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AN ANALYSIS OF GROWTH IN THE FIDDLER CRAB *UCA VOCANS*

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ABSTRACT

Measurements of 13 body variables were taken from 331 female and indifferent fiddler crabs collected at Ao Makam, Phuket, Thailand, Various combinations of these variables were utilized to assign crabs to molt classes and assessed by statistical and graphical procedures. Of the 13 variables, only abdomen width provided an adequated partitioning of the sample into molt classes when the data were subjected to probit analysis. This technique was inadequate to partition the first molt class, suggesting that putative molt class 1 is composed of several molt classes. There are probably more than 10 post-larval molts. The analysis provided information about the relative growth of various body parts. Certain lesser changes in the relationship between body parts occur between molt classes 2 and 3 and major changes appear between molt classes 1 and 2. After molt class 3, the proportions of body parts, except for abdomen width, are fixed.

INTRODUCTION

Over the past one hundred years much interest has been shown in growth patterns of marine organisms. Crustaceans have been especially carefully examined because of the episodic nature of their growth, size increases being manifested only at the time of the molt. Because it is so difficult to determine the age of crustaceans, there is little information on absolute growth and growth rates. The life span of the Amercian lobster is approximately 50 years (Herrick, 1896); of the crayfish, 15-20 years (Huxley, 1880), while most shore crabs have a much shorter life span (Calman, 1927; Williamson, 1903). For a few Crustacea there are data on mathematical relationships between size and age (Terao, 1928; Ingle, 1933), and the subject has been reviewed by Hartnoll (1982). A study including information on these subjects for the crab *Cancer* has recently appeared (Orensanz and Gallucci, 1988).

Where a species of crustacean can be raised in the laboratory, it is relatively simple to determine growth rates. Halcrow (1978) found that the growth rate in *Daphnia* decline with time, whereas in larval *Artemia,* the mitotic frequency increased in the second instar as compared to the first (Freeman, 1986). However, in field collections, growth rates cannot be directly determined and growth must be estimated from changes in body measurements. In such cases a standard measurement can be substituted for time. If X is some measureable character, *e. g.*, length, the growth rate will be the differential of X with respect to time. This also the case for Y, another character measured in the same units. The explicit growth rates are dX/dt and dY/dt. The relative growth rates are the growth rate per unit X and the growth rate per unit Y:

$$\frac{1}{X}\frac{dX}{dt} \quad \text{and} \quad \frac{1}{Y}\frac{dY}{dt}$$

Huxley (1932) postulated a relationship between the relative growth rate of Y and the relative growth rate of X such that:

$$\frac{1}{Y}\frac{dY}{dt} = \frac{1}{X}\frac{dX}{dt} \quad \text{or} \quad \frac{X}{Y}\frac{dY}{dX} = \beta$$

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Putting the equation in this form eliminates the time factor and creates the parameter β, the growth ratio (Richards and Kavanagh, 1945). It is the time-independent property of β that has endeared it to so many crustacean biologists, who are unable to measure accurately the time course of their subjects' growth. The solution to this equation is the famous allometric equation (Huxley, 1932).

$$Y = \alpha X^{\beta} \quad (\textit{vide}, \text{ Hartnoll, 1982, p. 156})$$

In this model, the size of a character Y is exponentially related to the size of some other character X by two parameters, α and β. Beta represents the growth ratio and alpha, called the initial growth index (Huxley and Tessier, 1936), is the initial size of a particular structure against which other variables may be measured (Lumer, Anderson and Hersh, 1942). For example, Anderson and Busch (1941), measuring growth in *Daphnia* antennae, used 1 mm as their α value, since the antennae were approximately that length during the first instar. Beta is useful in quantifying relative growth, since when it is equal to one, X and Y are growing isometrically; whereas if β varies from one, Y and X are growing allometrically relative to each other.

Generally, the allometric equation is put into logarithmic form, where it becomes amenable to analysis by linear regression techniques.

$$\ln Y = \ln \alpha + \beta \ln X$$

In 1886, Brooks proposed that the linear body dimensions of stomatopod crustaceans increased by a factor of 1.25 at each successive molt. Przibram (1931) modified this to 1.26, representing the linear increase accompanying the doubling of the volume of a sphere, *i.e.*, the cube root of 2. This is certainly too sweeping a generalization and is not the case for body length for juvenile specimens of the prawn *Macrobrachium rosenbergii,* for example, where body length and the cube root of weight grow almost isometrically ($\beta = 1.04$) (See Green, Richards, and Singh, 1977). There may be characteristic changes in dimensions at each molt, but these must be determined for each variable and for each species.

Our hypothesis is that crabs should exhibit characteristic relationships between body parts in each molt class. If so, a given individual could be assigned to a molt class (growth stage) by analyzing the length-frequency relationships between its body parts. For such an analysis, the body parts undergoing the most dramatic changes during molting must be determined.

MATERIALS AND METHODS

Specimens of *Uca vocans* were collected at Ao Makam, Phuket, Thailand, during the summers of 1984-1986. A variety of body dimensions was measured using a Nikon dissecting microscope fitted with an ocular micrometer for smaller specimens and a digital display calipers for the larger ones. The measurements shown in Figs. 1-3 were taken for each animal:

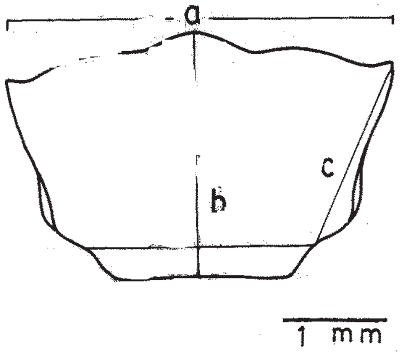

Figure 1. An outline drawing of the carapace of mature fiddler crab (*Uca vocans*). Line **a** represents anterior carapace width (ACW); line **b**, carapace length (CL); line **c**, carapace marginal length (CML); and line **d**, posterior carapace width (PCW) (measured between the bases of the fifth pair of walking legs).

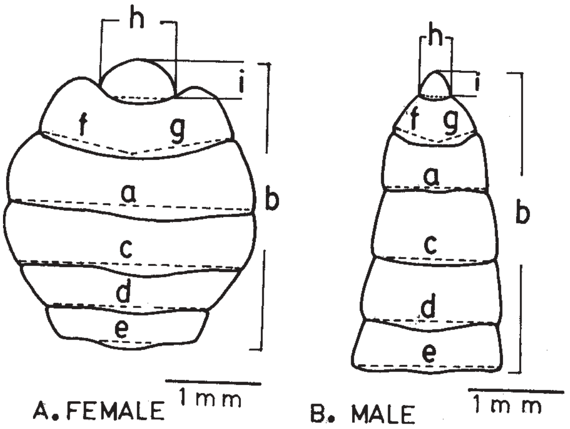

Figure 2. An outline drawing of the abdomen of mature female (A) and male (B) fiddler crabs (*Uca vocans*). Line **b** represents abdomen length (AL); lines **a**, **c-e** abdomen widths (AW); lines **f** plus **g** measure the width of the ultimate segment; and lines **h** and **i** measure the width and length of the telson.

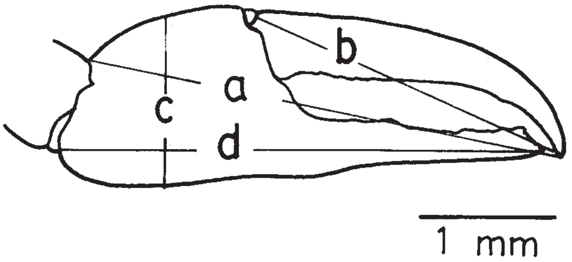

Figure 3. An outline drawing of the major cheliped of mature male fiddler crab (*Uca vocans*). Line **a** represents the length of the cheliped from the notch of the manus to the tip of the dactylus; line **b**, the length of the dactylus; line **c**, the width of the cheliped; and line **d**, the length of the propodus.

To differentiate between molt classes within these collections of crabs, all data were plotted on probability paper. As discussed below, probability paper permits discrimination among normally-distributed subpopulations, which overlap in the total distribution.

The statistical and graphical procedures utilized in the preparation of this paper were provided by the SYSTAT and SYGRAPH statistical and graphical packages of programs (Wilkinson, 1988a,b).

RESULTS AND DISCUSSION

A histogram defines the distribution of data less efficiently than does a probability plot (Harding, 1949; Cassie, 1954). In the latter, the values of a variable are plotted against the corresponding percentage points of some theoretical distribution (*e.g.*, the normal distribution). If the data are ordered from smallest to largest and are normally distributed, it is possible to predict an expected normal value corresponding to any data point. If probability paper is utilized, the observed values are plotted on the y-axis against the cumulative frequency of occurrence. A straight line indicates a normal distribution. A deviation from a straight line indicates the presence of a separate, normally-distributed subpopulation (class). Successive linear regions (sub-sets) of the probability plot can be extracted and analyzed further and if any of the sub-sets do not approximate a straight line when replotted on probability paper, a different breakpoint may be chosen and the entire set of data replotted. By a process of trial and error, adequate partitioning of the data can be obtained. Comparing the classes to a theoretical distribution (here, a normal distribution) provides a check on speculation.

Probability plots of neither chela length in males (Fig. 4) nor abdomen width in males or indifferent animals (Fig. 5,6) were capable of distinguishing between molt classes. Analysis of males was not pursued further in this study. Analysis of abdomen width in females gave a non-linear probability plot indicating several normally-distributed sub-populations (Fig. 7). A histogram of abdomen widths of females and indifferent animals combined shows significant deviations from a normal distribution (Fig. 8), and a probit plot of this data with a normal curve

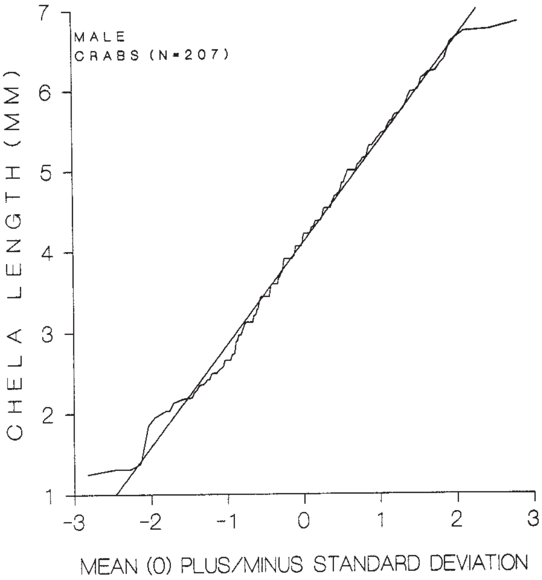

Figure 4. Probability plot of chela length of male crabs. The straight line represents the normal distribution of chela lengths of a population with a mean and standard deviation identical to that of the observed population. The latter shows no significant deviation from the normal distribution.

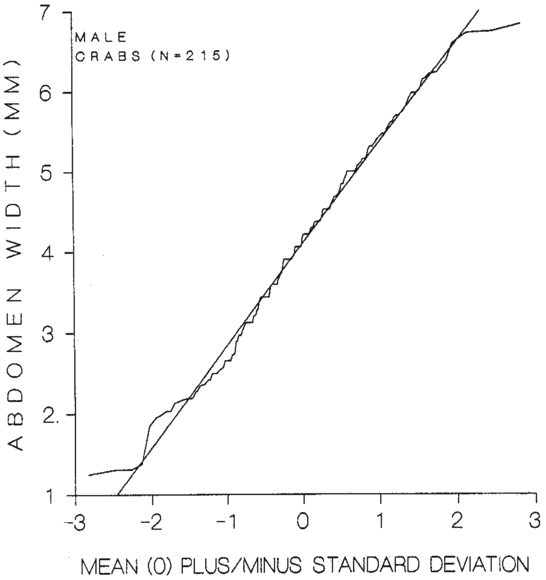

Figure 5. Probability plot of the abdomen width of male fiddler crabs.

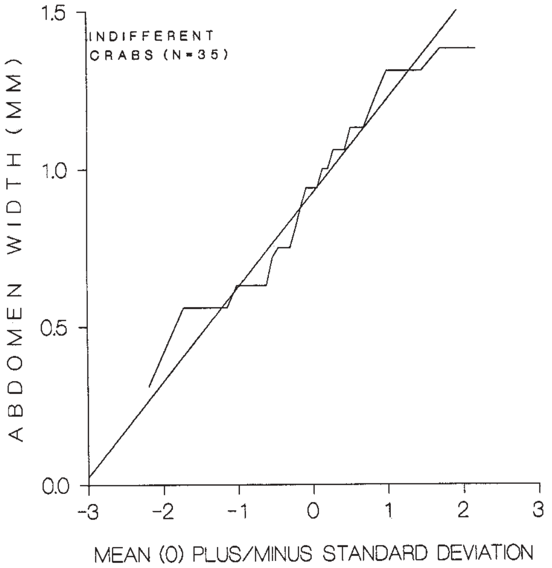

Figure 6. Probability plot of the abdomen width of indifferent crabs.

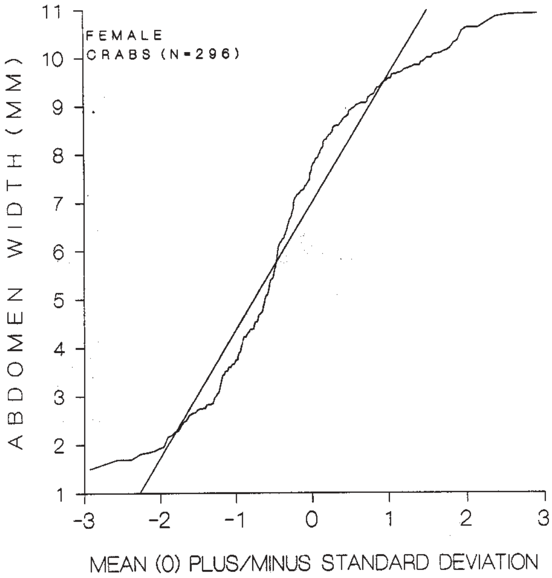

Figure 7. Probability plot of the abdomen width of female crabs.

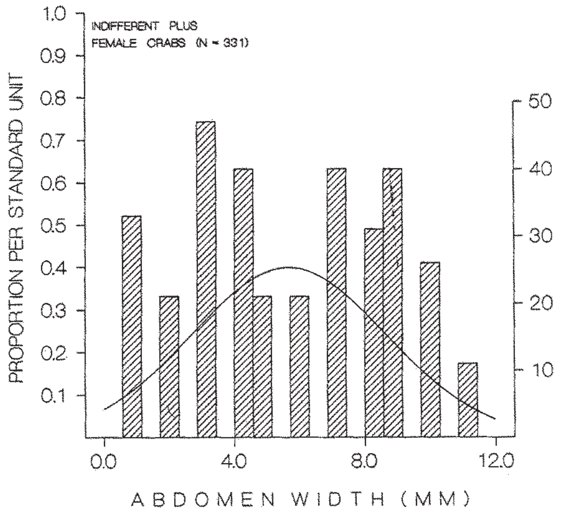

Figure 8. Histogram derived from abdomen width class data of indifferent and female crabs. Overlying the histogram is a plot of a normal curve having the identical mean and standard deviation. The scale to the right of the histogram measures the number of individuals in each bar. The scale to the left measures the proportion of cases falling in each bar divided by the sample standard deviation. Standardizing the Y-axis in this way makes for easier comparison with histograms based on different scales. The abdomen width data are not normally distributed.

overlay corroborates this conclusion. Ten breakpoints can be seen, which suggests that there are eleven subpopulations. These subpopulations are presumed to be molt classes. Figure 9B shows the lower limit of each sub-population superimposed on the probit curve from Figure 9A. If the cumulative frequency values of each of these putative molt classes is plotted on probability paper, the individual curves each show a normal distribution (Fig. 10). By this means, the heterogeneous field collection has been partitioned into sub-populations, each of which is normally distributed.

The data for the putative molt classes for female and indifferent animals are summarized in Table 1 and presented as graphs in Figure 11 and 12. Figure 11A is derived from a discriminant analysis involving a one-way analysis of variance (ANOVA) utilizing all the variates. The null hypothesis was that the molt classes were equivalent. Discriminants X and Y, byproducts of the ANOVA, were standardized to have a zero mean and unit standard deviation within a molt class and, consequently, they are comparable. When the discriminants were plotted against each other, the separation of the molt classes became evident. In plot 11A, fifty percent gaussian, bivariate ellipses are superimposed over each molt class. For most of the molt classes, approximately half of the data points are encompassed by their ellipse. This indicates in another way that the data within each molt class are normally distributed (*cf.*, Fig. 10). In Figure 11B the cumulative fraction (of the total N) for each class has been calculated, and the mean ± SD of abdomen widths for each is plotted against it. The line running through the points is a least squares linear regression line bounded by the 95% confidence interval of the slope. Since calculated mean class-points deviate non-randomly from the regression line, the overall data are not distributed normally.

The curves (Fig. 12 & 13) do not represent growth rates. The designation of the x-axis as molt class and the equal spacing given to each class cannot be interpreted as a time curve. Little information is available concerning the time periods between molts, although Needham (1950) suggests that it increases with age in some crustacea. The duration of these periods depends on ecological, behavioral and physiological factors beyond the scope of this work. What can be stated is that the increase in abdomen width is approximately 2.5 times greater before molt class 5 and about 1.5 times greater after molt class 5 than that of the other five variables.

The data in Table 2 are derived from that of Table 1. Here the increase in each of the six variables is calculated as a percentage of the previous molt class.

$$\{(\text{mean}_{(mcx+1)} - \text{mean}_{(mcx)})/\text{mean}_{(mcx)}\}*100$$

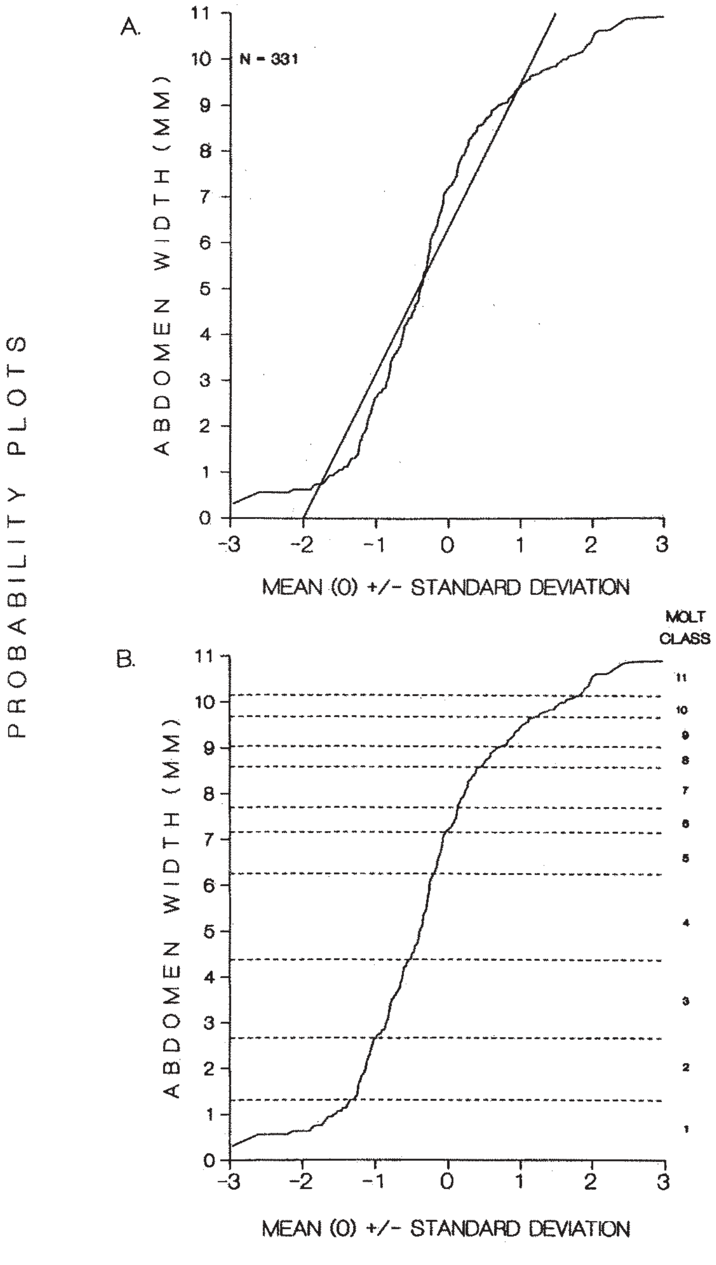

Figure 9. Probability plots of abdomen width of indifferent and female crabs ($\Sigma N = 35 + 296 = 331$). Plot A shows the least squares linear regression line, representing a normal curve of identical mean and standard deviation, superimposed over the probability plot. The deviations of the probability plot from the normal distribution appear as deviations from the linear overlay. These discrepancies suggest there are serveral normally-distributed populations within the data. Plot B shows the partitioning of the probability plot into eleven classes based on breakpoints in the curve.

Figure 14 is a plot of the data of Table 2. There is a sharp decline in percentage increase in the size of all body parts in the first 5 to 7 molt classes. Between molt classes 1 and 2, major size changes occur, especially in abdomen width. By the 10th molt, abdomen width has increased by a factor of almost 12; the other 5 variables, by a factor of 5.5 This is because the female's abdomen develops into a brood pouch. The comparable factor for male abdomen width is about 7.5. The changes in dimensions between molt class 1 and molt class 2 are so great as to suggest that molt class 1 consists of more than one class. Either the resolving power of the probit analysis was unable to partition this class further, or there were too few indifferent animals in the sample.

Once the putative molt classes were determined, allometric analyses provided information about the relative growth of various body parts. For example, the relationship between carapace length (CL) and abdomen width (AW) can be expressed by the allometric equation. Abdomen width is the independent variable and carapace length, the dependent variable. In molt class 1, $\alpha = 0.31$, the minimum width of the abdomen, and $\beta = -4$, so the allometric equation becomes: $CL = 0.31\ AW^{-4.0}$. The allometric relationship is different, however, in the 2 molt class, where $CL = 1.38\ AW^{1.9}$. The increase in β values between the 2 molt classes is due to a large relative increase in abdomen width compared to carapace length in the 1st molt class.

The β values for all molt classes and all variables are shown in Table 3 and facilitate comparisons of relative growth in the post-larval stages. The data show that, while lesser changes occur between classes 2 and 3, the major changes in relative proportions of crabs appear between molt class 1 and molt class 2. Between these molts, the ratio of abdomen length to abdomen width changes from about 0.41 in the smallest crabs to approximately 0.55 at the time abdominal sexual differences appear. In the largest male crabs, this ratio is 0.57 and in the largest females, 0.95. The length: width ratio of the chela varies from 4.94 in the smallest males to 2.35 in the largest. After molt class 3, the relative proportions of the crab's body, except for abdomen width, are fixed.

Table 3 also summarizes information on organisms categorized by the appearance of secondary sexual characters rather than by molt class. Some interesting features appear when we treat the data in this way. For instance, molt class 1 comprises all but the two largest indifferent animals, and it has an $\beta_{CL:AW}$ of -4.05. If the two largest specimens are included, the comparable $\beta_{CL:AW}$ rises to 9.35, the additional animals changing the $\beta_{CL:AW}$ value considerably. This suggests that carapace length is increasing relative to abdomen width. However, when animals, instead, are grouped into molt classes, it becomes apparent that carapace length grows only slightly between molt classes 1 and 2 in comparison to abdomen width.

Using a single characteristic to separate molt classes is difficult (see below). Of all the variables utilized, only female abdomen width proved a good discriminant. The statistical technique of cluster analysis may prove more useful, although molt classes other than the first are reasonably well delineated by probit analysis (Table 1: Figures 9-12). (However, note the qualification in the discussion on ANOVA below).

Two analyses of variance were performed to evaluate the significance of the differences between molt classes. In both analyses, molt classes were based on abdomen width measurements. One of the analyses compared molt classes by abdomen width alone; the other utilized all six variables. Both gave similar results (Table 4). There are highly significant differences ($p < 0.01$) between the molt classes, as shown by both univariate and multivariate ANOVAS when abdomen width is used. But when all variables are considered, only the first 5 molt classes differ significantly ($p < 0.01$) from each other. Significant interactions between the crabs, the variables, and the classes

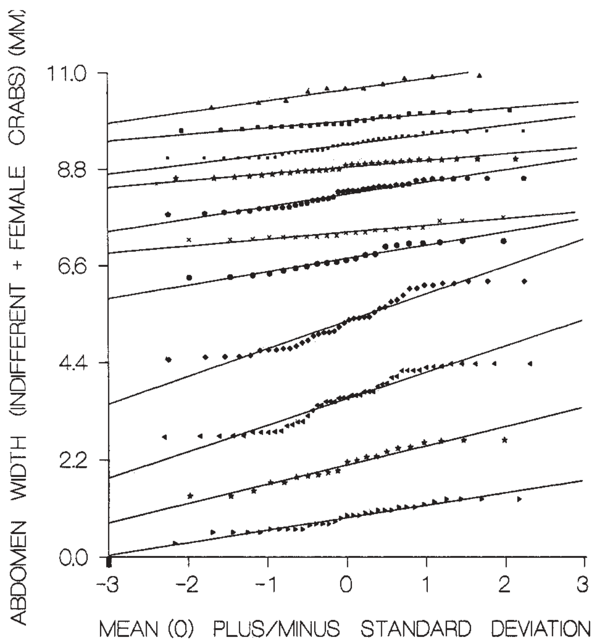

Figure 10. Probability plots of the eleven classes based on the probability plot of abdomen width of indifferent and female crabs. A least squares linear regression line, representing a normal curve of identical mean and standard deviation has been superimposed over each probability plot as an indicator of the adequacy of the partitioning process.

detract from the significance of the probit analysis. Some of this interaction is to be expected. For example, crabs increase in size from molt class to molt class, and consequently there is interaction between crab size and class. Similarly, the distribution of the numbers of crabs is such that larger and smaller crabs occur less frequently, engendering interaction with class. Since molt classes were assigned on the basis of a probit analysis of abdomen width, it is not surprising that the ANOVA of separation is better if abdomen width is considered alone, although it may be that a small number of variables will provide a more effective discrimination of classes in cluster analysis.

We are as yet unable to determine the number of post-larval molts in the fiddler crab. Since we believe that molt class 1 is composed of several classes, there are probably more than ten post-larval molts.

The technique of assessing growth by probability analysis is particularly suited to arthropods, where the requirements of the molt impose a step-like character to the growth curve. Such analysis has been aided by the availability of computer programs. By including cluster analysis and discriminant analysis, assigning individuals to a particular class may be expedited. These techniques are also applicable to organisms that show indeterminate growth, provided that some slope/rate difference (breakpoints) exist in the growth curve. These might occur at the time of sexual maturity or when some special structure or organ appears, or at points imposed by physiological constraints. Such techniques might be used, for instance, to assess the effects of stress on growth, with the proviso that a well-defined growth curve for the 'normal' organism exists. Deviations from the normal would appear as breakpoints and would signal stress-induced modification of growth.

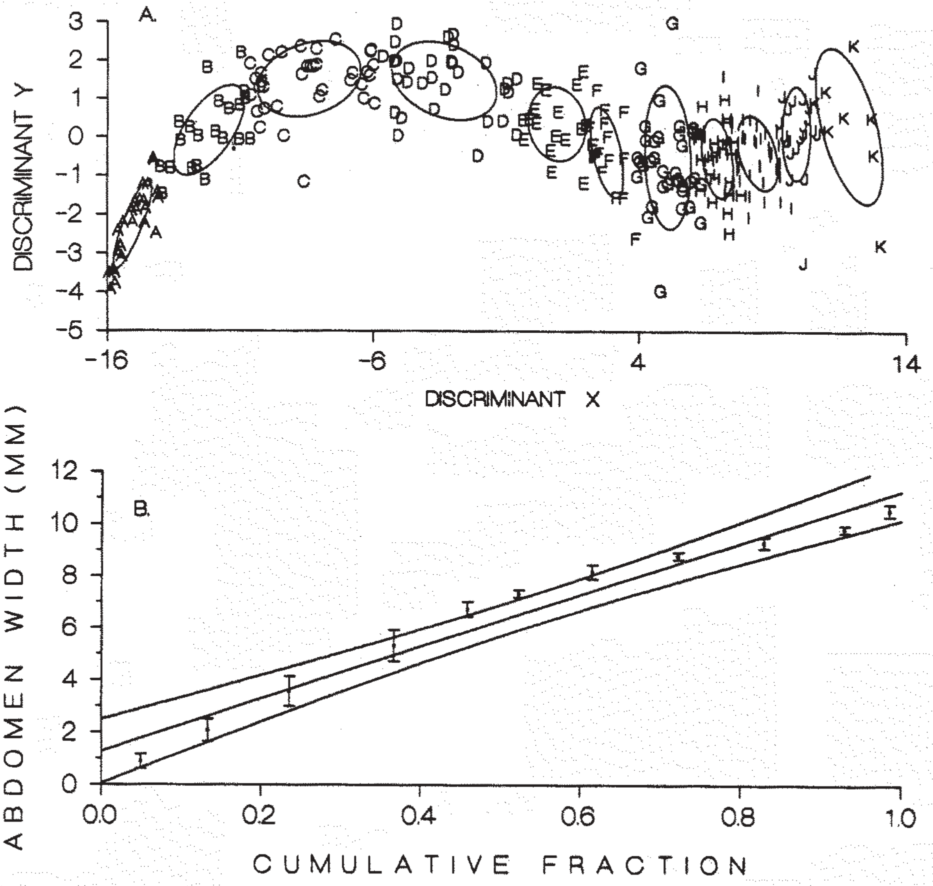

Figure 11. Plot A shows the results of a discriminant analysis based on a one-way analysis of variance (ANOVA). The eleven molt classes derived from abdomen width measurements were tested against the null hypothesis of no difference between them. As a by-product of the ANOVA, an X and a Y discriminant were produced based on all six variables. These discriminants were standardized to zero mean and unit standard deviation so they are directly comparable. They were than plotted against each other with each member of a molt class identified by letter (1 = A, 2 = B, *etc.*). Fifty percent gaussian, bivariate ellipses have been superimposed over the data with their centers located at the mean values for the X and Y discriminants. In plot B, the cumulative fraction (of the total N) for each member of the class was calculated and the mean ± SD plotted against it. A least squares linear regression line and the 95% confidence interval for the slope of the line is shown as an overlay.

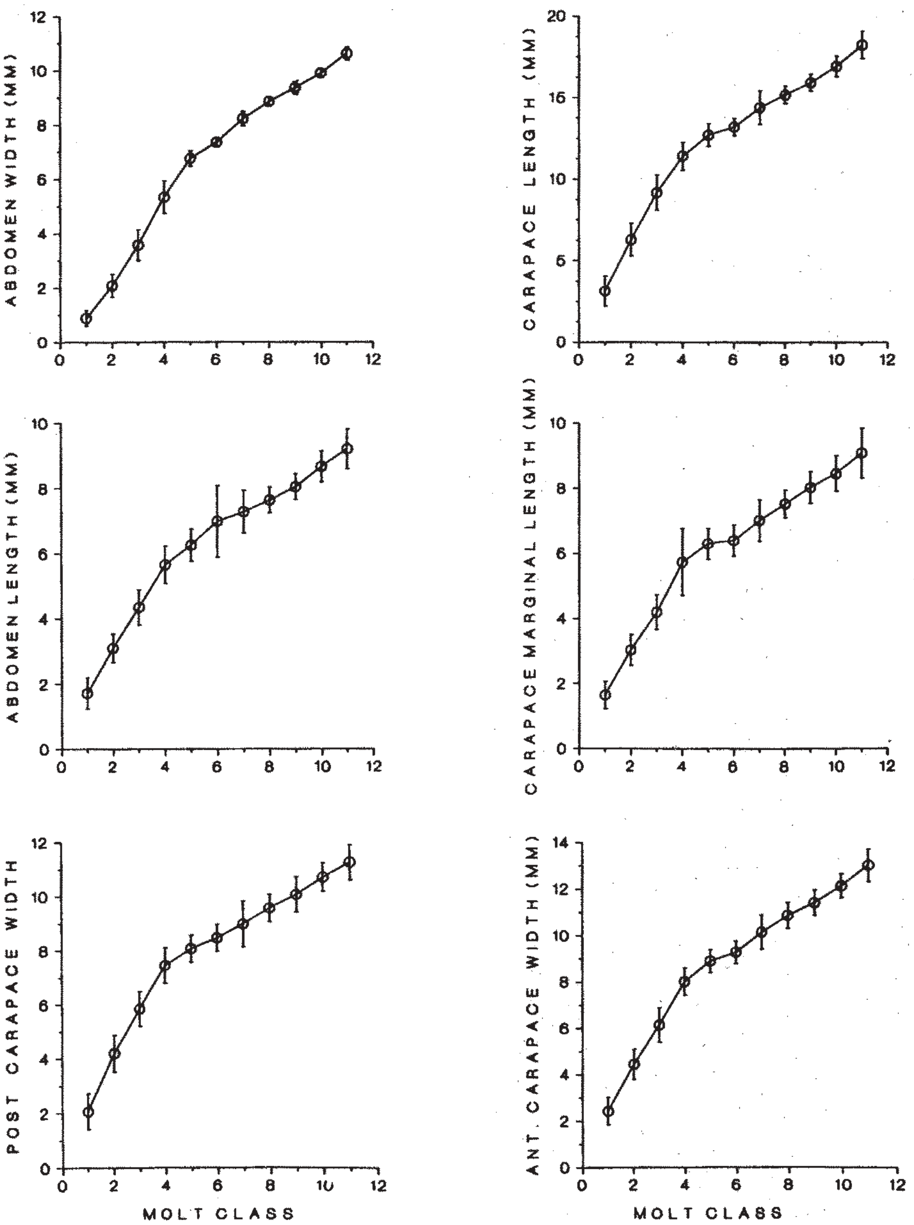

Figure 12. Shows the mean ± SD of the 6 body variables plotted against molt class. All 6 curves show a breakpoint between molt classes 4 and 6 in *Uca* (see also Huxley, 1924). These curves do not reach a plateau, suggesting that growth is ideterminate.

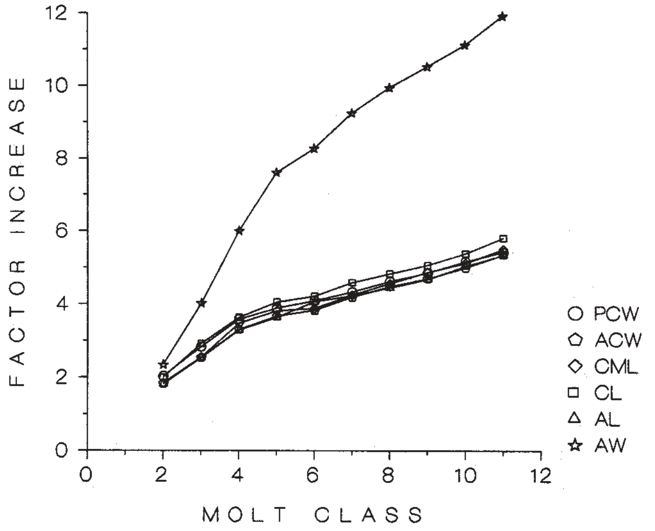

Figure 13. Shows the mean ± SD of the 6 body variables plotted against molt class. The 6 curves show a breakpoint following molt classes 4-6. The data from which these plots are derived comes from Table 1. This Fig. emphasizes the difference between abdomen width and the other 5 variables.

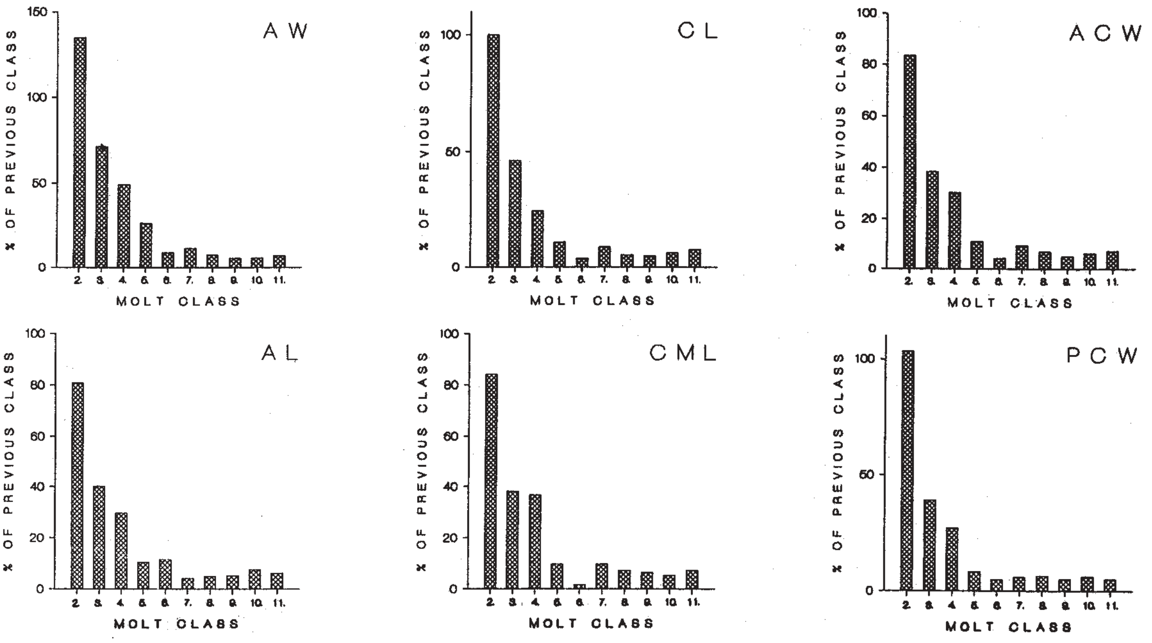

Figure 14. The bar graphs show the increase of the 6 body measurements in indifferent and female crabs as a percentage of the previous class (see Table 2). The sharp decline in percentage increase for the first 5-7 molt classes is followed by a plateau.

Table 1. Molt class data (Total N=350)

	VARIABLES	AW	AL	CL	CML	ACW	PCW
Molt Class 1 (Indifferent Crabs)	Number	33	33	41	41	41	41
	Minimum	0.31	0.75	1.31	0.81	1.25	0.81
	Maximum	1.31	2.56	4.94	2.50	3.50	3.25
	Mean	0.89	1.72	3.14	1.65	2.42	2.07
	Std. Dev.	0.28	0.47	0.92	0.42	0.59	0.66
Molt Class 2	Number	21	21	23	23	23	23
	Minimum	1.38	2.44	4.63	2.00	3.50	3.13
	Maximum	2.66	4.07	8.20	3.87	5.78	5.62
	Mean	2.09	3.11	6.28	3.04	4.44	4.21
	Std. Dev.	0.42	0.44	1.00	0.48	0.65	0.68
Molt Class 3	Number	47	46	47	37	37	37
	Minimum	2.72	3.06	7.27	2.98	4.64	4.89
	Maximum	4.38	5.31	10.94	5.16	7.50	7.16
	Mean	3.58	4.36	9.18	4.20	6.14	5.85
	Std. Dev.	0.57	0.54	1.06	0.53	0.75	0.64
Molt Class 4	Number	40	40	40	31	31	31
	Minimum	4.46	4.69	9.84	4.56	6.98	6.40
	Maximum	6.25	6.89	14.06	9.80	9.19	9.10
	Mean	5.34	5.66	11.43	5.74	8.00	7.44
	Std. Dev.	0.60	0.57	0.86	1.02	0.58	0.66
Molt Class 5	Number	21	21	21	18	18	18
	Minimum	6.33	5.66	11.56	5.47	8.04	6.67
	Maximum	7.16	7.64	14.33	7.51	10.12	8.74
	Mean	6.76	6.26	12.71	6.30	8.88	8.06
	Std. Dev.	0.29	0.49	0.70	0.47	0.48	0.50
Molt Class 6	Number	21	21	21	17	17	17
	Minimum	7.19	6.08	12.45	5.40	8.52	7.11
	Maximum	7.70	11.46	14.45	7.44	10.48	9.16
	Mean	7.36	6.99	13.22	6.40	9.26	8.46
	Std. Dev.	0.15	1.10	0.52	0.48	0.49	0.49
Molt Class 7	Number	40	40	40	36	36	36
	Minimum	7.76	6.14	11.96	6.18	8.96	7.02
	Maximum	8.59	9.84	17.82	9.28	12.26	11.26
	Mean	8.22	7.28	14.41	7.02	10.13	8.97
	Std. Dev.	0.27	0.66	1.03	0.64	0.73	0.85

Table 1. (continued)

	VARIABLES	AW	AL	CL	CML	ACW	PCW
Molt Class 8	Number	31	31	31	28	28	28
	Minimum	8.59	6.90	13.99	6.73	9.63	8.64
	Maximum	9.04	8.44	16.22	8.23	12.00	10.76
	Mean	8.85	7.64	15.18	7.53	10.84	9.56
	Std. Dev.	0.15	0.39	0.54	0.43	0.55	0.51
Molt Class 9	Number	40	40	40	37	37	37
	Minimum	9.06	6.94	14.74	6.80	9.98	8,52
	Maximum	9,68	8.91	17.42	9.14	12.68	11.40
	Mean	9.36	8.05	15.93	8.03	11.38	10.96
	Std. Dev.	0.22	0.40	0.52	0.49	0.55	0.65
Molt Class 10	Number	26	26	26	22	22	22
	Minimum	9.69	7.50	15.35	7.33	10.96	8.99
	Maximum	10.16	9.68	18.63	9.79	13.04	11.58
	Mean	9.90	8.67	16.94	8.46	12.10	10.70
	Std. Dev.	0.14	0.48	0.64	0.54	0.52	0.53
Molt Class 11	Number	11	11	11	8	8	8
	Minimum	10.20	7.90	16.74	7.78	11.95	10.05
	Maximum	10.92	10.10	19.58	10.36	14.03	12.17
	Mean	10.61	9.21	18.25	9.09	12.98	11.25
	Std. Dev.	0.24	0.61	0.84	0.77	0.69	0.65

Table 2. Growth of indifferent plus female crabs and percentage increase from previous class (mean values)

MOLT CLASS NUMBER	AW	AL	CL	CML	ACW	PCW
1	-	-	-	-	-	-
2	134.83	80.81	100.00	84.24	83.47	103.38
3	71.29	40.19	46.18	38.16	38.29	38.95
4	49.16	29.82	24.51	36.67	30.29	27.18
5	26.59	10.60	11.20	9.76	11.00	8.33
6	8.88	11.66	4.01	1.59	4.28	4.96
7	11.68	4.15	9.00	9.69	9.40	6.03
8	7.66	4.94	5.34	7.26	7.01	6.58
9	5.76	5.37	4.94	6.64	4.98	5.23
10	5.77	7.70	6.34	5.35	6.33	6.36
11	7.17	6.23	7.73	7.45	7.27	5.14

Table 2 (continued)

OVERALL INCREASES (MEAN VALUES) (MOLT CLASS 11/MOLT CLASS 1)

	FACTOR INCREASE
ABDOMEN WIDTH	11.90
ABDOMEN LENGTH	5.37
CARAPACE LENGTH	5.81
CARAPACE MARGINAL LENGTH	5.50
ANTERIOR CARAPACE WIDTH	5.37
POSTERIOR CARAPACE WIDTH	5.43

Table 3. Beta values of female and indifferent animals ($\Sigma N=347$)

MOLT CLASS	Dependent variable		Independent variables					
			CL	CML	ACW	PCW	AW	AL
1	CARAPACE LENGTH	(CL)	-	2.19	1.06	1.62	-4.05	2.22
	CARAPACE MARGINAL LENGTH	(CML)	0.26	-	0.38	0.94	-2.84	1.37
	ANTERIOR CARAPACE WIDTH	(ACW)	0.57	1.80	-	1.33	-3.62	1.85
	POSTERIOR CARAPACE WIDTH	(PCW)	0.46	1.65	0.65	-	-3.17	1.72
	ABDOMEN WIDTH	(AW)	-0.23	0.37	-0.24	0.26	-	0.49
	ABDOMEN LENGTH	(AL)	0.28	1.26	0.41	0.92	-1.38	-
2		(CL)	-	1.02	0.40	0.50	1.89	0.85
		(CML)	-0.23	-	-0.09	-0.01	1.05	0.22
		(ACW)	-0.02	0.72	-	0.26	1.49	0.55
		(PCW)	-0.05	0.68	0.13	-	1.43	0.51
		(AW)	-0.43	0.06	-0.34	-0.27	-	-0.12
		(AL)	-0.21	0.40	-0.07	0.00	1.05	-
3		(CL)	-	0.77	0.37	0.35	0.94	0.74
		(CML)	-0.25	-	-0.05	-0.08	0.35	0.22
		(ACW)	-0.07	0.51	-	0.13	0.65	0.48
		(PCW)	-0.10	0.47	0.13	-	0.61	0.45
		(AW)	-0.32	0.13	-0.15	-0.18	-	0.11
		(AL)	-0.23	0.25	-0.05	-0.08	0.37	-

Table 3 (continued)

MOLT CLASS	Dependent variable	Independent variables					
		CL	CML	ACW	PCW	AW	AL
4	(CL)	-	0.52	0.24	0.29	0.56	0.52
	(CML)	-0.22	-	0.09	-0.05	0.15	0.12
	(ACW)	-0.08	0.32	-	0.11	0.35	0.31
	(PCW)	-0.11	0.28	0.03	-	0.31	0.27
	(AW)	-0.25	0.09	-0.13	-0.09	-	0.08
	(AL)	-0.23	0.12	-0.10	-0.07	0.15	-
5	(CL)	-	0.46	0.21	0.30	0.36	0.44
	(CML)	-0.24	-	-0.11	-0.03	0.00	0.06
	(ACW)	-0.10	0.26	-	0.13	0.18	0.25
	(PCW)	-0.14	0.21	0.00	-	0.13	0.19
	(AW)	-0.20	0.12	-0.08	0.00	-	0.10
	(AL)	-0.24	0.07	-0.12	-0.04	0.00	-
6	(CL)	-	0.48	0.20	0.29	0.30	0.40
	(CML)	-0.26	-	-0.13	-0.05	-0.06	0.03
	(ACW)	-0.12	0.29	-	0.12	0.13	0.22
	(PCW)	-0.15	0.24	0.00	-	0.08	0.17
	(AW)	-0.20	0.17	-0.06	0.02	-	0.10
	(AL)	-0.22	0.14	-0.09	-0.01	-0.02	-
7	(CL)	-	0.43	0.20	0.32	0.29	0.43
	(CML)	0.49	-	-0.10	0.00	-0.05	0.07
	(ACW)	-0.06	0.26	-	0.17	0.13	0.26
	(PCW)	-0.11	0.19	0.00	-	0.07	0.19
	(AW)	-0.14	0.14	-0.04	0.07	-	0.15
	(AL)	-0.19	0.08	-0.09	0.01	-0.03	-
8	(CL)	-	0.40	0.19	0.25	0.26	0.39
	(CML)	-0.23	-	-0.10	-0.06	-0.06	0.04
	(ACW)	-0.09	0.24	-	0.10	0.11	0.22
	(PCW)	-0.14	0.17	0.00	-	0.05	0.16
	(AW)	-0.17	0.14	-0.04	0.01	-	0.12
	(AL)	-0.22	0.06	-0.10	-0.06	-0.05	-
9	(CL)	-	0.41	0.19	0.27	0.25	0.40
	(CML)	-0.22	-	-0.09	-0.03	-0.05	-0.07
	(ACW)	-0.09	0.25	-	0.13	0.10	0.25
	(PCW)	-0.14	0.19	0.00	-	0.05	0.18
	(AW)	-0.16	0.16	-0.02	0.04	-	0.14
	(AL)	-0.22	0.08	0.08	-0.09	-0.03	-

Table 3. (continued)

MOLT CLASS	Dependent variable	Independent variables					
		CL	CML	ACW	PCW	AW	AL
10	(CL)	-	0.39	0.18	0.27	0.24	0.38
	(CML)	-0.21	-	-0.10	-0.02	-0.06	0.06
	(ACW)	-0.08	0.24	-	0.13	0.10	0.22
	(PCW)	-0.13	0.18	-0.01	-	0.04	0.16
	(AW)	-0.16	0.14	-0.04	0.04	-	0.13
	(AL)	-0.20	0.08	-0.09	-0.01	-0.05	-
11	(CL)	-	0.38	0.16	0.24	0.25	0.38
	(CML)	-0.21	-	-0.11	-0.04	-0.05	0.06
	(ACW)	-0.09	0.23	-	0.11	0.10	0.22
	(PCW)	-0.14	0.17	-0.02	-	0.04	0.16
	(AW)	-0.16	0.14	-0.05	0.02	-	0.13
	(AL)	-0.21	0.08	-0.10	-0.03	-0.04	-

Indifferent crabs
Compare to Molt Class 1
ΣN=49

	Dependent variable	Independent variables					
		CL	CML	ACW	PCW	AW	AL
	(CL)	-	2.17	1.06	1.59	9.35	2.20
	(CML)	0.27	-	0.40	0.93	6.98	1.34
	(ACW)	0.58	1.79	-	1.31	8.34	1.83
	(PCW)	0.48	1.65	0.67	-	8.04	1.71
	(AW)	-0.20	0.41	-0.20	0.29	-	0.52
	(AL)	0.30	1.27	0.43	0.93	-1.32	-
Female Crabs	(CL)	-	0.91	0.60	0.67	1.08	0.86
	(CML)	0.14	-	0.29	0.34	0.75	0.50
	(ACW)	0.28	0.74	-	0.51	0.92	0.68
ΣN=298	(PCW)	0.24	0.68	0.40	-	0.86	0.63
	(AW)	0.18	0.61	0.33	0.39	-	0.55
	(AL)	0.15	0.56	0.30	0.35	0.76	-
Indifferent plus	(CL)	-	1.45	1.05	1.30	1.80	1.47
Female Crabs	(CML)	0.63	-	0.75	0.98	1.48	1.13
	(ACW)	0.77	1.28	-	1.14	1.64	1.31
	(PCW)	0.73	1.22	0.86	-	1.59	1.25
ΣN=347	(AW)	0.67	1.16	0.80	1.03	-	1.19
	(AL)	0.64	1.11	0.76	0.99	1.49	-

Table 4. Analysis of variance

Univariate Repeated Measures Analysis: Results of an Analysis of Abdomen Width Within crabs grouped by molt class

Source of Variation	S.S.	D.F.	M.S.	F
Molt Classes	1275	10	128	19805**
Error	0.6	100	0.006	

Multivariate Repeated Measures Analysis: Results of an Analysis of Abdomen Width

Source of Variation	F	D.F.	P
Molt Classes	194602	10,1	< 0.01**

Test of the Null Hypothesis of No Difference Between Molt Classes

Source of Variation	S.S.	D.F.	M.S.	F
Molt Class				
1 * 2	14.85	1	14.85	483**
Error	0.31	10	0.03	
2 * 3	12.36	1	12.36	380**
Error	0.33	10	0.33	
3 * 4	36.29	1	36.29	19761**
Error	0.02	10	0.002	
4 * 5	39.83	1	36.29	17104**
Error	0.02	10	0.002	
5 * 6	5.73	1	5.73	536**
Error	0.11	10	0.01	
6 * 7	4.24	1	4.24	4137**
Error	0.11	10	0.001	
7 * 8	7.29	1	7.29	30766**
Error	0.002	10	0.0002	
8 * 9	1.85	1	1.85	1170**
Error	0.02	10	0.002	
9 * 10	5.04	1	5.04	4235**
Error	0.01	10	0.001	
10 * 11	7.83	1	7.83	209**
Error	0.38	10	0.04	

Univariate Repeated Measures Analysis: Results of an Analysis with All Variables

Source of Variation	S.S.	D.F.	M.S.	F
Between Crabs grouped by molt class				
Molt Classes	13413	10	1341	948**
Error	382	270	1.42	
Between Crabs grouped by variables				
Variables	3084	5	617	2023**
Error	15.6	51	0.3	
Within Crabs grouped by molt class				
Molt Classes	5825	10	582.5	2528**
Interaction:				
Crabs * Classes	425	50	8.5	37**
Error	118	510	0.23	
Within Crabs grouped by molt class				
Variables	6120	5	1326	8425**
Interaction:				
Crabs * Variables	848	50	16.95	108**
Error	213	1350	0.16	

Multivariate Repeated Measures Analysis: Results of an Analysis with all Variables

Source of Variation	F	D.F.	P
Within Crabs Grouped by Variables			
Variables	6120	5,266	<0.01**
Interaction:			
Crabs * Variables	30	50,1216	<0.01**
Within Crabs Grouped by Molt Classes			
Molt Classes	6389	10,42	<0.01**
Interaction:			
Crabs * Molt Classes	16	50,194	<0.01**

Test of the Null Hypothesis of No Difference Between Classes: All Variables ANOVA

Source of Variation	S.S.	D.F.	M.S.	F
Molt Class				
1 * 2	22.6	5	4.5	45**
Error	5.1	51	0.1	
2 * 3	8.9	5	1.75	10**
Error	0.33	51	0.17	
3 * 4	16.2	5	3.23	10.6**
Error	0.02	51	0.31	
4 * 5	12.4	5	2.5	6.3**
Error	20.1	51	0.4	
5 * 6	3.6	5	0.72	0.86
Error	42.4	51	0.83	
6 * 7	6.2	5	1.2	1.74
Error	36.2	51	0.001	
7 * 8	3.4	5	0.7	1.8
Error	19.1	51	0.4	
8 * 9	0.41	5	0.8	0.96
Error	20.4	51	0.4	
9 * 10	2.4	5	1.0	0.43
Error	24.7	51	0.5	
10 * 11	6.2	5	2.2	1.5
Error	41	51	0.8	

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