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Does prism width from the shell prismatic layer have a random distribution?

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Abstract A study of the distribution of the prism width inside the prismatic layer of *Unio tumidus* (Philipsson 1788, Diss Hist-Nat, Berling, Lundæ) from Lake Neuchâtel, Switzerland, has been conducted in order to determine whether or not this distribution is random. Measurements of 954 to 1,343 prism widths (depending on shell sample) have been made using a scanning electron microscope in backscattered electron mode. A white noise test has been applied to the distribution of prism sizes (i.e. width). It shows that there is no temporal cycle that could potentially influence their formation and growth. These results suggest that prism widths are randomly distributed, and related neither to external rings nor to environmental constraints.

Introduction

Shell formation is a complex process, which is not fully understood. Molluscs absorb the components for their $CaCO_3$ shell from the surrounding water, and precipitate calcium carbonate in different forms, as prisms of calcite, lamellae of aragonite, or even vaterite (Martoja 1995). The shell is built by entrapping the crystals in a net of organic matter, composed mainly of proteins such as conchyoline. Essentially, three layers are secreted by the mantle (see Checa 2000, and Martoja 1995 for detailed reviews):

- an external layer (periostracum), which is an organic substance protecting the other parts of the shell;
- a middle vacuolized layer, which forms a structure called the antrum over time. These cavities become filled with crystals of calcium carbonate (i.e. aragonite), arranged perpendicularly to the outer periostracum, separated from it by a conchyoline membrane, and forming the outer prismatic layer;
- the nacreous layer, which is created by similar processes to those of the middle layer but is composed of lamellae of aragonite, parallel to the surface.

In the present paper, a test of possible cyclicity is proposed on the basis of detailed analyses of prisms from the shell prismatic layer, reflected in the measurement of their size (i.e. width). In other words, the objective is to demonstrate whether or not the distribution of prism width inside the prismatic layer is random. One of the consequences of such a study is to question if a potential relationship, e.g. correlation between prism width and growth lines, exists or not. Furthermore, such a study raises the question of the use of mineralized microstructures in environmental or climatic reconstructions when based on prismatic layer geometric properties. Indeed, this study suggests that there is no obvious relationship between prism width and growth lines at the surface of the shell in the case of freshwater bivalves from Lake Neuchâtel (Switzerland).

Materials and methods

Data collection: *Unio tumidus* (Philipsson 1788)

Unionidae shells from Lake Neuchâtel (46°55′ N, 6°50′ E; Bargetzi 1960) were collected during the summers of

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2004 (only dead shells) and 2005 (living and dead shells) in the area locally referred to as La Tène, situated west of the Thielle Canal (47°0′15″ N, 7°0′55″ E, Neuchâtel Canton, Switzerland). The following species were found:

- 321 living and 156 dead shells of *Unio tumidus*,
- 45 living and 11 dead shells of *Anodonta anatina*,
- 15 living shells of *Anodonta cygnea*.

In this paper, only *U. tumidus* (Philipsson 1788) will be studied, and only living shells from the same collection will be used for prism width study. *U. tumidus* (Fig. 1) has a mean length varying between 65 and 80 mm, a maximum length of 120 mm, a mean width of 30–45 mm, and a mean depth varying between 24 and 30 mm, depending on the shell's age. The width is about half the length. The shape is oblong, and the colour ranges from yellow-green to brown. *U. tumidus* prefers quiet waters such as lakes and rivers up to a maximum depth of 10 m. The maximal lifespan is 15 years on average but can reach more than 20 years (Turner et al. 1998). Mineral composition of *U. tumidus* shell is mainly aragonite (with traces of calcite or vaterite).

Internal composition of the shell

It is possible to see growth rings on the shell surface (Fig. 2a) as well as prisms (Fig. 2b) with a scanning electron microscope (SEM) in backscattered electron (BSE) mode. The number of prisms between two growth lines seems to vary. Two growth lines are even able to fuse, giving the impression that there is no relationship between prisms and growth lines. In thin section, the prisms and the lamellae appear more clearly (Fig. 2c,d). The prismatic layer seems to become thicker along the growth direction, and some rings are visible on the prisms as such, emphasizing their possible annual growth rhythm (prisms grow vertically inwards to the top, Fig. 2e,f; Checa 2000; Checa and Rodriguez-Navarro 2001; Dunca and Mutvei 2001).

Fig. 1 *Unio tumidus* (Philipsson 1788). The *black line* shows the cutting trace of the thin section

Growth prisms

Using SEM, it is possible to see the internal composition of the shell. In particular, it is possible to measure the width of each prism (Fig. 3; the microscope is calibrated, and the error in width measurement is <3%). There are two possible locations for prism measurement: (1) at the bottom of the prism, near the lamellae layer; (2) at the top of the prism, near the periostracum. In this paper, the second solution is chosen, i.e. the most external part of the prism was measured. The prisms are sometimes separated into two sub-prisms (Fig. 3), which is why the two measurements do not give the same results. Sub-prisms result from the fact that, during their vertical inward growth, bigger prisms expand laterally at the expense of smaller ones (Checa and Rodriguez-Navarro 2001). Therefore, the top of the prismatic layer is the older part and, consequently, the prism width at the top is acquired very early during prismatic layer formation (Checa et al. 2005). Thus, it was decided that the outside measurement of prism width be used, in order to be able to compare these results with the growth lines observed at the shell surface, and to identify a potential relationship between prisms and growth rings found on the shell surface. Curves plotted with these measurements (Fig. 4) show the distribution of the prisms' width acquired during shell formation. Depending on the shells, 954 to 1,343 prisms were measured. This means that 14,301 different prisms from 12 different shells of various ages (both left and right valves) constitute the database.

Signal and cyclicity

A signal is a temporal series characterized by its frequency, its trend and its autocorrelation. A signal varies with time. To analyze it, it is necessary to transform it and search for its characteristics. For this purpose, many methods exist, such as Fourier and wavelet analysis (Verrecchia 2004). Fourier analysis emphasizes the frequencies present in the signal. Wavelet analysis is able to decompose the signal at different levels to show the approximation and the detailed coefficients of the signal (Toubin et al. 1999). It is necessary to check if there is a general trend, or not, before any analysis of a signal can be conducted. A trend means that all the values change in the same direction. If there is any trend, it has to be removed. Then, it can be checked for any information that can be extracted, such as cycles. If not,

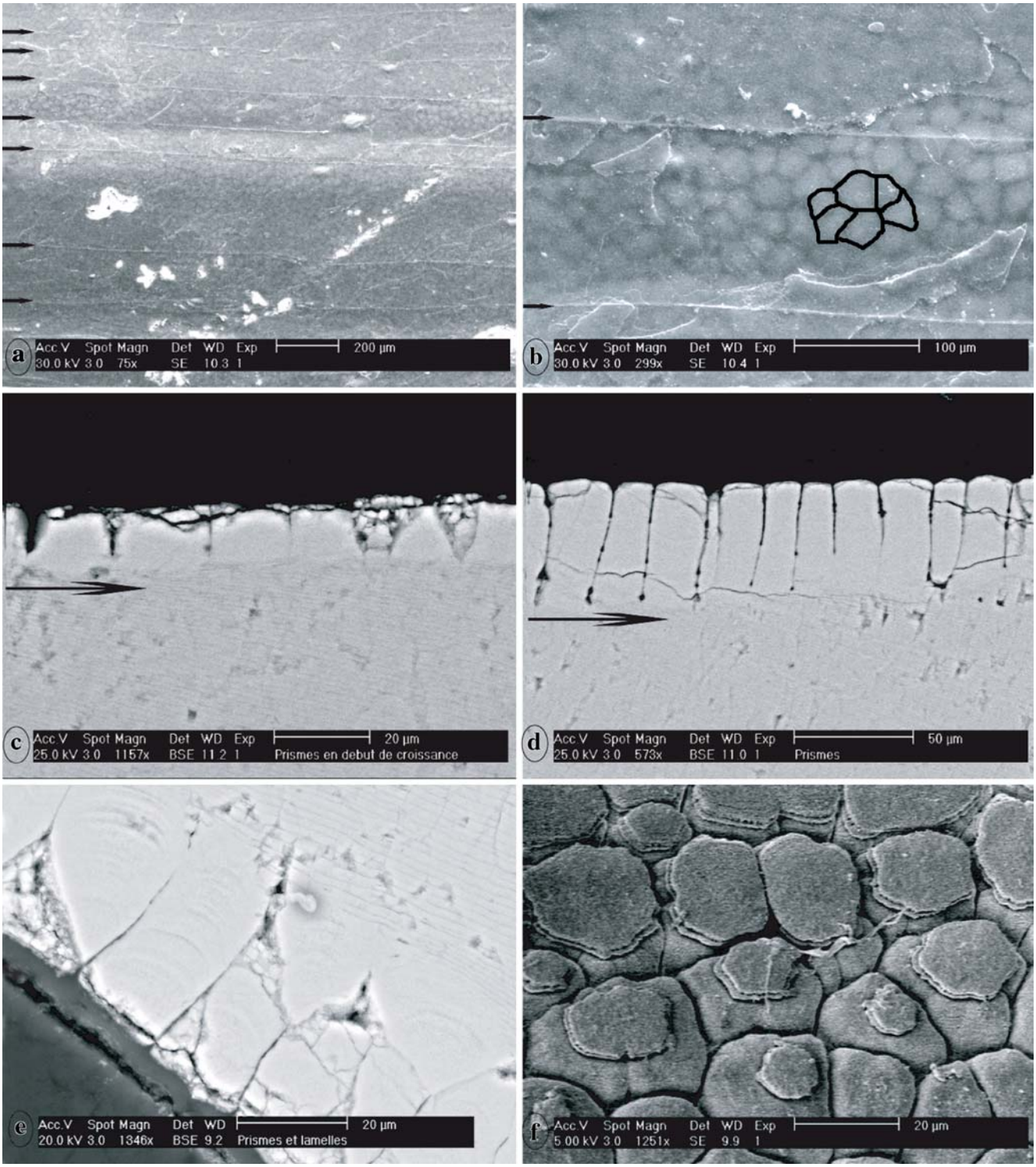

Fig. 2 Scanning electron microscope (SEM) images in conventional (**a**, **b**, **f**) and backscattered electron (BSE) mode (**c**–**e**). **a** Shell surface showing growth lines. Their spacing is not regular. **b** Shell surface of *Unio tumidus*, growth lines (*arrows*) and prisms (some limits drawn) can be observed. **c** Prismatic and lamellae layers (*arrow* limit between the two layers) at the beginning of shell growth. The prisms are squat, and no more than 15 µm high. **d** Prismatic and lamellae layers (*arrow* limit between the two layers) in the middle of the shell. Prisms can be >50 µm high. **e** Prismatic and lamellar layers showing the lamellae succession. **f** Shell surface after removing the periostracum. Prism growth is obviously vertical inwards, the older part of the prism being at the top

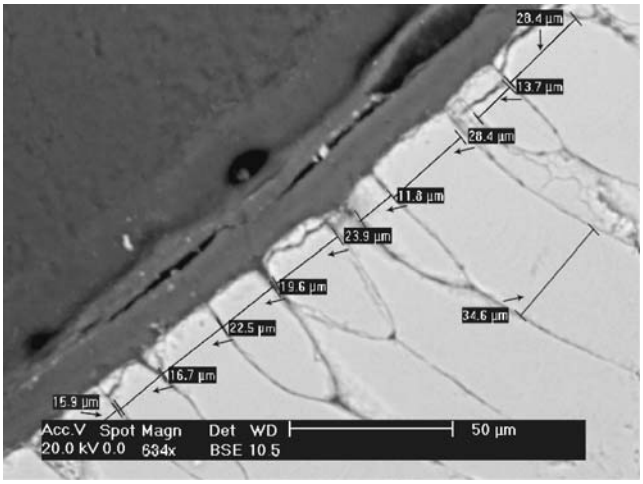

Fig. 3 Prism width measurements using SEM in BSE mode. The prisms are sometimes separated into two sub-prisms, so that there are two possibilities to perform the measurements: (1) at the bottom near the lamellae layer, and (2) at the top near the periostracum. The two measurements do not give the same results. The outside measurement was used in order to be able to compare the results with the lines on the surface (in the event of a relationship). In addition, as the prism grows inwards, this part is the oldest and the most stable

the signal is considered to be the result of random noise. In particular, it could be white noise.

White noise is a signal in which there is no autocorrelation, and that contains any frequency. If there is no particular frequency in the signal, that means there is no cyclicity to be detected and, consequently, no memory in the signal. Autocorrelation allows the detection of some regularity in a signal. So, the absence of autocorrelation means that a signal is not cross-correlated with itself, in any part of itself. If the autocorrelation function $R_f(\tau)$ of a signal f is given by

$$R_f(\tau) = E[f(\tau)f(t+\tau)]$$

where τ is the lag (used to shift the signal along itself by t increments), t the time, and E the expected value operator, the function is equal to 1 only when $\tau=0$ (because every part of the signal is correlated with itself), and is null everywhere else (because no part of the signal is similar, i.e. correlated, to another). The resulting function is a symmetric plot around a peak centred on lag 0. If the function value is not null around the centred peak, it means the signal has some correlated parts and, therefore, is not constituted by white noise. Otherwise, the signal is considered as a random function. In conclusion, for a white noise signal, the autocorrelation function has a peak only at 0, and no other noticeable values on the plot. Therefore, the autocorrelation function of a white noise looks like a Dirac function at 0.

The first step before using Fourier or wavelet analysis is to find some cycles in a signal, and to check if the signal is white noise or not. A test has been computed by J.-M. Vesin from EPFL in Lausanne, Switzerland, using Matlab®.

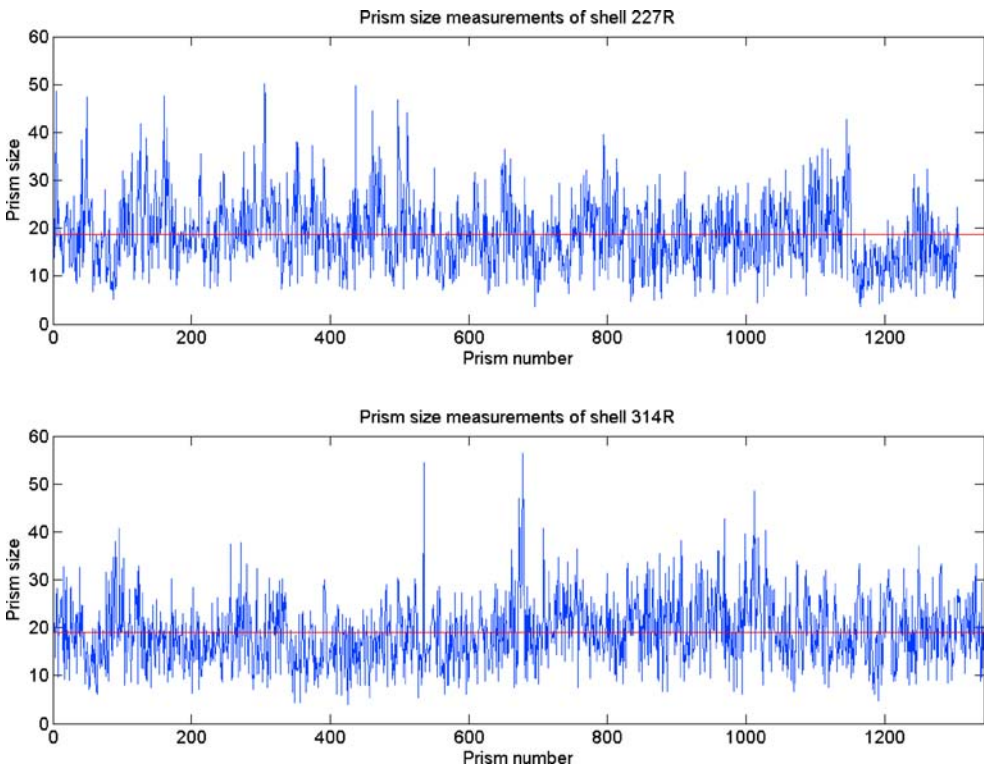

Fig. 4 Examples of plots (here, for shells 227R and 314R) showing prism measurements (width). On the *x* axis, prism number; on the *y* axis, prism width. *R* Right valve, *L* left valve, *red line* mean value

Table 1 Descriptive statistics of the prism width (in μm) compared to size parameters and age

Sample	Mean	Variance	Minimum	Maximum	Shell length (mm)	Shell width (mm)	Estimated age (year)
227R	18.6058	7.4555	3.64	50.10	106.55	48.42	11
261R	24.6144	9.6084	5.75	79.50	98.6	45.47	9
261L	25.1358	9.8888	4.51	87.10	97.66	45.97	9
314R	19.0268	7.0980	4.08	56.40	82.42	39.3	5
344R	16.0921	5.6422	3.70	36.20	72.7	36.16	11
344L	13.9341	5.1659	2.66	36.10	71.99	35.66	11
361R	19.4925	6.7179	3.81	57.30	52.34	25.82	3
416R	16.9999	6.4256	3.65	41.40	42.79	21.18	1
418R	20.5754	8.2228	4.16	67.00	62.28	31.16	3
418L	20.4860	6.9268	5.37	60.10	62.67	31.1	3
492R	16.0405	5.8264	3.59	37.50	33.66	17.63	1
492L	16.1551	5.9088	3.08	44.00	32.9	17.14	1

The test is used to verify the null hypothesis H_0 versus H_1, where H_0 is *the signal is white noise*, and H_1 is *the signal is not white noise*. The result of the test is less than 0.05 if it is white noise. If the test results in white noise signal identification, no cyclicity can be found in the recorded signal of the prismatic layer.

Results and discussion

It has been stipulated above that the aim of this paper is to check if there is any cyclicity, or not, in the width distribution of prisms. The objective is to verify if prism widths can be used as a proxy for environmental conditions. At first sight (Fig. 4), the width distribution of prisms looks like they have almost the same mean width along the growth direction. If this is true, it means that the prism widths do not vary significantly and that the differences seen in the recorded signal could be due to a random distribution. The signal resulting from the prism width distribution is probably a random process that could be defined as white noise. This point will be investigated further below.

In addition, it would be pertinent to use these data to perform a comparison between right and left valves. If the valves are perfectly symmetrical, then they must show the same pattern in all possible measurements and, in particular, in prism formation. Consequently, in addition to the test

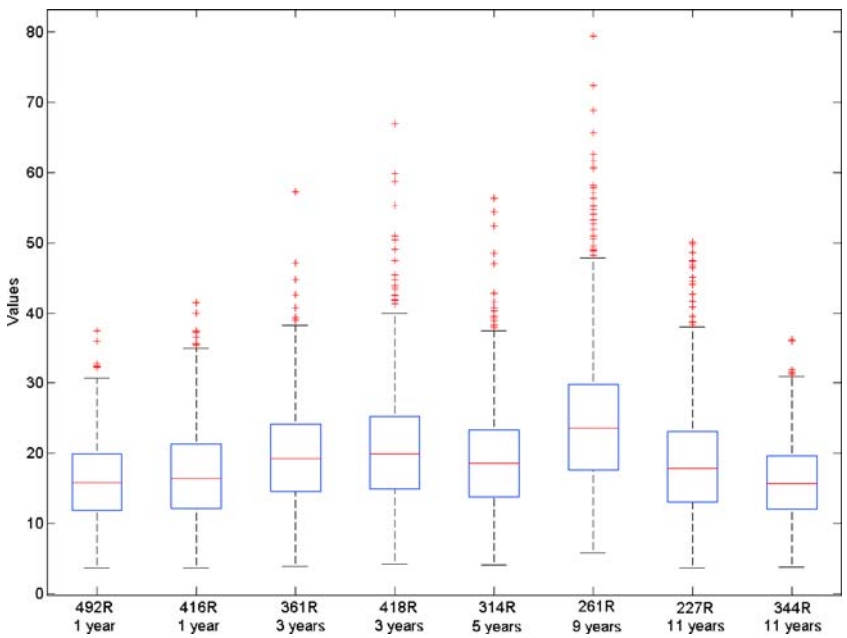

Fig. 5 Box plot of the prism width of the right valves from the shells studied. These box plots were used in order to compare variations between individuals. All the distributions vary with the same orders of magnitude

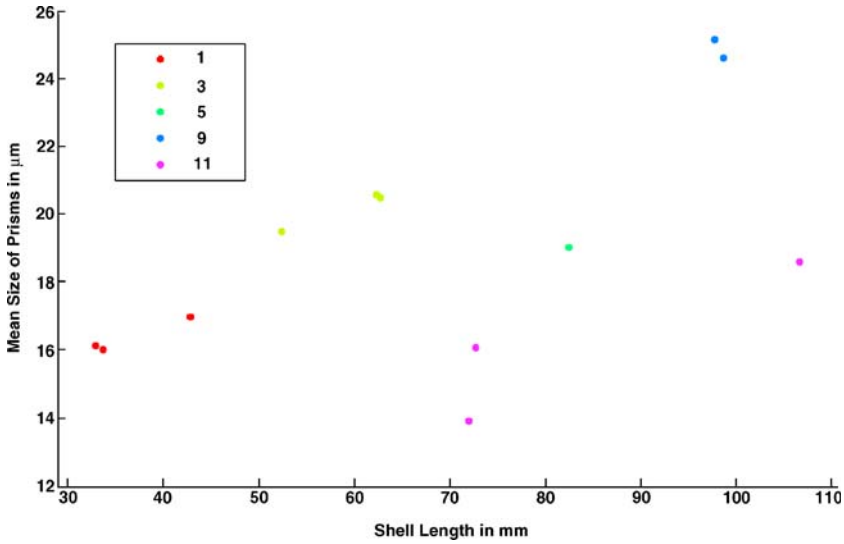

Fig. 6 Plot of the mean width of prisms versus the length of the shell, in terms of age (*in color*), showing that there is no relationship between prism width variation and the size of the shell (r=0.56)

of any cyclicity in prism width distribution, the right and left valves of a given shell have been compared to determine if they show the same pattern (cf. below).

Are there cycles in prism width distribution?

The descriptive statistics regarding the prism measurements are given in Table 1. All the means and variances seem to vary in the same way (Table 1; Fig. 5), even if some maxima are two or three times the value of others. These are outliers, and Fig. 5 shows that the magnitude of each distribution is the same. This fact is also illustrated in Fig. 6 where there is no relationship (r=0.56) between prism mean width, shell length and shell age. In addition to the results shown above—i.e. the signals seem to vary randomly around their mean value—it is possible that they do not show any particular trend during growth. Thus, the existence of cycles can be questioned. This is critical and must be proved using tests for white noise. Another pending question is related to the type of random distribution shown by the prism widths if these correspond to white noise.

Prisms grow vertically inwards (Checa and Rodriguez-Navarro 2001). One of the consequences of such a process is that prisms are randomly formed, and their number formed per day is variable. Therefore, as the prisms grow vertically (Dunca and Mutvei 2001), they do not result from a simultaneous period of growth when reaching the surface. In addition, Rhoads and Lutz (1980) noted that prisms are vertical, in order to protect the shell against dissolution. Some nuclei of prisms are caught in organic matter and continue to grow after their formation. This means that the growth lines visible on the surface are not directly related to prisms. They are instead related to lines in the lamellar layer (Richardson 1990). In fact, if there are different widths of prisms, it is because during their growth, prisms are in competition with each other to occupy space between the organic matter membranes (Rhoads and Lutz 1980; Checa 2000; Checa and Rodriguez-Navarro 2001; Checa et al. 2005).

The fact that the prisms are randomly distributed indicates that there is no cyclicity and that the signals reflect white noise. With the help of P. Vandergheynst, and the Matlab test of J.-M. Vesin (both EPFL, Lausanne, Switzerland), each signal has been studied as if it could be white noise. As noted above, the autocorrelation coefficient in white noise is null, which means that the autocorrelation function looks like a Dirac function, with a value of 1 only at step 0. Vesin's test allows a signal to be identified as white noise or not. If the value resulting from the test is <0.05, then the signal can be considered as white noise. The

Table 2 White noise test

Shell	Result	Conclusion
227R	0.0597	Not white noise
261R	0.0221	White noise
261L	0.0271	White noise
314R	0.0522	Not white noise
344R	0.0371	White noise
344L	0.0293	White noise
361R	0.0187	White noise
416R	0.1479	Not white noise
418R	0.1238	Not white noise
418L	0.0531	Not white noise
492R	0.0669	Not white noise
492L	0.0371	White noise

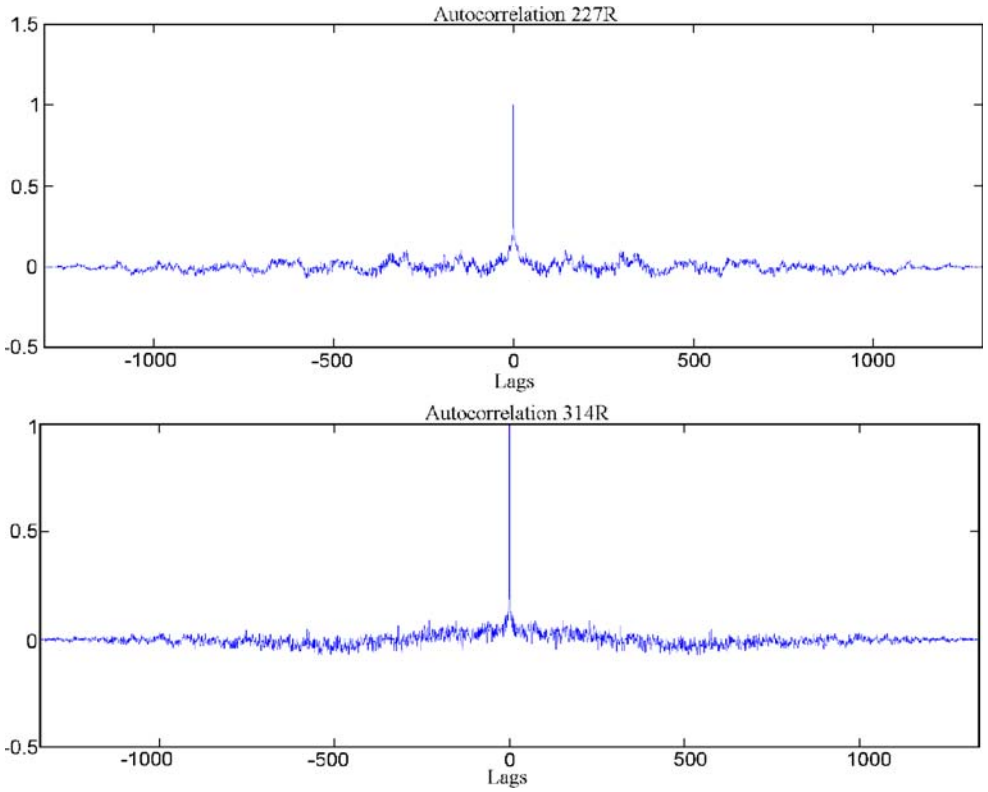

Fig. 7 Example of autocorrelation functions of the signals (shells 227R and 314R)

results of the white noise test are given in Table 2. Some signals are not white noise but the test value is not very far from 0.05. Looking at the autocorrelation functions (an example is given in Fig. 7), they have a Dirac shape. This means that the prism width distribution is random.

A question is still pending: to what distribution is the prism width distribution related? Prism width is distributed around a mean. For instance, do prism widths have a normal distribution? In order to find a possible model, the density histogram of the prism widths (Fig. 8) has been adjusted to various distributions of random variables. Results of best of fit distribution for one shell are given in Table 3. The same procedure and the same results have been obtained for the eight shells studied. A χ^2 test was used to compare some chosen distribution laws with the signal. The *dfittool* toolbox (Matlab®) served to compare the distribution laws with the density histogram (Fig. 8). Probability plots (Fig. 9) were calculated for each distribution in order to correctly adjust the density. The distributions chosen are (1) Birnbaum–Saunders, (2) gamma, (3) generalized extreme value, (4) inverse Gaussian, (5) lognormal and (6) normal. Based on these six estimations, the gamma distribution best fits shell 227R (Fig. 10). Results given in Table 3 demonstrate that the generalized extreme value and the gamma distributions are the most suited to fit prism width distribution. Nevertheless, regarding the histogram (Fig. 8), the gamma distribution seems to be a better model. The gamma distribution is also the best model in terms of the probability plot (Fig. 9).

For most of the studied shell signals, the gamma distribution is the best fit. Only one of these is better fitted by a normal distribution. The gamma distribution can be considered as an unusual choice because a normal distribution would have been more pertinent in order to

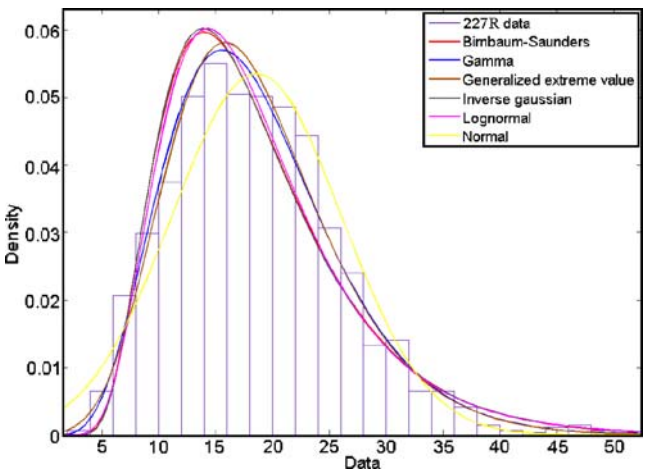

Fig. 8 Histogram of prism width distribution for shell 227R. The density function of each tested law has been drawn to estimate the best distribution

Table 3 Probability law estimation for shell 227R

Law	Estimated parameters	*p* value	Test results
Birnbaum–Saunders	17.0019 and 0.433462	No test	–
Generalized extreme value	–0.071652; 6.34189 and 15.3619	0.1511	H_0
Gamma	6.10888 and 3.0457	0.1170	H_0
Inverse Gaussian	18.6058 and 94.5827	No test	–
Lognormal	2.8394 and 0.423517	1.1060e-008	H_1
Normal	18.6058 and 7.4555	7.9830e-009	H_1

conclude that prism width distribution is related to Gaussian white noise. Nevertheless, knowing that the gamma distribution tends to a normal distribution, and that measured values are truncated at 0, it seems reasonable to obtain a gamma distribution as the best fit model.

Comparison of prism width for right and left valves

Previous unpublished work from the authors has statistically proven that right and left valves of *Unio tumidus*, *Anodonta anatina* and *Anodonta cygnea* from Lake Neuchâtel are identical regarding morphological parameters. Student t and Kolmogorov–Smirnov tests have been used to compare the two valves in terms of prism width distribution:

- for sample 261, the tests show that the means are different but the distributions are the same. Nevertheless, the difference between the means is <1 μm, so the means are virtually equal;
- for sample 344, the tests show that both the distributions and the means are different;
- for sample 418, the tests emphasize that the means and the distributions are the same;
- for sample 492, the distributions and the means are also the same.

In conclusion, although there is some variability between the right and left valves regarding prism width distribution, on average they show the same trend. If the histograms of width density are stacked for the two valves, it can be seen that they are very similar (Fig. 11). As a final comparison, quantiles of the two valves are shown to come from the same distribution (Fig. 12), which is not surprising because gamma distributions can be applied whatever the shell, as demonstrated above.

In conclusion, it has been proven in many papers (Clark 1975; Hall 1975; Whyte 1975; Mutvei and Westermark 2001; Goodwin et al. 2001) that the lines on the shell surface are related to cycles. Nevertheless, prism width distribution has been demonstrated to be a random variable following a gamma distribution. Therefore, prism widths are not related to the shell growth surface. The number of prisms formed by day is random,

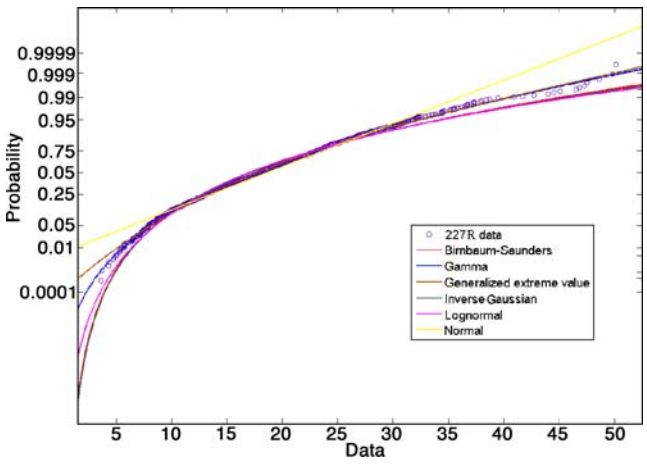

Fig. 9 Probability plot of prism width distribution for shell 227R. A probability plot was made for each distribution to find the best fit distribution to the natural data (see also Table 3)

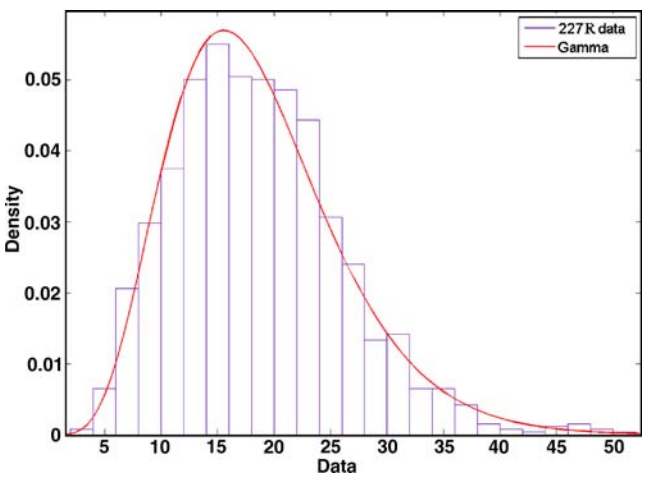

Fig. 10 Shell 227R histogram, with its estimated distribution density function

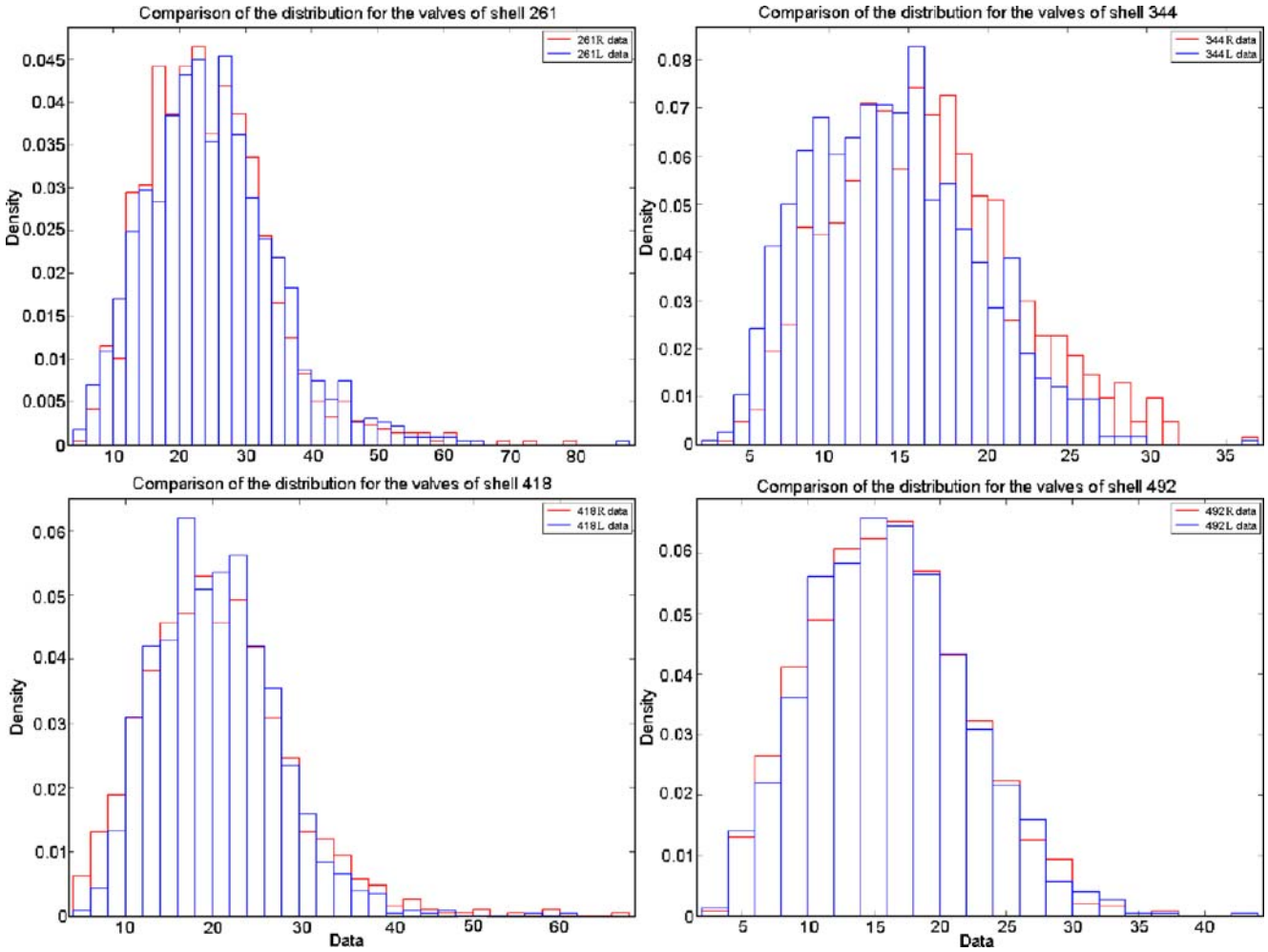

Fig. 11 Prism width histograms used for comparison between right and left valves

and not due to any known cycles. In addition, it has been shown that, even if there is a small difference between the widths of the prisms, their distribution is random for a given mean. Prism width also shows the same trend in the two valves.

In previous studies, Toubin et al. (1999) and Verrecchia (2004) demonstrated that bivalve shells record natural cycles. In particular, they used the Bertalanffy equation to estimate the mean growth rate. In Fig. 2, the growth rate varies between two lines. Other studies of subtidal samples (Richardson et al. 1980a, b, c; Richardson 1987a, b, 1990, 1996; Lonne and Gray 1988) show that the growth lines on the surface do not correspond to cycles, in contrast to intertidal ones where the endogenous rhythm of the animal is present. After a certain number of prisms are constructed, the shell needs to build a line in order to solidify the structure. Diurnal variations have no influence on the line formation. Consequently, how is it possible to know if the growth lines on the surface are a daily process? How can growth rate be used if it changes so frequently between two growth lines? Finally, the conclusions for marine environments seem true for freshwater lakes.

Conclusions

Many studies have been devoted to the use of shell surface or the lamellae layer of bivalves for environmental reconstructions. This paper does not discuss growth lines directly but the prismatic layer. The aim is to demonstrate whether or not the prism width inside the prismatic layer is random. This implies some consequences on the interpretation of prism growth related to shell growth. To date, no studies have demonstrated that prisms could be used to record natural cycles. In this paper, it has been proven that prism width distribution is random and assimilated to white noise. The random distribution—a gamma distribution—of prism width explains why they cannot be used as cycle

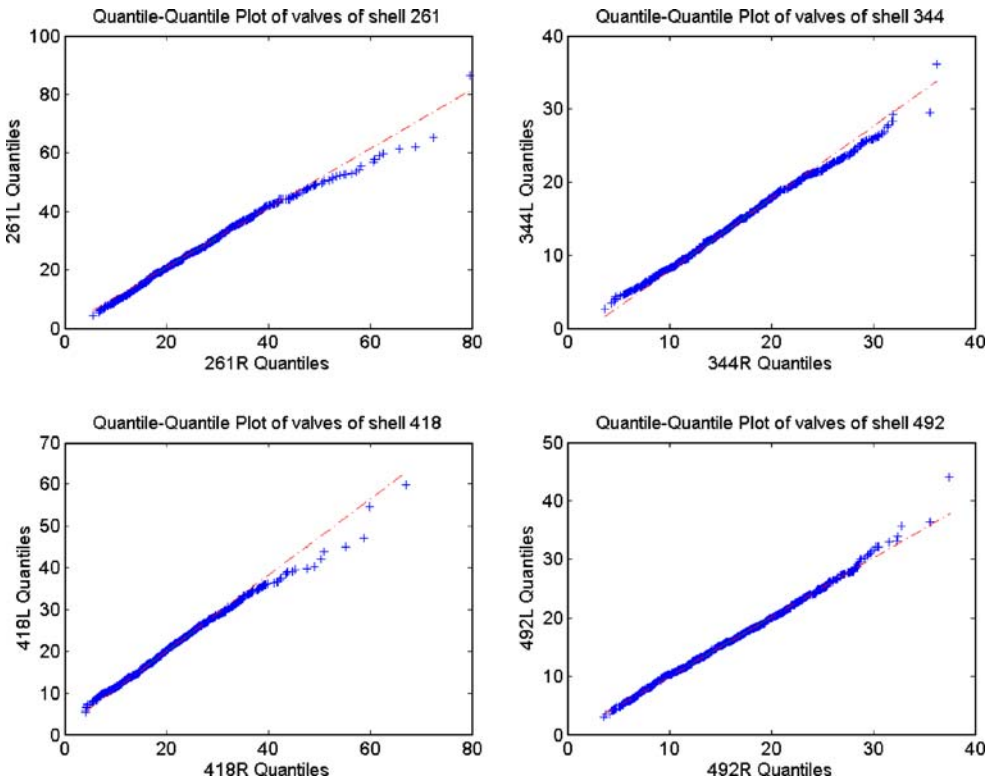

Fig. 12 Quantile comparison for prism width distribution of right and left valves

recorders. If their distribution is white noise, then they can be influenced neither by any cyclicity, nor by any environmental parameters. Similarly, subtidal bivalve surface growth rings cannot be used as environmental recorders because of variability due to their endogenous rhythm. This conclusion can also be applied to lacustrine shells in Lake Neuchâtel (Switzerland).

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