

Structural analysis and paleoenvironmental potential of dog cockle shells (*Glycymeris glycymeris*) in Brittany, northwest France



Clémence Royer^a, Julien Thébault^{a,*}, Laurent Chauvaud^a, Frédéric Olivier^b

^a Université de Brest, Institut Universitaire Européen de la Mer, Laboratoire des sciences de l'environnement marin (UMR6539 CNRS/IRD/UBO), rue Dumont d'Urville, 29280 Plouzané, France

^b Muséum National d'Histoire Naturelle, Département Milieux et Peuplements Aquatiques, UMR7208 BOREA MNHN/CNRS/P6/IRD, ISMER/UQAR, 310 allée des Ursulines, CP 3300 Rimouski (Québec), Canada, G5L 3A1

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ABSTRACT

To compensate for the lack of high resolution data on variation in environmental parameters before the establishment of monitoring networks, we evaluated dog cockle shells (*Glycymeris glycymeris*; Mollusca: Bivalvia) as archives for temperature and climate perturbations such as the North Atlantic Oscillation (NAO) over the last 50 years. Oxygen isotope compositions were measured from annual increments of shells collected from the Bay of Brest and the Chausey Islands in northwestern France. Simultaneously, sclerochronological analyses were performed on the same shells. Oxygen isotopic ratios measured in shells collected from the Bay of Brest were compared to *in situ* temperature and salinity data from monitoring stations and buoys in order to build a specific paleotemperature equation ($r^2 = 0.87$; $p < 0.001$) for the dog cockle. The specific equation was used to estimate sea surface temperatures around the Chausey Islands between 1966 and 1994. Standardized growth indices (SGI) calculated through sclerochronological methods were strongly correlated to oxygen isotope-derived temperatures. The SGI however did not capture the area's predominant climate pattern, the NAO. This study demonstrates that dog cockle shells can be used for long-term high-resolution reconstructions of past sea surface temperatures.

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1. Introduction

Since the end of the 20th century, global climate change has become a major focus of social, economic or political debate in nearly all developed and developing countries. The unequivocal consensus of the international scientific community is that human activities are changing the structure and functioning of the climate and nearly all of Earth's surface ecosystems. The world's coastal areas will be particularly affected by on-going and continued climate change (Jackson, 2001). In order to (i) decouple natural from anthropogenic influences on the climate, and (ii) develop methods for predicting and potentially reducing its impending effects, it is essential to estimate the magnitude of past long-term natural variability of certain key climatic and environmental variables (e.g. seawater temperatures). Modern "conventional" monitoring networks (electronic instruments, periodic water sampling) that perform high-frequency measurements of physico-chemical and biological parameters provide relatively recent historical information in the form of time series going back only a few decades. These methods do not encompass low frequency cycles of natural variation affecting coastal environments (Jackson, 2001).

Moreover, monitoring networks are sparse relative to the range of areas impacted by anthropogenic global climate change. Limited coverage of local coastal areas is likely to conceal important spatial disparities among different components of regional ecosystems. Therefore, reliable long term archives are needed that offer greater geographic coverage and adequate long-term sensitivity to the temporal scales on which climate change operates.

In this context, biological records have considerable potential for extending conventional climate records on a broad geographical scale, and over long periods of time. These so-called proxy records occur in sedimentary deposits and in many biomineral archives such as bivalve mollusc shells, corals, sclerosponges and coralline red algae (Gröcke and Gillikin, 2008; Halfar et al., 2008; Jones et al., 2009; Rosenheim et al., 2009). These organisms form their external calcium carbonate (CaCO_3) skeletons episodically, thus forming incremental growth lines that can be interpreted as a chronological record. Episodic growth patterns provide a sequential record of growth increments which can then be analyzed as a geochemical proxy (stable isotope ratios, elemental concentrations) for environmental conditions operating during growth of the shell or biomineral framework.

Analyses of most types of materials recovered from sediment cores can reveal the evolution of parameters over longer time intervals (10^7 years) but their temporal resolution is low and generally

* Corresponding author. Tel.: +33 2 98 49 86 47; fax: +33 2 98 49 86 45.

E-mail address: julien.thebault@univ-brest.fr (J. Thébault).

insensitive on decadal and shorter time scales. Other types of biogenic materials allow higher resolution paleoenvironmental reconstructions. Corals are well known as high-resolution paleoenvironmental archives (e.g. Tudhope et al., 2001) but molluscs can serve the same function on much broader geographic scales owing to their widespread distributions across a range of climate zones (polar, temperate and tropical) and environments (estuaries, coastal bays, continental shelves, hydrothermal vents, etc.). Molluscs also tend to form more distinct and easily discernible daily (circadian, circalunidian) to annual growth structures relative to corals and sediments. In doing so, molluscs can provide information on seasonal and intra-seasonal variations as paleoenvironmental archives (Goodwin et al., 2001; Schöne et al., 2005a).

In recent years bivalve mollusc shells have been successfully used in paleoenvironmental reconstruction of seawater temperature records (Schöne et al., 2011), phytoplankton dynamics (Thébault et al., 2009a) and climatic oscillations (Schöne et al., 2003; Carré et al., 2005). Mollusc shells may also provide detailed biological information concerning the organism's lifespan (Garcia-March and Marquez-Aliaga, 2007; Wanamaker et al., 2008), metabolism (Chauvaud et al., 2011), calcification rate (Thébault et al., 2009b) and the length of the growing season (Ivany et al., 2003; Miyaji et al., 2010).

The dog cockle (*Glycymeris glycymeris*, L., 1758) is a eurythermal bivalve mollusc found in surface areas of coarse-grained subtidal sediments. Its shell can reach a maximum length of 8 cm but averages around 4–6 cm in length. The dog cockle's minimum legal catch size of 4 cm corresponds to the minimum size for mature individuals, 9–10 years old. Spawning occurs throughout the year with the exception of two months in early winter (December–January) and two months in late summer (August–September; Morvan, 1987). *G. glycymeris* has a broad biogeographic distribution, inhabiting the north-eastern Atlantic continental shelf from Cape Verde to Norway in water depths of up to 100 m in areas with strong bottom currents (Savina and Pouvreau, 2004). The thick shell is nearly round (equilateral), symmetrical and composed of aragonite (Oliver and Holmes, 2008). Growth lines appear as concentric striations on the surface of the shell and within the valves (external and internal striations; Ramsay et al., 2000). A study of oxygen isotope composition of aragonite shells of *G. glycymeris* by Berthou et al. (1986) demonstrated that growth lines are formed annually, with their boundaries corresponding to winter shell growth cessations. Some *G. glycymeris* individuals can persist for up to two centuries (Ramsay et al., 2000; Reynolds et al., 2010). *G. glycymeris*' distribution, shell architecture and longevity thus make this organism an attractive subject for paleoenvironmental studies.

The objective of this study was specifically to determine whether dog cockle shells can be used as reliable archives of seawater temperature and climate perturbations such as the North Atlantic Oscillation (NAO) along the Brittany coast of northwest France. To execute this objective, our research sought (i) to determine whether oxygen isotopes were incorporated in dog cockle shells in isotopic equilibrium with surrounding seawater, (ii) to estimate how precisely seawater temperatures could be inferred from the oxygen isotope content of shell aragonite, and (iii) to assess the consistency of standardized growth indices (SGI) with past seawater temperature records and known NAO parameters.

2. Material and methods

2.1. Study sites

The shells analyzed in this study were dredged from two different sites (Fig. 1). A batch of live young specimens was collected from the Bay of Brest. Extensive monitoring of this collection site allowed us to check whether shells precipitate in isotopic equilibrium with

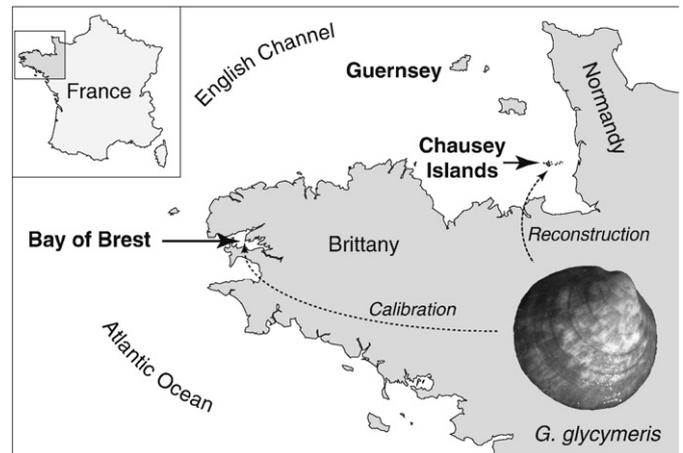


Fig. 1. Shell sampling localities in the Bay of Brest (calibration study) and near the Chausey Islands (paleoenvironmental reconstruction).

seawater and calibrate a specific paleotemperature equation as needed. A second batch of older live individuals was collected from the Chausey Islands in order to reconstruct long term standardized growth indices (SGI) and oxygen isotope-derived temperatures.

The Bay of Brest is a 180 km², semi-enclosed marine ecosystem connected to the Atlantic shelf (Iroise Sea) by a deep narrow strait (2 km width, 40 m depth; see Thébault and Chauvaud, 2012). It has an average depth of 8 m and is fed by two rivers, the Aulne (catchment area = 1792 km²) and the Elorn (catchment area = 379 km²), which provide up to 80% of the total freshwater input into the bay. Seawater temperature and salinity were monitored weekly from 1998 to 2010 at the SOMLIT-Brest station located at the outlet of the Bay of Brest (48°21'30"N, 4°33'06" W), using a Sea-Bird SBE 19 CTD profiler (conductivity, temperature and depth profiling instrument, Sea-Bird Electronics, Inc.). The automated buoy MAREL-Iroise provided records of physico-chemical parameters (temperature, conductivity, dissolved oxygen, pH, and turbidity) measured every 20 min at a location 50 m away from the SOMLIT-Brest station. Our study site, the Banc de la Cormorandière (48°20'26" N, 4°30'44" W), is a subtidal dune subject to strong tidal currents and located in the western part of the Bay of Brest, near its outlet (Northern part of Roscanvel bank; Thébault and Chauvaud, 2012). Lorrain (2002) showed that temperature and salinity conditions measured by SOMLIT and those measured along the southern side of the strait are similar and covary together. Young dog cockles ($n=4$; average age = 12.5 ± 2.4 years; Fig. 2) were collected alive on March 24th, 2010 using standard commercial fishing dredging equipment. Increments of the shells precipitated within the last decade were analyzed for their isotopic composition.

The Chausey Islands are located in the Normand-Breton Gulf (English Channel, France). These islands represent fragments of a submerged archipelago with exposed areas covering a total of 51 km² (emergent relative to the local tidal cycle, which has an amplitude of up to 14 m). Located 17 km from the Normandy coast, the islands are isolated from freshwater input and are too small for permanent river systems to develop. Seawater temperature and salinity have been regularly monitored two sites near the Chausey Islands since 1998 and 2000 by the Syndicat Mixte pour l'Équipement du Littoral (SMEL). The upper layer of subtidal sediments around the islands is largely dominated by *G. glycymeris* beds (Godet et al., 2009). Large live specimens ($n=27$; average size = 5.34 ± 0.31 cm; Fig. 2) were collected alive by dredging a shallow subtidal area (48°54'12" N, 1°50'36" W) on November 19th, 2009. These 27 samples were all used for sclerochronological analyses and 9 individuals (average age = 33.3 ± 2.6 years; Fig. 2) were further subjected to isotopic analyses.

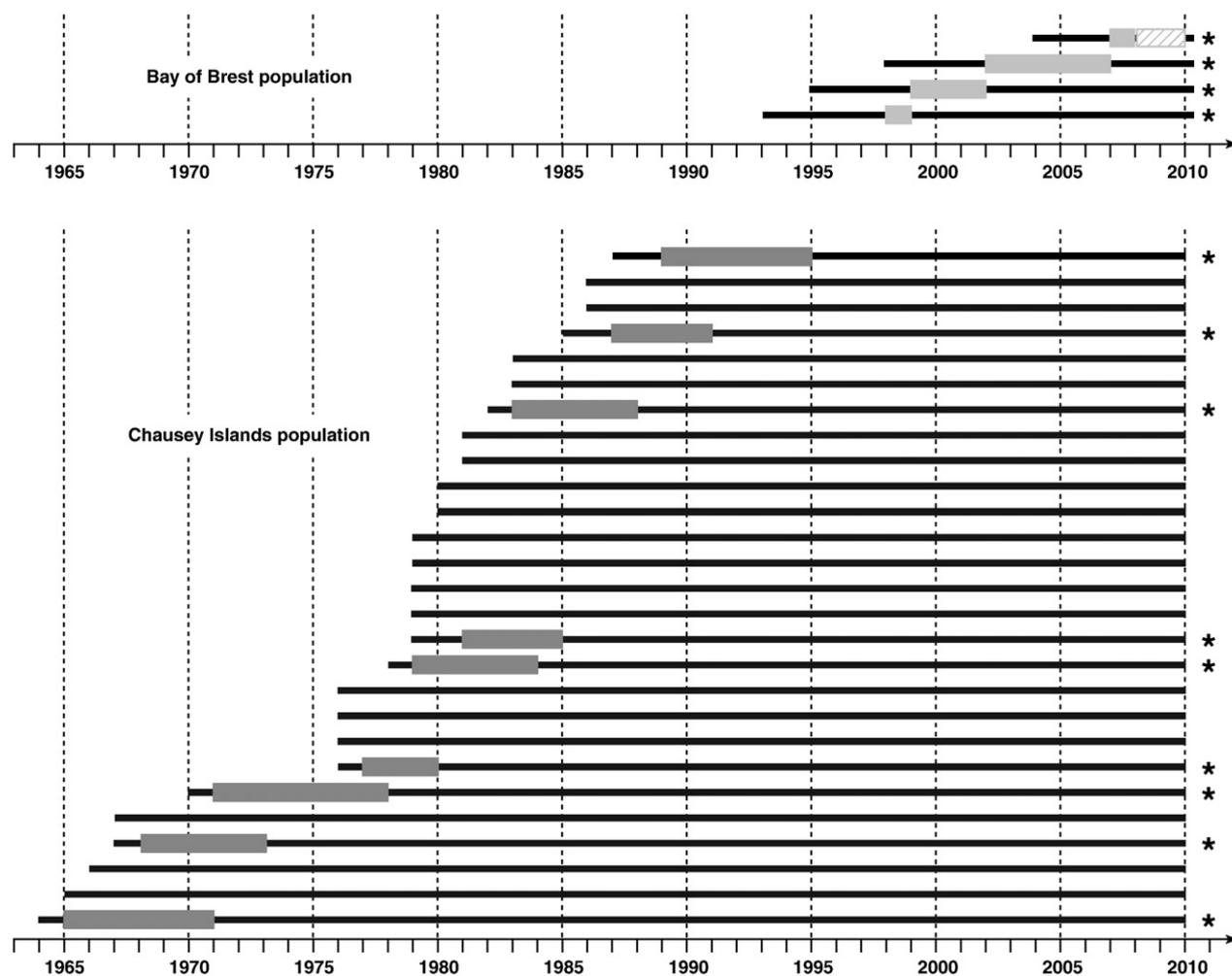


Fig. 2. Lifespans of the 4 dog cockle specimens collected from the Bay of Brest (upper panel) and of the 27 shells collected from the Chausey Islands site (lower panel). Asterisks indicate specimens analyzed for oxygen isotope composition. Gray rectangles delineate portions of shell sampled for isotopic analyses. Hatched rectangle indicates the shell portion of a specimen from the Bay of Brest that was used for validation of the paleotemperature equation.

2.2. Shell preparation

After collection, shells were immediately frozen and kept at $-18\text{ }^{\circ}\text{C}$ until further analyses. The left valve of the organism's shell was removed and cleaned with a brush to remove the periostracum, then gently rinsed with deionized water and air-dried. The sample valve was then mounted on a PVC cube with quick drying two-part epoxy resin. Depending on the shell, one or two 1-mm thick sections were cut from each valve perpendicular to the growth lines along the axis of maximum growth. Samples were sectioned with a low-speed precision saw (Struers-Secotom 10; rotation speed: 300 rpm; feed rate: $150\text{ }\mu\text{m s}^{-1}$) equipped with a 0.6 mm thick diamond-coated blade, continually cooled by deionized water. These sections were mounted on glass slides and ground first using a coarse abrasive (800 and 1200 grit size) and then polished with Al_2O_3 powder ($3\text{ }\mu\text{m}$, $1\text{ }\mu\text{m}$, and $0.25\text{ }\mu\text{m}$ grain size). Thick sections were ultrasonically rinsed with deionized water between each grinding or polishing step to remove residual abrasive material. The number of grinding or polishing steps depended on the final use of the thick section. For sclerochronological analyses (27 samples from the Chausey Islands site), sections were ground and polished down to a thickness of $240\text{ }\mu\text{m}$. Sections subjected to isotopic analyses (9 samples selected from the 27 specimens collected at the Chausey Islands, and 4 shells from the Bay of Brest) were ground and polished to a thickness of $800\text{--}900\text{ }\mu\text{m}$.

2.3. Sclerochronological analyses

The 27 sections cut from shells collected at the Chausey Islands were imaged using a Hamamatsu C4742-95 digital camera ($\times 6.3$) attached to a Leica MZ16 FM stereomicroscope ($\times 7.11$). Photo stitching software (Photoshop Elements 2.0) was then used to assemble images into a single, high-resolution mosaic map (Fig. 3a). The increments of each section were then dated relative to the ontogenetically youngest growth band formed in 2009. Increment width was measured using image analysis software dedicated to calcified structures (TNPC, French acronym standing for Numerical Treatment of Calcified Pieces, Noesis, France – www.tnpc.fr).

The main objective of these sclerochronological analyses was to relate shell growth rate variability to environmental conditions at the Chausey Islands site and, given a robust relationship between shell increments and known environmental parameters, to infer past environmental conditions from growth increment time series. Annual growth increment time series therefore require a correction for this ontogenetic trend in order to isolate environmental signals. A generalized von Bertalanffy growth function (gVBGF) was selected from among several functions that are used to apply age-related growth corrections (i.e. Gompertz, special VBGF, seasonal VBGF, logistic, and Richards model). The gVBGF was chosen because it provided the highest coefficient of determination for our

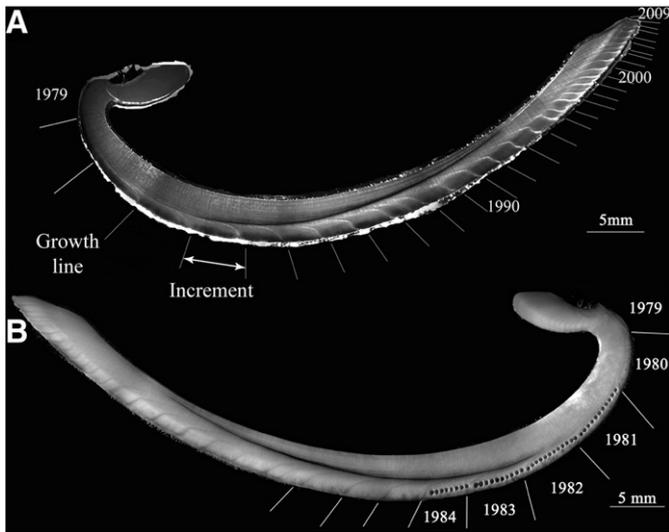


Fig. 3. (A) Cross-section of a dog cockle shell (240 µm thick) used for sclerochronological analyses, imaged by transmitted light. (B) 900-µm thick cross section of the same specimen, used for isotopic analyses and observed under reflected light. Each hole represents an extraction pit from which an aragonite fraction was collected and analyzed for oxygen isotopic composition.

dataset. The gVBGF was fitted to size-at-age data pairs belonging to the 27 samples (curvilinear distance umbo-growth line; mm-age in years) by an iterative nonlinear least-square method (Newton algorithm; see Brey, 2001 for details):

$$L(p)_t = L(p)_\infty \times \left(1 - e^{-K(t-t_0)}\right)^D \quad (1)$$

where $L(p)_t$ is the predicted shell length (*i.e.* curvilinear distance umbo-growth line in mm) at time t (year), $L(p)_\infty$ is the predicted mean asymptotic shell length (mm), K is the Brody growth coefficient (year^{-1}), the exponent D determines the shape of the curve (inflection point if $D > 1$), and t_0 is theoretical age (year) when shell length equals zero.

We subsequently applied a method used by dendrochronologists (*cf.* Briffa et al., 1990) and adapted for analysis of mollusc shells (Schöne, 2003) to calculate SGI. Growth indices were first calculated by dividing the measured growth increment by predicted growth increment (derived from the gVBGF) for each annual band:

$$GI_t = \frac{L_{t+1} - L_t}{L(p)_{t+1} - L(p)_t} \quad (2)$$

where GI_t is the growth index at time t (year), L_{t+1} is the measured shell length (mm) at time $t + 1$ (year), L_t is the measured shell length at time t , $L(p)_{t+1}$ is the predicted shell length at time $t + 1$, and $L(p)_t$ is the predicted shell length at time t . Growth indices were then standardized for each year according to Eq. (3):

$$SGI_t = \frac{GI_t - \bar{x}_{GI}}{\sigma_{GI}} \quad (3)$$

where \bar{x}_{GI} and σ_{GI} are the mean and the standard deviation of growth index time series for a given sample.

For each year of growth, SGI values were calculated for each sample and averaged in order to build a mean SGI chronology for the Chausey Islands sample population.

2.4. Oxygen isotope analyses

The oxygen isotope ratio ($^{18}\text{O}/^{16}\text{O}$) of marine biogenic carbonate is controlled by temperature and the oxygen isotope composition of the seawater from which it precipitates (Epstein et al., 1953). Because

both growth rate and the duration of growth (number of days of growth per year) decrease during the lifespan of bivalve molluscs (*cf.* Goodwin et al., 2003), shells were sampled only between the second and ninth year of growth (Fig. 2) in order to avoid overlap between closely spaced annual records. Shell aragonite fractions ($n=623$) were sampled from thick sections using an automated high-resolution microsampling device (MicroMill, New Wave Research) equipped with a 300-µm tungsten carbide drill bit (model H71.104.003, Gebr. Brasseler GmbH & Co. KG, Germany). Between 9 and 14 carbonate fractions were collected from the outer layers of annual growth increments corresponding to the ontogenetically youngest portions of shells (Fig. 3b). Drill holes were ca. 350 µm in diameter and provided aragonite fractions of 53 to 176 µg (mean = 98 µg). Aragonite samples were then acidified in 100% phosphoric acid at 70 °C for 470 s and analyzed using an automated Finnigan MAT Kiel III carbonate device coupled to a Finnigan MAT 252 isotope ratio mass spectrometer at the Stanford University Stable Isotope Laboratory. Shell isotopic ratios are reported in conventional delta (δ) notation (Epstein et al., 1953) relative to the VPDB standard. Repeated analyses of the international isotopic reference standard NBS-19 yielded reproducibility (1σ) of 0.05‰ VPDB.

To determine whether dog cockle shells are precipitated in isotopic equilibrium with seawater, we compared seawater temperature data from monitoring stations with those derived from oxygen isotope compositions of shells from the Bay of Brest. This analysis included aragonite samples corresponding to years 1998 to 2007 (Fig. 2). A first order challenge in reconciling real-time monitoring data with that of the potential proxy was that *G. glycymeris* shells do not preserve detectable daily increments between successive annual growth lines (given the resolution of methods and instruments used in this study). It was therefore impossible to assign an exact date to aragonite samples collected from shells. This problem was partly circumvented by calculating a theoretical $\delta^{18}\text{O}_{\text{aragonite}}$ seasonal record for the 1998–2007 study period based on temperature and salinity measurements from the SOMLIT-Brest station. In order to relate $\delta^{18}\text{O}_{\text{aragonite}}$ to environmental conditions, we used a fractionation equation empirically determined for biogenic aragonite by Grossman and Ku (1986). In their equation, $\delta^{18}\text{O}_{\text{water}}$ is reported as the SMOW value minus 0.20‰ in order to adjust the carbonate and water $\delta^{18}\text{O}$ measurements to the different scales on which they are measured (*i.e.* PDB and SMOW, respectively; Dettman et al., 1999). However, the most recent evaluations indicate that the PDB-derived CO_2 is enriched of 0.27‰ with respect to the CO_2 equilibrated with SMOW at 25 °C (Gonfiantini et al., 1995). Accounting for this new correction, the equation of Grossman and Ku (1986) translates to:

$$T(^{\circ}\text{C}) = 20.6 - 4.34 \times \left(\delta^{18}\text{O}_{\text{aragonite VPDB}} - \left(\delta^{18}\text{O}_{\text{water VSMOW}} - 0.27\right)\right). \quad (4)$$

The water oxygen isotope composition in the Bay of Brest was estimated using the linear relationship between $\delta^{18}\text{O}_{\text{water}}$ and salinity S (measured at SOMLIT-Brest) reported in Chauvaud et al. (2005):

$$\delta^{18}\text{O}_{\text{water VSMOW}} = 0.164(\pm 0.001) \times S - 5.38(\pm 0.02). \quad (5)$$

The first and last $\delta^{18}\text{O}_{\text{aragonite}}$ values for each annual increment were then compared with the predicted seasonal variation in $\delta^{18}\text{O}_{\text{aragonite}}$ for that year (based on SOMLIT data) in order to estimate timing and length of the growth period. We assumed that shell growth rate was constant throughout this period and interpolated the approximate date of formation from the relative distances between each aragonite sample pit for a given year.

Using the dates derived by the methods described above, $\delta^{18}\text{O}_{\text{aragonite}}$ temperatures were calculated using Eqs. (4) and (5)

and compared with seawater temperatures measured at the SOMLIT-Brest station. An offset between measured station temperatures and $\delta^{18}\text{O}_{\text{aragonite}}$ temperatures required derivation of a new paleotemperature equation. This equation was calculated as an ordinary least squares regression of *G. glycymeris* $\delta^{18}\text{O}_{\text{aragonite}}$ values on temperature and salinity data from the SOMLIT-Brest station. This equation was then checked by comparing (i) $\delta^{18}\text{O}_{\text{aragonite}}$ temperatures from 2008 to 2009 portions of shells (*i.e.* aragonite samples that were not used in calibrating of the new paleotemperature equation; Fig. 2), and (ii) seawater temperature data measured every 20 min at the MAREL buoy between 2008 and 2009.

In order to maximize the length and temporal resolution of the paleotemperature time series, aragonite samples were collected from 9 shells from the Chausey Islands site (ontogenetic ages 2 to 8; Fig. 2). We used $\delta^{18}\text{O}_{\text{aragonite}}$ values from these samples to reconstruct past variations of seawater temperature using our new paleotemperature equation, assuming an average seawater oxygen isotope composition of 0.34‰ VSMOW. This average $\delta^{18}\text{O}_{\text{water}}$ value was calculated using (i) the average salinity measured at the Chausey Islands site (May to October) over the last decade (34.87 ± 0.74) and (ii) the $\delta^{18}\text{O}_{\text{water}}$ –salinity relationship from the Bay of Brest. Oxygen isotope of seawater ($\delta^{18}\text{O}_{\text{water}}$) is strongly correlated with latitude (LeGrande and Schmidt, 2006), which is similar for the Brest and Chausey sites. Oxygen isotope-derived temperatures were then compared (i) to seawater temperatures from a station at Guernsey (St-Helier harbor data provided by the Guernsey Department of Fisheries; Fig. 1) between 1980 and 2008 and (ii) to seawater temperatures measured around the Chausey Islands between 1998 and 2009 (data provided by the SMEL buoy).

2.5. Environmental data and growth indices

The mean SGI chronology for the Chausey Islands population was compared to the North Atlantic Oscillation (NAO) and seawater temperature datasets from monitoring stations. The NAO is an atmospheric phenomenon related to latitudinal air mass movement between the subpolar and subtropical regions of the North Atlantic Ocean (Hurrell et al., 2003). It is responsible for most of the weather patterns (wind, temperature, moisture, *etc.*) in the North Atlantic, especially during the winter months. The NAO is usually monitored as the NAO index, which is defined as the normalized pressure difference between the Azores (the center of the high-pressure system) and Iceland (low-pressure system). In this study, the NAO was introduced as a time series of annual NAO index values calculated as the mean of January–March monthly values (data source: <http://www.cgd.ucar.edu/cas/jhurrell/indices.html>).

As seawater temperature is one of the main factors controlling growth of marine invertebrates, we compared SGI values with temperature data acquired by monitoring stations from 1998 to 2009, and by oxygen isotope analyses prior to 1998. An annual standardized temperature index (STI) was calculated to normalize the data (Schöne, 2003):

$$STI_t = \frac{T_t - \bar{x}_T}{\sigma_T} \quad (6)$$

where T_t is the mean annual temperature (°C) at time t , \bar{x}_T and σ_T are the mean and the standard deviation of the mean annual temperature time series.

2.6. Statistical analyses

In order to assess the quality of our master-chronology, we calculated the Expressed Population Signal (EPS) and the Subsample Signal Strength statistics (SSS; Briffa et al., 1990). Various authors regard EPS

and SSS values above 0.85 to be significant and indicative of a robust and reliable dataset (Wigley et al., 1984; Akkemik et al., 2005; Black et al., 2009).

The paleotemperature equation was checked by regressing empirically derived temperatures on measured temperatures for a given site (a linear model). This procedure yielded a slope of one that was verified by a Student's *t*-test. *A priori* residual analyses confirmed our assumptions of normality, independence, and homoscedasticity. Relationships between SGI, STI and NAO index were investigated with the Spearman rank correlation test. All statistical analyses were performed using R statistical analysis software.

3. Results

3.1. Sclerochronological analyses

Annual growth lines were easily resolved in thin sections of shells from the Chausey Islands population, allowing precise dating of each growth increment (Fig. 3). Some individuals exhibited supernumerary growth lines that were easily discernible in early ontogenetic stages of the shell, but more difficult to distinguish in later ontogenetic stages. We estimated that these supernumerary growth lines introduce a 1–3 year uncertainty in the actual age of the oldest shell samples.

The minimum and maximum ages of individuals used to build the mean SGI chronology were 23 and 46 years, respectively. The broadest annual increments, formed early in the organism's lifespan, measured less than 9 mm. Two groups of individuals were distinguished, separated by a period between 1970 and 1975 with relatively minor recruitment (at least in our sampling).

The mean SGI chronology spanned from 1965 to 2009 (Fig. 4). Due to the low sample density (only 2 shells for 1965 and 5 shells for the period 1967 and 1969), 95% confidence intervals were relatively broad before 1970. On another hand, confidence intervals were narrow for the period between 1987 and 2009 due to high sample density (27 shells). The relatively high EPS and SSS values (>0.89 and >0.90 respectively) for a minimum sample set of 2 shells allowed reliable reconstruction for the period between 1965 and 2009. Mean annual SGI varied from -1.176 in 1966 to 1.055 in 2002 (Fig. 4). SGI values were negative from 1965 to 1989 and positive from 1993 to 2009.

3.2. Calibration of the paleotemperature equation

Comparison of $\delta^{18}\text{O}_{\text{aragonite}}$ values measured from growth increments with those predicted by the equation of Grossman and Ku (1986) confirmed the assumption that growth lines within shells are produced annually ($r^2 = 0.82$; $p < 0.001$; Fig. 5A). Significant differences were observed between measured and predicted values

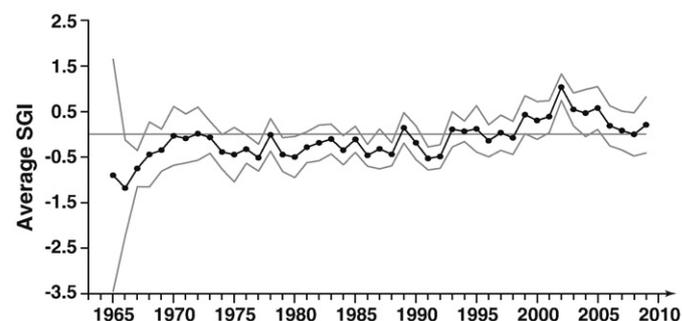


Fig. 4. Average annual SGI values of the 27 specimens of *Glycymeris glycymeris* collected at the Chausey Islands site (black dots and line). Gray lines represent the distribution limits at a 95% confidence interval. Expressed Population Signal (EPS) is 0.89.

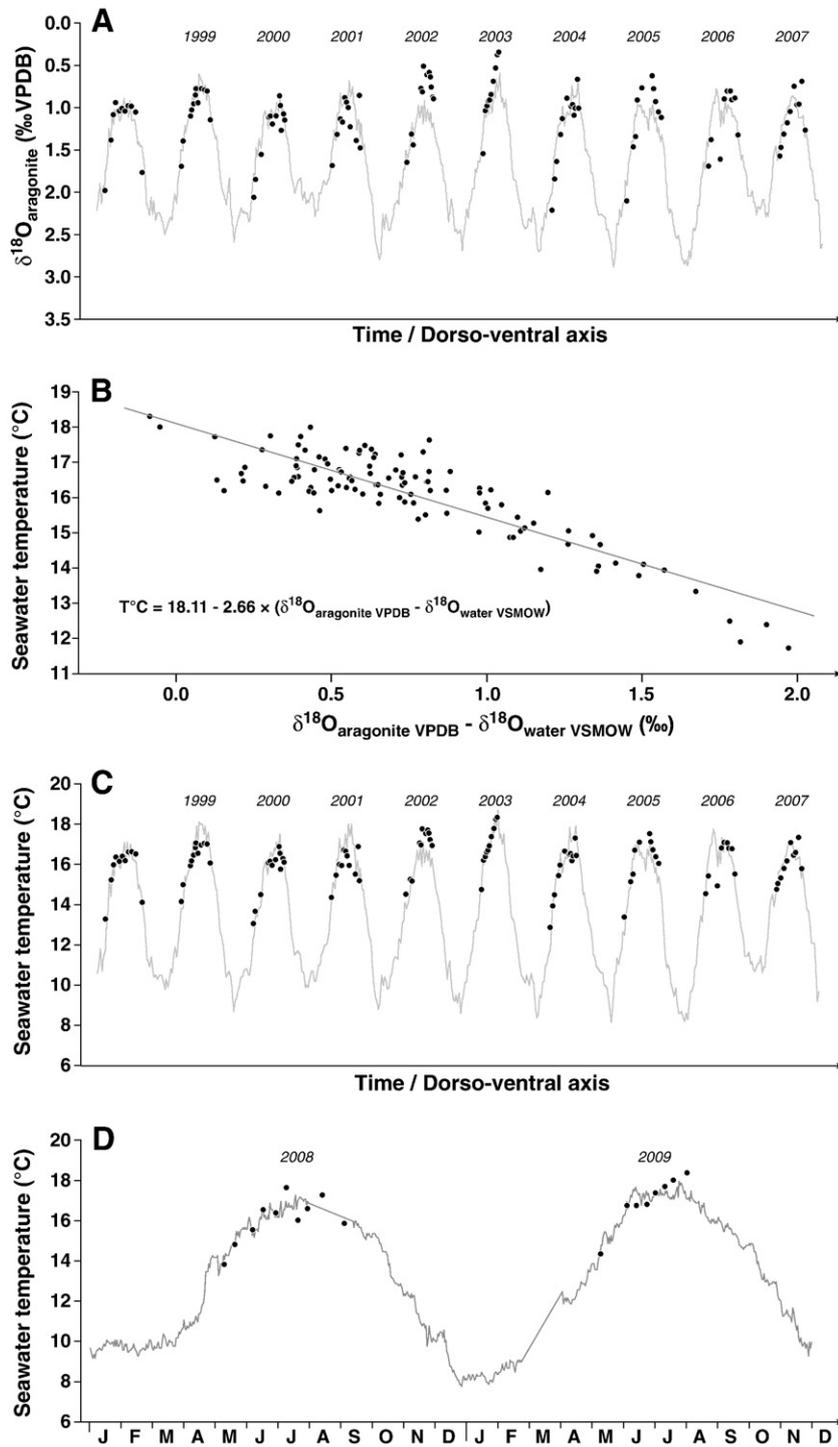


Fig. 5. (A) Time series of $\delta^{18}\text{O}_{\text{aragonite}}$ predicted from *in situ* (SOMLIT-Brest) temperature and salinity data using the Grossman and Ku (1986) equation (gray line) and time series of $\delta^{18}\text{O}_{\text{aragonite}}$ measured in four shells from the Bay of Brest (black dots). (B) Empirical relationship between seawater temperature ($^{\circ}\text{C}$) and ($\delta^{18}\text{O}_{\text{aragonite}} - \delta^{18}\text{O}_{\text{water}}$) derived by this study and calculated relative to VPDB and VSMOW standards, respectively. Observations are shown as black dots distributed around the trend predicted by Eq. (7) (gray line). (C) Time series of oxygen isotope-derived temperatures calculated from the paleotemperature equation specific to this study (Eq. (7); black dots) and measured temperatures in the Bay of Brest (gray line). (D) Comparison showing close overlap of the empirical paleotemperatures calculated from $\delta^{18}\text{O}_{\text{aragonite}}$ measurements (black dots), and *in situ* temperatures measured by the MAREL buoy (gray line) in the Bay of Brest for years 2008 and 2009.

after 2002 however, indicating the need of an additional paleotemperature equation ($r^2 = 0.87$; $p < 0.001$; Fig. 5B):

$$T(^{\circ}\text{C}) = 18.11(\pm 0.13) - 2.66(\pm 0.15) \times (\delta^{18}\text{O}_{\text{aragonite VPDB}} - \delta^{18}\text{O}_{\text{water VSMOW}}). \quad (7)$$

Uncertainties for the slope and intercept calculated according to 95% confidence intervals. Fig. 5C illustrates the significant correlation between seawater temperatures measured at the SOMLIT-Brest monitoring station and oxygen isotope derived temperatures calculated from Eq. (7). Reconstructed temperatures ranged from 12.7°C in 2004 to 18.3°C in 2003 and likely represent a period between early May and late October.

3.3. Validation

Eq. (7) allowed us to calculate a series of empirical seawater temperatures from $\delta^{18}\text{O}_{\text{aragonite}}$ values (T_{cal}) that were then compared to coeval temperature measurements from the MAREL buoy. The empirical temperatures corresponded to shell portions precipitated from 2008 to 2009 in the Bay of Brest. Note that the same specimen was also used for calibration (using shell portions accreted in 2007; Fig. 2). These data were then regressed on temperatures measured by the MAREL buoy (T_{meas}) using a linear model (multiple $r^2 = 0.99$; $p < 0.001$):

$$T_{\text{cal}} = 0.9964 \times T_{\text{meas}} \quad (8)$$

Oxygen isotope-derived temperatures were closely related to bottom water temperatures (Fig. 5D). The slope was not significantly different from one ($p = 0.966$), and average temperatures during the growth season were equivalent to both measured temperature (16.45 °C) and calculated temperature (16.39 °C, 95% confidence limits: 15.84–16.94 °C). The accuracy of our new paleotemperature equation was shown to be 0.34 °C (the standard deviation of the residuals). These results demonstrate that temperature records can be consistently reconstructed using a novel paleotemperature equation specifically derived from *G. glycymeris*. Comparison of temperatures calculated from the new equation and those calculated from Grossman and Ku (1986) equation showed that the use of the latter generic equation tended to overestimate temperature (Fig. 6). The over-estimation ranged from 0.1 °C to more than 2 °C, and was positively correlated to the absolute temperature value. These results demonstrate the critical importance of a specific paleotemperature equation for studies using the dog cockle as a proxy record.

3.4. Paleotemperature reconstruction

The methods described above were then used to reconstruct seawater temperature for the Chausey Islands from 1966 to 1994. Oxygen isotope composition for ontogenetically young portions of 9 shells, corresponding to partially overlapping growth periods (Fig. 2) were used as inputs to the final paleotemperature Eq. (7). Salinity varied between ± 0.74 between May and October at the study site. Given estimated effects of salinity on oxygen isotope partitioning, this variation introduced a ± 0.34 °C uncertainty to reconstructed temperature values. Reconstructed temperature variations resembled surface temperatures measured at the Chausey site between the months of June and November (Fig. 7). Overall, seawater temperatures measured from June to November were higher at the Chausey site than around Guernsey but we found a good correlation between

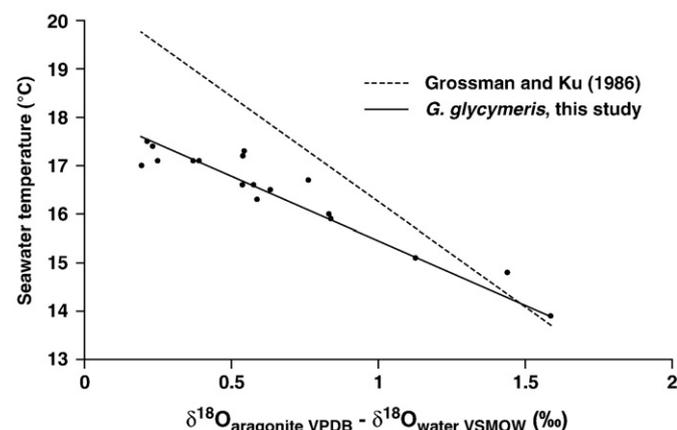


Fig. 6. Comparison of the temperature- $\delta^{18}\text{O}$ fractionation established in this study (solid line) with that reported in Grossman and Ku (1986; dashed line).

the datasets from these two sites for the years 1998 to 2008 ($n = 127$; $r^2 = 0.72$; $p < 0.001$). We compared oxygen isotopes-derived temperatures with Guernsey temperatures from 1980 to 1994 and found a strong and statistically significant correlation ($n = 163$; $r^2 = 0.78$; $p < 0.001$). The reconstructed and the measured variables seemed to fluctuate with a similar decadal periodicity. Reconstructed temperatures from the shell dataset indicate that the coldest summers occurred in 1967, 1975 and 1992 and the warmest years were 1981, 1993, 1994 and to a lesser extent, 1971.

3.5. Climate-shell growth relationships

Over the 1966 to 2009 study period, significant variations in mean SGI and STI were observed (Fig. 8A). These two time series exhibit a moderate but statistically significant, positive correlation ($n = 38$; $r^2 = 0.49$; $p < 0.05$). During two periods between 1966–1967 and 1976–1992, a significant decrease in shell growth was observed ($p < 0.05$). From 1999 to 2005, growth increased significantly ($p < 0.05$). Reconstructed temperatures and measured temperatures at the Chausey site confirm that the coldest summers occurred in 1966 and during the 1976–1992 period. These temperature records also showed that the hottest summers occurred during the 1999–2005 period (Fig. 7). These results indicate that temperature may regulate shell growth when it reaches a critical value. It should be noted that trends in the STI may be biased due to the absence of temperature data between 1994 and 1998.

With regard to longer term climate signals, no significant relationship could be determined for the mean SGI and the mean annual NAO index, but these two variables seemed to be slightly inversely related ($n = 45$; $r^2 = 0.18$; $p = 0.25$; Fig. 8B).

4. Discussion

The main objective of this study was to assess the potential of dog cockle shells (*Glycymeris glycymeris*) for use in paleoenvironmental reconstructions. Sclerochronological analysis of a population collected from the Chausey Islands provided plausible and robust mean Standardized Growth Indices (SGI). Sclerochemical analysis of the oxygen isotope composition of shell aragonite was applied to the Chausey Island samples and to an additional sample set collected from the Bay of Brest. The two sample sets allowed us to monitor population dynamics in tandem with our assessment of the organism's potential as a paleoenvironmental archive.

4.1. Sclerochronology of dog cockle shells

Annual increments in dog cockle shells are delimited by growth lines which can be either internal or external and are visible in cross section. The distribution of increments widths from the Chausey Islands sample set indicated that the *G. glycymeris* sample population comprised individuals born between 1964 and 1987. The relatively high degree of inter-individual variation in SGI also is similar to that observed for *Chione* sp. (Schöne, 2003), and may result from genetic factors or different responses to variations in environmental parameters. We attribute the slight increase in SGI variation observed after 1995 to low numbers of young individuals in our sample population and the ontogenetic decrease in annual increment widths as individuals age. Variation could also arise from supernumerary growth lines exhibited by some individuals, which may have induced small errors in the dating of annual increments (1 to 3 year age uncertainty for the oldest specimens). Supernumerary growth lines may result from growth hiatuses related to reproduction (Berthou et al., 1986), environmental perturbations (pollutants, exceptionally low temperature events, freshwater inputs, etc.) or anthropogenic disruptions such as dredging (Ramsay et al., 2000). Although variation in growth rates was non-negligible within the sample population analyzed here,

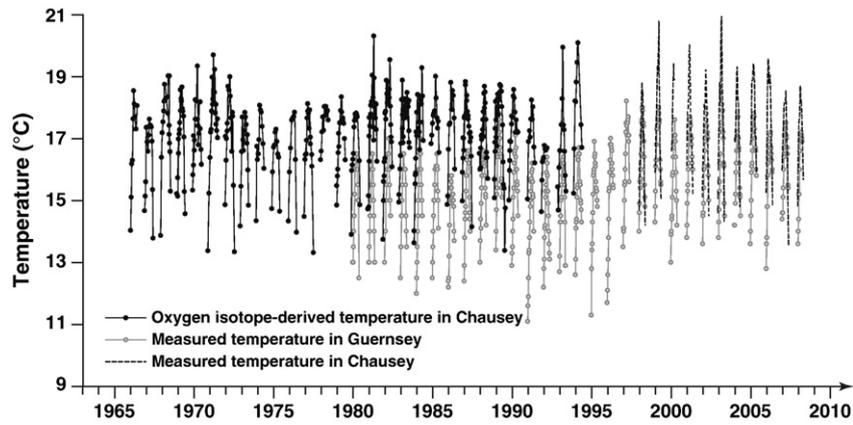


Fig. 7. Time series of oxygen isotope-derived temperature at the Chausey Islands site from 1966 to 1994 (black dots and line), temperatures measured *in situ* at a Guernsey monitoring station from 1980 to 2008 (gray circles and line), and at the Chausey Island monitoring station from 1998 to 2008 (black dotted line).

individuals exhibited strikingly similar growth trajectories, as evident from a robust mean annual SGI, and its relatively narrow associated uncertainties at the 95% confidence level. The EPS and SSS statistical tests described above confirmed that sclerochronological analysis of shells provided robust master-chronology.

4.2. Oxygen isotope-derived temperature of calcification

Isotopic analyses performed on sample populations collected from the two study localities were consistent and complementary. Dog cockle shells collected from the Bay of Brest were used to calculate a specific linear paleotemperature relationship and to get information about biological parameters such as the growth period. Along with the Bay of Brest sample population, shells from the Chausey Island site were used to assess *G. glycymeris*' potential in paleoenvironmental reconstructions.

Comparison of oxygen isotope-derived temperatures and water temperatures measured by several monitoring stations located in

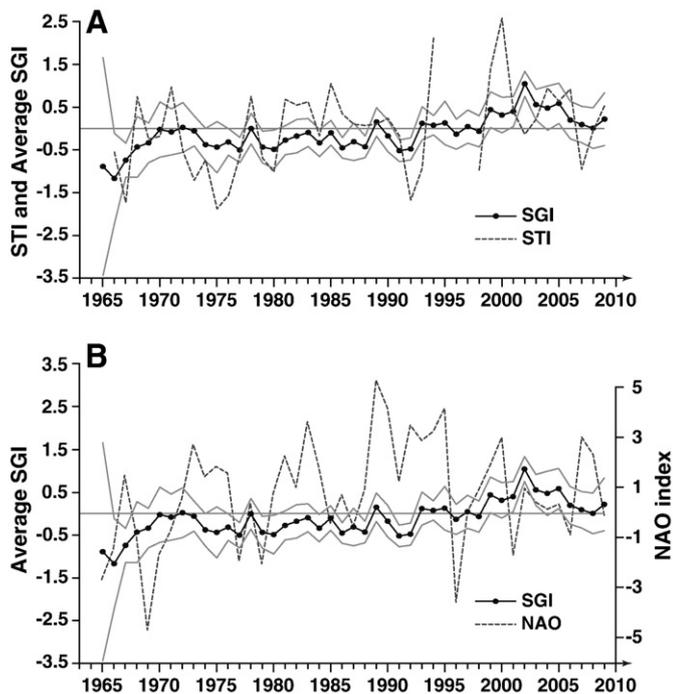


Fig. 8. (A) Time series of average annual SGI (black dots and line) and STI (dashed line). (B) Time series of average annual SGI (black dots and line) and NAO index (dashed line).

the Bay of Brest indicated that $\delta^{18}\text{O}_{\text{aragonite}}$ data corresponded to a May–October growth period for *G. glycymeris*. During early stages of the organism's lifespan, shell growth is apparently synchronized with the 6 warmest months of the year. This spring to autumn growth period has also been observed among other relatively long-lived bivalve species from the North Atlantic. For example, *Arctica islandica* exhibits an early-life growth increment width of 4–7 mm, similar to that of *G. glycymeris* (Schöne et al., 2005b). The mean increment width of an average *A. Islandica* specimen in its sixth year is 6 mm, which corresponds to a growth period of 185 days (Thébaud et al., 2009b). Our results confirm that lines demarcating growth increments correspond to winter growth cessation. While the paleotemperature equation reported in Grossman and Ku (1986) was developed for gastropods, foraminifera and scaphopods with an aragonite skeletal mineralogy similar to that of the Mollusca, our results show that the generic equation is non-ideal for temperature reconstructions using dog cockle shell aragonite. Contrasting paleotemperature equations suggest varying degrees of isotopic fractionation during biomineralization for different organisms. Dunbar and Wefer (1984) have previously shown that isotopic fractionation during biomineralization was species-specific. Using temperature measurements from monitoring stations and shell isotopic compositions, we developed a robust paleotemperature equation calibrated specifically for *G. glycymeris* ($r^2 > 0.87$). The new equation was then used to calculate temperature variations over the last decade at the Bay of Brest site and for the period between 1966 and 1994 at the Chausey Islands site. Oxygen isotope-derived temperatures were most strongly correlated to temperatures measured from June to November at both the Guernsey harbor station (between 1980 and 1994) and the Chausey Islands station. The robust correlation between reconstructed and measured values indicates that reconstructed temperature data for the 1965–1980 period faithfully reflect past seawater temperatures at the study localities. The reconstructed temperatures appeared to have a periodicity of around 10 to 15 years but we could not test this observation with further spectral analyses due to the insufficient duration of our time series, relative to the scale of the signal's apparent frequency.

Reconstructed temperatures from both the Bay of Brest and the Chausey Islands sites always exceeded 12.9 °C (Figs. 5, 7). We infer this temperature to be a thermal threshold for *G. Glycymeris* shell growth. The one-month offset between the growth periods observed at the Brest (May–October) and Chausey (June–November) localities, as well as differences in their respective reconstructed temperature minima (12.9 °C at Brest and 13.3 °C at Chausey), may result from differences in the water column structure at each site. Coastal waters in the Bay of Brest are often stratified during the summer (Chauvaud et al., 1998) whereas those of the Normand-Breton Gulf are always well-

mixed by intense tidal currents which induce a lack of vertical stratification (Hoch and Ménesguen, 1997) and a temporal shift in the development of phytoplankton blooms (Salomon and Breton, 1991). Dog cockle growth dynamics are also subject to fluctuations in their primary food source, phytoplankton, which bloom according to temperature and other marine environmental parameters (Eppley, 1972). Phytoplankton blooms usually occur during May in the Bay of Brest (SOMLIT-Brest data), but occur later in June in the Normand-Breton Gulf (Martin-Jezequel, 1983; Salomon and Breton, 1991). Other parameters such as nutrient dynamics (N, P, Si) also play an important role in development of phytoplankton blooms. Concentration and availability of nutrients determine their nature and intensity (Smith, 2006). The offset in seasonal time frames of dog cockle shell growth between the Chausey and Brest study sites may therefore be partly due to differences in nutrient dynamics.

4.3. *G. glycymeris*' potential as a paleoenvironmental archive

The significant correlation observed between reconstructed temperatures (STI) and the growth of dog cockle (SGI) is not surprising given the well-known effects of temperature in regulating metabolic activities of poikilotherm aquatic organisms (Kinne, 1964). We attribute the lack of correlation between NAO and SGI to the fact that the NAO primarily affects winter-time conditions in Northern Europe, during which time dog cockle shell growth is on hiatus. Through its effects on westerly winds (strength, moisture, direction), a positive phase of the NAO may cause a milder and moister winter in Northern Europe (Hurrell et al., 2003) but even these warmer effects were not detectable in shell growth trends. Analysis of the *G. glycymeris* SGI from our two study localities therefore suggests that the organism is not well suited for paleoenvironmental research concerning larger climate patterns such as the NAO.

In addition to temperature, nutrient and trophic conditions also play a fundamental role in bivalve growth (Bayne and Newell, 1983). Future studies of bivalve SGI trends should include chlorophyll *a* concentrations in the water column. Fatty acid biomarker analyses indicate that *G. glycymeris* individuals residing around the Chausey Islands feed on phytoplankton (diatoms) and brown macroalgae (Suroy et al., unpublished data). Changes in the availability of these food sources can directly influence bivalve growth (Mai et al., 1996; Chauvaud et al., 2001). *G. glycymeris*' SGI patterns may therefore reflect inter-annual variations of primary productivity. These potential effects could be queried in future studies by including trace element analyses (Ba/Ca, Mo/Ca, Li/Ca ratios) of shells, and other proxies related to phytoplankton dynamics (Thébault et al., 2009a; Thébault and Chauvaud, 2012).

In conclusion, *G. glycymeris* has excellent potential as a paleoenvironmental archive for periods of time encompassing several centuries because (i) this species appeared early in Cretaceous period (Oliver and Holmes, 2008) and is found throughout the subsequent fossil and archeological record (Stefaniuk et al., 2005), (ii) its lifespan can extend back two centuries (Reynolds et al., 2010) and (iii) seawater temperatures can be accurately estimated through sclerochronological and sclerochemical analyses of its shell. Therefore, dog cockles are a potential temperate equivalent to *Arctica islandica* shells (Scourse et al., 2006).

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