Graphical Estimation of Growth Parameters

By

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Introduction

For species in which there is no way of determining age it is often difficult to make estimates of growth parameters. MANZER and TAYLOR (1947), however, plotted individual lengths of recaptured soles against their lengths when tagged one year previously, and RICKER (1958) suggested that the plot so obtained could be used to estimate "maximum" length (L_∞) and, if the mean length at one age is known from other sources, annual increments. LINDNER (1953) plotted the lengths at recapture and release of shrimps at liberty for periods of up to only 40 days to obtain estimates of L_∞, and recommended this method as being suitable for species in which age is not easily determined. KOHLER (1963) used a similar method for cod at liberty for one and two years after tagging, and the present author examined growth data from marking experiments with whelks in the same way (HANCOCK, 1963a).

The validity of the results obtained by using this method for whelk data could not be assessed, because there is no known method of separating whelks into age-groups. The edible cockle (*Cardium edule* L.), however, although unsuitable for marking experiments, does possess well-defined winter growth checks, and the length at any age can be measured easily. It was therefore considered worth while to examine data from cockles to obtain some idea of the processes or errors involved in the method used by KOHLER (1963) and HANCOCK (1963a) of plotting length data of *individuals* of different ages, and to compare the results thus obtained with those from the more usual type of Ford-Walford plot which employs mean length at each age. The latter method, developed independently by FORD (1933) and WALFORD (1946), gives a similar interpretation of growth in length to VON BERTALANFFY'S (1938) growth equation (BEVERTON and HOLT, 1957). It should be said at once that the present results might be improved upon by examining a population containing older cockles than used here, i.e. so giving more mean length relationships on the graphs, but suitable data were not available. Nevertheless, the results serve to illustrate the underlying principles of the methods involved.

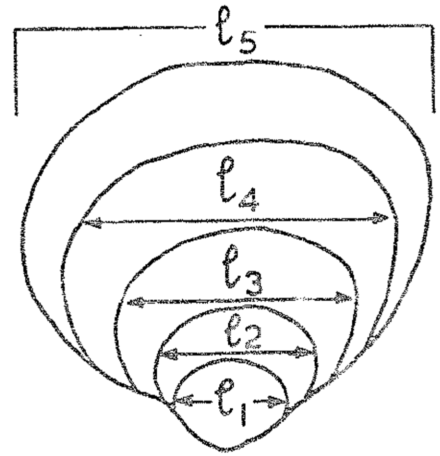

Figure 1. Shell-length measurements of cockles.

Method

Cockles in a large sample collected from a restricted locality of Llanrhidian Sands, South Wales, were examined for total shell length, age, and shell length corresponding to each winter growth check, i.e. l_1, l_2, l_3, etc. (Figure 1). Growth ceases each winter (HANCOCK, 1963b) and since these cockles were examined during the winter months the shell added between growth checks provides a measure of annual increments. In this area the majority of larvae are liberated at about the beginning of the growth season, so that the first winter ring usually encloses virtually the complete first year's growth. Using the data obtained it was possible to construct graphs to illustrate the following relationships

1. Ford-Walford plot

This normally involves plotting the mean length at any age (l_{t+1}) against the mean length (l_t) of animals one year younger (WALFORD, 1946). If the growth rate is fairly constant from year to year a straight line is usually obtained. In cockles, there may be marked variation in the amount of annual growth from year to year, but if enough age-groups are represented the points will still approximate to a straight line. The slope of this line is given by e^{-K}, its intercept on the y-axis by $L_\infty(1 - e^{-K})$, and its intercept on a 45° line, i.e. where $y = x$, is L_∞. K is the coefficient of catabolism of VON BERTALANFFY'S (1938) growth equation, and describes the rate at which the maximum or asymptotic length of the growth curve is reached (BEVERTON and HOLT, 1959). In addition, equal time intervals of more than a year may be useful for averaging out differences in annual growth, in which case the equation to the straight line

$$l_{t+T} = L_\infty(1 - e^{-KT}) + l_t e^{-KT}$$

should be used, where $T = 1, 2, 3 \ldots$, the time interval in years (GULLAND, 1964). For a time interval of say 2 years, the slope e^{-K} now becomes

Table 1

Mean lengths (mm) of cockles of year-classes 1955–1962 measured at the end of each growing season 1958–1962

(NR – No record)

Measured at end of	Year-class 1962	1961	1960	1959	1958	1957	1956	1955
1958	–	–	–	–	13·4	24·0	26·8	29·2
1959	–	–	–	13·2*	22·2	26·9	28·2	29·7
1960	–	–	13·8	22·0	26·0	NR	NR	NR
1961	–	12·9	22·9	26·7	28·5	NR	NR	NR
1962	12·6	21·1	26·0	28·4	29·8	NR	NR	NR

* Estimated value

The alternative method of plotting the increment $l_{t+1} - l_t$ against the original length l_t is often considered to be preferable (GULLAND, 1964), but since the present aim is to compare these results with those from Manzer and Taylor plots, the original Ford-Walford method is used.

The different methods of relating suitable data include:–

1(a) Using mean lengths of a selected year-class measured in each year of life, e.g. in Table 1, using the mean length of the 1958 year-class measured at the end of each year 1958 to 1962, i.e. 13·4, 22·2, 26·0 mm, etc. This plot describes the growth of a single year-class during several different years.

1(b) Taking the mean lengths of cockles of each year-class from the same population, and plotting them against the mean lengths of cockles from the same year-classes measured a year previously, e.g. Table 1, mean length of 1958 year-class at the end of 1962 against mean length of 1958 year-class at the end of 1961, 1959 year-class in 1962 against that in 1961, etc. This plot describes growth of different year-classes in the same year, i.e. 1962 in this instance.

1(c) Relating the mean lengths of different year-classes measured from one population in the same year, e.g. plotting mean length of 1958 year-class against 1959, 1959 against 1960, etc., all measured in 1962 (Table 1). Since these differences do not correspond to the growth of any fish this method should be used only when other methods cannot (GULLAND, 1964).

2. Back-measurement plot

This is a further application of the Ford-Walford plot, using data obtained by examining the previous growth history of animals of the same age. In cockles, the mean lengths at the end of each year of life of a group of cockles

Table 2

Mean lengths (mm) of cockles of year-classes 1958 and 1959 measured at the end of 1962 (i. e. 5 year-olds and 4 year-olds), showing the mean lengths of rings representing annual growth checks, as used for method (2)

Year-class	Growth season 1958	1959	1960	1961	1962
(A) 1958	13·0	20·8	26·2	29·1	29·8
(B) 1959	–	13·5	22·8	27·4	29·1

of a given age can be obtained by measuring the length of rings corresponding to annual growth checks on the shell (Figure 1 and Table 2). In fish this method is subject to errors arising from factors causing LEE's phenomenon (LEE, 1912), but in cockles at least one of these, the possibility of scale shrinkage, does not occur.

Method (2) differs from (1) above in that the relationship is based on measurements from the *same* individuals, not from groups of *different* animals from the same or different year-classes. Both methods (1) and (2) may include errors due to selection by fishing. RICKER (1958, p. 190) suggested that parameters obtained from method (2) would be most appropriate for production computation.

3. Manzer and Taylor plot

By plotting the length at recapture against the length at release, measurements from individuals at l_{t+1} are related to measurements at l_t from the *same* individuals. This is therefore not a typical Ford-Walford plot as in (1) above, not only because it employs *individual* measurements instead of mean lengths, but also because the related measurements are taken from the same, not different, animals. Similarly, when recaptures have been examined after two years at liberty, e.g. by KOHLER, the graph obtained again relates l_{t+2} to l_t of the *same individuals*. The method is therefore more like (2) above, but it relates not *mean* lengths but pairs of *individual* length measurements from the same individuals.

Results

1. *Ford-Walford plot*

Typical Ford-Walford plots were obtained (Figure 2 A–C) by using the mean shell lengths of cockles aged 1 to 5 years, this being the oldest group with cockles in useful numbers. With only four points on each graph and with variable annual growth, an exceptional year for growth could cause bias. However, fairly straight lines resulted, and the lines relating mean lengths of cockles separated by 2- and 3-year intervals could also be used to give a measure of the reliability of the estimates of L_∞ obtained (Table 3).

2. *Back-measurement plot*

The mean lengths at each age in their life of (A) 5 year-old and (B) 4 year-old cockles (Table 2) have been related as for a typical Ford-Walford plot at intervals of both one and two years, i.e. by plotting l_2 against l_1, l_3/l_2, etc. and also l_3/l_1, l_4/l_2, etc., all measurements being from the same cockles. Both ages were examined, the 4 year-olds because a larger sample was available than 5 year-olds and might be expected to give more reliable, if fewer, points on the graph. The graphs obtained from 5 year-olds (Figure 2D) were quite similar to those from method (1) (Figure 2 A–C), but here the deviations from a straight line reflect the effects of different growth seasons on the *same* cockles. The values of L_∞ are quite similar to those obtained from method (1), but the value of K obtained for 4 year-olds (0·82) was rather higher than for 5 year-olds (0·58 – Table 3).

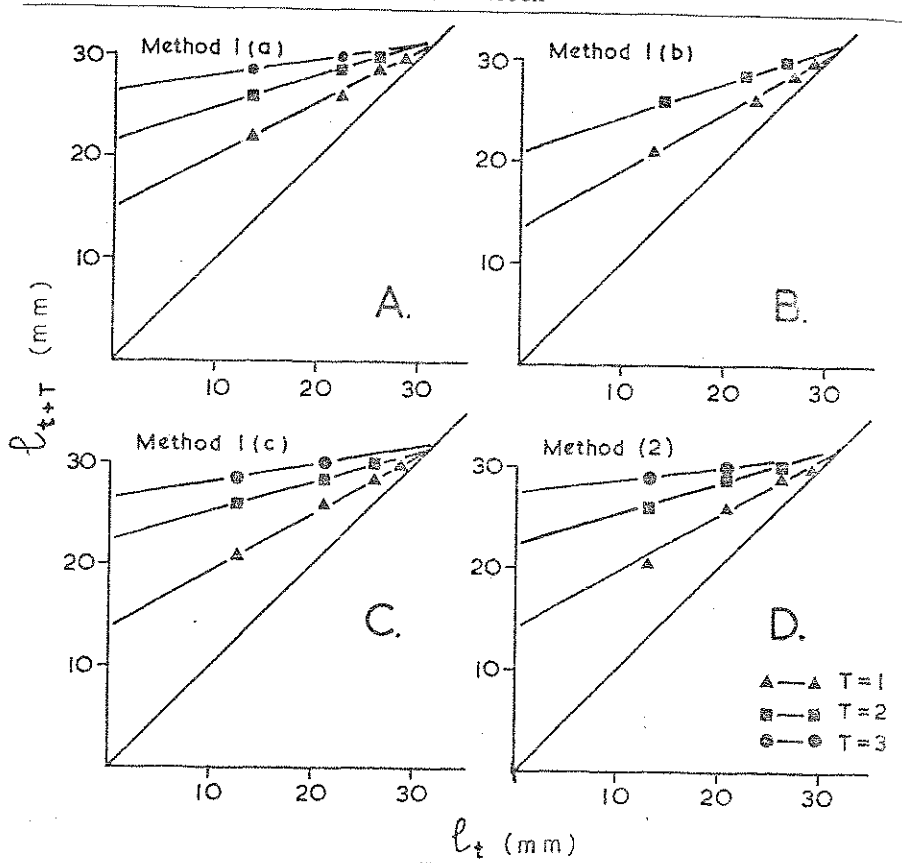

Figure 2. A–C, methods 1 (a–c), Ford-Walford plots (see text); D, method (2), back-measurement plot, for 5 year-old cockles.

Table 3

Parameters estimated by various methods

(see Figures 2, 3 and 4)

Method	Growth interval	Age of cockles included: – 5 years L_∞	K	4 years L_∞	K
Ford-Walford plot..............1(a)	one year	31·0	0·68	–	–
Ford-Walford plot..............1(b)	one year	31·2	0·58	–	–
Ford-Walford plot..............1(c)	one year	31·5	0·59	–	–
Back-measurement (means)......2(a)	one year	31·6	0·58	30·4	0·82
Back-measurement (individuals)..2(b)	one year	32·6	0·53	30·2	0·80
Manzer and Taylor plot.........(3)	one year	30·2	0·63	–	–
Ford-Walford plot..............1(a)	two years	31·5	0·58	–	–
Ford-Walford plot..............1(b)	two years	31·4	0·58	–	–
Ford-Walford plot..............1(c)	two years	31·5	0·62	–	–
Back-measurement (means)......2(a)	two years	30·8	0·73	30·4	0·85
Back-measurement (individuals)..2(b)	two years	32·4	0·55	29·9	0·89
Manzer and Taylor plot.........(3)	two years	31·6	0·55	–	–

Table 4

Manzer and Taylor plot. Equations by linear regression of values of l_{t+T} on l measured from individual cockles of different ages, i. e. 2 to 5 years

(see Figure 3)

Age of cockles	Relation ship	Regression formula	Correlation coefficient	Degrees of freedom	Intercept on $y = x$	K
		(a) One annual increment ($T = 1$)				
2..............	l_2/l_1	$l_2 = 0·746\, l_1 + 11·313$	0·60	5257	44·6	
3..............	l_3/l_2	$l_3 = 0·853\, l_2 + 6·150$	0·85	237	41·8	
4..............	l_4/l_3	$l_4 = 0·978\, l_3 + 1·612$	0·95	353	73·3	
5..............	l_5/l_4	$l_5 = 0·945\, l_4 + 2·244$	0·96	110	40·9	
All data combined		$l_{t+1} = 0·535\, l_t + 14·039$	0·90	5963	$L_\infty = 30·2$	0·63
		(b) Two annual increments ($T = 2$)				
3..............	l_3/l_1	$l_3 = 0·430\, l_1 + 20·079$	0·40	231	35·2	
4..............	l_4/l_2	$l_4 = 0·906\, l_2 + 7·739$	0·81	353	82·3	
5..............	l_5/l_3	$l_5 = 0·927\, l_3 + 5·516$	0·90	110	75·6	
All data combined		$l_{t+2} = 0·333\, l_t + 21·046$	0·77	698	$L_\infty = 31·6$	0·55

3. *Manzer and Taylor plot*

This was obtained by relating the measurements bounding the last annual increment of individual cockles aged two to five years. The resulting plot was therefore composed of points relating l_2 and l_1 of 2 year-old cockles, l_3 and l_2 of 3 year-old, etc. The data were too numerous to permit individual points to be plotted in Figure 3, but the regression line for y on x, i.e. l_{t+1} on l_t obtained by computer, has been shown. This line intersected the 45° line to give a value very similar to the estimates of L_∞ obtained from Ford-Walford plots (Tables 3 and 4). These had been considered to be quite reasonable for the area from which the cockles were gathered. The value of K calculated from the slope of the line was also similar.

From examination of the data from measurements for different ages, it was evident that the slopes of the lines relating l_{t+1} to l_t varied from year to year. The separate regression lines obtained by plotting measurements from individual cockles of different ages, i.e. l_2 against l_1 of 2 year-olds, separately from l_3 against l_2 of 3 year-olds, etc., have been shown in Figure 3. Table 4 also shows that the slope of each line is different from that of the combined line for unseparated ages, and the values obtained from intercepts with the 45° line were all different. The implications of this are discussed below.

4. *Back-measurement plot using individual, instead of mean, lengths*

In view of the results obtained by method (3) it was decided to re-examine the data used in method (2) above (back-measurement plot), this time plotting the individual measurements from which the mean lengths were taken. The results (Figure 4 and Table 5) behaved in a similar way to those from the Manzer and Taylor plot. The regression line from individual measurements combined from all age-groups (Table 3 – method 2(b) and Table 5) gave similar values of L_∞ and K to those obtained from mean lengths (Table 3 – method 2(a)), and its slope was again usually different from slopes for separate ages. This treatment is, of course, not applicable to data from other Ford-

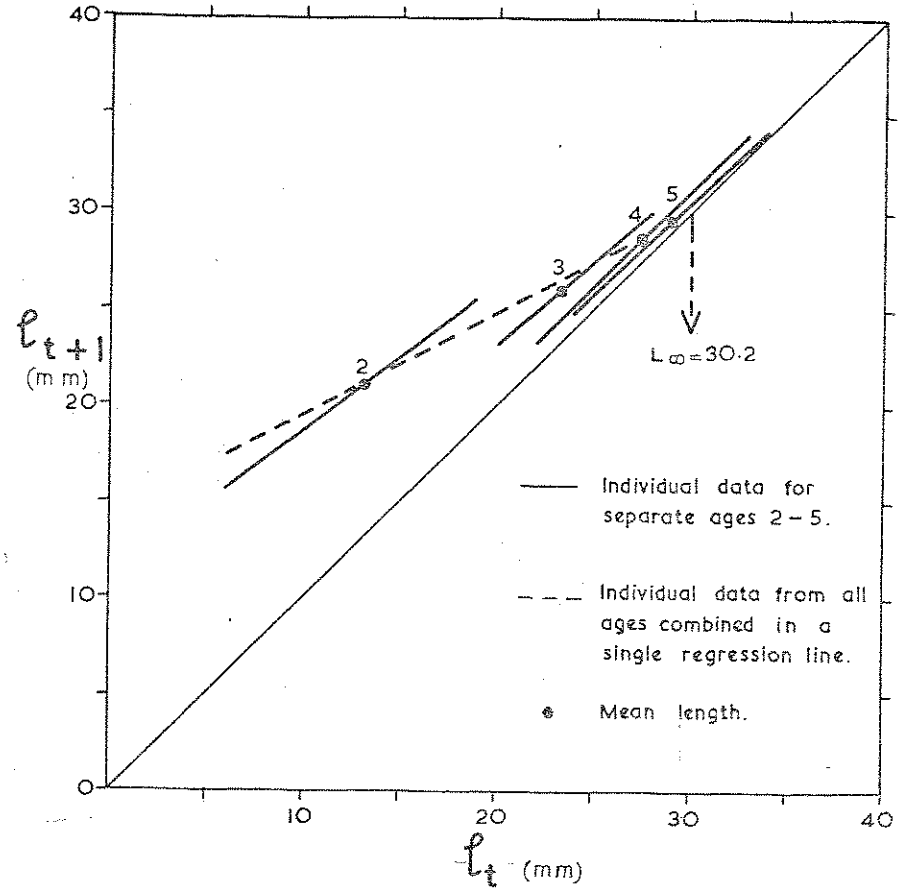

Figure 3. Manzer and Taylor plot (see also Table 4) of individual measurements from cockles aged 2–5 years, using regression lines l_{t+1} on l_t.

Age		Mean length (mm)	Range (mm)	Number in sample
2	l_2	21·1	14–27	5,259
	l_1	13·1	6–19	
3	l_3	26·0	22–31	239
	l_2	23·3	20–28	
4	l_4	28·4	24–34	355
	l_3	27·4	22–33	
5	l_5	29·8	24–35	112
	l_4	29·1	24–34	

Walford plots which are based on mean lengths at age of *different* animals, from which no equivalent pairs of observations from individuals are possible.*

* RICKER (personal communication) has since pointed out that unweighted regressions of l_{t+1} on l_t (which are both equally subject to error) are liable to bias, giving too small a slope and hence too small an L_∞ and too large a K. However, there seems to be no agreed method for determining the true "functional" relationship, but the comparisons between the various regressions should be valid, even though the rate of growth may have been underestimated.

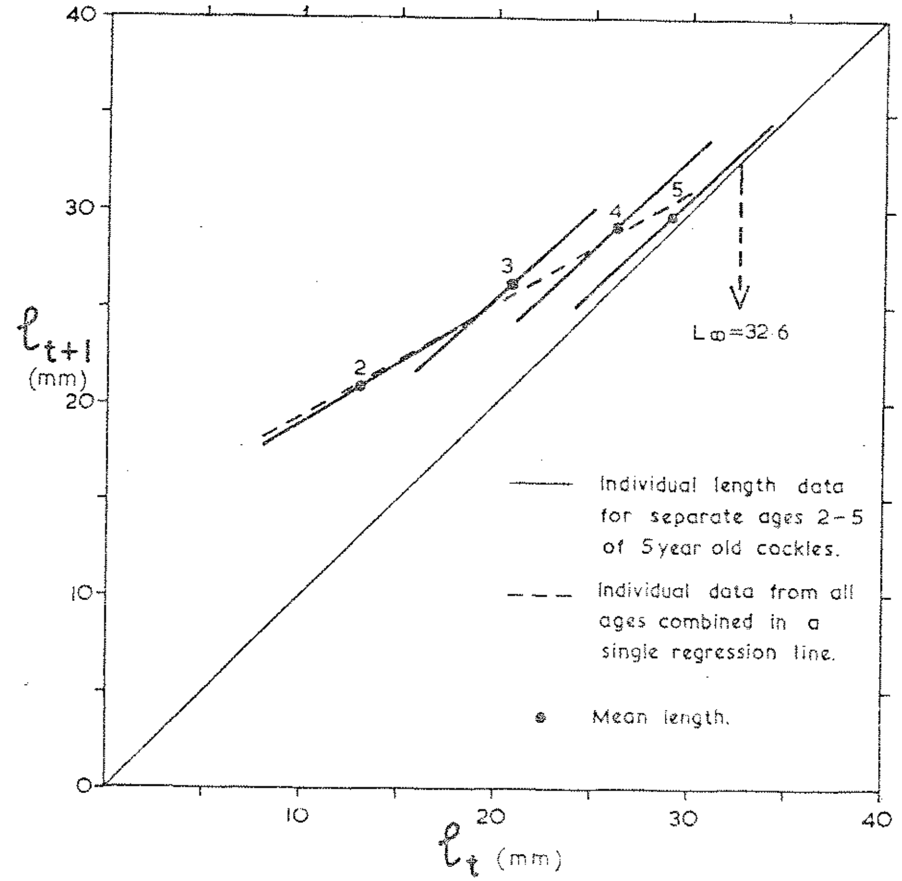

Figure 4. Back-measurement plot of individual measurements from 5 year-old cockles, using regression lines l_{t-1} on l_t (see also Table 5).

	5 year-olds Mean length (mm)	5 year-olds Range	4 year-olds (not plotted) Mean length (mm)	4 year-olds (not plotted) Range
l_1	13·0	8–19	13·5	9–18
l_2	20·8	16–25	22·8	18–27
l_3	26·2	21–31	27·4	22–33
l_4	29·1	24–34	28·4	24–34
l_5	29·8	24–35		
Number in sample	112		355	

Discussion and Conclusions

The results showed that estimates of growth parameters obtained from the various Ford-Walford plots, including back-measurement, were, except for the difference in K values from 4 and 5 year-old cockles, in good agreement. The higher K value (0·8) obtained by back-measurement of 4 year-old cockles may have resulted from the use of younger cockles, i.e. with only 3 points on the graph, particularly since the final increment represented a year of unusually

Table 5

Back-measurement plot. Individual measurements

Equations obtained by computer for linear regression of values of l_{t+T} on l_t measured from individual cockles of the same age, i.e. 4 or 5 years old (see Figure 4).

Relationship	Regression formula	Correlation coefficient	Degrees of freedom	Intercept on $y = x$	K
(A) 5 year-old cockles (1958 year-class)					
(a) One annual increment ($T = 1$)					
l_2/l_1	$l_2 = 0{\cdot}618\, l_1 + 12{\cdot}793$	0·62	110	33·5	
l_3/l_2	$l_3 = 0{\cdot}920\, l_2 + 6{\cdot}974$	0·86	110	87·2	
l_4/l_3	$l_4 = 0{\cdot}953\, l_3 + 4{\cdot}194$	0·92	110	89·2	
l_5/l_4	$l_5 = 0{\cdot}945\, l_4 + 2{\cdot}244$	0·96	110	40·8	
All data combined	$l_{t+1} = 0{\cdot}594\, l_t + 13{\cdot}244$	0·95	446	$L_\infty = 32{\cdot}6$	0·53
(b) Two annual increments ($T = 2$)					
l_3/l_1	$l_3 = 0{\cdot}506\, l_1 + 19{\cdot}564$	0·47	110	39·6	
l_4/l_2	$l_4 = 0{\cdot}841\, l_2 + 11{\cdot}594$	0·75	110	72·9	
l_5/l_3	$l_5 = 0{\cdot}927\, l_3 + 5{\cdot}516$	0·90	110	75·6	
All data combined	$l_{t+2} = 0{\cdot}328\, l_t + 21{\cdot}790$	0·76	334	$L_\infty = 32{\cdot}4$	0·55
(B) 4 year-old cockles (1959 year-class)					
(a) One annual increment					
l_2/l_1	$l_2 = 0{\cdot}803\, l_1 + 11{\cdot}942$	0·71	353	60·6	
l_3/l_2	$l_3 = 0{\cdot}932\, l_2 + 6{\cdot}116$	0·85	353	89·9	
l_4/l_3	$l_4 = 0{\cdot}978\, l_3 + 1{\cdot}612$	0·95	353	73·3	
All data combined	$l_{t+1} = 0{\cdot}451\, l_t + 16{\cdot}601$	0·91	1063	$L_\infty = 30{\cdot}2$	0·80
(b) Two annual increments					
l_3/l_1	$l_3 = 0{\cdot}653\, l_1 + 18{\cdot}544$	0·53	353	53·4	
l_4/l_2	$l_4 = 0{\cdot}906\, l_2 + 7{\cdot}739$	0·81	353	82·3	
All data combined	$l_{t+2} = 0{\cdot}174\, l_t + 24{\cdot}717$	0·46	708	$L_\infty = 29{\cdot}9$	0·89

poor growth, which would have affected the graph from only 4 years' measurements more than from 5 years'. It has already been suggested that more reliable results are to be expected from the use of older animals. More important is the fact that similar values of K and L_∞ were obtained using individual measurements for a back-measurement plot, and a Manzer and Taylor plot. This supports RICKER's (1958) suggestion that a Manzer and Taylor plot is a suitable method for estimating growth parameters. Examination of the data used (Table 1, under year-class 1958, and Table 2(A) for methods 1(a) and 2) and the results obtained (Table 3), suggests that selection by fishing has not been an important problem in the area sampled.

However, a factor of underlying importance to be considered in the use of the Manzer and Taylor plot is the variability of the slope of the line relating l_{t+1} to l_t for different ages of cockles. Each separate line represents the relationship between the amount of growth in one year of individuals covering a range of size and the total size they each achieved in previous year(s). This relationship was demonstrated more clearly in a previous paper (HANCOCK, 1963b, Plate 2), which showed that the smallest cockles at the end of the first year remained smallest at the end of the second and several subsequent growth seasons. Various combinations of the relative amounts of growth during the first two years will affect the slope of the line l_2 against l_1, for example a good first growing season followed by a bad one, and vice-versa. Table 2 shows how although the 1958 and 1959 year-classes reached a similar size in the first year, the 1959 year-class experienced better growth (to 22·8 mm) in the second year

than the 1958 year-class (to 20·8 mm), and the l_2/l_1 line for the 1958 year-class showed a smaller slope (Table 5). The slope of the line would be reduced by selective fishing. Clearly the individual regressions within pairs of age-groups tell nothing about average rate of growth. Tables 4 and 5 and Figures 3 and 4 show how the slopes l_{t+1} against l_t increase with increasing age, until by l_5/l_4 (Figure 4) the line is close and almost parallel to the 45° line, where $l_{t+1} = l_t$. The following table, giving data from a sample of 7 year-old cockles, also shows this:–

Regression	Slope	Correlation coefficient
l_2/l_1	0·602	0·609
l_3/l_2	0·820	0·846
l_4/l_3	0·746	0·806
l_5/l_4	0·840	0·852
l_6/l_5	1·039	0·969
l_7/l_6	0·996	0·986

It should be mentioned here that this sample was not used as an example of Ford-Walford plots, because growth during the first 3 years of life was affected by overcrowding. This will be discussed in a later paper.

FORD (1928, p. 295) obtained similar regression lines relating l_{t+1} to l_t from back-measurement of 4 year-old herring from Plymouth. They were:–

$$l_2 = 0{\cdot}675\, l_1 + 11{\cdot}68$$
$$l_3 = 0{\cdot}871\, l_2 + 6{\cdot}36$$
$$l_4 = 0{\cdot}727\, l_3 + 9{\cdot}07$$

but in 1933 (p. 344) he used the equation

$$y = 0{\cdot}53x + 13{\cdot}5$$

to describe the growth throughout the life of the same 4 year-old herring. The value of $L_\infty = 28{\cdot}7$ cm estimated from the latter equation is less than any of the values obtained from the equations for separate ages by intercept with the $y = x$ line. In the case of herring the effects of migration will be superimposed on seasonal changes in the environment, but with cockles migration does not occur.

RICKER (personal communication) has pointed out that, by and large, if the range (or better the standard deviation) of size of the animals in a year-class is decreasing the slope of such a plot will be less than 1, and vice-versa, so that a slope approximating to 1 indicates a range which is not changing. In cockle samples examined so far, the slope relating the first two growth seasons l_2 to l_1 has always been less than 1, though samples with increasing standard deviation from year to year had a greater slope than those with decreased standard deviation from l_1 to l_2. In younger cockles, the flatter slope also shows how the largest increments are added by the smallest cockles, which is in agreement with ideas on growth compensation (FORD, 1933; HODGSON, 1929). In later life, a slope approximating to unity shows that small and large cockles add similar length increments. RICKER (1958, p. 202) discussed growth "compensation" and "depensation", both of which may occur, and pointed out that in some fish populations there may be an increase in variability and range in length for a few years, followed by a phase of decreasing variability. This would result in early slopes of more than 1, followed by less than 1 in later life.

It is not however proposed to enter here into a full discussion on the growth of cockles. The purpose of this paper was to investigate the validity of the Manzer and Taylor plot for estimating growth parameters from tagging data, and the results have shown that the method is likely to give reasonable estimates provided that the tagged animals are drawn from several age-groups. If, by chance, a reasonable range of age is not covered amongst the individuals tagged, the slope of the line relating lengths at recapture to lengths at release will have a bias towards that of the most abundant age-group tagged, and estimates of L_∞ and K calculated from such lines could be quite erroneous. This is a likely occurrence in fisheries in which the stock in any year is dominated by one year-class. The data on lemon soles presented by Manzer and Taylor (1947) apparently covered a wide range of ages, but Kohler's (1963) data on cod recaptures seem to be restricted to very few age-groups and this may also help to explain the highly inconsistent values he obtained for K and L_∞. It should be mentioned that the values of K presented by Kohler from data at two-year intervals in fact represent K for two years, and should be halved for direct comparison with his one-year values of K.

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Summary

Growth parameters K and L_∞ of cockles have been estimated from Ford-Walford plots using mean lengths at each age, and the results compared with those based on pairs of individual measurements. The latter method, which has previously been used in the analysis of recapture data from species for which age is not known, gave similar results, but may be subject to errors where the data are drawn from a limited range of ages.

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