Influence of tides on microgrowth bands in *Cerastoderma edule* from Norway

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ABSTRACT: At an intertidal site on the island of Tautra in Trondheimsfjord, Norway, cockles *Cerastoderma edule* L. were sampled from 121 cm (Stn A) and 66 cm (Stn B) below tidal datum. Shells were sectioned longitudinally, polished, etched and photographed under a scanning microscope to reveal microgrowth bands. Tidal heights were calibrated against a tide recorder in Trondheim harbour, thus providing immersion times and tidal heights for Stns A and B. The tidal and growth band data were subjected to time-series analysis. At Stn A, immersion time is maximal at neap tides while tidal height is maximal at spring tides, whereas at Stn B, maxima of both values occur at spring tides. Although both neap and spring tides have a cycle of 28 tidal periods, a cross-correlation analysis should show a phase shift of 14 periods at Stn A and no phase shift at Stn B. The tide recorder data supported this hypothesis. If tides are a predominant influence on microgrowth bands similar patterns should be observed in band patterns. The data showed that this was the case. After correcting the data for changes in growth with age, growth was found to increase in February–March, decrease in April–May and was maximal in June. Our data clearly support the contention that it is tidal and not diurnal changes that influence microgrowth bands in intertidal populations of *C. edule*.

INTRODUCTION

Microgrowth bands in pelecypod shells were first reported by Barker (1964). He studied 4 marine species and suggested that there was a hierarchical structure to the bands with influences from a 6 h tidal cycle, from day/night temperature variations, from spring-neap tidal flow variations, and half-yearly and annual variations in temperature. House & Farrow (1968) studied cockles *Cerastoderma* (= *Cardium*) *edule* and concluded that the microgrowth bands were laid down in response to daily light and dark cycles. Farrow (1971, 1972) and Whyte (1975) both concluded that the bands caused by variations rates of shell growth were daily bands. Whereas House & Farrow concluded that the bands were laid down at night, Whyte suggested that this occurred during the day.

Evans (1972, 1975) studied the related N. American species *Clinocardium nuttalli* from a mixed tidal regime on the Pacific coast and found that there was a close relation between the number of growth bands

and the number of tides, thus implicating tidal rather than diurnal variations as the stimulus for the banding.

In an extensive series of field and laboratory studies, Richardson et al. (1979, 1980a, b, c) have shown that the microgrowth bands in *Cerastoderma edule* are tidally induced. From studies at different tidal levels they suggested that the amount of time immersed was of primary importance in determining the banding pattern. Rather than band width *per se* they recommended the distinctness of the banding as the best guide to tidal influence. Furthermore, they suggested from experimental data that there was a 5 % difference in growth rates between spring and neap tide periods. Richardson et al. could find no evidence of dark/light influence on the growth bands.

The method of Richardson et al. involved direct micrometer eyepiece measurements of the growth increments. The influence of tides was measured from samples taken at known points in the tidal cycles and tide-growth relationships calculated back from the sampling time (Richardson et al. 1980b), or from experimental transplants made after marking the shell by cold shock so that the following bands had a known starting point.

An alternative method of analysing the influence of

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tides on growth patterns is to measure microgrowth bands and to use time-series analysis methods to relate the patterns found to tidal regimes. This was the primary object of the present study. Whilst the findings of Richardson et al. were convincing, there is still doubt in the literature that growth patterns are tidally and not daily induced. The aim of this study is to test whether or not tidal regimes influence growth patterns using an independent method of analysis.

MATERIAL AND METHODS

Specimens of *Cerastoderma edule* L. were obtained from the island of Tautra, Trondheimsfjord, Norway (63°34'20" N, 10°38'00" E) on an east-facing sandy shore (500 m extent) between the island and the mainland (Fig. 1). Samples were taken from 2 tidal levels: Stn A, low down on the shore, and Stn B, higher up the shore. The tidal heights of the respective stations were assessed by reference to the tide recorder in Trondheim harbour. Tidal heights were calibrated against the Trondheim harbour recorder on 3 separate occasions and levels of Stns A and B related to sea level on the recorder. The tidal level of the 2 sites were (Stn A) 121 cm and (Stn B) 66 cm below datum point (level defined by Norges Geografiske Oppmålingsinstitutt, 1954). There is no difference in timing of tides between Tatura and Trondheim (Wendelbo 1970). Thus the time of immersion at each site and the maximum water height over each site could, after adjustment, be taken directly from the tide recorder. The average range of the unequal, semidiurnal Trondheimsfjord tide is 180 cm (Jacobson 1983).

Cerastoderma edule was sampled at low tide, by taking individuals of similar size (shell height < 25 mm) and hence all of presumed high growth rate. Animals were immediately killed by immersing in boil-

ing water. The left valve was later imbedded in resin (Serifix, Struers) and sectioned longitudinally from umbo to growing point. The section was then ground using successively finer silicon carbide powder (40, 25, 15 µm grain size) and polished in 3 operations using a polishing paste (Dialop compound, L. M. Van Moppes & Sons) containing diamond dust (3, 1 and 0.25 µm grain size). The surface was rinsed in 96 % ethyl alcohol between each operation. The surface was finally polished with a mixture of magnesium oxide and water. The polished surface was then etched with 0.12 M cold HCl for 45 s. A Jeol 35 C scanning electron microscope was used to photograph the shell surface using 300× enlargement, and coverage made from the growing edge inwards towards the umbo. During photography the surface of maximum growth (Pannella & MacClintock 1968) was kept in the screen centre to minimize distortion. Individual growth bands were then measured from a series of overlapping pictures using a Calcomp 9000 digitizer connected to a main-frame computer.

For the statistical analyses the immersion times at each level taken at the recorder and the growth bands were regarded as a sequence of observations ordered in time with an increment of 12 h 25 min, the theoretical time between 2 lunar high tides. Over more than 200 immersions this assumption gave an error of 0.3 % in the total number of high tides. The data series can, therefore, be regarded as equispaced and the variations found be analysed by time-series methods. A period in this context is defined as one increment of growth or one tidal cycle of 12 h 25 min, of which both were smoothed using a composite running median (4253H Twice, Velleman & Hoaglin 1981). The growth data also contained a seasonal trend which was removed by splitting the data set at its maximum value (leaving the maximum value with both sets) and treating each part as a separate linear trend; a method that gives a minimum loss of observed values (Chatfield 1975). The trend was removed by a first order differentiation $Y_t = X_{t+1} - X_t$, where Y_t is the new function and X_t is the old. The second half of the data was multiplied by -1. A Kendall's rank order correlation was then applied in order to test if the data still contained a trend (Legendre & Legendre 1983) before subjecting the data to further time-series analysis.

Following detrending the data were then subjected to autocorrelation analysis (see Chatfield 1975 for a recent review). A test of the significance of correlation values (5 % level), indicating whether the data set is randomly distributed, depends only on the number of observations (n) and is $\pm 2/\sqrt{n}$ (Chatfield 1975). The data were analysed on the University of Oslo's Dec 10 computer using the statistical package Minitab (Ryan et al. 1981).

Fig. 1. Location of sampling site (▲) on the island of Tautra in the Trondheimsfjord, Norway.

RESULTS

Tidal pattern at the sampling sites

The microgrowth bands were clearly discernible in our samples (Fig. 2). The tidal patterns, predicted from astronomical relationships for Stns A and B, are shown in Fig. 3. At level A the maximal immersion time corresponds to the neap tide period and the maximal water height occurs at spring tide. Both immersion time and tidal height fluctuate on a cycle of 28 periods but their maximal values are 14 periods out of phase with

time and tidal height for level A (Fig. 6a) showed that the 2 series had a common maximal positive correlation with a cycle of 28 to 29 periods, but with a phase shift of 14 periods, as shown by the displacement of the maximum from zero. Thus within limits of acceptable error the prediction is borne out, for level A, of two 28-period cycles 14 periods out of phase with each another.

The same analysis was carried out on tidal data for level B. Only the cross-correlation analyses are shown (Fig. 6b) since the procedure is the same as above. Only the cycle of 28 periods is apparent, thus bearing

Fig. 2. *Cerastoderma edule*. Surface of maximum growth of a longitudinally sectioned shell. Microgrowth bands are clearly discernible. Scale bar = 100 μ m

each other. Thus, theoretically at Stn A, where neap tide maximises immersion and spring tide tidal height, a cross-correlation analysis between immersion and tidal height should show a phase shift of 14 periods. On the other hand, at Stn B, where maximal values for immersion and tidal height occur at spring tides, a cross-correlation will not show any phase shift between the two.

Fig. 4 shows raw data from the tide recorder showing length of time immersed (Fig. 4a) and tidal height (Fig. 4b) at each tide at Stn A. Similar data was available for Stn B but is not shown. Autocorrelation analysis of the data for Stn A is shown in Fig. 5. The maximal positive correlation at Stn A for the length of time immersed (0.353 to 0.359) gives a cycle of 28 to 29 periods and for tidal height (0.405 to 0.406) also gives 28 to 29 periods. Correlation values greater than ± 0.16 are significant at 5 % level (Chatfield 1975). A cross-correlation analysis between maximal immersion

Fig. 3. Theoretical tidal cycle during spring tide (s) and neap tide (n). A and B indicate the levels of the sampling sites

out the prediction. There is however, a phase shift of 4 to 5 periods between immersion time and tidal height.

Effects of tidal patterns on microgrowth bands

If tides are the predominant influence on microgrowth bands in *Cerastoderma edule* similar patterns should be observed in the growth patterns as in the tidal patterns illustrated above.

Fig. 7 shows the 3 phases of the analysis of microgrowth patterns for a specimen from Stn A. The raw data is plotted in Fig. 7a, smoothed data in Fig. 7b and seasonally detrended data in Fig. 7c. Fig. 8 shows the smoothed and seasonally detrended data for a specimen from Stn B.

Autocorrelation of the above data shows (Fig. 9) that for Stn A the maximal positive correlations (Fig. 9a) are at periods 15 (0.201) and 28 (0.238). Thus the width of the growth bands shows fluctuations of period 14, as cycles of multiples of 14 only are distinguishable. Val-

ues greater than ± 0.14 are significant at the 5 % level.

For Stn B the maximal positive correlation (Fig. 9b) is at period 28 (0.317). Values greater than ± 0.16 are significant at the 5 % level. Thus at level B the growth bands show only one recurrence per 28-period tidal cycle, compared with two at level A.

Seasonal growth

In order to estimate seasonal growth, care must be taken to correct the data for changes in growth with age (see Richardson et al. 1980b). Richardson et al. gave a method to reduce the individual variation based on deducing a correction factor assuming the Von Bertalanffy equation holds. From analysis of annual growth checks for 40 individuals, the relationship between length (l) at Age n and Age n+1 was given by:

$$l_{n+1} = 0.81 (\pm 0.08) + 0.81 l_n$$

Fig. 4. Tidal data showing (a) the length of time (min) that level A is immersed; (b) maximum tidal height (cm) above level A at each high tide

Fig. 5. Autocorrelation of tidal data from level A. (a) Immersion time. (b) Tidal height. Maximum positive correlation occurs in both cases at period 28 to 29

The coefficient of determination, $R^2 = 0.98$ and maximum length along the perimeter (L) was calculated to be 4.26 cm. Richardson et al. (1980a) found that for a population of *Cerastoderma edule* from North Wales the relationship between the shell height (d), defined as the maximal width between the umbo and the growing edge, and the length (l) along the perimeter of the shell where (d) is measured was:

$$l = 1.543 d$$

For the Tautra population the relationship was:

$$l = 1.62 d (R^2 = 0.95).$$

Thus the correction factor for calculation of growth rates used here was $4.26 - 1.62 d$. As with Richardson et al. (1980b) growth was summed over 28 consecutive growth bands from the shell edge backwards, giving

Fig. 6. Cross-correlation between time immersed and maximum tidal height. (a) Tidal level A. There is a common fluctuation with period 28 as shown by the distance between the 2 positive maxima. The displacement of the positive maximum from zero indicates a phase shift between the 2 oscillations of 14 periods. (b) Tidal level B. There is a maximum positive correlation with period 28, and a displacement between the 2 oscillations of 4 to 5 periods

14 day periods, termed K14 by Richardson et al. The data from Tautra level B for the 4 individuals measured is shown in Fig. 10. Maximum growth occurs in June with little growth presumably between end of August

Fig. 7. *Cerastoderma edule*. Microgrowth band widths of shells from level A. (a) Original data. (b) Smoothed data. (c) Smoothed and detrended data

Fig. 8. *Cerastoderma edule*. Microgrowth band widths of shells from level B; smoothed and detrended data

Fig. 9. *Cerastoderma edule*. Autocorrelation of growth band width data. (a) From level A. Maximum positive correlation is at periods 15 and 28, giving a fluctuation of period 14. (b) From level B. Maximum positive correlation is at period 28

and February. After an initial increase in growth in February–March low growth occurred in April–May

DISCUSSION

These results show clearly that it is tidal patterns that influence growth rates in *Cerastoderma edule* from Tautra. They thus confirm the views of Richardson et al. (1980a, b, c) that microgrowth bands are laid down in response to tidal and not diurnal periodicity. Richardson et al. (1980c) have, by experimental studies, shown that the time immersed and the current flow both influence growth rates of *Cerastoderma edule*.

In this study a different method was used to test the hypothesis that microgrowth bands were tidally induced. Tidal patterns at 2 different shore levels showed different periodicities. At lower tide level (A) maximal immersion time occurred at neap tide whereas maximal tidal height (current flow) occurred at spring tide. Whilst both fluctuated over a frequency of 28 periods they were out of phase with each other by 14 periods (Fig. 6a), giving a resultant influence with a frequency of 14 periods. At the higher tidal level (B) maximal immersion time and maximal tidal height occurred at spring tide giving a frequency of 28 periods. The fact that immersion time and tidal height were out of phase with each other by 5 periods is probably due to non-cyclical effects from other environmental factors such as wind or wave action, that play a larger role here than lower down the shore. *Cerastoderma edule* taken from the 2 stations showed patterns in microgrowth bands (Fig. 9a, b) corresponding to the tidal periodicity (Fig. 6a, b), thus strongly supporting the hypothesis that tidal patterns control growth band formation. The finding that both immersion time and tidal height correlate with growth in natural populations agrees with the field and experimental results of Richardson et al. 1980a, b, c).

The annual pattern of growth of *Cerastoderma edule* from Tautra (Fig. 10) showed maximal growth in June. Similar maximal growth rates in June were reported by Richardson et al. (1980b) with populations from Sør-

Fig. 10. *Cerastoderma edule*. Mean growth band width averaged over 28 growth bands for 4 shells taken at level B, with standard error indicated

botn, Troms, Norway. The Sørbotn population showed no measurable growth between November and April, whereas the Tautra population showed growth beginning in February. Populations from North Wales (Richardson et al. 1980b) also showed growth starting in February. The Tautra population differed from that in North Wales in having a reduction in growth in March–April (Fig. 10) not present in the Welsh population. It is possible that gametogenesis diverts energy resources away from growth and the Tautra population had less available food at this period than the North Wales population. Diversion of energy resources away from growth in summer may cause growth checks as reported in *Mercenaria* populations from N. Carolina, USA. (Peterson et al. 1983). Maximal size in the Tautra population of $L = 42.6$ mm length was close to that found in North Wales by Richardson et al. (1980b).

Our results thus demonstrate that, after removing seasonal trends, tidal patterns are the dominating influence in the formation of microgrowth bands in *Cerastoderma edule*. Similar findings have been reported by Bourget (1980) for *Balanus balanoides*. Whilst we cannot extrapolate to other species there seems no obvious reason to believe that other intertidal species will show patterns influenced by daily (light/dark) cycles. The methods used here might offer a reasonably rapid way of testing this hypothesis. Preliminary studies have shown that clear microgrowth bands occur also in *Nucella lapillus*, *Patella vulgata*, *Littorina littorea* and in the periostracum of *Mytilus edulis*.

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