal molt is expensive in terms of the uncertainty in management advice, the necessity of assessing stocks under both the assumption of a terminal molt and the lack of a terminal molt, and finally, in terms of the research necessary to settle the question. For example, considerable effort has been

expended on a tagging study in Conception Bay, Newfoundland, in an effort to obtain definitive results.

In this paper, we review the published evidence on terminal molt in male snow crabs and present new data bearing on the problem. Emphasis is placed on determining the kinds of data, and the logical arguments, which will resolve the issue.

Statistical Evidence - Principal Components and Discriminant Functions

A major portion of the first paper on terminal molt in male snow crabs (Conan and Comeau 1986) was devoted to a principal component analysis and linear discriminant analysis. Conan and Comeau measured six size variables on crabs and computed the principal components on log-transformed data. When the crab data were plotted on the first two principal components, they fell in two clouds of points. Conan and Comeau assigned each animal to a cloud but it is not clear from their paper how they did this. They apparently either assigned animals to groups according as the observation was above or below the first principal component axis (the abscissa) or according as the observation was above or below an unspecified diagonal line. Either way, the separation was arbitrary since there was no concomitant information (ground truth) with which to establish a biological basis for defining categories. Thus, animals "in the middle" were not assigned to groups on the basis of any biological or statistical argument; the method of assigning animals to groups did not allow for any overlap of the distributions. Conan and Comeau noted that when measurements from additional males, caught by divers while the animals were in the process of mating, were plotted on the first two principal component axes all the animals fell into one cloud. They therefore suggested that these two clouds pertain to "mature" and "immature" animals (but see Ennis et al. 1989b). They then showed that, having assigned the animals to groups, they could duplicate the partition of the data with close to 100% accuracy using just two variables (chela height and carapace width). This shows only that four of the size variables are redundant. Specifically, the discriminant function analysis does not "confirm" the validity of the groupings from the principal component analysis. These two analyses succeed in showing that there are two clouds or groups of animals (large-clawed and small-clawed). This result is obvious from a scatter plot of the data and, as acknowledged by Conan and Comeau (1986), has been demonstrated by Powles (1968), Watson (1970), and Coulombe et al. (1985). The analysis also shows that a sample of breeding males from Bonne Bay fell in the cloud with large claws.

Note that an estimated misclassification rate for the discriminant function analysis pertains only to the reliability of the two-variable method for reproducing the arbitrary partition based on six variables. Similarly, the calculation of the probability of an animal falling into a particular group, as described by Conan and Comeau, pertains to the groups defined subjectively by Conan and Comeau. We belabor the point only to make it clear that these methods provide no objective, quantitative guidance in determining to which biological group a borderline data point has the greatest affinity. (A statistical method [mixture analysis] could be developed for determining the probability that a data point falls in a given statistical group, where the statistical groups are defined as the components of a mixture of two normal distributions. If one could assume that these statistical populations represent biological groups, then one would have an objective method for separating animals using statistical principles.)

Some other points should be made about Conan and Comeau's use of statistics. 1) They state that normality and homogeneity of variance are necessary conditions for the valid application of principal component analysis, and they used logarithmic transformation to achieve this. However, since principal component analysis is used as an exploratory

data-analytic technique, it is not necessary to assume normality or homogeneity of variance. (Linear discriminant functions are derived under these assumptions.) (See Morrison 1976.) 2) They assumed allometric (power function) relationships among body parts (see also Conan et al. 1988b), and indeed, the logarithmic transformation appeared to be successful in linearizing the relationship between chela height and carapace width over the range of data they had. However, our observations show that the linear relationship breaks down when a wider size range is considered (Figure 1). Hence, the allometric model does not appear to have much theoretical value. 3) The misclassification rate estimated by Conan and Comeau (1%) for the discriminant analysis is likely too optimistic because the linear discriminant classification rule was tested on the same data from which it was derived. A better approach is to use cross-validation (see Efron and Gong 1983), a leave-one-out sample reuse technique. Older techniques, which involve dividing the data into training and checking subsets, also provide reasonably good results.

To summarize, we find that the principal component analysis and linear discriminant analysis used by Conan and Comeau (1986) demonstrated that the data appear to fall into two groups associated with claw size, and that two variables are sufficient to see this natural grouping. There is no basis for judging the biological significance of these groups, i.e. for judging if the assignments to groups are consistent with any biological characteristics, because the animals did not come *a priori* from any known biological groups (i.e. there was no "ground truth" based on physiological, morphological, or behavioral characteristics). The analyses therefore do not provide any guidance for assigning borderline observations to biological groups. It is clear that these analyses do not provide any evidence for or against the theory of terminal molt.

Molting in Captivity

Conan and Comeau (1986) kept 110 large-clawed and 24 small-clawed males in the laboratory for 10 months from November, 1984, to September, 1985. All animals were "of the same size range", but the sizes were not specified. The shell conditions of the experimental animals were not given and no details of the experimental conditions (holding facilities, density of animals, etc.) were given. None of the 110 large-clawed males molted while 16 of the 24 small-clawed males (67%) molted. These results are difficult to accept at face value for several reasons.

1) If the large-clawed males were larger on average than the small clawed males, then a smaller proportion of the large-clawed animals would be expected to molt than of the small-clawed animals in the 10 months of the study. Large animals may have intermolt periods in excess of two years. Similarly, if the large-clawed group had a higher proportion of new-shelled animals than the small-clawed group, then one would expect a smaller proportion of the large-clawed group to molt. Finally, if large-clawed animals were held in more crowded conditions, or under conditions that were in some way less suitable, than the conditions under which the small-clawed crabs were held, then a smaller proportion of the large-clawed animals would be expected to molt. It is impossible to resolve these questions from Conan and Comeau's paper and, at any rate, such experiments are of limited value if the duration is as short as 10 months.

2) If the small-clawed animals had small carapaces, then one would expect them to molt every year so that close to 100% of the animals should have molted. Since only 67% of the small-clawed animals molted, this could be indicative of stress. (Conan and Comeau did not mention if any of the animals died during the experiment, e.g. while molting. However, in their reply to Donaldson and Johnson (1988), Conan et al. (1988a) describe subsequent aquarium work in which an unspecified proportion of small-clawed males died

either within the first six months of captivity or while in the process of molting.) If large-clawed animals are more "fussy" about the environmental conditions necessary for molting, then stressful conditions of captivity may have inhibited molting activity of the large-clawed animals.

Foyle (1987) kept 22 large-clawed male crabs in captivity for approximately 11 months. One crab molted. Its morphometry was: 92.8 mm carapace width, 18 mm chela height, 15.8 mm chela width.

In summary, interpretation of results from aquarium studies is difficult because of the possibility that artificial conditions of captivity affect the animals' behavior and physiology. Additionally, Conan and Comeau do not provide the necessary information on experimental conditions and experimental subjects to judge their experiment. Foyle (1987) reported one large-clawed male which molted in captivity.

Composition of Lightly Exploited Populations

Donaldson (1988) examined the types of conclusions that could be drawn from examination of the composition, by shell condition, of wild populations of males. He proposed two arguments.

Donaldson's First Argument

Donaldson reasoned that, if terminal molt exists, then among the largest body size classes in an unexploited or lightly exploited population there should be a buildup of old-shelled animals. This was not observed in the early years of the commercial fishery in the Southeast and Pribilof Districts of the Bering Sea, Alaska. Donaldson (1988 p. 104) reported:

year	effort pots lifted	landed weight (t)	% old-shell
1977-78	13,247	778.4	not available
1978-79	190,746	14,225.6	17.0%
1979-80	255,022	17,950.0	10.0%
1981	435,742	23,937.3	20.8%

Although the above figures refer to large and small-clawed animals combined, the proportion of old-shelled animals was also very low among the largest crabs (presumably large-clawed) captured in the National Marine Fisheries Service (NMFS) Bering Sea trawl surveys. These results suggest that large animals must be molting.

Donaldson's conclusion requires three assumptions: 1) that natural (or total) mortality is low so that animals don't die off before they have a chance to become old-shelled, 2) that conditions approximate a long-term steady-state, and 3) that large males are not capable of cleaning their shells of epibionts by scratching their backs with their claws, and thus appearing not to be old-shelled.

Natural mortality (assumption #1) is poorly known but is apparently quite low. The proportion of old-shelled animals among the large-clawed animals that would be expected for a given mortality rate can be computed as follows (under the assumption that

terminal molt exists). Let the annual survival rate $S (= e^{-Z})$ be constant for all large-clawed animals and assume equilibrium conditions (constant recruitment and constant mortality over time). Further, assume that it takes two years from the time of molting for an animal to develop an old shell. Then, if recruitment (to the population of large-clawed animals) is denoted by R , the number of new-shelled, large-clawed animals will be given by

$$\text{number of new-shelled, large-clawed animals} = R + RS .$$

The total number of large-clawed animals will be

$$\text{number of large-clawed animals} = R + RS + RS^2 + RS^3 + \dots$$

Hence, the proportion of new-shelled males among the large-clawed males will be

$$\begin{aligned} \text{proportion new-shelled} &= \frac{R + RS}{R + RS + RS^2 + RS^3 + \dots} \\ &= \frac{1 + S}{1 + S + S^2 + S^3 + \dots} \end{aligned}$$

The denominator of the above can be simplified to $\frac{1}{1 - S}$. Hence, the proportion of new-shelled males among the large-clawed males will be

$$\text{proportion new-shelled} = (1 + S)(1 - S) = 1 - S^2$$

and the proportion of old-shelled animals among the large-clawed animals will be

$$\text{proportion of old-shelled animals} = S^2 .$$

Thus, the expected proportion of old-shelled animals among those with large claws under the assumption of terminal molt is:

Z	S	proportion old-shelled	Z	S	proportion old-shelled
0.1	0.91	0.82	0.5	0.61	0.37
0.2	0.82	0.67	0.6	0.55	0.30
0.3	0.74	0.55	0.7	0.50	0.25
0.4	0.67	0.45	0.8	0.45	0.20

To explain the 10-20% old-shelled animals reported by Donaldson, one would need to assume an instantaneous mortality rate of $Z \geq 0.8 \text{ yr}^{-1}$ if terminal molt exists. This seems too high to be plausible.

Assumption #2 of near steady-state means, for example, that the absence of old-shelled large animals is not due to an epizootic or other natural catastrophe. The fact that Donaldson presented eight years of data seems to eliminate the possibility that approximate steady-state was not met (but see also below).

Finally, concerning assumption #3, Conan (personal observations, cited in Conan et al. 1988b p. 48-49) stated that "the relative cleanliness of the shell of the males is simply explained by the fact that males can reach the top of their carapace with their claws, while the shorter claws of the females do not allow them to remove epibionts such as sea anemones from the top of their carapaces". We examined commercial size (≥ 95 mm cw) males and found that only one third of the top of the carapace could be reached by the claws when light pressure was exerted on the claws; when sufficient pressure was applied to the claws to force them to the back of the carapace about one half of the carapace could be reached; however, it was difficult to effectively clean the shell with the claws in such an awkward position. We conclude there is no way a male snow crab can use its claws to clean its upper carapace. Also, the old-shelled condition is not defined solely by the presence of epibionts - old-shelled crabs have a darker carapace color and numerous scratches on the underside of the carapace.

Donaldson's (1988) data on population composition appear to be the most extensive available. Another data set, from Bonne Bay, Newfoundland, appears to represent another situation. This population had a very high percentage of old-shelled, large males in the mid 1980s (Ennis et al. 1989b), which would be consistent with the idea of a terminal molt. However, the population may not have been in a long-term equilibrium. For example, if a successful year class or set of year classes dominated the population then one would expect that when these year classes reached old age they would have a very low molting frequency which could give the appearance of a terminal molt. Over the 6 years the population has been observed, there appears to have been a large decline in the population of large and old-shelled males, followed by a pulse of recruitment. Also, the sampling method used was for divers to collect mating pairs. This sampling method may be biased towards the largest (reproductively most successful) animals which, because of their size, molt infrequently and are likely to have old shells (see Conan and Comeau 1986 p. 1718).

Donaldson's Second Argument

Donaldson's (1988) second argument is that, if terminal molt does not exist and if environmental conditions are unfavorable for molting in a given year (i.e. there is an unusually high incidence of "skip-molting"), then the proportion of old-shelled animals should rise; the following year, if environmental conditions return to normal, the old-shelled animals should molt and the proportion of old-shelled animals should decline. Conditions consistent with this scenario were observed from 1978-1981 and 1985-1987 (see Figures 2 and 3). Taylor et al. (1990) also noted that in some years in Newfoundland molting activity is reduced and he attributed this to unusually cold water temperatures. Thus, there is ample reason to believe that some years may have abnormally low incidences of molting. An alternative explanation for an increase in old-shelled animals in one year, followed by a decline in the next, is that there could be recruitment failure in the first year followed by normal or above average recruitment in the next year. Thus, if the alternative explanation is true, one should be able to detect a trough in the length frequency histogram or a gap in a scatter plot ("A" in Figure 4) that will cause an elevated level of old-shelled animals in the following year at a size that is one molt larger than the size where the trough or gap is located ("B" in Figure 4). Unfortunately, Donaldson did not present any length-frequency data to test this alternative explanation. For this sort of argument to be

compelling, it would be necessary to examine the data by claw type (large-clawed versus small-clawed).

In summary, the lack of an accumulation of large, old-shelled animals in Alaska before and during the early phase of the fishery is suggestive of no terminal molt. The high preponderance of large, old-shelled crabs in Bonne Bay is suggestive of terminal molt. A variety of possible explanations can be proposed to explain these findings. Hence, it seems to be extremely difficult to make a convincing argument based on population composition. The appearance of elevated levels of old-shelled crabs in one year (due to reduced molting activity), followed by a decline in the next (when molting resumes), is supportive of the no-terminal-molt hypothesis. Donaldson reported two incidences where this may be the case. An alternative explanation that should be ruled out is that the sudden occurrence of increased levels of old-shelled animals is due to a recruitment failure. Donaldson did not present the length frequency data necessary to check for this. To rigorously eliminate this alternative explanation one would apparently need to have information on claw sizes. Large male snow crabs are not capable of cleaning their carapaces with their claws.

Mouth Parts and Formation of New Carapace as Indicators of Molt Status

In order for a crab to molt, the new (second) carapace must be well formed. Such a new carapace should not occur in large-clawed animals if there is a terminal molt. We found two large-clawed males in the Bering Sea (Fig. 10) which clearly had well developed second carapaces indicating imminent molting. Ito (1970) showed that for large *C. opilio*, sampled by bottom trawl in the Japan Sea, peak occurrence of second carapaces preceded peak occurrence of newly molted (soft-shelled) crabs by one to two months. Thus, examination of carapaces can provide a powerful and direct method for quantifying molting activity. Unfortunately, examination of specimens for development of second carapace has not been routinely conducted. Hence, further study will be necessary to determine molting prevalences using this method.

Mouth part morphology has been used to determine the molt status (i.e. postmolt, intermolt, and premolt stages) of snow crabs (Moriyasu and Mallet 1986; O'Halloran and O'Dor 1988). Animals in premolt stages D_1 and D_{2-3} are said to be clearly committed to molting. Hence, these stages would not be expected to occur in large-clawed animals if terminal molt exists. There is also a D_0 stage, the beginning of the premolt stage, but in our experience this stage is very difficult to separate from the C_4 or intermolt stage. The D_0 stage is further divided into early D_0 and late D_0 , and the early D_0 stage is especially difficult to discern from the C_4 stage. Conan et al. (1988a p. 1502) also note the difficulty in identifying premolt stage D_0 . Hence, we do not feel that the presence or absence of males in the D_0 stage can be used to settle the question of whether or not there is a terminal molt.

We examined the mouth parts of 1123 hard-shelled, clearly large-clawed animals (molt status C - D) greater in size than 60 mm cw and collected by trawl in Conception Bay, Newfoundland, in March and April - May of 1988 and May of 1989. Our definition of "clearly large-clawed" is any animal above the upper dividing line in Figure 5. We deduce that these samples were obtained during the molting season based on the following information. Miller and O'Keefe (1981) reported that soft-shelled crabs can be found throughout most of the year in Conception Bay, Newfoundland, but the vast majority occur from April to September or possibly October. Animals do not feed in captivity for about a month after molting (O'Halloran and O'Dor 1988). Hence, assuming that animals are not trappable for a month after molting, the soft-shelled crabs caught in April must have molted

in March. Animals tagged in a soft-shelled condition achieve hard-shelled condition within three months after tagging (Taylor et al. in press). Hence, an animal which molted at the end of May would be catchable at the end of June and would then achieve a hard-shelled condition by the end of September; animals molting in June would still be present in soft-shelled condition in October but not after that. Since very few soft-shelled animals appear to be present after October, most of the molting activity has apparently finished by the end of May or June. Thus, we conclude that most of the molting in Conception Bay occurs from March to May-June.

Of the 1123 hard-shelled, large-clawed animals examined, two were clearly committed to molting. Capture data for these animals are as follows:

date captured	carapace width	chela height	chela width	shell condition	mouthpart stage
March, 1988	60 mm	12.4 mm	10.2 mm	new hard-shell	D ₁
May, 1989	74 mm	16.2 mm	14.1 mm	new hard-shell	D ₁

Inspection of the relationship between chela height and carapace width leaves little doubt that these animals were large-clawed (Figure 5). We also examined 718 clearly small-clawed animals in molt status C - D. Of these, 46 were in D₁ or above.

Since active premolting (stages D₁ - D₃) lasts for 6 - 9 weeks (O'Halloran and O'Dor 1988), and the molting season appears to be about three to four months long in Newfoundland, one would not expect to find many animals in active molt. This is because the exact timing of the molting season, the period of peak molting activity within the season, and the habitats where animals choose to molt, are poorly known. Also, large animals, regardless of claw size, may have intermolt periods of two or more years and, hence, would be particularly hard to find in an active molting state.

Conan and Comeau (1986) examined the mouth parts from 260 large-clawed animals caught in trawls taken from July to December, and also from 110 males (presumably large-clawed) taken in traps at an unspecified time of year (possibly also July to December). The size distribution and shell conditions of the animals were not given. They state (p. 1716) that none of the individuals was "in a premolt 'D' or molt 'A' stage". Here, there appears to be a problem: the "A" stage refers to the post-molt condition (see Moriyasu and Mallet 1986 p. 710; O'Halloran and O'Dor 1988 p. 168), not to molting animals. It does not make sense to look at the post-molt stage. All animals completing a molt, even animals molting to a terminal molt condition, would undergo a post-molt stage. Hence, the post-molt stage sheds no light on the terminal molt question. Conan and Comeau conclude that an upper, one-sided, 95% confidence limit on the proportion that initiate molting ever is 0.8%, i.e. virtually nil. However, this analysis suffers from several flaws:

1) some animals may not molt every year, so that their estimation procedure would apply to the proportion of animals molting at the time of sampling, rather than ever

2) the molting season for male snow crabs appears to be in the late winter - spring (Miller and O'keefe 1981; Conan et al. 1988a p. 1502, 1988b p. 49); thus, Conan and Comeau appear to have looked for initiation of molting and active molting after the molting season was largely over

3) the proper computation is not what proportion of the large-clawed animals are molting or about to molt; rather, it is what proportion of the animals that could potentially molt (i.e. are not in post-molt or new-shelled condition) are molting or about to molt; Conan and Comeau did not provide the necessary information

4) if animals about to molt do not feed, as reported by O'Halloran and O'Dor (1988) for aquarium-held animals which molted, then the animals caught in baited traps would not be expected to show signs of molting activity, and trapped animals should not be used to study molting activity as was done by Conan and Comeau.

5) Conan and Comeau reported (p. 1716) that "premolt and molting immatures are frequently found in trawl catches". However, they specifically did not report the number or proportion of animals with small claws that were molting in the catches from which they obtained the large-clawed animals. The absence of large-clawed animals in a molting condition is certainly not meaningful if molting small-clawed animals are also missing.

For these reasons, the mouth part data of Conan and Comeau (1986) do not appear to shed light on the question of terminal molt.

Conan et al. (1988a) addressed some of the above concerns. Concerning points 2 and 5 (seasonal timing of molting), they reported that no "premolt" animals were found among 6081 mature (i.e. large-clawed) animals and 2004 immature (i.e. small-clawed) animals caught by trawl from July to September, 1987. (They did not consider trapped animals since (pre)molting animals would not be susceptible to capture in baited traps (point 4).) From October to November (year not specified), they obtained the following results from trawling:

group	number examined	number in premolt stage
large-clawed	312	0
small-clawed	208	50 in D ₀

Note that no animals, large- or small-clawed, were found in active premolt stages D₁ or D₂₋₃. Thus, even among the small-clawed animals, Conan et al. did not find animals clearly committed to molting at the times they sampled. Animals in late D₀ molt in 8 to 12 weeks whereas animals can remain in early D₀ for several months according to O'Halloran and O'Dor's (1988) findings for laboratory animals. If Conan et al.'s animals were in late D₀ they would molt well before the molting season; therefore, they were presumably in early D₀. As explained above, we find that the distinction between intermolt (stage C) and beginning premolt (early stage D₀) is dubious. Therefore, we feel there was little evidence that either group of animals showed signs of molting activity. Also, Conan et al. did not provide a breakdown by shell condition, mouth part stage, or body size of the animals they examined. Some of the 520 animals they examined may have been post-molt, soft-shelled, or new-shelled. If so, then these animals could not be expected to molt and should not be used in a comparison of prevalence of molting among large- and small-clawed animals. The distribution of body size may have differed between the two groups of animals. In this case, comparisons of prevalence of molting would again not be appropriate.

To summarize, we found two large-clawed males from the Bering Sea with well developed second carapaces indicating imminent molting. We also found two clearly large-clawed animals from Newfoundland which were clearly in a premolt (D_1) condition. These should not occur if large-clawed animals have undergone a terminal molt. Conan and Comeau (1986) and Conan et al. (1988a) failed to find mouthparts indicating premolt status among over 6000 large-clawed animals examined. However, they looked at the time of year when molting activity of large crabs is lowest, and they couldn't even find any small-clawed crabs in active premolt (D_1 and $D_{2,3}$). They found 50 small-clawed animals in D_0 but we do not believe D_0 can be determined reliably. Our finding four large-clawed animals clearly committed to molting is strong, direct evidence against terminal molt; the failure of others to find molting, large-clawed animals can be explained by a variety of methodological problems, especially examination of crabs during inappropriate seasons.

Accounting for the Largest of the Large-clawed Animals

Consider the scatter plots of trap-caught animals in Figure 6 (from Ennis et al. 1989b, Fig. 1; Ennis et al. 1990). The largest of the small-clawed animals is approximately 91 mm cw. When animals of this size molt, they increase in size about 11 mm cw (Taylor and Hoenig 1990; similar results were also reported by Moriyasu et al. 1987). Thus, they would be expected to be about 102 mm cw when they reach their terminal molt, if terminal molt exists. The largest of the large clawed animals are over 130 mm cw, i.e. 30 mm larger than the largest small-clawed animals would be after they undergo their terminal molt. This suggests strongly that some of the large-clawed animals must be molting in order to account for the occurrence of the very large, large-clawed animals. Although the gap between the largest of the small-clawed males and the largest of the large-clawed males is especially great in Figure 6 (about 40 mm), similar diagrams have been produced for a wide variety of locations and years with gaps larger than 30 mm (Figures 1 and 7).

One possible alternative explanation for the observation that the largest of the small-clawed animals do not appear to account for the largest of the large-clawed animals is as follows (refer to Figure 8): suppose in the previous year, there was a gap in the length frequency distribution of small-clawed animals from 80-90 mm cw (e.g. due to a recruitment failure in the past). Then in the current year, there would be a gap in the length frequency diagram from 91 to 102 mm (that is, there were no small-clawed animals to recruit into the size category from 91 to 102 mm, assuming that molting occurs once a year). Thus, under "normal" conditions there might be small-clawed animals as large as 102 mm, and when these animals underwent their terminal molt they would account for the occurrence of large-clawed animals as large as 113 mm. This still does not account for the genesis of large-clawed animals in Bonne Bay from 114 to 130 mm cw; however, it is a potential explanation for scatter plots from other geographic locales. There is a way to test for this possibility. If the above scenario is true - i.e. that a recruitment failure in the past caused a temporary trough in the length frequency distribution - then (referring to Figure 8) in the next year (1989) one should find animals recruiting into the size class from 91 to 102 mm. It can be seen in Figure 6b that the largest size of the small-clawed animals in 1989 (approximately 96 mm) is slightly larger than the largest sizes of the small-clawed animals in 1988 (about 90 mm, Figure 6a). We note that it is highly unlikely that recruitment failures could account for the missing largest small-clawed animals in all the scatter plots examined, and gaps in the size-frequency distributions are rarely encountered.

Conan and Comeau (1986 p. 1718) state that "The size difference between larger morphometrically immature males and larger morphometrically mature ones in our data is

120 - 130 mm L_c (Fig. 4b) and can easily be covered over one molt to maturity". They suggest (p. 1718) that the wide gap in body size between the largest of the small-clawed animals and the largest of the large-clawed animals, reported by others, is "most likely a sampling artifact" and explain that "some types of gear such as traps or trawls which do not rake the sediment efficiently enough do not capture large morphometrically immature males which tend to conceal themselves more than mature ones, as shown by the aquarium experiments." Our examination of Conan and Comeau's Figure 4b reveals that the largest of the small-clawed males is 113 mm while the largest of the large-clawed males is 132 mm (difference of 19 mm.) We have found that trawl samples from several areas show a large gap in body size between the largest of the small-clawed animals and the largest of the large-clawed animals. Also, it remains to be proven if large small-clawed males are especially prone to concealing themselves in the sediments. The aquarium evidence that Conan and Comeau (p. 1711 and p. 1716) refer to is as follows: six small-clawed males ranging in size from 66 to 98 mm cw were placed in an 18 m³ aquarium with 12 large-clawed males ranging in size from 74 to 116 mm cw and 17 mature (multiparous) females. The bottom of the tank was covered with small gravel and large rocks. The small-clawed males "retreated to remote locations of the aquarium and displayed a hiding behavior by picking a stone and putting it on top of their carapace." This shows only that under crowded, artificial conditions, when males are competing for females, the small-clawed males may not be as aggressive or successful as large-clawed males with larger body sizes.

In summary, the largest of the large-clawed males must, by definition, be derived from the molting of non-terminally molted animals. Tagging studies have provided estimates of molt increments of approximately 11 mm cw for animals around 100 mm cw. Hence, there must, at some point in time, be non-terminally molted animals present that are within approximately 11 mm of the size of the largest large-clawed animals. This does not appear to be the case in a variety of situations if only small-clawed animals can molt. Therefore, there is strong circumstantial evidence that some of the large-clawed crabs must molt in order to account for the occurrence of the largest large-clawed animals.

Growth of Tagged Animals

A tagging study was initiated in 1987 in Conception Bay, Newfoundland, with one goal to determine if large-clawed animals molt. The relationship between chela height and carapace width was examined for 400 animals collected from Conception Bay in 1987 (Figure 5). Only animals which clearly fell in the upper cloud of Figure 5 (called "clearly large-clawed" animals) were tagged in 1987 and 1988 and 1989). T-bar tags were applied in the ecdysial suture according to methods described by Taylor and Hoenig (1990). To date, 93 large-clawed tagged animals have been recaptured of which two animals molted (Table 1). Nineteen animals tagged as small-clawed animals have been recaptured, of which 16 molted.

Because of the obvious importance of tagged animals in providing direct evidence against terminal molt, it is important to check carefully the tagging data for possible inconsistencies. We considered the following:

- 1) accuracy of measurements on recaptured animals
- 2) consistency of relationship between chela height and carapace width as well as between chela width and carapace width, at tagging and at recapture

3) consistency of shell condition at recapture with the time at liberty

4) reasonableness of increment in body size while at liberty

We measured the size of the recaptured animals several times (in blind trials) and are confident that the measurements are correct to the nearest millimeter. Animals were measured once at the time of tagging. Our own study (Taylor and Hoenig 1990) and studies in the literature (Hunt and Lyons 1986) suggest that single measurements of large crustacea are almost always within 3 mm of the correct value. Hence, there is little chance that the apparent growth of these specimens is due to measurement error. To further check for possible measurement errors, we compared the relationship between carapace width and chela width, and between carapace width and chela height, for the recaptured animals against the sample of 400 animals from Conception Bay from 1987. In both cases, the data from the recaptured animals were unremarkable.

The animal with tag number G3172 was at liberty for 120 d (4 mo). It was tagged as a new-hard-shelled (shell condition 2) animal (see Miller and O'Keefe (1981) for definitions of shell conditions) and recovered as a new-hard-shelled animal. The tagging results of Taylor et al. (in press) indicate that soft-shelled crabs can become hard in 2 months and virtually all become hard-shelled within three months. The laboratory study of O'Halloran and O'Dor (1988) indicate that crabs stop feeding for a month before molting. Hence, the 4 months at liberty were sufficient for the crab to fast for a month, molt, and recover to a hard-shelled condition. This presumes that molting took place in June. As described above, June appears to fall within the molting season of snow crabs in Conception Bay.

The other recaptured animal (tag G2138) was at liberty for 16 mo and was tagged and recaptured in the new-hard-shelled condition. Clearly, this animal had time to molt and recover to a hard-shelled condition.

The animal with tag number G3172 grew 15 mm while at liberty (from 85 to 100 mm cw). Results from the tagging study of Taylor and Hoenig (1990) indicate that the expected molt increment for an 85 mm male is 11.6 mm. Judging from their Figure 3, the probable range is at least ± 4 mm. Tagged animal G2138 grew 8 mm (from 95 to 103 mm cw). The predicted molt increment for this size is 11.0 mm. Thus, the magnitudes of the size increments are unremarkable. These molt increments are also consistent with the molt increments reported by Moriyasu et al. (1987) for an aquarium study.

In summary, clearly large-clawed animals were tagged to see if these animals molt. Two animals were recovered which molted. There is nothing remarkable about the tagging data to cast doubt on the validity of this information. Hence, this is strong, direct evidence against the idea of a terminal molt.

Other Evidence

Evidence from Similar Species

In the original paper on terminal molt of snow crabs, Conan and Comeau (1986) noted that, with the exception of the genus *Chionoecetes*, male crabs in the family Majidae are generally accepted to have a terminal molt. They then suggested that their work on *C. opilio* and their review of the literature on other species of *Chionoecetes* was sufficient to conclude that males of all species in the family Majidae undergo a terminal molt.

Donaldson and Johnson (1988) disagreed that males of all species of *Chionoecetes* undergo a terminal molt. In response, Conan et al. (1988a) acknowledged that terminal molt of males may not exist in all the species in the genus and also acknowledged that males of *C. opilio* in Alaska may not have completed their "evolution" towards complete terminal molt.

If the evidence were clear that males of all species in the Majidae undergo a terminal molt except *C. opilio*, then one would be well advised to consider carefully if *C. opilio* is really different from all other species in the family. However, universality of terminal molt is not accepted to be the case (Conan et al. 1988a, 1988b; Donaldson and Johnson 1988; Donaldson 1988; Jamieson et al. 1988) and, in fact, there is reason to believe that males in the genus *Chionoecetes* do not undergo a terminal molt (except, of course, for the question of *C. opilio* in Atlantic Canada). Therefore, circumstantial evidence from other species in the family does not provide strong evidence for (or against) terminal molt in *C. opilio* males.

Hormones and Y-organs

Conan et al. (1988a, 1988b) suggest that levels of the molting hormone crustecdysone are low and the Y-organs are reduced in large-clawed animals. They presented no new information but, rather, cited an unpublished work by Cormier (1986) for the level of crustecdysone. They gave no reference for Y-organs, and the only reference of which we are aware (Rioux 1988) is about females. E. Bataller is studying morphology of the Y-organ in males but does not yet have definitive results (A. Boghen, Université de Moncton, pers. commun., 23 March 1990). We have not had time to extensively review these works and offer only a few comments on interpretation of findings.

Levels of crustecdysone, and condition of the Y-organ, are likely affected by body size of the crab, position in the molt cycle (as evidenced by shell condition), and season of the year. Comparisons of levels of molting hormone and condition of the Y-organ between small- and large-clawed males can only be done after accounting for these factors, as suggested by Conan et al. (1988a) for crustecdysone.

Figure 9 (from Cormier 1986 Fig. 3.8) suggests over the size range from 92 to 114 mm cw, small-clawed males have higher levels of crustecdysone on average than large-clawed males. However, there is a great deal of overlap of the distributions which needs explanation. It is not clear what level of crustecdysone is necessary for molting to occur and how the levels change over the course of the molting cycle.

One line of evidence which would strongly contradict the theory of terminal molt would be if crustecdysone levels in hard-shelled, large-clawed males followed a bimodal distribution around the time of the molting season. Presumably, the lower mode would represent background levels for animals which will not molt in the near future whereas the upper mode would represent animals which will molt soon.

Examination of hormone levels and Y-organs is more involved than examination of mouthparts, and considerable work is necessary to determine the effects of size, season, and molting status on these variables. Thus, it may not be worthwhile to examine hormones and Y-organs unless they are indicative of future molting activity over a longer period of time than can be obtained from examination of mouthparts.

Limb Regeneration

Conan et al. (1988b p. 48) state that large-clawed males never regenerate limbs while small-clawed males do. They cite no references and provide no data. Consequently, there is no way to evaluate this evidence. We note that the absence of regenerating limb buds in large-clawed males could only be significant if small-clawed crabs of the same size have regenerating limbs.

In summary, the evidence does not support conclusively the idea that terminal molt is a family-wide phenomenon in the Majidae. We could not find support for the claims that the Y-organ tends to disappear in large-clawed males and that large-clawed males cannot regenerate lost limbs while small-clawed males of the same size can. The limited evidence on crustecdysone levels indicates that large-clawed males have lower levels of the molting hormone, on average, than small-clawed males of the same body size. However, the considerable overlap of the distributions of crustecdysone levels is difficult to reconcile with the idea that large-clawed males do not molt and have low levels of molting hormone.

General Conclusion

We conclude from our review of the available literature that the existence of a terminal molt in male snow crabs (*Chionoecetes opilio*) is not supported by the data or the analyses. Further, we have presented direct evidence, albeit limited, which contradicts the idea of a terminal molt in males of this species. We feel strongly that the statement of a consensus that male snow crabs are now considered to have a terminal molt indicated in the Proceedings of the International Workshop on Snow Crab Biology (Jamieson et al. 1988) was inaccurate and premature. Further research is required to resolve the question definitively but clearly the conclusion that a terminal molt exists in male snow crabs is untenable at this point in time.

Conan et al. (1988a) maintain that, because there is some misclassification when a discriminant function is used to assign animals to groups, the occurrence of a few large-clawed males which molt should not be considered to disprove the theory of terminal molt. We have taken a very conservative approach and examined only those males which were clearly in the upper cloud of points. However, if large- and small-clawed animals cannot be separated reliably, then it is impossible to disprove the existence of terminal molt, and terminal molt is not a scientific theory. We have tried to stress that the quantitative assessment of the prevalence of molting of large-clawed males is possible but that it is difficult because timing of the molting season is poorly known and because body size and shell condition are factors which affect the molting of individuals. Considerable work is necessary to arrive at a valid quantitative assessment of molting prevalence.

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Table 1. Tag and recapture data for two "clearly large clawed" animals which molted while at liberty.

characteristic	animal #1	animal #2
tag number	G2138	G3172
date tagged	May 14, 1988	May 11, 1988
carapace width at tagging	85 mm	95 mm
chela width at tagging	16.3 mm	17.8 mm
chela height at tagging	18.2 mm	20.5 mm
shell condition at tagging	new-hard-shelled	new-hard-shelled
date recaptured	Sept. 8, 1989	Sept. 8, 1988
time at liberty	482 d	120 d
carapace width at recapture	100 mm	103 mm
change in size while at liberty	15 mm (18%)	8 mm (8%)
chela width at recapture	?	unavailable ¹
chela height at recapture	23.1	unavailable ¹
shell condition at recapture	new-hard-shelled	new-hard-shelled

1) Specimen was returned without claws by fisherman.

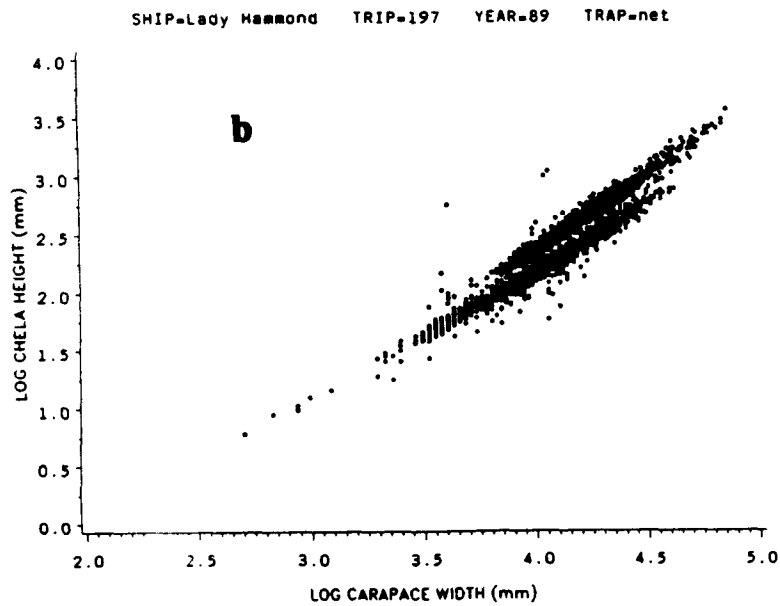
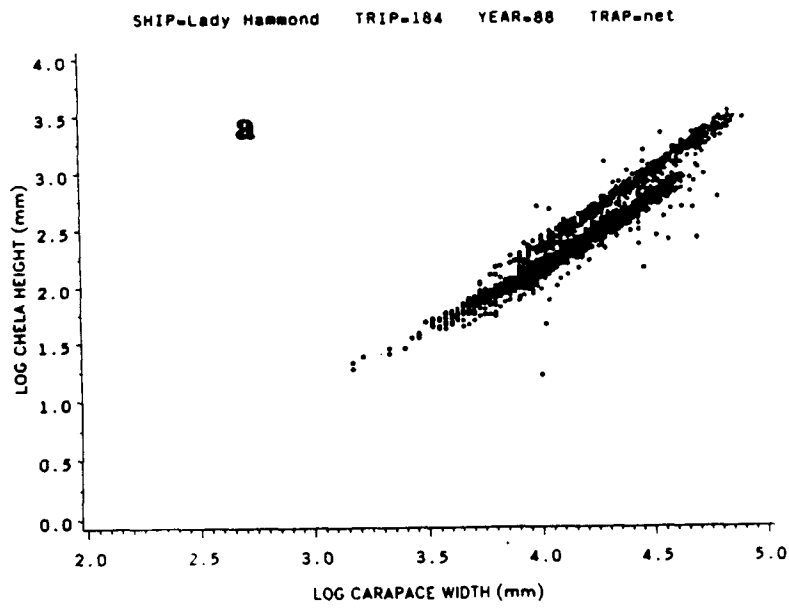


Fig. 1. Relationship between logarithm of chela height and logarithms of carapace width for trawled samples of male snow crabs from Newfoundland. Note that the logarithmic transformation does not completely linearize the relationship. a) data from 1988. b) data from 1989.

Fig. 2. Percentage of old-shelled males in trawl survey samples of male *C. opilio* from the Bering Sea as a function of body size (From Donalson 1988 Figures 5 - 8). Note that, among the largest size classes, the percentage of old-shelled animals rose in 1979 and 1980 and then declined in 1981.

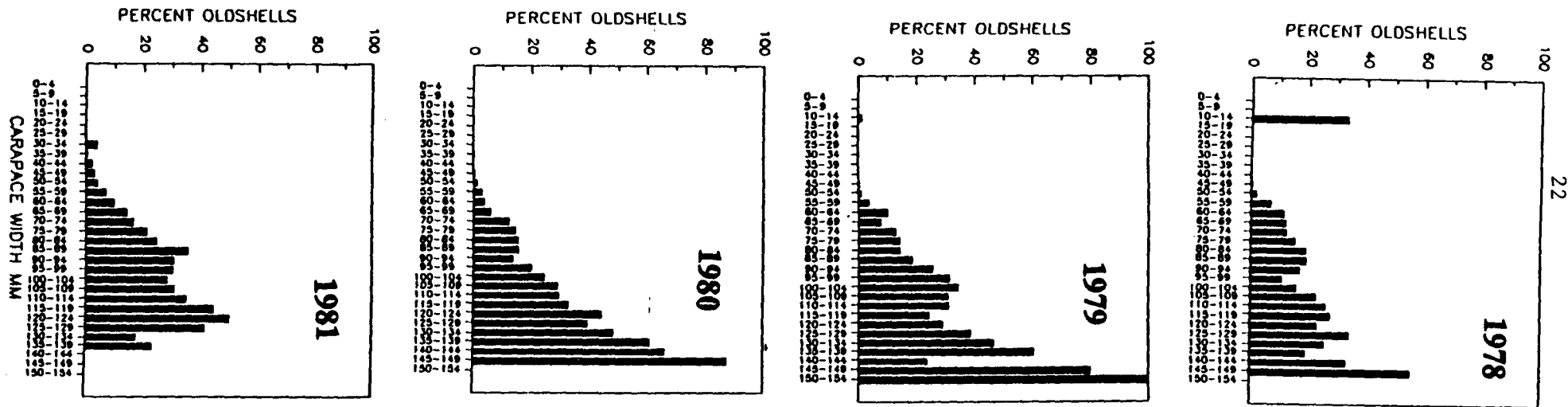
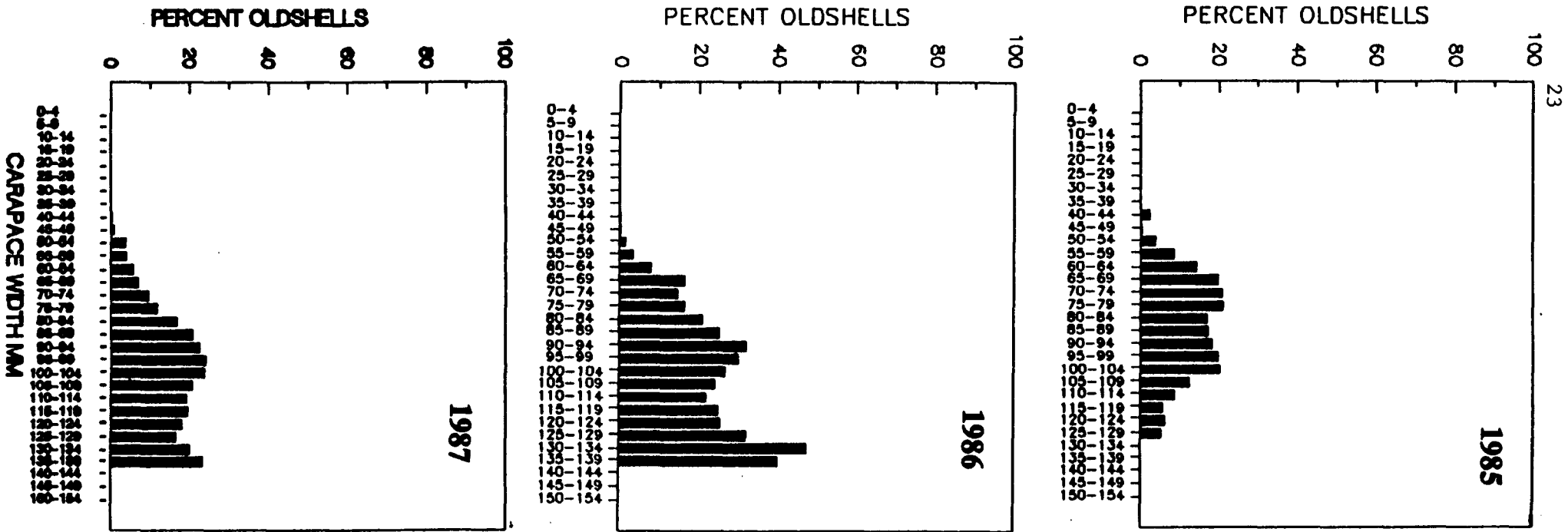


Fig. 3. Percentage of old-shelled males in trawl survey samples of male *C. opilio* from the Bering Sea as a function of body size (From Donalson 1988 Figures 12 - 14). Note that, among the largest size classes, the percentage of old-shelled animals rose in 1986 and then declined in 1987.



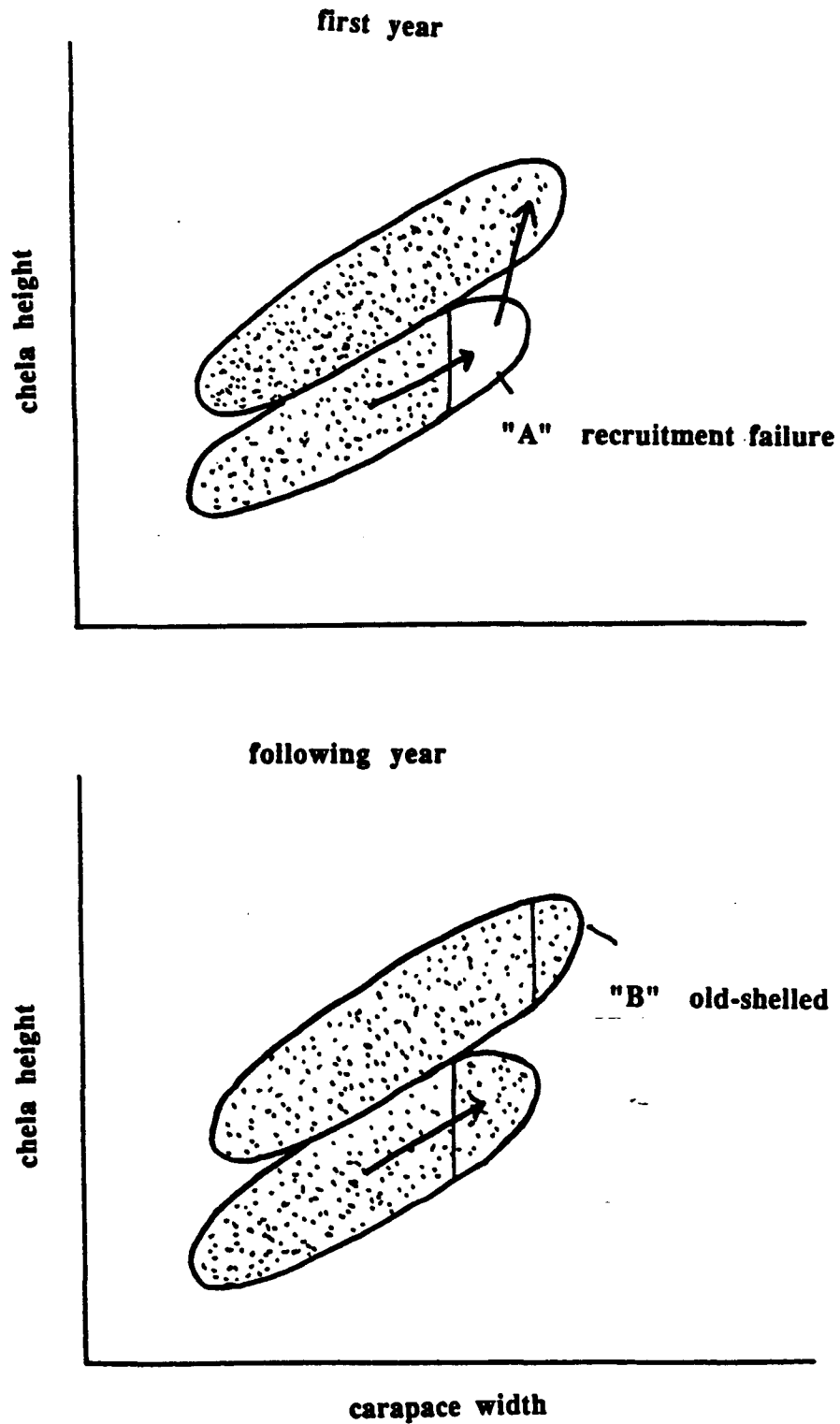


Fig. 4. Hypothetical situation leading to a temporary buildup of old-shelled males at the largest body sizes. Arrows show the fates of molting animals. Region "A" in the top part of the figure represents animals which are "missing" due to a recruitment failure some time in the past. These animals would normally molt to region "B" shown in the lower part of the figure. In the absence of these recruits, the animals in region "B" all age to the old-shelled condition.

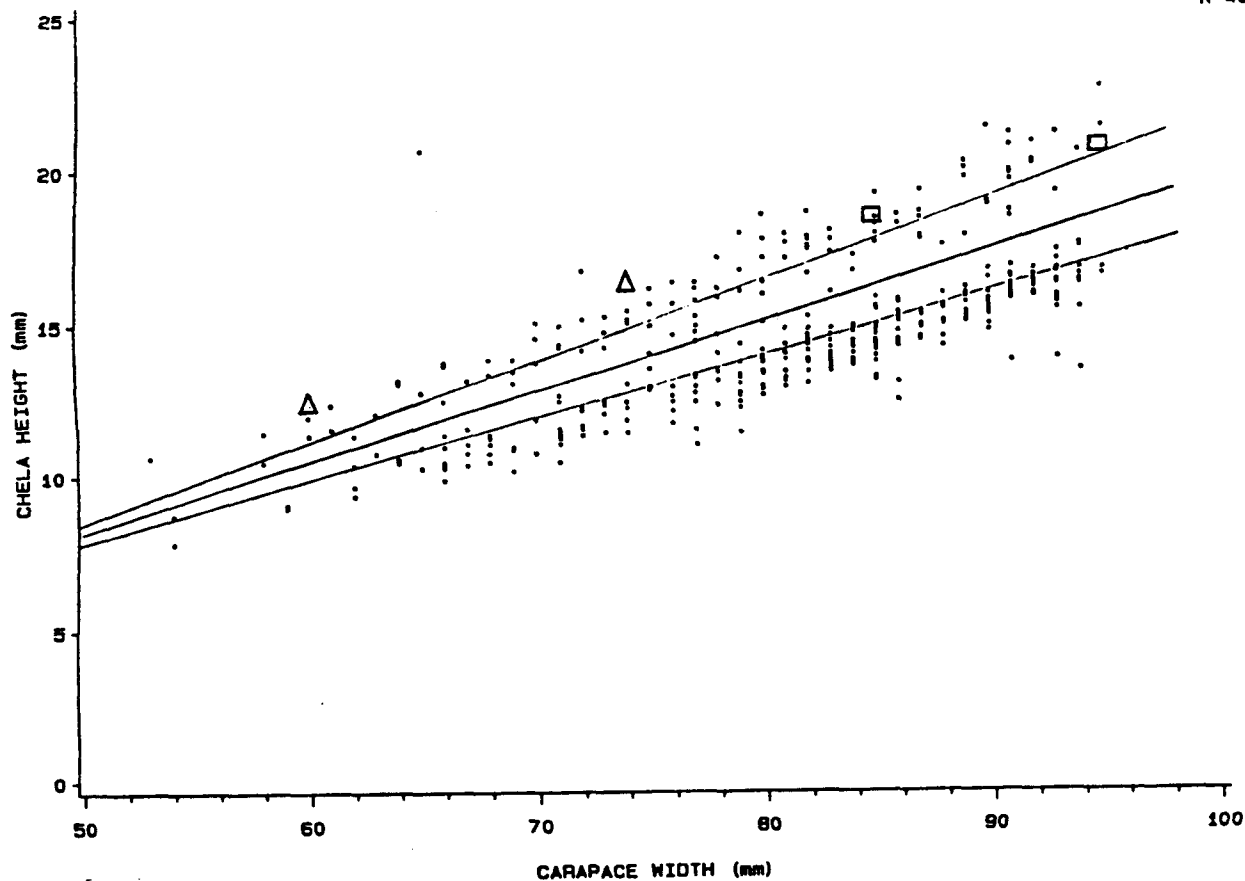


Fig. 5. Relationship between chela height and carapace width for a sample of 400 male *C. opilio* collected from Conception Bay in 1987 by trapping. The middle line appears to separate the two clouds of points well. Animals above the upper line are referred to as "clearly large-clawed" while those below the lower line are referred to as "clearly small-clawed". Lines were drawn by eye. Triangles refer to two animals with mouth parts indicating the D₁ phase of the molt cycle. Open squares refer to morphometry at tagging of two animals which subsequently molted.

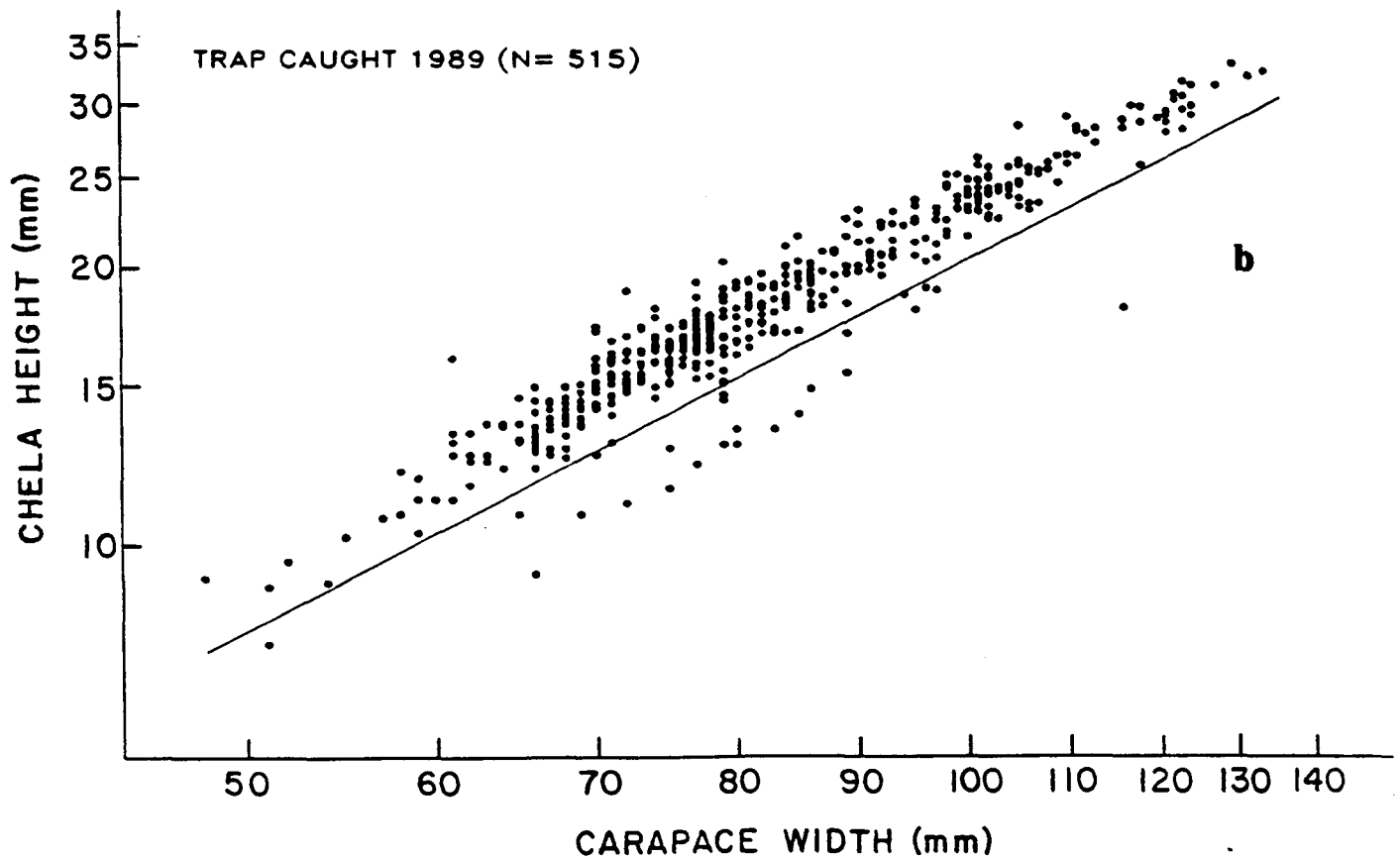
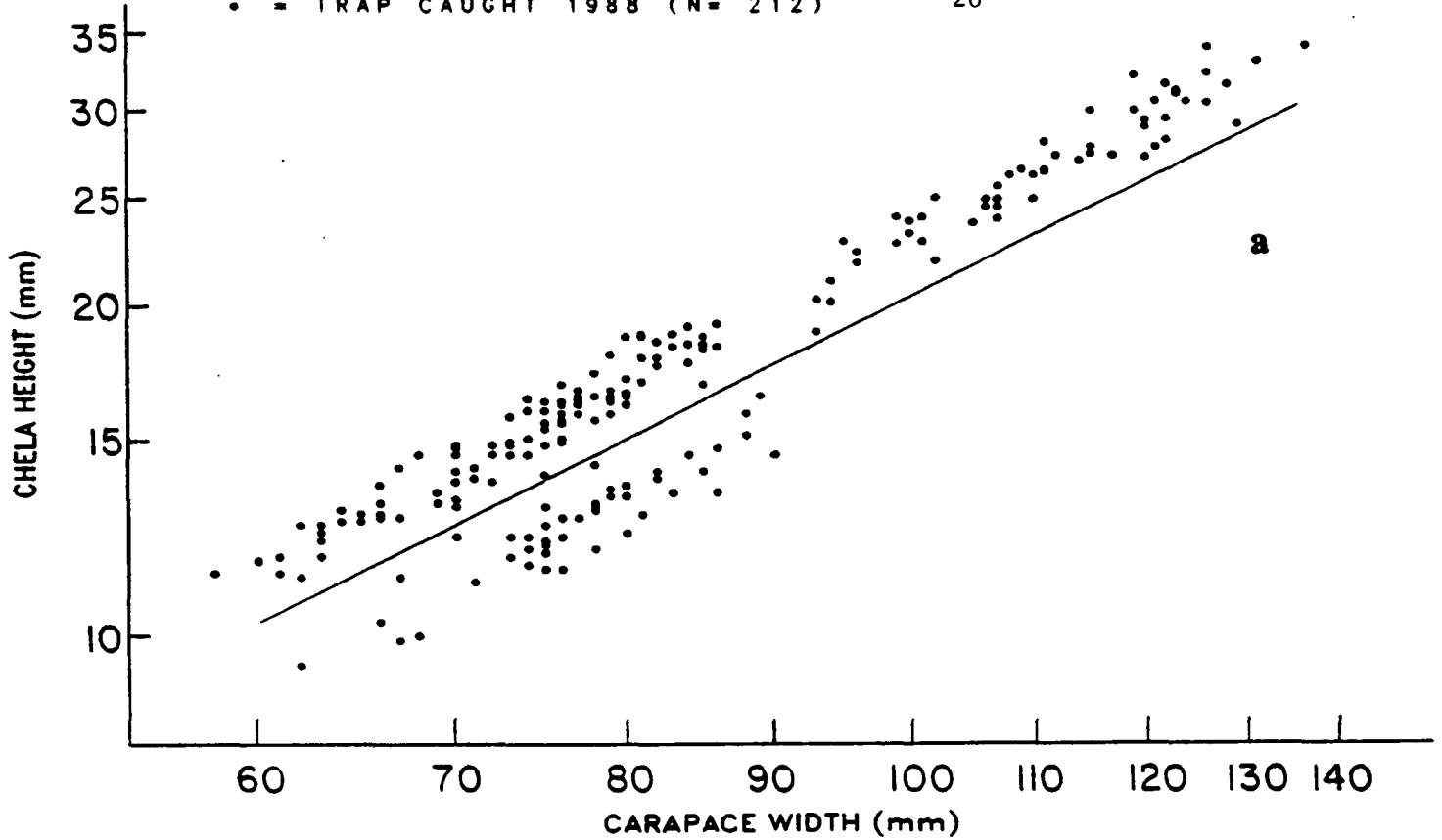


Fig. 6. Relationship between chela height and carapace width for trap-caught male *C. opilio* from Bonne Bay, Newfoundland. Note that the largest of the large-clawed animals are bigger than the largest of the small-clawed animals by about 40 mm. This suggests that, if terminal molt exists, the molt increment for the largest of the small-clawed animals must be about 40 mm to account for the occurrence of the largest of the large-clawed animals. a) 1988 data (from Ennis et al. 1989b Fig. 1). b) 1989 data (from Ennis et al. 1990).

INSHORE AVALON PENINSULA
MAY-1988

N=4027

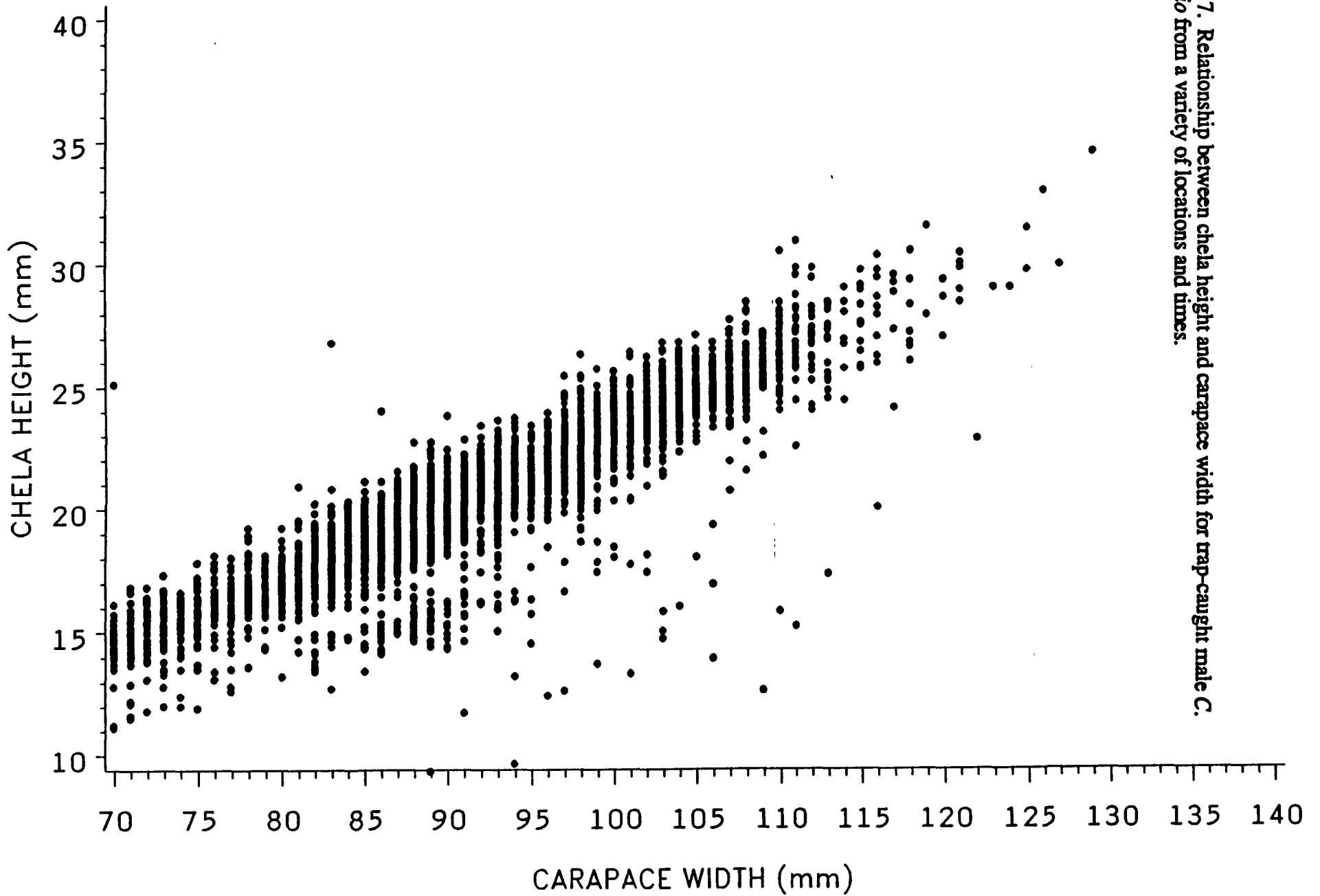


Fig. 7. Relationship between chela height and carapace width for trap-caught male *C. opilio* from a variety of locations and times.

OFFSHORE AVALON PENINSULA
MAY-1989

N=1205

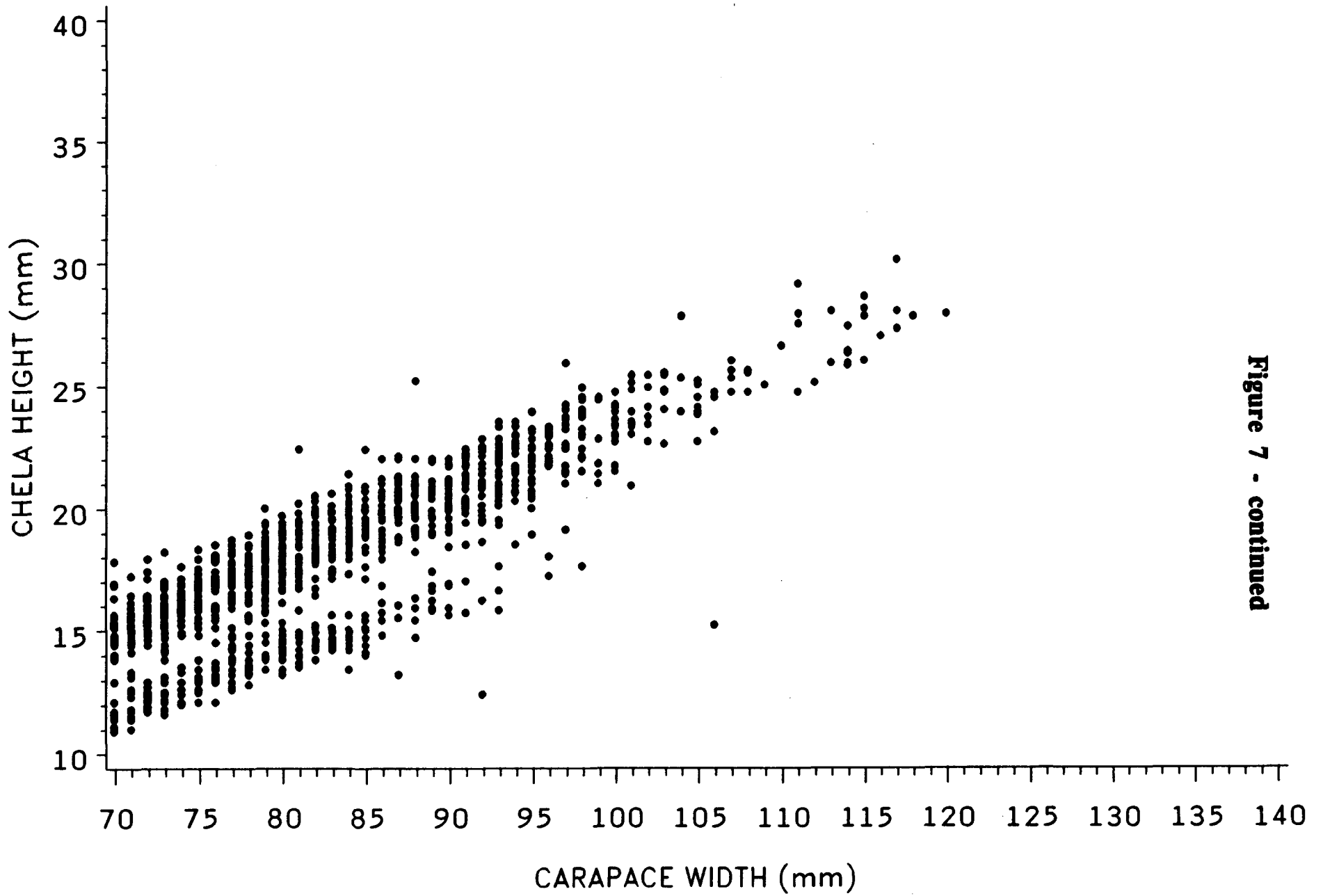


Figure 7 - continued

INSHORE AVALON PENINSULA
JUNE-1989

N=1690

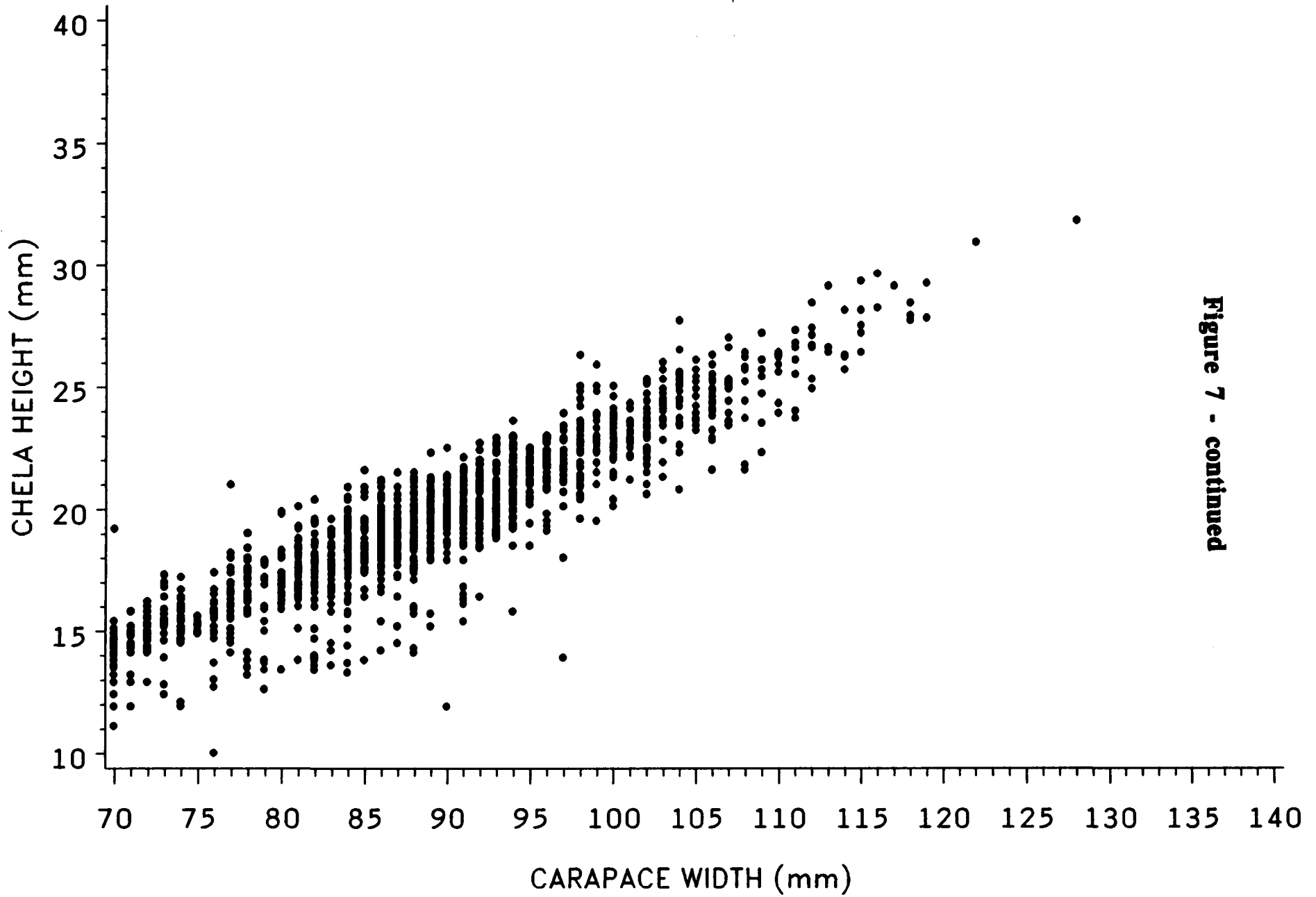


Figure 7 - continued

DOWNING BASIN
MAY-1989

N=573

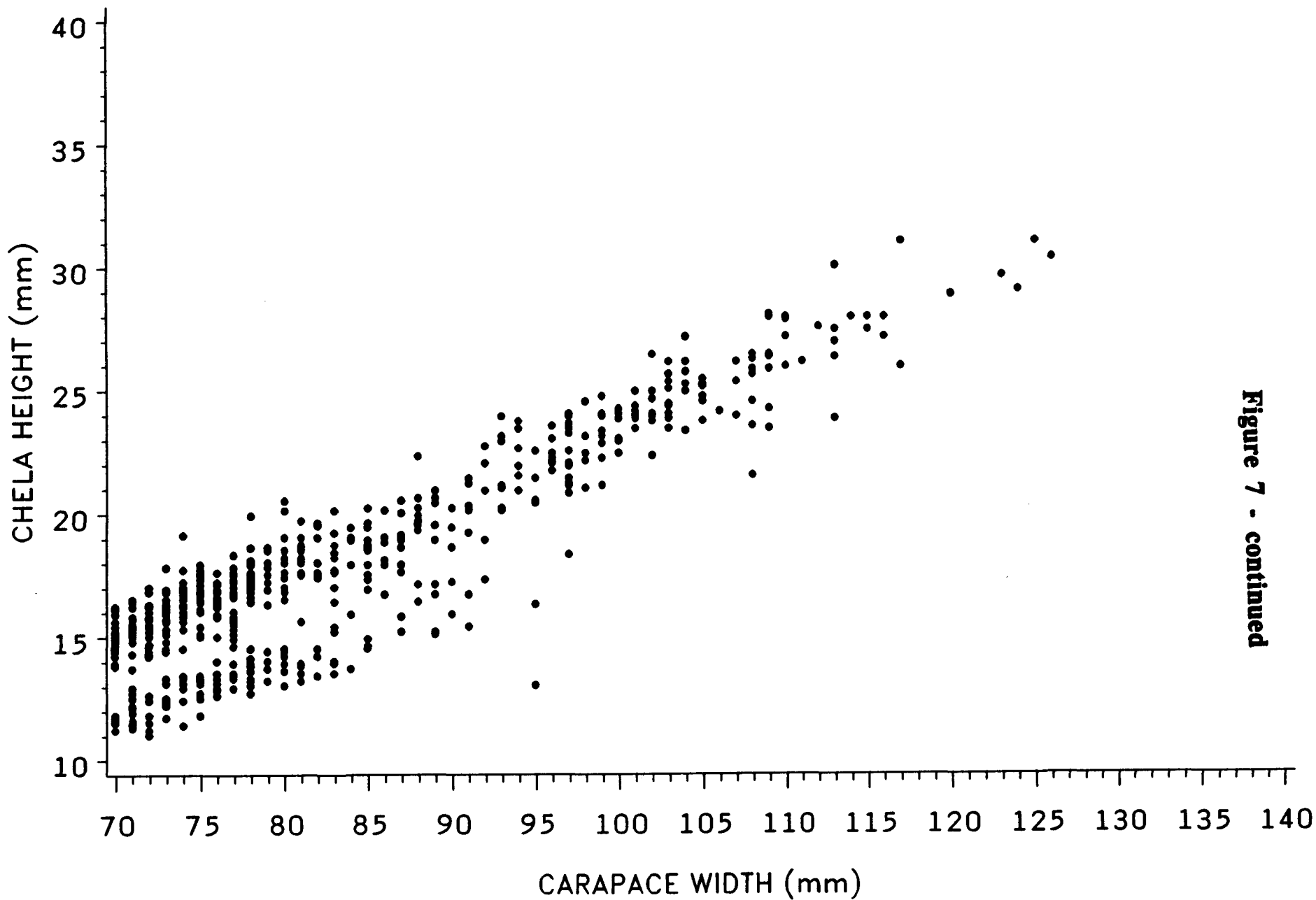
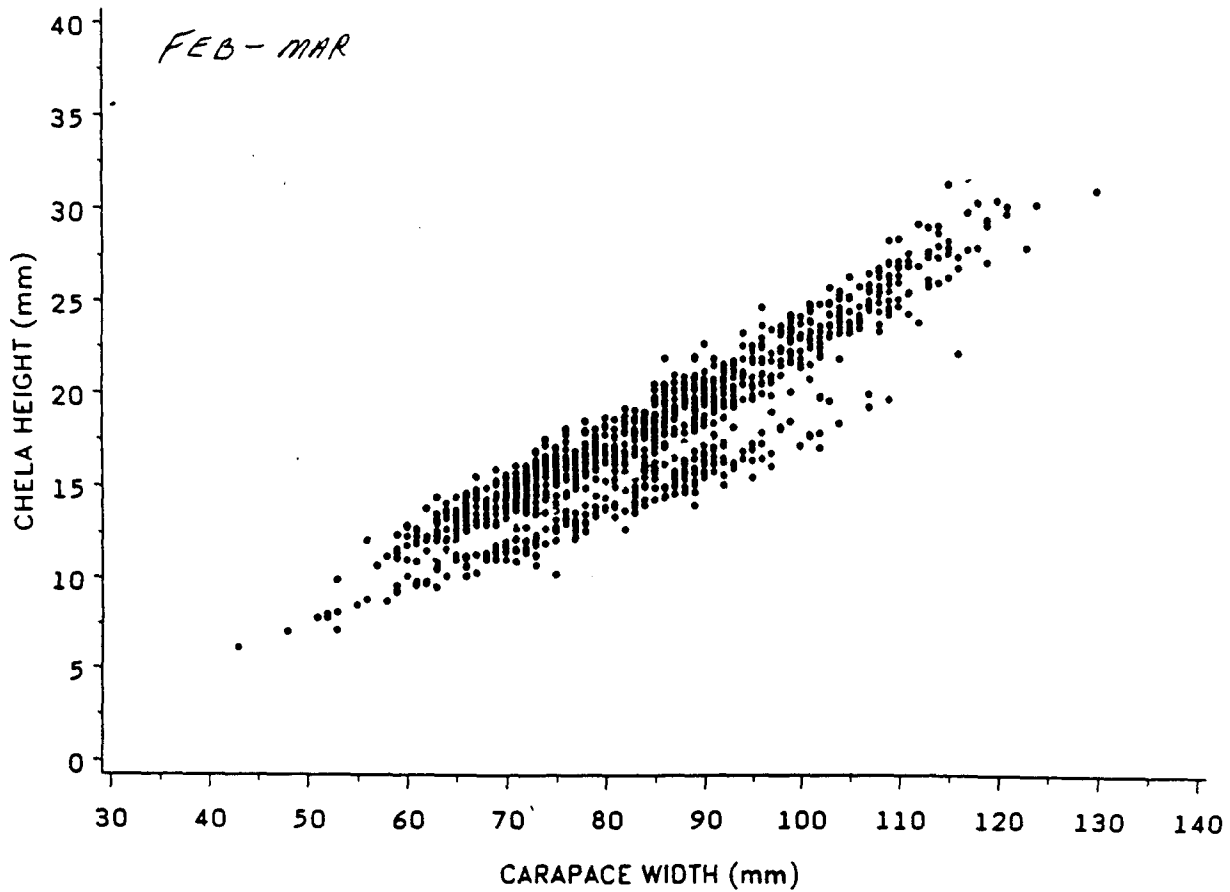
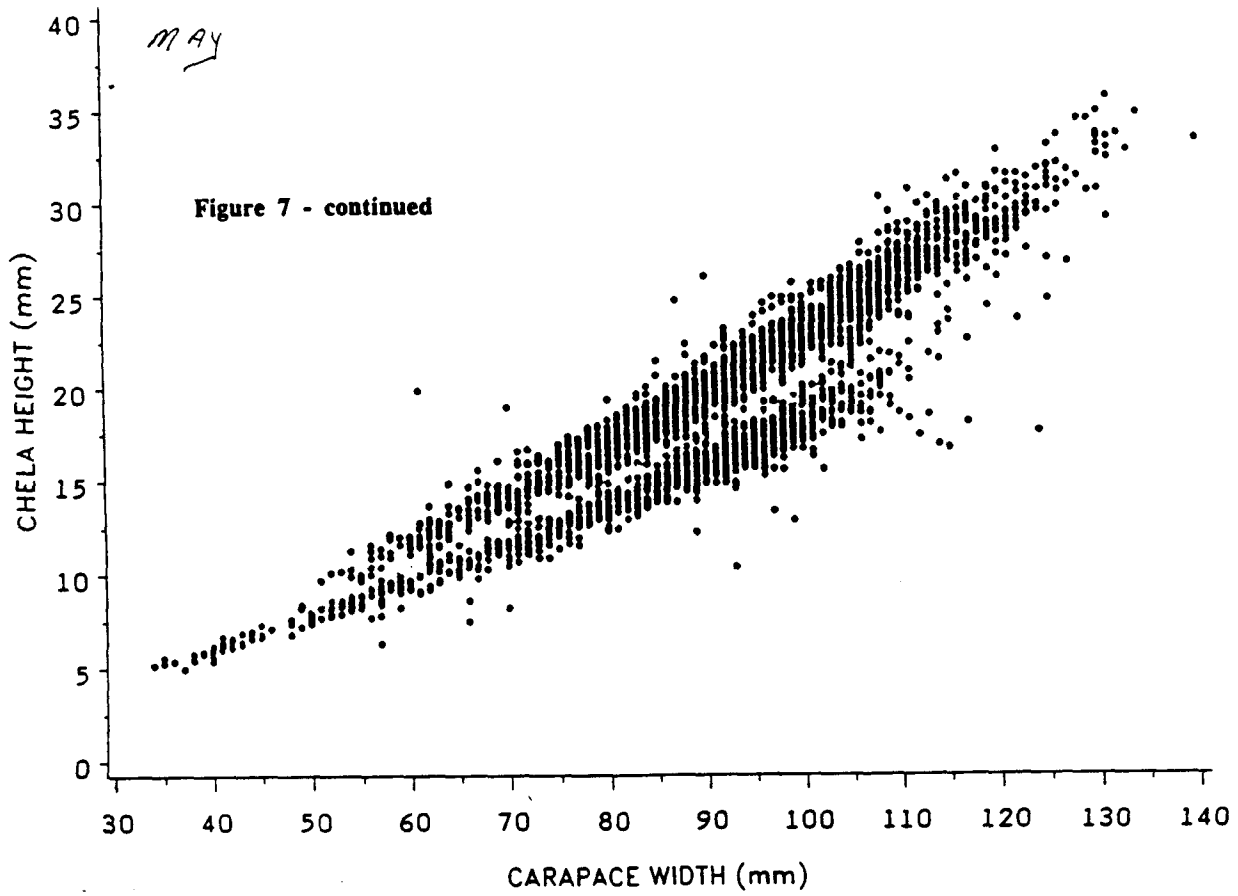
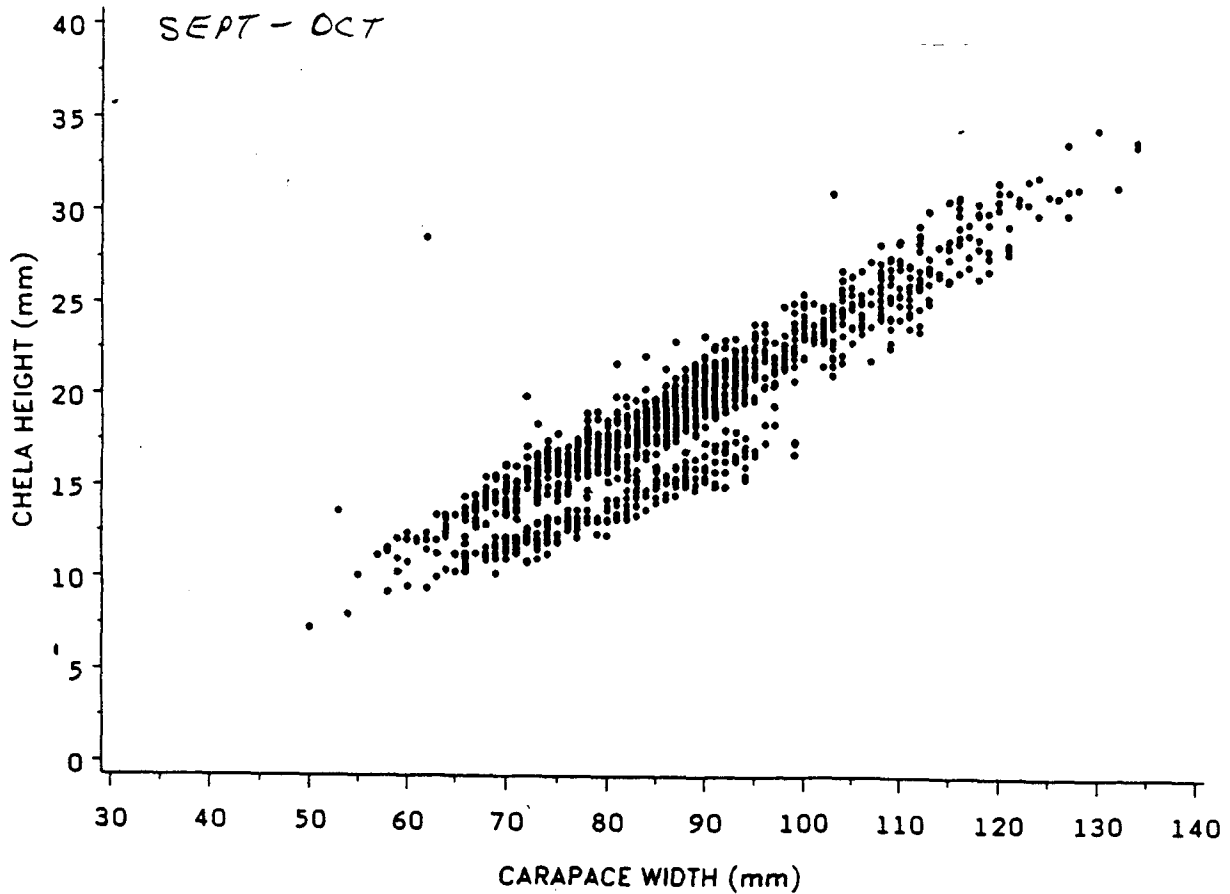
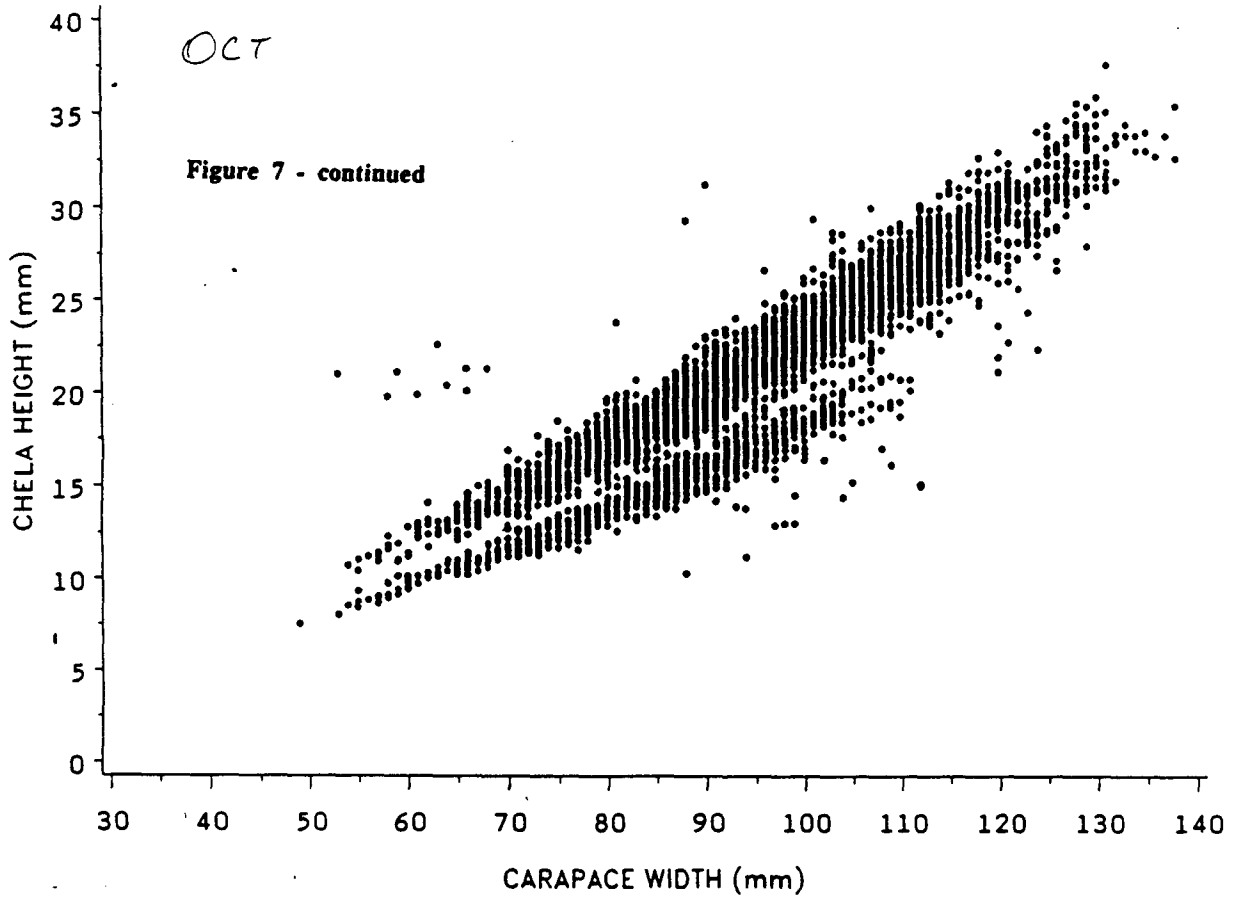


Figure 7 - continued





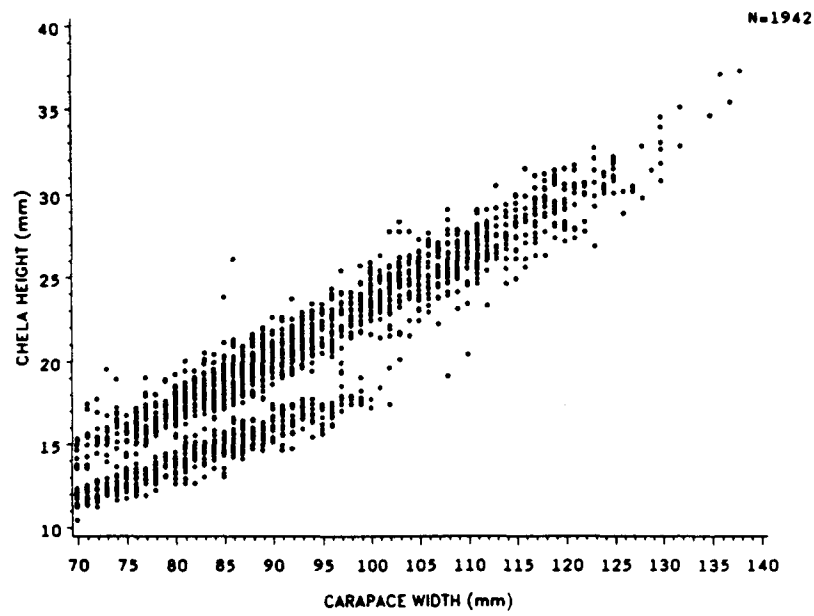
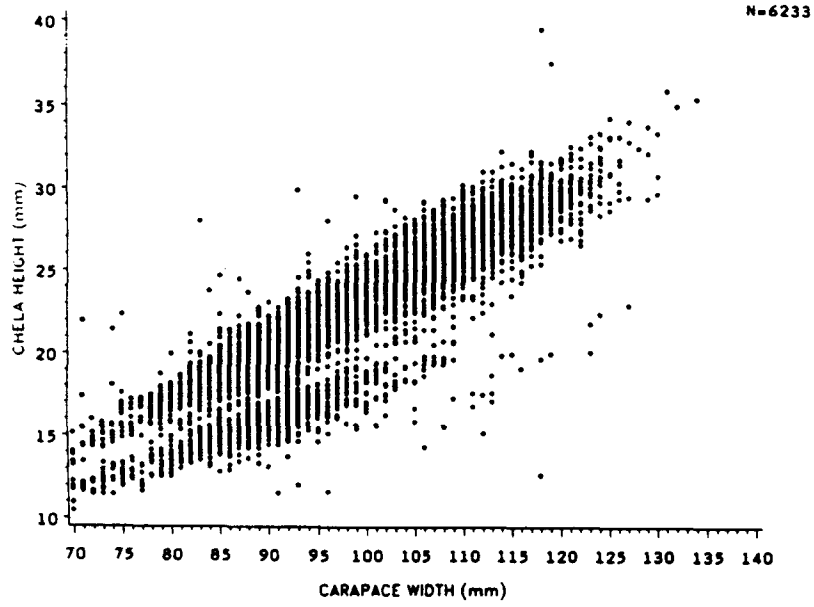


Figure 7 - continued

Bonavista Bay, Newfoundland, samples from pots from fall, 1988 (top) and fall, 1989 (bottom)

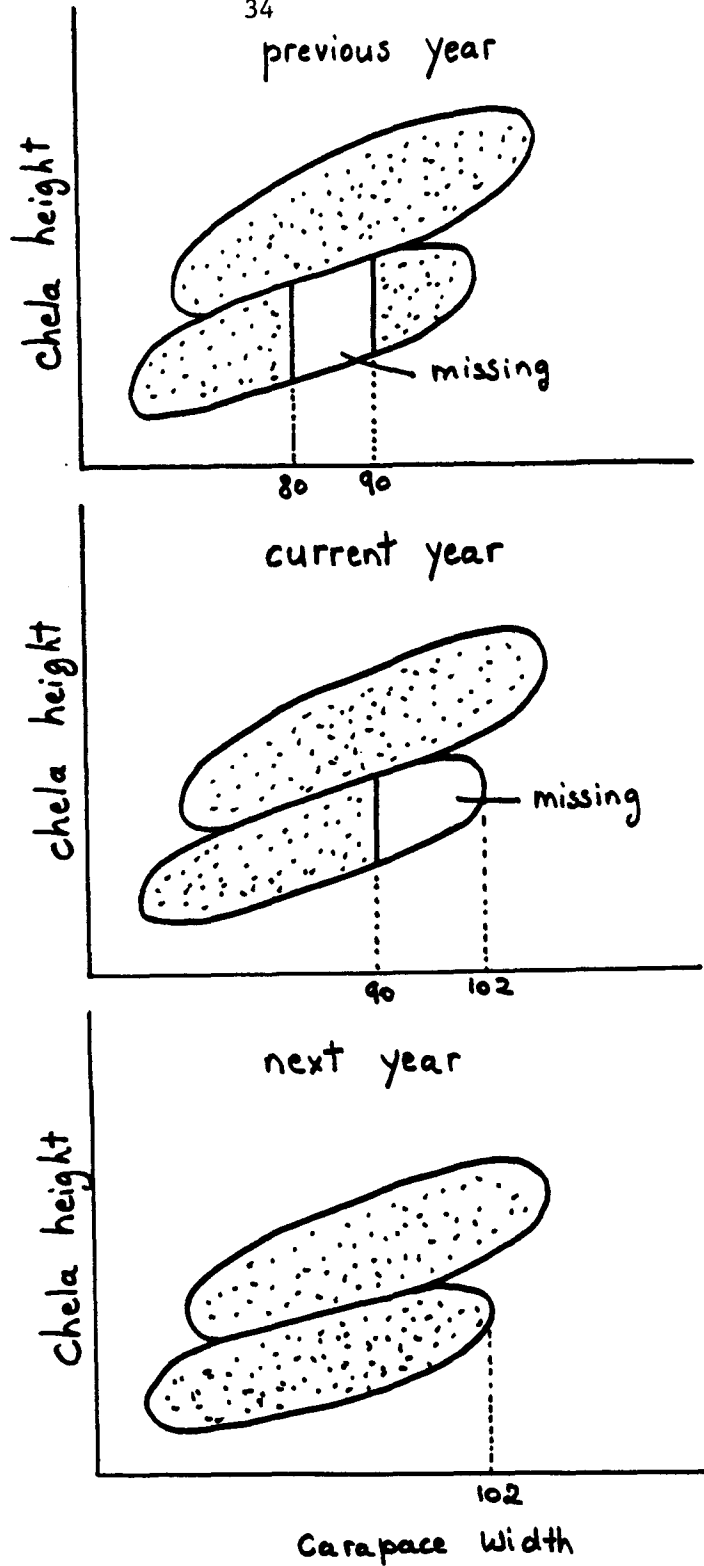


Fig. 8. Hypothetical situation illustrating how a "gap" in a scatter plot (top), due to a recruitment failure in the past, progresses to the right over time and eventually disappears (bottom). Middle panel illustrates how maximum size of small-clawed males can be temporarily reduced.

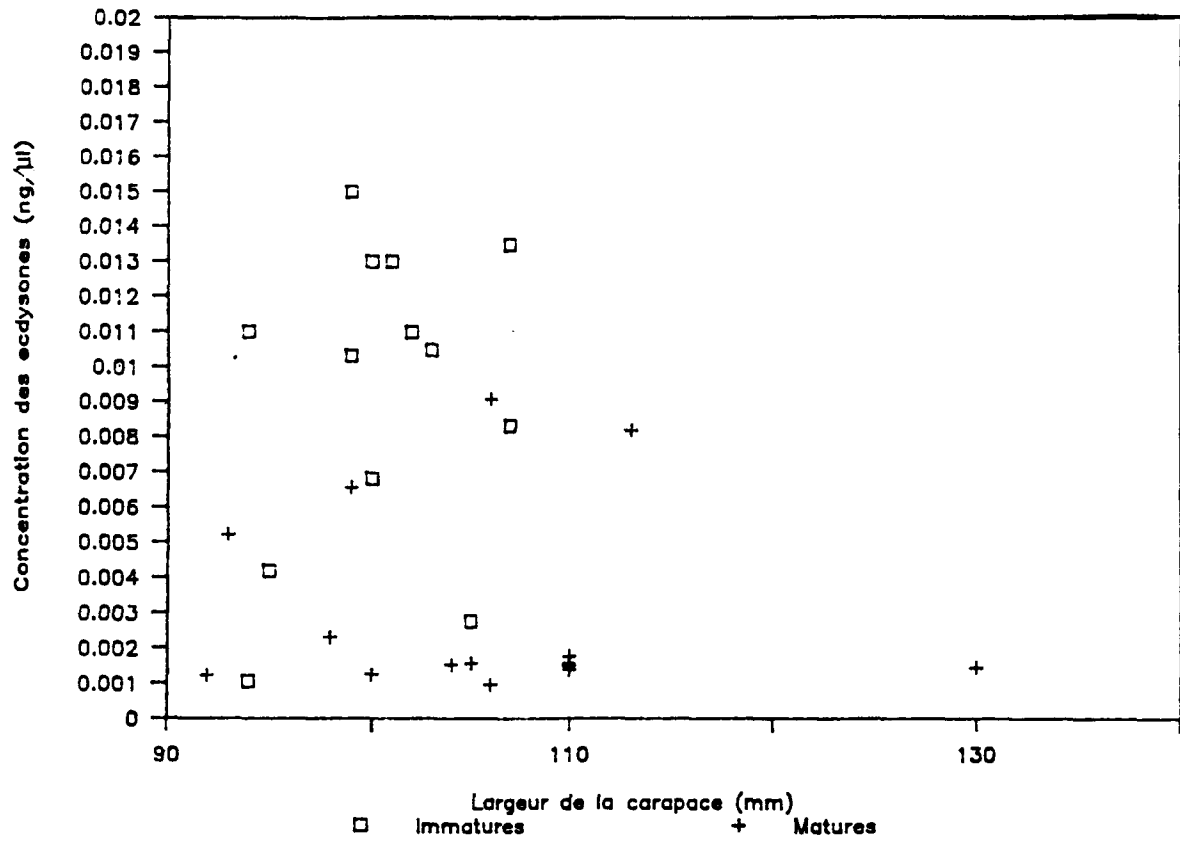


Figure 9. Concentration of ecdysones versus carapace width. Note the considerable overlap in the distributions of hormone concentrations for small-clawed and large-clawed males of similar body sizes. (From Cormier 1986 Fig. 3.8).

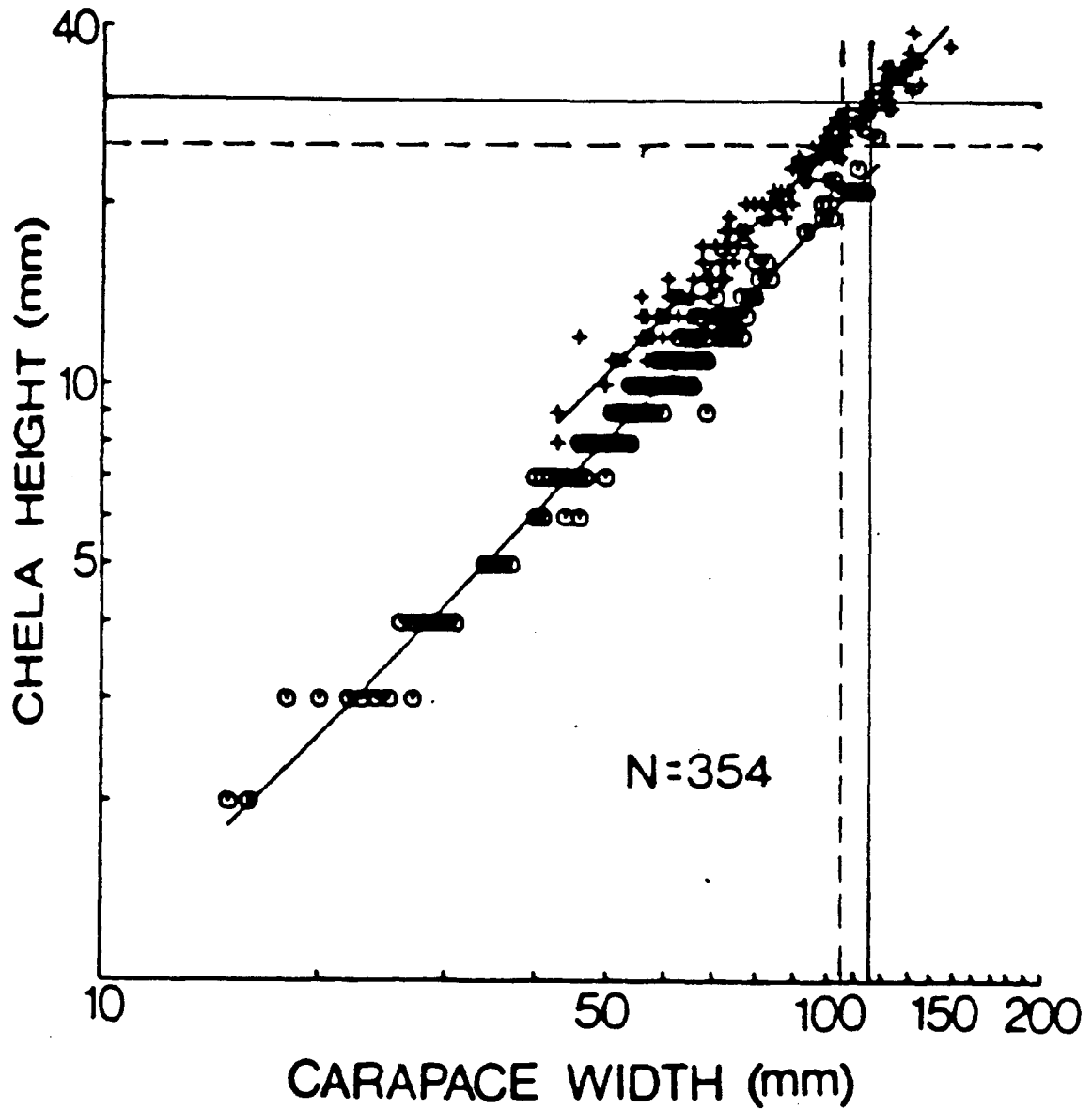


Fig. 10. Chela height and carapace width data for two male *C. opilio* from the Bering Sea with well developed second carapaces indicating imminent molting. By plotting the data on figure 9 from Somerton (1981), it can be seen that these two crabs are in the large-clawed cloud of animals.