

METRIC VARIATIONS IN POPULATIONS OF *CARCINUS MOENAS*

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(Text-figs. 1-8)

INTRODUCTION

In the years 1893, 1895 and 1898 careful measurements were made by Weldon and Thomson (Weldon, 1894, 1898) of the dimensions 'frontal width' and 'carapace length' (Fig. 2) in large numbers of young male *Carcinus moenas* from the beach at Plymouth. From a consideration of these data Weldon found that there was a continuous decrease in the ratio, frontal width/carapace length, with increase in body size, and further that at any particular body size the ratio was progressively smaller in succeeding years. He concluded that natural selection was at work on the population, differentially removing individuals with relatively wide frontal aperture. He suggested that since the building of the breakwater across Plymouth Sound in 1813 the amount of silt in the waters of the Sound had been continuously increasing, so that a relatively wide frontal aperture to the branchial chamber of *Carcinus* became increasingly deleterious to the animal. Weldon thought that his laboratory experiments bore out his conclusions. Both conclusions and experiments have been severely criticized by Cunningham (1928) and others, and there seems little doubt that the criticisms are sound.

The problem of the undoubted decrease in the ratio frontal width/carapace length remained. However, Huxley's demonstration (1932) of the widely occurring phenomenon of differential growth between different dimensions of the same body suggested a possible explanation of the change in the ratio in question, with increase in body size. The graph obtained by plotting frontal width against carapace length on double logarithmic paper (Needham, 1935) showed the straight line characteristic of most cases of differential growth. The graphs for the three years were three parallel straight lines, indicating that differential growth was essentially the same in all. There remained the problem of the vertical separation of the curves, that is, the successive decrease in the initial ratio frontal width/carapace length in succeeding years. The present work, an extension of Weldon's work on natural populations, was intended chiefly as an investigation of this problem. In addition, the suggested explanation of the change in the ratio with increase in body size was tested by measurements of the growth of actual individuals in the laboratory (Fig. 3).

MATERIAL AND METHODS

Three different populations were studied in three successive years, in the neighbourhood of Belfast. It was hoped that by choosing a locality in Larne Lough (Mill Bay) with much silt, one at Greencastle, in Belfast Lough, with

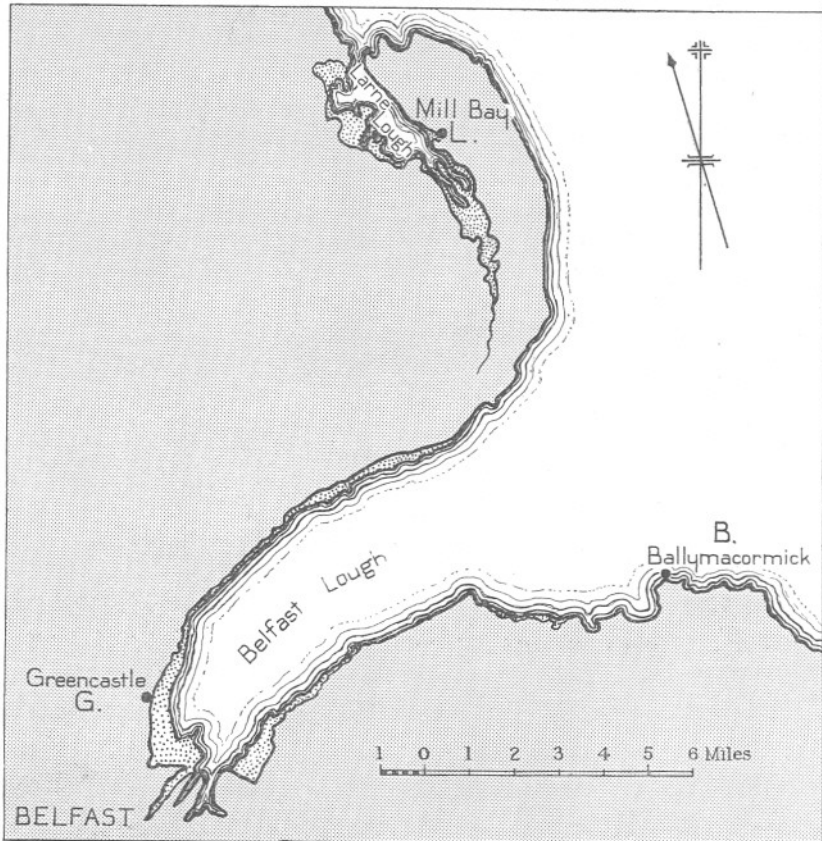


Fig. 1. Outline map of the north-eastern coast of Ireland, in the Belfast district, to show the three localities selected for the study of *Carcinus* populations, and the differences in their situation.

a moderate amount of silt, and Ballymacormick, facing the open waters of the Irish Sea and therefore comparatively free of silt, to detect any possible effect of this factor on the dimensions studied. The three localities will subsequently be referred to as L, G, and B respectively (see Fig. 1), followed by '36, '37 or '38 for the three years (1936, 1937, 1938). Samples of male *Carcinus* were collected from the three localities as nearly as possible at the same time each autumn. Orton's observations on the growth of individuals

in the field (Orton, 1936) indicated that they reach maturity in a single year, so that the bulk of each sample belonged to one season and was therefore homogeneous in this respect. The samples varied between 180 and 450 in number and covered a range of body size from 4 to 50 mm. Weldon's samples were much larger and covered a much smaller range of body size (10–15 mm.). The same dimensions as those of Weldon were measured (Fig. 2), but 'dentary margin' has not been extensively used in the subsequent analysis. Measurements were made with fine callipers on all individuals above 7 mm. carapace length. The smaller specimens were measured under a binocular microscope with a micrometer eyepiece. The error of measurement is estimated at not more than 1.5 %.

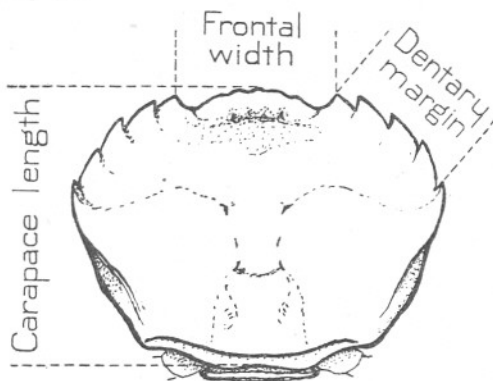


Fig. 2. Outline of carapace of *Carcinus moenas* to show dimensions measured.

The two dimensions, frontal width and dentary margin, were plotted against carapace length on double logarithmic paper. Group points were plotted, the grouping of individuals being at equal intervals on a logarithmic scale, except in the case of G '36 where the grouping was on a linear scale. There appeared to be no essential difference in the resulting graphs, but the logarithmic grouping gives even spacing of the points all along the logarithmic graph.

In the case of frontal width/carapace length the significance of possible differences between populations, in their growth curves, was tested mathematically. The Plymouth graphs (Needham, 1935) had taken the form of parallel straight lines corresponding to the equation of simple allometry (Huxley & Teissier, 1936), $y = bx^\alpha$, where α (the slope of the line) is constant in the three years, but b (the initial ratio y/x) decreases in succeeding years. In a case like this it is legitimate to test only for the significance of differences in b and assume that α is quite constant. An appropriate test, originally due to Teissier (1935), has been devised by Reeve and is here applied to the Belfast data.

The data for the nine populations were pooled and plotted on a single graph, double-logarithmically (Fig. 6). From this a mean value of α for all

nine, was obtained. Actually it was thought preferable to divide up the data into three sections according to body size, the sections to contain approximately equal numbers of individuals. The sections will subsequently be indicated by the suffixes 1, 2 and 3 to the appropriate population (L '36₁ and so on). Thus the data are divided into twenty-seven sections altogether. In correspondence with the division of the data three consecutive straight lines have been fitted to Fig. 6, their slopes giving the values of α appropriate to the three sections; the probability that α did, in fact, change with increase in body size was the main reason for dividing up the data. Although representing equal numbers of individuals the three sections do not cover equal ranges of body size (Fig. 6).

Using the appropriate mean values of α in each section, the value of b for every individual (about 3500 in all) was calculated from the allometry equation $y = bx^\alpha$, the calculation being performed in two steps (x^α and then y/x^α) using a log-log slide rule. From the series of values of b the mean, \bar{b} , was calculated for each of the twenty-seven sections and also the corresponding variance of b (Tables I-III). Any two populations were then considered to be significantly different in any section, if the difference, $\bar{b}_2 - \bar{b}_1$, between their mean values of b was greater than twice the standard error of the difference (i.e. more than twice the square root of the sum of their variances of b). The test was applied in two ways, which may be referred to as the general and the detailed tests. In the former, annual differences were tested by pooling the data of the three localities, and local differences in the same way by pooling the data for three years (Table I). This has the advantage of eliminating minor irregularities. In the detailed tests, the data for single populations were compared (Tables II, III). A significant difference is indicated by S and a non-significant difference by o, together with the sign of the difference. Differences greater than bare significance are marked by more S's, three times the standard error by SS, four times by SSS and so on.

Mr G. M. Spooner has kindly checked the results by an alternative test based on analysis of the variance.

RESULTS AND CONCLUSION FROM THE GRAPHICAL METHODS

Measurements of the growth of individuals show clearly that a decrease in the ratio frontal width/carapace length with increase in body size is manifest in the growth of the individual (p. 261). The data are shown in graphical form in Fig. 3, the short lines joining points representing the dimensions of successive exuviae. The slope of these lines varies around that of the whole population (dotted line), and the individual lines themselves are more or less normally distributed around the population curve. The extent of individual variation is perhaps worth noting. All measurements were carefully made by both workers, and there is little doubt that most of the variation is real. The population curve is a mean curve only (cf. Davenport, 1934; Needham, 1937).

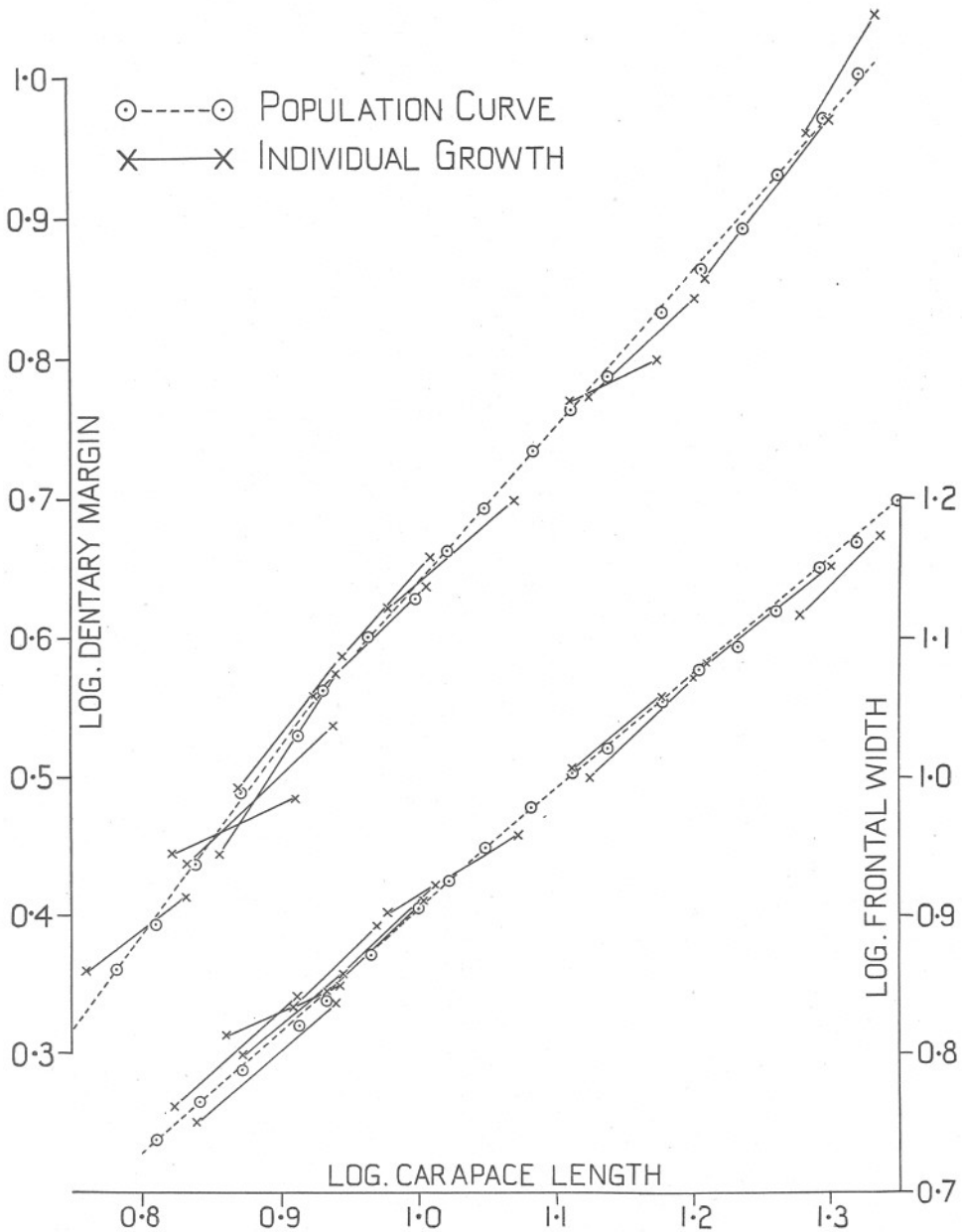


Fig. 3. Growth in frontal width and dentary margin relative to carapace length in individual male *Carcinus* kept in the laboratory, plotted for comparison, on the curve (dotted line) for the whole population in the same year and locality (Greencastle, 1937). Double logarithmic plotting. The lines join dimensions of successive exuviae.

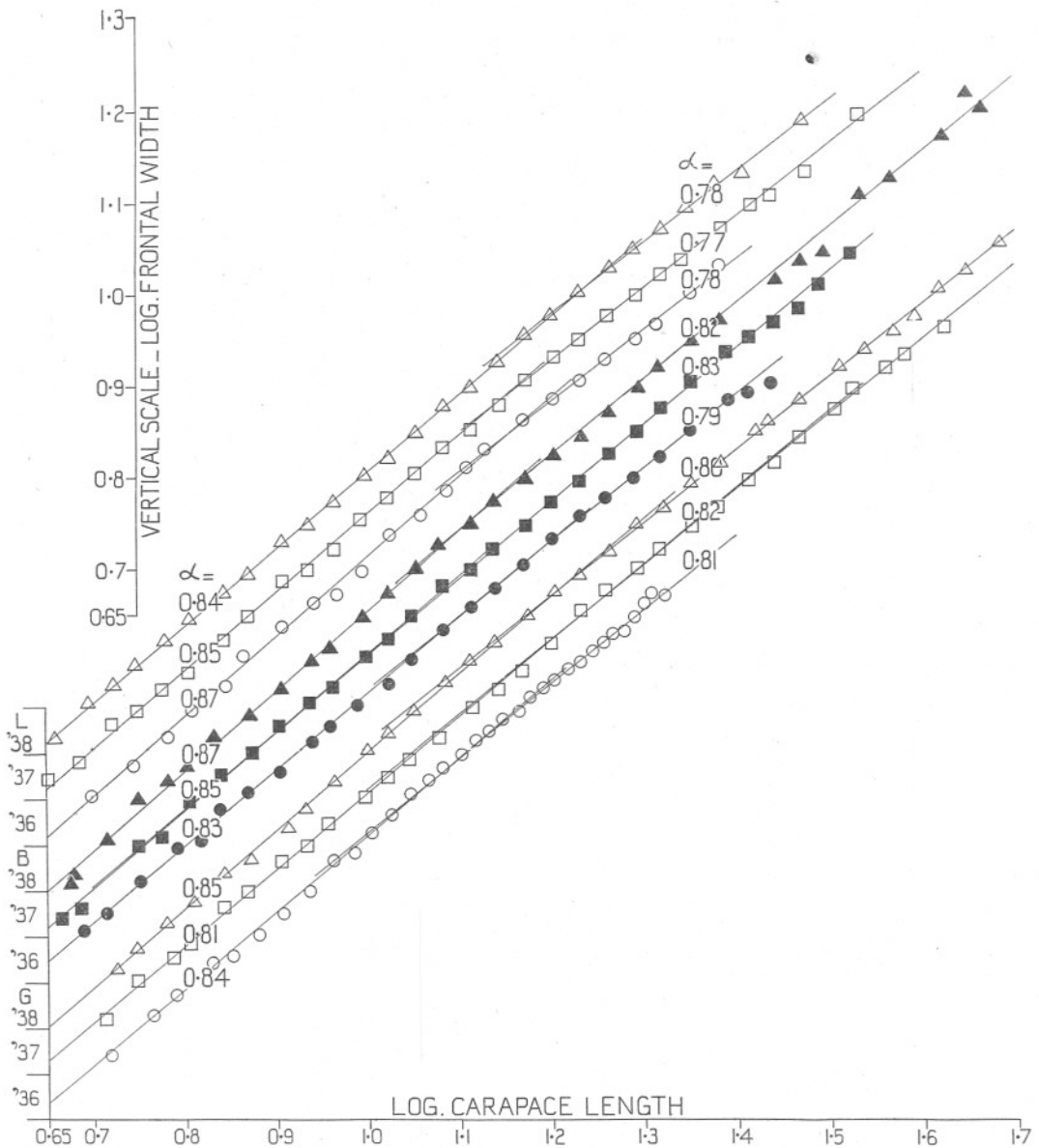


Fig. 4. Growth in frontal width relative to carapace length in nine populations of *Carcinus moenas* (males), from three localities, Greencastle (G), Larne (L), and Ballymacormick (B), in three successive years, 1936, 1937, 1938, to show the differences between the populations. Double logarithmic plotting. The curves are separated out, for clarity, by one large square of the graph paper, in the direction of the ordinate.

The curves of relative growth, frontal width/carapace length, for the Belfast populations (Fig. 4) are essentially similar to the Plymouth curves (Needham, 1935). It is clear, however, that the value of α is not absolutely constant over their much greater range of body size (p. 263), but decreases at larger body sizes. Two consecutive straight lines give reasonable fitting to the

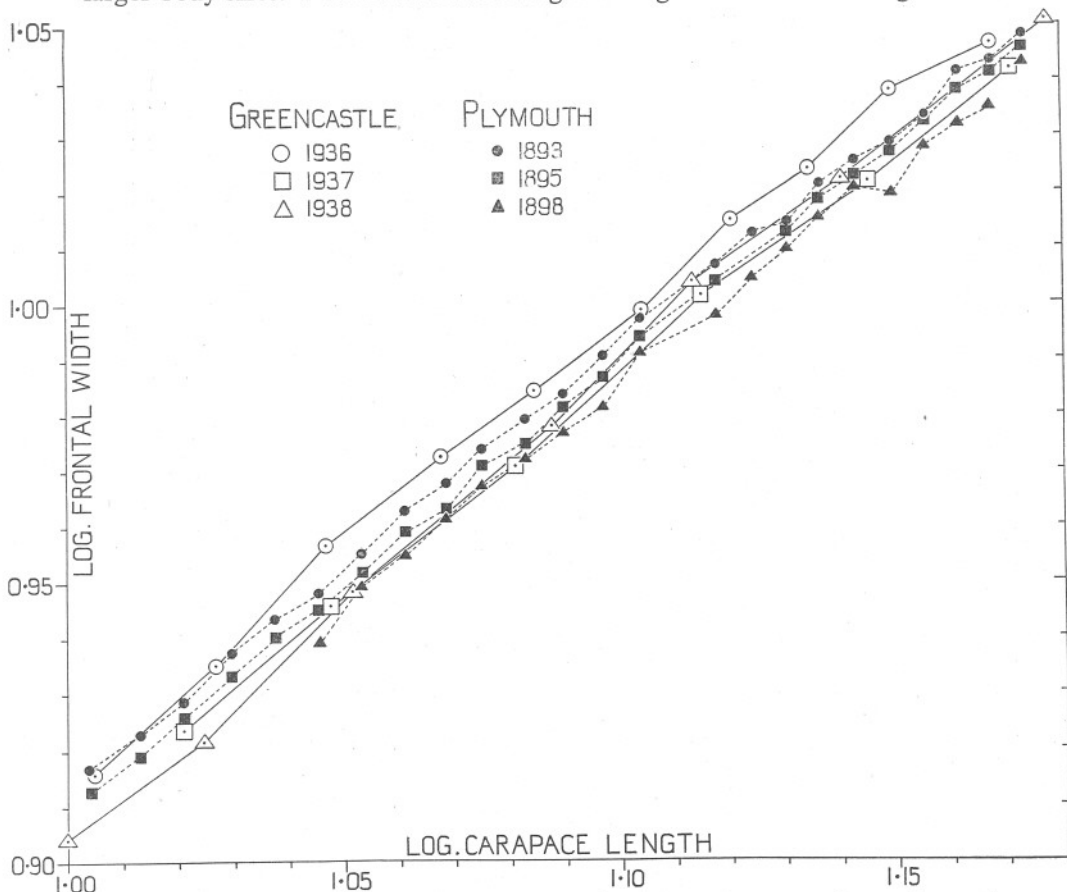


Fig. 5. The population curves for Greencastle male *Carcinus*, 1936, 1937, 1938, superimposed on those for Plymouth males, 1893, 1895, 1898, to show how the two sets overlap, and the parallel annual trend in the two localities. Double logarithmic plotting.

points, but it is probable that there is a continuous fall in α and that the three lines of Fig. 6 give a nearer approximation. For the sake of clarity the curves in Fig. 4 have been separated by one large square of the graph paper, in a vertical direction. At G and B there is a clear fall in b in '37, '38. The annual decrease is also shown by the wider gap between the curves L '38 and B '36 and between B '38 and G '36 (2-year interval) than between the curves in each locality, spaced at 1-year intervals. The value of α varies

somewhat in the different curves (0.81-0.87 for the first, and 0.77-0.83 for the second section), but an estimate of the standard error for one population (B '36) indicated that variation up to 0.08 was not significant. The division of the curves into two sections prevents a direct comparison with the Plymouth curves, but this has been done graphically in Fig. 5, where the latter are superimposed on the corresponding section of the G curves. The latter are possibly slightly higher than the Plymouth curves (higher value of b) and α is also possibly higher, but the differences are much less than the annual differences in the two localities. Since there is an interval of 40 years between the two groups of data it seems probable that the annual trends are not maintained over such long periods. At the same time they were, however, steadily maintained over a 5-year period at Plymouth, and the 2- and 3-year intervals show a correspondingly greater fall in b than the 1-year intervals of the Belfast data. The greater scatter among the points on the graphs of the latter is explained by the much smaller samples (p. 263).

Fig. 6 shows clearly that there is a real difference between the different populations in mean frontal width at corresponding body sizes. The grouping by body size was the same for all populations (except G '36, which is very distinct from the rest, therefore), so that the variation in carapace length (horizontal scatter of each group point) is due solely to chance variation in small samples. This variation is very small in the central region of the graph where there were large samples in the group. The variation in frontal width (vertical scatter of the points), on the other hand, shows considerable variation even in this region.

There is an interesting difference between different groups in the extent of this variation in frontal width, even in the central region. It is small in the groups with log carapace length = 1.0, 1.3 respectively, while in intermediate groups it shows a regular increase up to the group with log carapace length = 1.17, followed by a regular decrease.

The relative growth of dentary margin/carapace length is also essentially as at Plymouth, the value of α being about 1.2. Dentary margin shows positive allometry, therefore, whilst frontal width shows negative allometry. Carapace width shows virtual isometry relative to carapace length (plotting from the data of Day (1935)), so that the growth of the two sections of the carapace width (Fig. 2) is, as it were, compensatory. The possibility that b for dentary margin/carapace length shows regular trends as in the case of frontal width has not been investigated; it might possibly be expected to show an annual increase, in view of the 'compensatory' tendency noted above.

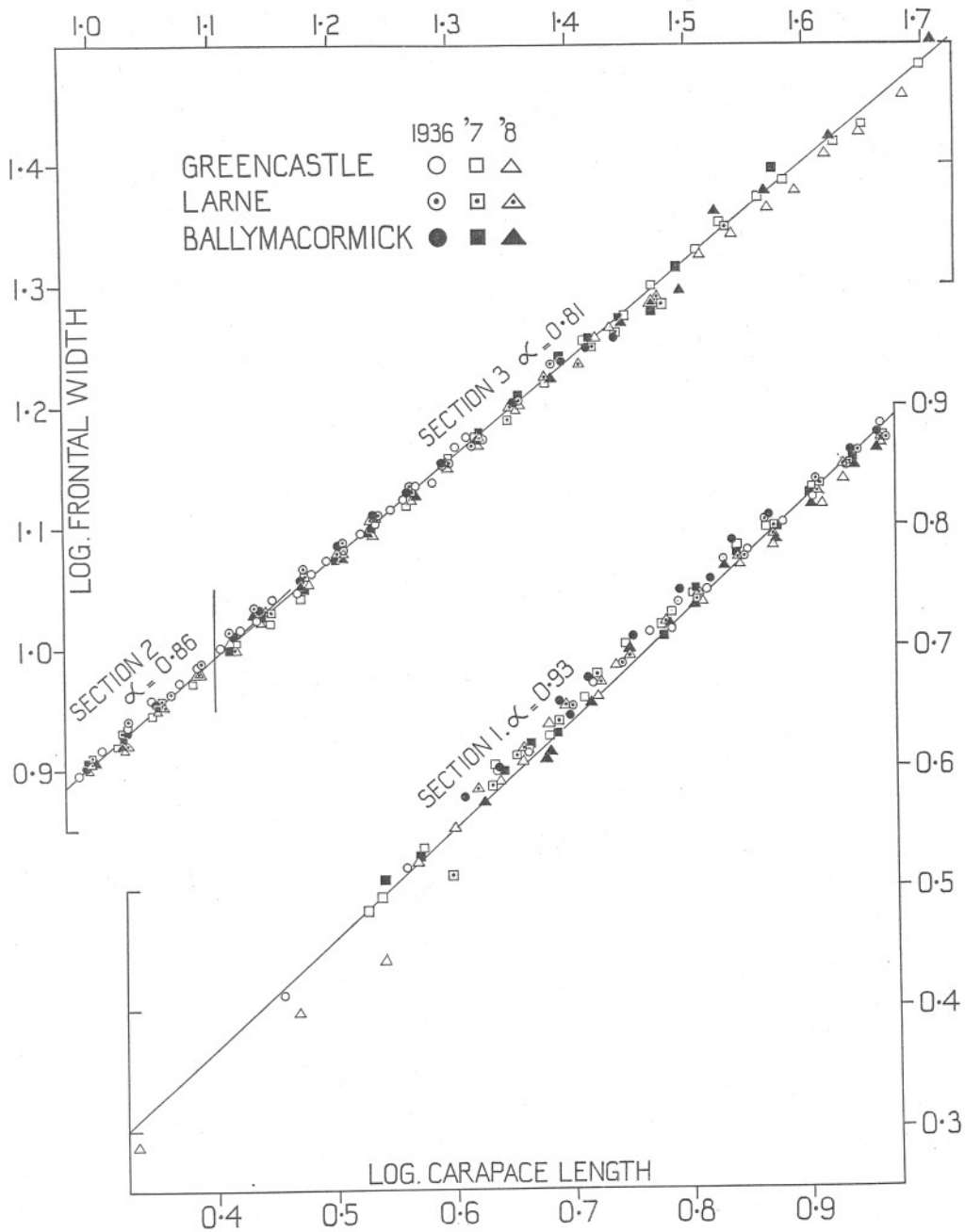


Fig. 6. Relative growth, frontal width/carapace length. Data (group points) for all nine Irish populations plotted on a single graph. Double logarithmic plotting. The curve is divided into three sections (1 in the lower graph and 2 and 3 above) containing approximately equal numbers of individuals. The slope of the line best fitting each section gave the values of α (0.93, 0.86, 0.81) used for the mathematical tests. It also shows: (1) variation in frontal width (vertical scatter of points) in each group is much greater than that in carapace length (horizontal scatter) due to chance variation in small samples only; (2) considerable differences between different groups in the extent of this variation in frontal width.

NOTES ON THE MATHEMATICAL TESTS

The assumption that α is the same for all nine populations, in any section, is fundamental to Teissier's test (p. 263); but, as indicated above (p. 267, Fig. 4), it is probable that α shows slight variations between the different populations, and it seems advisable to inquire how this might affect the validity of the tests. For an individual of average size (12 mm. carapace length) the substitution of $\alpha = 0.85$ for $\alpha = 0.80$ would produce a change in b of about 0.05, far greater than any difference recorded between the \bar{b} values for any two populations. The range of values of α shown on Fig. 4 indicates that the error in applying a mean value of α to a particular curve might well be of this order. Moreover, every point on the curve will be subject to this error, since the method of calculating b amounts to drawing a line through each point parallel to the mean curve. Again, in comparing two population curves, one having a real α value above the mean and the other below the mean, the difference $\bar{b}_2 - \bar{b}_1$ will be doubly affected by this error. If the true \bar{b}_2 were not less than the true \bar{b}_1 the apparent difference would be too large, while if it were less the errors would tend to cancel each other out; recorded differences may therefore be too large or too small. What they actually represent is a difference in b and α combined, the effect of α being often considerable (cf. Reeve, 1940, Text-fig. 4). Where two curves diverge their difference will be exaggerated, and where they approach or cross the difference may be reduced to insignificance. It seems probable that much of the apparent irregularity in significance from one section to another in the detailed test (Table II) may be due to this cause; the considerable reduction in this irregularity in the general test is also explained—the actual irregularities are partly smoothed out and therefore not so grossly exaggerated by subsequent treatment.

There are, however, a number of reasons for not discarding the tests as valueless. The contrast revealed between the magnitude of annual differences and that of local differences is independent of the factor just considered. The consistent trends in annual, local and sectional differences in variability of \bar{b} and in \bar{b} itself must also be real. The differences clearly show the relation between any two curves, whether they diverge, approach or cross, by the sign and magnitude of the difference in successive sections, so that an accurate picture is obtained which could not be accepted with confidence from the graphs alone. Moreover, since both b and α do apparently vary between populations, a figure based on both may legitimately be considered the best estimate of the extent of the difference between populations. In any case b depends on the value of α in previous sections of the growth curve, and the two parameters are interdependent (cf. Lumer, 1939). The values of \bar{b} shown in the tables give the mean position of that section of the curve in a vertical direction (i.e. direction of the ordinate)—the 'positional' value of Reeve (1940, p. 69). The differences between these \bar{b} values give the extent to which the curves are separated in the vertical direction, throughout the section, and not

merely at the beginning as would be the case with true values of \bar{b} . Thus the tests give valuable information about the differences between populations. Their only shortcoming is that they do not distinguish between differences due to b and those due to α . The Plymouth graphs strongly suggest that \bar{b} is much the more variable, and there is support from the Belfast data. Teissier (1936) found that local races of *Homarus*, *Haliotis*, *Littorina*, etc., differ in b but not in α , and the greater variability of b has been demonstrated by many workers.

In further justification of the tests it should be borne in mind that the use of a value of α (i.e. the adopted value) other than the true value increases the

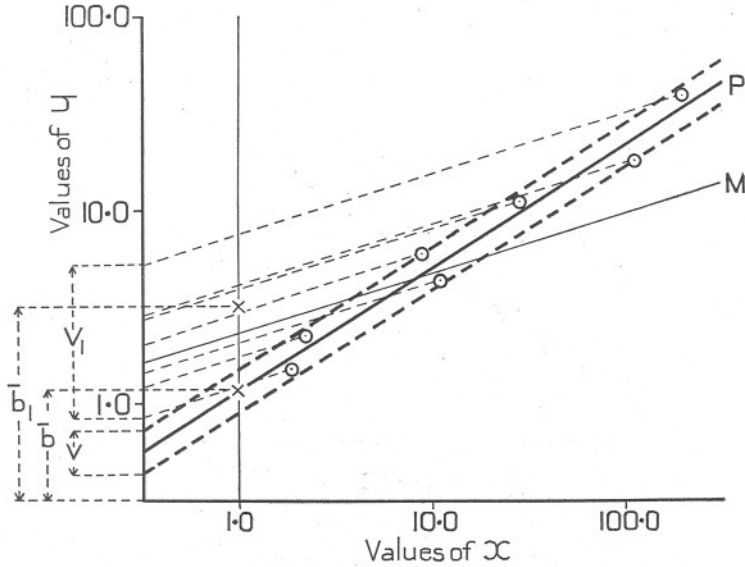


Fig. 7. Diagram to show the effect on \bar{b} and on the variation of b produced in a population curve by the substitution of the mean value of α for the true value. M =mean curve for all populations. P =curve for population in question. b and v = true value of b and of its range of variation. b_1 and v_1 =corresponding values obtained by using the mean value of α .

variance of b whether it increases or decreases the value of b itself (Fig. 7). The variance involves the square of the standard deviation, and since a difference, $\bar{b}_2 - \bar{b}_1$, must exceed $2 \times$ the square root of the sum of the two variances to be significant, there is every reason to believe that the test of significance is much more demanding than it would be with the true values of \bar{b} .

A possible source of error exists where the distribution of individuals is not uniform along the whole curve (or section). In the case of two curves not parallel to the mean curve, if one has many individuals near the beginning of the section and few in the second half, whereas the reverse holds for the other curve, then even if the two are virtually coincident (their α and b values both being the same) they will show very different apparent values of \bar{b} (Fig. 8).

In the present work every effort was made to ensure even distribution of individuals, and in any case those body sizes which were poor in individuals (the smallest and the largest) corresponded fairly closely in all populations.

If α is not constant over any considerable range of body size, but changes continuously throughout each section, as seems very probable, the value of \bar{b} obtained from the tests will be affected by this too. Here again the tests are of value; they still give an estimate of the *average* positional difference between two curves, in each section.

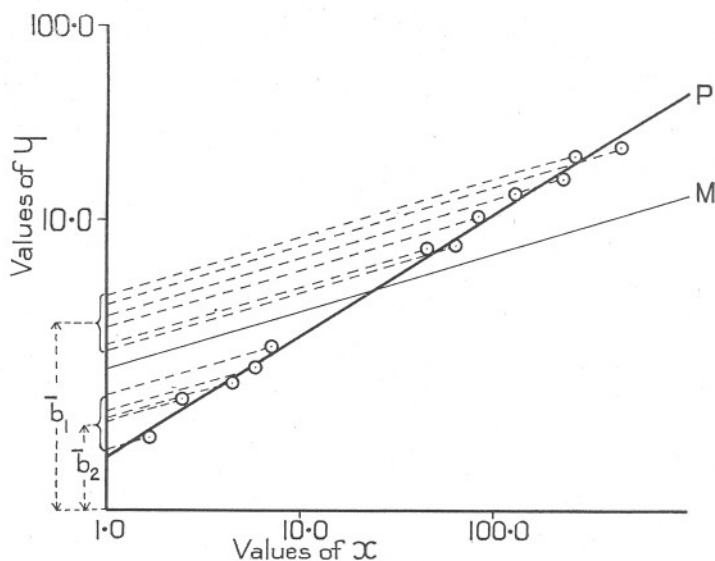


Fig. 8. Diagram to show how, when using the mean value of α instead of the true value, two coincident population curves give widely different values of b if there is not an even distribution of individuals along the curve. M = mean curve for all populations. P = coincident curves of the two populations in question. \bar{b}_1 and \bar{b}_2 = the mean values of b for the two populations.

RESULTS OF THE MATHEMATICAL TESTS

The value of b is given by y when $x=1$ in the allometry equation. Since the unit of x is a purely arbitrary quantity it may be taken as the value of x at the beginning of the particular section of the graph under consideration. In any case it will increase from section 1 \rightarrow 2 \rightarrow 3, following the fall in α . The change is far greater than the differences between the populations within any section, but this does not affect the significance of the latter (Tables I-III), which depend only on the values of b within that section.

From the general test (p. 264) it is seen (Table I) that the value of \bar{b} shows a regular annual decline, '36 > '37 > '38, and that there is a comparable regular sequence among the three localities, L, B, G, the widest frontal aperture being

TABLE I. THE GENERAL TEST

A. Yearly differences in \bar{b} , all localities combined

Year	Sec- tion	No. of indi- viduals	$Sb/n = \bar{b}$	Variance of $b \times n$	Variance of $\bar{b} \times 10^6$	Comparison between years	Sec- tion	Difference $\bar{b}_2 - \bar{b}_1$	Standard error of difference	Sign and significance of difference
1936	1	228	0.9798	0.3588	6.93330	1936-7	1	-0.002142	0.003027	-o
	2	458	1.1342	0.4558	2.17791		2	-0.011701	0.001913	+SSSSS
	3	320	1.2712	0.2360	2.31211		3	-0.008552	0.001921	+SSS
1937	1	421	0.9819	0.3939	2.22758	1937-8	1	-0.012239	0.002032	+SSSSS
	2	496	1.1225	0.3647	1.48542		2	-0.004127	0.001723	+S
	3	381	1.2627	0.1990	1.37464		3	-0.007568	0.001726	+SSS
1938	1	404	0.9697	0.3101	1.90477	1936-8	1	-0.010097	0.002973	+SS
	2	374	1.1183	0.2069	1.48313		2	-0.015828	0.001913	+SSSSSSS
	3	368	1.2551	0.2172	1.60852		3	-0.016120	0.001980	+SSSSSSS

B. Local differences in \bar{b} , all years combined

Locality	Sec- tion	No. of indi- viduals	$Sb/n = \bar{b}$	Variance of $b \times n$	Variance of $\bar{b} \times 10^6$	Comparison between localities	Sec- tion	Difference $\bar{b}_2 - \bar{b}_1$	Standard error of difference	Sign and significance of difference
Greencastle	1	425	0.9760	0.5562	3.08657	G-L	1	-0.002285	0.002345	-o
	2	535	1.1233	0.4993	1.74787		2	-0.003970	0.001957	-o
	3	423	1.2573	0.2921	1.63658		3	-0.009509	0.001726	-SSSS
Larne	1	327	0.9782	0.2574	2.41440	G-B	1	-0.000299	0.002492	-o
	2	347	1.1273	0.2504	2.08576		2	-0.003022	0.001849	-o
	3	387	1.2668	0.2004	1.34126		3	-0.007752	0.002095	-SS
Bally- macormick	1	301	0.9763	0.2817	3.11949	L-B	1	+0.001986	0.002316	+o
	2	446	1.1263	0.3318	1.67204		2	+0.000948	0.001939	+o
	3	259	1.2651	0.1840	2.75299		3	+0.001757	0.002022	+o

found in the most silty locality. However, whereas the annual differences are quite significant (except '36₁-'37₁), local differences are not (except G-L₃ and G-B₃). Mr Spooner's analysis of variance leads to the same conclusions: there are significant annual differences in all sections but local differences are only significant in section 3. The annual differences on the other hand decrease slightly, section 1 → 2 → 3.

The detailed tests (p. 264) reveal a number of irregularities which repay further investigation. The analysis of variance shows that the irregularities are greater than the variance within samples and are therefore significant. They are of the order of magnitude of the local differences but much smaller than the annual differences. The irregularities are greatest in section 1 and about half as great in 2 and 3. It seems possible that they are of the same nature as the local differences, that is, due to quite local causes.

The differences between '36 and '38 are consistently more significant than over either of the 1-year periods (Table II), showing that the annual differences are definitely progressive. This is most marked at B; at G, L there are often marked differences over a 1-year interval. In no 1-year interval is the difference significant in all three sections, but only at G '36-'37 is it insignificant in two of the three sections and usually it is far in excess of the limit of significance. In both G and B the order of the significance for 1, 2 in '36-'37 corresponds to that for 2, 3 in '37-'38 (-0 and +SSSSS for G, and +0 and +SSS for B), and this might be taken to indicate that the annual growth of *Carcinus* was approximately one section of the range of body size. However, the observations of Orton (1936) definitely disprove this. In any case the feature is not shown by L and is probably quite fortuitous.

L is anomalous in a number of respects. Its annual differences are smaller and less consistent than at G and B. In L₁ there is a significant increase in *b* from '36 to '38, instead of the usual decrease, and similarly in L₃ '37-'38.

Annual differences are greatest at Greencastle, the intermediate locality, and least at Larne.

The detailed tests bear out the general conclusion that local differences are less marked than annual differences: only 14/27 differences are significant as against 21/27 for the latter (Table II, B). Four of the nine comparisons show two sections insignificant (one only in the annual tests) and in seven of the nine the sign of the difference changes between sections 1 and 3, indicating that the two curves in question have crossed each other. In three sections ('36₂, '37₃, '38₂) none of the differences are significant, and only in '37₂ and '38₃ are all the three differences significant.

The value of the standard deviation of \bar{b} has been calculated by Mr Spooner and shows interesting features. It decreases regularly '36 > '37 > '38 as does \bar{b} itself, but the decrease is relatively greater; the decrease is shown in all sections (1 > 2 > 3) and in all localities (L least). Similarly there is a regular sequence in the localities G > B > L, involving all sections (1 most) and all years ('38 least). On the other hand, it is noteworthy that the locality sequence

TABLE II. THE DETAILED TEST. TEST FOR SIGNIFICANCE OF DIFFERENCES BETWEEN MEAN VALUES OF b FOR DIFFERENT POPULATIONS

Year, place and section	Difference $b_2 - b_1$	Standard error of difference	Sign and significance of difference		
A. Yearly differences in each locality					
Greencastle	$^{36}_1 - ^{37}_1$	-0.008889	0.0050170	-0	
	$^{37}_1 - ^{38}_1$	+0.024508	0.0033407	+SSSSSS	
	$^{36}_1 - ^{38}_1$	+0.015619	0.0047223	+SS	
	$^{36}_2 - ^{37}_2$	+0.021141	0.0030878	+SSSSSS	
	$^{37}_2 - ^{38}_2$	-0.000728	0.0028660	-0	
	$^{36}_2 - ^{38}_2$	+0.020413	0.0028940	+SSSSS	
	$^{36}_3 - ^{37}_3$	+0.001239	0.0030720	+0	
	$^{37}_3 - ^{38}_3$	+0.017874	0.0028627	+SSSSS	
	$^{36}_3 - ^{38}_3$	+0.019113	0.0029460	+SSSSS	
Larne	$^{36}_1 - ^{37}_1$	-0.012786	0.0057155	-S	
	$^{37}_1 - ^{38}_1$	-0.003160	0.0032420	-0	
	$^{36}_1 - ^{38}_1$	-0.015946	0.0055009	-S	
	$^{36}_2 - ^{37}_2$	+0.005934	0.0030020	+0	
	$^{37}_2 - ^{38}_2$	+0.009408	0.0030578	+SS	
	$^{36}_2 - ^{38}_2$	+0.015342	0.0031353	+SSS	
	$^{36}_3 - ^{37}_3$	+0.012393	0.0031780	+SSS	
	$^{37}_3 - ^{38}_3$	-0.004677	0.0023130	-S	
	$^{36}_3 - ^{38}_3$	+0.007716	0.0033029	+S	
Ballymacormick	$^{36}_1 - ^{37}_1$	+0.006632	0.0041770	+0	
	$^{37}_1 - ^{38}_1$	+0.017908	0.0039674	+SSS	
	$^{36}_1 - ^{38}_1$	+0.024540	0.0045804	+SSSS	
	$^{36}_2 - ^{37}_2$	+0.008349	0.0029770	+S	
	$^{37}_2 - ^{38}_2$	+0.004014	0.0028480	+0	
	$^{36}_2 - ^{38}_2$	+0.012363	0.0031220	+SSS	
	$^{36}_3 - ^{37}_3$	+0.012938	0.0039740	+SS	
	$^{37}_3 - ^{38}_3$	+0.009298	0.0037840	+S	
	$^{36}_3 - ^{38}_3$	+0.022236	0.0036730	+SSSSS	
B. Local differences in each year					
1936	G-L	1	+0.013672	0.0067446	+S
		2	-0.000385	0.0044283	-0
		3	-0.009889	0.0036235	-S
	G-B	1	-0.007756	0.0054313	-0
		2	+0.003628	0.0031804	+0
		3	-0.011891	0.0035270	-SS
	L-B	1	-0.021428	0.0062193	-SS
		2	+0.004013	0.0044710	+0
		3	-0.002002	0.0039560	-0
1937	G-L	1	+0.009775	0.0036729	+S
		2	-0.015592	0.0029880	-SSSS
		3	+0.001265	0.0025690	+0
	G-B	1	+0.007765	0.0036222	+S
		2	-0.009164	0.0028770	-SS
		3	-0.000192	0.0036030	-0
	L-B	1	-0.002010	0.0036470	-0
		2	+0.006428	0.0028050	+S
		3	-0.001457	0.0032016	-0
1938	G-L	1	-0.017893	0.0028600	-SSSSS
		2	-0.005456	0.0029326	-0
		3	-0.021286	0.0026702	-SSSSSSS
	G-B	1	+0.001165	0.0036121	+0
		2	-0.004422	0.0028300	-0
		3	-0.008768	0.0031180	-S
	L-B	1	+0.019058	0.0036959	+SSSS
		2	+0.001034	0.0030968	+0
		3	+0.012518	0.0030692	+SSS

is the reverse of that due to \bar{b} itself (p. 272). In the same way the regular decrease in the standard deviation through the three sections ($1 > 2 > 3$) is accompanied by a considerable increase in \bar{b} itself.

The standard deviation is a measure of absolute variability; by dividing it by \bar{b} the coefficient of variability is obtained. The annual differences in S.D. are so great ('38 only 75 % of the value for '36) that the much smaller decline in \bar{b} itself ($1\frac{1}{2}$ % only) has little effect and the coefficient of variability also

TABLE III. THE DETAILED TEST. THE MEAN OF \bar{b} AND ITS VARIANCE IN THE DIFFERENT POPULATIONS

Year, locality and section	No. of individuals	\bar{b}	$(Sb)^2/n$	$S(b^2)$	Variance of $b \times n$	Variance of $\bar{b} \times 10^6$	
Greencastle	'36 1	119	0.9788	114.0038	114.2587	0.2549	18.1527
	2	218	1.1356	281.1373	281.3675	0.2302	4.8662
	3	118	1.2644	188.6444	188.7129	0.0685	4.9616
	'37 1	146	0.9877	142.4222	142.5707	0.1485	3.7015
	2	176	1.1145	218.6014	218.7452	0.1438	4.6688
	3	159	1.2632	253.6925	253.8050	0.1125	4.4781
	'38 1	160	0.9632	148.4291	148.5347	0.1056	4.1509
	2	141	1.1152	175.3583	175.4276	0.0693	3.5106
	3	146	1.2453	226.4045	226.4832	0.0787	3.7175
Larne	'36 1	29	0.9652	27.0117	27.0339	0.0222	27.3399
	2	51	1.1360	65.8153	65.8529	0.0376	14.7451
	3	104	1.2743	168.8738	168.9613	0.0875	8.1684
	'37 1	145	0.9779	138.6606	138.7959	0.1353	6.4799
	2	160	1.1301	204.3277	204.4361	0.1084	4.2610
	3	149	1.2619	237.2610	237.3037	0.0427	1.9363
	'38 1	153	0.9811	147.2579	147.3516	0.0937	4.0291
	2	136	1.1207	170.7989	170.8923	0.0934	5.0871
	3	134	1.2666	214.7989	215.0213	0.0608	3.3386
Bally-macormick	'36 1	80	0.9865	77.8605	77.9322	0.0717	11.3449
	2	189	1.1320	242.1835	242.3700	0.1865	5.2488
	3	98	1.2763	159.6314	159.7025	0.0711	7.4795
	'37 1	130	0.9799	124.8281	124.9305	0.1024	6.1061
	2	160	1.1236	202.0098	202.1016	0.0918	3.6085
	3	73	1.2633	116.5105	116.5542	0.0437	8.3143
	'38 1	91	0.9620	84.2150	84.2939	0.0709	9.6337
	2	97	1.1196	121.5951	121.6370	0.0419	4.4996
	3	88	1.2540	138.3914	138.4374	0.0460	6.0084

shows a marked annual decline. The difference between localities in the S.D. is much less marked than the annual differences, but the coefficient of variability shows more marked differences from the fact that the value of \bar{b} itself shows the reverse order ($L > B > G$). This effect is even more marked in the sequence between sections where the inverse increase in \bar{b} , section $1 \rightarrow 2 \rightarrow 3$, is much greater.

This last feature, a decrease in the variability of b with increase in body size, does not necessarily imply a corresponding decrease in the variability of y . It can be shown by calculation that a decrease in the variability of b is not inconsistent with a constant *relative* variability of y (i.e. with an increasing *absolute* variability of y , the S.D. increasing as \sqrt{y}). It would be interesting to know whether, in the present case, y does show constant relative

variability—for a decreasing variability of b is consistent with a considerable range in the variability of y , both above and below the standard of constant relative variability.

It is clear that the above phenomenon results from the fact that the value of b depends not on that of x or y alone but on the ratio between them. A decreasing variability of b with increase in body size implies an increasing correlation between y and x (i.e. a more constant ratio y/x). This result seems to demand an explanation but cannot be considered further at this point.

DISCUSSION

The results of the present work show a close similarity to those of Weldon (1894); the ratio frontal width/carapace length decreases with increase in body size in *Carcinus moenas*, and it may further show a progressive decrease, at corresponding body size, from year to year. The observations on individual growth (Fig. 3) are sufficient to show that the former is a feature of differential growth in the individual, as the population curves, derived from Weldon's Plymouth data, had suggested (Needham, 1935). In this connexion, however, it is only fair to point out that since the population curve is only the mean of very variable individual curves (p. 264) it is possible that its essential form might not be changed if some natural selection agency were systematically eliminating individuals with relatively wide frontal aperture, or with a relatively high value of α . At present, however, there is no evidence concerning the possible effect of such a factor on the curve of relative growth.

Previous criticisms (Cunningham, 1928, etc.) have probably been sufficient to prove that the amount of silt in the water could not be such a factor in the present case, but the deliberate choice of localities in the Belfast studies, according to the amount of silt, has enabled a clear demonstration of this. Frontal width is consistently greatest at Larne, where, according to Weldon's hypothesis, it should be smallest; it is smallest at Greencastle, where it should be intermediate, so that silt cannot be a determining factor.

The yearly decline in the ratio is undoubtedly the most interesting feature of the data. The previous suggestion (Needham, 1935) that it depended simply on an initial difference in the ratio at the outset of growth seems reasonable. Teissier (1934) has suggested similar differences in proportion in the Zoea larva to account for the same phenomenon in the closely allied genus *Portunus*. Since local differences are so insignificant in comparison with annual differences (p. 274) it seems probable that the cause of the annual differences in larval proportions must be sought in factors which affect all localities equally, for example, climatic, affecting the atmosphere, or hydrographic. The annual changes are clearly not continuous over long periods; at Plymouth b decreased by 0.007 in 5 years, so that in about 650 years it would approximate to zero! That the Belfast data overlap the Plymouth data of 40 years earlier also suggests that periods when b decreases are offset by others showing an annual

increase. Whether the change follows a regular cyclic course, as in the case of fluctuations in animal numbers in many species (Elton, 1924), or is quite irregular cannot be decided without more data. There is strong evidence for the latter alternative however (Kemp, 1938). Hydrographic conditions in the Atlantic show considerable annual changes which appear to be quite irregular. It seems a priori probable that for marine animals hydrographic conditions may be the most important influence, far more so than direct climatic conditions.

It is of interest that there is a distinct sex difference in b in the same year (evidence from the data of Weldon), since local differences in any year are so small. However, this is presumably a genetic difference, quite independent of environmental factors.

The insignificance of local differences is indeed remarkable. The three localities differ in respects other than that of silt. Larne is very sheltered, with a very muddy substratum and with an admixture of fresh water, while B is a rocky coast exposed to the open sea; in all respects G is intermediate. Thus a number of local differences might be expected to combine to produce distinct local differences in relative proportions. The absence, in fact, of any such marked effects suggests that the animals may be relatively insensitive to most differences in local conditions. Considerable differences between local populations of terrestrial species are often recorded (Dice, 1940), but there it is probable that genetic differences may be at work; there is much less isolation among marine forms.

Such small local differences as there are (Table II B) do not follow the expected sequence; G is not intermediate and the order is $L \rightarrow B \rightarrow G$ (p. 272). There is only one obvious factor which distinguishes G from the other two and might account for its position in the sequence: there is a local effluent from Belfast, and the general effect of a large city on the Lough may be considerable. The sequence $G \rightarrow B \rightarrow L$ does, further, agree with their geographical latitude.

The anomalous features of the populations at L (p. 274) may well be due to its sheltered position, causing a general damping down of all environmental fluctuations. The constant outflow of fresh water might also have some effect, particularly on marine hydrographical changes. The tendency towards annual increases in b in some sections of the L data may well be due to these factors.

Local differences clearly exist (p. 274), but they are smaller and less consistent than annual differences. The fact that they tend to be more marked in section 3 than at smaller body sizes (p. 274) suggests a continuously operating type of influence, that is, a local environmental factor. At the same time it is just possible that initial differences are alone responsible: they would automatically increase with body size.

The probability that α changes continuously with body size means that the law of simple allometry (p. 267) does not strictly apply. This does not detract from the essential value of the law, however, and the assumption of a constant

value of α over a section of the growth curve is justified by the facilities it provides for testing differences between populations, varieties and species. Reeve (1940) and others have already shown the value of the law, even as an approximation, in solving taxonomic problems. The idea of a regular change in proportions with increase in body size, and the very simple equation which effectively expresses the relation, have opened up possibilities which have not yet been fully exploited.

Another apparent criticism (p. 264), namely, that the curve of relative growth obtained by plotting the data of a large sample (population curve) is only a statistical mean and not an expression of individual growth (Davenport, 1934) does not detract from the value of the curve. The growth of an individual is as much a statistical mean (of the activity of its cells) as that of a population or of a species. The population curve is a population characteristic and may be used with the same confidence as any recognized character, morphological or otherwise. Again, the superiority of a mathematical estimate over purely descriptive morphological characters, as a permanent record, is undoubted.

No reason for the change in relative frontal width with increase in body size has been advanced. It may be a secondary effect of the contrasted (and apparently complementary) increase in relative size of the dentary margin (p. 268). The dentary margin corresponds roughly to the branchial region of the carapace and if, as seems probable, the surface area of the gills increases in simple proportion to the volume of the body as a whole, the dimension in question might be expected to increase relative to other dimensions of the body (roughly to the power $\sqrt{\frac{3}{2}} = 1.23$ approx., which is roughly the value of α actually recorded for dentary margin/carapace length). If the relative decrease in frontal width is a compensatory result of this it must further be supposed that other considerations demand approximate isometry between total carapace width and carapace length.

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It is hoped to deposit the original data, too bulky to be included here, with the library of the British Museum, Natural History.

SUMMARY

1. Measurements of *Carcinus*, comparable to those taken by Weldon at Plymouth 40 years ago, have been made on material from three Irish localities, the observations in each area extending over three years. The three localities afford different environments, one having no silt, one a moderate amount and the other much silt.

2. The results support the view that the change in the ratio frontal width/carapace length with increase in body size is due to differential growth in the individual and is not caused, as Weldon supposed, by the continuous removal through natural selection of those crabs with a relatively wide frontal aperture. Measurement on the growth of individuals confirms this view.

3. A striking fact which emerged from Weldon's work was that the ratio mentioned above showed a successive diminution in each of the three years covered by the observations. A precisely similar diminution has been found at each of the Irish localities, and it is shown that the annual differences are mathematically significant.

4. The results disprove Weldon's hypothesis that the change in the ratio is correlated with the slow accumulation of silt in Plymouth Sound. The Irish locality with most silt has the widest frontal aperture and the intermediate locality the narrowest. It is also shown that the yearly trend towards a lower value for the ratio cannot be continuous, for the rate of change is too rapid to be maintained indefinitely, and the values obtained in the Irish localities overlap those at Plymouth 40 years earlier. Possible explanations of the changes are discussed.

5. The differences between populations from the three localities in any year are much less marked than the annual differences at one locality, and are not generally significant. Though small, however, they do show a consistent sequence among the three localities (but not corresponding to the order for siltiness).

6. The equation of simple allometry, $y = bx^\alpha$, applies to the data, at any rate as a useful approximation. The mean of b , and the variance of b , show consistent annual, and local differences in magnitude, and a regular change with increase in body size. The sequence for b itself may either correspond with that for its variance or run precisely counter to it.

7. The relation of individual growth to the mean curve of growth for a whole population is indicated and the value of the latter discussed.

8. A possible explanation of the differential growth of the dimension frontal width is advanced.

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