

# Time series analysis of sclerochronological data

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**Abstract.** Due to the versatility of sclerochronological data and distinct research objectives, recent contributions to the investigation of accretionary growth in biogenic hardparts differ in their employ of time series analysis tools. However to a certain extent techniques are similar and finding a comprehensive model could be of heuristic value, improving the interpretation of the both types of sclerochronological data i.e. isotope composition as a function of accretion width and increment width as a function of time. An idea for creating a practicable comprehensive model is briefly discussed after highlighting some previous research work done by various authors.

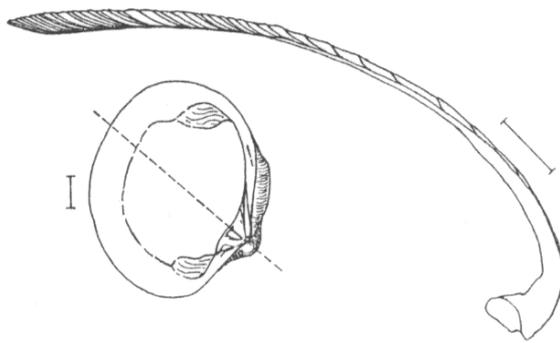
*Keywords:* Increments; Stable isotopes; Time series analysis; Palaeobiology; Palaeoenvironment

## Introduction: Skeletons as a data source

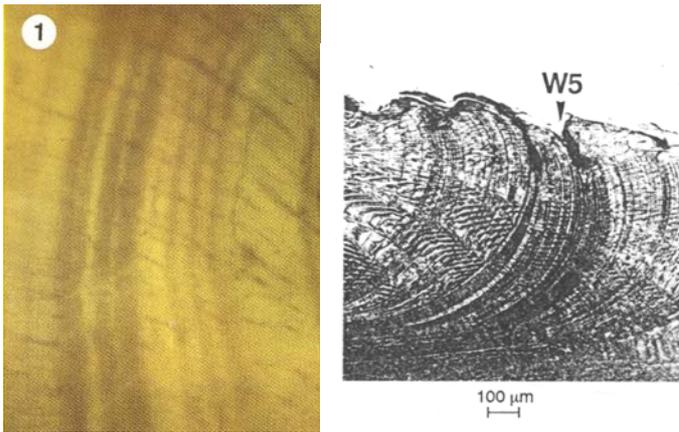
Sclerochronology deals with the accretionary growth of biogenic hardparts. Given that growth is subject to periodic environmental variation, the skeletons of animals such as a bivalve shell or a coral reef are usually patterned by **growth increments** and lines of arrested growth (Fig.1 (a), (b)). Recognizing an assumedly daily or seasonal variation within these patterns allows to determine the duration of accretion of a certain amount of skeletal material. Thus a time series can be gained by relating the skeletal thickness along the growth axis to time (Fig.1 (a), (b)) or by relating increment width to increment number. As the first derivative of skeletal thickness with respect to time increment width is another expression for growth rate (Fig.1 (b), (c); e.g. SATO 1999, MARCHITTO 2000, SCHÖNE et al. 2002, GOODWIN et al. 2003).

Another source of sclerochronological data are **stable isotope** analyses performed with samples sequentially taken along a skeletal profile. The resulting isotope curves are often sinusoid indicating seasonality and thus demonstrating a relation to time which appears to be independent from the stripe pattern of growth increments (Fig.1 (d); e.g. LEDER et al. 1996, STEUBER 1996, SURGE et al. 2001, WILKINSON & IVANY 2002, GOODWIN et al. 2003, BUICK & IVANY 2004, NAKASHIMA et al. 2004, STRAIGHT et al. 2004, WATANABE et al. 2004).

Sclerochronological analyses have been carried out for numerous purposes and for a great ecological and taxonomic spectrum of recent and extinct animal groups including corals (LEDER et al. 1996, WILKINSON & IVANY 2002), brachiopods (JAECKS 2000), bivalves (STEUBER 1996, SATO 1999, MARCHITTO et al. 2000, SURGE et al. 2001, SCHÖNE et al. 2002, WILKINSON & IVANY 2002, GOODWIN et al. 2003, IVANY et al. 2003, BUICK & IVANY 2004, GOODWIN et al. 2004, NAKASHIMA et al. 2004, SCHÖNE et al. 2004, WATANABE et al. 2004), gastropods (LATAL et al. 2004), amphibians (STEYER et al. 2004), sharks (MCFADDEN et al. 2004), teleost fishes (WILKINSON & IVANY 2002), archosaurs (ERICKSON et al. 2004, THOMAS & CARLSON 2004, STRAIGHT et al. 2004), and mammals



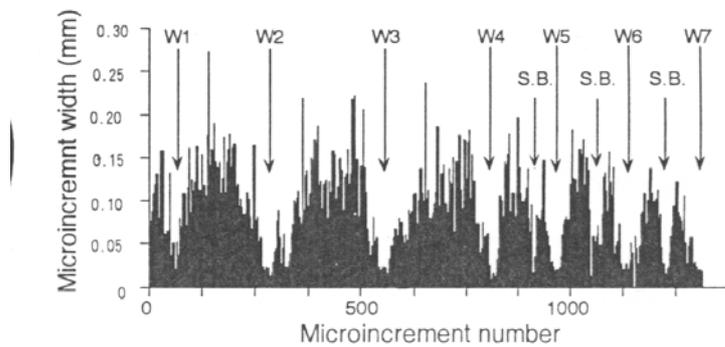
(a) Profile through a bivalve shell showing annual lines of arrested growth (scale bars: 1 cm).



(b) Shell patterned by growth increments:

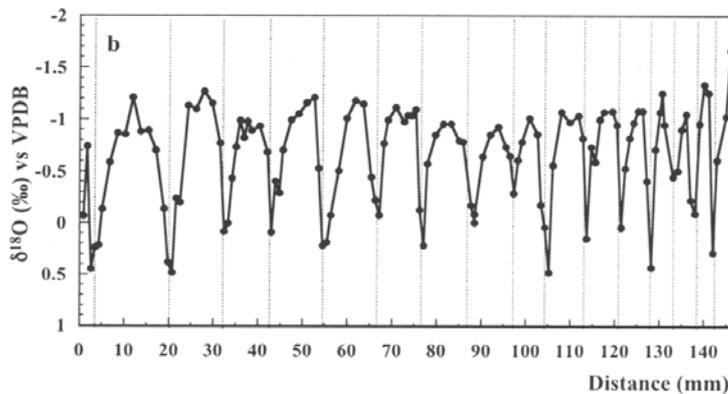
$$s_n = \sum_{j=1}^n i_j = s(t_n) = \int_0^{t_n} (i) dt$$

shell thickness  $s$ ,  
 increment number  $n$ ,  
 increment width  $i$ , time  $t$ ,  
 period  $T = dt = 1$  day.



(c) plot of increment width/ increment number revealing growth rates  $g$ :

$$g(t_n) = d s(t_n) / dt = i_n.$$



(d) variation of  $\delta^{18}\text{O}$  and  $\delta^{13}\text{C}$  values along the growth axis:

$$\delta = \delta(s(t_n)).$$

**Fig.1.** Types of sclerochronological data obtained from (a, b) shell profiles: (b) shell thickness (c) increment number/ growth rate, and (d)  $\delta$  values as time series (images from MARCHITTO et al. 2000, SATO 1999, HAMPE 1991, WILKINSON & IVANY 2002, in the order of appearance).

(FRICKE & O'NEIL 1996, WILKINSON & IVANY 2002, CERLING et al. 2004, FERANEC 2004, FOX & FISHER 2004, HOPPE et al. 2004, RINALDI & COLE III 2004, ZAZZO et al. 2002). However there are techniques and problems several approaches have in common, some of whom are discussed below.

## Applying methods of time series analysis

### Noise removal

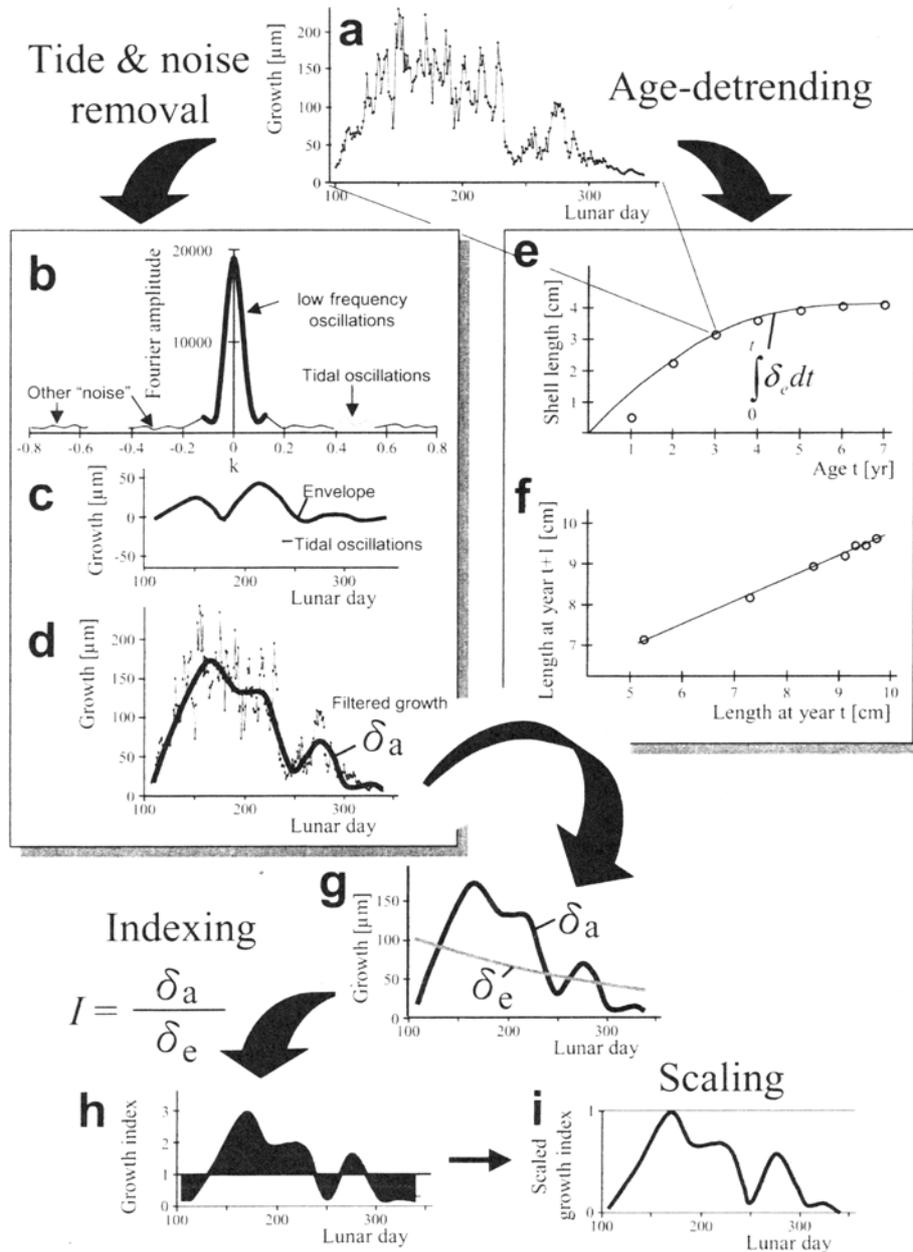
Unlike isotope profiles which often comprise relatively few data points and lack high-frequency variation, growth rate curves obtained from measurements of daily increments tend to show some high-frequency noise, caused by environmental or physiological signals which cannot be resolved. One way to remove these interfering signals is the application of a **low-pass filter** such as a moving average filter (according to BORRADAILE 2003: pp. 201- 203, see FERANEC 2004, p. 3007). Another type of low-pass filter, a Savitzky-Golay filter, was used by SCHÖNE et al. 2004 in order to enhance the long-term trend within an isotope profile from a long-living specimen of the bivalve *Artica islandica* (page 220).

SCHÖNE et al. 2002 applied **Fourier transformation** to reveal cyclic growth patterns in an increment width/ lunar day time series of an intertidal bivalve shell (see Fig.2, further discussion of the method follows). Before transforming the data back they removed tidal oscillations and high-frequency noise in order to isolate the temperature signal which was in the focus of their investigation (Fig.2 (b), (c), (d); SCHÖNE et al. 2002: pp. 135- 136). Applying a moving average or similar low-pass filter can improve the legibility of data in a following Fourier analysis (according to BORRADAILE 2003: page 211), a way which was followed by SCHÖNE et al. 2004.

### The meaning of trends

Growth is often regulated by **ontogenesis** resulting in an age-dependence of growth rates (Fig.3, e.g. STEUBER 1996, MARCHITTO et al. 2000, SCHÖNE et al. 2002, ERICKSON et al. 2004). Furthermore it can cause a swap in life style and/or habitat, or otherwise influence the animal's physiology and consequently the parameters of its skeletal accretion. Changes in growth rate or isotope composition due to ontogenesis are usually reflected in sclerochronological data sets as **trends**. Fig.3 illustrates the effect of age-dependent growth rates in the increment width/ increment number plot (Fig.3 (a)) and in an isotope profile (Fig.3 (b)). However interpreting trends requires taking into account that they can also represent cyclic environmental variation with a period too long to be recognized in a time series comprising the growth period of one animal hard part (BORRADAILE 2003, pp. 209-210, see for example FERANEC 2004, page 307).

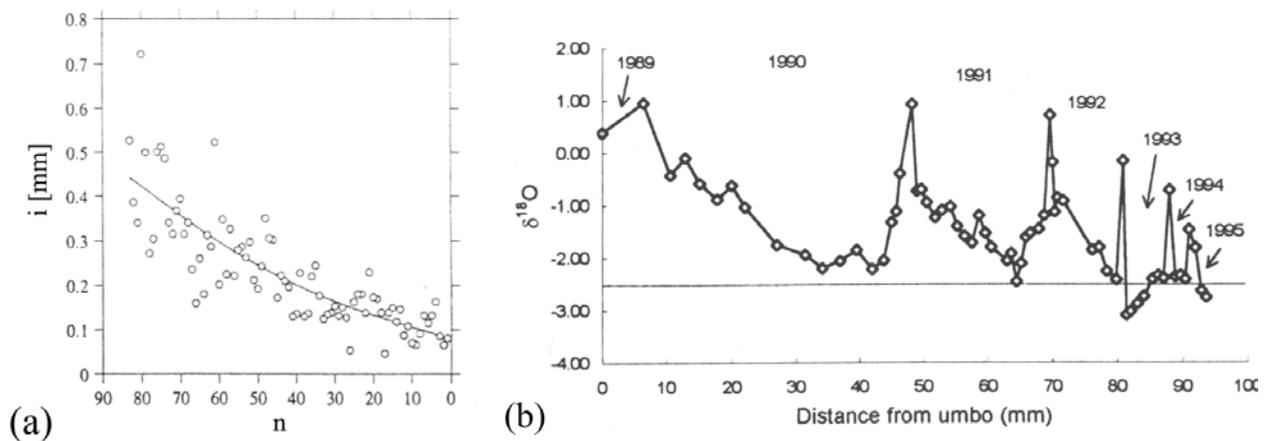
Detecting trends can be performed utilizing different techniques, e.g. a moving average filter of very high order or a **regression analysis** can reveal long-term change in a data set (BORRADAILE 2003, page 209). Since growth curves of animals are often sigmoidal or at least show a significant decrease of growth rate with age, exponential regression functions such as logistic growth equations (see ERICKSON et al. 2004, STEYER et al. 2004), the Gompertz equation (see MARCHITTO et al. 2000) and



**Fig.2.** (a) An increment width/ lunar day time series. (b) Its Fourier transform shows different oscillation types. (c) Back-transformed tidal oscillations [hardly visible] and their envelope. (d) Back-transformed low-frequency oscillations plotted in a diagram with the curve from (a). (e) Exponential curve representing age-dependent growth. (f) A Ford-Walford plot allows to determine the parameters for the exponential model in (e). (g) The filtered growth curve from (d) and the age-dependent growth curve derived from (e). (h) Daily growth indices, gained from dividing the filtered growth curve (d) by the age-dependent growth curve derived from (e). (i) Scaled daily growth indices from (h), allows the deduction of water temperatures (from SCHÖNE ET AL. 2002).

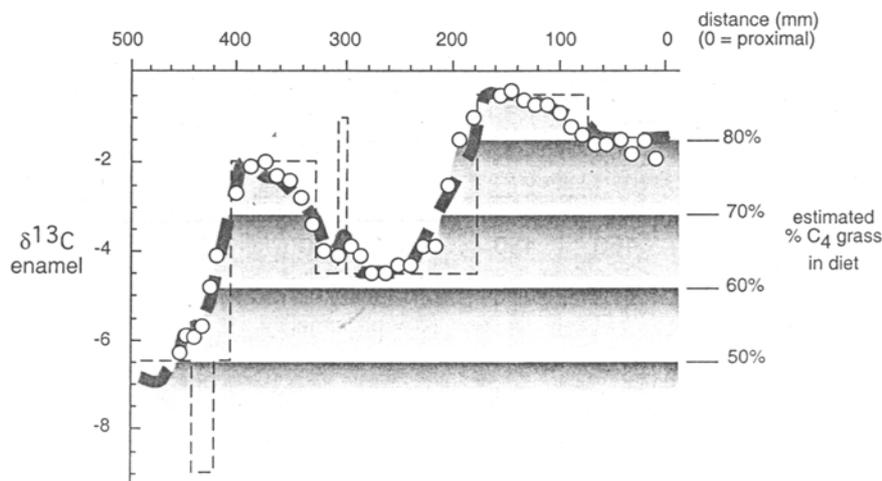
the Bertalanffy equation (see Fig.2 above: “Age-detrending” in (e), (f); SCHÖNE et al. 2002, BUICK & IVANY 2004) are often applied for modeling the age trends. Sometimes the ontogenetic effect is marginal and a simple linear or quadratic relationship between annual skeletal accretion and time can be assumed, as demonstrated by STEYER et al. 2004 for a species of temnospondyl amphibians (STEYER et al. 2004 pp. 197- 198).

An example of another kind of trend was contributed by PASSEY & CERLING 2002, who observed a



**Fig.3.** (a) Growth rates decreasing with age lead to a shortening of increment width. A trend curve can be deduced via regression (changed after MARCHITTO et al. 2000). (b) A similar signal in an isotope profile: Growth rates decreasing with age lead to a shortening of the annual shell width (which comprises one cycle of a seasonal isotopic variation) in spite of the constant duration of one period (after GOODWIN et al. 2003).

long-term change in the carbon isotope composition of a recent hippopotamus tooth (isotope profile shown in Fig.4). The shift of  $\delta^{13}\text{C}$  values, which are proxies for the diet composition of grazing and browsing terrestrial herbivores, proved the transition from a  $\text{C}_3$ -rich to a more  $\text{C}_4$ -rich diet (PASSEY & CERLING 2002, pp. 3231- 3232).



**Fig.4.** A trend in the carbon isotope composition of tooth enamel caused by a long term diet change. Signals underlying such a diet change can differ (e.g. environmental variation, migration or effects of ontogenesis) and thus have to be discussed using additional information (after PASSEY & CERLING 2000).

### Seasonality

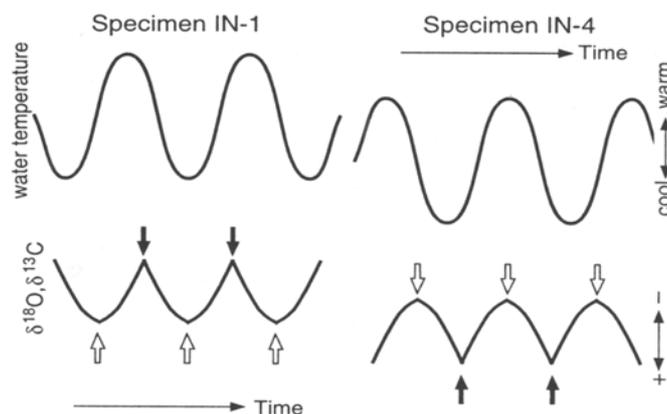
After subtracting trends from a time series, the stationary residual signal is to be analysed for renewal processes, such as seasonal climatic variation (BORRADAILE 2003, pp. 197- 199). Fig.1 (c), (d), 2, 3 (b), 4, 6, and 8 show seasonal variation in sclerochronological data sets, pointing out that seasonal climatic cycles can constitute a prominent periodical signal in both isotope profiles (Fig.1 (d), 3 (b), 10; see also SURGE et al. 2001, FERANEC 2004, STRAIGHT et al. 2004, SCHÖNE et al. 2004); and increment width/ increment number plots (Fig. 1(c), 2, 6, 8; see also Schöne et al. 2004). As demon-

strated in Fig.2 and 3 (b) seasonal variation need not to follow an exact sine curve but can show rather strong intra-annual variation. In fact the publication by SCHÖNE et al. 2002, from whom Fig.2 was taken, deals with modelling intra-annual variation of growth rates in order to deduce daily temperatures.

**Autocorrelation** and **Fourier analysis** are two of the techniques for finding periodicities. While autocorrelation measures the alikeness of a time series  $y(t)$  with itself after the elapse of a certain lag time ( $y(t+L)$ ; the correlation is close to 1 if lag time  $L$  is a dominant period), Fourier analysis transforms a wave pattern into a spectrum of sine and cosine functions whose wavelengths and amplitudes reflect the actual wave parameters occurring in the time series (techniques according to BORRADAILE 2003: pp. 205- 212, see also Fig.2 (b)). The problem with these methods is the partial inadequacy of sclerochronological data: the rather short time span reported in one skeletal element, the low density of data points in isotope profiles (see Fig.1 (d), 3 (b)) and the overall imprecision inherent in many geological renewal processes (see also BORRADAILE 2003: pp. 207- 208). However there are data sets from corals and long-living bivalves where they have been applied successfully (e.g. SCHÖNE et al. 2004: p. 215- 216).

### Growth cessations

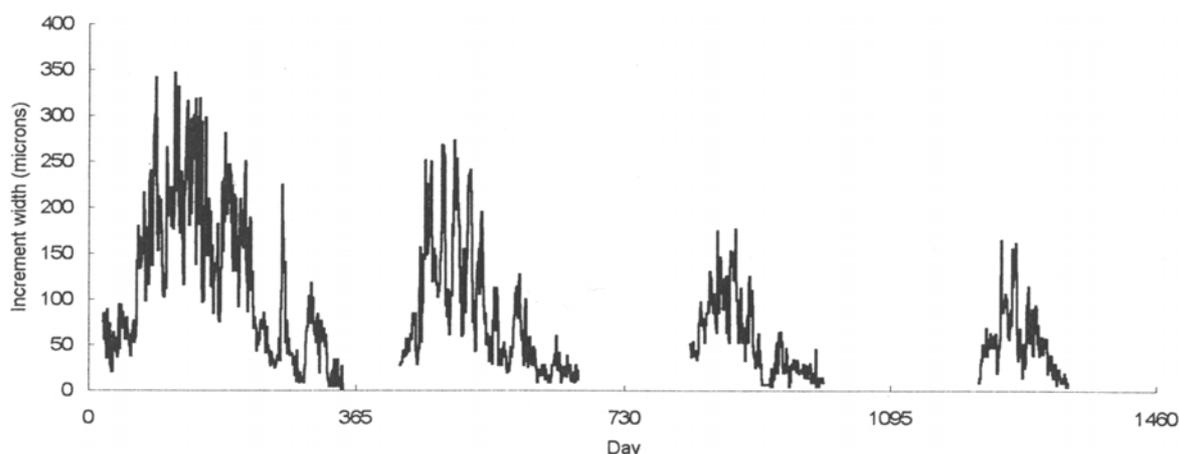
A bias of deducing average annual temperatures from bulk samples of fossil shells are seasonal growth cessations, which can be recognized in oxygen isotope profiles as sharp bends (see Fig.1 (d), 3(b) and 5). Fig.5 illustrates how a sinusoid environmental signal is preserved in a bivalve shell when summer and winter shutdowns of accretion occur as a consequence of crossing thermal thresholds which are set by the shell producer's physiology: Lower amplitudes of seasonality are measured (e.g. GOODWIN et al. 2003, WILKINSON & IVANY 2002: p.110- 112, NAKASHIMA et al. 2004).



**Fig.5.** Long (black arrow) and short (white arrow) periods of growth cessation as a consequence of crossing thermal thresholds in summer- and wintertime. Note the difference in isotope curves when average annual temperatures differ (after NAKASHIMA et al. 2004).

An additional effect results from the shortening of growth period with age, a phenomenon, which produces trends in isotope profiles as in Fig.3 (b) and leads to a decrease of increments per annum in increment width/ increment number plots as in Fig.6 (see GOODWIN et al. 2003). In some bivalve species a more drastic ontogenetic change occurs: Assumedly due to the onset of sexual maturity both iso-

tope fluctuation and annual shell growth abruptly decrease to a notable extent (according to NAKASHIMA et al. 2004, pp. 304- 306).



**Fig.6.** Increment width as of function of time: Note the ontogenetic trend of decreasing annual increment number and decreasing daily increment width (after Goodwin et al. 2003).

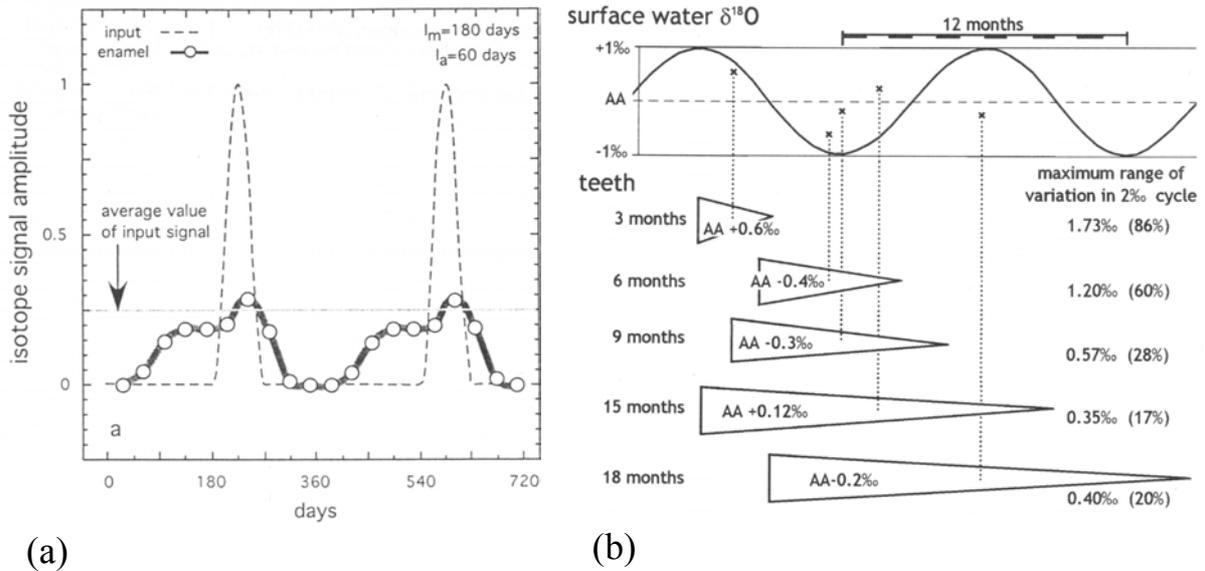
### Time-averaging and attenuation

Some authors investigated the effects of long-term enamel hardening in terrestrial vertebrates, namely PASSEY & CERLING 2002, HOPPE et al. 2004, KOHN 2004, PASSEY & CERLING 2004, and STRAIGHT et al. 2004: Isotopic compositions of enamel phosphate tend to preserve attenuated environmental signals as a consequence of continually incorporating the momentary isotope ratio over longer periods of enamel hardening. The modelled effect of this kind of time-averaging is illustrated in Fig.7 (a): High peaks are flattened and broadened (into the direction of older enamel). In order to recover the original signal PASSEY & CERLING 2002 developed a mineralization model which regards the measured  $\delta$  value of a model increment as a sum of a sequence of input  $\delta$  values which contribute with different loadings. They applied the model to isotope data from a hippopotamus tooth: The result for the  $\delta^{13}\text{C}$  curve is shown in Fig.4 (dashed line). Fig.7 (b) illustrates the attenuation of a harmonic seasonal  $\delta^{18}\text{O}$  variation for differing enamel mineralization times (after STRAIGHT et al. 2004).

### Profiles in comparison

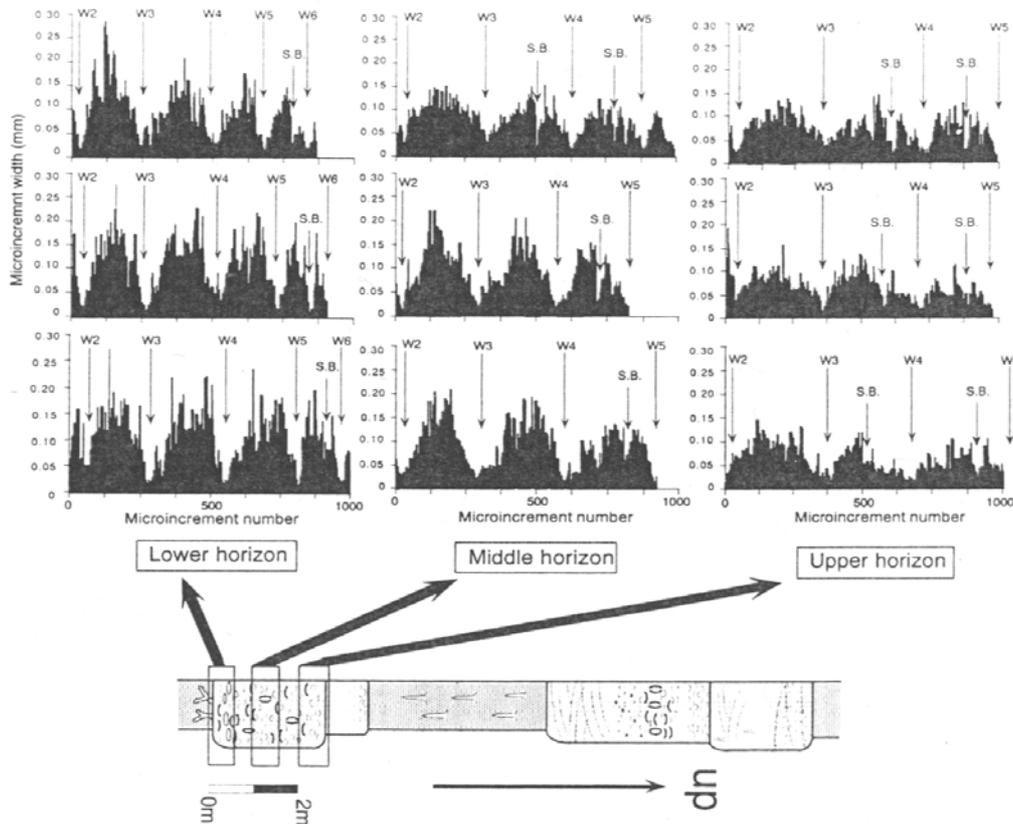
Comparing the skeletal records of several specimen greatly expands the potentials of sclerochronology: Dissimilarities in age-dependent growth of related species reveal evolutionary shifts in ontogenesis, termed **heterochronous evolution** (see e.g. IVANY et al. 2003). ERICKSON et al. 2004 proved notable differences in the growth rates of tyrannosaurid species by comparing the curves of their annual accretion.

Performing skeletal profile comparisons of specimen from successive horizons in a sedimentary profile is useful for the detection of **shifts in a species' ecological niche** and/ or its environment: Fig.8 shows in several specimen from a succession of horizons an increasing number of daily increments per annum and a decrease of increment width. According to SATO 1999 such a change of life-history traits may reflect the increase of mean annual water temperature.



**Fig.7.** (a) Modeled attenuation of an isotope input signal (dashed line) due to a long period of enamel mineralization (after PASSEY & CERLING 2004). (b) Scheme illustrating attenuation effects which are reached with differing hypothetic mineralization periods and for differing deviations from the average  $\delta$  value (AA) of an harmonic input signal (after STRAIGHT et al. 2004).

Another idea for a multi-specimen approach was published by GOODWIN et. al 2004: Fossil shells from the same accumulation site can be investigated for **spatial or temporal mixing** by analyzing quantitatively the similarity of  $\delta^{18}\text{O}$  profile parameters. The results allow to draw conclusions concer-



**Fig.8.** Increment width/ increment number plots of several individuals from successive horizons show a trend towards longer growth periods and lower daily increment widths (after SATO 1999).

ning the taphonomy of the fossil site. In a similar way the correlation between isotopic patterns of bovid teeth from a single fossil site enabled ZAZZO et al. 2004 to conclude that the species had a preferred season of birth and he found that the individuals to whom the teeth belonged had died at different times implying a long-term formation of the deposit.

Since sclerochronology may be regarded as an animal counterpart to dendrochronology MARCHITTO et al. 2000 discussed the possibility of creating a **composite chronology** by correlating the increment patterns of extremely long-living individuals of the bivalve *Arctica islandica*: They found that correlation between shell specimen was possibly high enough to allow a linkage of individual sclerochronologies into a 1000-year calendar.

### Look-out: Ideas for a comprehensive model

Though there are some recent sclerochronological analyses which combine isotope and increment data, e.g. the approaches by SCHÖNE et al. 2004, BUICK & IVANY 2004 and WATANABE et al. 2004, and many others, which employ practical comprehensive models for analysing either increment patterns (such as the one by SCHÖNE et al. 2002, see Fig.2) or isotope variation (for example the best-fit sinusoid method by WILKINSON & IVANY 2002), there is no generalized model unifying different data sources, animal groups and objectives of investigation.

A generalized sclerochronological model could begin with the assumption of an unaltered environmental signal ( $\mathbf{Env}_1$ ) which results in an accretion of a certain increment width ( $\mathbf{i}$ ) as a function of time ( $\mathbf{t}$ ) and which comprises periodical signals ( $\mathbf{p}_i$ ), a trend ( $\mathbf{tr}_1$ ) and a residual signal ( $\mathbf{res}_1$ ):

$$\mathbf{i}(\mathbf{t}) = \mathbf{Env}_1(\mathbf{t}) = \Sigma \mathbf{p}_i(\mathbf{t}) + \mathbf{tr}_1(\mathbf{t}) + \mathbf{res}_1(\mathbf{t}). \quad (1)$$

Equation (1) is to be expanded by a function of physiological alteration ( $\mathbf{alt}$ ) comprising e.g. the age-dependent growth ( $\mathbf{age}$ : can be a sigmoidal curve added to  $\mathbf{Env}_1$ ) and a cessation function ( $\mathbf{ces}$ , which can only adopt the values 0 for cessation of growth or 1 for accretion in progress):

$$\begin{aligned} \mathbf{i}(\mathbf{t}) &= \mathbf{alt}[\mathbf{Env}_1(\mathbf{t})] = \mathbf{alt}[\Sigma \mathbf{p}_i(\mathbf{t}) + \mathbf{tr}_1(\mathbf{t}) + \mathbf{res}_1(\mathbf{t})] \\ &= \mathbf{ces}(\mathbf{t}) \cdot \mathbf{age} [\mathbf{p}_i(\mathbf{t}) + \mathbf{tr}_1(\mathbf{t}) + \mathbf{res}_1(\mathbf{t})]. \end{aligned} \quad (2)$$

This model is related to isotope compositions ( $\delta$ ) in that the latter ones are no direct function of time but of shell thickness ( $\mathbf{s}$ ) which is the sum of increment widths  $\mathbf{i}$  (see also Fig.1 (b)). The isotope signal ( $\mathbf{Env}_2$ ) is not affected by physiological alteration (with the possible exception of disequilibrium precipitation in some shell-producing animals which shall not be considered in this model):

$$\begin{aligned} \delta(\mathbf{t}) &= \mathbf{Env}_2(\mathbf{s}(\mathbf{t})) \\ &= \mathbf{Env}_2(\int (\mathbf{i})d\mathbf{t})(\mathbf{t}) \\ &= [\Sigma \mathbf{p}_j(\mathbf{t}) + \mathbf{tr}_2(\mathbf{t}) + \mathbf{res}_2(\mathbf{t})](\int \mathbf{alt}[\mathbf{Env}_1(\mathbf{t})]d\mathbf{t})(\mathbf{t}). \end{aligned} \quad (3)$$

The equations (2) and (3) each can contain a number of parameters which are determined during the process of searching for the best-fitting curves. Another model assumption would be that some of the  $\mathbf{p}_i$  and  $\mathbf{p}_j$  cycles are in fact one and the same signal and thus should be synchronous.

The aim of the suggested approach is to use the additional information gained by analyzing both the isotope profile and the increment pattern more effectively and to find a close approximation to the actual environmental signals via some kind of forward modelling.

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