

Analysis of ontogenetic growth trends in two marine Antarctic bivalves *Yoldia eightsi* and *Laternula elliptica*: Implications for sclerochronology



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ABSTRACT

There is an increasing use of marine species as palaeoclimate recorders for the marine realm. These archives provide novel baseline records of past oceanographic variability in regions devoid of instrumental observations. Here we report results of a study of the ontogenetic growth pattern of two Antarctic marine bivalve molluscs: *Yoldia eightsi* and *Laternula elliptica* from West Antarctic Peninsula populations using negative exponential detrending technique and multi-taper method spectral analysis. Our data show that the growth of both *Y. eightsi* and *L. elliptica* follows a general negative exponential trend over their longevity. However, our analyses also identified an innate 9.06 year periodic endogenous growth rhythm in the growth increment pattern of *Y. eightsi* and two innate periodic growth rhythms, 5 and 6.6 year period, were found in *L. elliptica*. We hypothesize that the *Y. eightsi* endogenous growth rhythm may be related to the reallocation of energetic resources between somatic growth and gametogenesis although more biological data are required to test this hypothesis. Further work into *L. elliptica* biology is required to understand the possible meaning of the innate growth rhythms found for this species. The identification of growth rhythms is important not only for their biological significance but also in sclerochronological analysis because of their importance in developing palaeoenvironmental reconstructions.

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1. Introduction

Shell growth in marine bivalve molluscs has been studied from many different perspectives. Growth markings (rings, checks or lines) both on and in the shell provide useful information about the biology, ontogeny and environment of the living mollusc and its population (Richardson, 2001). These markings can be formed periodically (e.g. annual, tidal) or be formed as a result of a disturbance event that causes metabolic stress to the animal, hindering or even inhibiting growth (e.g. Richardson, 1988; Shumway and Parsons, 2006; Abele and Philipp, 2012). From a fisheries perspective, shell markings provide practical information about the age structure of populations necessary for sustainable exploitation of wild stocks and impacts of fishing activity (e.g. Richardson and Walker, 1991; Ramsay et al., 2000, 2001). More recently the study of long-lived bivalve molluscs to investigate past oceanographic variability over the past centuries to millennia has become one of the fastest growing fields in palaeoclimatology (e.g. Black et al., 2009; Butler et al.,

2009a; Wanamaker et al., 2012; Reynolds et al., 2013; Schöne, 2013; Mette et al., 2016).

Endogenous ontogenetic growth rhythms have been found in several marine bivalve species. For example endogenous semi-diurnal growth rhythms in shell formation have been identified in *Cerastoderma edule* (Richardson et al., 1980) and *Tapes philippinarum* (Richardson, 1988). These rhythms are characterized by the relatively weak cycles overprinted on the stronger cycles that correspond to the emersion-immersion cycles. Other species such as *Argopecten irradians*, *Notovola meridionalis* and *Patinopecten yessoensis* exhibit reduced or even interrupted shell growth during gametogenesis due to the allocation of energetic resources towards gonad and gamete production (Shumway and Parsons, 2006), although this process seems to be species specific.

This study focuses on the examination annually-resolved growth pattern of Antarctic infaunal bivalve *Yoldia eightsi* (Courthouy 1839) and compares the ontogenetic signals within the growth increment series of this species with those to another key species in Antarctic shallow water benthic ecosystems, *Laternula elliptica*. *Y. eightsi* is one of the most abundant species in Antarctic and Subantarctic waters. It is found buried in the upper 2–3 cm of soft sediment bottoms from

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depths of 4 m down to 824 m in dense but patchy communities (Davenport, 1988, 1989; Dell, 1990; Nolan and Clarke, 1993). *Y. eightsi* possesses a maximum lifespan (MLSP) of 60 years and has been reported to occur in densities up to 1500 individuals per m² (Davenport, 1989; Peck and Bullough, 1993; Nolan and Clarke, 1993). Whilst juveniles (size ≤ 10 mm, shell length) grow at approximately the same rate in summer and winter, in adults (size between 10 mm and 30 mm) winter growth declines relative to summer and it ceases in the largest individuals (Peck et al., 2000). *L. elliptica*, with a moderate MLSP of 33 years in populations around King George Island, can be found between 5 and 30 m depth in dense communities in Antarctic coastal waters, inhabiting muddy, gravelly and sandy bottoms within the upper 50 cm of the sediment (Hardy, 1972; Mercuri et al., 1998; Ahn et al., 2001; Brey et al., 2011).

The major growth increments in the shells of both species have been shown to be annually formed. In the case of *L. elliptica* this was done by the development of $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ records (Brey and Mackensen, 1997), whereas in the case of *Y. eightsi* it was demonstrated by the use of catch and release techniques (Peck and Bullough, 1993), ^{45}Ca incorporation into the shell (Nolan and Clarke, 1993) and margin incremental analysis of intra-annually collected specimens (Román-González, 2011; Román-González et al., 2015 in submission). Therefore absolutely-dated life histories can be constructed based on the analysis of the growth patterns present in their shells. This characteristic is essential in the development of sclerochronologies and scleroclimatological proxies based on both the growth patterns and isotopic composition of the shell. The process of removing the ontogenetic signal from the shell growth pattern, whilst at the same time preserving as far as possible the external environmental signal, is called detrending (Briffa and Jones, 1990; Cook et al., 1995; Cook and Peters, 1997a,b); it is therefore crucial to fully characterize the species' ontogeny to enable the growth increment series to be used as a scleroclimatological proxy. A commonly used detrending methodology in sclerochronology involves the use of negative exponential (NE) curves to remove the primary ontogenetic signal (Briffa and Jones, 1990; Cook et al., 1995; Cook and Peters, 1997a,b; Butler et al., 2010), i.e. fast growth during the first years of life followed by an exponential reduction in growth rate as the species' maximum size is approached; this signal accords with the von Bertalanffy general model (Von Bertalanffy, 1938). Regional curve standardization (RCS) is an alternative method to NE detrending. In the RCS method individual growth-increment series are aligned by ontogenetic age instead of by calendar date in order to produce a regional, non-climatic age-trend detrending function (Briffa et al., 1992; Cook et al., 1995; Esper et al., 2003; Butler et al., 2010). The advantage of using RCS over more deterministic methods such as NE detrending is that RCS provides the ability to retain a greater proportion of long-term (lower frequency) variability and remove much of variance associated with ontogeny (Briffa et al., 1992; Cook et al., 1995; Esper et al., 2003; Butler et al., 2010). However, RCS requires a greater number of crossdated specimens than NE detrending to attain the same level of confidence in the resulting indices (Briffa et al., 1992). The aim of this study is to examine the ontogenetic growth patterns present in *Y. eightsi* and *L. elliptica* by the use of the RCS and NE detrending methods. The hypotheses here analysed are i) that there will be a difference between detrending methods (NE and RCS) and ii) one of the detrending methods will provide a more suitable approach depending on each species ontogenetic growth trend. Understanding species ontogeny is especially relevant in the development of climatological archives.

2. Materials and methods

2.1. Collection and laboratory procedures

One hundred and seventy four specimens of *Y. eightsi* were live-collected in 1988 by British Antarctic Survey (BAS) scuba divers in Factory Cove, South Orkney Islands ($60^{\circ}43'\text{S}, 45^{\circ}36'\text{W}$) from ≤ 8 m depth, whilst 250 *L. elliptica* specimens were collected between 1986

and 2010, both alive and dead, by the Alfred Wegener Institute for Polar and Marine Research (AWI) from the south-western coast of King George Island from depths between 10 and 25 m (Brey et al., 2011) (Fig. 1).

For *Y. eightsi* soft tissues were removed and the shells were cleaned and air-dried. A total of 47 specimens were subsampled based on length across the maximum growth axis. The selected articulated valves were separated and one valve was embedded in polyester resin (MetPrep, KLEER-SET, 24 h curing time) and cut along the maximum growth axis using a precision saw (IsoMet 5000 saw; cf. Scourse et al., 2006). The exposed internal surface of the shell was ground using abrasive carborundum paper (P400, P1200, P2500 and P1200/4000) and polished using diamond polishing paste (3 μm Ø). The exposed cut and polished surface was etched in 0.01 M HCl for 30 min. Acetate peel replicas were prepared by adding ethyl acetate to the etched surface of the shell and immediately after rolling an acetate sheet (Agar Scientific, 35 μm in thickness) over the shell surface. Acetate peels were air-dried for 60 min and then mounted on microscope slides for identification and measurement of the growth increments under transmitted light microscopy (5 \times magnification using a Lumenera Infinity3 colour camera). *L. elliptica* samples were prepared using similar techniques as described in Brey et al. (2011).

Peels were assessed and photographed in a Color View Imaging System for *L. elliptica* and Image Pro for *Y. eightsi* under a transmitted light microscope. The annually-resolved growth increments were measured in the hinge plate for *L. elliptica* and along the shell margin for *Y. eightsi* as the peel replica technique (cf. Scourse et al., 2006) provided insufficient resolution to identify the growth increments in the hinge plate.

2.2. Statistical analysis

Growth increment series for each specimen of each species were aligned ontogenetically and averaged for each ontogenetic year and by doing so, an averaged growth per ontogenetic year class was obtained

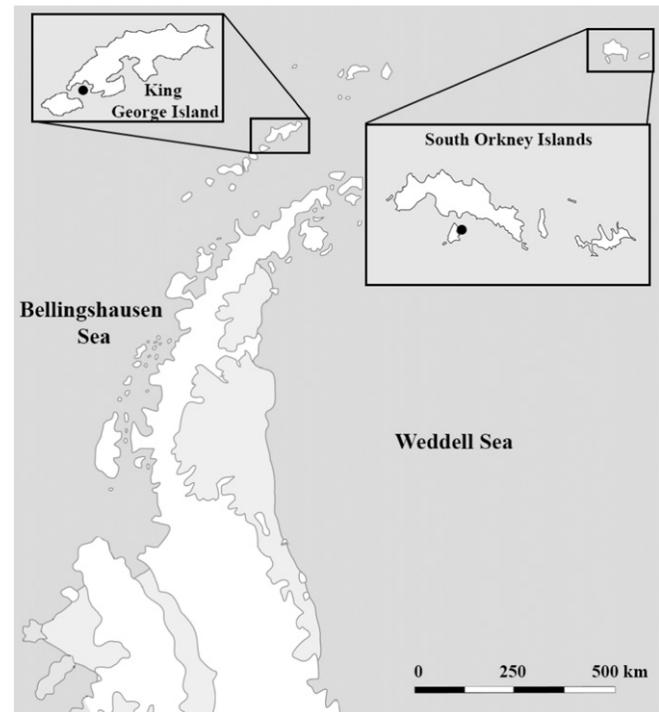


Fig. 1. Map showing the Antarctic Peninsula and two insets with the sampling locations (black dots) of Signy Research Station at the South Orkney Island ($60^{\circ}43'\text{S}, 45^{\circ}36'\text{W}$), where *Y. eightsi* samples were collected, and King George Island ($62^{\circ}02'\text{S} 58^{\circ}21'\text{W}$), where *L. elliptica* samples were collected.

independently of the corresponding calendar year (e.g. the first ontogenetic year of one specimen could have been 1970 whereas in other specimen could have been 1979). This averaged ontogenetic growth curve is traditionally termed the regional curve in the RCS literature (Cook et al., 1995; Esper et al., 2003, 2009). A source of error in the RCS technique is due to the misalignment of the individual series during the first years of growth due to missing increments, termed pith offset (Briffa et al., 1992; Cook et al., 1995; Esper et al., 2009). This means that either the number of missing increments needs to be estimated based on the size of the shell, the portion of the umbo eroded and the shape growth increment pattern or alternatively consider that there is no pith offset and assume the first measured growth increment as the first ontogenetic increment. This second option is especially viable if the analysed specimens present similar biometric characteristics and a similar degree of conservation, as this was the case of our samples no correction for pith offset was carried out. This inevitably results in the indices being somewhat biased although the potential effects on chronologies will be limited once the series are aligned by calendar date instead of ontogenetic age (Cook et al., 1995; Esper et al., 2009). Nonetheless, in order to provide a possible estimation of the error due to the lack of pith offset correction, the standard deviation and standard error of the original uncorrected series and a set of growth series with randomly introduced offsets were compared. To produce these offset series a random offset between -5 and $+5$ years was introduced to the individual specimen-specific growth increment series, then growth by ontogenetic year class was averaged (i.e. regional curve construction); this process was repeated 30 times. Finally standard deviation and standard error of the 30 offset series were calculated per year class.

The NE ontogenetic growth trend was removed by first carrying out a regression on the regional curve fitted to a NE model, which produced an empirically-calculated NE detrending curve. The NE model applied is defined by:

$$f(x) = y_0 + a * e^{-(b*x)}$$

where $f(x)$ is shell growth (μm), y_0 is the animal size at $f(\infty)$, x represents age (year), a is the intercept or size at first year of life and b is the slope or rate of change in shell growth. y_0 , a and b are empirical constants which must be calculated for each species. The NE detrending curve calculated was then subtracted from the original regional curve to generate residuals. As a result of this detrending process, the data were normalized to the population mean shell growth. Positive deviations from the mean represent enhanced population shell growth whereas negative deviations represent a decrease in population shell growth, with values close to zero representing a homeostatic balance in shell growth. It is important to note that as the time series are ontogenetically aligned rather than calendar-date aligned the environmental drivers of shell growth are not affecting the RCS curve as they are reduced to a noise signal within the ontogenetic growth.

An analysis of the standard error was carried out in order to estimate the effect upon variability of decreasing sample depth associated with increasing biological age in the RCS, created by a deficiency of ontogenetically old specimens. A cut-off point of sample depth was adopted as a compromise between series length and stable data variability. This was set at 50% reduction of the maximum standard error, for which the equivalent sample depth was 21 Y. *eightsi* and 87 L. *elliptica* specimens. Below this cut-off point data should be interpreted cautiously as the low sample depth and increased variability may lead to erroneous interpretations.

Multitaper spectral analysis (MTM) was used to analyse the growth cycles present in the residual ontogenetic growth pattern (ROGT, Mann and Lees, 1996). The program K-Spectra (v3.4.3, SpectraWorks Inc.) was set for a comparison against red noise, i.e. temporally integrated white noise, for narrowband and harmonic signals (Ghil et al., 2002). K-Spectra was configured with a resolution = 2 and number of tapers = 1. Frequencies were tested against their amplitude relative to the

estimated background noise (i.e. narrowbands) and using an F-test for periodic signals (i.e. harmonics) (Ghil et al., 2002). Robust noise background estimation and a log fit of the misfit between the robust estimated background noise and the spectral density were also tested.

3. Results

3.1. Y. *eightsi*

Y. *eightsi* specimens presented an age range between 22 and 58 years of age and shell length varied between 33.9 and 28.2 mm (Appendix, Fig. 1a). Data on population recruitment and age–shell length relationship are provided in Appendix Fig. 2a and Fig. 3a respectively and results on the lack of pith offset correction are provided in Appendix Fig. 4. Sample depth in the RCS curve started to decline above 20 years of age and only six specimens reached 45 years of age. The ontogenetic trend appeared to present a smooth decline during the first two decades of life (Fig. 2a). The resolved empirical detrending curve applied to the Y. *eightsi* specimens is: $y = 272.868 + 331.241 * \exp^{-(0.0905 * x)}$ ($R^2 = 0.572$) (Fig. 2a). The standard error analysis showed a rapid decline with increasing sample depth (Fig. 3a). A compromise of a minimum of 21 specimens, which corresponds to 37 ontogenetic years in the age-distributed analysis, was selected as a cut-off point. Interpretations of data beyond this cut-off point have to be interpreted cautiously due to the increasing influence of individual shell bias in masking the population growth pattern. An endogenous growth rhythm with a variable period and apparent cycles centred on 24, 32 and 41–42-ontogenetic years with a possible fourth cycle at 52 ontogenetic years can be observed (Fig. 4a). However the relatively high variability in the data resulting from the low number of long-

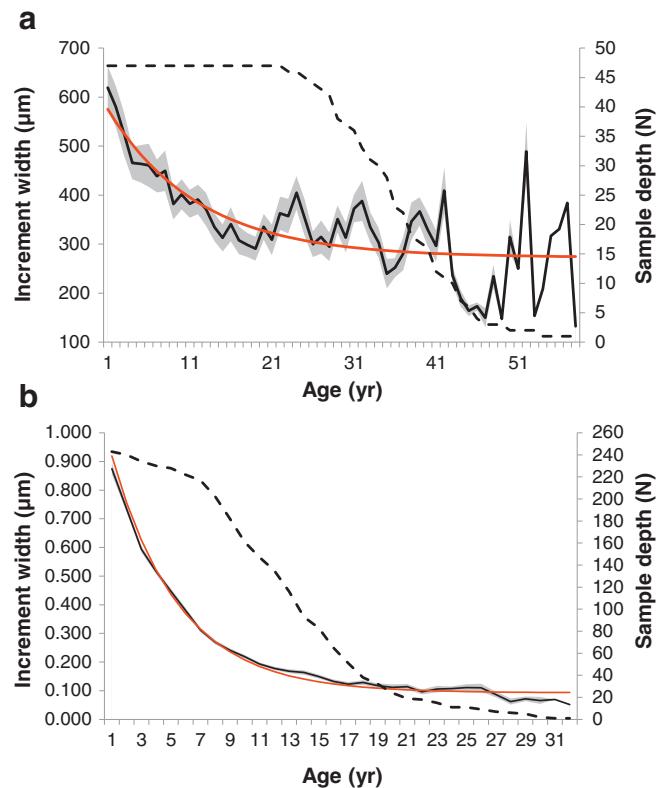


Fig. 2. Ontogenetic growth trend (solid black) of: a) 47 Y. *eightsi* and b) 244 L. *elliptica* specimens and the negative exponential detrending curves (solid red) (Y. *eightsi*: $y = 272.868 + 331.241 * \exp^{-(0.0905 * x)}$; L. *elliptica*: $y = 0.0808 + 0.965 * \exp^{-(0.1961 * x)}$). Grey-shaded area represents the \pm standard error. Dashed black line: sample depth.

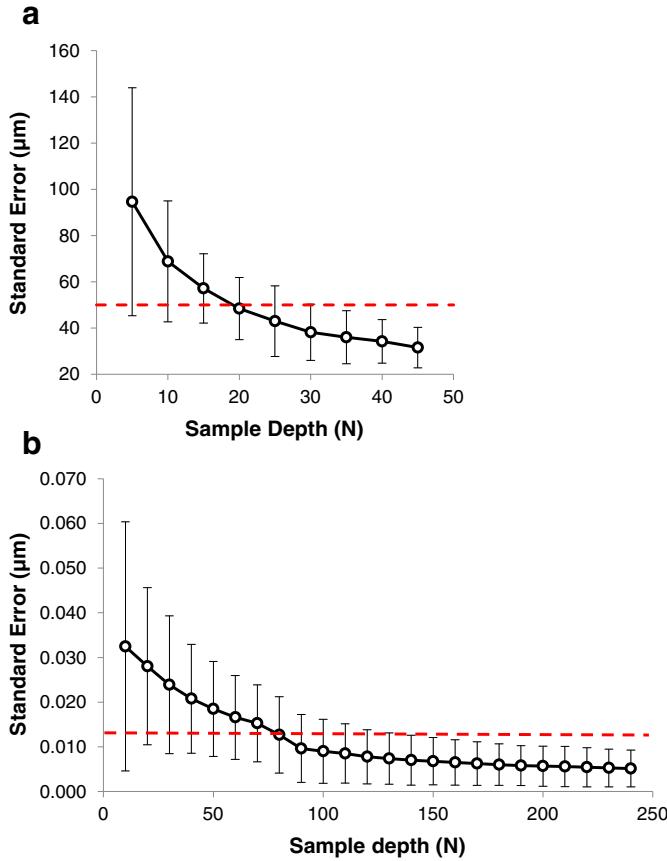


Fig. 3. Standard error analysis of: a) *Y. eightsi* and b) *L. elliptica*. The plot shows decreasing standard error as sample depth/size is increased. Red dashed line represents the sample depth cut-off point for data variability stability. Whiskers represent \pm standard deviation.

lived specimens included in the analysis makes it more difficult to confirm the forth cycle. The residuals of the ROGP after removing the NE detrending curve are shown in Fig. 4a.

The MTM analysis identified two narrowband frequencies that passed both the amplitude versus estimated background noise and the F-test: $f_{Y1} = 0.0869$ (90% significance level, SL) and $f_{Y2} = 0.4990$ (90% SL). These two frequencies correspond to periods of: $T_{Y1} = 11.5$ years and $T_{Y2} = 2$ years respectively (Appendix Fig. 5). Due to the fact that T_{Y1} does not correspond with the periodicity observed in the shell growth series (Figs. 2 and 4), a more conservative approach was considered. MTM analysis was carried out again after a 15 year high pass filter was applied to the detrended series, this removed the data variability above the 15 year threshold, and more conservative settings were used in K-Spectra (resolution = 2, number of tapers = 1). We chose the 15 year threshold as we know from observing the shell growth series (Figs. 2 and 4) that the periodicity of the growth rhythm is between nine and eleven years and a 15 year high pass filter removes much of the variability that is not relevant for this study. This analysis produced a single significant frequency of $f_{Y3} = 0.1103$ (99% SL) corresponding with $T_{Y3} = 9.06$ years (Fig. 5a), which is much more similar to what can be observed in the shell growth series.

3.2. *L. elliptica*

L. elliptica specimens ranged between 14 and 33 years of age and shell length varied between 33.8 mm and 115.8 mm (Appendix, Fig. 1b). Data on population recruitment and age–shell length relationship are provided in Appendix Fig. 2b and Fig. 3b respectively. Sample depth declined rapidly for individuals older than 10 years

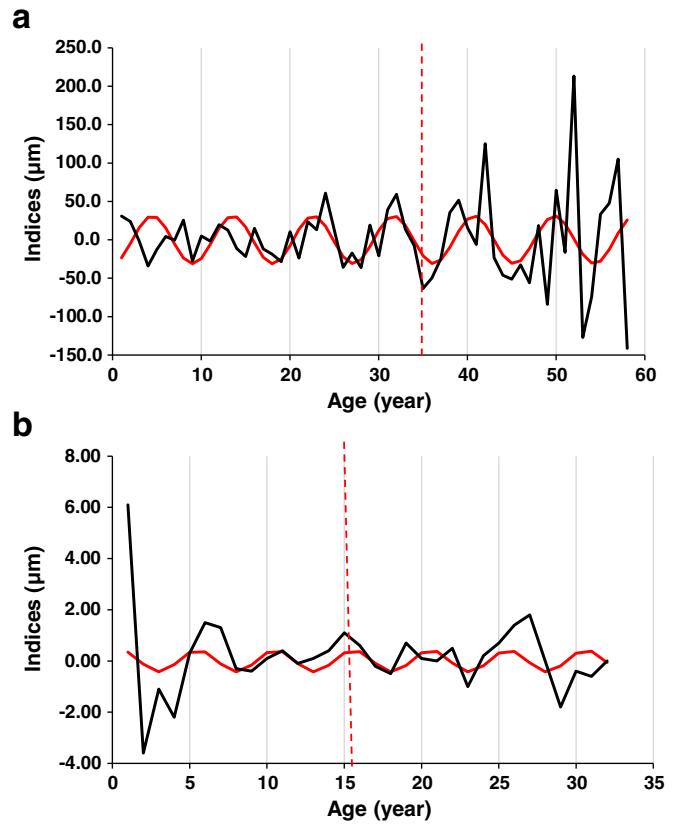


Fig. 4. Residuals of the ontogenetic growth series (thick solid black line) after the empirical detrending curve was removed for: a) *Y. eightsi* and b) *L. elliptica*. Thin solid black line represents the normalized series average. The solid red line is the MTM spectral analysis and centre weighted band pass filtered data using the significant power spectra (9.06 years in (a) and 5 years in (b)). Red dashed line represents the sample depth cut-off point for data variability stability.

(Fig. 2b) and only 11 specimens were older than 25 years. *L. elliptica* does not appear to present an endogenous shell growth rhythm apart from the negative exponential growth trend. The standard error analysis showed a rapid decline of data variability with increasing sample depth stabilising around $N = 120$ (Fig. 3b), corresponding with 14 ontogenetic years in the age-distributed analysis. The resolved empirical detrending curve applied to the *L. elliptica* specimens is: $y = 0.0808 + 0.965 * \exp(-(0.1961 * x))$ ($R^2 = 0.996$) (Fig. 2b). The ROGP after removing the NE detrending curve is shown in Fig. 4b.

The MTM analysis found two single frequencies that passed both the amplitude versus estimated background noise and the F-test: $f_{L1} = 0.0693$ (95% CI; $T_{L1} = 14.4$ years) and $f_{L2} = 0.1514$ (90% CI; $T_{L2} = 6.6$ years; Appendix Fig. 5). To allow a comparison with *Y. eightsi* results, a 15 year high pass filter was applied to the NE detrended *L. elliptica* series. MTM analysis was also repeated using K-Spectra settings of resolution = 2 and number of tapers = 1. The analysis resulted in two significant frequencies $f_{L3} = 0.1523$ (90% CI; $T_{L3} = 6.6$ years) and $f_{L4} = 0.2002$ (95% CI; $T_{L4} = 5$ years; Fig. 5b).

4. Discussion

Endogenous shell growth rhythms are innate variations of growth within an individual independent of outside environmental factors. These endogenous rhythms can be caused by cyclical innate variations in resource allocation to growth and probably reflect trade-offs between growth and other energetic life history requirements (e.g. Richardson, 1988; Shumway and Parsons, 2006; Abele and Philipp, 2012). One possible explanation for the innate growth rhythm in *Y. eightsi* may be

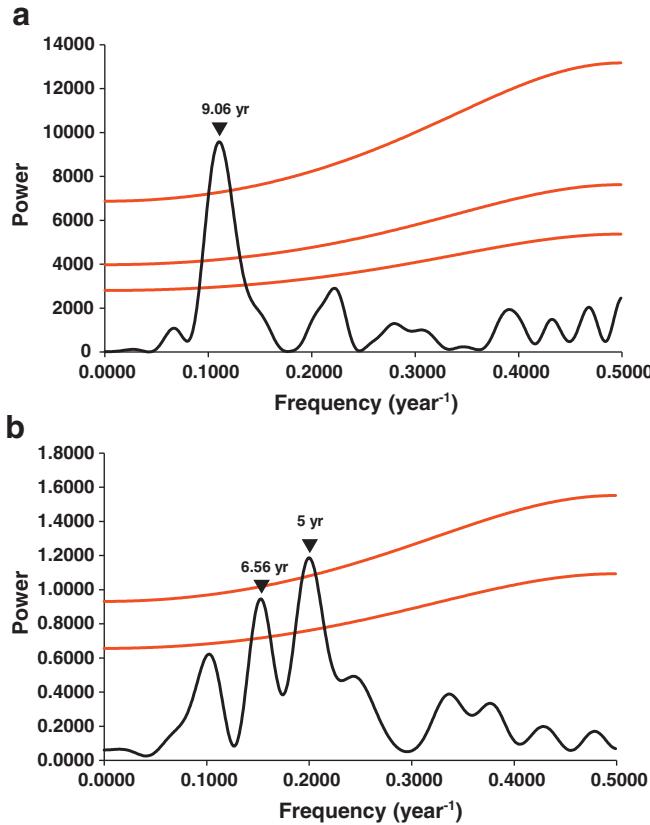


Fig. 5. Spectral analysis for a) *Y. eightsi* and b) *L. elliptica* from the multi-taper method (MTM) showing the spectral frequencies (black line) and the 90%, 95% and 99% (in the case of *Y. eightsi*) significance levels (red lines in ascending order). The period of significant frequencies is also indicated.

related to spawning events during its life history. Shell growth can be limited as a result of the preferential allocation of energy resources to developing gonads and the production of gametes (Shumway and Parsons, 2006). Spawning in *Y. eightsi* may be constrained by the available resources needed for gametogenesis and finally spawning to occur. In many species spawning occurs annually providing energy resources have been accrued. In *Y. eightsi* the build-up of sufficient resources for spawning to occur may take several years to achieve and this is manifest in innate rhythmic changes in shell growth. The beginning of this cyclicity coincides with previous studies on *Y. eightsi* growth and the onset maturity in the same sampling location (Nolan and Clarke, 1993; Peck et al., 2000). Nolan and Clarke (1993) reported the *Y. eightsi* population at Signy Island to have a wide range in age although recruitment could be sporadic in areas of high adult density. Peck et al. (2000) reported a personal observation by J.G. Colman in which animals showed gonad development at around 13 mm of shell length and they were considered fully mature at around 20 mm of shell length. Since the specimens used in our study were all over 28 mm in shell length and therefore considered fully mature, it would be interesting to select specimens of 13 mm and 20 mm in shell length and investigate the number of cycles of the ROGP present in the shell record. However, the process of resource reallocation during gametogenesis seems to be species-specific in that some species show significant shell growth during periods of active gametogenesis (e.g. Urrutia et al., 1999) whereas others (including: *A. irradians*, *N. meridionalis* and *P. yessoensis*) show none (Shumway and Parsons, 2006). Resource limitation has been suggested to be a major factor dictating marine animal adaptations and life history characteristics in Antarctica (Clarke, 1988, Clarke and Peck, 1991). This has been used to explain the seasonal decoupling of shell growth and body mass increase in the Antarctic

rhynchonellid brachiopod *Liothyrella uva* (Peck et al., 1991). As a result of the seasonally scarce and intermittent food supply, and the strong interannual variation in phytoplankton blooms, resources available for *Y. eightsi* in the Antarctic mean that it may take several years to accumulate enough resources for successful gamete production. This also relates to the hypothesis suggested by Peck et al. (2000) regarding the decoupling between shell growth and tissue mass growth in juvenile *Y. eightsi* specimens: i) shell and tissue growth were decoupled with shell growth remaining constant throughout the year and tissue growth being limited to the austral summer when energetic resources are available and ii) shell and tissue growth are not decoupled and are constant throughout the year in which there is a production of storage compounds used for tissue growth during the austral winter. If it is confirmed that the ROGP relates to gamete production, then shell and tissue growth coupling would be much more closely related than expected surpassing seasonality in the environmental parameters. The developmental strategy in which several years are needed in order to undergo gamete production successfully is not unheard of, with species such as the Arctic Woolly Bear Caterpillar (*Gynaephora groenlandica*; Wocker, 1874) requiring between 7 and 14 years of resource stocking in order to undergo metamorphosis, with long periods of diapause during the Arctic winter (Kukal et al., 1988; Morewood and Ring, 1998). As the basal energetic budget of *Y. eightsi* remains unknown it is not yet possible to test this hypothesis. In addition, little is known about its reproductive cycle, energetic budget and reproductive cycle.

Due to the short length of both the *Y. eightsi* and *L. elliptica* time series we have to interpret the results of the MTM cautiously. In order to be sure that the significant frequencies are not just due to statistical chance the significance levels (SL) have to be about $1 - (1/N)$ (Ghil et al., 2002) for *Y. eightsi* the minimum SL is 0.98 and for *L. elliptica* is 0.96. Although there is some degree of uncertainty in the spectral data mainly due to the short length of the series, the internal growth rhythm is still obvious in the raw growth increment series. The specific period at which this cyclicity occurs, although still biologically relevant, is of secondary significance in this study. The analysis carried out to determine the error associated with no pith offset correction suggests that internal growth rhythm is still significant even when no pith offset correction was applied (Appendix Fig. 4) for at least a \pm five year offset, which is what is expected in *Y. eightsi* due to umbo erosion. In the case of *Y. eightsi*, the conservative MTM analysis did find a significant frequency f_{Y3} ($T_{Y3} = 9.06$ years, 99% CI), which complies with this criterion of being at a significance level of at least 98%. On the other hand, the more flexible MTM did highlight two periodicities ($T_{Y1} = 11.5$ years and $T_{Y2} = 2$ years) at lower significance level (90% CI). Therefore the 15 year high pass filter and the more conservative settings in the MTM analysis seem to have removed some of the variability highlighted by the flexible MTM. The periodicity highlighted by the conservative MTM ($T_{Y3} = 9.06$ years) coincides with the period of the rhythm observed in the growth increment series (24, 32 and 41 and 52 ontogenetic years; Figs. 2a and 4a); this indicates that the results provided in the conservative MTM are more robust than those from the flexible MTM. Regarding the shorter periodicity $T_{Y2} = 2$ years (flexible MTM), this is probably due to high frequency variability in the data and was not even highlighted by the conservative MTM. In the case of the frequencies found in *L. elliptica*, the flexible MTM analysis highlighted two significant frequencies f_{L1} ($T_{L1} = 14.4$ years, 95% CI) and f_{L2} ($T_{L2} = 6.6$ years, 90% CI) whereas in the more conservative MTM after the 15 year high pass filter was applied the frequencies highlighted were $f_{L3} = 0.1523$ ($T_{L3} = 6.6$ years, 90% CI) and $f_{L4} = 0.2002$ ($T_{L4} = 5$ years, 95% CI). The fact that f_{L1} was not found significant in the conservative MTM is because this result is spurious as it encompasses a significant period of the entire length of the *L. elliptica* time series (i.e. 32 years). Cook et al. (1995) discussed the relationship between series length and signal detection as “the segment-length curse”, the authors stated that the maximum fluctuation detectable possible is limited in theory by the maximum length of series and in a more

pragmatic way by a third of the length of the series. This adds to our opinion that T_{L1} , which is almost half of the length of the series, in *L. elliptica* should be considered cautiously. Having both MTM analysis highlighted a periodicity around 6.6 years (f_{L2} and f_{L3}) indicates that there is a cyclicity in the data that is more difficult to observe in the increment growth series than that one found in *Y. eightsi*. The shorter periodicity found by the conservative MTM ($T_{L4} = 5$ years) was even more significant than T_{L3} ; this can indicate that two cyclicities are present in *L. elliptica* ontogeny. Alternatively, considering how similar the periods of these two frequencies (f_{L3} and f_{L4}) are, it can also mean that they are part of the same cyclicity with a period of between 5 and 6.6 years.

In terms of population dynamics these innate growth rhythms should not represent a handicap (i.e. a period of slow growth in the regional ontogenetic growth pattern, ROGP, in a year of abundant resources) if the population receives sufficient recruitment each year, which seems to be the case with the *Y. eightsi* population in Factory Cove (Peck and Bullough, 1993), although Nolan and Clarke (1993) demonstrated of sporadic *Y. eightsi* recruitment at Signy Island. In addition Peck and Bullough (1993) suggested the possibility of density-dependent control on recruitment based on the low abundance of young individuals in the presence of adults. A normally distributed population, in terms of age class, would be able to take advantage of plentiful years, with some of the individuals (those at the low growth part of the cycle) allocating resources towards gametogenesis and others (those at the rapid growth part of the cycle) allocating resources towards somatic growth.

These ontogenetic cycles are important not only for their biological relevance but also for other research fields such as the development of sclerochronological archives based on annually-resolved growth increments measured in the shells of marine bivalves (e.g. Butler et al., 2009b). Sclerochronological analysis uses growth patterns in carbonate structures of molluscs as a proxy for environmental/climatological parameters (with shell growth shown to be dependent on parameters such as food availability or water temperature (e.g. Reynolds et al., 2013; Schöne, 2013; Bušelić et al., 2015), and as a chronological template for geochemical analysis. Detrending methods are a crucial part of dendrochronological and sclerochronological studies, since they remove low frequency trends (i.e. biological and climatological) and aim to preserve the underlying high frequency external environmental component present in the growth of these organisms. The ontogenetic deviations from the mean observed in *Y. eightsi* (Fig. 4a) were not expected and are not removed by the standard use of negative exponential detrending. On the other hand *L. elliptica* shows a more conventional pattern in ROGP with minimal deviations from mean growth (Fig. 3c). Although the selection of the cut-off point for stable data variability (Fig. 4) was made as a subjective compromise between series length and data variability, this is not necessarily optimal. However, the reduced number of long-lived specimens of *Y. eightsi* is still a limiting factor.

In conclusion, data presented here shows a 9.06 year endogenous growth cycle present in individuals of the *Y. eightsi* population at Signy Island and two endogenous cycles, 5 years and 6.6 years, in *L. elliptica* specimens from King George Island. Whether this pattern is specific to the Signy Island and King George Island populations or is common to all *Y. eightsi* and *L. elliptica* populations is still to be determined. In the development of palaeo-climatological proxies, ontogenetic biological trends have to be removed whilst preserving as much as possible the low-frequency climatic variability. This study therefore presents a logical step forward in the development of more accurate climatological proxies for Antarctic coastal waters based on shell increments from Antarctic bivalves. The use of the RCS detrending method is recommended instead of the more commonly used negative exponential detrending in order to remove ontogenetic cyclicities present in the data. Further research into *Y. eightsi* and *L. elliptica* growth trends is required before the potential of this species as a climatological

proxy can be fully realized. Current warming trends in the Southern Ocean could itself pose a potential risk to *Y. eightsi* via the environmental forced disruption of the internal rhythm that may be biologically or ecologically essential.

Compliance with ethical standards

This piece of research is part of the outcome of the ongoing PhD programme of A. Román-González, which presents multiple affiliations: Cardiff University, Bangor University and British Antarctic Survey.

All applicable international, national, and/or institutional guidelines for the care and use of animals were followed.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <http://dx.doi.org/10.1016/j.palaeo.2016.05.004>.

References

- Abele, D., Philipp, E., 2012. Environmental control and control of the environment: the basis of longevity in bivalves. *Gerontology* 59 (3), 261–266. <http://dx.doi.org/10.1159/000345331>.
- Ahn, I.Y., Chung, H.S., Choi, K.S., 2001. Some ecological and physiological features of the Antarctic clam, *Laternula elliptica* (King and Broderip) in a nearshore habitat on King George Island. *Ocean Polar Res.* 23 (4), 419–424.
- Black, B.A., Copenheaver, C.A., Frank, D.C., Stuckey, M.J., Kormanyos, R.E., 2009. Multi-proxy reconstructions of northeastern Pacific sea surface temperature data from tree and Pacific geoduck. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 278, 40–47. <http://dx.doi.org/10.1016/j.palaeo.2009.04.010>.
- Brey, T., Mackensen, A., 1997. Stable isotopes prove shell growth bands in the Antarctic bivalve *Laternula elliptica* to be formed annually. *Polar Biol.* 17, 465–468. <http://dx.doi.org/10.1007/s003000050143>.
- Brey, T., Voigt, M., Jenkins, K., Ahn, I.Y., 2011. The bivalve *Laternula elliptica* at King George Island – a biological recorder of climate forcing in the West Antarctic Peninsula region. *J. Mar. Syst.* 88, 542–552. <http://dx.doi.org/10.1016/j.jmarsys.2011.07.004>.
- Briffa, K.R., Jones, P.D., 1990. Basic chronology statistics and assessment. In: Cook, E.R., Kairiukstis, L.A. (Eds.), *Cook ER Methods of Dendrochronology*. Kluwer Academic Publishers, Dordrecht, The Netherlands, pp. 137–152.
- Briffa, K.R., Jones, P.D., Bartholin, T.S., Eckstein, D., Schweingruber, F.H., Karlén, W., Zetterberg, P., Eronen, M., 1992. Fennoscandian summers from AD 500: temperature changes on short and long timescales*. *Clim. Dyn.* 7, 111–119. <http://dx.doi.org/10.1007/BF00211153>.
- Bušelić, I., Peharda, M., Reynolds, D.J., Butler, P.G., Román-González, A., Ezgeta-Balić, D., Vilibić, I., Grbec, B., Hollyman, P., Richardson, C.A., 2015. *Glycymeris bimaculata* (Poli, 1795) – a new sclerochronological archive for the Mediterranean? *J. Sea Res.* 95, 139–148. <http://dx.doi.org/10.1016/j.seares.2014.cook07.011>.
- Butler, P.G., Scourse, J.D., Richardson, C.A., Wanamaker, A.D., Bryant, C.L., Bennell, J.D., 2009a. Continuous marine radiocarbon reservoir calibration and the C-13 Suess effect in the Irish Sea: results from the first multi-centennial shell-based marine master chronology. *Earth Planet. Sci. Lett.* 279 (3–4), 230–24. <http://dx.doi.org/10.1016/j.epsl.2008.12.043>.
- Butler, P.G., Richardson, C.A., Scourse, J.D., Witbaard, R., Schöne, B.R., Fraser, N.M., Wanamaker, A.D., Bryant, C.L., Harris, I., Robertson, I., 2009b. Accurate increment identification and the spatial extent of the common signal in five *Arctica islandica* chronologies from the Fladen Ground, northern North Sea. *Paleoceanography* 24, PA2210. <http://dx.doi.org/10.1029/2008PA001715>.
- Butler, P.G., Richardson, C.A., Scourse, J.D., Wanamaker Jr., A.D., Shammon, T.M., Bennell, J.D., 2010. Marine climate in the Irish Sea: analysis of a 489-year marine master chronology derived from growth increments in the shell of the clam *Arctica islandica*. *Quat. Sci. Rev.* 29, 1614–1632. <http://dx.doi.org/10.1016/j.quascirev.2009.07.010>.
- Clarke, A., 1988. Seasonality in the Antarctic marine environment. *Comp. Biochem. Physiol. B* 90, 461–473. [http://dx.doi.org/10.1016/0305-0491\(88\)90285-4](http://dx.doi.org/10.1016/0305-0491(88)90285-4).

- Clarke, A., Peck, L.S., 1991. The physiology of polar marine zooplankton. In: Sakshaug, E., Hopkins, C., Oritsland, N. (Eds.), Proceedings of the Pro Mare Symposium on Polar Ecology, Trondheim. Polar Res Vol. 10, pp. 355–369. <http://dx.doi.org/10.1111/j.1751-8369.1991.tb00659.x>.
- Cook, E.R., Peters, K., 1997a. Calculating unbiased tree-ring indices for the study of climatic and environmental change. *The Holocene* 7, 361.
- Cook, E.R., Peters, K., 1997b. Calculating unbiased tree-ring indices for the study of climatic and environmental change. *The Holocene* 7 (3), 361–370. <http://dx.doi.org/10.1177/095968369700700314>.
- Cook, E.R., Briffa, K.R., Meko, D.M., Graybill, D.A., Funkhouser, G., 1995. The ‘segment length curse’ in long tree-ring chronology development for palaeoclimatic studies. *The Holocene* 5, 229–237. <http://dx.doi.org/10.1177/095968369500500211>.
- Davenport, J., 1988. The feeding mechanism of *Yoldia* (= *Aequiyooldia*) *eightsi* (Courthouy). *Proc. R. Soc. Lond. B Biol. Sci.* 232, 431–442. <http://dx.doi.org/10.1098/rspb.1988.0005>.
- Davenport, J., 1989. Feeding, oxygen uptake, ventilation rate and shell growth in the Antarctic protobranch bivalve mollusc *Yoldia eightsi* (Courthouy). *Proc Br Antarct Surv Spec Top Award Scheme Symp*, pp. 57–63.
- Dell, R.K., 1990. Antarctic Mollusca. *R. Soc. N. Z. Bull.* 27, 1–311.
- Esper, J., Cook, E.R., Krusic, P.J., Peters, K., Schweingruber, F.H., 2003. Tests of the RCS method for preserving low-frequency variability in long tree-ring chronologies. *Tree-ring Res.* 59 (2), 81–98.
- Esper, J., Frank, D., Büntgen, U., Kirdyanov, A., 2009. Influence of pith offset on tree-ring chronology trend. In: Kazka, R., Malik, I., Owczarek, P., Gärtner, H., Helle, G., Heinrich, I. (Eds.), (2009): TRACE – Tree Rings in Archaeology, Climatology and Ecology. Vol. 7: Proceedings of the DRENDROSYMPORIUM 2008, April 27th–90th 2008, Zakopane, Poland. GFZ Potsdam, Scientific Technical Report STR 09/03, Postdam, pp. 205–210.
- Ghil, M., Allen, M.R., Dettinger, M.D., Ide, K., Kondrashov, D., Mann, M.E., Robertson, A.W., Saunders, A., Tian, Y., Varadi, F., Yiou, P., 2002. Advanced spectral methods for climatic time series. *Rev. Geophys.* 40 (1), 1–11–41. <http://dx.doi.org/10.1029/2001RG000092>.
- Hardy, P., 1972. Biomass estimates from some shallow-water infaunal communities at Signy Island, South Orkney Island. *Br. Antarct. Surv. Bull.* 31, 93–106.
- Kukal, O., Heinrich, B., Duman, J.G., 1988. Behavioural thermoregulation in the freeze-tolerant Arctic caterpillar, *Gynaephora groenlandica*. *J. Exp. Biol.* 138, 181–193.
- Mann, M.E., Lees, J.M., 1996. Robust estimation of background noise and signal detection in climatic time series. *Clim. Chang.* 33, 409–445. <http://dx.doi.org/10.1007/BF00142586>.
- Mercuri, G., Iken, K., Ledesma, B., Dubois, R.F., 1998. On the distribution pattern and density of the Antarctic infaunal bivalve *Laternula elliptica* in Potter Cove, King George Island. *The Potter Cove Coastal Ecosystem, Antarctica. Ber Polarforsch* Vol. 299, pp. 137–143.
- Mette, M.J., Wanamaker Jr., A.D., Carroll, M.L., Ambrose Jr., W.G., Retelle, M.J., 2016. Linking large-scale climate variability with *Arctica islandica* shell growth and geochemistry in northern Norway. *Limnol. Oceanogr.* 61 (2), 748–764. <http://dx.doi.org/10.1002/lnco.10252>.
- Morewood, W.D., Ring, R.A., 1998. Revision of the life history of the High Arctic moth *Gynaephora groenlandica* (Wocke) (Lepidoptera: Lymantriidae). *Can. J. Zool.* 76, 1371–1381. <http://dx.doi.org/10.1139/z98-085>.
- Nolan, C.P., Clarke, A., 1993. Growth in the bivalve *Yoldia eightsi* at Signy Island, Antarctica, determined from internal shell increments and calcium-45 incorporation. *Mar. Biol.* 117, 243–250. <http://dx.doi.org/10.1007/BF00345669>.
- Peck, L.S., Bullough, L.W., 1993. Growth and population structure in the infaunal bivalve *Yoldia eightsi* in relation to iceberg activity at Signy Island, Antarctica. *Mar. Biol.* 117, 235–241. <http://dx.doi.org/10.1007/BF00345668>.
- Peck, L.S., Brockington, S., Brey, T., 1991. Growth and metabolism in the Antarctic brachiopod *Liothyrella uva*. *Philos. Trans. R. Soc.* 352, 851–858. <http://dx.doi.org/10.1098/rstb.1997.0065>.
- Peck, L.S., Colman, J.G., Murray, A.W.A., 2000. Growth and tissue mass cycles in the infaunal bivalve *Yoldia eightsi* at Signy Island, Antarctica. *Polar Biol.* 23, 420–428. <http://dx.doi.org/10.1007/s003000050463>.
- Ramsay, K., Kaiser, M.J., Richardson, C.A., Veale, L.O., Brand, A.R., 2000. Can shell scars on dog cockles (*Glycymeris glycymeris* L.) be used as an indicator of fishing disturbance? *J. Sea Res.* 43, 167–176. [http://dx.doi.org/10.1016/S1385-1101\(00\)00006-X](http://dx.doi.org/10.1016/S1385-1101(00)00006-X).
- Ramsay, K., Richardson, C.A., Kaiser, M.J., 2001. Causes of shell scarring in dog cockles *Glycymeris glycymeris* L. *J. Sea Res.* 45 (2), 131–139. [http://dx.doi.org/10.1016/S1385-1101\(01\)00050-8](http://dx.doi.org/10.1016/S1385-1101(01)00050-8).
- Reynolds, D.J., Butler, P.G., Williams, S.M., Scourse, J.D., Richardson, C.A., Wanamaker Jr., A.D., Austin, W.E.N., Cage, A.G., Sayer, M.D.J., 2013. A multiproxy reconstruction of Hebridean (NW Scotland) spring sea surface temperatures between AD 1805 and 2010. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 386, 275–285. <http://dx.doi.org/10.1016/j.palaeo.2013.05.029>.
- Richardson, C.A., 1988. Exogenous and endogenous rhythms of band formation in the shell of the clam *Tapes philippinarum* (Adams et Reeve, 1850). *J. Exp. Mar. Biol. Ecol.* 122, 105–126. [http://dx.doi.org/10.1016/0022-0981\(88\)90179-7](http://dx.doi.org/10.1016/0022-0981(88)90179-7).
- Richardson, C.A., 2001. Molluscs as archives of environmental change. *Oceanogr. Mar. Biol.* 39, 103–164.
- Richardson, C.A., Walker, P., 1991. The age structure of a population of the hard-shell clam *Mercenaria mercenaria* from Southampton Water, England, derived from acetate peel replicas of shell sections. *ICES J. Mar. Sci.* 48, 229–236.
- Richardson, C.A., Crisp, D.J., Runham, N.W., 1980. An endogenous rhythm in shell deposition in *Cerastoderma edule*. *J. Mar. Biol. Assoc. U. K.* 60, 991–1004.
- Román-González, A., 2011. Climate Change in the Antarctic: the Search for Sclerochronological Proxies (Dissertation) Bangor University, Bangor, North Wales, United Kingdom.
- Román-González, A., Scourse, J.D., Richardson, C.A., Peck, L.S., Bentley, M.J., Butler, P.G., 2015. In Submission: A Sclerochronological Proxy for Antarctic Coastal Waters Based on the Marine Bivalve *Yoldia eightsi* (Jay, 1839) from the South Orkney Islands.
- Schöne, B.R., 2013. *Arctica islandica* (Bivalvia): a unique paleoenvironmental archive of the northern North Atlantic Ocean. *Glob. Planet. Chang.* 111, 199–225. <http://dx.doi.org/10.1016/j.gloplacha.2013.09.013>.
- Scourse, J., Richardson, C., Forsythe, G., Harris, I., Heinemeier, J., Fraser, N., Briffa, K., Jones, P., 2006. First cross-matched floating chronology from the marine fossil record: data from growth lines of the long-lived bivalve mollusc *Arctica islandica*. *The Holocene* 16 (7), 967–974. <http://dx.doi.org/10.1177/0959683606h1987rp>.
- Shumway, S.E., Parsons, G.J., 2006. *Scallops Biology, Ecology, and Aquaculture*. Elsevier, Amsterdam; Boston 9780080480770.
- Urrutia, M.B., Ibarrola, I., Iglesias, J.I.P., Navarro, E., 1999. Energetics of growth and reproduction in a high-tidal population of the clam *Ruditapes decussatus* from Urdaibai Estuary (Basque Country, N. Spain). *J. Sea Res.* 42, 35–48. [http://dx.doi.org/10.1016/S1385-1101\(99\)00017-9](http://dx.doi.org/10.1016/S1385-1101(99)00017-9).
- Von Bertalanffy, L., 1938. A quantitative theory of organic growth (inquiries on growth laws. II). *Hum. Biol.* 10, 181–213.
- Wanamaker Jr., A.D., Butler, P.G., Scourse, J.D., Heinemeier, J., Eiriksson, J., Knudsen, K.L., Richardson, C.A., 2012. Surface changes in the North Atlantic meridional overturning circulation during the last millennium. *Nat. Commun.* 3, 899. <http://dx.doi.org/10.1038/ncomms1901>.