

Functional Maturity and Terminal Molt of Male Snow Crab, *Chionoecetes opilio*

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Bivariate and multivariate analyses of allometric relationships between chela size and carapace size of snow crab, *Chionoecetes opilio*, show that mature males are recognizable by morphometry. The most simple procedure is to plot logarithms of chela height (C_h) against logarithms of carapace width (L_c). Data from mature and immature males fit into two distinct ellipses with parallel major axes. The discriminant function $Y = -0.78893 \log_e L_c + 0.614488 \log_e C_h + 1.76051$ will assign individuals to the correct groups in 99% of cases (for mature males: $Y > 0$). Spermatophores are present in the vasa deferentia of all males larger than 60 mm L_c . The molt to morphometric maturity occurs later at L_c sizes ranging from 60 to 120 mm; it is identified as final. Only morphometrically mature males larger than 96 mm L_c have been observed to mate efficiently with multiparous females in intermolt and be functionally mature. In the catch, as many as 40% of males larger than the minimal legal size of 95 mm can be immature.

L'analyse bivar  e et multivar  e des relations d'allom  trie entre la taille de la pince et la taille de la carapace du crabe des neiges, *Chionoecetes opilio*, permet d'identifier ais  ment par morphom  trie les m  les matures. Une m  thode simple consiste    porter graphiquement les logarithmes des hauteurs de pinces (C_h) en fonction de ceux des largeurs de carapace (L_c). Suivant l'  tat de maturit  , les donn  es s'aggr  pent en deux ellipses d'axes majeurs parall  les. La fonction discriminante $Y = -0.78893 \log_e L_c + 0.614488 \log_e C_h + 1.76051$ permet d'identifier des individus dans 99% des cas (pour les m  les matures: $Y > 0$). Des spermatophores sont pr  sents dans les canaux d  f  rents des m  les de taille L_c sup  rieure    60 mm. La maturit   morphom  trique appara  t apr  s une mue terminale qui s'effectue entre $L_c = 60$ et 120 mm. Seuls les m  les morphom  triquement matures de taille L_c sup  rieure    95 mm s'accouplent efficacement avec des femelles multipares en intermue et sont fonctionnellement matures. Jusqu'   40% des m  les captur  s, dont la taille L_c est sup  rieure    la taille minimale l  gale de 95 mm sont immatures.

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The snow crab, *Chionoecetes opilio* (Brachyura, Majidae), is one of the most valuable species harvested in Atlantic Canada. Only males are commercially exploited by the fishery, and a minimum legal size of 95 mm carapace (cephalothorax) width (L_c) has been enforced since 1973. This size is the smallest acceptable by processors for mechanized meat extraction. Male snow crab are generally believed to mature and mate before they reach 95 mm L_c (Powles 1968; Watson 1970). Watson (1970) concluded that male snow crabs reach maturity between 51 and 72 mm L_c . Since 1970 it has frequently been assumed that the snow crab stocks were protected from recruitment overexploitation because females were not harvested and because all males were thought to mature and have the opportunity to mate before they reached the minimum legal size.

Teissier (1933, 1935) and Hartnoll (1963) have shown that male majid crabs show a differentiation of the chelae, a change in allometry, when they reach maturity. When the logarithms of chelae measurements are plotted against the logarithms of some standard measurements of carapace size, this results in three segments of straight lines. The first segment, for small crabs, is characteristic of the "prepubertal" stage; it leads,

without discontinuity, to an angular point marking a transition. The prepubertal molt leads to the second segment which is characteristic of the pubertal stage. The third segment is parallel to the second, but shifted in ordinate. The discontinuity between the second segment and the third is caused by the pubertal molt or molt to maturity during which the chelae increase considerably in volume in one abrupt step. The molt to maturity may occur over a large range of carapace size. In many species of majid crab, large immature males may be two to three times larger than the smallest mature ones. The molt to maturity is believed to be the last one, the "final" or "terminal molt," in most species.

Powles (1968), Watson (1970), and Coulombe et al. (1985) have observed such a differentiation in the claw of *C. opilio* at maturity. The overlap of the immature/mature carapace size reported by Watson (1970) is short. In contrast, Powles (1968) and Coulombe et al. (1985) observed a wider overlap of carapace sizes, suggesting that immature crabs could be found in the commercial catch at sizes greater than 95 mm L_c . However, Coulombe et al. (1985) questioned whether these morphometrically "immature" crabs larger than 95 mm L_c were actually functionally immature.

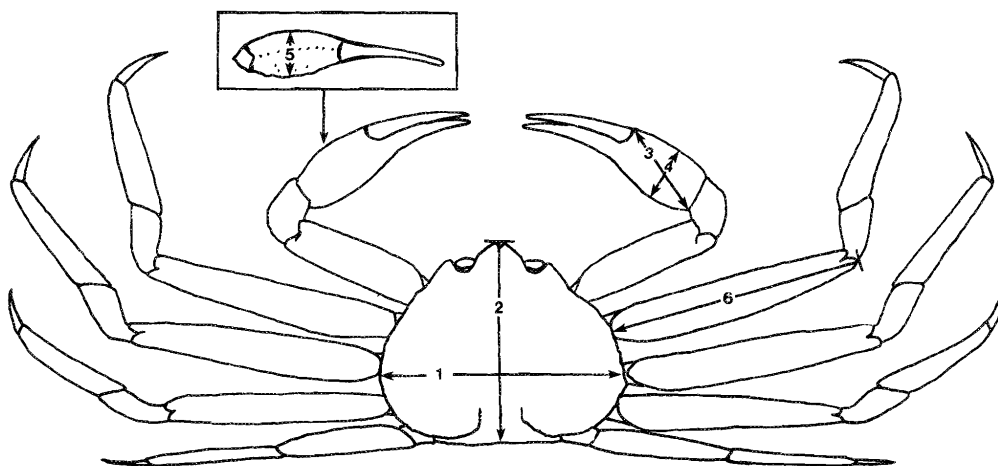


FIG. 1. Standard measurements taken on male snow crab: 1, cephalothorax length; 2, cephalothorax width; 3, chela length; 4, chela height; 5, chela width; 6, 2nd pereiopod meropodite length. Dorsal view of chela is shown in rectangle.

Somerton (1980) developed a tool for estimating the size of sexual maturity in crabs. His technique is based on a computer algorithm for iteratively fitting two regressions lines starting simultaneously from the two extremities of the range of observations. However, Somerton's technique was not designed to respond to the goal of precisely attributing individual observations to the mature versus immature subgroups. Somerton (1981) later mentioned that in *Chionoecetes* it is difficult to distinguish by simple means mature males from immature ones on the basis of allometry alone.

We have analyzed morphometric data on maturity of male snow crabs and compared these results with observations on the presence of spermatozoa in the vasa deferentia and observations on functional maturity made on mating pairs in their natural habitat and in an aquarium. Our goal was to develop a simple nondestructive tool to allow efficient discrimination of mature males from immature ones for fishery management surveys. We analyzed the discriminant value of several standard measurements made on the chela and the carapace for identification of mature and immature individuals. We first used multivariate tools allowing for synergic discriminatory effects of several standard measurements. The multivariate approach also allowed identification of the two most efficient parameters for a simple bivariate discrimination tool. We attempted to develop a technique based on Fisher's discriminant function to efficiently assign individuals to either of the two categories by a criterion of highest probability.

To verify the existence of a terminal molt at the onset of maturity, we thereon applied the discriminant function for identifying mature males in the catch. We checked for the occurrence of molting within the group of mature males by aquarium and field experiments.

Materials and Methods

Sea Sampling

Male snow crabs were collected by trawling. Previous authors (e.g. Watson 1970) have used trapping to collect large animals and beam trawling to collect small- and medium-sized ones. We used a Bay of Biscay *Nephrops* otter trawl with a 25-m opening designed for capturing semiburied crustacean species. The *Nephrops* trawl catches snow crabs of a wide range of sizes efficiently. We believe that it is less selective for

immature and recently molted crabs than traps. Conan and Maynard (1986) have shown by underwater television that small crabs tend to bury themselves in soft bottom sediment. The trawling was conducted over the summer of 1984 in Baie des Chaleurs and over the snow crab fishing grounds in the southwest Gulf of St. Lawrence.

A sample of mating snow crab pairs was collected by SCUBA divers (G. Y. Conan and R. W. Elner, DFO, Biological Station, St. Andrews, N.B.) in Bonne Bay (Newfoundland) during May 1984 at depths of 20–35 m during the spring inshore mating migration described by Hooper (1986) and Taylor et al. (1985). An additional sample of commercial sized crabs was obtained from Baie de Chaleurs using standard commercial traps.

Aquarium Experiment

During April 1985, 18 males of 66–116 mm L_c were selected for sizes within and above the range of maturity differentiation described by Watson (1970) as 51–72 mm L_c . The males were placed in an 18-m³ tank holding 17 multiparous females, i.e. females having already mated and spawned at least once (Paul 1984). Six females bore bright orange, freshly layed eggs and 11 females bore older eggs showing conspicuous eye spots. The bottom of the tank was covered with small gravel and large rocks as observed on natural mating grounds in Bonne Bay. The temperature ranged from 2 to 3°C and the salinity was 32. Observations on mating behavior were made on a 24-h basis over a period of 14 d. An underwater video camera ("Subsea" system) and a recorder were used for continuous observations. Male crabs were measured for biometric characteristics, and at the end of the experiment their vasa deferentia were dissected for identification of spermatophores.

In a long-term rearing experiment, 110 morphometrically mature males and 24 morphometrically immature ones of the same size range were kept for 10 mo from November 1984 to September 1985, through the period of "white" crabs (i.e. molting) in the commercial catch. The crabs were monitored for occurrence of molts.

Biological Analysis of Data

Biometric measurements were made to the nearest milli-

metre using a modified vernier caliper (Watson and Wells 1970). Six standard measurements were taken on snow crabs as indicated in Fig. 1.

All males in the aquarium experiment and a subsample of males from the sea sampling were used for direct reading of physiological maturity: a smear of the vasa deferentia was examined at low magnification for the presence of spermatophores under a light transmission microscope (Powles 1968).

For reading the molt stages we have used the simple technique described by Drach and Tchernigovtzeff (1967), and successfully adapted to snow crabs by Moriyasu and Mallet (1986). The endite of the second maxilliped is removed *in vivo* using a pair of forceps and is observed in transmitted light under a low-resolution microscope. The presence/absence and morphology of developing setae inside the old tegument allow easy and accurate identification of molters (A stage) postmolts (B), intermolts (C), and premolts (D). The operation is harmless for the crab.

Statistical Analysis of Data

We used a principal component analysis (PCA) on log transformations of the measurements to identify which variables (measurements) were redundant and could be discarded and which variables were the most representative of the size factor and of the sexual differentiation factor (Conan et al. 1985). A log transform is used to linearize the allometric data:

$$C_w = a(w)L_c^{b(w)}$$

which becomes

$$\log_e C_w = \log_e a(w) + b(w) \log_e L_c$$

where C_w = chela width, L_c = carapace width, a and b are parameters, and w is the index for width. The transformation normalizes the dispersion of points around the linear regression lines and stabilizes the variances of the dispersion of points along the regression lines. These conditions are required by the PCA.

The graphics output of the PCA is set as described by Lebart et al. (1979). The data are centered and reduced. The observations are projected onto the planes defined by the principal components taken two at a time. The variables are also projected onto the plane, as vectors of unit length. A circle of radius 1 (unity) is centered on the origin of axes, and it represents the maximal extent of the vectors if they are fully defined within the plane considered. Dummy observations (observations that do not take part in the computation of the PCA, but are projected onto the planes) may be used for identifying locations within the swarms of data points. In this application, we used as dummy observations sets of measurements made on males in mating couples observed in the wild.

We further proceeded from the output of the PCA with a bivariate discriminant analysis for observations made on the two variables chosen for best sharing two properties: (1) identified in the PCA as being suitable for discriminating mature from immature individuals (i.e. best representing the sexual differentiation factor versus the growth factor) and (2) most suitable for practical measurements. Fisher's bivariate discriminant analysis can be visualized as an orthogonal (rectangular) projection of the data points from the plot of chela sizes versus carapace width onto a line perpendicular to the line discriminating (separating) most adequately the two swarms of points to be contrasted. The new coordinates of the data points

TABLE 1. Percentage of variance explained by the principal components analysis for observations from Baie des Chaleurs ($N = 217$).

Axis	Percentage of variance
1	98.05
2	1.14
3	0.55
4	0.13
5	0.11
6	0.03

read along the perpendicular are called discriminant scores. An implicit *a priori* condition is that the variance and the covariances between variables (here, chela size and carapace width) be the same for the two swarms contrasted (Cooley and Lohnes 1971). We compared the variance/covariance matrices by a test described in Morrison (1976). The sets of data points that are contrasted must be identified before the analysis. The output is (1) a linear function allowing "recognition" of individuals in further analysis, (2) an estimate of the variance of coordinates on the orthogonal projection (discriminant scores) allowing calculation by *t* test of the cumulative probability for any individual to pertain to either group, and (3) an estimate of the probability of misclassification in future analysis, based on the overlap of the two distributions on the orthogonal projection.

We also used a more traditional tool, the Powles (1968) index of morphometric maturity, in which the chela length is multiplied by the claw width. The index is plotted against carapace width on a log - log scale for identification of immature versus mature males. It can be shown that if the relationships between chela width (C_w) and cephalothorax width (L_c) and claw height (C_h) and L_c are allometric, then the relationship between the index $C_w \cdot C_h$ and L_c is also allometric:

$$C_w = a(w)L_c^{b(w)}$$

$$C_h = a(h)L_c^{b(h)}$$

$$I = C_w \cdot C_h = a(w) \cdot a(h) \cdot L_c^{b(w) + b(h)}$$

$$I = aL_c^b$$

The justification for a composite index using the product of two measurements would be to reduce multivariate data to a simple bivariate case without restricting the information to bivariate measurements.

We set confidence limits on observed proportions of molters for checking how substantial was their presence within categories. Confidence limits on non-zero proportions are set by reading isopleths for the binomial distribution (Dixon and Massey 1957). Confidence limits on observed null proportions are set by assuming a Poisson distribution for occurrence of rare events:

$$p(x) = \frac{e^{-m} m^x}{x!}$$

where p is the probability of x occurrences in the sample and m is the mean number of occurrences in a distribution of samples of given size n within the population. At the $p = 0.05$ level, a zero observation is obtained when m approximates 3, and the proportion of events (individuals of given category) within the population is

$$P = \frac{m}{n}$$

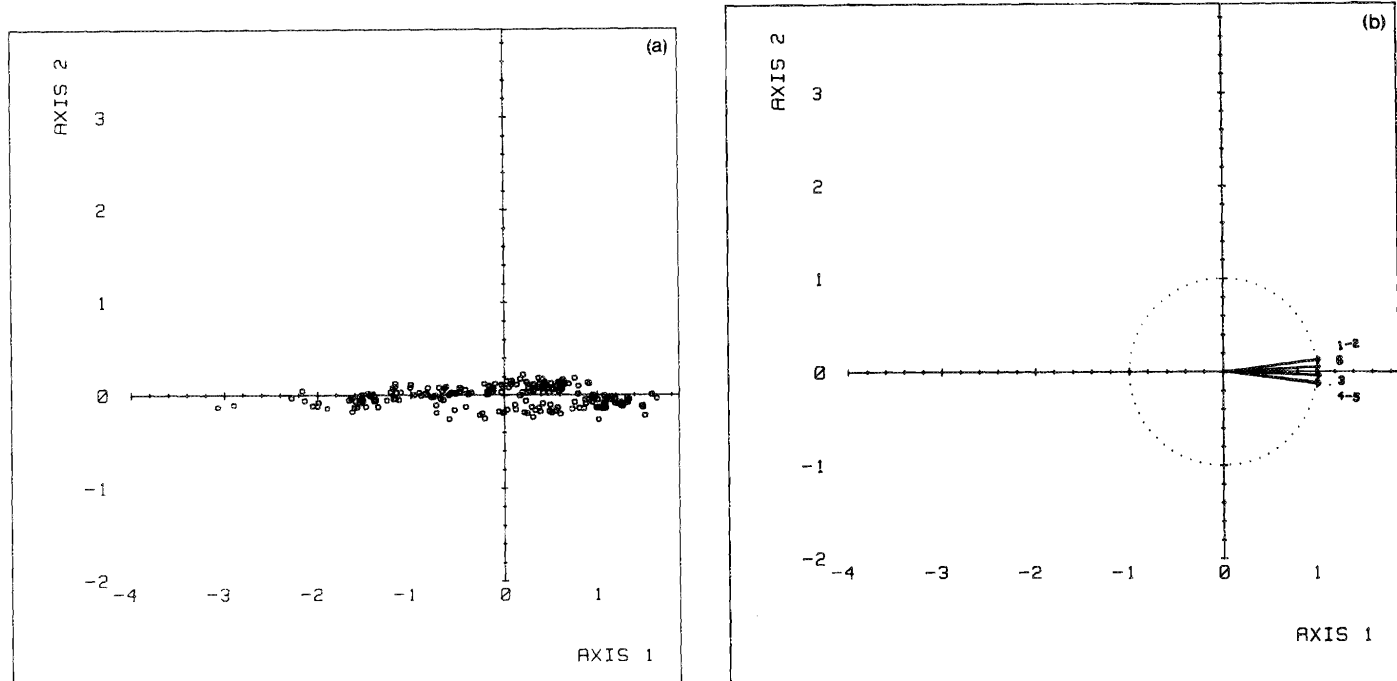


FIG. 2. Principal component analysis on six variables (carapace length, carapace width, chela length, chela height, chela width, and 2nd pereiopode meropodite length). (a) Representation of observations ($N = 217$). Two discrete swarms of points elongated along axis 1 are attributed to immature males (positive direction of axis 2) and mature males (negative direction of axis 2). (b) Representation of the variables as vectors (1, carapace width; 2, carapace length; 3, chela length; 4, chela height; 5, chela width; 6, 2nd pereiopode meropodite length). Variables 1 and 2 are redundant, as are variables 4 and 5. Variables 1 and 2 are orientated along the major axis of the ellipses and represent a size factor. Variables 4 and 5 are the most efficient in discriminating the two swarms of points and are correlated with a sexual differentiation factor.

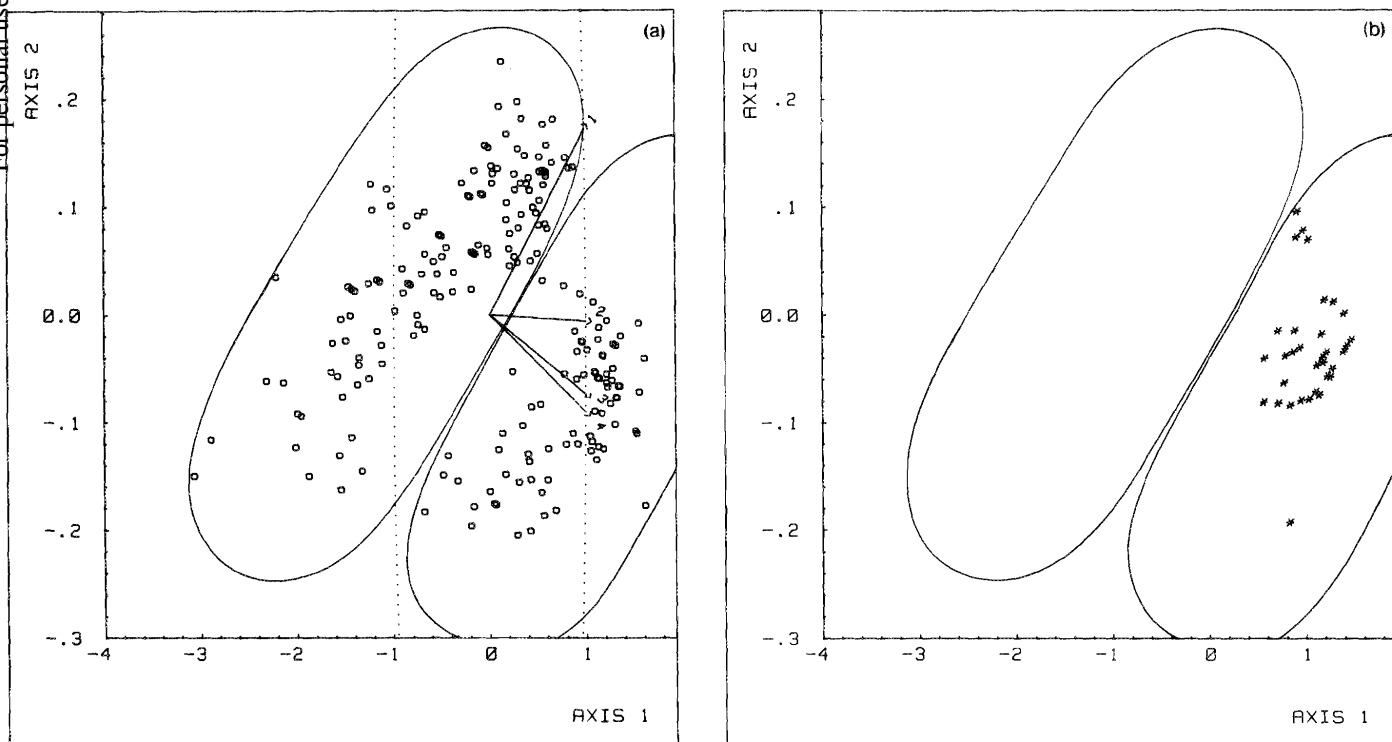


FIG. 3. Principal component analysis on four variables (1, carapace width; 2, chela length; 3, chela height; 4, chela width). (a) Simultaneous magnified representation of the variable as vectors and of the observations ($N = 217$). Variables 1 and 2 are parallel to the major axis of the swarms of points and represent a size factor. Variables 3 and 4 are the most efficient in discriminating the two swarms of points and are correlated with a sexual differentiation factor. (b) Numbers represent the projection of dummy observations: measurements taken on males from mating pairs from Bonne Bay. The arbitrarily drawn contours outline the location of observations from Baie des Chaleurs. The dummy observations fit into the contour of the lower swarm of points, and are therefore identified as representing mature animals.

TABLE 2. Correlations between variables and principal axes of the principal components analysis for observations from Baie des Chaleurs ($N = 217$).

Axis	Carapace		Chela		2nd pereopode meropodite length	
	Width	Length	Length	Height	Width	
1	0.990443	0.989806	0.995751	0.99678	0.988837	0.985572
2	0.123476	0.126781	0.04683	0.11891	0.13429	0.050159
3	-0.05236	-0.05686	-0.01163	-0.02131	-0.01857	0.0161517
4	0.010479	0.0099	-0.07745	0.013512	0.036758	0.007312
5	0.000775	-0.00045	0.012826	-0.06157	0.049822	-0.00138
6	-0.03059	0.029059	-0.00008	-0.00023	-0.000492	0.000604

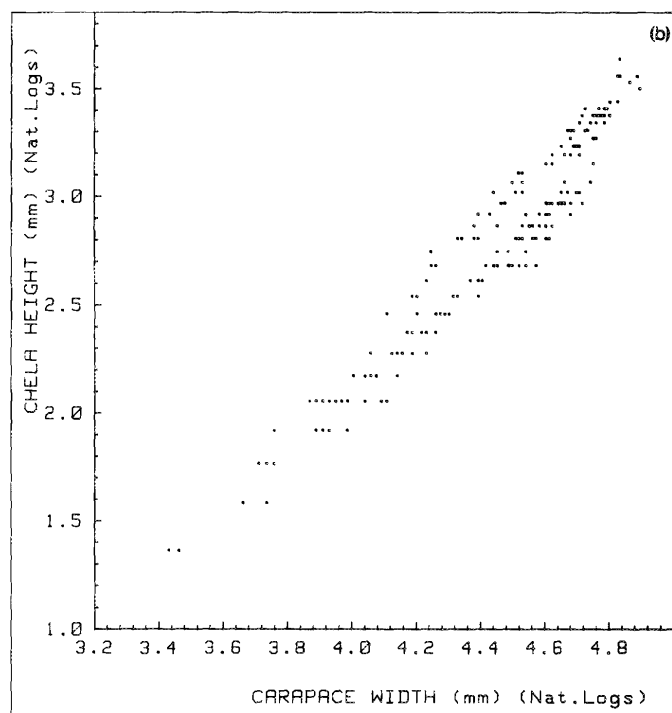
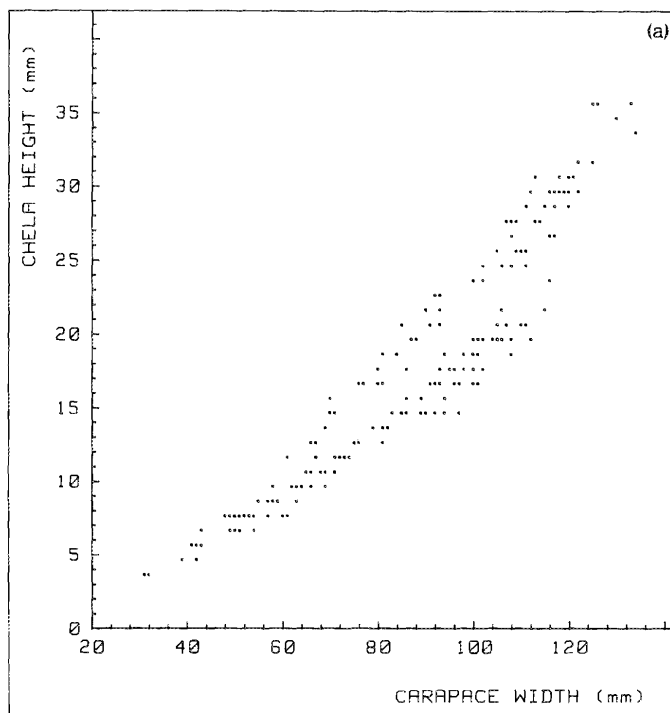


FIG. 4. Relationship between chela height and carapace width for male snow crabs from Baie des Chaleurs. (a) Linear scale ($N = 217$); (b) logarithmic scale ($N = 217$).

All statistical procedures were conducted on an HP 9845B computer using custom designed programs. The programming technique for the discriminant analysis can be found in Davies (1971).

Results

Component one explains most of the variance in the PCA (98%) (Table 1). Component two explains only 1.14% of the variance, about twice as much as component three. Therefore, for further graphic analysis in the PCA we proceeded only with projections in the plane defined by the first and second components. On the projection of the observations (Fig. 2a), two swarms of points are elongated at a slight angle with the first axis. On the projection of the variables (Fig. 2b), all variables appear to be almost entirely defined within the plane: the plane will suffice for graphic analysis. Variables 1 and 2 overlap and are redundant; one measurement of either carapace width or length would be sufficient. Variables 1 and 2 have the same orientation as the major axes of the swarms of points; they efficiently represent the growth factor. Variables 4 and 5 (chela

height, chela width) are highly correlated between themselves and define the most open angles with variables 1 and 2 (less correlated); variables 4 and 5 are almost redundant and they are the most efficient to discriminate the two swarms of points by representing the sexual differentiation factor. This graphic analysis is confirmed in Fig. 3a where observations and variables are represented simultaneously on a magnified non-isotropic scale.

When the data from Bonne Bay (independent measurements made on males from mating couples in their natural environment) are projected as dummy observations in Fig. 3b, the points are accurately positioned within the contours defined by the lower swarm; we therefore identify this swarm as data points representing functional adults.

Carapace width and chela height were selected as the most suitable variables for a bivariate analysis because (1) they appeared to efficiently represent, respectively (Table 2), the size (major axis of swarms of points) and the sexual differentiation and (2) they are easy to measure. Graphs of chela height versus carapace width for Baie des Chaleurs data are presented on an arithmetic scale in Fig. 4a and on a logarithmic scale in Fig. 4b.

The two swarms of points are conspicuous on both graphs. The logarithmic transformation linearizes the shape of the swarms and stabilizes the variance. The relationships between chela height and carapace width are therefore typically allometric. The two swarms in Fig. 4b could be circumscribed in two elongated ellipses with parallel major axes. The swarms widely overlap in abscissa and ordinate. The major axes apparently differ in ordinate intercept but not in slope. There is no conspicuous angular point suggesting a prepubertal molt along the swarm of immature points.

A graph of the Powles index versus carapace size on a logarithmic scale provided identical results, and did not allow better discrimination between swarms of points. For this set of data the Powles index, as compared with a simple bivariate plot, does not enhance visual discrimination between the swarm of points because the chela length and width measurements are highly correlated and carry almost redundant information (Fig. 2b).

The points pertaining to either of the mature/immature groups identified on the PCA plots for Baie des Chaleurs data were processed in a bivariate discriminant analysis which was 99% efficient in allocating points to the right groups, although the variance/covariance matrices for the two sets of points were significantly different at the 0.01 level. We generalized the discriminant analysis to 784 data points from the whole southwest Gulf of St. Lawrence (Fig. 5) in order to develop a discriminant function representative for the whole fishery. The data points had previously been attributed to immature/mature groups by graphic PCA. The resolution of the cutting line statistically fitted by the analysis remained good although the variance along the Y and X variables increased due to slight local variations in allometry (Fig. 6a). Morphometrically immature males ranged in size from 31 to 120 mm L_c and morphometrically mature males from 52 to 137 mm L_c . The histograms of the discriminant scores (orthogonal projection of the points on either side of the cutting line onto a perpendicular) slightly overlap, possibly due to initial a priori misclassification of a few points (Fig. 6b) in the graphic PCA. However, the analysis forecasts that 99% of the observations will be correctly assigned to either group (Table 3) when the discriminant function $Y = -0.7889259 \log_e L_c + 0.6144883 \log_e C_h + 1.7605142$ is used. If $Y < 0$, the individual is immature; if $Y > 0$, the individual is mature. Alternatively, the function $C_h = 0.015554 L_c^{1.5787}$ can be plotted on graph paper. All points of chela height versus carapace width plotted below this line will identify immature individuals, and all points above the line will identify mature ones. The probability for an individual to pertain to either group can be calculated as follows:

$$\text{immatures: } Z = (S - 244.5752)/4.6488$$

$$\text{matures: } Z = (S - 222.9641)/4.6488$$

where Z is a standard normal deviate and S is the discriminant score where

$$S = 104.7737 \log_e L_c - 81.6074 \log_e C_h.$$

The two-tailed cumulative probability can be read from tables of the standard normal deviate. The variance/covariance matrices for the two sets of points were significantly different at the 0.01 level. Results of discriminant analysis for alternative measurements used as standards by other authors are presented in Table 3 as a reference for analysing data sets defined by different measurements (Powles 1968; Watson 1970).

TABLE 3. Discriminant functions allowing identification of morphometrically mature versus immature males as a function of carapace width (L_c), chela height (C_h), chela length (C_l), and chela width (C_w).

Discriminant functions (immature: $Y < 0$; mature: $Y > 0$)	%	Normal deviate indicating probability for an individual to pertain to either group	
		Immatures	Matures
$Y = -0.7915457 \log_e L_c + 0.6111111 \log_e C_l + 1.3591466$	99.1	$Z = (136.7477 \log_e L_c - 245.9584)/4.730$	$Z = (136.7477 \log_e L_c - 105.5755 \log_e C_l - 223.5834)/4.730$
$Y = -0.7889259 \log_e L_c + 0.6144883 \log_e C_h + 1.7605142$	99.0	$Z = (104.7737 \log_e L_c - 81.6074 \log_e C_h - 244.5752)/4.6488$	$Z = (104.7737 \log_e L_c - 81.6074 \log_e C_h - 222.9641)/4.6488$
$Y = -0.802818 \log_e L_c + 0.5962242 \log_e C_w + 1.9761339$	98.9	$Z = (93.4585 \log_e L_c - 69.4083 \log_e C_w - 240.4603)/4.5715$	$Z = (93.4585 \log_e L_c - 69.4083 \log_e C_w - 219.5614)/4.5715$

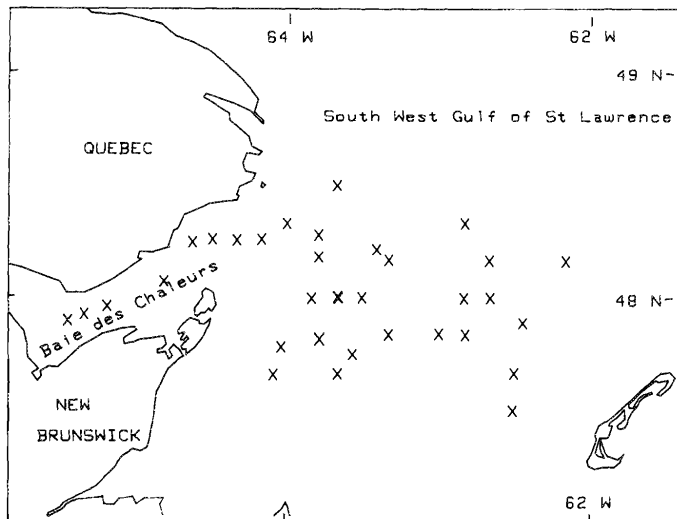


FIG. 5. Geographic location of sampling sites in Baie des Chaleurs and southwest Gulf of St. Lawrence.

An additional minimal size constraint increases the efficiency of the discrimination. In Fig. 6a, it appears that the swarm of points representing immatures is slightly curved. This results in a few points towards the lower range of sizes being located above the discriminant line and therefore classified erroneously as pertaining to mature animals. To avoid this artefact, we suggest identifying all males smaller than 50 mm L_c as immature.

The discriminant function was used for identifying morphometrically mature males in the sea sampling data and the aquarium experiment. All morphometrically mature males bore spermatophores in their vasa deferentia, but the smaller ones (below 95 mm) bore many more spermatophores than the larger ones, except in Bonne Bay. Small morphometrically mature males identified as "pygmies" by fishermen usually bore highly turgid vasa deferentia, also found in some large males from couples collected by diving in Bonne Bay. All males larger than 60 mm bore spermatophores independent of their morphometric state of maturity.

In the aquarium experiment, 12 males were morphometrically mature, ranging in size from 74 to 116 mm L_c , and 6 were morphometrically immature, ranging in size from 66 to 98 mm L_c . All males bore spermatophores. Complete mating behavioral sequences (Watson 1970, 1972) were observed for three couples of morphometrically mature males and hard-shell females, immediately after hatching of an old brood and prior to extrusion of the new brood. None of the females molted. Seven morphometrically mature males initiated mating behavior with hard-shell females but were disturbed by bachelors. Two morphometrically mature and six morphometrically immature males did not initiate any mating behavior. The morphometrically immature 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. Morphometrically mature males initiated mating behavior (precopulatory embrace) with five of six females bearing orange, recently spawned eggs, but the embrace never lasted more than 30 min and copulation was never achieved.

Of the 110 morphometrically mature males maintained in the aquarium from November to September, none molted. At a 95% probability level we may therefore assume that no more

than 2.7% may have molted under similar conditions. Meanwhile, 16 of 24 morphometrically immature ones molted, which yields confidence limits at the 95% level of 46–85% for molting incidence within the immature group under similar conditions.

Of 260 morphometrically mature males sampled from the catch in *Nephrops* trawls from July to December at depths ranging from 40 to 160 m and of 110 males caught in traps, no individuals were ever found in a premolt "D" or molt "A" stage. At the 95% level we may therefore assume that no more than 0.8% of morphometrically mature males in the wild initiate molting. Premolt and molting immatures are frequently found in trawl catches.

Discussion

Identification of Morphometrically Mature Males

The bivariate discriminant function developed for logarithms of carapace width and chela height allows efficient identification of morphometric maturity of males. The variance/covariance matrices of the mature and immature swarms of points significantly differed, but the discriminant analysis was robust enough to provide accurate results. Bivariate discriminant analyses on logarithms of chela length and chela width versus carapace width provide very similar results, and the associated discriminant functions (Table 3) may also be used, although in our experience precise measurements are more difficult to take.

The discriminant function appears to be efficient for data originating from a geographic area as wide as the southwest Gulf of St. Lawrence (Fig. 5). It may be robust enough to allow discrimination in most other geographic stocks, although some geographic variation in allometry may be anticipated (Davidson et al 1985).

Precise measures are required with a modified caliper such as that described by Watson and Wells (1970); otherwise, the variances of the variables increase and the tool may lose considerable discriminative power. Coulombe et al. (1985), for instance, concluded that the immatures could not be distinguished easily from the mature individuals by morphometry; however, the dispersion of the sets of points they provided was much greater than ours, and they used as an equation for the cutting line a constant ratio between claw size and carapace width for the slope and a zero value for the elevation (Watson 1970). Even for field identification this approach is incompatible with an allometric relationship between variables. For field identification we would suggest a more rigorous approach: a simple arithmetic plot of chela height (C_h) versus carapace width (L_c) and check for location above (mature) or below (immature) the predrawn curve $C_h = 0.01555 L_c^{1.5787}$ obtained from the equation of the cutting line in the discriminant analysis. If the measurements are precise enough, 99% of the identifications will be accurate.

Morphometric versus Functional Maturity

The equivalence of the presence of spermatophores in the vasa deferentia and morphometric maturity, defined by a change of allometry in the chela size versus carapace width, was questioned, with reason, by Coulombe et al. (1985). Watson (1970) apparently found that all males bearing spermatophores were also morphometrically mature; this was in an

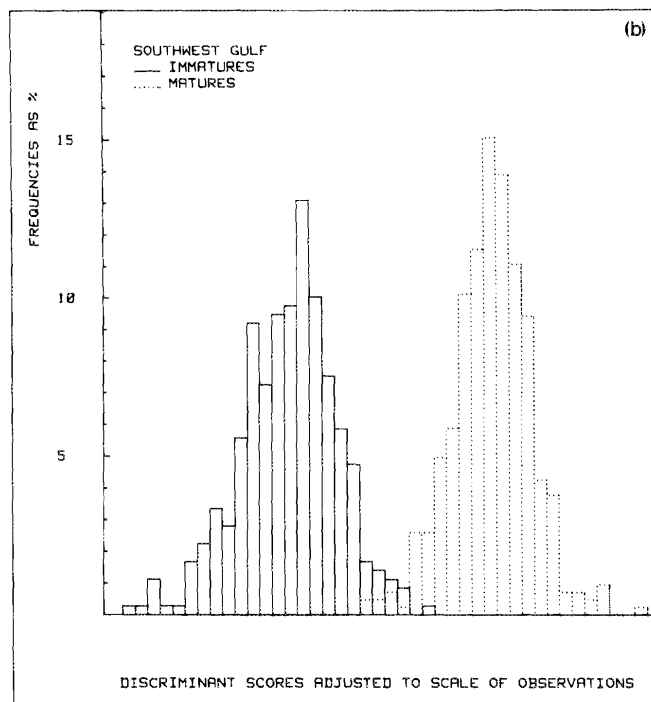
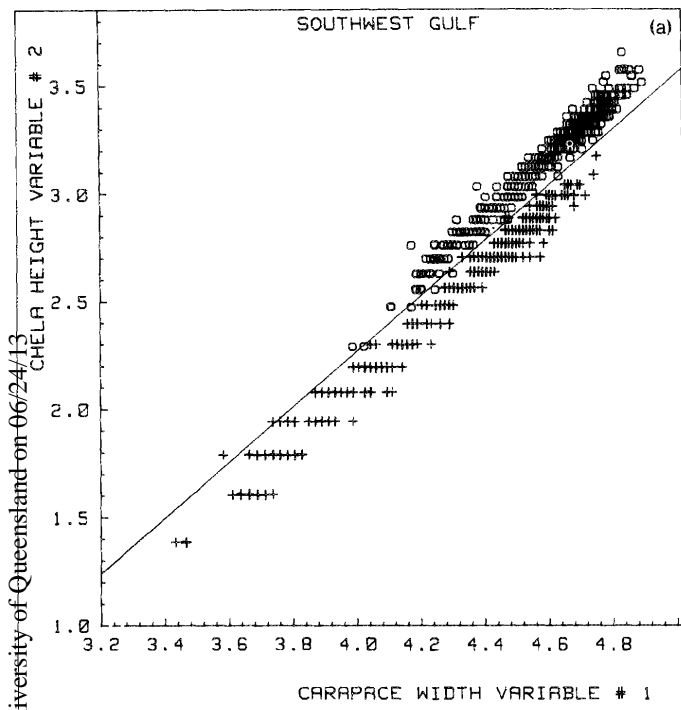


FIG. 6. Discriminant analysis of observations from southwest Gulf of St. Lawrence. (a) Representation of the cutting line separating the two swarms of points. The discrimination is about 100% efficient (\circ = mature males, $+$ = immature males). $N = 784$. (b) Histograms of discriminant scores (projection of points on a line perpendicular to the cutting line). There is very little overlap. The discrimination is about 100% efficient. $N = 784$.

early stage of exploitation of the fishery. Our data provide different information. In the subsamples of dissected males we occasionally found morphometrically mature individuals with mature spermatophores in the vasa deferentia, while all morphometrically immature males larger than 60 mm L_c already bore spermatophores.

Our observations made while SCUBA diving in Bonne Bay and during aquarium experiments provide a biological interpretation for the differentiation of the claw of males at maturity. We observed that males carry the females for up to 3 wk before mating. The female, which is much smaller than the male, is held facing her mate. The chela of the male firmly grasps two to three legs along one side of the female. There is strong competition between males in mating pairs and numerous aggressive bachelors at this time. The female is carried in one claw extended outwards high above ground while fencing takes place with the other claw extended outwards in the opposite direction. If we compare the position of the dummy observations representing males collected in the field during the act of mating (Fig. 3b) with the contours of the volume defining the swarms of points of the morphometrically mature and immature animals collected by trawling (Fig. 3a), we may observe that all functionally mature animals are confined towards the larger carapace sizes within the swarm. Some functionally mature animals, however, have small chelae which position them close to the immature swarm. The dummy observations in the PCA indicate that the size factor modeled by the carapace size of the male is probably of great advantage in this competition. However, the contribution of the sexual differentiation factor modeling differentiation of secondary sexual characters is a prerequisite. The differentiation of the chela in mature males as a secondary sexual character is probably functionally justified by the mating embrace behavior. However,

the size of the claw does not seem to provide an advantage in the competition between males. As shown by our data, males with a chela at the smallest portion of the range but of otherwise large body are successful in achieving precopulatory embrace and most likely in mating.

It used to be assumed that all males larger than the minimum commercial size of 95 mm L_c reached functional maturity at sizes ranging from 51 to 72 mm L_c , grew, and had the chance to mate at least once before being captured. This assumption is usually made after referring to Watson (1970), but is challenged by two of our observations:

(1) Morphometrically immature individuals can be found up to a size of 120 mm L_c . In certain samples, up to 40% of the males larger than 95 mm L_c may be immature. In the aquarium experiment, none of the morphometrically immature males that bore spermatophores and were as large or larger than active morphometrically mature males initiated any precopulatory behavior.

(2) Our data show that morphometrically and physiologically mature males as small as 60 mm L_c can be captured by trawling. However, we have no indication that these crabs are functionally mature, i.e. able to carry females during the long precopulatory embraced phase and copulate. The smallest male in copulating pairs found in Bonne Bay had a carapace width of 96 mm. Similar size for onset of functional maturity has also been reported by Paul et al. (1983) for the closely related species *C. bairdi*. Small mature males called "pygmies" by the fishermen usually have their vasa deferentia loaded with spermatophores, while larger ones reveal much smaller quantities of genital products. The production of spermatophores seems to be a continuous process with continuous accumulation prior to mating. The vasa deferentia of pygmy males appear never to be emptied by mating. There is no indication that the pygmies

do efficiently contribute to mating and reproduction.

In heavily harvested stocks (southwest Gulf of St. Lawrence), large morphometrically mature males above commercial size frequently bear few spermatophores; this was never observed in lightly exploited stocks such as Bonne Bay and never reported in old records from the southwest Gulf (Powles 1968). We believe that in heavily exploited stocks the proportion of males caught as soon as they reach morphometric maturity becomes very high. Little time, if any, is given to the functionally mature males for accumulating spermatophores and efficiently mating.

A New Interpretation of the Life Cycle of *C. opilio*

Our biological observations and our morphometric analysis bring new interpretations of the life cycle of *C. opilio*. The mating pattern we observed is similar to that described by Paul (1984) for *C. bairdi*. We definitely observed morphometrically mature males mating with hard-shell multiparous females immediately after hatching of the previous brood and without any sign of molting. We believe that previous observations by Watson (1970, 1972) of females molting prior to mating actually recorded mating of primiparous (virgin) females. This is an exceptional event which occurs during the terminal molt to maturity of the female. Mating of hard-shell males and multiparous females is the common rule in the wild.

It was previously believed (Watson 1970) that (1) male *C. opilio* simultaneously reached morphometric maturity (differentiation of the claw) and gonad maturity (production of spermatophores), (2) all males were mature beyond a critical carapace width of 60 mm, and (3) they kept on growing beyond the molt to maturity. We suggest that production of spermatophores is already initiated for most males when they reach 60 mm L_c but that the "true" functional maturity is eventually reached much later. A special molt, which coincides with the differentiation of the claw for grabbing the female, is required. This morphometric maturity is reached around 60 mm by very few individuals and can be delayed to sizes of up to 120 mm L_c (Fig. 4b). Such individuals are functionally immature, do not even demonstrate behavioral precopulatory sequences, and actually tend to hide under stones in an aquarium when mating activity is taking place, although they all carry spermatophores in their vasa deferentia. Such life history patterns are the common rule among majid crabs (Hartnoll 1963 for review), and so far the genus *Chionoecetes* was considered an exception. We also believe that among morphometrically mature animals only the larger ones (approximately 95 mm and more) are functionally mature, i.e. apt to grab a female, carry it around (precopulatory embrace), and mate. This agrees with independent observations made by Taylor et al. (1985) although their interpretation of the facts differs.

The twofold range of sizes (60–120 mm) over which morphometric maturity is reached is not exceptional; ranges as wide as three- to four-fold have been described in other species of majid crabs. The molt to morphometric maturity in majid crabs of other genera is always described as the last molt or terminal molt.

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. The wider gap sometimes reported between these sizes and attributed to growth is most likely a sampling artifact. 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 the mature ones, as shown by the aquarium experiments, or do not appear on the mating grounds, as shown by Bonne Bay diving observations. The *Nephrops* trawl allowed us to catch a more representative sample of the population.

Our tank-rearing observations and molt stage identifications do confirm that morphometrically mature males extremely seldom, if ever, molt. We never observed molting of morphometrically mature males while morphometrically immature ones of the same size range molted. We never found morphometrically mature males in premolt stages, while morphometrically immature males in premolt stages were common in the *Nephrops* trawl catch. We strongly suspect that the common assumption that male *C. opilio* keep growing after the molt to morphometric maturity is an illusion resulting from incorrect identification of morphometrically mature individuals.

Implications for Fisheries Management

As suggested by Comeau (1985), one practical consequence of this peculiar life history is that the legal size of 95 mm does not "protect" the fecundity of the stock. Many male snow crabs are caught by the fishery before they mature at sizes ranging up to 120 mm. Further, there is no evidence that sublegal morphometrically mature males can efficiently mate in their natural environment with multiparous females. Such males have been described to mate with primiparous females in an aquarium (Watson 1970), but no mating involving primiparous females has been observed by us in the wild, and it is likely to be a very rare event. This situation is not necessarily critical; most species start to be harvested before maturity. However, one must be aware that the reproductive potential of a harvested snow crab stock will not remain as high as in a virgin stock even if the fishery is restricted to males and if these males all have a carapace width larger than a minimal legal size of 95 mm. The proper legal size for avoiding the capture of mature males would be 120 mm, but this would not allow for a harvested biomass sufficient to sustain a fishery.

Another practical consequence is that a minimal legal size is not an efficient tool for achieving the best yield per recruit. The harvestable stock comprises two types of individuals within most of the size range: immature males that grow and mature ones that have stopped growing. At an early state of exploitation, most individuals captured in the southern Gulf of St. Lawrence were mature ones accumulated over many years. As the fishery developed, old mature males tended to be fished out. The proportion of "whites" (animals recently molted to maturity) increased. The proportion of immatures about to reach maturity also increased within the catch. In terms of yield per recruit, all individuals that stop growing should be immediately harvested. This cannot be efficiently regulated by size because (1) the terminal molt is reached by different individuals at any of the sizes harvestable, (2) recently molted individuals are of poor commercial quality, and (3) individuals that stopped growing below the legal minimum size are not harvested and will never contribute to yield.

To protect fecundity of the stock and to achieve maximal yield per recruit, a selective gear catching only mature animals should be designed. This goal is not impossible; we have observed in an aquarium and in situ by diving that mature and

immature crabs display different behavioral patterns and segregate. Several leads are presently being studied.

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