A Computer Technique for Estimating the Size of Sexual Maturity in Crabs[1]

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A new computer technique for estimating the size of 50% sexual maturity from crab
morphometric data is described. Using nonhierarchical cluster analysis, crabs are assigned to
either of two maturity groups based on the size of one body dimension relative to another. The
size of 50% maturity is then estimated by using nonlinear regression to fit a logistic function to
percent maturity and size estimates. The size of 50% maturity in the eastern Bering Sea was
estimated to be 102.8 and 101.9 mm (carapace length) for male and female *Paralithodes
camtschatica* and 114.7 mm (carapace width) for male *Chionoecetes bairdi*. These estimates are
similar to estimates for these species obtained previously by other techniques.

Key words: crabs, growth, sexual maturity, *Paralithodes, Chionoecetes*

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On trouvera dans l'article qui suit la description d'une nouvelle méthode par ordinateur
grâce à laquelle la taille où 50% des crabes sont sexuellement matures peut être estimée à
partir de données morphométriques. Par le truchement d'une analyse de groupes non hiérar-
chiques, les crabes sont classés dans l'un ou l'autre de deux groupes de maturité, selon la taille
d'une partie du corps en relation avec celle d'une autre partie. La taille de 50% de maturité est
ensuite estimée par régression non linéaire qui adapte une fonction logistique aux estimations
de pourcentage de maturité et de taille. La taille de 50% de maturité dans le secteur oriental
de la mer de Béring a été estimée à 102,8 et 101,9 mm (longueur de carapace) chez *Paralithodes
camtschatica* mâle et femelle, et 114,7 mm (largeur de carapace) chez *Chionoecetes bairdi* mâle.
Ces estimations sont semblables à celles déjà obtenues chez ces espèces par d'autres méthodes.

SIZE of sexual maturity is primary information needed
for managing the harvest of a species of crab. Al-
though maturity can be determined either by histo-
logical examination of the gonads or by inspection for
the presence of secondary sexual characteristics, these
techniques sometimes prove to be time consuming and
difficult to apply in the field. Consequently, many in-
vestigators have recognized that crabs may change
shape at maturity and have chosen the relatively easy
task of measuring several morphological features on a
number of specimens and determining at what size the
relative growth of these features changes (Wallace et
al. 1949; Watson 1970; Brown and Powell 1972; Kanno
1972). In this paper I briefly review the use of this
method and discuss a computer program which esti-
mates the size of sexual maturity from morphometric
data.

Hartnoll (1978) recently described the manner in

which the relative growth of various features of a
crustacean's body changes during ontogeny. During
postlarval development, a crustacean normally displays
two phases of relative growth, a juvenile and an adult
phase. In some cases a prepuberty phase, consisting of
the first few postlarval instars, is also present. Within
each phase the size of one body dimension relative to
another can be described by the allometric growth
equation, $Y = \beta X^a$, where Y is the relative dimension
(usually a limb measurement), X is the reference
dimension (usually a carapace measurement), and β
and a are undetermined coefficients. When plotted on
a double logarithmic scale, the allometric growth equa-
tion becomes a straight line, $\log Y = \log \beta + a \log X$
(Fig. 1A–D).

The various patterns that juvenile and adult phase
lines assume can be categorized into four types. In the
first type (Fig. 1A), all individuals mature at a specific
value of X, and the two phase lines meet at this point.
Since juveniles and adults near the size of sexual
maturity differ primarily in the rate of relative growth,
as indicated by the slopes of the phase lines, rather
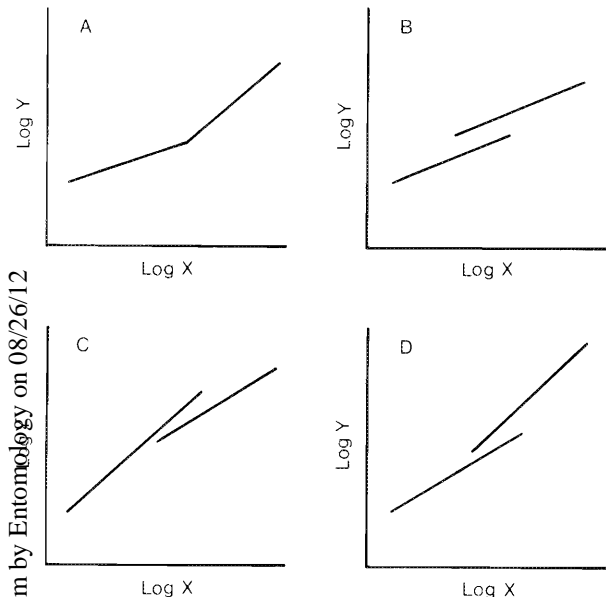than in the actual relative size of the two body dimen-

FIG. 1. Four patterns assumed by juvenile and adult phase lines. In A, sexual maturity occurs at a specific value of X and the phase lines meet at this point. In B, the relative growth rate (slope of the phase lines) does not change at maturity, although there is a relatively large increment in the Y dimension. Intermediate cases are shown by C and D which typify a female and male pattern, respectively, when the Y dimension is an appendage measurement and the X dimension is a carapace measurement.

tions, the sexual maturity of an individual cannot be readily determined by inspection. In the second type (Fig. 1B), sexual maturity occurs over a range of sizes and the phase lines overlap. At sexual maturity an individual abruptly grows in the Y dimension relative to X, but the relative growth rate after maturity remains the same as before. If the increment gained at maturity is sufficiently large, as it usually is for secondary sexual characteristics, juveniles and adults can be distinguished by their appearance. For most crabs, the pattern of phase lines is probably intermediate between these two types and resembles either Fig. 1C or D.

Methods for Determining the Size of 50% Sexual Maturity

The size of sexual maturity is the easiest to determine when the pattern of phase lines is similar to that in Fig. 1A because the problem is simply one of finding the size at which the two phase lines meet. In an earlier paper (Somerton 1980), I described a computer program which estimates this size by finding the best fit of a pair of intersecting straight lines. Starting with an initial estimate of the intersection point on the X axis, the program splits the data into two subsets, one with X values smaller than the initial value (juveniles)
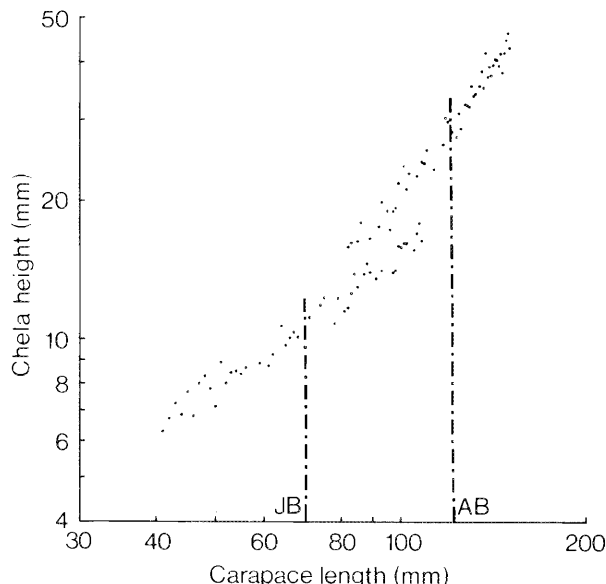

FIG. 2. A synthetic set of morphometric data is split into three subsets according to two values of X, a juvenile bound (JB) and an adult bound (AB), chosen by the user. Data to the left of JB are known to be from juveniles, data to the right of AB are known to be from adults, and data between JB and AB are from an unknown mixture of juveniles and adults.

and one with X values greater than the initial value (adults). Linear regression is used to fit a straight line to each subset of data with the two lines being constrained to meet at the initial value of the intersection point. The intersection point is then changed slightly, the data are repartitioned, and the lines are fit iteratively until the intersection point resulting in the minimum residual sum of squares is found. This method, however, does not work satisfactorily when the phase lines overlap because the data cannot be separated into juvenile and adult subsets at some value of X.

To find the size of sexual maturity in those cases where the relative growth phase lines overlap, two separate problems must be solved. First, all data must be assigned to either the juvenile or the adult category. Second, the proportion of data classified as adult must be determined as a function of X and the X value at which this proportion reaches 50% estimated. This sequence of operations is shown in Fig. 2–4 for a synthetic set of data.

Assigning data values to either of the two maturity groups was done by a technique similar in its basic concept to nonhierarchical cluster analysis (Anderberg 1973). Two values of X, a juvenile bound (JB) and an adult bound (AB), are chosen such that the X axis is divided into three regions; the leftmost region containing data only from individuals known to be juveniles, the rightmost region containing data only from individuals known to be adults, and the middle region containing data for an unknown mixture of juveniles
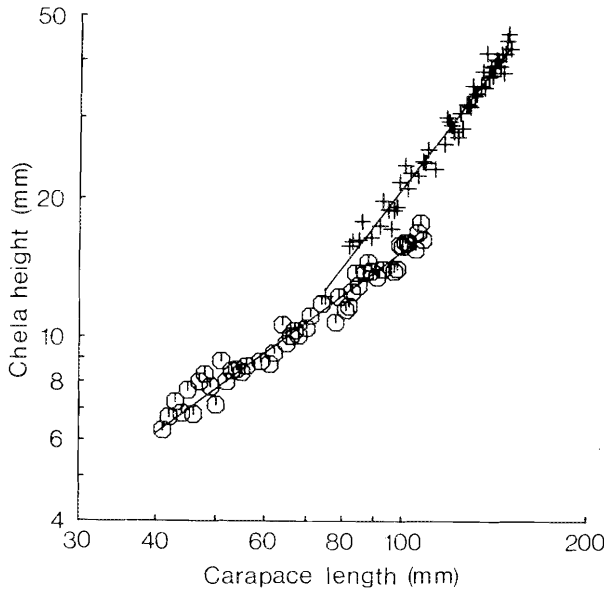
FIG. 3. All values in the synthetic data set are classified as either juvenile, represented by circles, or adults, represented by pluses, using the algorithm described in the text. Notice that the smallest value classified as adult is probably better classified as a juvenile. Such misclassification contributes to the variance of the estimated size of 50% maturity.
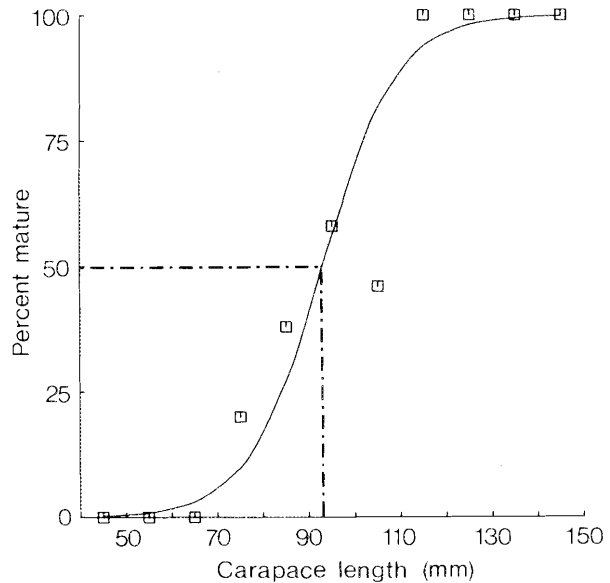

FIG. 4. A logistic curve is fit to the percent of the data classified as adult by size. The size of 50% maturity is then estimated by evaluating the logistic curve at 50%.

and adults (Fig. 2). Preliminary estimates of the two phase lines are made by fitting straight lines, using linear regression, to the known juvenile and adult data. The lines are extrapolated into the middle region and the difference in Y direction between every data point in the middle region and each of the two lines is calculated. Data points are then tentatively assigned to the closest line, that is, they are tentatively classified as either juvenile or adult and combined with the data with known maturity. The phase lines are recomputed, the distance between every point in the middle region and each of the two lines is recalculated, and the points are again assigned to the closest line. This process is repeated iteratively until no points switch from one phase line to another on two successive iterations. Figure 3 shows the fit of the two lines to the synthetic data set.

After the iterative process converges, a statistical test is made to determine if the resulting two lines fit the data better than a single line. If the fit is not significantly better, there is little justification for using two lines to describe the data and, consequently, some other method must be used to determine sexual maturity. The test statistic is

$$T = \frac{(RSS_{1\ \text{line}} - RSS_{2\ \text{line}})/2}{RSS_{2\ \text{line}}/(N - 4)}$$

where $RRS_{1\ \text{line}}$ is the residual sum of squares (RSS) about a single line fit to the data, $RSS_{2\ \text{line}}$ is the RSS

about two lines fit to the data, and N is the number of data points (Draper and Smith 1966). The test statistic has an F distribution with 2 and $N - 4$ df.

To estimate the size of 50% sexual maturity, the X axis is transformed back to a linear scale and divided into a number of equal-width size intervals. For each interval, the proportion of the data classified as mature is determined. A logistic function is fit to these proportions using the methods discussed in Appendix 1 and the resulting equation is then evaluated to find the size at which 50% of the individuals are mature (Fig. 4).

The above procedures were incorporated into a computer program (MATURE). A listing of the program and a User's Guide are available from the author.

Examples

Program MATURE was used to find the size of 50% maturity for three sets of relative growth data from the eastern Bering Sea: (1) Chela height and carapace length measurements for male Alaska king crab (*Paralithodes camtschatica*) obtained from Wallace et al. (1949); (2) Chela height and carapace length measurements for female Alaska king crab obtained from the same source; and (3) Chela height and carapace width measurements for male Alaska tanner crab (*Chionoecetes bairdi*) collected by the author on a 1975 National Marine Fisheries Service cruise to the eastern Bering Sea. The partitioning of each data set into immature and mature relative growth phases is shown in Fig. 5–7.

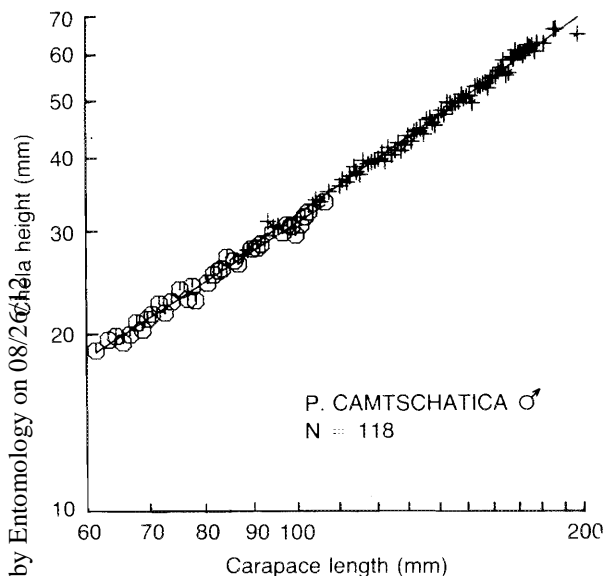The estimated size of 50% maturity is shown below

FIG. 5. Maturity classification of morphometric data for male Alaska king crab from the eastern Bering Sea. Circles represent juveniles and pluses represent adults.
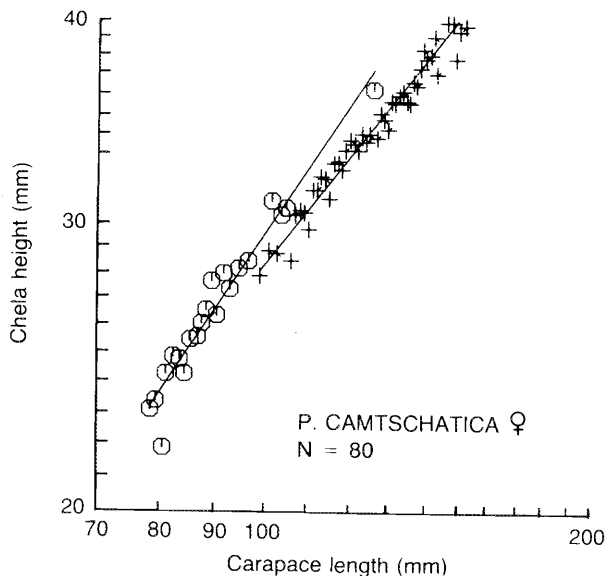

FIG. 6. Maturity classification of morphometric data for female Alaska king crab from the eastern Bering Sea. Circles represent juveniles and pluses represent adults.

for the three sets of data:

Data set	Size of 50% maturity
P. camtschatica ♂	102.8 mm carapace length
P. camtschatica ♀	101.9 mm carapace length
C. bairdi ♂	114.7 mm carapace width

These estimates are similar to those obtained for the same species by other methods. Wallace et al. (1949) reported the size of 50% maturity for female king crab, based on the presence of eggs on the pleopods, as 96 mm carapace length. Wallace et al. (1949) stated that the smallest observed mature male king crab, based on histological examination of the vas deferens, was 90 mm; however, an estimate of the size of 50% maturity was not given because too few crabs were examined. Brown and Powell (1972) reported 113 mm as the size of 50% maturity for male tanner crab near Kodiak Island based on reproductive tract weight. Variances of the estimated sizes of 50% maturity were not calculated because, as discussed below, the sample sizes were too small.

Estimation of the Variance of the Size of 50% Maturity

Estimates of the size of 50% maturity produced by program MATURE have two components of variability, one due to variability of percent maturity values about the fitted logistic equation (fitting error), and one due to the probability of classifying morphometric data into the wrong maturity category (misclassification error). The estimation of total variability is com-

plicated because the two components are neither strictly additive nor strictly multiplicative, and, in addition, only one of the components, fitting error, is estimable using standard analytic techniques (Appendix 1). However, if a sufficiently large sample of morphometric data is available, an estimate of total variability can be obtained by calculating the variance among independent estimates of the size of 50% maturity based on randomly chosen subsamples of data.

The method of estimating total variability consists of randomly partitioning a data set into N subsets, using program MATURE to estimate the size of 50% maturity for each subset, and then calculating the variance among the N estimates. There are three questions, however, which must be considered before using this method: (1) how much data is required? (2) how many subsets of data should be drawn? and (3) how well does the estimate of fitting error calculated by program MATURE approximate total variability? Although specific answers to these questions depend upon the characteristics of the data being analyzed, general guidelines are provided by the following example based on chela height and carapace width measurements from 1066 male *Chionoecetes opilio*.

The effect of sample size on estimates of total variability was examined by partitioning the *C. opilio* data into N subsets where N varied from two to eight. Each level of subsampling was replicated five times, with each replicate consisting of a different selection of N data subsets. For each replicate, the variance of the N estimates of the size of 50% maturity and the mean of the N estimates of fitting error were calculated. The five replicate estimates of both total variability and fit-
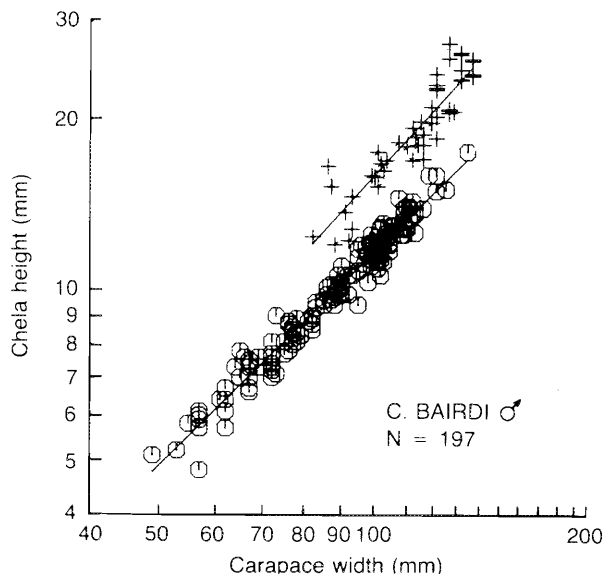
FIG. 7. Maturity classification of morphometric data for male Alaska tanner crab from the eastern Bering Sea. Circles represent juveniles and pluses represent adults.
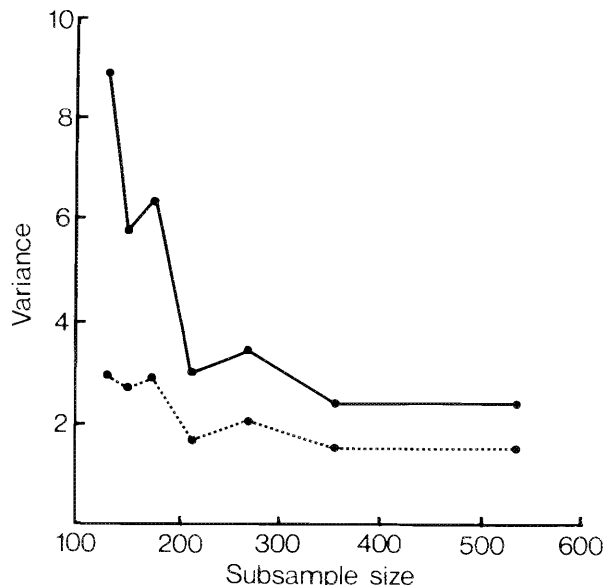

FIG. 8. Total variance (solid line) and fitting error (dotted line) of the estimated size of 50% maturity for male *C. opilio* are shown plotted against average subsample size. The 1066 values comprising the data set were randomly divided into *N* subsets where *N* varied from two to eight. Thus, average subsample size varied from 1066/8 to 1066/2. Total variance was calculated as the variance of *N* independent estimates of the size of 50% maturity. Fitting error was calculated for each of the *N* subsets using the methods described in Appendix 1 and then averaged.

ting error were averaged and plotted against average sample size (Fig. 8). For *C. opilio*, both total variability and fitting error decrease asymptotically as sample size increases and only small gains in precision of the estimate of 50% maturity are obtained by increasing sample size beyond 350.

Although in this case a sample size of 350 is sufficient to produce a precise estimate of the size of 50% maturity, it is too small to adequately estimate variance. For example, if a sample of 350 were divided into three subsamples of 116, the estimated variance would be roughly equal to 9.0 (Fig. 8); however, the variance of the size of 50% maturity based on the whole sample of 350 would be equal to only 2.4. Thus, variance estimates based on small subsamples tend to overestimate true variances. If, however, a sample of 1000 were divided into three subsamples, the estimated variance would be quite similar to the true variance.

Either of two methods can be used to estimate variance of the size of 50% maturity depending on sample size. The first method, which is recommended for large samples, is simply to divide the sample into *N* subsamples and calculate the variance among the *N* independent estimates of the size of 50% maturity. The choice of *N* involves a trade-off between precision of the estimate of variance, which increases as the number of subsamples increases, and the potential for overestimating the true variance, which increases as subsample size decreases. Three subsamples are a reasonably good compromise. This method of estimating variance will produce an estimate which is conservative in the sense that the true variance will always be less than the estimated value.

The second method, which is recommended for small samples, requires the variance to be calculated repetitively from a variable number of subsamples as was done in the example. Nonlinear least squares is used to fit a curve to the estimated variance as a function of sample size. An estimate of the variance for the complete sample is then obtained by extrapolating this curve to the appropriate sample size. The extrapolated variance estimate, however, is not necessarily conservative.

In some situations, the estimate of fitting error calculated by program MATURE may be a reasonably good approximation of total variability. Figure 8 shows that as subsample size increases, fitting error becomes an increasingly greater proportion of the total variability. At the largest subsample size (533), fitting error is 62% of total variability. When the relative growth phase lines are well separated and the likelihood of misclassification appears to be low, fitting error can probably be safely used as an estimate of total variability.

Use of the Size of 50% Maturity as a Measure of the Median Size of Maturity

The size of 50% maturity can be interpreted as the size at which a randomly chosen individual has a 50%

chance of being mature. Under certain conditions, the size of 50% maturity can also be interpreted as the median size of maturity. The difference between these interpretations is subtle and is best demonstrated with an example.

If the sizes of maturity of all members of a population were known, one could construct a maturation probability density function expressing the probability of an individual maturing at a particular size. Integrating this density function would result in a cumulative probability distribution function (CDF1) expressing the probability of an animal maturing at or less than a particular size. The 0.5 probability level on this function corresponds to a size at which 50% of a cohort is expected to be mature. This size, by definition, is the median size of sexual maturity. Since it is rarely possible to obtain individual sizes of maturity, the size of sexual maturity is typically estimated from the observed percent mature within a number of size intervals. Percent maturity versus size is also a cumulative probability distribution function (CDF2); however, this function expresses the probability that a randomly chosen individual of a partciular size will be mature which is different than the probability expressed by CDF1. The difference between CDF1 and CDF2 is most pronounced when growth ceases at sexual maturity. In such cases, the median size of adults is exactly the same as the median size of maturity, but the size of 50% maturity is less than this size. As factors such as rapid growth and high mortality reduce the accumulation of adults within the maturing size range, CDF2 approaches CDF1 and the size of 50% maturity becomes a better approximation of the median size of maturity.

To determine how good this approximation is, a computer model was developed which simulated the growth, mortality, and maturity of a population of male *C. bairdi*. Individual crabs matured according to a CDF1 which ranged from 0.01 for crabs 90 mm wide to 0.99 for crabs 130 mm wide. The 50% level on this CDF1 (median size of maturity) was 109.5 mm. Crabs grew according to the relationship $S_{i+1} = A + BS_i$ where S_i and S_{i+1} are the carapace widths before and after molting and A and B are parameters which for juveniles were set at 4.17 and 1.19 (W. Donaldson, unpublished data) but which for adults were varied between model runs to simulate varying degrees of decreasing growth. All crabs were assumed to molt annually and to have an instantaneous natural mortality rate of 0.25.

A simulation run consisted of adding a cohort of juveniles each year and allowing them to grow, mature, and die along with crabs recruited in previous years. After 15 simulated years, the percent mature in each 1-mm size interval was calculated. The size of 50% maturity was then estimated by linearly interpolating between the two size intervals with percent maturities bracketing 50%. The following table summarizes the results of five simulation runs in order of decreasing

adult growth.

Run No.	Adult growth parameters		Size of 50% maturity in mm
	A	B	
1	4.17	1.19	109.5
2	16.32	1.07	109.5
3	16.32	0	109.2
4	5.00	0	106.6
5	0	0	100.2

In the first run, adults grew at the juvenile rate. In the second run, adults grew at their observed rate (Donaldson unpublished data). For both cases the size of 50% maturity was the same as the median size of maturity. In the third and fourth runs adults grew at slower rates which were independent of crab size. For these cases the size of 50% maturity slightly underestimated the median size of maturity. In the fifth run, adults cease growth. For this case, the underestimate of the median size of maturity was quite pronounced.

The distinction between the size of 50% maturity and the median size of maturity is important for species such as *C. bairdi* where males continue to grow after maturity but females do not. To express the sizes of maturity for both sexes on a comparative basis, the size of 50% maturity should be computed for males, but for females, the median size of adults should be computed because both measures are estimates of the same life history feature: the median size of sexual maturity.

Discussion

Previous studies using relative growth to determine the size of sexual maturity of crabs plotted body measurements on either a linear scale (Brown and Powell 1972) or a double logarithmic scale (Wallace et al. 1949) and determined by eye the size at which the relative growth rate changed. This method may work satisfactorily when the adult and juvenile relative growth phase lines meet at the size of sexual maturity. However, an abrupt change in slope will not be evident when the phase lines overlap to any extent. The technique described in this paper, which is incorporated into program MATURE, will find the size of 50% sexual maturity when there is overlap, provided the two phase lines are statistically different.

Better precision in the estimate of the size of 50% maturity will be achieved if special attention is paid to two aspects of sampling. First, when the relative dimension (Y) is a leg measurement, care must be taken to avoid measuring legs which are incompletely regenerated because such measurements will not only add variability about the phase lines, but they could also result in adults being misclassified as juveniles. For species which are bilaterally symmetrical with respect to the limb being measured, partially regenerated legs can usually be recognized by comparing right and left sides of a crab's body. This cannot be done for those crabs, such as many anomurans, which are not bilat-

erally symmetrical. One method which may be useful for detecting partial regeneration in this case is to take an additional measurement of the limb proximate to the plane of autonomy (Edwards 1972), for example, the width of the coxa, and compare this to the dimension being studied. The ratio of limb measurement to coxa width should be abnormally small for regenerated appendages.

The second aspect of sampling requiring special attention concerns the size range of the animals being sampled. The larger the ranges of the two size regions containing individuals of known maturity, the better program MATURE will be able to classify the data values in the size range containing individuals of unknown maturity. This dictates that an attempt should be made to sample a broad range of sizes. However, if the data known to be from juveniles show a change in slope after being plotted on a double logarithmic scale, the species may have a prepuberty relative growth phase. In such cases, the data to the left of the slope change should be excluded from the analysis.

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Appendix 1
Notes on Fitting the Logistic Equation

The logistic equation has several uses in fisheries. Besides describing percent maturity as a function of size, it is also used in toxicology experiments to describe percent survival as a function of dosage level and it is used to describe fishing mortality as a function of age (selection ogive). Until recently the methods in Berkson (1944) were used to fit the logistic equation to data, but new computer techniques for fitting nonlinear equations make this method obsolete. The following is a brief description of how to fit the logistic equation and how to estimate the value of X at which Y is equal to 50%.

Berkson's (1944) method of fitting the logistic equation consists of transforming it into a linear form, then using weighted linear regression (Draper and Smith 1966) to estimate the two parameters. The logistic equation is expressed as

$$Y = \frac{1}{1 + Ae^{BX}}$$

where Y is a proportion, X is the midpoint of a class interval, and A and B are undetermined parameters. The linearized form of this equation is

$$\log\left(\frac{1-Y}{Y}\right) = \log A + BX$$

where log represents the natural logarithm. Weighting factors used in the regression are $NY(1-Y)$ where N is the number of observations in each class interval.

The logistic equation can be fit to data better by using nonlinear least squares (Draper and Smith 1966). Routines for doing nonlinear least squares are usually included in statistical software packages (e.g. SPSS, IMSL, BMD) available at most computer centers. These routines typically require some initial estimates of the two parameters, A and B, and iteratively improve these estimates until some level of precision has been achieved. Berkson's (1944) method can be used to obtain these initial parameter estimates. Weighting factors should be used in the nonlinear regressions, with weights equal to $N/Y(1-Y)$.

The X value corresponding to any Y can be calculated from

$$\hat{X} = \frac{\log\left(\frac{1-Y}{Y}\right) - \log A}{B}$$

which when evaluated at a Y value of 0.5 equals

$$\hat{X}_{0.5} = \frac{-\log A}{B}.$$

The variance of $\hat{X}_{0.5}$ (fitting error) can be approximated using the Delta method (Seber 1973). The first order approximation is

$$\mathrm{Var}(\hat{X}_{0.5}) = \left(\frac{1}{AB}\right)^2 \mathrm{Var}(A)$$
$$+ \left(\frac{\log A}{B^2}\right)^2 \mathrm{Var}(B) - \frac{2\log A}{AB^3}\mathrm{Cov}(AB)$$

where Var and Cov represent variance and covariance.