PERIODICITY STRUCTURES IN THE BIVALVE SHELL: ANALYSIS OF STUNTING IN *CERASTODERMA EDULE* FROM THE BURRY INLET (SOUTH WALES)

by G. E. FARROW

ABSTRACT. Individuals of *Cerastoderma edule* from the Burry Inlet are smaller than those from any other British cockle population. This stunting results from the situation of the cockle flats near neap high water mark, and is due to arrested growth during periods in the tidal cycle when the shells were exposed to the air. This, together with the longer winter stoppages, leaves cockles from high water neap level some two-thirds of the size of their contemporaries from low water spring level. The external width of a winter ring and the sharpness of its incision into the shell profile become more acute higher up the shore. Greater prominence of the crossed-lamellar structure in the outer shell layer is associated with winter reduction in growth rate; the lamellae become markedly deflected if an actual stoppage, marked by a dark periostracal band, takes place. Application of these results to the geological record would lead to a precise differentiation of littoral environments and enable the recognition of stunting in fossils.

THE Burry Inlet, like the Thames whose cockle populations have already been described (Farrow 1971), is an estuarine area and one of the three most important commercial sites in the country (Hancock and Urquhart 1966, fig. 1). Its environment is, however, different in several important respects:

(*a*) The unusually high situation of the cockle flats, caused by the marked silting up of the Inlet.
(*b*) The large tidal range (10 m at major spring tides).
(*c*) Greater instability of the substratum, caused by migration of the river channel and exposure to gales.

In this stringent habitat fully grown cockles rarely exceed 30 mm in length, compared with over 50 mm for examples from Barra in the Hebrides.

The present work owes much to the co-operation of the Burnham-on-Crouch Fisheries Laboratory whose staff have been engaged since 1958 in a study of the population dynamics of the *Cerastoderma edule* (L.) community. The present experiments on daily growth patterns thus effectively supplement a sound framework of macroshell growth analyses (Hancock and Simpson 1962; Hancock 1965, 1967). 'Transect F' of Hancock and Urquhart (1966, figs. 4–6) was levelled accurately and living cockles collected from stations 40 m apart. Specimens from this transect, preserved immediately after collection and subsequently oven dried, were supplied by Dr. D. A. Hancock and these form the main basis of this paper. The location of the transect within the estuary is shown in text-fig. 1.

TRANSECT DATA

Abundance and distribution of age-groups. Text-fig. 2 shows the abundance of the various year-groups present along the sand-flat in February 1969. Cockles in their first, second, and sixth winters are most abundant; in the intervening years spatfalls

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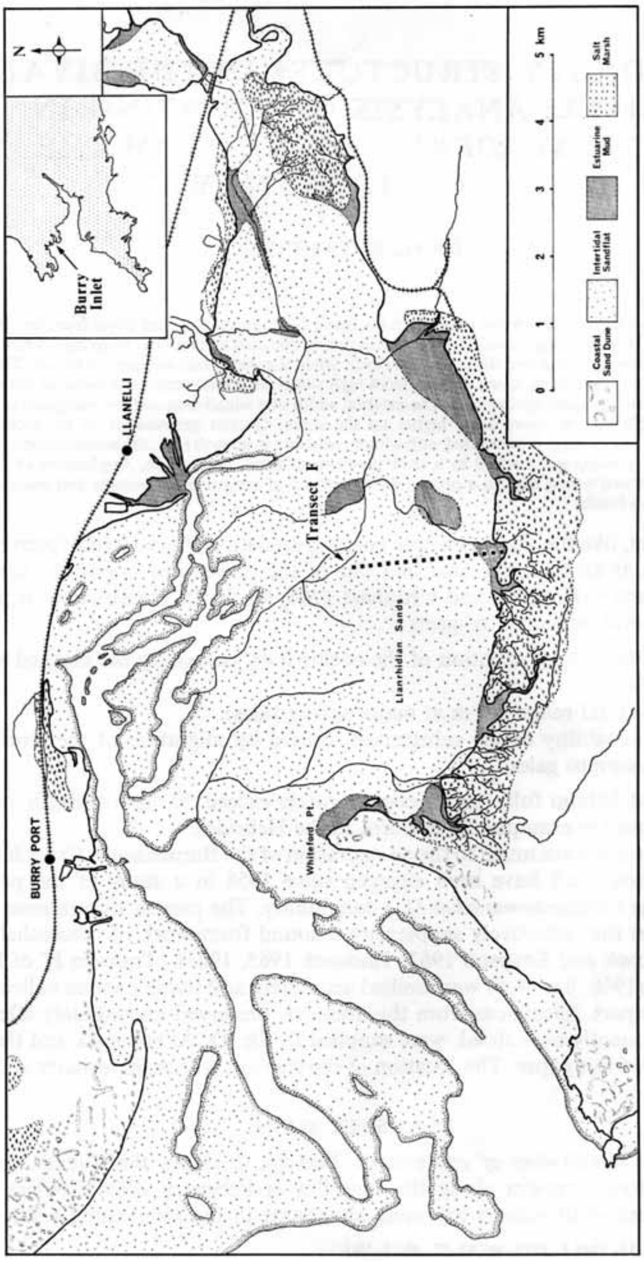
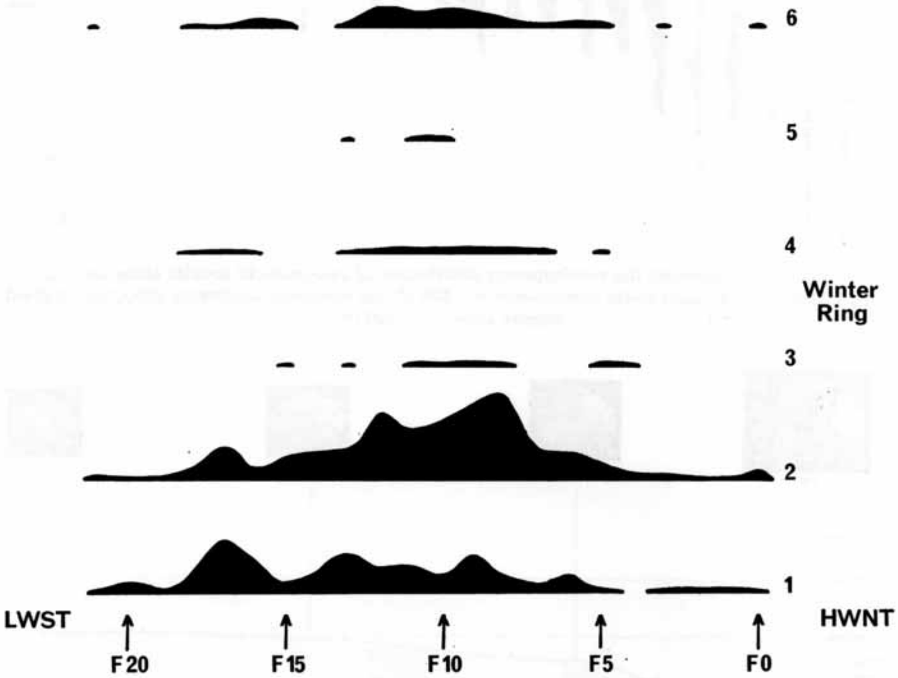


TEXT-FIG. 1. Map showing the distribution of Recent sediments and the location of Transect F within the Burry Inlet, based on Admiralty Chart no. 1167. All cockles described in the text are from this transect.

were insignificant. Densities of up to 7000/m^2 are recorded for the 1967 year-group and this spatfall was selected for study since it was the most widely distributed along the transect. The density distribution of the other year-groups is broadly similar.

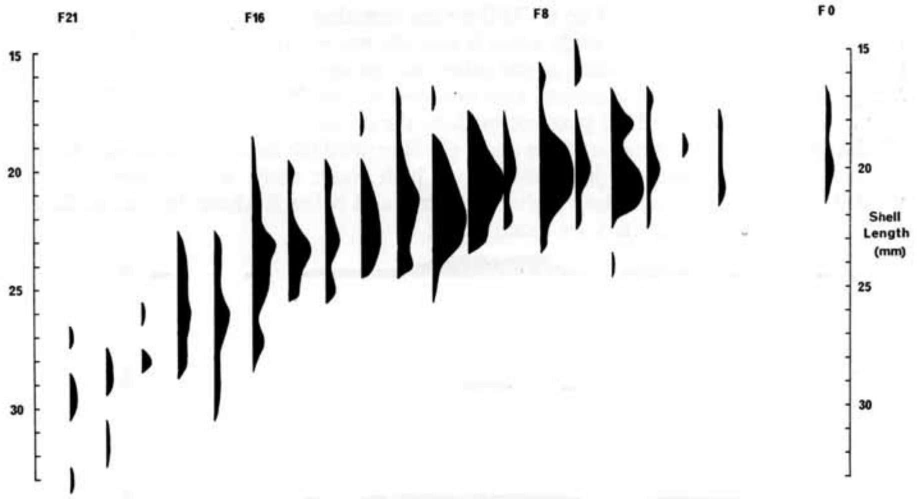
Size-frequency distribution of cockles with two winter rings. Text-fig. 3 shows the variation in shell length of the 1967 year-group along the transect, sampled on 14 May 1969. Modal specimens from stations 250 m apart are illustrated for comparison on text-fig. 4. Densest settlement occurred just below neap high water mark where three stations yielded more than 5000/m^2. Both higher than this, and below it where the steeper flank of the flat is reached, densities are much lower.



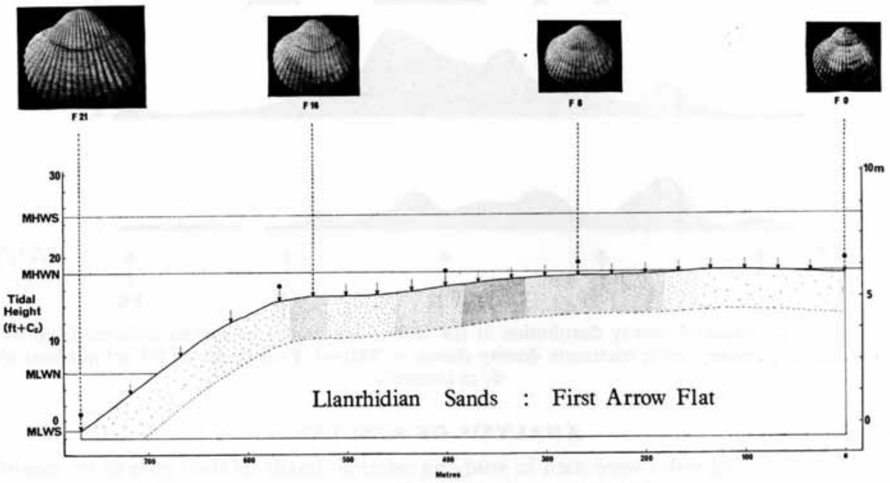
TEXT-FIG. 2. Curves of density distribution of the various age-groups of cockles collected from the transect in February 1969; maximum density shown = 7000/m^2. Plots based on 0·1 m^2 quadrats at 40 m intervals.

ANALYSIS OF RESULTS

Two sets of samples were used in studying internal details of shell growth by means of acetate peels of radial valve sections: the first a random series of shells from the February survey; the second a complete series of shells, one being selected from a sample of six modal individuals sent from Burnham for each station (text-fig. 3), obtained on 14 May 1969. Since chance preservation of shells in the fossil record does not usually permit large numbers to be examined it is of some value to compare the



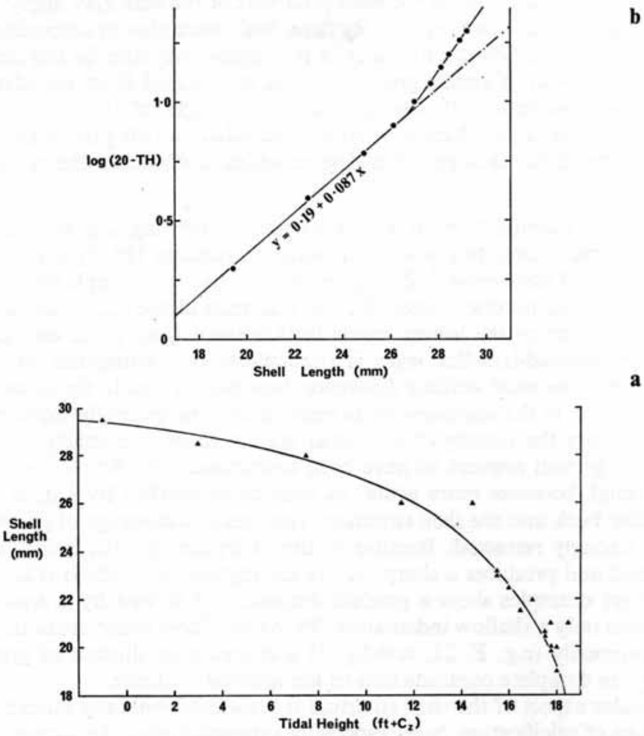
TEXT-FIG. 3. Curve showing the size-frequency distribution of two-year-old cockles along the transect on 14 May 1969; greatest width corresponds to 1400 of one particular centimetre group/m²; highest density shown = 5500/m².



TEXT-FIG. 4. Diagram showing the shore profile of Transect F (from Hancock and Urquhart 1966, fig. 6). Cockles selected from the mode at four stations each separated by about 250 m demonstrate the striking reduction in shell length on the higher parts of the flats (which is also apparent in their relative size at the first winter ring). Black dots indicate the location of specimens illustrated on Pl. 9; stipple density is proportional to density of cockle settlement.

results obtained. External measurements of shell length were carried out by the staff at Burnham on all shells collected during the May survey.

Relationship of shell length to position on tidal flat. The striking visual correlation may be seen on text-fig. 4; this is also apparent in the cockle's relative size at the first winter ring. Text-fig. 5*a* shows that when plotted out arithmetically the rate of reduction in total growth increases sharply on the higher parts of the flats. Plotting points from the fitted curve of text-fig. 5*a* on a logarithmic scale resolves growth characteristics into two groups, both of which are related logarithmically to tidal height. The bulk of the population may be fitted to the curve:



TEXT-FIG. 5. Graphs illustrating the relationship between modal shell length and tidal height: *a*, plotted arithmetically; *b*, plotted logarithmically from the curve fitted to *a*. Chart Datum (C_z) = −14 ft O.D. (Newlyn).

$$y = 0{\cdot}19+0{\cdot}087x,$$

where $y = \log(20-\text{tidal height in feet}+C_z)$,

$x = \text{shell length in mm};\ C_z = \text{Chart Datum}.$

This relationship seems to hold on the flats down to a point (text-fig. 5*b*) corresponding to a tidal height of about 11 feet, after which a second function is operative. However, text-fig. 3 indicates that values of modal shell length on the lower part of the transect may be in error owing to sparsity of individuals, so that it would be unwise to attach undue significance to these two categories. Nevertheless it seems unlikely that tidal cover *per se* can explain the observed variation completely. The fact that the rate of reduction in growth increases on the most level part of the flats may imply that friction causes a decrease in tidal current velocity here, and hence also in suspended matter on which the cockles feed. Greater turbidity in this region may also be important.

The theoretical limit of cockle growth may be determined from the above relationship at the point where $x = 0$. The resulting tidal height of 18·5 feet is only inches above the highest level at which cockles are recorded; which proves that the higher Burry cockles must be 'stunted' to a degree which approaches the maximum theoretically possible.

Winter rings. The internal form of a cockle's first winter ring is governed strongly by its position on the shore; this is seen in both the random (Pl. 8) and modal (Pl. 9) samples. Because of poor growth during the initial months the high shore shell F. 0 is still very thin during its first winter (Pl. 8A) and may already truly be referred to as 'stunted' by reference to the longer, much thicker shells from lower on the shore; the inner complex crossed-lamellar layer is particularly thin compared with F. 14 for example (Pl. 8B). The most striking difference, however, is seen in the external width of the winter ring and in the sharpness of its incision into the generally smooth outer shell profile. Shells from the vicinity of low water springs show a relatively shallow trough beneath which growth appears to have been continuous (Pls. 8C, 9E). Moving up the shore this trough becomes more acute, its base being marked by a dark periostracal band extending back into the shell structure. This marks a stoppage of growth when the mantle was strongly retracted. Because of this stoppage, growth before and after is relatively rapid and produces a sharp nick in the highest shore shells (Pls. 8A, 9A), but the lower shore examples show a gradual diminution followed by a gradual increase which produces only a shallow indentation (Pl. 9D, E). These wider areas are often more noticeable externally (e.g. F. 21, text-fig. 4) and create an illusion of greater winter susceptibility, in complete contradiction to the internal evidence.

One particular aspect of the shell structure is associated with any interruption of the normal pattern of calcification, being especially apparent during the winter. The crossed

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EXPLANATION OF PLATE 8

Acetate peels showing daily increments during the first autumn and winter in three specimens of *Cerastoderma edule* selected at random from different stations along Transect F, Burry Inlet:

A. High-shore specimen (F. 0) showing disturbance ring and sharp winter ring: shell much thinner than lower shore individuals, especially the inner complex crossed-lamellar layer.

B. Mid-shore specimen (F. 14) showing markedly cyclical growth pattern, broader winter ring and thicker shell.

C. Low-shore specimen (F. 21) showing continuous, uniform growth and very broad winter ring; because of the much greater thickness of this shell only part of the outer shell layer can be illustrated.

Dark lines in A and B extending back from the winter rings into the shell structure mark a cessation of growth.

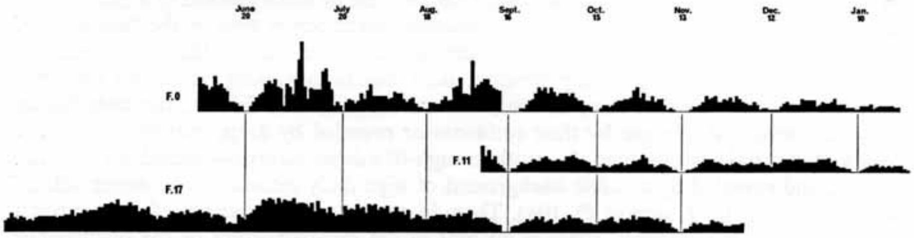
lamellae become extremely prominent, appearing to transgress the growth lines; immediately before the stoppage they extend strongly outwards (Pl. 9A); after it they appear inconspicuous. Marked deflections in the orientation of the lamellae take place across the dark periostracal band.

Disturbance rings. The problem of separating disturbance rings from those of annual origin can be tackled statistically by external growth-ring analysis (Craig and Hallam 1963), though this is a somewhat lengthy procedure. Preparation of an acetate peel of a shell takes only five minutes, and from it the two can be distinguished at a glance even at low magnification. Pl. 8A shows an autumnal disturbance ring in the first year of growth; Pl. 10A an autumnal disturbance during the second year on the same specimen. Although the interruptions may produce dark bands extending back into the shell structure in the same fashion as truly annual rings, albeit fainter, the disturbance rings are readily diagnosed by their suddenness; revealed by deep, narrow slots in the outer shell profile (rather than the gentle trough-like depressions associated with annual rings); and revealed by a stable background of high daily increments on either side of the disturbance (well seen in Pl. 10A). Thus, in contrast to the pattern of daily growth preceding winter stoppages, there is no hint in the microstructure of the disturbance to come. Subsequent growth is at a rate identical to that prior to the stoppage, and this is a reflection of some kind of physical rather than biological disturbance, for with a spawning ring, for example, resumption of growth is gradual and background values may not be attained for some weeks (Pannella and MacClintock 1968, Pl. 6, fig. 2).

Comparison of high and low shore cockles shows that physical disturbances are commonest on the higher parts of the flats; the external expression of an autumn disturbance ring in the first year can be seen on F. 8, text-fig. 4. Pl. 10 shows growth during the second autumn for shells from three stations along the transect: F. 0 has a pronounced disturbance ring, but the indentation of the outer shell profile of F. 14 at the same period is scarcely perceptible; F. 21 from low water springs exhibits very uniform growth throughout the period. Physically induced disturbances are severe only during the autumn (House and Farrow 1968; also for cockles inhabiting sand in the Thames, Farrow 1971). The reason for this is to be sought in the equinoctial tides, as is explained in the following section.

Cyclicity in the pattern of daily growth. Study of microstructural periodicities demonstrates the close control of tidal cyclicity on the growth of cockles from different transect stations. Again this is shown as well by random samples (text-fig. 6) as by individuals carefully selected from the mode at each station (text-fig. 7). On text-fig. 6 are plotted second year summer and autumn daily increments for the random series of cockles. A 29-day tidally controlled cyclicity can be identified, even in the low shore F. 17, but this becomes attenuated during the autumn with growth stoppages occurring at the beginning and end of each cycle in the high shore F. 0. The modal specimens (text-fig. 7) show that the severity of such stoppages decreases as low water mark is approached; further, it shows that this effect is pronounced only around the time of the equinoctial tides. The probable reason for this is illustrated on text-fig. 8 and outlined briefly below.

The higher shore cockles are situated very close to mean high water of neap tides (text-fig. 4), which means that at certain seasons when the tidal range is small the flowing tide never reaches them and they may be left high and dry for days on end. The degree to which observed disturbances correlate with predicted occurrences of very low high water is shown on text-fig. 8. Even at other periods some individuals may be covered by only a few inches of water, and during the summer this evidently leads to a disturbance of growth (text-figs. 6, 7). Throughout the year it is the resumption of vigorous growth following neap-tide deceleration which produces the marked cyclicity. The reduced effect nearer low water springs enables more continuous growth to take place, though in the second year individual daily increments are not necessarily greater here than higher on the shore, for shells like F. 21 have already reached a comparatively large size as a consequence of much more prolonged growth during their first autumn than higher shore shells (text-fig. 7) which are still quite small. It is thus possible to relate the amplitude of the cyclicity to position on the shore, values for each lunar cycle being tabulated in Table 1. Variation in the amplitude and attenuation of the cyclicity is thus the key to understanding why the higher shore specimens are stunted.



TEXT-FIG. 6. Daily increment plots for three shells selected at random from different transect stations, showing summer and autumn growth in the second year. The amplitude of the cyclical growth pattern is considerably greater in the higher shore specimen F. 0 than in F. 17; in the autumn the pattern becomes attenuated as a result of periodic growth disturbances. Shells collected in February 1969; maximum increment = 150 μm.

PALAEOECOLOGICAL IMPLICATIONS

Two aspects of the Burry Inlet experiment are of especial value to the palaeontologist. First, all specimens studied were collected in life position and the results obtained can thus be applied readily to *in situ* infaunal fossils. Second, two series of shells were analysed side by side; a random collection of single cockles from unselected transect stations and shells from a quantitative survey which were statistically selected from the modal shell length value for regularly spaced stations. The fact that the results could be

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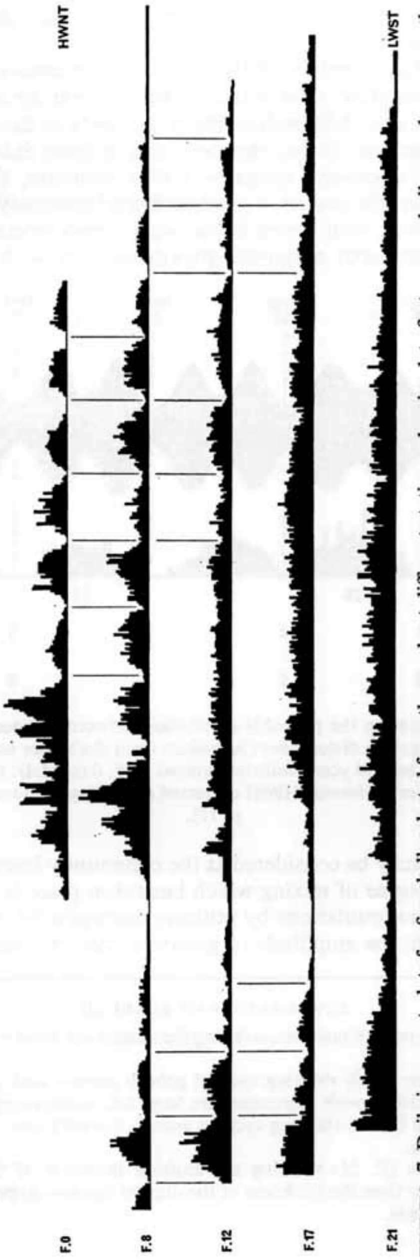
EXPLANATION OF PLATE 9

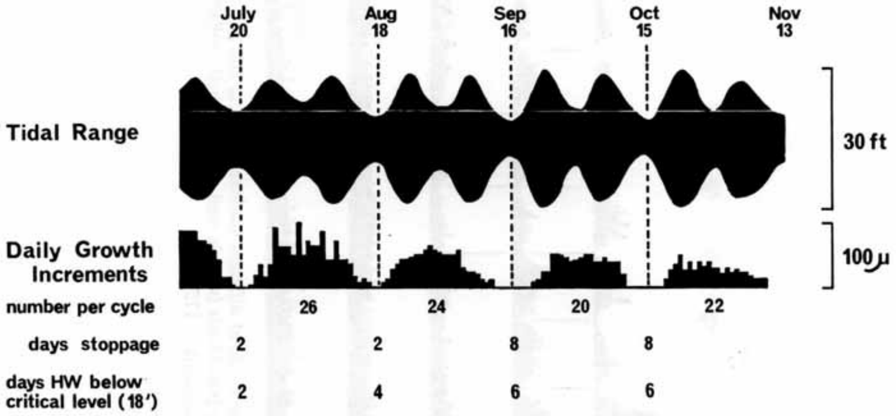
Acetate peels showing cross sections of the first winter ring in modal specimens of *Cerastoderma edule* from successively lower along Transect F: (A) F. 0 (B) F. 8 (C) F. 12 (D) F. 17 (E) F. 21. Transgressive crossed-lamellar structure is particularly evident in the higher shore individuals immediately prior to the winter stoppage. Progressive increase in width of the winter ring with increasing depth is well shown: in the lowest example growth appears to have been continuous, but dark periostracal bands indicating stoppage seem to be present in the remainder. Position of the stations is indicated on text-fig. 4: Scale bar = 200 μm.



TEXT-FIG. 7. Daily increment plots for five shells selected from the mode at different stations, showing late first year and all second year growth. The greater amplitude in the growth pattern of the higher shore individuals is again well shown. Shells collected on 14 May 1969: maximum increment = 175 μm.

compared closely is encouraging for the extrapolation into the fossil record where numbers sufficient for statistical work are but rarely found.

The palaeoecological implications of the work are best assessed on two levels. First, that of the individual mollusc. Five minutes spent preparing an acetate peel for the internal analysis of any one shell enables many incidents in the life of that shell to be recognized. Winter rings can be distinguished readily from disturbance rings by their external profile and transgressive crossed-lamellar structure, thus enabling the true life span to be calculated: the season of greatest disturbance may be compared with the season of death: the month with lowest winter water temperature can be obtained from the correlation of pronounced autumnal growth cyclicity with the equinoctial tides. Secondly, implications may be considered at the community level. Here it should prove possible to assess the degree of mixing which has taken place between different faunal elements in dead shell accumulations by utilizing discrepancies in, for example, winter ring characteristics or in the amplitude of growth cycles. In considerations of possible



TEXT-FIG. 8. Diagram illustrating the probable correlation between the occurrence of very low high tides and the incidence of growth disturbances in cockles from the higher parts of the flats during late summer and autumn of the second year. Daily increments = F. 0 (modal): tidal values for each spring and neap tide from *Whitaker's Almanac* (1968) corrected according to Hancock and Urquhart (1966, p. 15).

EXPLANATION OF PLATE 10

Acetate peels showing daily growth increments during the second autumn for the three shells illustrated on Plate 8:

A. High-shore specimen (F. 0) showing cyclical growth pattern and a pronounced disturbance ring, before and after which growth increments are large (cf. winter rings).

B. Mid-shore specimen (F. 14) showing cyclical growth but with only a slight indentation in the smooth outer shell profile.

C. Low-shore specimen (F. 21) showing the uniform thickness of the growth increments: a cyclicity in the type rather than the thickness of the diurnal bands is apparent if the plate is viewed from the side at a low angle.

stunting in any fauna internal analysis of periodicity structures may reveal its cause, whether it be a prolonged winter cessation of growth or repeated physical disturbance caused by periodic subaerial exposure.

The most novel application of this experiment to the fossil record would undoubtedly lie in palaeotidal analysis. It would be most exciting to extend the semi-quantitative assessment of intertidal environments using amplitude measurements, of the type presented in Table 1, in conjunction with the equation formulated from text-fig. 5. Even extending the use of periodicity structures into sub-tidal régimes is likely to prove rewarding to judge from the work of Rhoads and Pannella (1970, p. 158, fig. 9) who have illustrated the extremely uniform growth of deep-water molluscs, where spawning disturbances replace winter temperature and physical disturbance rings as the most conspicuous interruptions of the normal calcification process. Periodicity in the type rather than the thickness of diurnal increments seems to characterize the growth of those molluscs living in sublittoral habitats which are nevertheless influenced by tidal flux: compare *Cerastoderma edule* from extreme low water springs (Pl. 10c, viewing at a low angle) with *Tridacna squamosa* (Pannella and MacClintock 1968, pl. 7) and *Nucula proxima* from −6 m (Rhoads and Pannella 1970, fig. 9*b*). With further examples to act as standards molluscan growth characteristics could become most useful indicators of contemporary water depth in ancient seas. Before having confidence in such estimates, however, additional experiments on living molluscs must be undertaken. First, there is the question of how widespread is the tidally controlled cyclicity characteristic of the Burry Inlet cockles; it is certainly difficult to perceive in the Thames fauna where it is swamped by other ecological variables (Farrow 1971). Future studies should be undertaken not only on a wider range of cockle habitats but on a wider spectrum of organisms, for there is no reason to suppose that *Cerastoderma* should be more prone to physical growth controls than any other carbonate-secreting animal.

TABLE 1. Variation in amplitude of tidally controlled growth cycles in *Cerastoderma edule* from stations at different heights along Transect F, Burry Inlet, S. Wales

Transect number	*20 June*	*19 July*	*18 Aug.*	*16 Sept.*	*15 Oct.*		*Mean amplitude (May–Sept.)*	*Tidal height of Stations (in ft + MLWS)*
Upper shore								
F. 0	10	19	11	13	8	8	13·3	18·8
F. 8*	13	15	8	14	10	7	12·5	18·7
F. 11/12	5	7	8	10	4	5	7·5	17·5
F. 17	5	5	6	7	4	5	5·7	16·0
Lower shore								

Amplitude = maximum daily increment − minimum daily increment per lunar monthly cycle (mm × 160); all values represent the average of measurements from text-figs. 6 and 7 except F. 8* which was obtained from text-fig. 7 only. MLWS (Mean low water spring tide) = −15 ft O.D. (Newlyn).

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G. E. FARROW
Department of Geology
The University
Hull

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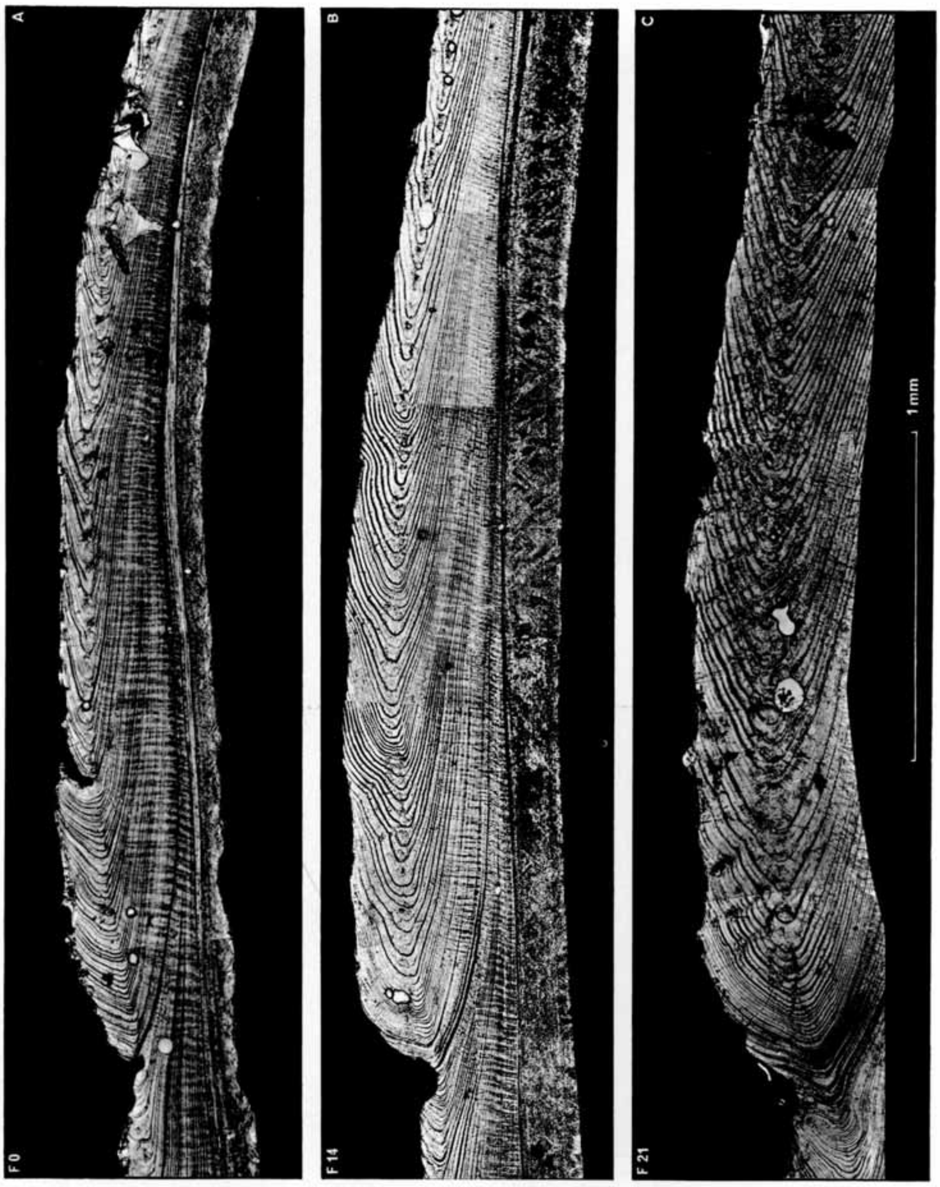

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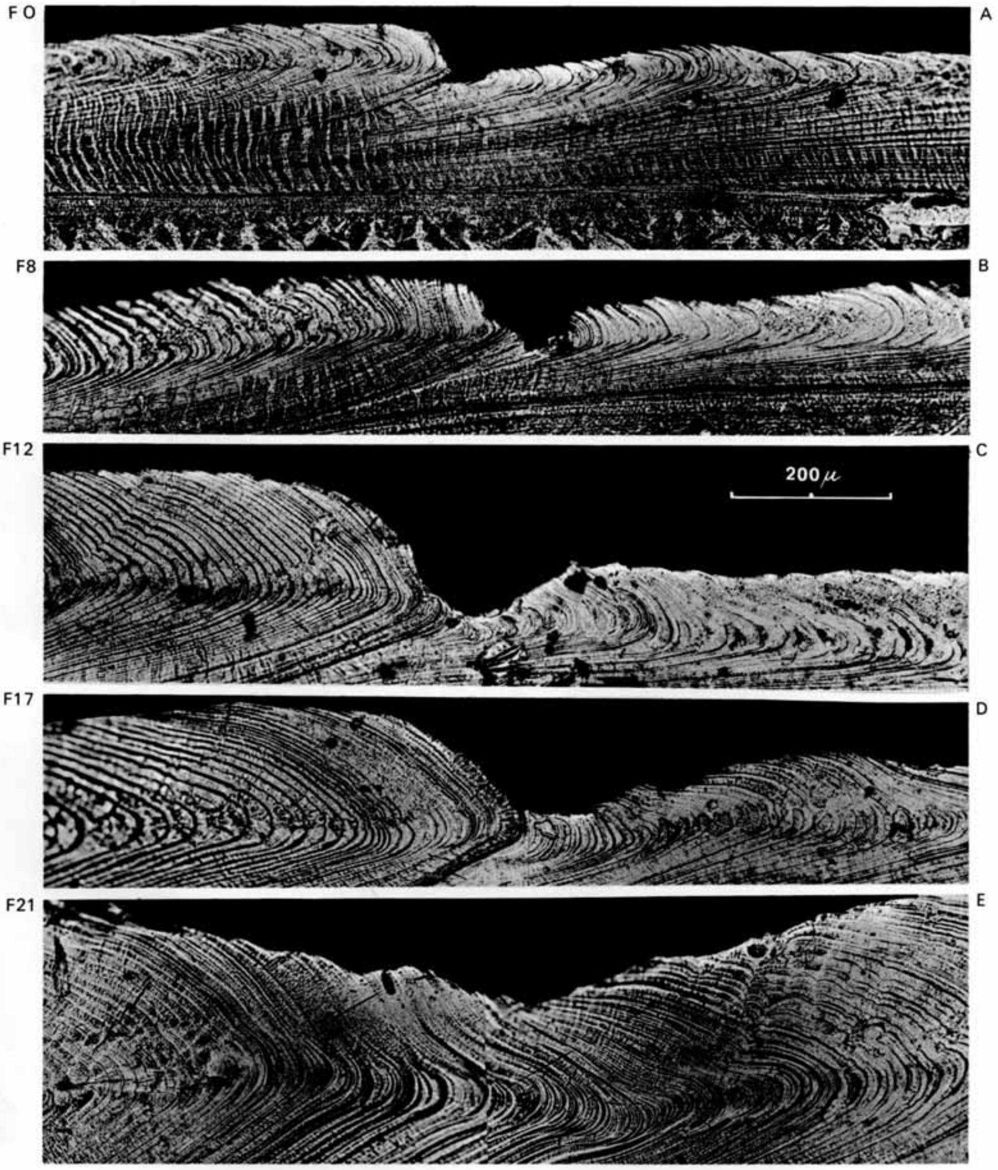

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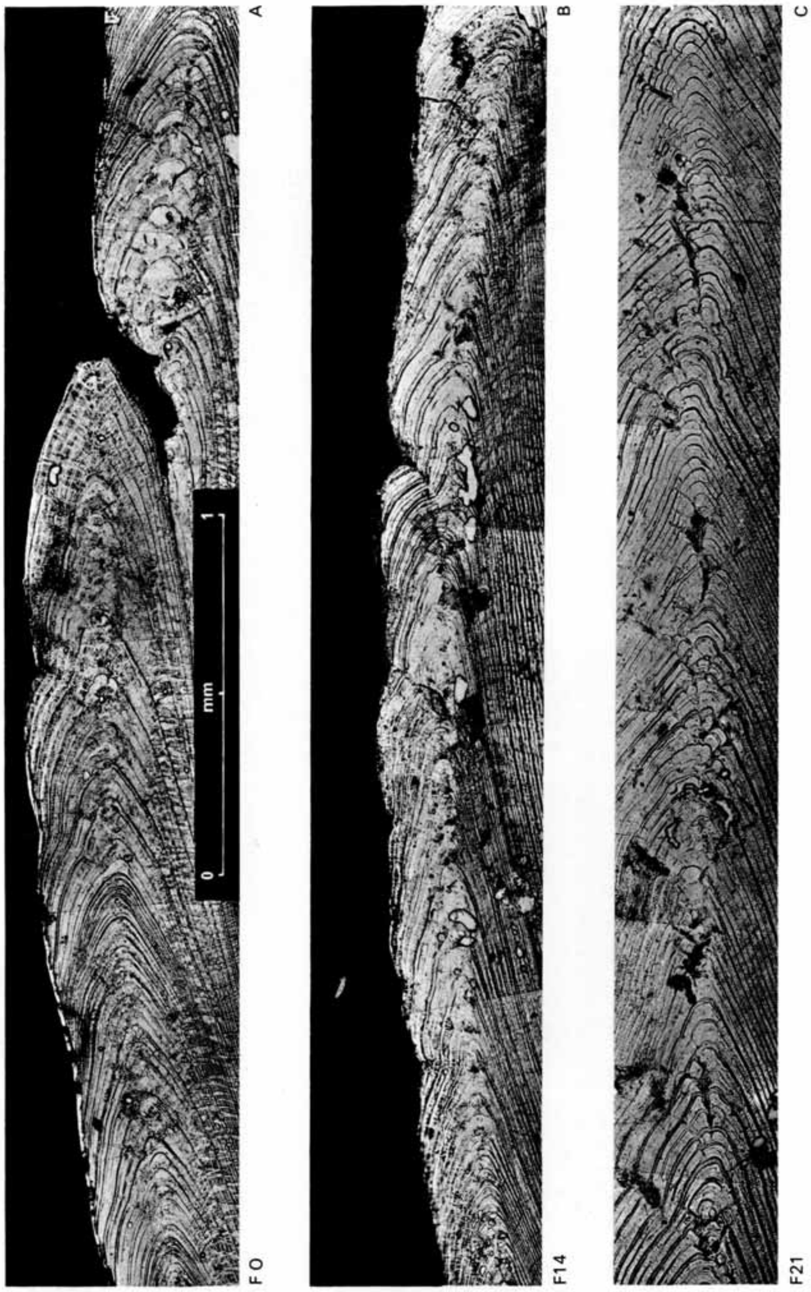

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