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# Growth anomalies in *Protothaca thaca* (Mollusca, Veneridae) shells as markers of ENSO conditions

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**ABSTRACT:** Environmental variations can be recorded in bivalve shells, and this proxy information can be crucial for paleoceanographic studies in regions where other proxies (e.g. corals) are absent. We present the first sclerochronological study of *Protothaca thaca* (Mollusca, Veneridae), a common upper subtidal bivalve, characterized by a high temperature tolerance, from the SE Pacific Ocean (12 to 45° S). *P. thaca* is present in archaeological deposits and Holocene marine terraces, making it a potentially useful paleo-environmental recorder, particularly in respect to El Niño Southern Oscillation (ENSO) reconstructions. The sclerochronological analysis of recent *P. thaca* shells from Peru and Chile was done by microscopy of thin sections and acetate peel replicates; it shows that a clear 'summer check' (SC) is formed in the shell when sea surface temperature (SST) exceeds 18°C for several weeks. Under La Niña conditions in summer, SCs can be absent due to lower SST and enhanced productivity. During the strong 1997–1998 El Niño, long-lasting high summer SST produced an SC >520 µm wide. The relative width of SC on fossil shells may thus be an indicator of paleo-ENSO events. Our sclerochronological analysis has established a temporal framework in *P. thaca* shells, providing precise time-series analytical profiles, which is a prerequisite for future calibration of geochemical proxies.

**KEY WORDS:** Bivalve · *Protothaca thaca* · Peru · Chile · Sclerochronology · El Niño Southern Oscillation

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## 1. INTRODUCTION

Bivalve shell growth is a step by step process. Growth layers are successively added at the edge and inner surface of the growing shell. The thickness of the increments and the frequency at which they are added are governed not only by animal physiology (e.g. reproduction, ontogeny), but also by environmental variations (e.g. tidal cycle, water temperature, storm events, food availability). The study of shell microstructure periodicities, sclerochronology, can thus give information on both life history and environmental variations that occurred throughout the lifetime of the animal (reviews by Lutz & Rhoads 1980, Richardson 2001). Yearly to daily periodicities can be observed in the succession of shell increments. Growth rings (also named 'checks' or 'breaks') are formed in the shell when growth is reduced or stopped during temperature extremes, e.g. in

summer and/or winter (e.g. Jones & Quitmyer 1996). The growth rings can be counted to deduce the lifespan of fossil and living specimens (Jones 1983 and references therein). Many bivalve species deposit micro-growth increments, usually named 'daily growth increments'; their width and number per year generally decreases with ontogeny (Hall et al. 1974, Jones 1981, Tanabe 1988). Formation of daily increments and some of their variability in width are related to tidal rhythms (e.g. Richardson 2001, Schöne et al. 2002a, 2003) and temperature (Kennish & Olsson 1975, Jones 1981, Goodwin et al. 2001, Schöne et al. 2005). Schöne et al. (2002b) used age-detrending methods and Fourier filters to remove the ontogenic trend and tidal cycles from daily growth data in *Chione cortezi* and extract a sea surface temperature (SST) signal.

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The SE Pacific region is of particular importance for understanding the El Niño phenomenon. El Niño events along the Peruvian and north Chilean coasts result in a considerable increase in SST; e.g. during the very strong 1982–1983 El Niño, SST rose by 10°C during several weeks (Arntz 1986). At present, marine sediment records off Peru and Chile do not provide sufficient resolution to document such short term climatic events. Corals could provide high-resolution proxy records of El Niño occurrences, but in the cool waters of the Humboldt Current there are no coral species that can be used for paleo-environmental reconstructions.

Mollusc shells could supply a proxy record of El Niño events. The presence of easily readable shell growth anomalies may provide evidence of ENSO related events for specific Holocene periods. Bivalve shells (*Chione subrugosa* and *Trachycardium procerum*) from Peru have recorded the 1982–1983 El Niño both in the shell microstructure (growth anomaly) and in the shell isotopic signature (Rollins et al. 1987, Perrier et al. 1994). Similar features have been observed in fossil *T. procerum* shells and this is interpreted as reflecting El Niño occurrences during the Mid-Holocene period (Perrier et al. 1994). Carré et al. (2005) determined  $\delta^{18}\text{O}$  in archaeological *Mesodesma donacium* shells to study early Holocene El Niño events. However, the use of *M. donacium* shells as archive of El Niño event occurrences is problematic, since this species is particularly sensitive to temperature increases. *M. donacium* populations suffered high mortality during the 1982–1983 and 1997–1998 El Niño events (Arntz & Tarazona 1990, Barriga & Quiroy 2002).

*Protothaca thaca* may be a more appropriate environmental and paleo-environmental recorder, because its high temperature tolerance (Urban 1994) makes it one of the most resistant species to the effects of El Niño events in the SE Pacific region. A study of *P. thaca* shell geochemistry (El Jouhari et al. 2001) indicates that the 1997–1998 El Niño was registered in the stable oxygen isotope composition of the carbonate. Moreover, *P. thaca* is found in Holocene archaeological deposits of Peru (Reitz 1988, Moore 1991, Perrier et al. 1994) and in Pleistocene marine terrace units in southern Peru and Chile (Ortlieb et al. 1992, 1996). *P. thaca* may thus potentially provide useful palaeoceanographic and paleoclimatic data along the coast of the East Pacific Ocean, south of central Peru. However, unlike other Veneridae species, e.g. *Mercenaria mercenaria* (Jones & Quitmyer 1996), *Artica islandica* (Witbaard 1997, Buick & Ivany 2004), *Chione* sp. (Schöne et al. 2002a), and *Protothaca staminea* (Takesue & van Geen 2004), *P. thaca* shells do not have conspicuous growth patterns. Therefore, a study of *P. thaca* was undertaken to determine if temporal and environmental information can be extracted from growth patterns

in its shell. This study aimed to provide the sclerochronological framework for future geochemical analysis oriented towards a validation of *P. thaca* for paleo-El Niño reconstructions.

This is the first sclerochronological analysis of the Peruvian-Chilean *Protothaca thaca* shell. It is based on (1) microscopic observations on thin sections and acetate peel replicates and (2) correlation between growth increment widths and water temperature recorded during growth. Our study shows that a 'summer check' (SC) is formed in the shell when SST is >18°C for >3 wk. Under La Niña summer conditions, SCs can be absent. Finally, the widest SCs are related to the strong 1997–1998 El Niño, emphasising the potential of *P. thaca* shell as recorder of past ENSO events.

## 2. MATERIALS AND METHODS

### 2.1. Samples

*Protothaca thaca* is a subtidal marine bivalve (Veneridae) that lives up to an age of 7 yr in shallow water depth (maximum 20 m), just below the surface of sandy substrates (Urban 1994, Urban & Campos 1994). It has a wide distribution range (12 to 45°S) and lives in water temperatures between 5 and 26°C (Urban 1994). Urban (1994) showed that *P. thaca* survives El Niño events, thanks to its high lethal temperature threshold (LT50 = 27.9°C) and high tolerance to rapid temperature increases (<50 % mortality in the case of an abrupt increase by 14°C). *P. thaca* specimens were studied at 2 sites: Pocoma, Peru (17°25'S, 71°22'W) and El Lenguado, Chile (23°46'S, 70°28'W) (Fig. 1A).

The 4 Pocoma shells studied belong to a population for which the growth of individuals was followed from at least May 2003 to September 2003; 85 individuals were put in net-bags fixed to the bottom *in situ*. Once per month, the *Protothaca thaca* specimens were removed and immersed for 3 h in a bucket with seawater and 100 ppm of calcein; 2 specimens were taken after each marking, while the others were replaced *in situ* until the next marking. Then 4 specimens, 2 specimens with an initial marking from May 15, 2003 (PC77, PC134) and 2 with an initial marking from July 16, 2003 (PC50, PC127) were used for growth increment measurements. These specimens were sacrificed on 16 July 2003 (PC77), 14 August 2003 (PC50) and 21 September 2003 (PC127), (PC134). Daily SST data were obtained from the Ilo Station of the Instituto del Mar del Perú (IMARPE), which is near the Pocoma site (Fig. 1A).

Shells of dead *Protothaca thaca* were collected on the beach at El Lenguado in December 2000. Only specimens with articulated valves, i.e. from individuals

that had died only a few days earlier, were used. From this sample, 6 specimens were randomly selected for the study of shell growth anomalies.

## 2.2. Sclerochronological methodology

The *Protothaca thaca* shell consists of 2 aragonitic layers, an inner homogeneous layer and an outer prismatic layer, where the growth increments are largest and can be more easily observed (Fig. 1B). Growth marks were identified by macroscopic observation of the shell surface, light microscopy and scanning electron microscopy (SEM). Shells were cut along their maximum growth axis using a high precision diamond saw (Isomet 5000 Buehler). The 4 Pocoma shell sections were polished and acetate peel replicates were made after etching with 10% acetic acid for 30 s. Microstructural growth units and growth anomalies were identified by combining diffused and transmitted light microscopic observations of thin sections and acetate peels, and SEM imaging (Philips 505). The width of each thinnest growth increment was measured on the acetate peel replicates of the 4 Pocoma samples under an optical microscope with a precision of 5  $\mu\text{m}$ . One valve of each of the 6 El Lenguado specimens was cut as stated above and the

thickness of the major growth anomalies was measured on thick polished sections with a precision of 5  $\mu\text{m}$  under an optical microscope with diffused light.

## 3. RESULTS

### 3.1. Microgrowth increments

The thinnest clearly bounded growth increments have a width of 10 to 120  $\mu\text{m}$  and are limited by a 3 to 5  $\mu\text{m}$  thick line of organic matter (black in transmitted light, etch-resistant) (Fig. 1C). These microgrowth increments are thinner in the last stages of life of the individual, reflecting the growth rate decrease related to ontogeny (see Fig. 3). Increment width variations at the margin of sample PC127 showed cycles varying from 6 to 14 increments. The beginning/end of each cycle are characterized by a small groove on the surface of the shell, as reported in other bivalves (e.g. *Chione cortezi*: Schöne et al. 2002a); this cyclic pattern is thought to coincide with tidal cycles. As tidal mode here is semidiurnal with a diurnal inequality (see Dirección de Hidrografía y Navegación; <http://www.dhn.mil.pe>), the microgrowth increments defined above can thus be interpreted as 'daily' growth increments.

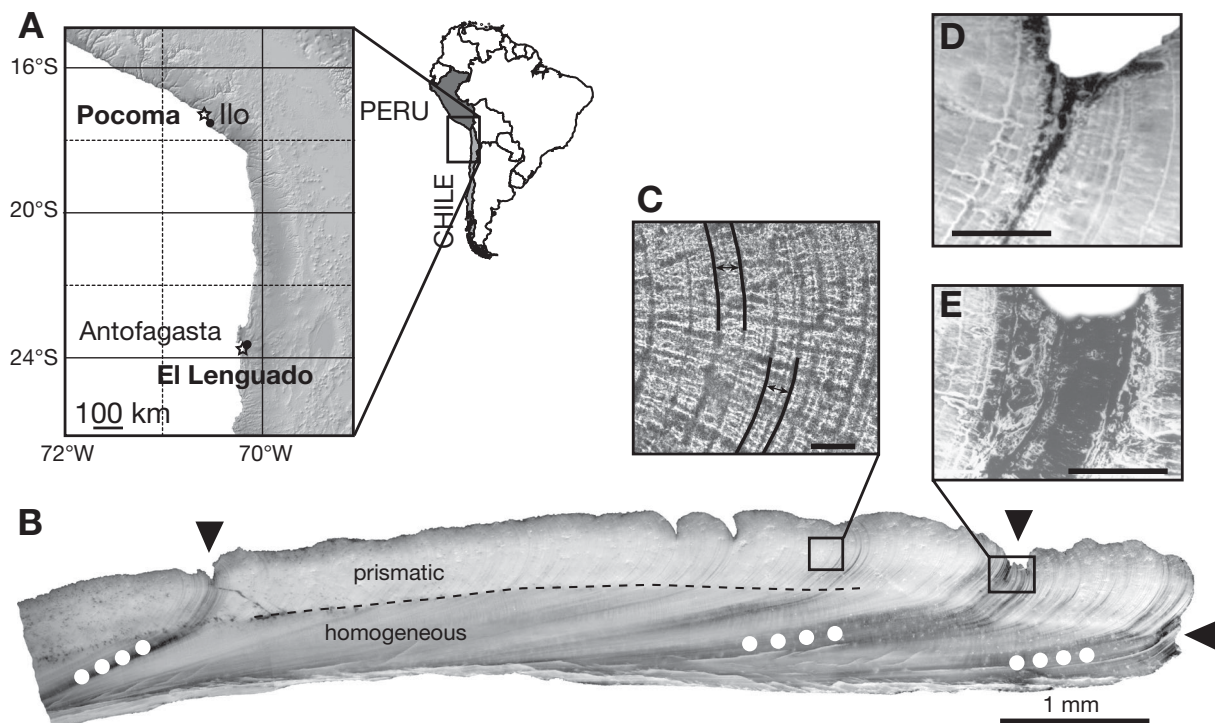


Fig. 1. (A) Sampling sites (stars). (B–E) *Protothaca thaca*. Structures and microstructures of the aragonitic shell. (B) Major growth anomalies (MGA); black triangles: surface grooves; white dotted lines: thick organic-rich layers (polished thick section, diffused light). (C) Daily growth increments. Arrows: growth rings of 1 day (acetate peel replicate, transmitted light). (D) Sporadic growth anomaly (retro-diffused electron SEM image). (E) MGA (retro-diffused electron SEM image). Scale bars for (C)–(E)= 100  $\mu\text{m}$

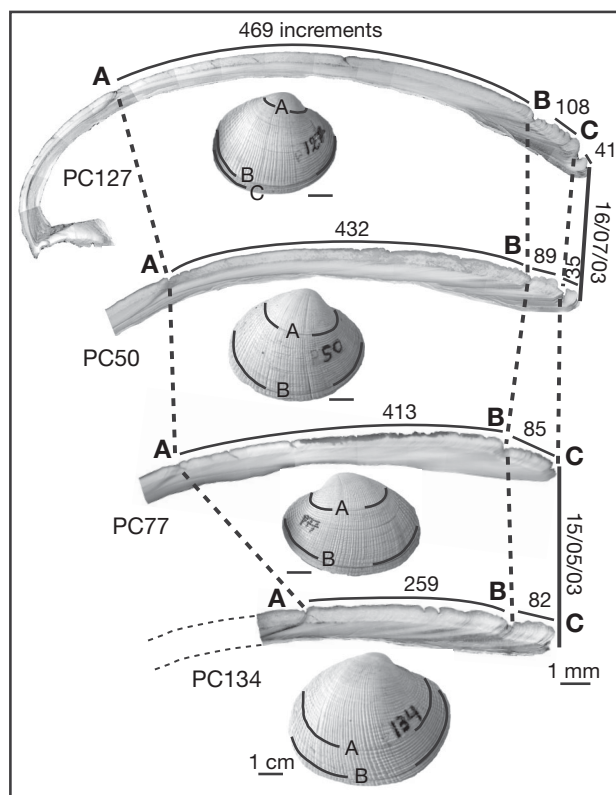


Fig. 2. *Protothaca thaca*. Identification of major growth anomalies (MGAs) in 4 shells (identification nos. given) from Pocoma (Peru). A, B and C are MGAs on valves (scale bar = 1 cm) and on thick polish sections (diffused light; scale bar = 1 mm); no. of daily growth increment between MGAs given above each section. Solid vertical lines and dates (right): end of growth. MGAs connected by dotted lines between shells

### 3.2. Major growth anomalies (MGAs)

Growth anomalies in *Protothaca thaca* shells consist of an organic-rich layer associated with a depression on the surface of the shell (Fig. 1B). Relatively thin growth anomalies, 5 to 40  $\mu\text{m}$  thick (Fig. 1D), which are irregularly distributed in the shell are interpreted as short non-periodic stress events like storms, predation attempts, etc. These irregular growth anomalies might also be related to spawning events, as *P. thaca* reproduction can occur in various months of the year (Henríquez et al. 1981).

Major growth anomalies (MGAs) are characterized by organic-rich layers of 50 to 400  $\mu\text{m}$  thickness and a more conspicuous groove at the surface of the shell (Figs. 1B & 2). The microgrowth increment width is drastically reduced in MGAs (Fig. 3). We observed 3 MGAs (denoted A, B and C in Fig. 2) in *P. thaca* shells from Pocoma. The relative position of MGAs A and B in the shells depends on the age of the individual: in young individuals with an elevated growth rate (e.g.

PC127; Fig. 2, top), the distance between A and B is greater than in older individuals (e.g. PC134; Fig. 2, bottom). If MGAs A and B (and, by extension, C) represent records of the same events in the Pocoma population, the age dependence of the position of A and B should be reproducible. The distances umbo–A and A–B were measured on the surface of 21 Pocoma shells and these age-dependent distances were highly correlated ( $R^2 = 0.94$ ). Pocoma *P. thaca* of different ages have thus recorded the same events at different periods in their life. MGA C is located at the ventral margin of Shells PC77 and PC134, which can be dated precisely thanks to the staining experiment. The calcein baths were highly stressful for the specimens, and lengthwise growth ceased after the first marking. Thus, for the PC77 and PC134 samples, the end of MGA C is recorded at around 15 May 2003. The position of MGA C in PC127 and PC50 is determined by intercomparison of the shells and shell sections (Fig. 2).

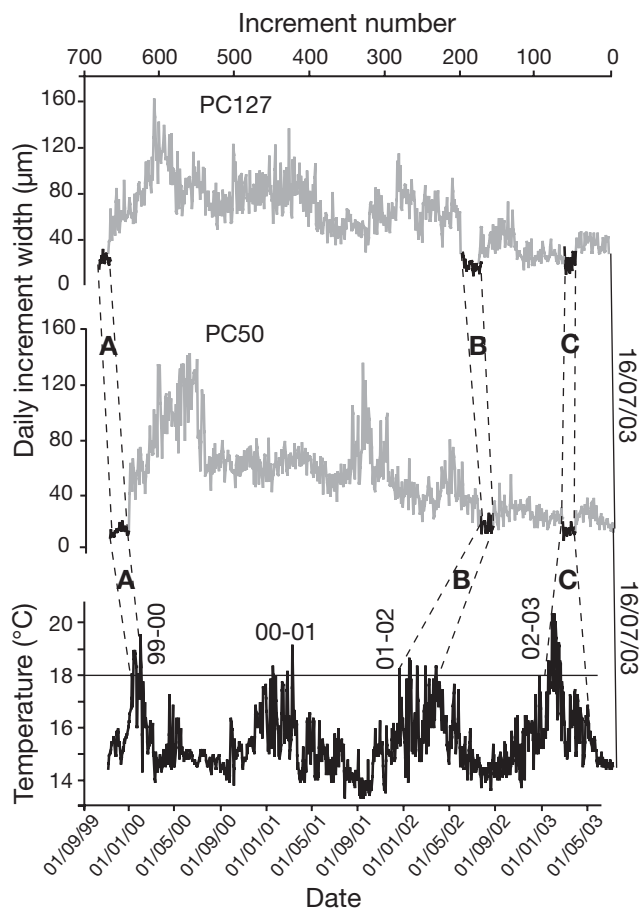


Fig. 3. Relation between recorded sea surface temperature (SST, bottom panel) and daily growth increment width variations in *Protothaca thaca* shells PC127 and PC50. Major growth anomalies A, B and C represented by small daily increments ('summer checks') are in black and related to the corresponding high summer SSTs. Solid lines at right: end of growth



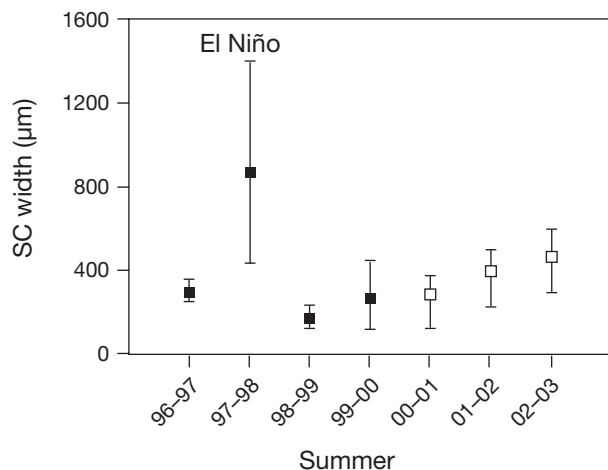


Fig. 4. *Protothaca thaca*. Means, minima and maxima of 'summer check' (SC) widths in shells (mean and range;  $n = 42$  SC). Filled squares: El Lenguado (Chile) ( $N = 6$ ). Empty squares: Pocoma (Peru) ( $N = 7$ )

To analyze which events induced the formation of MGA in the *Protothaca thaca* shells, microgrowth increment width variations were correlated with SST (Fig. 3); similar patterns were observed in PC77 and PC134 (not shown). MGA C occurred before mid-May 2003 (austral autumn) and <50 increments were counted between MGA C and the date on which the specimens were sacrificed. MGA C thus corresponds to the austral summer 2002–2003. The MGA that occurred before MGA C, i.e. MGA B, is assigned to the austral summer 2001–2002. The number of 'daily' growth increments between A and B greatly exceeds the number of days in 1 year (Fig. 2). MGA A is therefore interpreted to correspond to summer 1999–2000 (Fig. 3). The overall decrease in growth rate and the decrease in the number of increments counted from summer 2000 to the date of sacrifice are in agreement with ontogenic development. The summers 1999–2000, 2001–2002 and 2002–2003 were those for which SST exceeded  $18^{\circ}\text{C}$  either almost continuously for >3 wk (1999–2000, 2002–2003) or repeatedly over 3 mo (2001–2002). When these SST conditions are not reached, no MGA is observed in the *P. thaca* shells (summer 2000–2001 between A and B). MGA were called 'summer check' (SC).

### 3.3. MGAs and El Niño

In the 6 El Lenguado specimens of *Protothaca thaca* collected in December 2000, 4 MGA were identified and assigned to the summers between 1996–1997 and 1999–2000. The MGA attributed to the strong 1997–1998 El Niño event was characterized in most of the

shells by an alternation of normal growth (light-coloured layers) and reduced growth (organic-rich layer), rather than by a continuous thick organic-rich layer. A total of 42 SCs measured in 13 specimens, including those from Pocoma, showed that the strong 1997–1998 El Niño event led not only to the widest SC of the population (mean width  $868\text{ }\mu\text{m}$ ; significantly wider than SC from other years,  $p < 0.001$ ) but also to the most varied individual response (Fig. 4).

## 4. DISCUSSION

### 4.1. Environmental significance of MGAs

Shell growth reduction or cessation is linked not only to specific SST conditions, but rather to a combination of environmental changes, including salinity and reduced food availability. In addition to other environmental and physiological parameters, food availability is one of the most important factors that controls molluscan shell growth rate (Witbaard 1996, Sato 1997, Schöne et al. 2005). The absence of SC—showing 'normal' summer growth—may indicate not only anomalously reduced SST (La Niña period), but also favourable environmental conditions. La Niña events generally lead to an increase in primary production, as reported for the 1996–1997 and 1998–1999 periods (Thomas et al. 2001, Carr et al. 2002). We surmise that the La Niña 2000–2001 summer induced both lower SST (see Fig. 3) and higher productivity.

### 4.2. MGAs and El Niño

Several studies showed that the strong 1997–1998 El Niño event along the Peruvian-Chilean coast was characterized by the occurrence of 2 El Niño maxima (June–July 1997 and December 1997–January 1998) separated by a relaxation period (Blanco et al. 2001, Carr et al. 2002, Escribano et al. 2004). During the El Niño pulses, SST, salinity and oxygenation of the water column increased (Escribano et al. 2004). The spatial pattern and concentrations of chlorophyll closely followed those of the SST, with low values during El Niño peaks and high values during the relaxation period (Thomas et al. 2001, Carr et al. 2002, Escribano et al. 2004). This succession of environmental conditions that were either potentially unfavourable (El Niño peaks with high SST and low primary production) or favourable (relaxation period with lower SST and highest productivity) during the 1997–1998 El Niño event may explain the specific microstructural pattern of the *Protothaca thaca* El Niño SC as well as the variable individual response observed.

## 5. CONCLUSIONS

The sclerochronological analysis of recent Peruvian-Chilean *Protothaca thaca* indicates that the width variations in microgrowth increments may be related to the tidal cycle. Two types of growth anomalies were evidenced. The finest growth anomalies were interpreted as temporary stress events, while MGAs were attributed to anomalous summer environmental conditions, e.g. high SST over a longer time period, and named 'summer check'. During La Niña events, reduced summer SST and enhanced primary productivity lead to the absence of SC formation. The lifespan of bivalves (i.e. the time span of environmental variations registered) established from counting of MGAs should be used with caution, particularly in fossil specimens, as the environmental conditions which determine the formation of annual growth rings must be identified for each species and environment. In specimens collected in 2000, long-lasting high SST and associated environmental changes related to the 1997–1998 El Niño event led to the widest SC. We conclude that SC widths in fossil *P. thaca* shells are a proxy of paleo-ENSO events.

More work is needed to define the environmental conditions that induce SC formation in *Protothaca thaca* shells, particularly with regard to primary production. This study provides a basis for the interpretation of *P. thaca* shell microstructures, an essential step towards the calibration of proxies in modern shells. Geochemical analyses of shells, which are currently under way, should provide new clues to identify and evaluate the relative importance of the different environmental parameters responsible for MGA formation in *P. thaca* shells.

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## LITERATURE CITED

- Arntz WE (1986) The two faces of El Niño 1982–1983. *Meeresforsch* 31:1–46
- Arntz WE, Tarazona J (1990) Effects of El Niño 1982–83 on benthos, fish and fisheries off the South American Pacific coast. In: Glynn PW (ed) *Global ecological consequences of the 1982–83 El Niño-Southern Oscillation*. Elsevier, Amsterdam, p 323–360
- Barriga ER, Quiroy MR (2002) Impacts of El Niño and La Niña events on the populations of clams (*Mesodesma donacium*, Lamarck 1818) along the Southern Peruvian coast. *Investig Mar* 30:137–135
- Blanco JL, Thomas AC, Carr ME, Strub PT (2001) Seasonal climatology of hydrographic conditions in the upwelling region off northern Chile. *J Geophys Res* 106:11454–11467 (2000JC000540)
- Buick DP, Ivany LC (2004) 100 years in the dark: extreme longevity of Eocene bivalves from Antarctica. *Geology* 32:921–924
- Carr ME, Strub PT, Thomas AC, Blanco JL (2002) Evolution of 1996–1999 La Niña and El Niño conditions off the western coast of South America: a remote sensing perspective. *J Geophys Res C* 107:3236, doi:3210.1029/2001JC001183
- Carré M, Bentaleb I, Fontugne M, Lavallée D (2005) Strong El Niño events during the early Holocene: stable isotope evidence from Peruvian sea shells. *Holocene* 15:42–47
- El Jouhari L, Pierre C, Saliège J, Ortlieb L, Soler P (2001) Calibration of the oxygen isotopic composition of bivalve shells (*Protothaca thaca*, Veneridae) from the northern Chile coast. *EOS Trans Am Geophys Union, Fall Meet Suppl* 82, PP11A-0449
- Escribano R, Daneri G, Farias L, Gallardo VA and 7 others (2004) Biological and chemical consequences of the 1997–1998 El Niño in the Chilean coastal upwelling system: a synthesis. *Deep-Sea Res Part II* 51:2389–2411
- Goodwin DH, Flessa KW, Schöne BR, Dettman DL (2001) Cross-calibration of daily growth increments, stable isotope variation, and temperature in the Gulf of California bivalve mollusk *Chione cortezi*: implications for paleo-environmental analysis. *Palaaios* 16:387–398
- Hall CA Jr, Dollase WA, Corabato CE (1974) Shell growth of *Tivela stultorum* (Mawe, 1826) and *Callista chione* (Linnaeus, 1758) (Bivalvia): annual periodicity, latitudinal differences, and diminution with age. *Paleogeogr Paleoclimatol Paleoecol* 15:33–61
- Henríquez R, Barboza P, Taipa E, Toro C (1981) Variación anual de la gónada de la almeja *Protothaca thaca* (Molina, 1782): análisis histológico. *J Cienc Mar* 34
- Jones DS (1981) Annual growth increments in shells of *Spisula solidissima* record marine temperature variability. *Science* 211:165–167
- Jones DS (1983) Sclerochronology: reading the record of the molluscan shell. *Am Sci* 71:384–391
- Jones DS, Quitmyer IR (1996) Marking time with bivalve shells: oxygen isotopes and season of annual increment formation. *Palaaios* 11:340–346
- Kennish MJ, Olsson RK (1975) Effects of thermal discharges on the microstructural growth of *Mercenaria mercenaria*. *Environ Geol* 1:41–64
- Lutz RA, Rhoads DC (1980) Growth patterns within the molluscan shell, an overview. In: Rhoads DC, Lutz RA (eds) *Skeletal growth of aquatic organisms: biological records of environmental change*, Vol 1. Plenum Press, New York, p 203–255
- Moore JD (1991) Cultural responses to environmental catastrophes: post-El Niño subsistence on the prehistoric north coast of Peru. *Latin Am Antiq* 2:27–47
- Ortlieb L, Ghaleb B, Hillaire-Marcel C, Macharé J, Pichet P (1992) Déséquilibres U/Th, rapports allo/isoleucine et teneurs en <sup>18</sup>O des mollusques de dépôts littoraux pléistocènes du sud du Pérou: une base d'appréciation chronostratigraphique. *CR Acad Sci Paris* 314 (Ser II):101–107
- Ortlieb L, Diaz A, Guzman N (1996) A warm interglacial episode during oxygen isotope stage 11 in northern Chile. *Quat Sci Rev* 15:857–871

- Perrier C, Hillaire-Marcel C, Ortlieb L (1994) Paléogéographie littorale et enregistrement isotopique ( $^{13}\text{C}$ ,  $^{18}\text{O}$ ) d'événements de type El Niño par les mollusques holocènes et récents du Nord-Ouest péruvien. *Geogr Phys Quat* 48:23–38
- Reitz EJ (1988) Faunal remains from Paloma, an archaic site in Peru. *Am Anthropol* 90:310–322
- Richardson CA (2001) Molluscs as archives of environmental changes. *Oceanogr Mar Biol Annu Rev* 39:103–164
- Rollins HB, Sandweiss DH, Brand U, Rollins JC (1987) Growth increment and stable isotope analysis of marine bivalves: implications for the geoarchaeological record of El Niño. *Geoarchaeol* 2:181–197
- Sato S (1997) Shell microgrowth patterns of bivalves reflecting seasonal change of phytoplankton abundance. *Paleontol Res* 1:260–266
- Schöne BR, Goodwin DH, Flessa KW, Dettman DL, Roopnarine PD (2002a) Sclerochronology and growth of the bivalve mollusks *Chione* (*Chionista*) *fluctifraga* and *C. (Chionista) cortezi* in the northern Gulf of California, Mexico. *Veliger* 45:45–54
- Schöne BR, Lega J, Flessa KW, Goodwin DH, Dettman DL (2002b) Reconstructing daily temperatures from growth rates of the intertidal bivalve mollusk *Chione cortezi* (northern Gulf of California, Mexico). *Paleogeogr Paleoclimatol Paleoecol* 184:131–146
- Schöne BR, Tanabe K, Dettman DL, Sato S (2003) Environmental controls on shell growth rates and delta O-18 of the shallow-marine bivalve mollusk *Phacosoma japonicum* in Japan. *Mar Biol* 142:473–485
- Schöne BR, Houk SD, Freyre Castro AD, Fiebig J, Oschmann W (2005) Daily growth rates in shells of *Arctica islandica*: assessing sub-seasonal environmental controls on a long-lived bivalve mollusk. *Palaaios* 20:78–92
- Takesue RK, van Geen A (2004) Mg/Ca, Sr/Ca, and stable isotopes in modern and Holocene *Protothaca staminea* shells from a northern California coastal upwelling region. *Geochim Cosmochim Acta* 68:3845–3861
- Tanabe K (1988) Age and growth rate determinations of an intertidal bivalve, *Phacosoma japonicum*, using internal shell increments. *Lethaia* 21:231–241
- Thomas AC, Blanco JL, Carr ME, Strub PT, Osses J (2001) Satellite-measured chlorophyll and temperature variability off northern Chile during the 1996–1998 La Niña and El Niño. *J Geophys Res* 106:899–915 (1999JC000052)
- Urban HJ (1994) Upper temperature tolerance of ten bivalve species off Peru and Chile related to El Niño. *Mar Ecol Prog Ser* 107:139–145
- Urban HJ, Campos B (1994) Population dynamics of the bivalves *Gari solida*, *Semele solida* and *Protothaca thaca* from a small bay in Chile at 36° S. *Mar Ecol Prog Ser* 115: 93–102
- Witbaard R (1996) Growth variations in *Arctica islandica* L. (Mollusca): a reflection of hydrography-related food supply. *ICES J Mar Sci* 53:981–987
- Witbaard R (1997) Tree of the sea. The use of the internal growth lines in the shells of *Arctica islandica* (Bivalvia, Mollusca) for the retrospective assessment of marine environmental change. PhD thesis, Rijksuniversiteit, Groningen

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