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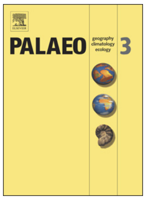

Analysis of ontogenetic growth trends in two marine Antarctic bivalves *Yoldia eightsi* and *Laternula elliptica*: Implications for sclerochronology

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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.

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 m^2 (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 δ^{18}O and δ^{13}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°43′S, 45°36′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× 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. eight*si 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

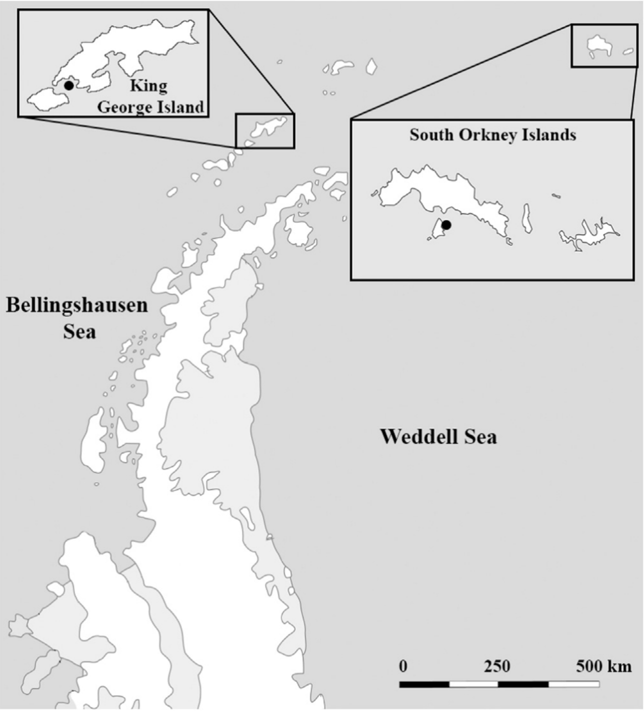

Fig. 1. Map showing the Antarctic Peninsula and two insets with the sampling locations (black dots) of Signy Research Station at the South Orkney Island (60°43′S, 45°36′W), where *Y. eightsi* samples were collected, and King George Island (62°02′S 58°21′W), where *L. elliptica* samples were collected.

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