

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

Earl G. Dawe, David M. Taylor, John M. Hoenig, William G. Warren, and Gerald P. Ennis

Department of Fisheries and Oceans, Science Branch, P.O. Box 5667, St. John's, Nfld. A1C 5X1, Canada

Robert G. Hooper

NICOS/Biology Department, Memorial University of Newfoundland, St. John's, Nfld. A1B 3X9, Canada

William E. Donaldson

Alaska Department of Fish and Game, 211 Mission Road, Kodiak, AK 99615, USA

and A. J. Paul and Judy M. Paul

Institute of Marine Science, Seward Marine Center, University of Alaska-Fairbanks, Box 730, Seward, AK 99664, USA

Dawe, E. G., D. M. Taylor, J. M. Hoenig, W. G. Warren, G. P. Ennis, R. G. Hooper, W. E. Donaldson, A. J. Paul, and J. M. Paul. 1991. A critical look at the idea of terminal molt in male snow crab (*Chionoecetes opilio*). *Can. J. Fish. Aquat. Sci.* 48: 2266–2275.

Whether or not male snow crab (*Chionoecetes opilio*) undergo a terminal molt when they develop large chelae is reviewed. Evidence supporting terminal molt includes laboratory studies in which large-clawed animals failed to molt and field studies which failed to find large-clawed males with mouth parts indicating imminent molting. Both studies were poorly documented. The field studies were largely conducted during inappropriate seasons and molt status based on a questionable mouth part stage. There is also an unsubstantiated claim that large-clawed animals fail to form limb buds for limb regeneration during the next molt and an inconclusive study of the degeneration of the Y-organ. We present new data against terminal molt including capture of large-clawed males with internal carapaces indicating impending molts, capture of two large-clawed animals with mouth parts indicating active premolting, recovery of two tagged large-clawed animals which molted while at liberty, and that the largest small-clawed animals usually are not large enough to account (through growth in a single molt) for the largest of the large-clawed animals. Also, one large-clawed male reportedly molted in captivity. We conclude that the existence of a terminal molt in male snow crab is not proven.

On reexamine si le crabe des neiges mâle (*Chionoecetes opilio*) entreprend une mue finale lorsqu'il développe de grosses pinces. Les indices à l'appui d'une mue finale comprennent des travaux en laboratoire dans lesquelles des crabes à grosses pinces n'ont pas mué et des études sur le terrain qui n'ont pas réussi à trouver des mâles à grosses pinces aux pièces buccales indiquant une mue imminente. Ces études sont mal documentées; les travaux sur le terrain ont été surtout effectués durant les mauvaises saisons et l'état de mue se fondait sur un stade de pièce buccale mal défini. On trouve également l'affirmation non démontrée selon laquelle les animaux à grosses pinces ne forment pas de bourgeons pour régénérer les membres durant la mue suivante et une étude non concluante de la dégénérescence de l'organe Y. Nous présentons de nouvelles données réfutant la mue finale : la capture de mâles à grosses pinces à la carapace interne indiquant une mue imminente, la capture de deux mâles à grosses pinces aux pièces buccales indiquant une pré-mue active, la recapture de deux crabes à grosses pinces étiquetés qui ont mué dans la nature et le fait que que les plus gros animaux à petites pinces sont trop petits pour atteindre la taille des plus gros à grosses pinces en une seule mue. En outre, on signale la mue d'un mâle à grosses pinces en captivité. Nous concluons que la mue finale du crabe des neiges n'est pas prouvée.

Received November 8, 1990  
Accepted June 6, 1991  
(JA795)

Reçu le 8 novembre 1990  
Accepté le 6 juin 1991

The idea that male snow crab (*Chionoecetes opilio*) undergo a terminal molt was suggested by Miller and O'Keefe (1981). Conan and Comeau (1986) claimed proof of a terminal molt and linked it with the development of large chelae. Donaldson and Johnson (1988) and Donaldson (1988) challenged these assertions and Conan et al. (1988a) and Conan et al. (1988b) defended the idea of 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

7 of the 38 workshop participants remain unconvinced. Recently, Conan et al. (1990) reiterated their conviction of a terminal molt.

Terminal molt means, according to Conan and Comeau (1986, p. 1718), that "morphometrically-mature" (i.e. large-clawed) males "extremely seldom, if ever, molt." The alternative is that these males molt commonly although possibly less frequently than "morphometrically-immature" (i.e. small-clawed) males. We find the terms "morphometrically-mature" and "morphometrically-immature" confusing because the

relationships of male chela morphometry to sexual maturity and mating capability remain unclear (Ennis et al. 1988, 1990). Because of this confusion, we prefer to use the terms "large-clawed" and "small-clawed" when referring to chela morphometry, and we concentrate only on the question of whether large-clawed males can molt.

Intermolt period is known to increase with the size of the animal for a variety of crustacean species. Therefore, any comparison of molting frequency between large- and small-clawed males must account for sizes of the animals in order to attribute differences in molt frequency to claw size.

The question of whether or not terminal molt exists has important implications for stock assessment and fishery management. If only small-clawed animals molt, then the proportion of the sublegal-sized population with large claws will never reach the Canadian legal harvest size of 95 mm carapace width (cw). 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. Also, if terminal molt exists, data on age composition of carapaces could be used to estimate mortality of large-clawed animals by catch curve methods.

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

### Statistical Treatment of Morphometric Data

A major portion of the first paper on terminal molt in male snow crab (Conan and Comeau 1986) was devoted to a principal component analysis and linear discriminant function analysis. This analysis appears to have been misunderstood by a number of biologists who work on snow crabs. Conan and Comeau measured six size variables on crabs and computed the principal components on log-transformed data. When the data were plotted on the first two principal component axes, they formed two clouds of points. The investigators assigned each animal to a cloud, but it is not clear from their paper how they did this. They apparently assigned animals to groups according to whether the observation was either above or below the first principal component axis (the abscissa) or an unspecified diagonal line. Either way, the separation was arbitrary because 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. However, Ennis et al. (1990) have shown that males from both clouds are capable of mating successfully. Therefore, we prefer to avoid terms which relate the clouds to states of maturity and use instead the descriptive terms "large-clawed" and "small-clawed" because the two groups can essentially be obtained more easily by looking at the relationship between chela height and carapace width. Conan and Comeau 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 six 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 only 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, 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, Newfoundland, fell in the cloud with large claws. It does not prove in any way that large-clawed animals are less likely to molt than small-clawed animals.

We 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 the six variables. Similarly, the calculation of the probability of an animal falling into a particular group, as described by Conan and Comeau (1986), pertains to the groups they subjectively defined. We stress the point only to make it clear that these methods do not provide objective, quantitative guidance in determining to which biological group a borderline data point has the greatest affinity.

Since Conan and Comeau's (1986) method of classification is complicated and essentially subjective, we have chosen to use a simpler subjective procedure which gives essentially the same results. We simply examine a scatter plot of chela height on carapace width and subjectively divide the data points into two clouds.

We also note that mixture analysis can be used to determine 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 (or lognormal) distributions (Warren 1990). If one could assume that these statistical populations represented biological groups, then one would have an objective method for separating animals using statistical principles (see Warren 1990 for an application of the method to a snow crab population).

### Molting in Captivity

Conan and Comeau (1986) kept 110 large-clawed and 24 small-clawed males in the laboratory for 10 mo 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 and details of the experimental conditions (holding facilities, density of animals, etc.) were not given. None of the 110 large-clawed males molted, while 16 of the 24 small-clawed males (67%) molted. 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 if the intermolt period increases with size. 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. However, it is worth noting that Conan et al. (1988a) and Conan et al. (1990) described

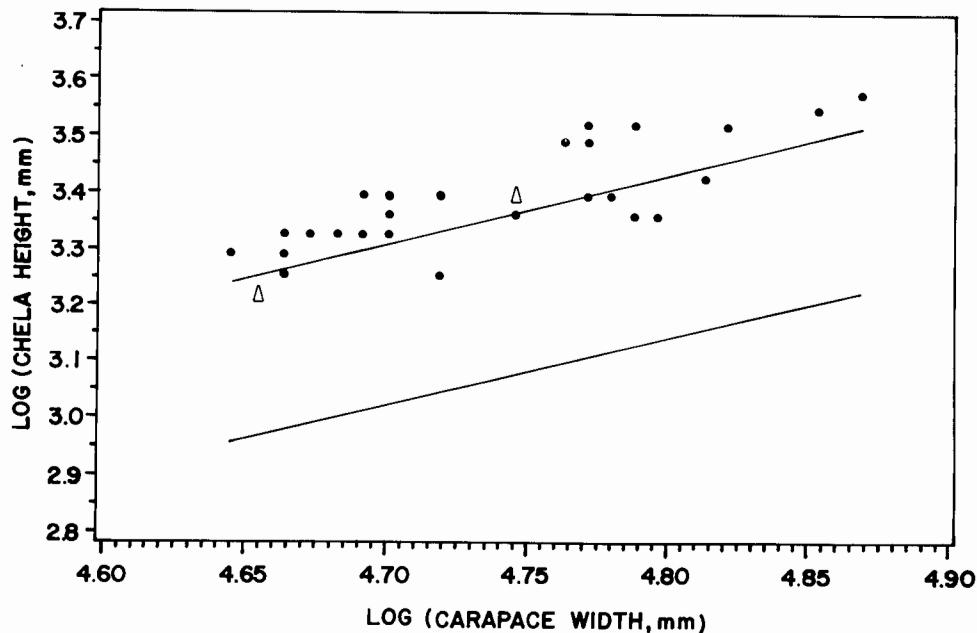


FIG. 2. Relationship between the logarithm of the chela height and the logarithm of the carapace width for Bering Sea *C. opilio* with well-developed second carapaces indicating imminent molting. Open triangles are from Dawe et al. (1990); closed circles are from the current study. The two lines, from Somerton (1981), indicate the central tendencies for clouds of large- and small-clawed animals.

TABLE 1. Samples of trawl-caught male snow crab collected from Conception Bay, Newfoundland, for examination of mouth parts.

(a) Sampling times and sample sizes				
Time	Sample size,			
	large-clawed males	small-clawed males	Large-clawed molters	Small-clawed molters
March 3, 1988	14	38	1	4
April 25 – May 5, 1988	216	168	0	27
May 12–23, 1989	819	315	1	15

(b) Information on large-clawed males in active premolt					
Date captured	Carapace width (mm)	Chela height (mm)	Chela width (mm)	Shell condition	Mouthpart stage
March 1988	60	12.4	10.2	Hard-shell	D <sub>1</sub>
May 1989	74	16.2	14.1	Hard-shell	D <sub>1</sub>

The D<sub>0</sub> stage is further divided into early D<sub>0</sub> and late D<sub>0</sub>, and the early D<sub>0</sub> stage is especially difficult to discern from the C stage. Conan et al. (1988a, p. 1502) also noted the difficulty in identifying premolt stage D<sub>0</sub>. Hence, we do not feel that the presence or absence of males in the D<sub>0</sub> stage can be used to address the question of whether or not there is a terminal molt.

We examined the mouth parts of 1049 hard-shelled, clearly large-clawed animals (molt status C and D) greater in size than 60 mm cw and collected by trawl in Conception Bay, Newfoundland, from March to May 1988 and May 1989 (Table 1a). Our definition of “clearly large-clawed” is any animal above the upper dividing line (based on 1987 data) in Fig. 3. We assume that the timing of our sampling was during the molting season which appears to occur from March to May–June in Conception Bay (Miller and O’Keefe 1981; Dawe et al. 1990). However, the timing of the peak of the molting season appears to be poorly known.

Of the 1049 hard-shelled, large-clawed animals examined in 1988–89, two were clearly committed to molting (Table 1b). Inspection of the relationship between chela height and carapace width leaves little doubt that these animals were large-clawed (Fig. 3). We also examined 521 clearly small-clawed animals in molt stages C to D (i.e. with hard carapaces) which had a similar size composition as the large-clawed animals (mean size of small-clawed animals = 73 mm with standard deviation = 9.0 mm; mean size of large-clawed animals = 76 mm with standard deviation = 13.5 mm). Of the small-clawed males, 46 (9%) were in D<sub>1</sub> or above. Clearly, we did not find a large percentage of either large- or small-clawed males in active premolt. However, it is notable that the sampling in the first part of the molting season (March) was extremely small (38 small-clawed and 14 large-clawed).

Conan and Comeau (1986) examined the mouth parts from 260 large-clawed males caught in trawls from July to December, and also from 110 males (presumably large-clawed) taken in traps at an unspecified time of year. The size distribution and shell conditions of the animals were not given. They stated that none of the individuals was “in a premolt ‘D’ or molt ‘A’ stage.” However, stage “A” (postmolt) sheds no light on the terminal molt question, since even animals molting to a terminal molt condition would undergo a postmolt stage. Conan and Comeau concluded that an upper, one-sided, 95% confidence limit on the proportion that ever molt is 0.8%, i.e. virtually nil. However, this analysis suffers from several flaws:

(1) Some animals may not molt every year. Also, not all the animals that will molt during the year will be in premolt stage at the exact same time. Therefore, Conan and Comeau’s procedure estimates the proportion of animals molting at the time of sampling, rather than during the whole year or during any subsequent period of life.

(2) The molting season for male snow crab appears to be in the late winter – spring (Miller and O’Keefe 1981; Conan et al. 1988a, 1988b); thus, Conan and Comeau looked for initiation

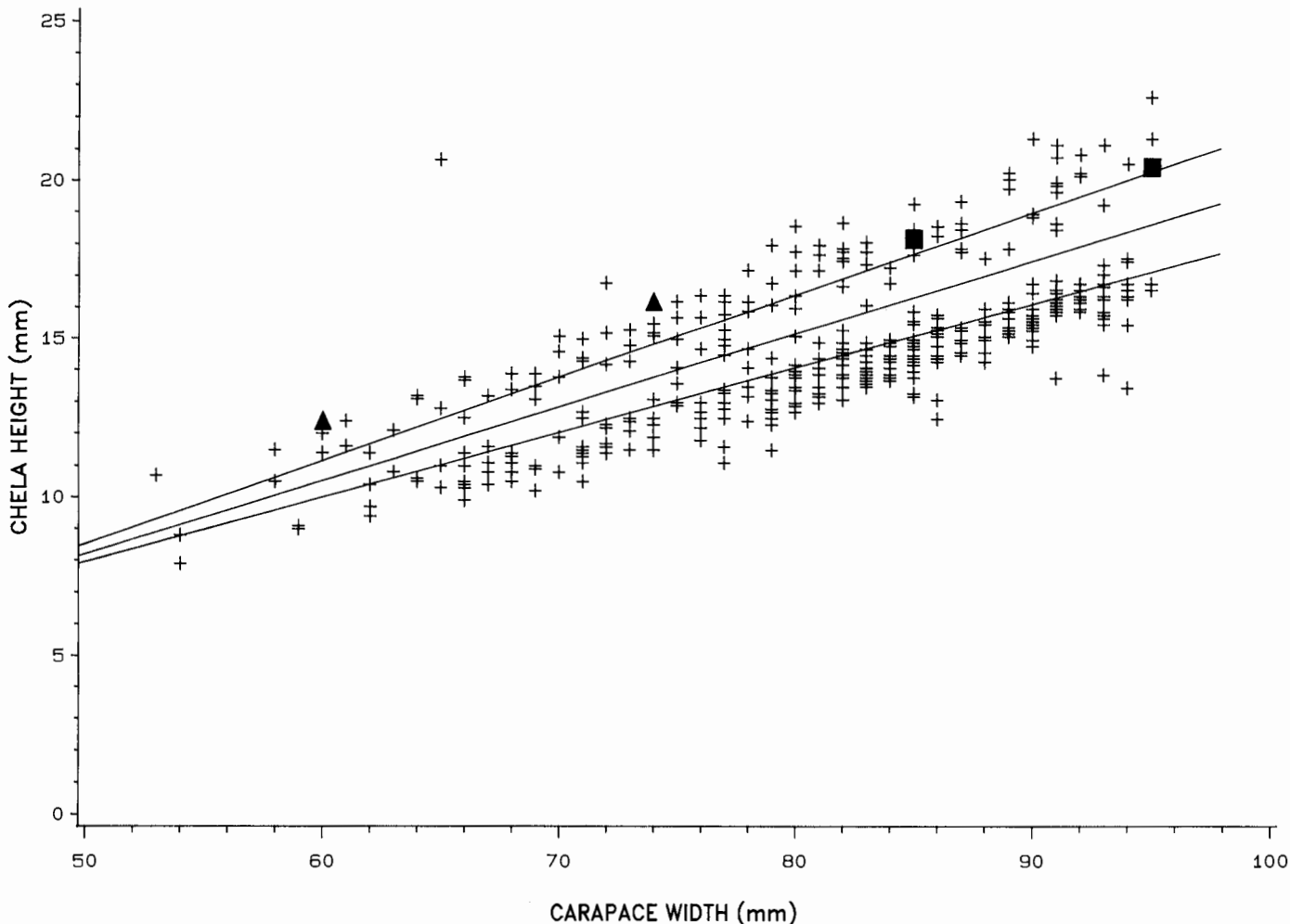


FIG. 3. Relationship between chela height and carapace width for a sample of 400 male *C. opilio* collected from Conception Bay, Newfoundland, in 1987 by trapping. The middle line appears to separate well the clouds of large-clawed and small-clawed animals. We refer to animals above the upper line as "clearly large-clawed" and those below the lower line as "clearly small-clawed." Lines were drawn by eye. Triangles refer to two animals with mouth parts indicating the D<sub>1</sub> phase of the molt cycle (i.e. clearly committed to molting). Squares refer to the morphometry at time of tagging of two animals which subsequently molted.

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 hard-shelled) are molting or about to molt; such information was not provided.

(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 that "pre-molt and molting immatures are frequently found in trawl catches." However, they did not specifically 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); they reported that no "pre-molt" 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 <sub>0</sub>

Note that no animals, large- or small-clawed, were found in active premolt stages D<sub>1</sub> to D<sub>3</sub>. Thus, even among the small-clawed animals, they did not find animals clearly committed to molting at the times they sampled. Animals in late D<sub>0</sub> molt in 8-12 wk whereas animals can remain in early D<sub>0</sub> for several months according to O'Halloran and O'Dor's (1988) findings

for laboratory animals. If Conan et al.'s males were in late  $D_0$ , most would apparently molt well before the molting season; therefore, most were presumably in early  $D_0$ . As explained above, we find that the distinction between the intermolt stage C and the beginning of premolt, especially early stage  $D_0$ , is dubious. Therefore, we feel that there was little evidence that either group of animals showed signs of imminent 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 soft-shelled (including crabs with brittle carapaces whose chelae are easily shattered by thumb pressure). If so, then these animals could not be expected to be preparing for another 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.

Conan et al. (1990) reported on additional observations of crab mouth parts. Their report suffers from the same deficiencies of their earlier papers: lack of detail concerning the specimens examined, sampling at an inappropriate time of the year, and apparent heavy reliance on stage  $D_0$  upon which to base interpretations. (They reported results for stages  $D_0$  and  $D_1$  combined; however, the  $D_0$  stage is unreliable in our opinion, and they sampled from October to November, i.e. 3–6 mo before molting, when they should have encountered very few animals in  $D_1$ .)

### Origin of the Largest of the Large-Clawed Males

Consider the scatter plot of trap-caught animals from Conception Bay, Newfoundland, in Fig. 4. The largest of the small-clawed animals was 102 mm cw except for a single animal of 116 mm cw. When animals of this size molt, they increase in size about 12 mm cw according to results from tagging studies carried out in Conception Bay (Taylor and Hoenig 1990). Thus, the animals would be expected to be about 114–117 mm cw when they reach their terminal molt, if terminal molt exists. The largest of the large-clawed animals was 134 mm cw, i.e., at least 20–30 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.

The gap between the largest of the small-clawed males and the largest of the large-clawed males in Conception Bay is about 32 mm. Similar diagrams have been produced for a wide variety of locations and years (Dawe et al. 1990). However, interpretation of such data depends critically on the availability of reliable estimates of growth increments (see below).

Conan and Comeau (1986) stated 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." Examination of that figure reveals, however, that the difference is actually about 19 mm as opposed to 10 mm. In a later paper, Conan et al. (1990) acknowledged that gaps larger than 30 mm occur and stated "A size increment at molt of 30 mm is well within the range of possibility for a 120 mm male. Miller and Watson's (1976) data suggest average growth increments of 20% or more." A 20% increment in size is not sufficient to account for the observed gaps in the scatter plots discussed by

Conan et al. (1990). Furthermore, Miller and Watson reported an average growth increment of 18.4% for captive animals larger than 57 mm (and larger average percentage increments only in size categories smaller than 57 mm). The greatest individual molt increment observed in their data on large (57–100 mm cw) experimental males was about 22%. Even if all males were capable of such large increments, this would result in a size increment of only 26 mm for a 120 mm cw male, i.e. not large enough to account for the observed gaps.

The available estimates of growth increments are quite variable, as shown in the table below:

Reference	Method	Average increment at 120 mm		
		Source	mm	%
Taylor and Hoenig 1990	Tagging	Conception Bay	12	10.0
Moriyasu et al. 1987	Aquarium		16	13.3
Miller and Watson 1976	Aquarium		22	18.4
Comeau et al. 1989	Modal analysis	Bonne Bay	30	25.0
G. P. Ennis, unpubl. obs.	Field/aquarium	Bonne Bay	29	24.1

The only estimates higher than those reported by Miller and Watson are for Bonne Bay, Newfoundland, and these are for animals considerably smaller than 120 mm. We estimated increments for Bonne Bay animals at 120 mm cw based on the assumption that the percentage increase is the same as for small animals. For this reason, the estimates are probably too high. Also, the estimate from Comeau et al. (1989) pertains to molting animals which retained the small-claw state. Comeau et al. (1989) reported that animals molting to the large-claw state have smaller increments which "agree with the size increment presented by Miller and Watson (1976) for larger crabs." Thus, available growth estimates do not account for the gaps in sizes observed in nature.

The large gap in size between the largest small-clawed animals and the largest large-clawed animals could also be explained by recruitment failure in the past, which could result in the absence of a given size group of small-clawed males. This appears to have been the case in Bonne Bay, Newfoundland, in the 1980s. Comeau et al. (1989) and Comeau et al. (1991) showed that the maximum size of the small-clawed males in Bonne Bay increased steadily over a period of several years. However, gaps within size–frequency distributions (which would also be evident if recruitment failed) are rarely encountered. Furthermore, it is unlikely that recruitment failure could account for the missing largest small-clawed animals in all the scatter plots examined (Dawe et al. 1990).

Another possibility suggested by Conan and Comeau (1986) is 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." The aquarium evidence to which Conan and Comeau referred suggests only that under crowded, artificial

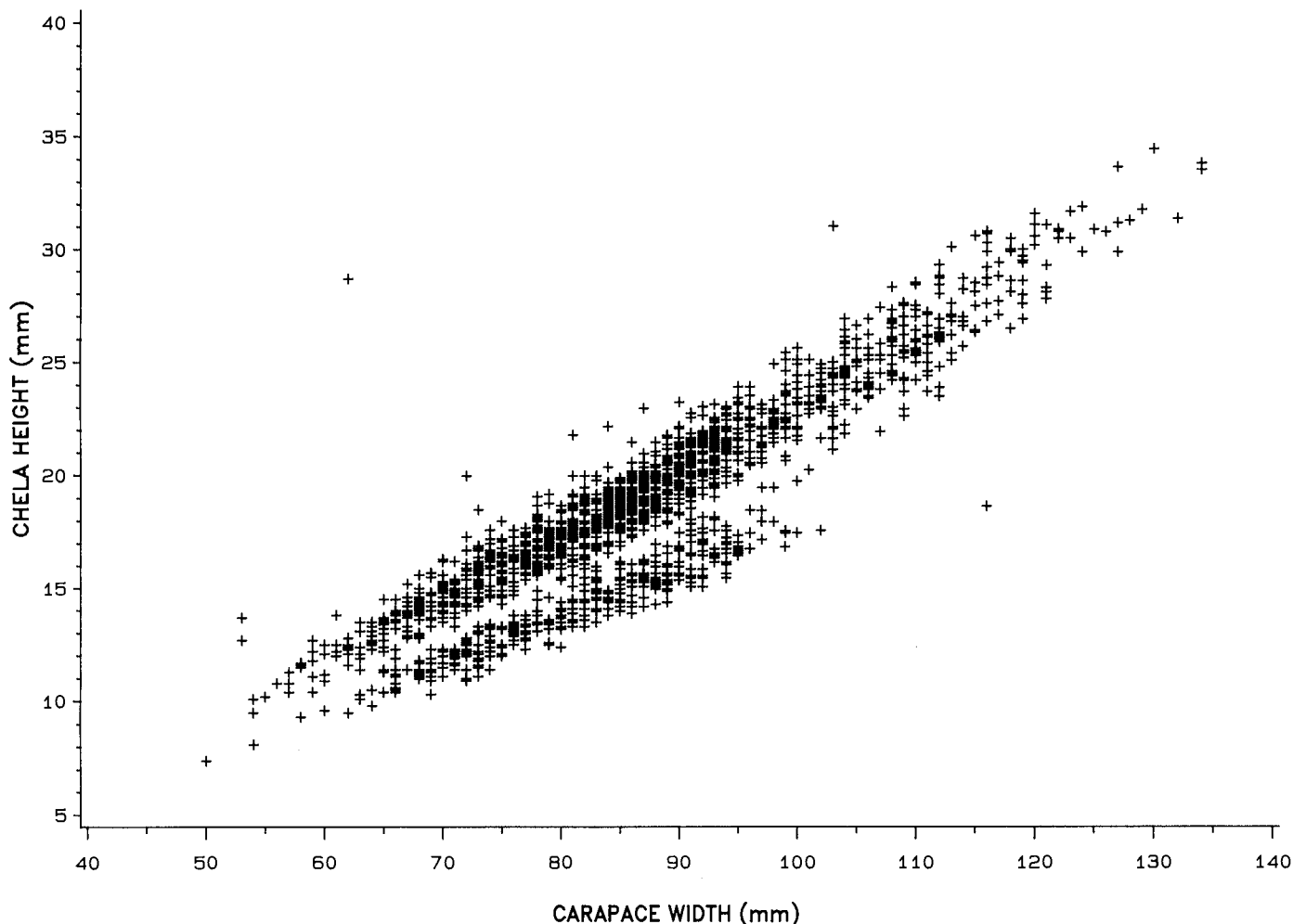


FIG. 4. Relationship between chela height and carapace width for male *C. opilio* from Conception Bay, Newfoundland, captured in traps in September–October 1989.

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 and may exhibit a “hiding behavior” by placing stones on their backs.

Conan et al. (1990) advanced one more explanation for the size gap between the largest of the small-clawed males and the largest of the large-clawed males. They suggested that the body size at which males make the transition in claw size may vary from year to year. In some years, the animals may develop large claws at a large body size, thus giving rise to extremely large, large-clawed males. In a subsequent year, the transition may be made when the males have a small body size, thus eliminating the largest of the small-clawed males from the population and widening the size gap. This is a new and speculative hypothesis concerning size-synchronized molting and the effects of annual variability. The only supporting evidence given by Conan et al. is that, in the Gulf of St. Lawrence, the magnitude of the gap has differed according to three field surveys conducted at widely separated times. A mixture of sampling gears was used in these studies, so the results are not interpretable. Another study which reported yearly changes in the magnitude of such gaps was described by Comeau et al. (1991) who showed that the maximum size of small-clawed males and the minimum size of large-clawed males in Bonne

TABLE 2. Comparison of times at liberty for recaptured animals tagged in large-clawed versus small-clawed condition in May 1988 in Conception Bay, Newfoundland.

Time at liberty (mo)	Large-clawed (no. of recaptures (%))	Small-clawed (no. of recaptures (%))
4–5	33 (49)	4 (21)
13–17	34 (51)	15 (79)

Bay changed over a period of several years in the 1980s. They interpreted these changes as a response to changing crab densities. In our opinion, these observations do not provide evidence for Conan et al.’s (1990) proposed annual variability in the size at transition to the large-claw state.

### Growth of Tagged Animals

A tagging study was initiated in 1987 in Conception Bay, Newfoundland, with one of the goals 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 (Fig. 3). Only animals which clearly lay above the upper line or below the lower line in Fig. 3 were tagged in 1988 and 1989. T-bar tags were applied in the



TABLE 3. Tag and recapture data for two "clearly large-clawed" animals from Conception Bay, Newfoundland, which molted while at liberty.

Characteristic	Animal 1	Animal 2
Tag No.	G2138	G3172
Date tagged	May 14, 1988	May 11, 1988
Carapace width at tagging (mm)	85	95
Chela width at tagging (mm)	16.3	17.8
Chela height at tagging (mm)	18.2	20.5
Shell condition at tagging	New-hard-shelled	New-hard-shelled
Date recaptured	Sept. 8, 1989	Sept. 8, 1988
Time at liberty (d)	482	120
Carapace width at recapture (mm)	100	103
Change in size while at liberty (mm)	15 (18%)	8 (8%)
Chela width at recapture (mm)	?	Unavailable <sup>a</sup>
Chela height at recapture (mm)	23.1	Unavailable <sup>a</sup>
Shell condition at recapture	New-hard-shelled	New-hard-shelled

<sup>a</sup>Specimen was returned without claws by fisherman.

ecdysial suture according to methods described by Taylor and Hoenig (1990). To date, 67 large-clawed and 19 small-clawed tagged animals have been recaptured from the first experiment in 1988 (Table 2). Two large-clawed animals (Table 3; Fig. 3) and 13 small-clawed animals molted while at liberty. Note that the small-clawed animals recovered were at liberty for longer periods of time, on average, than the large-clawed animals (Table 2), thus providing the small-clawed animals more opportunity to molt than the large-clawed animals.

One of the large-clawed males which molted 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 4 mo at liberty were sufficient for the crab to fast for a month, molt, and recover to a hard-shelled condition before recapture (Taylor et al. 1989). This presumes that molting took place in June which, as already noted, is quite possible for snow crab in Conception Bay. The other large-clawed male recaptured 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. Dawe et al. (1990) noted that the growth increments of these two large-clawed males were consistent with growth estimates from tagging studies.

## Other Evidence

### Hormones and Y-Organs

Conan et al. (1988a, 1988b) suggested 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 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 and A. Boghen are studying morphology of the Y-organ in males and report the following (A. Boghen, Université de Moncton, April 9 and 26, 1991, pers. comm.): there is a full or partial transformation of the Y-organ sometime after the male snow crab attains large-claw status and this transformation seems to correspond to the degenerative process described for other species; however, the results are not definitive although they are consistent with the

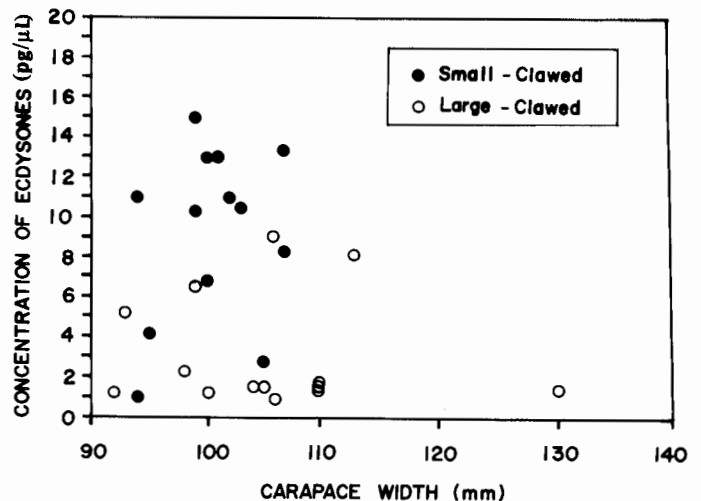


FIG. 5. Concentration of ecdysones versus carapace width for male *C. opilio* (from Cormier 1986, fig. 3.8). Note the considerable overlap in the distributions of hormone concentrations for small-clawed and large-clawed males of similar body sizes.

idea of a terminal molt. They believe that the Y-organ continues to show some activity for an unknown period of time after the molt to the large-clawed state.

Levels of crustecdysone, and condition of the Y-organ, are probably related to 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 5 (from Cormier 1986, fig. 3.8) suggests that over the size range from 92 to 114 mm cw, small-clawed males have higher levels of crustecdysone on average than comparably sized large-clawed males. However, there is a great deal of overlap of the distribution 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.

It is possible to establish experimentally the physiological ability of a crab to molt. For example, Havens and McConaughy (1990) questioned the conventional wisdom that female blue

crab (*Callinectes sapidus*) undergo a terminal molt. As part of their study, they ablated the eyestalks of captive animals to eliminate the production of molt-inhibiting hormone. They concluded that mature females were physiologically capable of molting (the Y-organ continues to produce the molting hormone), since their experimental animals all molted (except three which died shortly after the ablation.)

### Limb Regeneration

Conan et al. (1988b, p. 48) stated that large-clawed males never regenerate limbs, while small-clawed males do. They cited no references and provided no data. Consequently, there is no way to evaluate this. We note that the absence of regenerating limb buds in large-clawed males could only be considered significant if small-clawed crabs of the same size have regenerating limbs. Conan et al. (1990) reported that they found no reference to any experiment showing that limbs of postpuberal (i.e. large-clawed) majids can regenerate, but they did not report finding any experiments showing the contrary, either. It would be possible to bring similarly sized large- and small-clawed males into the laboratory, remove a limb, and look for signs of limb regeneration.

### 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* were sufficient to conclude that males of all species in the family Majidae undergo a terminal molt. This view was challenged by Donaldson and Johnson (1988) and Donaldson (1988). In response to Donaldson and Johnson, Conan et al. (1988a) conceded that terminal molt of males may not exist in all species of the genus *Chionoecetes* and, in referring to the rather minor degree of differentiation in claw size occurring in *Chionoecetes* (relative to that in other majids), stated that "This may suggest that *Chionoecetes* have not yet fully made the choice for a terminal molt as other genera of majids." They further acknowledged that some populations of *C. opilio* may undergo a terminal molt, while others do not. However, in Conan et al. (1990), it is again suggested that terminal molt occurs throughout the genus without providing any new evidence for the other species of *Chionoecetes*. That conclusion is not consistent with the observation of Donaldson and Johnson that large-clawed male *C. bairdi* molted in holding pens.

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 within the family is not accepted to be the case. Therefore, circumstantial evidence from other species of majids does not provide strong evidence for (or against) terminal molt in *C. opilio* males.

### Conclusions

We conclude from our review of the available literature that the existence of a terminal molt, or a greatly reduced molting frequency, in large-clawed or large-bodied or old male snow crab (*Chionoecetes opilio*) is probable but not well supported

by the data or the analyses. We have presented direct evidence, albeit limited, which is not consistent with the idea of a terminal molt in males of this species. Further research is required to resolve the question, but clearly the conclusion that a terminal molt exists in male snow crab is untenable at this point.

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 molting history (as indicated by shell condition) are factors which affect the molting of individuals. These factors must be accounted for if a valid quantitative comparison of molting prevalences is to be made between large-clawed and small-clawed male snow crab.

### Acknowledgments

We thank Scott Akenhead, Don Parsons, and Michel Comeau for comments on an earlier draft and Eric Bataller and Andrew Boghen for sharing unpublished results with us. David Somerton graciously provided source material from his 1981 paper on tanner crab. Paul Collins and Noel Cadigan helped with the graphics.

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