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PART N, REVISED, VOLUME 1, CHAPTER 14: BIVALVE SCLEROCHRONOLOGY AND GEOCHEMISTRY

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Bivalve shells act as unique skeletal diaries. They can provide precisely dated, unprecedented ultra high-resolution (daily, seasonal, annual) records of life history traits, as well as records of climate changes in environmental settings from which only limited data exist. Bivalve sclerochronology seeks to deduce these records from the growth patterns preserved in shells and is a term that was introduced for similar studies on corals (BUDDEMEIER & MARAGOS, 1974). Sclerochronological techniques have been successfully applied to many different fields, including paleoclimatology, archeology, biology, evolution, and retrospective environmental biomonitoring. The full potential of bivalves for such studies becomes evident through the following considerations.

Many bivalve species are extremely long lived (THOMPSON, JONES, & DREIBELBIS, 1980; ZOLOTAREV, 1980; STROM & others, 2004), and thus, they are perfectly suited as long-term paleoclimate archives. For example, the ocean quahog, *Arctica islandica* (LINNAEUS, 1767), lives for more than 500 years (JONES, 1983; ROPES & MURAWSKI, 1983; SCHÖNE, FIEBIG, & others, 2005; WANAMAKER, SCOURSE, & others 2008; BUTLER & others, 2011), *Neopycnodonte zibrowii* WISSHAK & others, 2009, for more than 545 years (WISSHAK & others, 2009), and the European freshwater pearl mussel, *Margaritifera margaritifera* (LINNAEUS, 1758), exceeds a lifespan of 200 years (MUTVEI & WESTERMARK, 2001). Each specimen of such long-lived species opens a multi-century window into the climatic past. Moreover, such long-lived species allow the construction of master chronologies (much like tree rings) to extend the paleoclimate records beyond the lifetime of an individual animal (JONES, ARTHUR, & ALLARD, 1989; MARCHITTO & others, 2000; SCHÖNE & others, 2003; BUTLER & others, 2010).

Throughout their lifetime, and assuming sufficient growth rates, bivalves sensitively and faithfully record changes—in chronological order—of the ambient physico-chemical environment, in particular temperature (HENDERSON, 1929; KENNISH & OLSSON, 1975), food availability (ANSELL, 1968; PAGE & HUBBARD, 1987; SATO, 1997), salinity (DAVIS & CALABRESE, 1964; MARSDEN & PILKINGTON, 1995), and water quality (FRANTSEVICH & others, 1996; MUTVEI & others, 1996; RAVERA & others, 2007). Environmental changes are encoded in the shells in the form of variable growth rates (KENNISH & OLSSON, 1975; KOIKE, 1980) and geochemical properties (JONES, WILLIAMS, & ROMANEK, 1986; WEFER & BERGER, 1991; GILLIKIN, DE RIDDER, & others, 2005).

Among aquatic organisms, bivalves exhibit an unrivaled biogeographic distribution, extending from the poles to the equator, from the deep sea to shallow waters, and from marine to freshwater habitats. Therefore, they can provide environmental data from many different settings. In addition to their wide spatial distribution, they also have a long geologic history and cultural significance. Bivalves occur abundantly in the fossil record, documenting more than 500 million years of evolutionary history. On human time scales, they were important food resources for historic and prehistoric people. A vast number of shells of short-lived species (e.g., *Mercenaria* spp., *Spisula* spp., *Chione* spp., *Phacosoma* spp.; JONES, WILLIAMS, & ARTHUR, 1983; TANABE & OBA, 1988; GOODWIN & others, 2001;

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Surge & Walker, 2006) are preserved in many archeological shell middens and shell-bearing deposits in nearly all coastal environments. These midden deposits provide an inexhaustible resource for studies on seasonal mobility patterns and resource use by past populations, as well as paleoclimate and paleoseasonality studies (Coutts, 1970; Koike, 1975; Quitmyer, Jones, & Arnold, 1997; Andrus & Crowe, 2000; Hallmann & others, 2009; Miyaji & others, 2010).

The most important prerequisite for chronological research, however, is precise time control. Therefore, the following section provides an overview of concepts of periodic growth pattern formation in bivalves.

SHELL CALENDARS

Periodic growth patterns are prerequisite for sclerochronological analyses because they permit a precise temporal alignment of the shell record. Such growth patterns result from periodic changes in the rate of shell deposition associated with variations in chemical composition and crystallographic properties. Growth lines separate the growth pattern into time slices of almost equal duration, so-called growth increments (Barker, 1964; Jones, 1980; Ropes & others, 1984). Growth increments and adjoining growth lines form a shell calendar and provide an ideal means to measure time. A variety of different periodic growth patterns have been recognized in bivalve shells, including annual, lunar-monthly (apogee + perigee fortnight cycle), fortnightly, solar-daily (circadian, ~24 hr), lunar-daily (circalunidian, Palmer, 1995; diurnal, ~24.8 hours), semidiurnal (ciratidal, Palmer, 1995; 12.4 hours) and ultradian (time scales of minutes and hours).

Growth increments and lines are typically studied in the outer or middle shell layer of cross-sectioned valves (cut perpendicular to the growth lines; Fig. 1). Several preparation techniques have been developed to visualize growth patterns (Clark, 1980; Kennish, Lutz, & Rhoads, 1980; Tevesz & Carter, 1980; Richardson, 1987; Schöne, Dunca, & others, 2005). The term outer shell layer generally refers to the outer layer of a microstructurally two-layered (outer + inner) or the outer and middle layer of a three-layered (outer + middle + inner) shell, although some workers refer to the outer and middle shell layers as the outer and inner sublayers of an outer shell layer (Schöne, Radermacher, & others, 2011). In polished cross sections, growth lines appear as dark lines and growth increments as white bands under reflected light (Fig. 1). In some species (e.g., *Mercenaria* spp.), dark and light increments revealed under reflected light (translucent and opaque, respectively, under transmitted light) are formed during periods of slow (dark increment) and fast (light increment) growth, and a couplet represents a period of annual growth (Quitmyer, Jones, & Arnold, 1997). Etching of polished cross sections forms a three-dimensional relief of etch-resistant ridges and stronger etched growth increments. When combined with dyes (Fig. 1), portions with elevated levels of certain substances (e.g., sugars) can be visually enhanced (Mutvei, 1979; Schöne, Dunca, & others, 2005). In acetate peels (transmitted light), however, growth lines appear as dark lines, whereas in thin sections, growth lines appear as translucent zones and growth increments as opaque bands (Richardson, 1987; Wanamaker, Heinemeier, & others, 2008).

In the absence of diagenesis or taphonomic alteration, the outer shell layer and portions of the middle shell layer provide a complete and undisturbed shell record (Fig. 2). These two layers are located at the shell margins, below the periostracum, and are precipitated from the outer extrapallial fluid (EPF) by mantle activity (Crenshaw, 1980). The outer EPF is secreted from the outer epithelium mantle cells (Vander Putten & others, 2000; Hansen Klünder & others, 2008). In some species, such as *A. islandica* [but not *Saxidomus gigantea* (Deshayes, 1839); Hallmann & others, 2009], the outer EPF also forms parts of the hinge plate. During shell opening, new

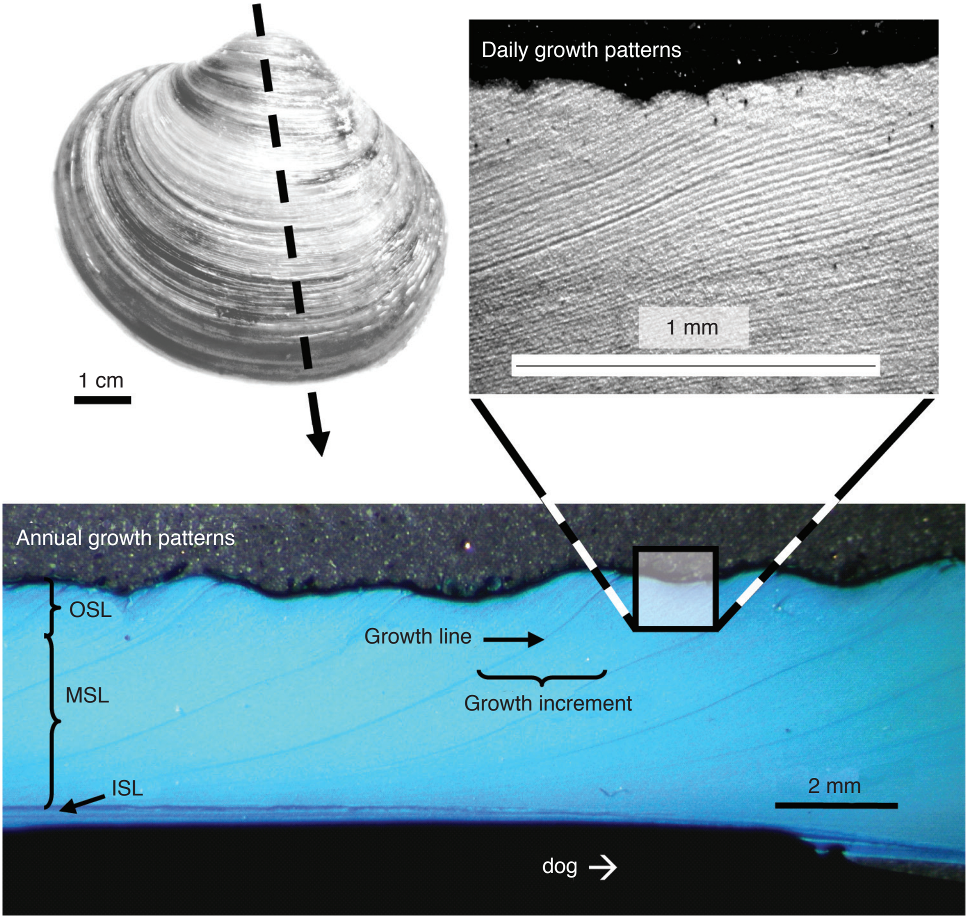

Fig. 1. Internal annual and daily growth patterns in cross sections of *Arctica islandica*, which have been immersed in Mutvei's solution. Organic-rich, etch-resistant growth lines are stained dark blue; growth increments appear in lighter shades of blue; *dog,* direction of growth; *OSL,* outer shell layer; *MSL,* middle shell layer; *ISL,* inner shell layer (new).

shell material is accreted along all shell margins and inner surfaces, i.e., along the outer and middle shell layers by the outer EPF and along the inner shell layer by the inner EPF (which is secreted from inner epithelium mantle cells; Vander Putten & others, 2000; Hansen Klünder & others, 2008) (Fig. 2). Bivalve shells increase in height, overall size, and/or thickness by accretion of new shell material to all three shell layers. Shell dissolution may occur repeatedly during extended periods of shell closure (for example, during seasonal anoxia, winter or summer extremes), but only along the inner shell surfaces (inner shell layer and the inner portions of the middle shell layer; Fig. 2) (Crenshaw, 1980). Therefore, the inner shell layer and the inner portion of the middle shell layer cannot be used as a calendar-dated climate archive. Shell dissolution during shell closure does not affect the outer shell layer and the outermost portion of the middle shell layer (Fig. 2). In many species, small to large portions of the shell margins are in direct contact with each other during shell closure (Fig. 2). Evidently, no dissolution can occur under such circumstances in these shell portions.

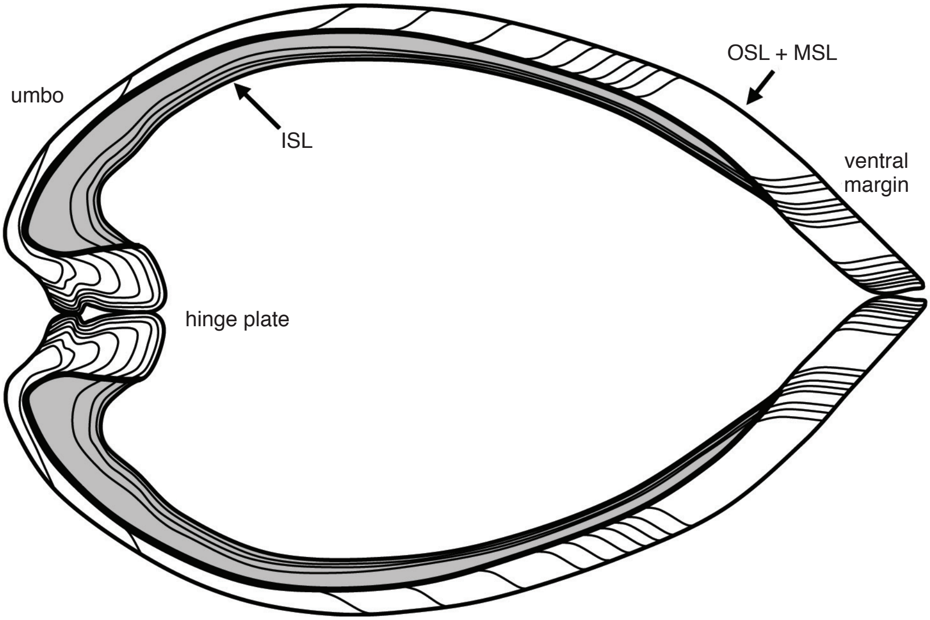

FIG. 2. Schematic representation of different shell layers and growth patterns in cross-sectioned valves of *Arctica islandica,* offshore northeastern Iceland. Growth patterns are formed at growth margins (ventral margin, hinge plate, inner shell layer) by mantle activity during shell opening. *OSL+MSL,* outer and middle shell layers (white); *ISL,* inner shell layer (grey); *thick line* separating MSL and ISL, pallial myostracum (new).

The outer shell layer and the outer part of the middle shell layer can grow by accreting new shell material, but they do not lose material during anaerobiosis. The hypothesis by GORDON and CARRIKER (1978) that growth lines are caused by anaerobiosis must therefore be rejected, at least for the outer and part of the middle shell layers.

Growth line formation requires a gradually waning and/or waxing of biomineralization rate as well as changes in chemical and crystallographic properties. A sudden growth cessation followed by resumption of shell growth with similar rates as before would be almost impossible to recognize. The formation of growth lines clearly does not require complete closure of the shell, because growth lines are present even in permanently widely gaping shells such as *Panopea* spp. This genus cannot completely close its valves, because its siphons are too large to be fully retracted into the shell.

Slow shell growth (and growth line formation) is associated with elevated amounts of organic material relative to calcium carbonate. This is chemically indicated by increased levels of phosphorous and sulfur at the growth lines (TANABE, 1988) as well as higher amounts of mucopolysaccharides and glucosamids (SCHÖNE, DUNCA, & others, 2005). Slow-growing shell portions are also associated with a significant change in crystal size, habitus, and orientation. In porcelaneous bivalves, the growth lines often consist of irregular, simple prisms, whereas the substance of growth increments is structurally more complex, e.g., composite prismatic, crossed lamellar, and/or complex cross lamellar (ROPES & others, 1984; Fig. 3). Both variations in proportion of organic matrix and differences in crystal fabrics are essential for distinguishing between growth lines and growth increments.

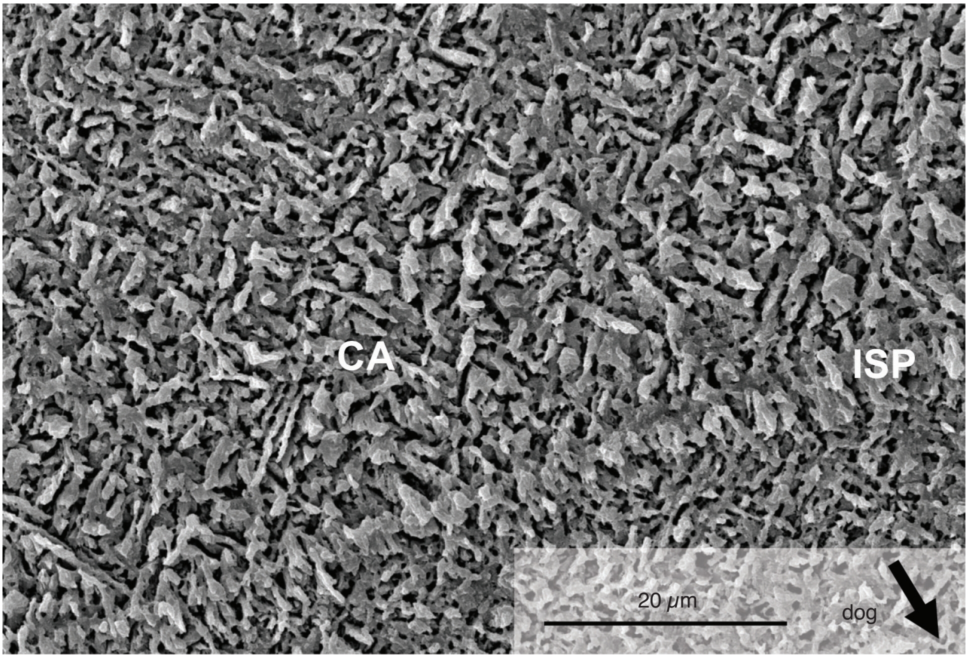

FIG. 3. Crystal fabrics in the middle shell layer (see Fig. 1) of *Arctica islandica*. Annual growth lines consist of irregular simple prisms and irregular spherulitic prisms (*ISP*), whereas the annual increments are composed of crossed acicular (*CA*) crystal fabrics; *dog,* direction of growth (new).

Notably, some specimens exhibit indistinct growth lines. If shell growth proceeds at a slow rate for an extended period of time, growth lines can appear broad and frayed, as in *Mercenaria* from Florida. In such cases, JONES (1980) and JONES and QUITMYER (1996) recommended the use of the terms white (opaque in thin sections) increments and dark (translucent in thin sections) increments (=growth line).

DAILY GROWTH PATTERNS

Many bivalves form daily growth patterns in their shells. Such daily microgrowth patterns are ideally studied in fast growing, young portions of the shells. Especially during optimum growth conditions, the number of microgrowth (µm-scale growth) increments and lines in some pectinids and giant clams (*Tridacna* spp.) corresponds to the number of solar days that elapsed during the time interval represented by these shell portions (CLARK, 1974, 1975; PARSONS & others, 1993; WATANABE & OBA, 1999; CHAUVAUD & others, 2005). These findings suggest that the microgrowth patterns are formed with circadian periodicity (CLARK, 1975). In fact, pectinids and some other taxa can track light and dark changes by simple to complex photoreceptors located at the mantle edge (DAKIN, 1910).

In intertidal settings, bivalve shells exhibit distinct, tidally controlled growth patterns (Fig. 4). Shell growth stops when the bivalves are aerially exposed during low tide and commences when they are submerged during high tide (HOUSE & FARROW, 1968; EVANS, 1972; OHNO, 1989; GOODWIN & others, 2001; MIYAJI, TANABE, & SCHÖNE, 2007). During exposure, most species keep their valves tightly closed and retract the mantle into the shell. However, the growth line forms shortly before and/or after aerial exposure. In habitats with semidiurnal tides, two growth lines and two increments (=two circatidal growth patterns) are formed per

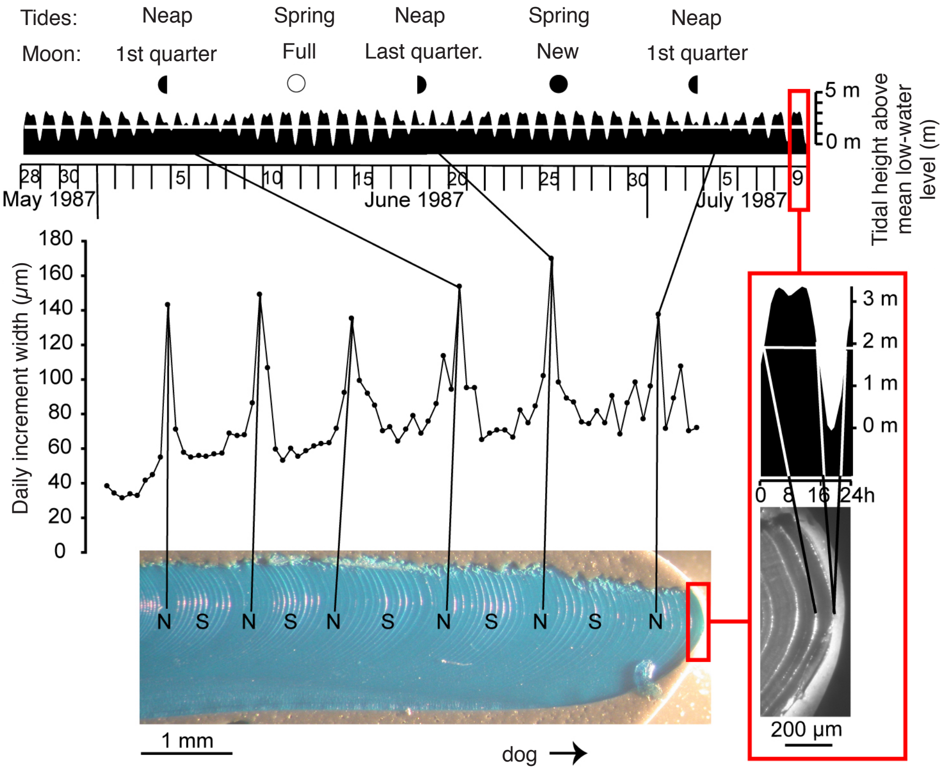

FIG. 4. Lunar daily and fortnightly growth patterns in shell of intertidal bivalve *Saxidomus gigantea,* Pender Island, British Columbia. Growth increments form during high tide and growth lines during low tide. At this setting, tides occur on a semidiurnal basis, i.e., twice a day. Therefore, two (circatidal) growth increments and two growth lines are formed per lunar day (=circalunidian growth pattern). Circalunidian growth patterns are arranged in bundles of approximately 14 (fortnightly bundles). Broad increments with weakly developed growth lines are formed during neap tides (*N,* half moon), whereas narrow increments with distinct growth lines are deposited during spring tides (*S,* full or new moon). The last increment at ventral margin was formed approximately between midnight and late afternoon on 9 July 1987. The formation of last microgrowth line at ventral margin started at a tidal height of less than 2 m during early evening, before this specimen was collected in the evening (=shell exposed to the air); *white horizontal line* in the tidal calendar denotes position on shelf where shell was collected; *dog,* direction of growth (adapted from Hallmann & others, 2009).

lunar day. For unknown reasons, growth lines produced during the daytime are more prominent than those formed during nighttime. Due to increased environmental stress (e.g., water agitation), growth lines formed during spring tides are more distinct than those formed during neap tides (Fig. 4). The distance from the shoreline determines the number of growth increments and lines in the shell. For example, in the high intertidal zone, bivalves can be aerially exposed for several days during spring tides without forming growth lines and increments, while specimens lower in the intertidal zone are periodically immersed and aerially exposed depending on tides. Therefore, in bivalves from the high intertidal, the number of growth increments and lines can be significantly fewer than in specimens living farther away from the coast (OHNO, 1989). In addition, growth increment widths are typically broader in shells from the low intertidal than in mid-intertidal settings, because the time interval during which the bivalves can form shell is linked to the duration of water immersion, which increases from high to low intertidal settings. Shorter immersion periods during spring tides also result in narrower growth increments, whereas neap tide increments are wider (Fig. 4). Wider and narrower lunar daily increments alternate regularly and form distinct bundles of ~13 to 15. Bundles with ~13 circalunidian increments correspond to a spring tide-to-spring-tide-cycle from new moon to full moon (14 solar days, 13.5 lunar days, perigee), whereas those containing ~5 circalunidian increments correspond to a full-moon-to-new-moon-cycle (15.5 solar days, 15 lunar days, apogee). It should be added that tidal growth patterns are not limited to intertidal bivalves. Although less distinct, they have also been observed in subtidal bivalves (Thompson, Jones, & Dreibelbis, 1980; Schöne, Houk, & others, 2005; Schöne & Giere, 2005).

At first glance, daily and semidiurnal growth patterns of bivalve shells seem to be fully controlled by environmental cues. However, when transplanted from their natural habitat and kept under constant immersion in tanks, intertidal bivalves continue to form tidal growth patterns for several weeks (Richardson, 1987). The persistence of such cycles under isolation from environmental entrainment suggests the presence of endogenous timekeeping mechanisms, so-called biological clocks (Pittendrigh & Bruce, 1957; Richardson, Crisp, & Runham, 1979; Williams & others, 1982; Williams & Pilditch, 1997). These endogenous rhythms govern the bivalve's physiology (Beentjes & Williams, 1986; Kim & others, 2003; Rodland & others, 2006, 2009; García-March, Sanchís Solcona, & García-Carrascosa, 2008).

Although the link between shell growth and physiological processes has not yet been directly confirmed, it is plausible for the following reasons. Physiological activity exerts a strong control over the biomineralization process, because crystal formation in bivalve shells is mediated by organic matrices secreted by epithelial cells of the mantle (Mann, 1983; Simkiss & Wilbur, 1989; Crenshaw, 1990; Watabe, Kingsley, Kawaguchi, 1993; Addadi & others, 2006). These organic matrices determine the type of crystal fabrics, i.e., the morphological appearance of newly formed crystals. However, the type of organic matrices secreted by the mantle cells depends on the physiological state of the animal. Likewise, physiological activity determines the relative proportion of calcium carbonate and organic materials in each shell portion. Since the physiological activity exhibits oscillatory changes that are controlled by biological clocks, shell growth patterns will reflect these periodic changes in the form of growth increments and growth lines. In porcelaneous bivalves, shell portions with a lower proportion of organic matrix (requiring less energy to produce) and a higher $CaCO_3$:organics ratio (=growth increments) regularly alternate with shell portions with irregular simple prismatic crystal fabrics and a lower $CaCO_3$:organics ratio (=growth lines) (see Ohno, 1989; Schöne, Radermacher, & others, 2011).

Endogenous rhythms parallel environmental cycles such as light and dark, and ebb or flood, but the periods, as such, are generated by the biological clock (Palmer, 1974; Rensing, Meyer-Grahle, & Ruoff, 2001). Environmental periods act as pacemakers that constantly reset the endogenous clocks. In the absence of environmental cues, the animal establishes free-running periods that can vary slightly in period length ("circa"dian = near daily) among species and among individuals, but are close to 24 hours. Through this flexibility in period length, circadian clocks can occur universally in organisms entrained by the light/dark cycle or the tidal cycle. For organisms exposed to semidiurnal tides, Palmer (1995) suggested the presence of two circadian clocks linked in anti-phase, so that each cycle comprises approximately 12.4 hours. In other organisms, the two circadian clocks run in phase, and ensure that the cycle length remains at approximately 24 hours. After several weeks under continuous immersion in the laboratory, intertidal bivalves switch from circalunidian to circadian rhythms (Kim & others, 2003). The anti-phase relationship between the two circadian clocks changes into an in-phase relationship.

Through endogenous rhythms, the organism can anticipate environmental changes, e.g., the approaching low or high tide, or the day or night. Circadian oscillators are encoded by genes (Lowrey & Takahashi, 2004). The importance of circadian clocks lies in their ubiquity among organisms, including mollusks (Block & Wallace, 1982; Roberts & Xie, 1986; Takahashi, Nelson, & Eskin, 1989; Kim & others, 2003). In fact, these genes have been found in all three domains of life, namely Eukarya, Bacteria, and Archaea (Dunlap, 1999; Harmer, Panda, & Kay, 2001; Lowrey & Takahashi, 2004). Circadian clocks occur likewise in motile (crabs, fish, diatoms) and sessile organisms (Palmer, 1974). Together with their ubiquity among organisms today, the occurrence of biological clocks in single-celled organisms near the root of the phylogenetic tree suggests that endogenous rhythms developed early during evolution. However, the length of the fundamental period of the circadian clock may have changed over time, because the Earth rotated faster around its axis in the distant geological past and the days were significantly shorter (Wells, 1963; Runcorn, 1975).

ULTRADIAN GROWTH PATTERNS

At higher magnification, a number of subdaily growth increments and lines can often be discerned within daily and semidiurnal growth increments. These growth patterns are referred to as ultradian (subdaily, infradian, intradaily) growth increments and lines and possibly represent physiological oscillations at time scales of minutes to hours (Rodland & others, 2006). It seems unlikely that ultradian physiological activity patterns are solely genetically predisposed. For example, Rodland and others (2006) found a strong temperature dependence of ultradian shell gaping activity. The temperature dependence suggests that ultradian cycles reflect chemical reactions. Actually, the ultradian metronome is a fundamental and universal necessity for orchestrated intracellular coherence and ensures a proper functioning of cell division and chemical reactions (Lloyd & Murray, 2005).

ANNUAL GROWTH PATTERNS

Nearly all hitherto studied bivalve species produce distinct annual growth lines in their shells (Hall, Dollase, & Corbató, 1974; Jones, 1980; Brey & Mackensen, 1997). These major dark growth lines can often be discerned by the naked eye on the outer shell surface of young specimens. These growth lines are often associated with depressions (grooves) formed during time intervals of slow shell growth when the mantle was retracted into the shell. However, reliable annual increment analyses require sections through the valves. At high magnification, annual growth lines appear as bundles of closely spaced microgrowth lines (Barker, 1964; Hall, Dollase, & Corbató, 1974). Daily increment widths decrease gradually toward annual growth lines and increase gradually afterward. This is an important feature to distinguish annual growth lines from disturbance lines. Disturbance lines can form, for example, during a major storm, and are characterized by abruptly changing microgrowth increment widths.

Periodically recurring environmental stimuli, in particular temperature, seem to be an important trigger for annual growth line formation (Davenport, 1938; Clark, 1975; Kennish & Olsson, 1975; Jones, 1983; Bucci & others, 2010). Temperature sets the limits for shell growth. For example, if temperature drops below ~5 °C, *Margaritifera margaritifera* forms a winter growth line (Dunca & Mutvei, 2001). However, in many species, shell growth ceases above and below species-specific temperature thresholds. Consequently, both a summer and a winter growth line can be present in settings with large seasonal temperature extremes (Clark, 1979; Koike, 1980; Sato, 1995; Jones & Quitmyer, 1996; Schöne & others, 2002). For example, *Mercenaria mercenaria* (Linnaeus, 1758), grows its shell between 9 and 31 °C, and forms distinct growth lines below and above these temperatures, respectively (Ansell, 1968). North of Virginia, winter temperatures drop below 9 °C, and *M. mercenaria* forms winter growth lines, whereas south of North Carolina, shell growth slows during the summer (Clark, 1979). At the transition zone in the Middle Atlantic region, both winter and summer growth lines are present in this species (Jones & Quitmyer, 1996).

Despite the undeniable importance of environmental controls on shell growth rates, the formation of annual growth lines is probably controlled by a combination of environmental stimuli, physiology, and endogenous rhythms. According to Brockington and Clarke (2001), in many marine benthic invertebrates, environmental stimuli such as the photoperiod, food supply, and temperature entrain endogenous rhythms and control the annual physiological activity. Several observations suggest that mollusks can actively maintain the duration of the growing season through the use of circadian biological clocks. For example, shell growth of *Arctica islandica* decreases and eventually stops for a time interval of about two months (Schöne, Houk, & others, 2005). However, the timing of the annual growth line formation differs in surface and bottom waters. Above the thermocline, growth retardation starts in September, whereas in settings below the thermocline, growth rate decreases in December. Irrespective of the season, specimens from different habitats strongly reduce and eventually stop biomineralization about four weeks after the seasonal temperature maximum. In bottom waters, the warmest season is during breakdown of the thermocline and downward mixing of warm surface waters. Apparently, the animals use circadian time gauges to measure the time elapsed since the seasonal temperature maximum.

According to Jones (1980), growth line formation in *Arctica islandica* and *Spisula solidissima* (Dillwyn, 1817) falls together with the spawning phase of the reproductive cycle. Therefore, the annual growth breaks in these species were referred to as spawning breaks. However, even premature specimens of *A. islandica* form annual growth lines at the same time as mature individuals. Thompson, Jones, and Dreibelbis (1980) suggested that the premature bivalves mimic reproduction (foreshadowing). Temperature-induced spawning cycles have also been identified in other species (Loosanoff & Davis, 1963; Castagna & Kraeuter, 1977; Sato, 1995). The timing and number of annual spawning events may also differ in a single species across latitudinal gradients. For example, *Mercenaria mercenaria* along the southeastern United States spawn multiple times per year (Dalton & Menzel, 1983), whereas specimens in the northern part of their biogeographic range have only a single spawning break (Loosanoff, 1937; Kassner & Malouf, 1982). Whether or not spawning breaks exist or another factor triggers annual growth line formation in these bivalves, the clockwork precision at which the animal forms annual growth patterns suggests an endogenous timekeeping mechanism.

APPLICATIONS OF GROWTH PATTERN ANALYSIS

Growth pattern analyses offer a broad spectrum of potential applications in biology, ecology, archeology, and climate research. The following section summarizes selected applications.

The number of daily growth increments between annual growth lines can be used to estimate the duration of the growing season and to assign precise dates to each shell portion (approximately to the nearest two to four weeks; Hallmann & others, 2009). Furthermore, if the shutdown temperatures and the physiological tolerance of a species are known, such data can reveal how seasonal temperature patterns and overall climate has changed through time and across latitudinal gradients (ANSELL, 1968; HALL, DOLLASE, & CORBATÓ, 1974; TANABE & OBA, 1988; SCHÖNE, OSCHMANN, & others, 2004).

Microgrowth patterns of intertidal bivalve shells are particularly useful for archeological research, e.g., to gain insight into shellfish collection practices of ancient human populations (COUTTS, 1970; KOIKE, 1975; ANDRUS & CROWE, 2000). In young specimens where microgrowth patterns are easy to recognize, the date of collection can be estimated to within about two weeks by growth increment counts (HALLMANN & others, 2009). By comparing the lunar daily growth pattern with the tidal calendar, it is even possible to estimate the time of collection (daytime or nighttime) and the tidal position (high or low intertidal) (Fig. 4). The tide calendar can be used to make predictions on the expected growth patterns, because shell growth only occurs during high tide and microgrowth line formation around low tide. Furthermore, the tidal growth patterns from the distal shell margins can reveal if the shells were collected during neap tides or spring tides. Distinct microgrowth patterns would suggest the shells were obtained during spring tides, whereas weakly developed structures would suggest collection during neap tides. Shell collection during spring tides can be facilitated by the light provided by the full moon. Whether a growth line or a growth increment is developed provides details on how the shells were collected, by swimming during high tide (by adults) or simple shelling at low tide (by all individuals).

Variations in increment width can be also be used to estimate seasonal environmental conditions, especially water temperature. Temperature exerts the greatest control on shell growth (KENNISH & OLSSON, 1975; HENRY & NIXON, 2008). Higher growth rates typically correspond well with higher temperatures. However, most species exhibit an optimum growth temperature, above or below which growth rate sharply declines. The species-specific relationship between shell growth and temperature must be carefully investigated prior to using increment widths as an independent temperature proxy. In addition to temperature, other environmental factors have been reported to influence growth rate, e.g., food quality and availability (ANSELL, 1968; WITBAARD, DUINEVELD, & BERGMAN, 2001), water quality (DUNCA, SCHÖNE, & MUTVEI, 2005), and population density.

Lunar daily growth patterns in bivalve shells have been used to test geophysical calculations of solar day length in Earth history, as well as the changing distance between Earth and Moon (BERRY & BARKER, 1968; PANNELLA, 1972; RUNCORN, 1975). A higher number of lunar daily increments in fortnight bundles suggests that the Earth rotated faster in the past, and that the solar days were shorter. Furthermore, such data reveal that the length of day did not decline at a uniform rate throughout Earth history. During the late Paleozoic and early Mesozoic, nearly all landmasses were combined in the supercontinent Pangea. The Earth's rotation slightly increased during that time interval and counterbalanced the overall slowdown of rotational speed (ROSENBERG & RUNCORN, 1975).

Annual growth patterns of bivalves have recently led to the astounding finding that bivalves are among the longest lived animals. In fact, they might be the longest lived, noncolonial animals producing periodic accretionary hard parts. Some species can live for many centuries (THOMPSON, JONES, & DREIBELBIS, 1980; ZOLOTAREV, 1980; SHAUL & GOODWIN, 1982; JONES, 1983; MUTVEI & WESTERMARK, 2001; SCHÖNE, FIEBIG, & others, 2005; WANAMAKER, SCOURSE, & others, 2008; WISSHAK & others, 2009). In conjunction with their capability to record environmental changes in their shells, such species are highly suitable tools for long-term climate reconstruction (NOAKES & CAMPBELL, 1992; MARCHITTO & others, 2000; SCHÖNE & others, 2003; STROM & others, 2004, 2005; WANAMAKER, HEINEMEIER, & others, 2008; BUTLER & others, 2010).

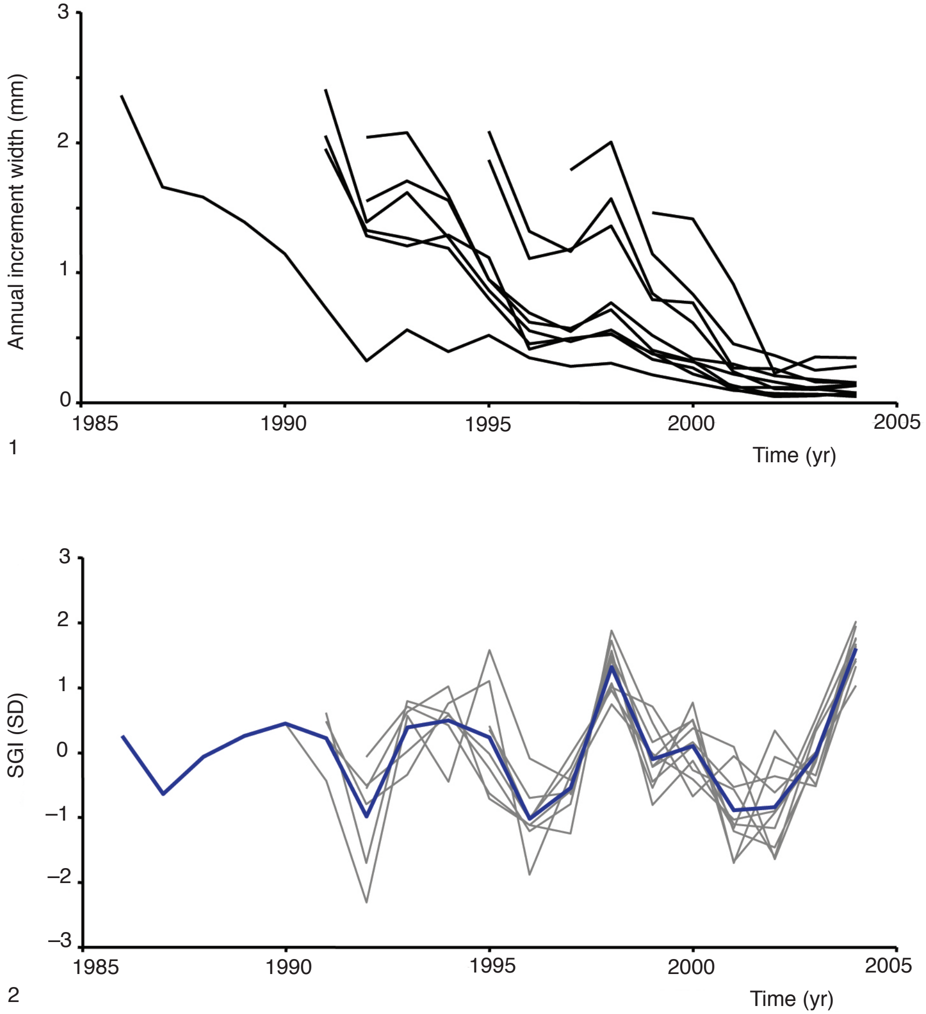

FIG. 5. Annual growth increment width chronologies from freshwater pearl mussels, *Margaritifera laevis* (HAAS, 1910), Teshio River, Japan; *1,* growth rates decreasing with increasing ontogenetic age; *2,* after correction for age-related growth trends, individual growth time series exhibit a high degree of running similarity; *SGI,* standardized growth index; *SD,* standard deviation units (adapted from Schöne, 2008).

Variations in annual shell growth rate can function as environmental recorders. Shell growth rates vary through ontogeny and in response to environmental conditions. Therefore, studying the environmental signals requires the removal of age-related growth trends from the observed (measured) shell growth (m). Annual growth rate decreases significantly with increasing age (Fig. 5.1). For example, during the first seven years of life, *Arctica islandica* can grow up to ~2 cm in shell height per year. This rapid growth allows the bivalve to quickly escape the high-predation window (WANINK & ZWARTS, 1993) and provides the body size needed for reproduction (CARGNELLI & others, 1999). At an age of 13 or so, annual shell growth

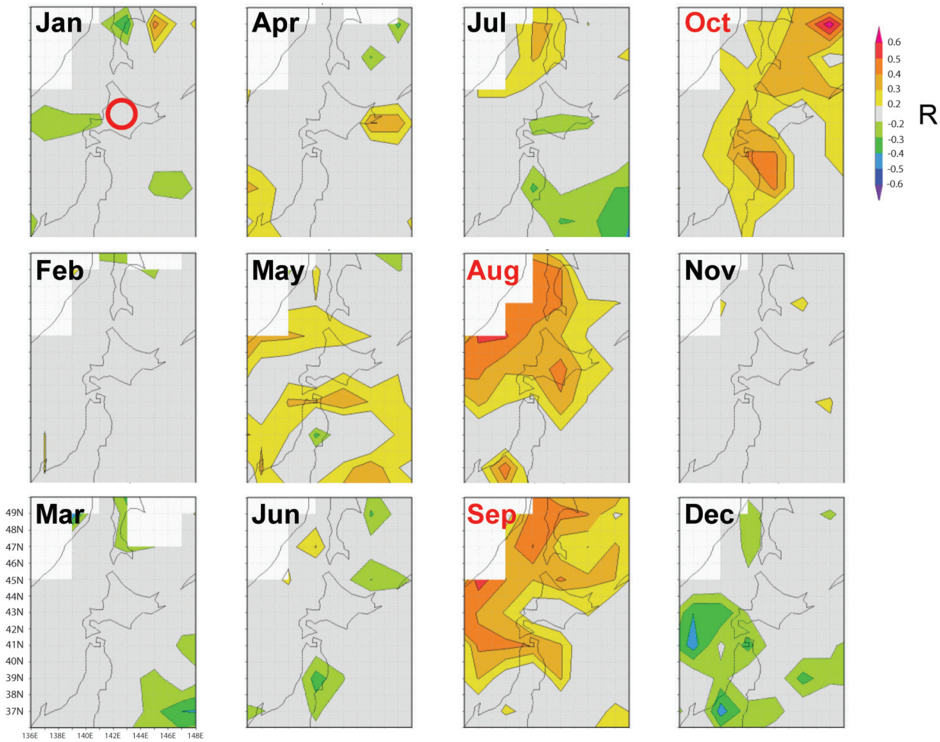

FIG. 6. Variations in relative shell growth of *M. laevis,* Teshio River, Japan, depicted in Figure 5.2, are highly positively correlated with ambient temperature during summer (August–October); *red circle* indicates locality where shells lived (new).

decreases exponentially to rates as low as 10 µm per year at age 350 (SCHÖNE, FIEBIG, & others, 2005). The decreasing rate of shell growth can be estimated by applying a well-established, nonlinear growth equation such as the von Bertalanffy curve (VON BERTALANFFY, 1934, 1938) to the measured annual increment width (m) time series. The predicted increment width (p) time series reflects the ideal or hypothetical shell growth. Elimination of ontogenetic growth trends (i.e., the computation of growth indices, I) is accomplished by dividing measured (m) by predicted (p) (=estimated, see above) growth increment widths ($I = m / p$). Subsequent standardization transforms the growth index (I) chronology into a standardized growth index (SGI) time series and removes the high correlation between the mean and the variance, i.e., the heteroscedasticity. SGI values are dimensionless measures of annual shell growth (Fig. 5.2). Positive values reflect faster than average growth, negative values the opposite. SGI values of different specimens can be directly compared to each other and to environmental chronologies (JONES, ARTHUR, & ALLARD, 1989; MARCHITTO & others, 2000). Typically, SGI values of bivalves are strongly correlated with temperature (JONES, ARTHUR, & ALLARD, 1989; MARSH & others, 1999) (Fig. 6), food availability and/or quality (SCHÖNE & others, 2003), or co-varying, large-scale climate indices. For example, STROM and others (2004, 2005) found a strong agreement between variations in shell growth and the Pacific Decadal Oscillation. For proper interpretation of SGI data, it is relevant to know the duration of the growing season and how seasonal growth rates vary. Also, it is required to test whether the duration of the growing season changes through ontogeny (Goodwin, Schöne, & Dettman, 2003). Such information can be obtained from daily increment analyses.

Climate reconstructions based on bivalves are not limited to the lifespan of a single individual. By stitching together SGI chronologies of multiple bivalves with overlapping lifespans, it is also possible to construct uninterrupted master chronologies (Schöne & others, 2003; Schöne, Dunca, & others, 2004; Strom & others, 2004, 2005; Black & others, 2008, 2009; Butler & others, 2010) (Fig. 5.2). The method of combining individual chronologies is known as crossdating and has been developed by dendrochronologists. Crossdating is performed by wiggle-matching of the time series. These composite chronologies or master chronologies can span several mollusk generations and are capable of providing millennial-scale paleoclimate data (Jones, Arthur, & Allard, 1989; Marchitto & others, 2000; Schöne & others, 2003; Schöne, Dunca, & others, 2004; Strom & others, 2004, 2005; Black & others, 2008, 2009; Butler & others, 2010).

Annual growth patterns have also been used to investigate processes of evolutionary change. For example, Jones and Gould (1999) combined sclerochronologic age with size and morphological shape information for Jurassic *Gryphaea* to specify the mode of heterochrony for this pedomorphic bivalve. Their work demonstrated that larger phyletic shell sizes of Lower Jurassic taxa were not attained through extended longevity, but solely by maintaining high juvenile growth rates in later life stages. A different set of Middle to Upper Jurassic gryphaeans exhibited an evolutionary trend toward extended lifespan, but not size increase or heterochrony. Goodwin, Anderson, and Roopnarine (2008) demonstrated that phylogenetic valve development of Neogene tropical American corbiculids underwent peramorphic changes. The ancestral growth pattern in *Lenticorbula? idonea* Conrad, 1833, was characterized by a uniform rate of increase in shell height age. Two derived forms, however, showed accelerated shell height growth at initial ontogenetic stages and shell thickening, as well as a marked change in growth direction during later ontogenetic stages.

SHELL GEOCHEMISTRY AND SHELL GROWTH PATTERNS

Environmental variations are geochemically recorded while the shells grow. In combination with growth pattern analysis, this makes bivalve shells potentially high-resolution recorders of paleoclimate and paleoseasonality.

STABLE ISOTOPES

Stable carbon isotope ratios of bivalve shells

$$\delta^{13}C_{shell} = 1000 \cdot \left(\frac{^{13}C}{^{12}C} shell \, / \frac{^{13}C}{^{12}C} VPDB - 1 \right)$$

where VPDB is the Vienna-Pee Dee Belemnite standard, can theoretically provide information on the carbon isotope ratio of dissolved inorganic carbon (DIC) and, therefore, reflect changes in primary productivity and remineralization (Mook & Vogel, 1968). Plants preferentially take up the light carbon isotope ^{12}C during photosynthesis, which increases the relative abundance of ^{13}C in the remaining water. During growth, bivalves in surface waters sample the carbon isotope ratio of the ambient environment in their shells, i.e., more positive $\delta^{13}C_{DIC}$ values occur during times of increased primary productivity, whereas oxidation of organic matter decreases the $\delta^{13}C_{DIC}$ and $\delta^{13}C_{shell}$ values. However, bivalves also incorporate metabolic CO_2 into their shells and, more importantly, many species seem to incorporate increased amounts of respiratory CO_2 through their lifetime, which results in more negative $\delta^{13}C_{shell}$ values as the bivalve grows older (McConnaughey & Gillikin,

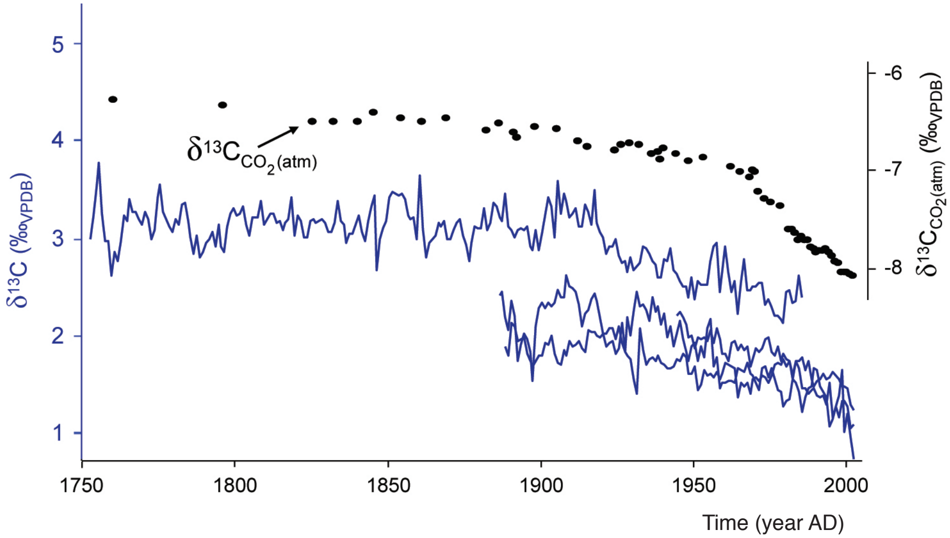

FIG. 7. Annually resolved stable carbon isotope chronologies of four *A. islandica* specimens from the North Atlantic (*blue*) reflect the oceanic Suess effect, i.e., the negative $\delta^{13}C$ shift of dissolved inorganic carbon (*black*). Note that $\delta^{13}C_{shell}$ values differ among localities, owing to differences in the local dissolved inorganic carbon (DIC) pool. None of the shell carbon isotope curves shows ontogenetic trends, but a large decadal-scale variability (new; data from Schöne, Radermacher, & others, 2011).

2008). This finding diminished earlier hopes to use bivalve shells as recorders of DIC changes (MOOK & VOGEL, 1968). More recent studies, however, suggest that long-lived bivalves do not exhibit such ontogenetic $\delta^{13}C_{shell}$ trends, enabling the possibility to study past carbon cycle dynamics in the ocean or track the anthropogenic CO_2 increase in the atmosphere and the oceans (Suess effect; BUTLER & others, 2011; SCHÖNE, WANAMAKER, & others, 2011) (Fig. 7).

Metabolic (vital) effects do not seem to affect the most widely used geochemical proxy of bivalve shells, the oxygen isotope ratio, or $\delta^{18}O_{shell}$, defined by the formula:

$$\delta^{18}O_{shell} = 1000 \cdot \left(\frac{^{18}O}{^{16}O}\ shell \Big/ \frac{^{18}O}{^{16}O}\ VPDB - 1 \right).$$

In fact, almost all studied bivalves are known to precipitate their shells in oxygen isotopic equilibrium with the ambient water (MOOK & VOGEL, 1968; for exceptions, see OWEN & others, 2008; HALLMANN & others, 2009). Therefore, changes in $\delta^{18}O_{shell}$ values are related to variations of temperature and the $\delta^{18}O$ value of the ambient water ($\delta^{18}O_{water}$) (UREY, 1947; EPSTEIN & others, 1953). If the temperature is known, $\delta^{18}O_{shell}$ values can be used to estimate salinity variations through time (INGRAM, CONRAD, & INGLE, 1996). However, if the $\delta^{18}O_{water}$ value during the time of shell formation is known or assumed to be constant, $\delta^{18}O_{shell}$ functions as a reliable paleothermometer (JONES, ARTHUR, & ALLARD, 1989; WEFER & BERGER, 1991; WEIDMAN & JONES, 1994; DETTMAN, REISCHE, & LOHMANN, 1999; SURGE, LOHMANN, & DETTMAN, 2001; CARRÉ & others, 2005; SCHÖNE, FIEBIG, & others, 2005; WANAMAKER & others, 2006; IVANY & others, 2008), because the fractionation of oxygen isotope ratios between $CaCO_3$ and water is then solely controlled by temperature (the equilibrium isotope effect). Temperature estimates based on $\delta^{18}O_{shell}$ values have been used to confirm the annual periodicity of growth line formation (JONES, WILLIAMS, & ARTHUR, 1983) and to demonstrate that bivalves do not grow year round, but only within a species-specific temperature range (EPSTEIN & others, 1953).

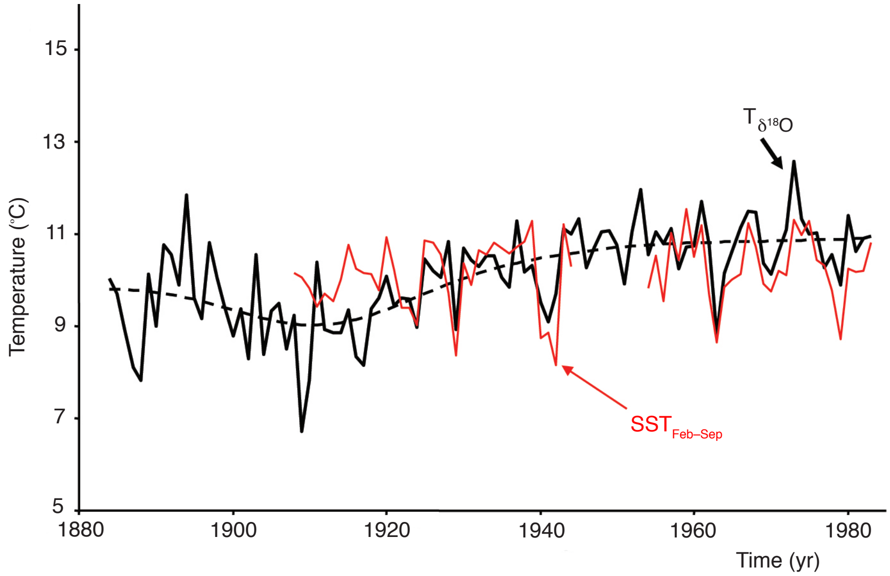

FIG. 8. Annually resolved temperatures reconstructed from oxygen isotope values (*black*) of shells (*A. islandica*) from the southern North Sea closely resemble ambient sea surface temperatures (SST) (new; data modified from Schöne, Freyre Castro, & others, 2004).

As demonstrated by various experiments, a 1‰ change in $\delta^{18}O_{shell}$ corresponds to a temperature change of ~4.3 °C (EPSTEIN & others, 1953; GROSSMAN & KU, 1986; DETTMAN, REISCHE, & LOHMANN, 1999; BÖHM & others, 2000). A shift in $\delta^{18}O_{shell}$ toward more positive values indicates colder temperatures, whereas more negative values reflect warmer temperatures. In conjunction with modern carbonate preparation devices, highly sensitive mass spectrometers can measure sample sizes of 10 to 50 µg obtained by micromilling (DETTMAN & LOHMANN, 1995) with an external precision of less than 0.08‰ (DETTMAN & LOHMANN, 1995; SPÖTL & VENNEMANN, 2003; FIEBIG, SCHÖNE, & OSCHMANN, 2005). This enables temperature reconstructions on seasonal to subdaily time scales, depending on growth rates, to the nearest 0.35 °C (Fig. 8). Shell growth patterns ensure that the temperature record derived from $\delta^{18}O_{shell}$ is placed into a precise temporal context.

However, the $\delta^{18}O_{shell}$ paleothermometer only provides legitimate results when the oxygen isotope ratio of the ambient water is known, and this is rarely the case for prehistoric environments. Recently, a new carbonate paleothermometer has been introduced (GHOSH & others, 2006), which is based on the relative abundance of doubly and singly substituted carbonate isotopologues (mass 47: $^{13}C^{17}O^{17}O$, $^{12}C^{18}O^{17}O$, $^{13}C^{18}O^{16}O$; mass 46: $^{12}C^{17}O^{17}O$, $^{13}C^{17}O^{16}O$, $^{12}C^{18}O^{16}O$, mass 45: $^{12}C^{17}O^{16}O$, $^{13}C^{16}O^{16}O$; mass 44: $^{12}C^{16}O^{16}O$) in the carbonate lattice. The so-called Δ47 (clumped isotope) thermometer is defined as

$$\Delta 47 = \left(\left(\frac{R47_{measured}}{R47_{random}}-1\right)-\left(\frac{R46_{measured}}{R46_{random}}-1\right)-\left(\frac{R45_{measured}}{R45_{random}}-1\right)\right)\cdot 1000$$

where R47, R46, and R45 represent measured and stochastic ratios of isotopologues 47/44, 46/44, and 45/44, respectively. Current analytical methods limit the carbonate clumped isotope paleothermometer to uncertainties in temperature of ~ ±1 °C for ~10 mg samples (CAME & others, 2007; EILER, 2007; AFFEK & others, 2008) and to ±2 °C for ~5 mg samples (Ghosh & others, 2006).

Another isotope-based paleothermometer is based on calcium isotopes (Nägler & others, 2000:

$$\delta^{44}Ca_{shell} = 1000 \cdot \left(\frac{^{44}Ca}{^{40}Ca} shell / \frac{^{44}Ca}{^{40}Ca} std \right) ,$$

where *std* = standard. However, the T-δ^{44}Ca fractionation curves for different cultured foraminiferan taxa and inorganic precipitates exhibit largely different slopes, ranging from 0.24‰ to 0.02‰ per 1 °C (Nägler & others, 2000; Hippler & others, 2002; Gussone & others, 2003). Vital effects also seem to govern the T-δ^{44}Ca relationship in bivalves.

Other light stable isotope ratios have been used to extract environmental information from the organic matrix of bivalve shells. Carroll, Romanek, and Paddock (2006) suggested that the hydrogen isotope ratios (δD_{shell}) of freshwater bivalves may function as an independent proxy for $\delta^{18}O_{water}$. However, the large samples required for some of these analyses require whole shells. For example, δ^{15}N of *M. mercenaria* shells has been used to trace wastewater input in estuarine ecosystems (Carmichael & others, 2008). O'Donnell and others (2003) identified the type of food ingested by *Mercenaria* spp. based on the analysis of δ^{13}C, δ^{15}N, and δ^{34}S values. Strontium isotopes in freshwater shells reportedly reflect pH changes (Mutvei & Westermark, 2001).

MINOR, TRACE, AND RARE EARTH ELEMENTS

Metal to calcium (Me/Ca) ratios of bivalve shells likely contain a host of paleoenvironmental information. Extraction of such data, however, is less straightforward than for stable isotopes, and many studies have pointed out strong biological controls on minor and trace elements in bivalve shells.

The boron concentration of marine bivalve shells might provide suitable proxies for salinity and freshwater pulses (Roopnarine & others, 1998). Various elements have also been suggested as proxies for phytoplankton dynamics (Stecher & others, 1996; Vander Putten & others, 2000; Thébault, Chauvaud, & others, 2009: Ba/Ca, but see Gillikin & others, 2006; Thébault, Chauvaud, & others, 2009: Mo/Ca; Langlet & others, 2006: Mn/Ca). Li/Ca ratios for *A. islandica* are strongly correlated with lithium levels in the water and may be used as indicators of basalt weathering (Thébault, Schöne, & others, 2009). Some trace and rare earth elements can also provide information on anthropogenic pollution (Bau, Merschel, & Kulaksiz, 2010). Pb/Ca ratios of *M. mercenaria* seem to reflect the leaded gasoline peak in the 1970s (Gillikin, Dehairs, & others, 2005). Higher trace metal levels in shells may reflect values in the environment (Pitts & Wallace, 1994; Gundacker, 2000; Mutvei & Westermark, 2001; Pearce & Mann, 2006; Bellotto & Miekeley, 2007; Hansen Klünder & others, 2008), but may also be linked to the trophic level (Ravera & others, 2003, 2005, 2007). According to some studies, however, shell chemistry is not an ideal bioindicator of pollution (Palmer & Rand, 1977; Szefer & others, 2002).

In comparison to other Me/Ca ratios, Sr/Ca and Mg/Ca are by far the best studied. Both are considered to provide serviceable paleothermometers (Hansen Klünder & others, 2008). Analyses of these Me/Ca ratios of bivalve shells and hard parts of other organisms were complemented by inorganic precipitation experiments (Kinsman & Holland, 1969; Mucci, Canuel, & Zhong, 1989). With increasing temperature, Sr/Ca and Mg/Ca ratios of abiogenic aragonite decreases (Kinsman & Holland, 1969; Gaetani & Cohen, 2006), whereas those of abiogenic calcite increase (Kinsman & Holland, 1969). In addition, precipitation rate has been shown to affect the Sr/Ca ratio of calcite. Due to its orthorhombic crystal structure, Sr levels are significantly higher in aragonite than in rhombohedral calcite. The Sr/Ca and Mg/Ca ratios of bivalves, however, are much lower than expected from thermodynamic equilibrium. Furthermore, both Me/Ca values can vary in contradictory ways among different species, among different sites and even among different contemporaneous specimens from the same locality. For example, a negative correlation was found between temperature and Sr/Ca ratios in the aragonitic portion of *Mytilus edulis* LINNAEUS, 1758 (DODD, 1965), whereas GILLIKIN, LORRAIN, and others (2005) reported the opposite for *Saxidomus gigantea* (aragonite). Sr and Mg levels may also correlate with growth rate (SWAN, 1956) and ontogenetic age (FREITAS & others, 2005; SURGE & WALKER, 2006). These findings suggest that bivalves actively control which elements reach the site of calcification. In fact, trace impurities can control the type of $CaCO_3$ crystal formed in the shell. According to a recent paper, after mathematical elimination of vital effects, Sr/Ca and Mg/Ca ratios of *A. islandica* are inversely correlated to temperature (SCHÖNE, ZHANG, & others, 2011).

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