

SCLEROCHRONOLOGICAL STUDIES IN THE HUMBOLDT CURRENT SYSTEM, A HIGHLY VARIABLE ECOSYSTEM

MARC GOSSELIN,* C. E. LAZARETH AND L. ORTLIEB

IPSL/LOCEAN, UPMC/CNRS/IRD/MNHN, Centre IRD France Nord, 32 avenue Henri Varagnat,
93143 Bondy CEDEX, France

ABSTRACT The Humboldt Current that bathes the west coast of South America is affected by different influences at daily to decadal periodicities. Environmental influences such as upwelling or coastal trapped waves as well as climate influences such as El Niño southern oscillation and Pacific decadal oscillation events interact and modify the thermocline depth of this Humboldt Current System. The position of this thermocline plays a key role in Humboldt Current System functioning by driving sea surface temperature (SST) and primary production variations. As filter feeders, bivalves are particularly affected by SST and primary production, and their shells can provide information about these two environmental factors. Using sclerochronology, we studied three bivalve species from different ecological niches living along the Peruvian–Chilean coast. Depending on the species, thick or thin sections, etched or not, were studied using an optical microscope. Increment thicknesses were measured at the surface of the shell and/or in cross-section. Moreover, the mineralogical composition of the different layers of the studied shells was determined on thin sections by Fourier transform infrared spectroscopic analyses. Growth results were then interpreted tentatively in terms of environmental variations. For the free-living, short-lived Pectinidae *Argopecten purpuratus*, the daily growth rhythm is linked to the solar period whereas growth amplitude seems to be related to the occurrence of spawning events, probably triggered by specific water temperature patterns. tidal regime and SST seem to be the major environmental parameters that govern shell growth rhythms and/or increment thickness for two nearshore species—the Mytilidae *Choromytilus chorus* and the Veneridae *Eurhomalea rufa*—which grow more slowly and have a life span longer than *A. purpuratus*, and have a strong potential for paleo-environmental and paleo- El Niño southern oscillation reconstruction. These results need to be confirmed studying multiple shells to quantify individual growth variations and to enhance the significance of the findings on the different environmental parameters recorded in the growth patterns of the South American bivalve species studied.

KEY WORDS: Sclerochronology, Bivalve, Humboldt Current System, Chile, Peru, El Niño Southern Oscillation, Coastal trapped waves, Upwelling

INTRODUCTION

The west coast of South America is bathed by the Humboldt Current, a paradoxical ecosystem characterized by high-nutrient, low-chlorophyll waters off the coast and highly productive areas close to the coast as a result of the upwelling of cold, nutrient-rich deep waters (Gonzalez et al. 1998, Hutchins et al. 2002). Consequently, the Peruvian and Chilean coastal upwelling region, which accounts for 0.1% of the ocean surface area, is the most productive zone in the world (10% of the world's fish catch) (Chavez et al. 2008). Nevertheless, this productivity is fragile because the Humboldt ecosystem is submitted to various environmental and climate phenomena that occur at daily to decadal periodicity. Upwelling is affected by daily to weekly periodicities (Rutllant & Montecino 2002, Escribano et al. 2004). Intraseasonal variations, as well, play an important part in the physical and chemical variability of the Pacific Ocean (Gushchina & Dewitte 2011 and references therein). Along the Chilean–Peruvian coast, oceanic and atmospheric intraseasonal variations (from 40–70 days) are driven by coastal trapped waves (CTWs) (Hormazabal et al. 2001, Hormazabal et al. 2002, Hormazabal et al. 2006). El Niño Southern Oscillation (ENSO) events also affect this region at seasonal to interannual timescales (Rasmusson & Carpenter 1982, Rutllant & Montecino 2002). During warm ENSO events (El Niño), which last several months (usually between 9 mo and 24 mo), several environmental parameters—such as sea surface

temperature (SST), sea level, wind regime, surface currents, thermocline depth, and rainfall—may be modified significantly according to the strength of the event (e.g., Blanco et al. 2002, Carr 2002). Furthermore, the Pacific decadal oscillation (PDO), an oceanographic–climatic phenomenon that has some similarities to ENSO, impacts the whole Pacific basin at a decadal periodicity (Zhang et al. 1997, Montecino et al. 2003).

Numerous studies have examined the complex interactions between climate and environment within the Humboldt Current System (HCS; e.g., see the special issue by Werner et al. 2008). Some of these studies reported how disturbances in the thermocline depth impact the SST but also sea level and phytoplankton productivity (Rutllant & Montecino 2002, Rutllant et al. 2004, Hormazabal et al. 2006, Montecino et al. 2006). During a downwelling (upwelling) phase of CTWs, the thermocline depth increases (decreases), which decreases (increases) the nutrient input in more shallow waters (Hormazabal et al. 2006). In addition, the CTW downwelling (upwelling) phase is associated with warmer (colder) SST conditions such as El Niño–like (La Niña–like) events (Hormazabal et al. 2006). Indicators need to be developed to assess the impact of such climate variability on the HCS. Indicators help to set up an objective index, allowing characterization of the state of a system. Thus, the information gathered, through indicators on ecological response of HCS species, could indeed help in setting up sustainable management of the marine resources within this ecosystem (Fernandez et al. 2000, Tarazona et al. 2003, Corrège et al. 2004, Thatje et al. 2008).

A promising record of coastal climate variability may be obtained from mollusc shells through the use of sclerochronology.

*Corresponding author. E-mail: Marc.Gosselin@ird.fr, mar.gosselin@gmail.com

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Sclerochronology is the study of the hard, mineralized parts of some organisms such as corals, fish, molluscs, and algae, with the aim of counting their growth bands and reconstructing the life history of the organisms through analysis of the biomineralization processes that drive skeletal growth (e.g., Druffel & Griffin 1995, Panfili et al. 2002, Schöne et al. 2008, Halfar et al. 2011). Such a tool can thus be used to understand more completely the biology of the organism studied (Buddemeir 1978, Jones 1983, House 1995, Schöne 2008, Schäfer et al. 2011) and to specify the environmental conditions in which the organism grew (e.g., Bessat & Tabeaud 1998, Hendy et al. 2003, Schöne 2008, Wanamaker et al. 2011). The low temperatures of the HCS (mean SST, 19.3°C at 4° S to 12.8°C at 42° S) do not allow development of corals typically used in sclerochronological studies (Cortes 1997, Hoegh-Guldberg 1999). In the southeast Pacific region bathed by the HCS, bivalves can be an interesting alternative for sclerochronological studies. Indeed, benthic mollusc communities such as bivalves and gastropods are interesting indicators of the environment because they thrive in a wide range of environments, and many species are relatively sedentary and can record both acute and chronic stress events (Fano et al. 2003). During shell formation, environmental variations are recorded via increment thickness change (sclerochronology) and variations of some element content in the shell, such as stable isotopes and trace metals (sclerochemistry) are also retained (Schöne et al. 2002, Hallmann et al. 2009). In the HCS, bivalves are the third marine resource (by weighted catch) after fish and algae and have a relatively broad ecological diversity within the intertidal zone (i.e., colonizing different substrates such as mud, sand, and rock). In addition, because of their generally high growth rate, bivalves record environmental parameters at a high resolution (i.e., daily), which is crucial in a highly variable environment such as the HCS. Last, the Chilean–Peruvian coast has many archaeological and fossil sites that contain mollusc shell remnants, which allow studies of paleoceanographic variations (paleotemperature and paleoproductivity) after the essential calibration step on modern shells of the same species and same individual age-verified specimens.

The objectives of our study are to show the kind of information that can be obtained using sclerochronology on HCS coastal bivalve species and to expose the different ways of obtaining information on environmental and climatic parameters potentially recorded in bivalve shells. Three bivalve species from different ecological settings living along the Chilean–Peruvian coast were chosen. This sclerochronological study was conducted to set the shell structures and their mineralogy as well as to gather information on the shell growth patterns and build the temporal framework essential to establish and interpret future time series.

MATERIALS AND METHODS

Three species—*Argopecten purpuratus*, *Choromytilus chorus*, and *Eurhomalea rufa*—were chosen for their wide geographical distribution along the coasts of Peru and northern Chile and/or because they are harvested commercially. The studied species are filter-feeding bivalves but with different life habits. The specimens were sampled in the Antofagasta region of Chile (Fig. 1, Table 1) as drifted material, recently dead, and with their valves still connected. Information about their growth and their period of reproduction at the sampling sites is presented in Table 1. Except for *E. rufa*, for which no information exists concerning its resistance to specific climatic events, these species are tolerant to moderate El Niño events (Urban 1994). The sclerochronological study was carried out in the outer layer because the growth line succession is observed more easily in that layer. This was done from sections for *C. chorus* and *E. rufa*, and directly from the external surface for *A. purpuratus*. The bivalve *E. rufa* presented a clear pattern in the umbo, which was thus also studied.

Argopecten purpuratus (Lamarck, 1819)

The scallop *Argopecten purpuratus* is an infralittoral vagile species living on muddy sand bottoms. In addition, *A. purpuratus* is an important economic resource in Peru, harvested commercially for local and international markets. Its population

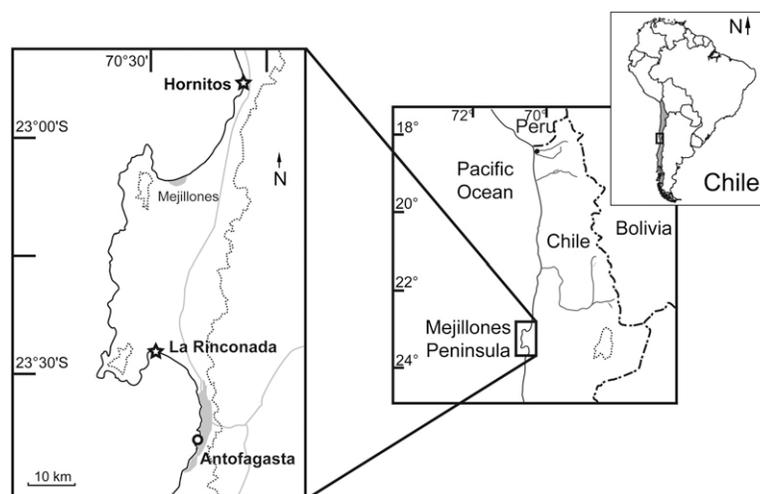


Figure 1. Location of the sampling sites (stars) around the Mejillones Peninsula, Chile. The circle marks the location of the sea surface temperature sensor (CENDHOC, Centro Nacional de Datos Hidrograficos y Oceanograficos de Chile).

TABLE 1.
Southeastern Pacific mollusc species on which sclerochronological studies have been done.

Species	<i>Argopecten purpuratus</i> Lamarck, 1819	<i>Choromytilus chorus</i> Molina, 1782	<i>Eiarhomalea rufa</i> Lamarck, 1819	<i>Protothaca thaca</i> Molina, 1782	<i>Mesodesma donacium</i> Lamarck, 1818*	<i>Concholepas concholepas</i> Bruguière, 1789	<i>Trachycardium procerum</i> Sowerby, 1833
Order, superfamily, family	Pterioidea, Pectinacea, Pectinidae	Mytiloidea, Mytilacea, Mytilidae	Veneroidea, Veneracea, Veneridae	Veneroidea, Veneracea, Veneridae	Veneroidea, Veneroidea, Mesodesmatidae	Neogastropoda, Muricoidea, Muricidae	Veneroidea, Cardioidea, Cardiidae
Geographical distribution (Alamo & Valdivieso 1987, Guzmán et al. 1998)	From Paíta, Peru, to Coquimbo, Chile	From Callao, Peru, to Strait of Magellan, Chile	From Gulf of Panama, Panama, to Concepcion, Chile	From Callao, Peru, to Chonos Archipelago, Chile	From Chimbote, Peru (Alamo & Valdivieso 1987, Guzmán et al. 1998) to Chiloe Island, Chile	From Callao, Peru, to Magellan Strait, Chile	From Baja California, Mexico, to Bahía Independencia, Peru
Habitat (Alamo & Valdivieso 1987, Guzmán et al. 1998)	Infralittoral, subtidal; muddy, coarse sand	Mesolittoral, infralittoral; rocky shore, rocky patches, pebbles covered by sand	Infralittoral, intertidal, sand between rocks	Infralittoral, subtidal, coarse sand	Intertidal, fine sandy beach, high wave energy	Subtidal (adults), intertidal (juveniles); rocky shore, rocky patches	Intertidal, muddy, sandy bay
Reproduction	Main spawning period between September and April throughout the year during ENSO event (Cantillanez et al. 2005)	Continuous gonadal activity, main spawning period in austral spring (Stotz et al. 2007)	Main spawning period August to October	Continuous gonadal activity (current study)	Gonadal activity from June to December, spawning between October and January (Riascos 2009)	Continuous gonadal activity, main spawning period between April and September (Castilla & Cancino 1976)	Quasicontinuous gonadal activity, main spawning periods in austral summer (maximum, February and March) and in austral spring (maximum, October and November) (Ortiz Galarza 2011)
Growth at Antofagasta, Chile	90 mm in 0.86–1.43 y (Avendaño & Cantillanez 2005, Thébault et al. 2008)	120 mm in 3.7–8 y (Lopez et al. 2008)	45–63 mm in 2–3 y (Lay-Salas 1966)	50 mm in 6 y (Henríquez et al. 1981)	65 mm in 3 y (Riascos et al. 2009)	100 mm in 1.65–6 y (Manríquez et al. 2008)	ND
Mean increment thickness	341 ± 139 µm (current study)	82 ± 57 µm (current study)	40 ± µm (current study)	10–120 µm (Lazareth et al. 2006)	ND	2 µm (Guzmán et al. 2007)	ND
Estimated mean growth rhythm	1 increment/day (current study)	2 increments/day, minimum (current study)	1.5 increments/day (current study)	3–7 increments/wk (Lazareth et al. 2006)	1 or 2 increments/day Riascos et al. 2009)	40–50 layers/day (Manríquez et al. 2008)	2 increments/day (Manríquez et al. 2008)

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TABLE 1.
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Species	<i>Argopecten purpuratus</i> Lamarck, 1819	<i>Choromytilus chorus</i> Molina, 1782	<i>Eurhemalea rufa</i> Lamarck, 1819	<i>Protothaca thaca</i> Molina, 1782	<i>Mesodesma donacium</i> Lamarck, 1818*	<i>Concholepas concholepas</i> Bruguère, 1789	<i>Trachycardium procerum</i> Sowerby, 1833
Environmental control on shell growth rhythm	Circadian rhythm (current study, Thébault et al. 2008) and lunar periodicity (current study)	Tidal rhythm, at least at each low tide (current study)	Tidal rhythm, low tide intensity (current study)	Probably tidal rhythm (Lazareth et al. 2006)	Tidal rhythm, low tide intensity (Lazareth et al. 2006)	Probably circadian rhythm (Guzmán et al. 2007)	ND
Sclerochronological use for temporal framework	Daily increment (current study, Thébault et al. 2008)	Annual pronounced notch, seasonal notch, weekly dark ring, daily increment (current study)	Summer check, monthly dark band and bundle, daily increment (current study)	Summer check (Lazareth et al. 2006)	Summer check, semimonthly check between 2 nd and 3 rd years (Carré et al. 2005a)	Nycthemeral differentiation, subhourly increment (Guzmán et al. 2007, Lazareth et al. 2007, Valderrama 2008)	ND
Sclerochronological and chemical element used to record environment	Increment amplitude and oxygen isotope as temperature recorder (current study, Thébault et al. 2008)	Oxygen isotope as temperature recorder (Jones 2010)	ND	Oxygen isotope as temperature recorder (Lietard 2007)	Oxygen isotope as temperature recorder (Carré et al. 2005a)	Oxygen isotope as temperature recorder and radiocarbon and stable carbon isotopes as upwelling recorders (Perrier et al. 1994, Andrus et al. 2005)	Oxygen isotope as temperature recorder and radiocarbon and stable carbon isotopes as upwelling recorders (Perrier et al. 1994, Andrus et al. 2005)

* The northern limit distribution of *M. donacium* has been updated (Valentín Mogollón, pers. comm., 2009). Main information on taxonomy, ecology and sclerochronology are reported for 6 species, including the 3 studied in the current work. ENSO, El Niño southern oscillation; ND, no data.

is affected positively during El Niño events (Wolff 1985). A shell growth rhythm of 1 increment/day was proposed by Thébaud et al. (2008) from wild-specimen populations. The shell of *A. purpuratus* studied is 84 mm long and was collected on the beach of La Rinconada on December 1, 2000. La Rinconada (northern Chile, 23°28', 70°30' W) is a well-documented marine reserve (Avendaño & Cantillanez 2005, Avendaño et al. 2007, Piñones et al. 2007) situated 15 km to the northeast of Antofagasta in the southern bay of the Mejillones peninsula (Fig. 1). In the La Rinconada embayment, coastal upwelling occurs throughout the year and is stronger in summer (Piñones et al. 2007). This upwelling brings nutrient-rich cool waters (~13 to ~16°C) to the surface (Avendaño et al. 2007), inducing phytoplankton blooms (Thébaud et al. 2008). SST time series between September 26, 2000 and November 26, 2000, were provided at a daily resolution by the Centro Nacional de Datos Hidrográficos y Oceanográficos de Chile—Servicio Hidrográfico y Oceanográfico de la Armada de Chile (CENDHOC-SHOA) from the closest recording station, the Antofagasta harbor.

Choromytilus chorus (Molina, 1782)

A sessile giant mussel, *Choromytilus chorus* (Mytilidae) populations live near Antofagasta on upper infralittoral rocky patches covered partially by sand. This species was exploited extensively at the beginning of the 20th century and might be a good candidate for new exploitation development (Thiel et al. 2007). Information on biological cycle and growth parameters of *C. chorus* are, however, scarce in the northern part of its extension range. To our knowledge, no study has been published previously on the sclerochronology of *C. chorus* shells. The studied specimen is 84 mm long and was collected on the backshore December 27, 2005, at Hornitos Bay (22°52' S, 70°17' W). The Hornitos site is located to the north of the Mejillones peninsula, 60 km north of Antofagasta (Fig. 1). It is bordered by a fine-sand beach with a slight slope and an intertidal width of ~70 m (Jaramillo et al. 2001). Unfortunately, no SST data were available for the Hornitos site.

Eurhomalea rufa (Lamarck, 1819)

The Veneridae *Eurhomalea rufa* lives in meso- or infralittoral sandy bottoms, burrowed in the sediment at a depth of less than 10 cm. To our knowledge, only 1 population study has been conducted on this species, at Hornitos (Lay-Salas 1966). No sclerochronological study has been undertaken on *E. rufa* shells. The studied *E. rufa* shell was collected December 27, 2005, on the foreshore of Hornitos, one small locality where this species has been indexed in northern Chile (Fig. 1). The peristomial length of the studied specimen is 64.5 mm.

Sample Preparation and Analysis

For each species, the shell structure and the increment features were studied both on the external surface and inside the shell. The right valve of each shell was first cut along the axis of maximum growth using a linear precision saw (Isomet 5000; Buehler). One half valve of each sample was then glued on a glass slide or embedded in epoxy. For proper observation and measurement acquisition, especially with regard to shell increment patterns, specific shell preparations were made according

to the species. The embedded half valves were cut again to obtain shell sections of different thicknesses—thin, 12 µm and 140 µm; thick, 2–3 mm. To improve the observation and identification of the shell growth structures, some polished shell sections were etched using the Mutvei's solution (Schöne et al. 2005). The combination of weak acetic acid, Alcian blue (or an equivalent), and glutaraldehyde highlights the organic-rich growth lines as darker stained ridges.

Fourier transform infrared spectroscopic analyses (Equinox 55, Bruker), a nondestructive method, were done on thin sections to determine the mineralogical composition of the different layers of the studied shells (Bertaux et al. 1998).

Observations and pictures of the growth patterns of the external layer and the umbo of the different species were conducted and acquired, respectively, using an optical microscope (BX60, Olympus) with diffused and transmitted natural or UV light (to observe organic matter-rich layers). The sclerochronological work on growth increments was done using Visilog V6.481 software with an adapted "sclerochronological module" (Noesis Co.) (Gosselin et al. 2007).

A wavelet analysis was done on the increment thickness of the *Argopecten purpuratus* specimens and on the corresponding SST time series. The wavelet analysis routine of Torrence and Compo (1998) allows one to determine the significant periodicities for each of the two time series, and the common periodicities by using the cross-wavelet analysis. In addition, phase difference (lag) between the two time series was calculated using a MATLAB wavelet routine for ecological data (Cazelles et al. 2008).

RESULTS

All studied shells were composed of at least two layers of different colors and/or mineralogical composition. Mollusc shells, which grow by the addition of successive increments, consist of a mix in variable proportions of organic matter and calcium carbonate (Rhoads & Lutz 1980, Dauphin et al. 2003). An increment is defined herein as a couplet of an organic matter-rich and a calcium carbonate-rich growth line.

Shell Structure and Mineralogy

Argopecten purpuratus

The external surface of the *Argopecten purpuratus* shell is characterized by well-developed radial ribs and delicate, concentric sheets (Fig. 2A). Because of the natural abrasion effect, the older part of the shell, close to the umbo, has more subdued superficial structures. Consequently, only the part of the shell from 60–84 mm from the umbo was studied (Fig. 2B). The shell of *A. purpuratus* is made of three layers (Fig. 2C). The outer and the inner layers are made of calcite whereas the middle one is aragonitic. The conspicuous sheets observed on the external surface of the shell are difficult to identify in thin section. Indeed, in the shell cross-section, the marks of those external sheets are only visible in the first few micrometers of the outer shell layer (Fig. 2D, black arrows).

Choromytilus chorus

Under a varnished black periostracum, this blue mussel presents thin external growth marks (Fig. 3). The shell is composed of two layers: a blue calcitic outer layer and a white

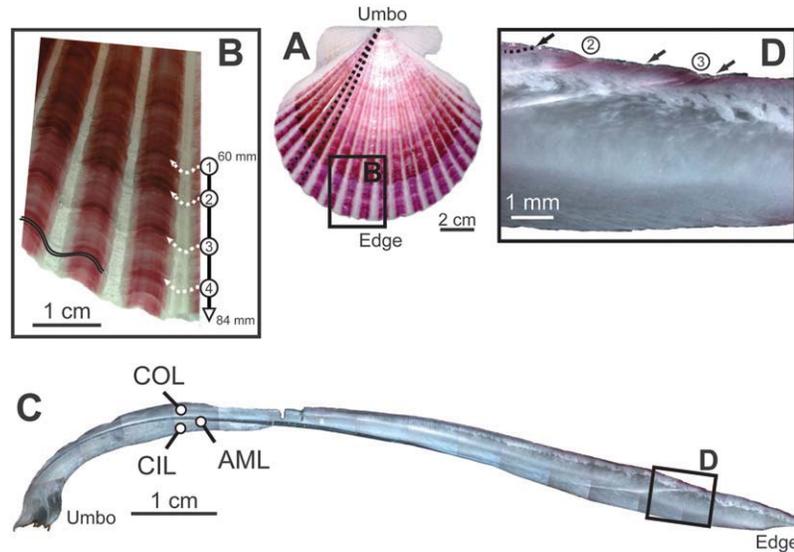


Figure 2. The *Argopecten purpuratus* shell. (A) View of the external part of the shell. Radial ribs are marked by the dotted black lines. (B) Focus on the external part of the shell where increments were measured. Black lines to the left follow a pair of external growth increments. The 4 growing phases are indicated (numbered circles with white arrows). These growing phases are delimited by zones of growth reduction (see text for details). (C) Thin section viewed under diffused light, with umbo to the left and growing edge to the right. AML, aragonitic middle layer; CIL, calcitic inner layer; COL, calcitic outer layer. (D) Detail of the thin section showing the limits of phases 2 and 3. Note that, in the cross-section, the mark of the increments, which is clearly observed on the shell surface, is only visible in the first micrometers of the external part of the outer layer (3 examples noted by a black arrow; one broken black line is added for the far left black arrow).

aragonitic inner layer (Fig. 3A). In the calcitic layer, thin, white growth lines are observed in the thin section when highly polished (with a 0.25- μm grid) or etched (Fig. 3D). These growth lines start parallel to the inner layer and then follow a slight slope until they curve abruptly toward the surface of the shell.

Eurhomalea rufa

The external shell surface of *Eurhomalea rufa* presents thin concentric growth marks and two major growth anomalies, one at 21.1 mm and the other at 46.9 mm from the umbo (Fig. 4A,

black lines and black arrows). The shell is made of two aragonitic layers, a white outer layer and a translucent inner layer, when observed under diffused light (Fig. 4A). The outer layer shows a succession of narrow dark and broad white curved growth lines (Fig. 4B). The dark lines, which are in relief after Mutvei etching and are fluorescent under UV light, are organic matter-rich lines (Fig. 4D). In some parts of the outer layer, the white growth lines become thinner whereas the dark growth lines become larger, forming dark bundles that fuse as thick dark bands in the inner layer (Fig. 4B). The umbo consists of a succession of wide white and dark bands that apparently mimics the set of bundles observable all along the shell (Fig. 4C).

Sclerochronological Features

Argopecten purpuratus

Between 60 mm and 84 mm from the umbo, 64 increments (concentric sheets) were measured at the external shell surface (Fig. 3B). The distance between those sheets ranged between 81 μm and 666 μm , with an average of $341 \pm 139 \mu\text{m}$ (Fig. 5A). For the wavelet transform analysis, we considered first that the animal died on December 1, 2000 (collection date), and attributed 1 day to each increment according to the hypothesis of an uninterrupted daily shell growth as proposed by Thébault et al. (2008) for the species. Using December 1 as the death date, a phase difference (lag) of 6.3 days was observed between the sclerochronological and the SST series. Considering that the main driver of shell growth is SST, we assumed that the specimen stopped growing almost 1 wk before collection. Consequently, November 26, 2000, was thus allocated to the edge of the *Argopecten purpuratus* shell. The 64 increments identified in our shell would have thus been formed between September 24, 2000, and November 26, 2000.

The sclerochronological profile can be divided in 4 phases, each delimited by a growth rate decrease (Fig. 5A), which is

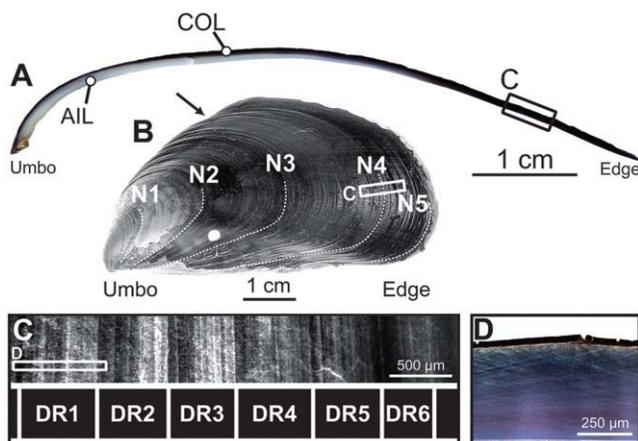


Figure 3. The giant mussel *Choromytilus chorus* shell. (A) Thin section (reflected light), with umbo to the left and growing edge to the right. AIL, aragonitic inner layer; COL, calcitic outer layer. (B) View of the outer surface of the right valve with the 5 notches shown by the white dotted lines (N1–N5). The arrow points to the remarkable pronounced fourth notch along the margin. (C) Detail of the shell outer surface (transmitted light) in which 6 weekly dark rings (DR1–DR6) are observed (black band delimited by white lines). (D) Thin section under diffused light showing the infra-daily growth lines.

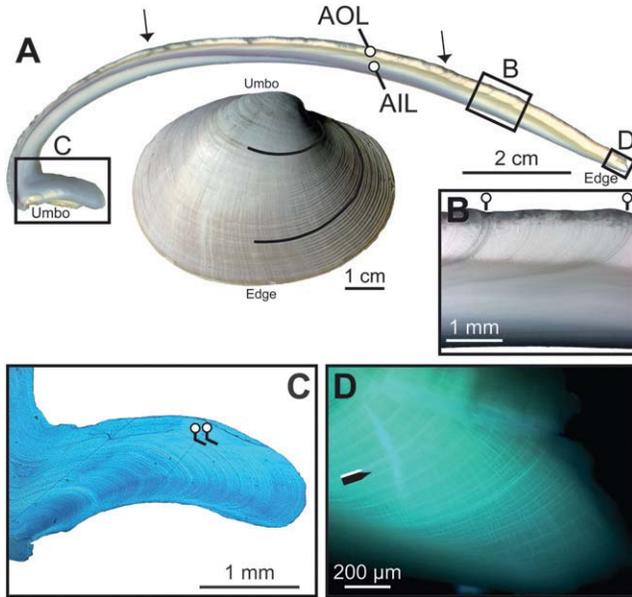


Figure 4. The *Eurhomalea rufa* shell. (A) Outer view of the valve (below) and thin section (above, diffused light) with the 2 annual growth anomalies “summer checks” (bold lines on the whole valve; arrows on the thin section) shown. AIL, aragonitic inner layer; AOL, aragonitic outer layer. (B) Detail of the thin section with 2 monthly bundles (black circles). (C) View of the umbo in thin section after Mutvei’s solution etching (under diffused light). The 2 monthly bundles in (B) appear in (C) as 2 monthly dark bands (black circles). (D) Detail of the shell margin area (under reflected UV light). Daily increments are formed by a couplet of 1 narrow, dark organic-rich line and a broad, white CaCO_3 -rich line. Under UV light, the organic-rich line fluoresces (white arrow) and the broad CaCO_3 -rich line appears darker (black arrow).

identified by a darker growth mark at the surface and a white line inside the shell (Fig. 2B–D). These 4 phases lasted 18, 22, 14, and 10 days, respectively (Fig. 5A). From September 24 to November 26, the mean daily SST recorded in Antofagasta harbor was $16.8 \pm 1^\circ\text{C}$, with an overall increase from 15–19°C (Fig. 5A). The SST changes during that period are characterized by 4 successive phases of increase and decrease (Fig. 5A). The wavelet analysis shows that shell increment thickness and daily SST follow a significant similar pattern (Fig. 5B, C, respectively), with a common periodicity of 17 days throughout the study period (cross-wavelet analysis, Fig. 5D).

Choromytilus chorus

The external surface of *Choromytilus chorus* presents 5 notches characterized by V-shaped marks on the margin side (Fig. 3B). These notches were located, respectively, at 15.3, 24.8, 34.9, 48.6, and 59.3 mm from the umbo. The fourth notch is more pronounced than the others (Fig. 3B, black arrow). In addition, a succession of dark rings, visible with the naked eye, is observed at the surface of the shell (Fig. 3C). Eleven to 12 dark rings were counted between 2 notches, for a total of 60 dark rings for the whole shell. At a higher magnification, under transmitted light, the shell surface presents thin growth increments that form a succession of color bands of variable dark-red intensities (Fig. 3C). These thin growth increments were particularly well evidenced within 6 successive dark rings

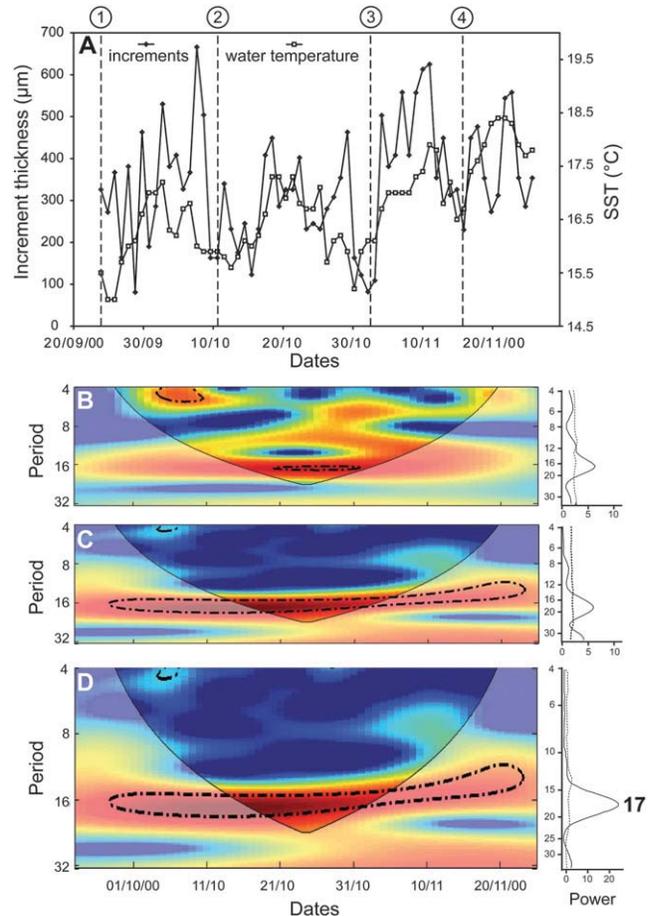


Figure 5. Sclerochronological results obtained on *Argopecten purpuratus* compared with sea surface temperature (SST; sensor CENDHOC-SHOA Centro Nacional de Datos Hidrográficos y Oceanográficos de Chile–Servicio Hidrográfico y Oceanográfico de la Armada de Chile). (A) Increment thickness changes at the *A. purpuratus* shell surface and SST variations between September 26, 2000, and November 26, 2000. Four cycles of increase and decrease are delimited by the vertical dotted lines (circled numbers 1–4). The numbers and the vertical dotted lines refer to the 4 numbers and the white arrows in Figure 2B. (B, C) Coherence wavelet analysis and periodograms (right) of the 2 time series, presented in (A) increments (B) and SST (C). The colors correspond to the range of correlation, dark blue (0) to dark red (1). Note the common periodicity throughout the 17 days of the times series (dotted bold line). (D) Cross-wavelet analysis and periodogram (right) of growth increment thickness and SST changes. Note the common periodicity throughout the 17 days along the times series (dotted bold line). The dotted area in the wavelets panel and the peaks above the dotted line in the periodograms are significant at a 95% confidence interval.

around the fourth notch, and this zone was thus selected for growth increment thickness measurements (Fig. 3C). Fifty-six increments, with an average thickness of $62.1 \pm 23 \mu\text{m}$, were counted from the shell surface, which corresponds to a mean of 9.3 increments per dark ring (Fig. 3C).

To confirm these observations, the internal growth pattern was analyzed on a thick etched section (Fig. 3D). The area between the second and the fourth notches (N2–N4; 24 dark rings) was selected because the internal growth pattern was clearer in that part of the shell. Between the second and the

fourth notch, 348 organic matter-rich growth lines were counted in delimiting increments, with a mean thickness of $81.7 \pm 57 \mu\text{m}$ (Fig. 6). Because 24 dark rings were present between notches N2 and N4, there was an average of 14.5 organic matter-rich growth lines per dark ring (Fig. 6). The difference in increment number depending on the shell preparation (9.3 vs. 14.5 for shell surface vs. thick section, respectively) is a result of the fact that thick sections allow a more detailed observation of growth structures than the shell surface. The increment thickness variation is characterized by successive increases and decreases, with each cycle of increase and decrease including 27 ± 6 organic matter-rich growth lines (Fig. 6, dotted lines).

Eurhomalea rufa

The sclerochronological study of the *Eurhomalea rufa* shell was done in the umbo and in the outer shell layer. In the umbo, 30 dark bands were counted (Fig. 4C). Those dark bands had an average thickness of $35 \pm 8 \mu\text{m}$ and were separated by white bands that were, on average, $180 \pm 68 \mu\text{m}$ thick. The relative distances between the dark bands in the umbo and between each bundle in the outer shell layer are linked ($R^2 = 0.98$) by about 1 order of magnitude. This indicates that the dark bands (umbo) and the bundles (outer shell layer) result most probably from a common “forcing” and formed concomitantly. Between the 2 external shell surface growth anomalies (Fig. 4A, black arrows), 11 bundles, with their corresponding dark bands in the umbo, were counted. Between the second growth anomaly (46.9 mm) and the edge (64.5 mm), 10 bundles were counted. In this last portion of the shell, 450 growth increments, with a mean thickness of $39.7 \pm 19 \mu\text{m}$, were measured.

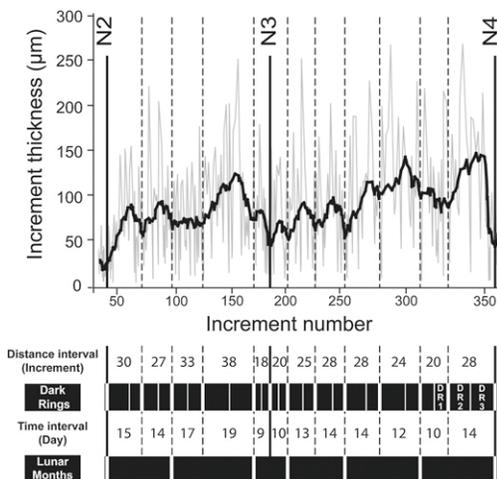


Figure 6. Sclerochronological profile (thin gray lines) of *Choromytilus chorus* between the seasonal marks N2 and N4 (Fig. 3B), with a moving average (thick black line) of 14 days. The 348 increments counted correspond to 6 mo of growth. Dotted lines delimit the semimonthly lunar cycle (2 dark rings, see Fig. 3C). The correspondence, at different temporal resolutions, between growth marks (intradaily increments, weekly dark rings) and time intervals (lunar day and month) is shown below. The 3 numbered dark rings (DR) refer to the dark rings from DR1–DR3 from Figure 3C.

DISCUSSION

Sclerochronology Applied to Pacific South American Molluscs

After the earliest studies (Clark 1974, Rhoads & Lutz 1980), the sclerochronological tool has been applied to many bivalve species in numerous latitudes (Hall et al. 1974, Beukema & Meehan 1985). A growing interest in this research field developed during the first years of the 21st century, and some areas such as the northern hemisphere have been the subject of various studies for climatic reconstruction (see Wanamaker et al. (2011) and references therein). In the northeastern Pacific Ocean, paleoclimate studies have been carried out recently on bivalve shells of the long-lived species *Panopea abrupta* (e.g., Black et al. 2009). Along the west coast of South America, the sclerochronological tool was used at the beginning of the 1990s as part of paleobiogeographical studies of shell midden (Rollins et al. 1990, Perrier et al. 1994). Lately, sclerochronology, with the help of sclerochemistry, has been used in environmental and climatic reconstructions (Andrus et al. 2005, Carré et al. 2005a, Carré et al. 2005b, Lazareth et al. 2006, Guzmán et al. 2007, Thébault et al. 2008).

The sclerochronological research along the coast of Chile and Peru must take into account the specificity of the HCS and must focus on understanding the different spatiotemporal phenomena driving climate variations—specifically, upwelling (daily to weekly), CTWs (intraseasonal), ENSO (interseasonal to interannual), and PDO (interdecadal) events (e.g., see the special issue by Werner et al. (2008)). These phenomena impact the thermocline depth with variations in SST and in primary production. Sea surface temperature and primary production affect the growth of mollusc species and can be recorded in their shells. Most HCS South American mollusc species already studied using sclerochronology have short or medium life spans (i.e., <10 y). Nevertheless, thanks to their high growth rate, these species can be studied at a high temporal resolution (i.e., daily), which make them useful for studying weekly to interannual environmental variations of the HCS.

We studied three bivalve species living along Chilean–Peruvian coast by means of sclerochronology. First, their growth patterns were analyzed and a temporal framework was suggested for each of the three species. Then, from the different growth marks observed, we studied the different phenomena influencing the HCS at suitable spatiotemporal scales in the light of previous sclerochronological and sclerochemical studies carried out in South America.

Characterization of Three HCS Bivalve Species: Growth Patterns and Temporal Frameworks

Argopecten purpuratus

In previous sclerochronological studies done on the external shell part of *Argopecten purpuratus* from La Rinconada, a mean daily growth of $330 \mu\text{m}$ was measured (Thébault 2001, Thébault et al. 2008). A very similar value was found in our study ($341 \mu\text{m}$) for a specimen from the same locality collected 1 y later. In 64 days, our specimen grew in length from 60–84 mm. To reach the same size, the *A. purpuratus* population from La Rinconada needed the same time in 1999 whereas they needed 192 days in 2001 (e.g., Avendaño & Cantillanez 2005). Thus, in 1999 (Thébault et al. 2008) and in 2000 (this study), *A. purpuratus*

growth rates were high. In 1999 and October/November 2000, La Niña conditions were prevailing. SOI index data from the Bureau of Meteorology, National Climate Centre site, Australia. Consequently, *A. purpuratus* may have a higher growth rate during La Niña episodes, at least in the La Rinconada locale of northern Chile, even though populations of this species are known to show a bloom during El Niño conditions (Arntz & Valdivia 1985, Arntz & Tarazona 1990, Diaz & Ortlieb 1993). As suggested by Thébault et al. (2008), we surmise that the favorable individual growth conditions experienced at La Rinconada are linked to intensified upwelling conditions and high nutrient availability.

Besides this favored growth, we observed a 17-day periodicity for both growth increment variations and daily SST, and 4 phases of increment thickness variations of about 16 days each (Fig. 5). In addition, abrupt growth drops are observed when SST decreased between these phases (Figs. 2B–D and 5A). It was shown for the European *Pecten maximus* that there is an energetic balance between the reproductive activity and the somatic growth throughout the year (Paulet et al. 2006). Cantillanez et al. (2005) reported that *Argopecten purpuratus* individuals may realize successive spawning events over consecutive periods of ~20 days. These successive spawning events are possibly controlled by specific temperature changes (i.e., strong diurnal fluctuations and phytoplankton concentration changes) (Avendaño & Cantillanez 1997). Consequently, the 17-day SST period, the 4 16-day shell growth phases, and the known ~20 days spawning event periodicity (Cantillanez et al. 2005) support a close relationship between spawning periodicity and thermal variations in *A. purpuratus*.

Choromytilus chorus

The increment pattern of *Choromytilus chorus* shell, as described from the thick section (i.e., 14.5 increments per dark ring) and a dozen of dark rings between each notch may be related to a circalunidian rhythm controlled by tidal cycles. Indeed, in the study area, the tidal rhythm is characterized by 2 “daily” low tides. If we consider that 1 increment is formed at each low tide (i.e., 2 increments/day (Fig. 3D)), a dark ring (14.5 increments) would form every week (Fig. 3C). The cycle of increment thickness change, containing, on average, 27 increments (Fig. 6), thus lasts around 15 days, with the hypothesis of 2 increments/day. This cycle is in agreement with a growth pattern that follows a fortnightly tidal range fluctuation cycle as described in other species (e.g., Pannella 1976, Richardson 1990, Carré et al. 2005a). Based on the hypothesis of 2 infradaily increments per day, the time span between the second and fourth notches on the *C. chorus* surface would correspond to a 6-mo span (12 cycles; Figs. 3B, 6). Consequently, the conspicuous notches on the *C. chorus* shell would represent seasonal growth anomalies related to the equinox and solstice spring tides that take place alternately every 3 mo (Fig. 6).

The studied *Choromytilus chorus* specimen presented 5 notches and might thus be around 15 mo old. Considering the collection date (end of December 2005), the fourth, more pronounced notch would have been formed 3 mo earlier, in September 2005. This corresponds to the austral spring equinox spring tide, when spawning events usually occur for this species (Stotz et al. 2007). A notch in the *C. chorus* shell corresponding to such an event is very likely because spawning events imply an energetic reallocation phenomenon that leads to a shell growth

decrease (Navarro 1988). In addition, it has been reported that, for this species, spawning events can be triggered by a salinity decrease (Navarro 1988). At Hornitos, salinity decreases occur through a seasonal freshwater resurgence in the upper infratidal area along the beach, which occurs in September (Riascos 2009, Riascos et al. 2009). Altogether, the presence of a pronounced notch, allocated to spring tides, and the co-occurrence of spawning events with a seasonal decrease in salinity of coastal waters, support our temporal resolution hypothesis of 2 increments/day.

The bivalve *Choromytilus chorus* is a slow-growing species (Thiel et al. 2007, Lopez et al. 2008). Following the von Bertalanffy equations reported in Lozada et al. (1971) and Norambuena and Solis (1978), a size of 60 mm is reached between 28 mo and 40 mo. Our sclerochronological data (59.3 mm in 15 mo) imply a higher growth rate during the juvenile stage than in the populations of Chiloe (Lozada et al. 1971) and of Coquimbo (Norambuena & Solis 1978). We infer that this growth difference is probably a result of latitude. In northern Chile, environmental conditions are more favorable than in southern Chile because of a higher SST and a higher productive upwelling (Stotz et al. 2007). Indeed, the von Bertalanffy data from Coquimbo and from Chiloe come from populations of *C. chorus* farther south than our population from Hornitos (600 km and 2100 km, respectively). Another hypothesis could be a difference in measurement between the sclerochronology method and the caliper method. Last, Jones (2010) studied 4 specimens of *C. chorus* from Arica, Chile, 600 km north of Hornitos, using isotopic analysis. From oxygen isotope seasonal profiles, Jones (2010) inferred an age between 1 y and 2 y for shells from 80–105 mm, with a daily mean growth rate of 200 μm . Based on these data, the mean growth rate of the specimens of 1.5 y and 80 mm was 153 μm . This is very close to our results of 159 $\mu\text{m}/\text{day}$ for our specimen of 1.4 y and 84 mm, and reinforces our sclerochronological findings on *C. chorus* growth rhythm.

Eurhomalea rufa

Thirty bundles were counted in the *Eurhomalea rufa* shell, with 11 of them between the 2 growth anomalies shown in Figure 4A. We assume that 1 bundle is formed every month (i.e., 1 mo of shell growth separates 2 bundles) and that the growth anomalies are annual. The studied specimen would thus be 30 mo old, with an inferred birth around June 2003. The growth anomalies would thus correspond to January 2004 and 2005, and may be considered annual growth marks similar to the “summer checks” described for the Chilean Veneridae *Protothaca thaca* (Lazareth et al. 2006).

Between the second growth anomaly and the edge, 450 increments and 10 bundles were counted. Based on the same hypothesis, the time span between the second growth anomaly and the edge would be about 11 mo. One month of shell growth would thus include 41 increments (450/11)—in other words, a mean of 1.5 increments/day. At Hornitos, the tidal cycle is semidiurnal, with diurnal inequality. During a monthly cycle, *E. rufa* would thus form one growth line both at the lower low-water stage of the semidiurnal cycle (28 lines/mo) and at the higher low-water stage of the diurnal cycle (14 lines/mo), for a total of 42 lines/mo. A growth rhythm controlled by the tidal cycles has already been proposed for other bivalve species (Evans 1972, Carré et al. 2005a). However, additional investigations should be undertaken to clarify the respective effect of

environmental parameters such as the tidal range and/or SST on the other aspect of *E. rufa* growth pattern through the study of its increment thickness variations.

According to our sclerochronological analysis and shell growth rhythm hypothesis, the studied specimen reached its size (64.5 mm) in 30 mo. This is in accordance with the study of Lay-Salas (1966) who found that, between 2 y old and 3 y old, *E. rufa* shells have a size of 45–63 mm. Our assumption of an average of 1.5 increments/day is thus supported by this convergence, even if additional sclerochronological analyses remain necessary.

The growth modalities of the three studied bivalve species depend on various parameters that influence shell growth in terms of (1) time taken by the species for each growth cycle, (2) the frequency of the biomineralization processes (i.e., the rhythm of growth), and (3) the thickness of the growth increment (i.e., the amplitude of growth). The mobile Pectinidae *Argopecten purpuratus* shell growth pattern follows a solar influence with 1 increment/day. Tidal regime and SST seem to be the major environmental parameters that govern shell growth rhythms and/or increment thicknesses for the two nearshore studied species *Choromytilus chorus* and *Eurhomalea rufa*.

Characterization of the HCS Environment at Different Temporal Scales Using Bivalve Shells

The understanding of the growth patterns and temporal frameworks of the shells of our three bivalve species can shed light on HCS function. A wise use of the different growth marks and their specific periodicities can provide insight into the different environmental and climate phenomena. The phenomena that affect the HCS at their own specific periodicities are PDO (interdecadal), ENSO (interseasonal to interannual), CTW (intra-seasonal), and upwelling (weekly). Previous studies on South American molluscs attempted to use shells as recorders of main factors of environmental variations by studying not only the growth patterns of shell striae (sclerochronology) but also the variations in the shell's chemical components (sclerochemistry) (Perrier et al. 1994, Andrus et al. 2005, Carré et al. 2005a, Lazareth et al. 2006, Lietard 2007, Thébault et al. 2008, Valderrama 2008, Sadler et al. 2012). Sclerochronological studies on Chilean and Peruvian molluscs provide information on growth rhythm for a few species (Table 1).

Interdecadal Periodicity

The PDO is a climate phenomenon that impacts the Chilean–Peruvian coast at an interdecadal scale and can deeply affect marine resources, such as the regime shifts between anchovy and sardine fisheries (Chavez et al. 2003). However, exact mechanisms involved in PDO and its effect on HCS still need to be determined (Bakun & Broad 2001).

In this regard, a sclerochronological and/or sclerochemical study could provide valuable information on HCS variations under PDO influence. However, PDO variations along the Chilean and Peruvian coasts have not yet been studied using sclerochronology because fast growth and a life span less than 10 y of the South American mollusc used until now precluded such studies.

Nevertheless, species with long life spans and annual marks like *Eurhomalea rufa* (“summer check” mark) and *Choromytilus*

chorus (pronounced notch mark) may allow such studies with the help of cross-dating tools, which have been used successfully on trees, corals, and bivalves (e.g., DeLong et al. 2007, Black et al. 2009, Butler et al. 2010).

Interseasonal to Interannual Periodicities

The El Niño southern oscillation is a climate phenomenon that impacts the Chilean–Peruvian coast from interseasonal to interannual scales. Bivalve populations may be affected from one year to another depending on the strength and/or duration of the ENSO event. Thus, Urban and Tarazona (1996) noticed changes in the reproductive strategy of the Peruvian bivalve *Gari solida*, with successive shifts between somatic and gonadal production before, during, and after the 1992 to 1993 El Niño.

Among our three studied species of bivalves, the thickness variations of the monthly (bundle) and annual (summer check) growth marks of *Eurhomalea rufa* as well as the seasonal (notch) and annual (pronounced notch) growth marks of *Choromytilus chorus* could be used as recorders of environmental variations induced by ENSO in the HCS.

Several bivalve species have been studied using sclerochronology to test their potential as recorders of ENSO events, tracking SST or productivity variations (e.g., Perrier et al. 1994, Andrus et al. 2005, Carré et al. 2005a, Lazareth et al. 2006, Thébault et al. 2008, Sadler et al. 2012). These sclerochronological studies are often used to build the temporal framework essential to establishing and interpreting geochemical time series. The arid coasts of southern Peru and northern Chile are a suitable area for oxygen isotope studies because they receive little land freshwater inputs, which can disturb seawater salinity and thus the interpretation of oxygen isotope data. From a fortnightly periodicity based on a sclerochronological study, $\delta^{18}\text{O}_{\text{shell}}$ studies on modern *Mesodesma donacium* specimens led to the establishment of a paleotemperature equation that was then applied to fossil shells to give an insight into ENSO event occurrences for the past 5,000 y in northern Chile (Carré et al. 2005b). A similar study done on modern and Holocene shells of the Cardiidae *Trachycardium procerum* from shell middens of northern Peru shows a decrease of -1.7‰ in $\delta^{18}\text{O}$ data corresponding to the warming of surface waters during the 1982/1983 strong El Niño event (Perrier et al. 1994). However, when the thermal resistance threshold of a species is passed, such as during strong ENSO events, the specimen can cease growing, inducing a gap in the environmental record. This is the case of the Veneridae *Protothaca thaca*, which stops growing during too long and too warm summers (Lazareth et al. 2006). Similarly, the Pectinidae *Argopecten purpuratus* shells hardly detect ENSO events, despite their equatorial origin and their physiological tolerance of high temperatures (Wolff 1985). Such shell growth stops, related to environmental stress such as that caused by ENSO, imply that environmental variability is not recorded in the shell for that period (Jones et al. 2009). If no growth stop occurred during ENSO events, the radiocarbon signature of the shells could potentially provide information on such events. In Peruvian *Trachycardium procerum*, which survived the 1982/1983 El Niño event, a decrease in $\delta^{18}\text{O}_{\text{shell}}$ and an increase in radiocarbon were measured (Andrus et al. 2005). The decrease in $\delta^{18}\text{O}_{\text{shell}}$ was interpreted as reflecting the El Niño-related SST increase whereas the increase in radiocarbon was interpreted as reflecting a decrease in the upwelling of deep radiocarbon-depleted waters during El Niño events

(Andrus et al. 2005). Moreover, Jones (2010) noted that the sessile Mytilidae *Choromytilus chorus*, through its shell $\delta^{18}\text{O}$ signature, records seasonal variations of SST with a high intraspecific variability. This observation underlines the need to choose the sampling size carefully, with an adequate number of shells, to represent the mean growth patterns of the population. A good knowledge of species' growth behavior is thus needed for an accurate interpretation of shell geochemical records.

Intraseasonal Periodicity

The HCS is affected by CTWs at an intraseasonal periodicity, mainly from 40–70 days (Shaffer et al. 1997). These CTWs move southward from the equator along the west coast of South America. They are generated by Kelvin oceanic waves, which are formed primarily by eastward equatorial Pacific winds (Shaffer et al. 1997). The upwelling and downwelling phases of these oceanic waves impact southeastern Pacific coastal waters by modifying the thermocline depth, which modulates the upwelling intensity and the ENSO SST effect (e.g., Rutllant & Montecino 2002). These waves can be followed via the SST and sea-level variations they generate. To our knowledge, no sclerochronological studies have investigated CTWs, which act on the HCS at an intraseasonal timescale. Yet, this periodicity might be resolved using South American mollusc sclerochronological studies.

The three bivalve species of our sclerochronological study may be used as recorders of intraseasonal CTWs from their daily growth marks as well as from the weekly dark rings of *Choromytilus chorus* and monthly bundles of *Eurhomalea rufa*. Rutllant et al. (2004) showed that warm and cold SST periods lasting from 15–20 days were observed off central Chile during the 1996 La Niña and 1997 El Niño events. Those SST periods were associated with intraseasonal CTWs inducing upwelling/downwelling cycles in the thermocline depth. This physical phenomenon could be at the origin of the common 17-day periodicity that we observed by wavelet analysis in October and November 2000 in the SST data set and in the increment thickness data set of *Argopecten purpuratus*. Thus, intraseasonal CTWs may affect bivalve physiology indirectly through variations in thermocline depth by modulating their growth patterns.

To extract periodicities specific to CTWs, singular spectrum and wavelet analysis can be done (e.g., Gedalof et al. 2002, Hormazabal et al. 2002, Hormazabal et al. 2006, Black et al. 2009). Such data processing could be done on sclerochronological and sclerochemical profiles obtained from shells from different areas, sampled along the latitudinal gradient of the Chilean–Peruvian coast, to follow the CTWs moving southward from the equatorial region.

Weekly Periodicity

The deep, cold waters rich in nutrients that reach the surface (coastal upwelling) act on both the SST and primary production at weekly periodicities. At such periodicities, a sclerochronological study needs high temporal resolution (i.e., daily growth marks). However, such a high temporal resolution generally requires a higher investment than other structures of lower temporal resolution (e.g., annual periodicity).

Generally, bivalves grow by the addition of 1 or 2 increments/day (Table 1). For instance, the Pectinidae *Argopecten purpuratus* forms 1 daily increment following a circadian

rhythm, whereas the Mytilidae *Choromytilus chorus* produces 1 daily increment at each low tide, and the Veneridae *Eurhomalea rufa* produces 1.5 mean increments/day, depending on the intensity of each low tide. In other molluscan species, the increment deposition may even occur at an infradaily rhythm. Thus, the gastropod *Concholepas concholepas* shows two infradaily growth structures: an alternation of dark and translucent “increments” allowing nycthemeral differentiation as well as a succession of 40–50 layers per day (Guzmán et al. 2007, Lazareth et al. 2007). Such high temporal resolutions in mollusc sclerochronology to study oceanic physical–biological processes that occur at a daily periodicity in the HCS.

The activity (intensity and frequency) of upwelling cells along the Chilean–Peruvian coast affects both SST and primary production variations. Oxygen isotope shell ($\delta^{18}\text{O}_{\text{shell}}$) data on *Mesodesma donacium* have been used as recorder of upwelling intensity because upwelling waters are colder than surface ones (Carré et al. 2005a). Studying the intensity and frequency of the upwelling events, which bring cold deep waters enriched with nutrients and ^{12}C up to the surface, can provide information on primary production. Andrus et al. (2005) showed that an increase in the shell stable carbon isotope ($\delta^{13}\text{C}_{\text{shell}}$) signature of the Peruvian bivalve *Trachycardium procerum* was interpreted as a decrease in primary production (Perrier et al. 1994). The seasonal activity of the upwelling has also been studied using geochemical analysis in the Veneridae *Protothaca staminea*; stable carbon isotope values less than -0.5‰ correspond to spring or summer coastal upwelling events in the Humboldt bay (40.8° N , California) (Takesue & Van geen 2004). More recently, Sadler et al. (2012) proposed that $\delta^{13}\text{C}_{\text{shell}}$ variations in *Mesodesma donacium* shells are mainly the result of $\delta^{13}\text{C}_{\text{DIC}}$ changes. Lower $\delta^{13}\text{C}_{\text{shell}}$ values correspond to lower $\delta^{13}\text{C}_{\text{DIC}}$ values and to an increase in upwelling intensity. However, strong evaporation in bays, or freshwater input can disturb the interpretation of primary production signals obtained from $\delta^{18}\text{O}_{\text{shell}}$ and $\delta^{13}\text{C}_{\text{shell}}$ data. In addition, the intensity of coastal upwelling episodes can be recorded by studying the radiocarbon shell variations of bivalve shells as an indicator of water mass age; the deep water mass being older than subsuperficial ones (Andrus et al. 2005). Sclerochemical analyses can also be used to study past upwelling activities in the HCS. Using fossil shells for paleoreconstruction purposes, Teusch et al. (2002) used stable oxygen and carbon isotopes in Turritellidae and suggested that upwelling intensities were more pronounced during some periods of the Pleistocene along Chilean coasts. Lastly, Sadler et al. (2012) studied *Mesodesma donacium* bivalve shells from Ica (15° S , Peru) and showed a difference in mean upwelling intensity ($0.5\text{‰ } \delta^{13}\text{C}_{\text{shell}}$) between modern and Inca periods.

Environmental and Climatic Event Interactions

Various environmental and climatic events take place in the HCS, affecting SST and primary production at different spatiotemporal scales—the warm and cold phases of interdecadal PDO and interseasonal to interannual ENSO, the modulation of thermocline depth by intraseasonal CTWs, and the frequency and intensity of weekly upwelling. Their interactions enhance the complexity of the system and, thus, the difficulty of extracting valuable information from sclerochronological and sclerochemical data sets.

In the HCS, chlorophyll *a* (Chl *a*) variability, an index of phytoplankton biomass, is latitude dependent and is associated

with ENSO perturbations (e.g., Correa-Ramirez et al. 2012). Coastal upwelling intensity affects Chl *a* variability through the supply of nutrients (Patti et al. 2008). Thus, ENSO and upwelling events can interact on Chl *a* variability and indirectly on bivalve growth. Some sclerochronological results can thus be difficult to interpret. An increase in growth rate of bivalve shells in the HCS can indeed be the result of two antagonist phenomena: an (1) El Niño (La Niña) event increases (decreases) the mean SST, which has a positive effect on the growth of bivalve species originating from tropical (polar) regions; and (2) nutrient input via upwelling, which has a positive effect on bivalve growth. During an El Niño event, the warming of surface water along the Chilean–Peruvian coast deepens the thermocline, reducing the nutrient pool that usually reaches the surface. The study of the chemical components of bivalve shells could provide an insight into the respective influence of an ENSO or upwelling event when a growth variation is observed. In fact, oxygen isotopes are used to record the SST variations induced by El Niño event, as described earlier. Moreover, the study of periodicity variation of $\delta^{18}\text{O}_{\text{shell}}$ could be used to separate the respective influence of upwelling (weekly periodicity) or ENSO event (interannual periodicity). Last, ^{14}C and $\delta^{13}\text{C}_{\text{shell}}$ signatures can be used as archives of upwelling intensities (as discussed earlier). Other proxies, such as trace metal elements, have been used in different archives (bivalves, corals) to investigate upwelling and ENSO events through SST or productivity variations in other oceanic regions; Ba/Ca, Mo/Ca, or Sr/Ca have indeed been used to track upwelling and coastal environmental variations (e.g., Lea et al. 1989, Gillikin et al. 2006, Montaggioni et al. 2006, Thébault et al. 2009). Looking at combinations of such archives in multiproxy studies should help separate the respective impact of distinct environmental variabilities in the HCS.

Moreover, because ENSO and CTWs act, in part, at a similar periodicity (interseasonal vs. intraseasonal, respectively), it is still difficult to characterize their respective effects from raw sclerochronological and sclerochemical profiles. Thus, singular spectrum and wavelet analysis could give an insight into the respective effect of the CTW and ENSO events on the variations in SST in the HCS. Indeed, Gushchina and Dewitte (2011) established that a strong link exists between intraseasonal tropical variability and ENSO events. They found that Kelvin waves, from which CTWs form, preceded weak El Niño events by half a year. They also showed changes in the relationship (positive/negative) between intraseasonal variations and El Niño events at a decadal, PDO-related, periodicity.

To understand the complex environmental and climatic phenomena taking place in the HCS, sclerochronological and sclerochemical studies using cross-dating tools, multiproxy archives, and wavelet data processes could be of great help in future investigations.

CONCLUSION AND FUTURE WORK

We studied three bivalve species living along the Chilean–Peruvian coast (*Argopecten purpuratus*, *Choromytilus chorus*, and *Eurhomalea rufa*). By means of sclerochronology, their growth patterns were analyzed and a temporal framework was suggested for each of the three species. Solar and/or lunar regimes seem to be the major environmental parameters that govern shell growth rhythms and/or increment thicknesses for

the three studied species. The bivalves *C. chorus* and *E. rufa*, which grow more slowly and have a longer life span than *A. purpuratus*, are better fit for paleo-environmental and paleo-ENSO reconstructions. Daily, weekly, monthly, and annual marks appear in the growth patterns of the three bivalves studied, which should make them useful for investigating the climatic and environmental events taking place in the HCS at multiple periodicities. However, the results presented here need to be confirmed by replicating such studies on several individuals of the same age to enhance the significance of the study. The study of environmental and climatic events using sclerochronology and shell geochemistry requires careful selection of the mollusc species. In addition, several points can improve the choice of the bivalve species used in a sclerochronological study. First, it is necessary to focus on the raw material—the bivalve shell itself. Essential structural aspects are clear growth increments as well as growth marks related to specific timescales. Second, bivalve species need to have specific ecological characteristics such as a large geographical range to make large-scale studies easier, a sensitivity to climatic events but with a sufficient ecological range to survive, and a growth activity during most of the year and during temperature extremes to set up a reliable paleotemperature equation. Last, methodological aspects—in particular, the choice of the study site—need to be taken into account. For example, the calibration step requires that the site be monitored with concomitant records of bivalve growth and environmental parameters. And, conducting a paleoreconstruction study requires paleontological and archaeological sites with bivalve shells preserved from temporal alterations (diagenesis).

A highly variable environment such as the HCS requires tools capable of recording its variations over a wide range of periodicities. Upwelling, CTW, ENSO, and PDO events contribute to this environmental and climatic variability. The thermocline depth is modified by these different events at their own time-scales (respectively, daily to weekly, intraseasonally, interseasonally to interannually, and on a decadal scale). The thermocline variation translates into changes in SST and in the qualitative and quantitative productivity of phytoplankton. These two environmental factors are critical to bivalve growth.

Sclerochronological studies on HCS mollusc shells provide access to these different timescales, from daily to interannual. Studying shells of modern specimens using sclerochronology can thus provide important information on bivalve growth parameters as well as on the SST and productivity variations during the bivalve's growth.

Complementing sclerochronology with isotope studies (^{18}O , ^{13}C , ^{14}C), and eventually trace metals, is a promising way to discriminate between the respective effects of upwelling/ENSO events on the environment. In addition, wavelet data processes could give an insight into CTW events, and cross-dating tools could be used to study PDO variability. Last, multiproxy studies could broaden the understanding of the climatic and environmental context in the HCS. Such studies could then be applied to fossil species for paleotemperature and paleoproductivity reconstructions.

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LITERATURE CITED

- Alamo, V. & V. Valdivieso. 1987. Lista sistemática de moluscos marinos del Perú. Lima: Instituto del Mar del Perú. 183 pp.
- Andrus, C., G. Hodgins, H. Sandweiss & D. Crowe. 2005. Molluscan radiocarbon as a proxy for El Niño-related upwelling variation in Peru. *Geol. Soc. Am.* 395:13–20.
- Arntz, W. E. & J. Tarazona. 1990. Effects of El Niño 1982–83 on benthos, fish and fisheries off the South American Pacific coast. In: P. W. Glynn, ed. *Global ecological consequences of the 1982–83 El Niño-southern oscillation*. Amsterdam: Elsevier. pp. 323–360.
- Arntz, W. E. & E. Valdivia. 1985. Incidencia del fenómeno El Niño sobre los mariscos en el litoral peruano. In: W. E. Arntz, A. Landa & J. Tarazona, eds. *El Niño: su impacto en la fauna marina*. Lima, Peru: Boletín Instituto del Mar del Perú. pp. 91–101.
- Avendaño M. & Cantillanez M. 1997. Necesidad de crear una reserva marina de ostiones en el banco de la Rinconada (Antofagasta II region, Chile). *Estudios Oceanol.* 16:109–113.
- Avendaño, M. & M. Cantillanez. 2005. Growth and population structure of *Argopecten purpuratus* at La Rinconada Marine Reserve, Antofagasta, Chile. *Cienc. Mar.* 31:491–503.
- Avendaño, M., M. Cantillanez, G. Thouzeau & J. B. Pena. 2007. Artificial collection and early growth of spat of the scallop *Argopecten purpuratus* (Lamarck, 1819), in La Rinconada Marine Reserve, Antofagasta, Chile. *Sci. Mar.* 71:197–205.
- Bakun, A. & K. Broad. 2001. Climate and fisheries: interacting paradigms, scales, and policy approaches. Presented at the IRI-IPRC Pacific Climate-Fisheries Workshop. Honolulu, HI.
- Bertaux, J., F. Frohlich & P. Ildefonse. 1998. Multicomponent analysis of FTIR spectra: quantification of amorphous and crystallized mineral phases in synthetic and natural sediments. *J. Sediment. Res.* 68:440–447.
- Bessat, F. & M. Tabeaud. 1998. La croissance corallienne: un marqueur des environnements actuels et passés. *Ann. Geogr.* 599:16–32.
- Beukema, J. & B. Meehan. 1985. Latitudinal variation in linear growth and other shell characteristics of *Macoma balthica*. *Mar. Biol.* 90:27–33.
- Black, B. A., C. A. Copenheaver, D. C. Frank, M. J. Stuckey & R. E. Kormanyos. 2009. Multi-proxy reconstructions of north-eastern Pacific sea surface temperature data from trees and Pacific geoduck. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 278: 40–47.
- Blanco, J. L., M. E. Carr, A. Thomas & P. Strub. 2002. Hydrographic conditions off northern Chile during the 1996–1998 La Niña and El Niño events. *J. Geophys. Res.* 107:1–19.
- Buddemeir, R. 1978. Sclerochronology: a data source for reef systems models. *Band Atoll Res. Bull.* 220:25–32.
- Butler, P. G., C. A. Richardson, J. D. Scourse, A. D. Wanamaker, Jr., T. M. Shammon & J. D. Bennell. 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.
- Cantillanez, M., M. Avendaño, G. Thouzeau & M. Le Penneç. 2005. Reproductive cycle of *Argopecten purpuratus* (Bivalvia: Pectinidae) in La Rinconada Marine Reserve (Antofagasta, Chile): response to environmental effects of El Niño and La Niña. *Aquaculture* 246:181–195.
- Carr, M. E. 2002. Estimation of potential productivity in eastern boundary currents using remote sensing. *Deep Sea Res. Part II Top. Stud. Oceanogr.* 49:59–80.
- Carré, M., I. Bentaleb, D. Blamart, N. Ogle, F. Cardenas, S. Zevallos, R. M. Kalin, L. Ortlieb & M. Fontugne. 2005a. Stable isotopes and sclerochronology of the bivalve *Mesodesma donacium*: potential application to Peruvian paleoceanographic reconstructions. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 228:4–25.
- Carré, M., I. Bentaleb, M. Fontugne & D. Lavallee. 2005b. Strong El Niño events during the early Holocene: stable isotope evidence from Peruvian sea shells. *Holocene* 15:42–47.
- Castilla, J. C. & J. Cancino. 1976. Spawning behaviour and egg capsules of *Concholepas concholepas* (Mollusca: Gastropoda: Muricidae). *Mar. Biol.* 37:255–263.
- Cazelles, B., M. Chavez, D. Berteaux, F. Ménard, J. Vik, S. Jenouvrier & N. Stenseth. 2008. Wavelet analysis of ecological time series. *Oecologia* 156:287–304.
- Chavez, F. P., A. Bertrand, R. Guevara Carrasco, P. Soler & J. Csirke. 2008. The northern Humboldt Current System: brief history, present status and a view towards the future. *Prog. Oceanogr.* 79:95–105.
- Chavez, F., J. Ryan, S. Lluch-Cota & M. Niquen. 2003. From anchovies to sardines and back: multidecadal change in the Pacific Ocean. *Science* 299:217–221.
- Clark, G. R., II. 1974. Growth lines in invertebrates skeletons. *Annu. Rev. Earth Planet. Sci.* 2:77–99.
- Correa-Ramirez, M. A., S. E. Hormazabal & C. E. Morales. 2012. Spatial patterns of annual and interannual surface chlorophyll-a variability in the Peru–Chile current system. *Prog. Oceanogr.* 92:8–17.
- Corrège, T., M. Gagan, J. Berck, G. Burr, G. Cabioch & F. Le Cornec. 2004. Interdecadal variation in the extent of South Pacific tropical waters during the younger Dryas event. *Nature* 428:927–929.
- Cortes, J. 1997. Biology and geology of eastern Pacific coral reefs. *Coral Reefs* 16:39–46.
- Dauphin, Y., J. P. Cuif, J. Doucet, M. Salome, J. Susini & C. T. Williams. 2003. *In situ* mapping of growth lines in the calcitic prismatic layers of mollusc shells using X-ray absorption near-edge structure (XANES) spectroscopy at the sulphur K-edge. *Mar. Biol.* 142:299–304.
- DeLong, K., T. Quinn & F. Taylor. 2007. Reconstructing twentieth-century sea surface temperature variability in the southwest Pacific: a replication study using multiple coral Sr/Ca records from New Caledonia. *Paleoceanography* 22:PA4212.
- Diaz, A. & L. Ortlieb. 1993. El fenómeno “El Niño” y los moluscos de la costa peruana. *Bull. Inst. Français Etudes Andines* 22:159–177.
- Druffel, E. R. M. & S. Griffin. 1995. Regional variability of surface ocean radiocarbon from southern Great Barrier Reef corals. *Radiocarbon* 37:517–524.
- Escribano, R., G. Daneri, L. Farías, V. A. Gallardo, H. E. González, D. Gutiérrez, C. B. Lange, C. E. Morales, O. Pizarro, O. Ulloa & M. Braun. 2004. Biological and chemical consequences of the 1997–1998

- Ortiz Galarza, K. 2011. Biología reproductiva de “concha corazón” *Trachycardium procerum* (Sowerby, 1833). (Cardiidae, Pelecypoda) Lima (PE). *Biologist (Lima)* 9:66–97.
- Panfili, J., H. Troadec, P. Wright & H. de Pontual. 2002. Manual of fish sclerochronology. IFREMER-IRD. Brest, France. 464 pp.
- Pannella, G. 1976. Tidal growth patterns in recent and fossil mollusc bivalve shells: a tool for the reconstruction of paleotides. *Naturwissenschaften* 63:539–543.
- Patti, B., C. Guisande, A. R. Vergara, I. Riveiro, I. Maneiro, A. Barreiro & A. Bonanno. 2008. Factors responsible for the differences in satellite-based chlorophyll a concentrations between the major global upwelling areas. *Estuar. Coast. Shelf Sci.* 76:775–786.
- Paulet, Y.-M., A. Lorrain, J. Richard & S. Pouvreau. 2006. Experimental shift in diet $\delta^{13}\text{C}$: a potential tool for ecophysiological studies in marine bivalves. *Org. Geochem.* 37:1359–1370.
- Perrier, C., C. Hillaire-Marcel & L. Ortlieb. 1994. Paléogéographie littorale et enregistrement isotopique (^{13}C , ^{18}O) d'évènements de type El Niño par les mollusques Holocènes et récents du Nord-Ouest Péruvien. *Géogr. Phys. Quat.* 48:23–38.
- Piñones, A., J. C. Castilla, R. Guínez & J. L. Largier. 2007. Nearshore surface temperatures in Antofagasta Bay (Chile) and adjacent upwelling centers. *Cienc. Mar.* 33:37–48.
- Rasmusson, E. M. & T. H. Carpenter. 1982. Variations in tropical sea surface temperature and surface wind fields associated with the southern oscillation/El Niño. *Mon. Weather Rev.* 110:354–384.
- Rhoads, D. C. & R. A. Lutz. 1980. Skeletal growth of aquatic organisms: biological records of environmental change. New York: Plenum Press. 750 pp.
- Riascos, J. M. 2009. Thriving and declining: population dynamics of the macha (*Mesodesma donacium*, Bivalvia, Mesodesmatidae) along a latitudinal gradient of the Humboldt Current upwelling system. Bremen: Bremen University. PhD dissertation 124 pp.
- Riascos, J. M., D. Carstensen, J. Laudien, W. E. Arntz, M. E. Oliva, A. Guntner & O. Heilmayer. 2009. Thriving and declining: climate variability shaping life-history and population persistence of *Mesodesma donacium* in the Humboldt upwelling system. *Mar. Ecol. Prog. Ser.* 385:151–163.
- Richardson, C. A. 1990. Tidal rhythms in the shell secretion of living bivalves. In: P. Brosche & J. Sundermann, eds. Earth's rotation from eons to days. Berlin: Springer-Verlag. pp. 215–226.
- Rollins, H. B., D. H. Sandweiss & J. C. Rollins. 1986. Effect of the 1982–1983 El Niño on bivalve mollusks. *Natl. Geogr. Res.* 2:106–112.
- Rollins, H. B., D. H. Sandweiss & J. C. Rollins. 1990. Mollusks and coastal archaeology: a review. In: N. P. Lasca & J. D. Donahue, eds. Archaeological geology of North America. Geological Society of America. Boulder, CO. pp. 467–478.
- Rutllant, J. & V. Montecino. 2002. Multiscale upwelling forcing cycles and biological response off north-central Chile. *Rev. Chil. Hist. Nat.* 75:217–231.
- Rutllant, J. A., B. Rosenbluth & S. Hormazabal. 2004. Intraseasonal variability of wind-forced coastal upwelling off central Chile (30°S). *Cont. Shelf Res.* 24:789–804.
- Sadler, J., M. Carré, M. Azzoug, A. J. Schauer, J. Ledesma, F. Cardena, B. M. Chase, I. Bentaleb, S. D. Muller, M. Mandeng, E. J. Rohling & J. P. Sachs. 2012. Reconstructing past upwelling intensity and the seasonal dynamics of primary productivity along the Peruvian coastline from mollusk shell stable isotopes. *Geochem. Geophys. Geosyst.* 13:17.
- Schäfer, P., H. Fortunato, B. Bader, V. Liebetrau, T. Bauch & J. J. G. Reijmer. 2011. Growth rates and carbonate production by coralline red algae in upwelling and non-upwelling settings along the Pacific coast of Panama. *Palaios* 26:420–432.
- Schöne, B. R. 2008. The curse of physiology: challenges and opportunities in the interpretation of geochemical data from mollusk shells. *Geo. Mar. Lett.* 28:269–285.
- Schöne, B. R., E. Dunca, J. Fiebig & M. Pfeiffer. 2005. Mutvei's solution: an ideal agent for resolving microgrowth structures of biogenic carbonates. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 228:149–166.
- Schöne, B. R., E. Dunca, H. Mutvei & U. Norlund. 2004. A 217-year record of summer air temperature reconstructed from freshwater pearl mussels (*M. margaritifera*, Sweden). *Quat. Sci. Rev.* 23:1803–1816.
- Schöne, B. R., D. H. Goodwin, K. W. Flessa, D. L. Dettman & P. D. Roopnarine. 2002. Sclerochronology and growth of the bivalve mollusks *Chione* (Chionista) *fluctifraga* and *C.* (Chionista) *cortezii* in the northern Gulf of California, Mexico. *Veliger* 45:45–54.
- Shaffer, G., O. Pizarro, L. Djurfeldt, S. Salinas & J. Rutllant. 1997. Circulation and low-frequency variability near the Chilean coast: remotely forced fluctuations during the 1991–1992 El Niño. *J. Phys. Oceanogr.* 27:217–235.
- Stotz, W., L. Caillaux, C. Olivares, M. Valdebenito, D. Lancellotti, J. Aburto, C. Cerda, J. Morales, P. Guajardo, V. Jiménez & C. Mondaca. 2007. Criterios de explotación de recursos bentónicos: informe final proyecto fondo de investigación pesquera 2005–42. Universidad Católica del Norte. Antofagasta, Chile. 424 pp.
- Takesue R. K. & A. Van geen. 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.
- Tarazona, J., D. Gutierrez, C. Paredes & A. Indacochea. 2003. Overview and challenges of marine biodiversity research in Peru. *Gayana (Zool.)* 67:206–231.
- Teusch, K. P., D. J. Jones & W. D. Allmon. 2002. Morphological variation in turritelid gastropods from the Pleistocene to recent of Chile: association with upwelling intensity. *Palaios* 17:366–377.
- Thatje, S., O. Heilmayer & J. Laudien. 2008. Climate variability and El Niño southern oscillation: implications for natural coastal resources and management. *Helgol. Mar. Res.* 62:5–14.
- Thébault, J. 2001. *Argopecten purpuratus* (Lmk.): calibration d'un capteur eulerien de la variabilité de l'environnement côtier dans l'Océan Pacifique Sud (Rinconada, Chili). Brest: University de Bretagne Occidentale. 43 pp.
- Thébault, J., L. Chauvaud, S. L'Helguen, J. Clavier, A. Barats, S. Jacquet, C. Pécheyran & D. Amouroux. 2009. Barium and molybdenum records in bivalve shells: geochemical proxies for phytoplankton dynamics in coastal environments? *Limnol. Oceanogr.* 54:1002–1014.
- Thébault, J., G. Thouzeau, L. Chauvaud, M. Cantillanez & M. Avendaño. 2008. Growth of *Argopecten purpuratus* (Mollusca: Bivalvia) on a natural bank in northern Chile: sclerochronological record and environmental controls. *Aquat. Living Resour.* 21:45–55.
- Thiel, M., E. C. Macaya, E. Acuna, W. E. Arntz, H. Bastias, K. Brokordt, P. A. Camus, J. C. Castilla, L. R. Castro, M. Cortes, C. P. Dumont, R. Escribano, M. Fernandez, J. A. Gajardo, C. F. Gaymer, I. Gomez, A. E. Gonzalez, H. E. Gonzalez, P. A. Haye, J. E. Illanes, J. L. Iriarte, D. A. Lancellotti, G. Luna-Jorquera, C. Luxoro, P. H. Manriquez, V. Marin, P. Munoz, S. A. Navarrete, E. Perez, E. Poulin, J. Sellanes, H. H. Sepulveda, W. Stotz, F. Tala, A. Thomas, C. A. Vargas, J. A. Vasquez & J. M. A. Vega. 2007. The Humboldt Current System of northern and central Chile. *Oceanography and marine biology*, vol. 45. Boca Raton, FL: CRC Press-Taylor & Francis. pp. 195–344.
- Torrence, C. & G. P. Compo. 1998. A practical guide to wavelet analysis. *Bull. Am. Meteorol. Soc.* 79:61–78.
- Urban, H. J. 1994. Upper temperature tolerance of ten bivalve species off Peru and Chile related to El Niño. *Mar. Ecol. Prog. Ser.* 107:139–145.
- Urban, H.-J. & J. Tarazona. 1996. Effects of El Niño/southern oscillation on the population dynamics of a *Gari solida* population (Bivalvia, Psammobiidae) from Bahía Independencia, Peru. *Mar. Biol.* 125:725–734.
- Valderrama, I. 2008. Calibration de la relation température de l'eau: isotopes stables de l'oxygene et du carbone dans la coquille d'un

- gasteropode littoral (*Concholepas concholepas*) du Perou–Chili. Paris: UPMC. 33 pp.
- Wanamaker, A. D., K. J. Kreutz, B. R. Schöne & D. S. Introne. 2011. Gulf of Maine shells reveal changes in seawater temperature seasonality during the Medieval Climate Anomaly and the Little Ice Age. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 302: 43–51.
- Werner, F., R. G. Lough, A. Bertrand, R. Guevara Carrasco, P. Soler, J. Csirke & F. P. Chavez. 2008. The northern Humboldt Current System: ocean dynamics, ecosystem processes and fisheries. *Prog. Oceanogr.* 79:198–207.
- Wolff, M. 1985. Abundancia masiva y crecimiento de preadultos de la concha de abanico peruana (*Argopecten purpuratus*) en la zona de Pisco bajo condiciones de El Niño 1983. In: W. L. Arntz & J. Tarazona, eds. El fenómeno El Niño y su impacto en la fauna marina. Lima Callao: Instituto del Mar del Perú. pp. 87–89.
- Zhang, Y., J. M. Wallace & D. S. Battisti. 1997. ENSO-like interdecadal variability: 1900–93. *J. Clim.* 10:1004–1020.