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The ormer (*Haliotis tuberculata*): A new, promising paleoclimatic tool

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ABSTRACT

This study aimed to investigate the environmental controls on the oxygen isotope composition of shells of the European abalone, *Haliotis tuberculata*. Seasonal $\delta^{18}O$ profiles from the outer prismatic layer of four abalone shells, collected live in northwest Brittany (France) in 2002 and 2012, were compared to local temperatures and salinities. According to the findings herein, $\delta^{18}O$ variations in abalone shells corresponded to seasonal variations, and thus, shell composition represented a reliable tool for aging and growth studies. Seawater temperatures estimated from the abalone collected in 2012 reflected the in situ measured temperatures, but the reconstructed temperatures from shells of the three specimens collected in 2002 deviated from measured temperatures by 2.5 °C. This overestimation of temperatures corresponded to a "kinetic effect" related to very high annual abalone growth rates; thus, it could be corrected by applying $+0.53‰$ to the $\delta^{18}O_{shell}$. This methodology was then applied to a fossil (6000 cal yr BP) collected in the Bay of Biscay. Given the worldwide distribution of both live and fossilized abalones, the results of the present study showed that this genus represents a promising paleoclimatic tool.

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1. Introduction

Knowledge of past environmental variations is a prerequisite for understanding possible future climate changes in a warming world. Environmental parameters, such as ocean temperature and salinity, have been directly measured only over a relatively short instrumental period (Hurrell and Trenberth, 1999; Smith and Reynolds, 2003). For time intervals prior to 1860, stable oxygen isotope values of carbonates serve as an important temperature proxy. The temperature dependency of oxygen isotope fractionation has been quantified for inorganically precipitated calcite (Urey, 1947; McCrea, 1950; O'Neil et al., 1969; Kim and O'Neil, 1997). The temperature dependency of oxygen isotope fractionation has also been established for living organisms, both in the field and in laboratory cultures, for corals (Reynaud-Vaganay et al., 1999), mollusks (Epstein et al., 1953; Grossman and Ku, 1986), and planktonic foraminifera (Erez and Luz, 1983; Bernis et al., 1998; Barras et al., 2010). Thus, analysis of the oxygen isotope values ($\delta^{18}O$) in mollusk shells can provide a precise determination of the temperature of the water in which the animals lived (Krantz et al., 1984; Kennedy et al., 2001; Chauvaud et al., 2005).

Shells of bivalves have received considerable attention in paleoclimate studies; in particular oysters (Kirby et al., 1998; Kirby, 2001; Lartaud et al., 2010; Ullmann et al., 2010; Harzhauser et al., 2011), scallops (Hickson et al., 1999; Chauvaud et al., 2005; Johnson et al., 2009), mussels (Donner and Nord, 1986; Freitas et al., 2005), and clams (Arthur et al., 1983; Schöne et al., 2004; Gillikin et al., 2005; Schöne et al., 2005). However, the shells of gastropods are often more difficult to use. This problem can be partly attributed to the morphology of gastropod shells and partly to the difficulty in preparing cross-sections to reveal internal growth patterns (Schöne et al., 2007; Radermacher et al., 2009; Tao et al., 2013). Internal growth patterns are useful to place the geochemical data into a temporal context. So far, no aging technique based on growth pattern analyses has been established and validated for abalones (Ward, 1986; Day and Fleming, 1992; Erasmus et al., 1994; Day et al., 2001). The use of stable oxygen isotopes was proposed as an alternative method for aging abalone shells in determining growth rates for fisheries management (Gurney et al., 2005; Kim and Hudson, 2007; Naylor et al., 2007; Roussel et al., 2011) and stock discrimination (Lee et al., 2002). To our knowledge, stable isotopes of abalone shells have not been employed to reconstruct paleo-environmental changes.

Abalones are widely distributed in temperate and tropical waters throughout the world (Shepherd and Steinberg, 1992). *Haliotis* species

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generally live in shallow, rocky, subtidal habitats, although some can also be found in the lower intertidal zone (Shepherd, 1973). They are largely sedentary and rarely move more than a few tens of meters within several months (Clavier and Richard, 1984; Clavier and Chardy, 1989; Dixon et al., 1998). Currently, partly due to their commercial value, the biology and ecology of abalone species are fairly well known. The only species in Europe is *Haliotis tuberculata* L.; it achieves a maximum shell length of 14 cm, and is found in the best fishing areas of Brittany and the Channel Islands.

Like many gastropods, abalone growth varies with the season, food availability, population density, temperature, local hydrography, and stress (review in Day and Fleming, 1992; Huchette, 2003). *H. tuberculata* grow faster in spring and summer than during the rest of the year (Clavier and Richard, 1986; Roussel et al., 2011). However, many gastropods and bivalves stop growing during the coldest or warmest months of the year; thus, their shells do not provide a good record of winter or summer temperatures (Arthur et al., 1983; Wefer and Berger, 1991; Chauvaud et al., 1998; Surge et al., 2001; Schöne, 2013). *H. tuberculata* growth slows down during the lowest temperatures, but there is no evidence that the shells stop growing in winter (Roussel et al., 2011). The zones of slow growth can be considered as 'growth checks', because they are used to determine the approximate age of *H. tuberculata* shells (Forster, 1967). Growth checks occur in winter in for abalone species, such as *H. australis* and *H. mariae* (Poore, 1972; Shepherd et al., 1995), but in summer (due to reproduction) for others species, such as *H. discus hannai* and *H. discus* (Sakai, 1960; Kojima, 1995). However, in many species, e.g., *H. corrugate* and *H. fulgens*, regular growth checks are not discernable (Shepherd and Avalos-Borja, 1997; Shepherd and Turrubiates-Morales, 1997).

Haliotis comprises more than 100 species, and each has a shell with a specific microstructural arrangement. The shell is typically bilayered with an inner nacreous layer (aragonite) and an outer prismatic layer (Bøggild, 1930). Depending on the species, the outer layer is composed of calcite, aragonite, or both of these $CaCO_3$ polymorphs. *H. tuberculata* is one of the species with an outer layer containing both aragonite and calcite polymorphs (Kessel, 1935). However, this outer layer has been difficult to characterize. It was first thought to be mainly composed of calcite with some aragonite enclosed within the calcitic prisms (Mutvei, 1985; Dauphin et al., 1989). However, based on scanning electron microscope analyses, Dauphin et al. (2014) showed an irregular distribution of calcite and aragonite in the outer part of the shell. Thus, the imbricated structure of *H. tuberculata* is composed of an inner nacreous layer, which is aragonitic; a middle layer, mainly composed of prismatic calcite; and an outer layer of prismatic aragonite.

The aim of this study was to investigate the possibility of using *H. tuberculata* shells as biological archives of environmental conditions. We analyzed the oxygen isotopic composition of samples obtained from the outer prismatic layer of four modern abalone shells from northern Brittany and one fossilized abalone from the Bay of Biscay.

2. Materials and methods

2.1. Abalone sampling

A total of five abalone shells were used in the present study. Three abalones (AB1–AB3), were collected on the 1st of May 2002, near the small port of Primel in northwest Brittany, France (Fig. 1). The fourth abalone (AB4) was collected on the 12th of January 2012, close to the coastal monitoring site "Estacade" at the port of Roscoff (Fig. 1). A fossilized abalone (AB5) was retrieved from an archaeological site at Ponthezières (Saint-Georges d'Oléron, Charente-Maritime, Fig. 1), along the coast of the Bay of Biscay. It was dated to the Late Neolithic period (~6000 cal yr BP, Laporte, 1994; Laporte et al., 1998). The four modern abalones were collected by scuba divers, between 10 m (for AB4) and 20 m (for AB1–AB3) depth. The maximum shell lengths of specimens AB1–AB5 were 92, 112, 123, 96, and 75 mm, respectively.

2.2. Environmental parameters

Weekly sea surface temperature (SST) and salinity measurements were obtained from the Service d'Observation en Milieu LITtoral (SOMLIT observatory, http://www.sb-roscoff.fr/Somlit/) at the coastal monitoring site of Estacade at the port of Roscoff for the period of 1997–2011 (Figs. 1, 2A). These data corresponded to specimens AB1–AB3, which were collected at Primel. Indeed, monitoring of environmental parameters also performed in Primel region, but with one
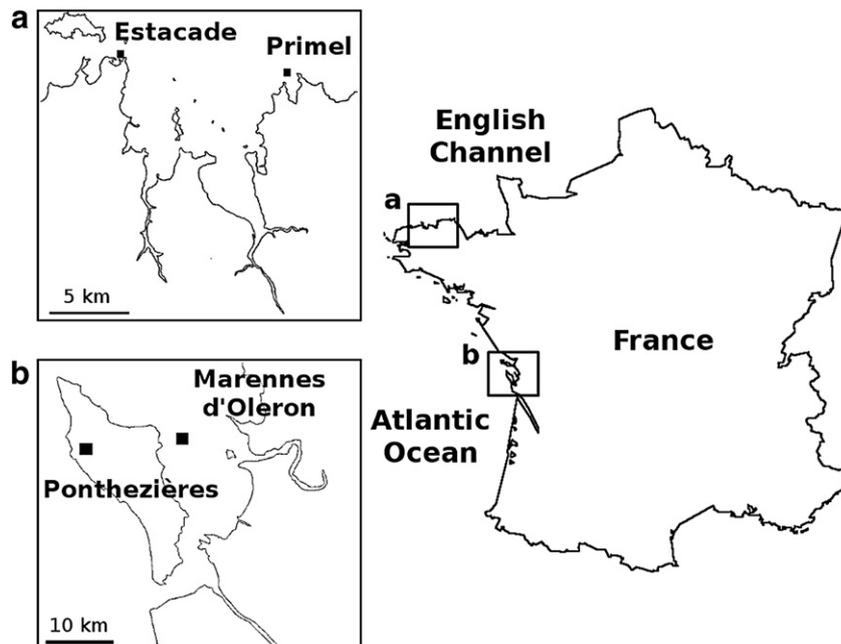

Fig. 1. Locations of abalone sampling sites. (a) Three abalones were collected at Primel in 2002 (AB1–AB3) and one was from Estacade, collected in 2012 (AB4); (b) The fossilized abalone was found at Ponthezières, an archaeological site in the Bay of Biscay. Environmental parameters were derived from observation sites at Estacade in northwest Brittany (SOMLIT observatory), and at Marennes d'Oléron in the Bay of Biscay (IFREMER observatory).
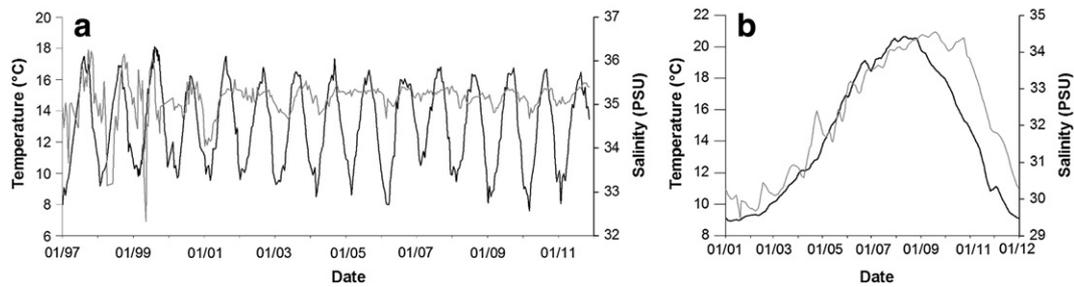
Fig. 2. Sea surface temperatures (°C, dark lines) and salinities (PSU, gray lines). (a) Measurements taken at the coastal monitoring site Estacade of the Roscoff marine experimental station (SOMLIT) for the period of 1997–2011; and (b) measurements taken at Marennes d'Oléron and averaged for 1995 to 2003 (IFREMER).

measurement every two months, showed that both environments were comparable with a mean absolute error of 0.2 °C and 0.6 PSU between 1997 and 2001 (data from E. Thiebaut, Station Biologique de Roscoff). Temperatures derived from the oxygen isotopes in AB5 were compared to modern temperatures measured at Marennes d'Oléron, a station near the archaeological site of Ponthezières, (data from IFREMER, http://www.ifremer.fr/envlit/, Fig. 1). The available seasonal temperature and salinity data were averaged weekly over the period of 1995–2003 to obtain annual reference cycles (Fig. 2b).

2.3. Isotope sample collection

Each shell was carefully cleaned, and external epibionts were removed with successive acetic acid baths. The outer layer of the shell was carefully ground to avoid shell damage caused by boring organisms, with a Dremel hand-held drill, equipped with a 0.3 mm tungsten carbide grinding tip. Samples were acquired from the outer shell surface along the fine growth lines (Fig. 3). Growth lines were ground down until a sufficient amount of material was obtained for analysis (ca. 50–100 μg). This technique allowed the collection of large amount of sample without drilling too deeply (<200 μm). Shell powder samples were analyzed to determine the stable oxygen isotope composition. The results are reported in per mil (‰) relative to the Vienna Pee Dee Belemnite (V-PDB) standard. Samples that weighed over 100 μg were split into two sub-samples.

For abalones AB1 to AB3 (94, 139, and 130 samples, respectively), isotope analyses were performed in 2002 with an automated Finnigan

MAT Kiel III carbonate device coupled to a Finnigan MAT 252 isotope ratio mass spectrometer at Stanford University (California, USA). We analyzed a total of 363 shell samples, 75 NBS-19 standards (National Institute of Standards and Technology, NIST SRM 8544), and 37 SLS-1 standards (Stanford Isotope Lab Standard). The routine analysis of NBS-19 and SLS-1 in this study yielded standard deviations of 0.05‰ and 0.07‰ for $\delta^{18}O$, respectively. Additionally, 78 (21%) shell sample measurements were replicated, and we measured an average standard deviation of 0.05‰ for $\delta^{18}O$.

For abalones AB4 and AB5 (91 and 68 samples, respectively), samples were processed in a Thermo Finnigan MAT 253 continuous flow isotope ratio mass spectrometer coupled to a Gas Bench II at the University of Mainz (Germany). Carrara marble, calibrated relative to NBS-19, was used as an external standard. Precision errors were as small as 0.04‰. To compare the results obtained in the two laboratories, five samples from AB3 were analyzed in 2012 at the University of Mainz. The average difference was as low as 0.09 ± 0.08‰ between analyses made in 2002 and 2012 in the two different laboratories.

2.4. Dating isotopes signals

Each drilled sample was located on the shell along a curved line, from the apex to the peristomal margin (outer lip), following the respiratory holes (Fig. 3). Because samples were taken at equidistant intervals across the shell (on average, every 1.5 ± 0.5 mm), more carbonate samples were derived from the fast-growing portions of shell which were formed during spring and summer.
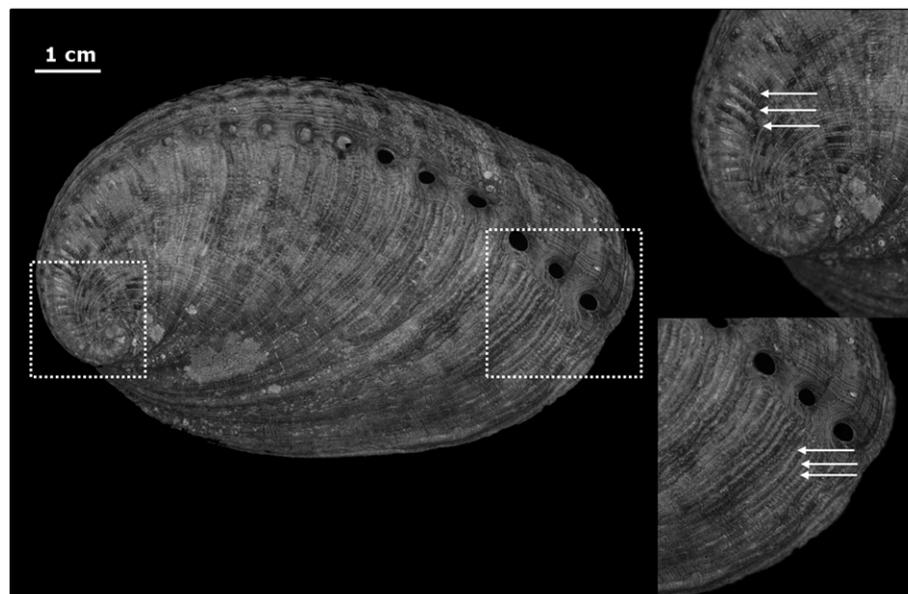

Fig. 3. Shell from abalone AB1 showing sampling grooves (some marked with white arrows) from milling procedure to collect shell powder for stable oxygen isotopic analyses.

An accurate date of formation was assigned to each carbonate sample drilled on the shells based on temporal synchronization of the derived oxygen isotope and the instrumental SST.

Here, the temporal synchronization was treated as a 1-dimensional (1D) signal recording problem, as introduced previously by Nasreddine et al. (2009a). This framework was previously applied in marine biological archives to estimate the growth law of fish otoliths, and with shape geodesics, it has been used for stock or species identification (Nasreddine et al., 2009b). Because the $\delta^{18}O$ measurements were correlated to in situ temperatures, it could be considered a modulated waveform of the temperature signal. Formally, the recording problem is stated as a search for the transformation that optimizes some similarity measure between a reference signal, i.e., the temperature and the deformed signal, $\delta^{18}O$ (Nasreddine et al., 2009a). This issue is stated as the optimization of an energy involving a data-driven term, which evaluates the similarity between the deformed $\delta^{18}O$ signal and the reference signal of temperature, and a regularization term that ensures the transformation remains smooth. At the end of this process, the deformed $\delta^{18}O$ signal and the in situ temperature were significantly correlated (Spearman correlation on the five abalones: synchronization method $= -0.89$, all $P < 0.001$) validating samples dating.

2.5. Outer layer composition

As mentioned in the Introduction, the outer layer of *H tuberculata* has a complex composition, constituted of both aragonite and calcite (Mutvei, 1985; Dauphin et al., 1989; Dauphin et al., 2014). Therefore, we performed a Raman micro-spectrometry analysis on the surface of each shell, and we compared the spectra to reference spectra of aragonite and calcite (free database: Handbook of Raman spectra, http://www.ens-lyon.fr/LST/Raman/). These determinations of outer layer composition thus validated our choice of paleo-temperature equation. Raman scattering investigations were performed at room temperature with excitation at 514.5 nm radiation from an argon/krypton ion laser (Coherent, Innova) and a T64000 multichannel Raman spectrometer (Jobin–Yvon, Horiba) equipped with a nitrogen cooled CCD detector. The Raman spectra were recorded under an Olympus BX41, with backscattering geometry, and an X-50 LF objective with a laser power of 50 mW per sample, which resulted in a spot size of 4 μm. The Raman scattered light was filtered with a holographic Super Notch filter and analyzed with a single monochromator (600 gratings mm^{-1}). The spectra were accumulated twelve times with exposure times of 20 s.

The reference spectrum of aragonite and calcite differed by the group of peaks located between 150 and 300 cm^{-1}. In particular, aragonite spectrum exhibited a peak at 209 cm^{-1} as spectra obtained at the shell surface of the four modern abalones and also the fossilized abalone (Fig. 4).

2.6. $\delta^{18}O_{shell}$ relationship to SST

Based on Dauphin et al. (2014) and Raman micro-spectrometry analyses, the outermost layer of the abalone shells is mainly composed of aragonite. The temperature at the time of shell formation was thus backcalculated with the empirical equation for aragonite sampled in mollusk shells given by Grossman and Ku (1986); we also applied the small modification required on $\delta^{18}O_w$ described by Sharp (2006):

$$T(°C) = 21.8 - 4.69\left(\delta^{18}O_S - \left(\delta^{18}O_W - 0.27\right)\right) \qquad (1)$$

here, $\delta^{18}O_S$ is the oxygen isotopic value of the shell aragonite relative to V-PDB, and $\delta^{18}O_w$ is the oxygen isotopic value of the water relative to the Vienna Standard Mean Ocean Water standard (VSMOW). The $\delta^{18}O_w$ was calculated for each sampling date with the $\delta^{18}O_w$/salinity relationship developed by Chauvaud et al. (2005) in Brittany, where the salinity was measured in situ; thus, we solved the following equation:

$$\delta^{18}O_w = 0.164 * salinity - 5.38. \qquad (2)$$

For the four modern abalones, we used environmental parameters measured at Estacade between 1997 and 2011: salinity measurements were used to calculate $\delta^{18}O_w$, and temperature measurements were used to compare to the temperatures estimated from oxygen isotope composition. For the fossilized abalone, AB5, no data were available for the Neolithic period; therefore, $\delta^{18}O_w$ was calculated either from the annual cycle of salinity (Fig. 2b) or from a constant annual salinity, was obtained by averaging the salinity measured at Marennes d'Oléron over the period of 1995–2003. This salinity was 32.65 ± 2.11 PSU, which gave a $\delta^{18}O_w$ of −0.03‰. The temperatures estimated from the isotopic composition of AB5 were compared to the average temperature measured at Marennes d'Oléron (Fig. 2b).
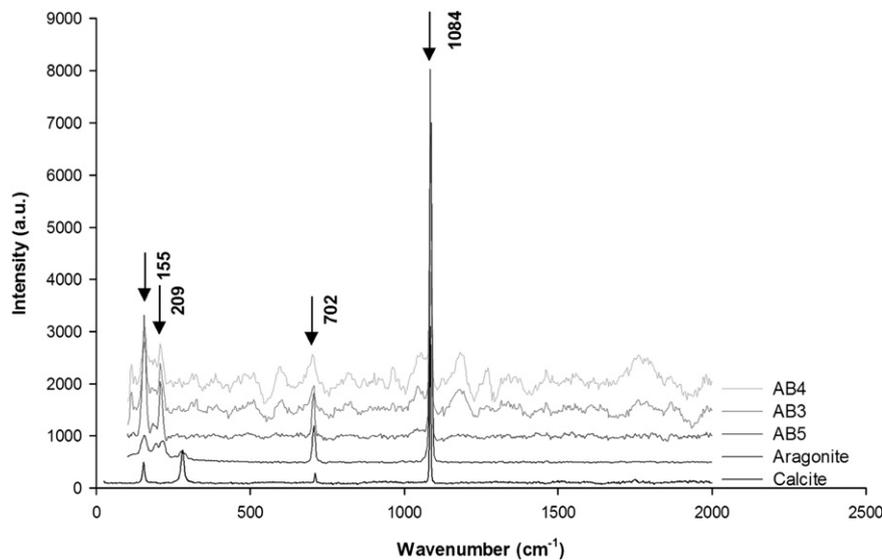

Fig. 4. Comparison of Raman spectra acquired on the surface of modern (AB3 and AB4) and fossilized abalones (AB5) with aragonite and calcite references in the 100–2000 cm^{-1} region. The main signature of aragonite (peaks at 155, 209, 702 and 1084 cm^{-1}) is clearly visible in the abalone spectra. For clarity, the spectra are shifted, and the background was corrected for luminescence.

3. Results

3.1. Oxygen isotope samples

The sampling points were re-distributed for each abalone with synchronization method (Fig. 5). Range of oxygen isotope values of AB1–AB3 was between 0.63 and 2.48‰ and homogeneous on the common period of 1999–2001 (one-way ANOVA, P = 0.165). It was higher on AB4 varying from 1.36 and 3.14‰ and larger on AB5 from −0.52 to 2.63‰ (Table 1). For further analyses, only complete oxygen isotope oscillations (winter to winter) were retained because the synchronization with the temperature was easier with complete oscillations and therefore better. Moreover, exclude oxygen isotopes samples corresponding to the first growth year allowed to avoid possible contamination with the middle calcitic layer or the inner nacreous layer due to erosion of the outer layer in this region.

Once the oxygen isotopes samples were placed in temporal context, the growth rate of each abalone was estimated (Table 2). The shell length at the first winter for AB4 and AB5 were estimated as isotopic samples began at 40 and 30 mm from the apex (Table 2). The annual growth rates of AB4 were 1.5 fold lower than those of abalones collected in 2002 (AB1–AB3). The annual growth rates of the fossilized abalone were comparable to those of AB4 until the third winter; in the following fourth year, the AB5 growth rate fee below that of AB4.

3.2. $\delta^{18}O_{shell}$ relationship to SST

Temperature was estimated from oxygen isotope values and compared with the instrumental SST (Fig. 6). Temperatures calculated from AB1–AB3 were higher than the SST measured at Estacade with a mean absolute error (MAE) of 2.5 °C (Fig. 6a). This overestimation was general and above 2 °C either during summer periods of fast growth

Table 1
Details of oxygen isotope samples for each abalone. Samples only analyzed when they were located at a distance farther than 20 mm from the apex and displayed complete oscillations (winter-to-winter). $N_{initial}$: the number of samples drilled on each specimen; N_{kept}: the number of samples retained for analysis; $\delta^{18}O_{shell}$ (in ‰): the range of oxygen isotope variability among individual specimens; W: winter. The number of complete oscillations was counted from winter-to-winter, which corresponded to the years of growth and the time period analyzed.

Abalone	$N_{initial}$	N_{kept}	$\delta^{18}O_{shell}$	Complete oscillations	Years of growth	Period
AB1	94	83	0.65–2.37	W1–W4	1st–3rd	1999–2001
AB2	139	121	0.63–2.48	W1–W4	1st–3rd	1999–2001
AB3	130	120	0.65–2.46	W1–W6	1st–5th	1997–2001
AB4	91	82	1.36–3.14	W2–W6	2nd–5th	2007–2010
AB5	68	45	−0.52–2.63	W2–W4	2nd–3rd	

(May to November: MAE = 2.4 °C) or during winter periods of slow growth (December to April: MAE = 2.9 °C) and whatever the year of growth considered (1st year for AB1–AB3: MAE = 2.6 °C, 3rd year for AB1–AB3: MAE = 2.3 °C, 5th year for AB3: MAE = 2.8 °C). On the contrary, the temperatures estimated from AB4 were close to the measured SST, with a MAE of 1 °C (Fig. 6c). The estimated temperatures were in accordance with the SST during the first two years, but in the two following years, the lowest temperatures were not estimated. The temperatures estimated from the isotopic composition of the fossilized abalone (AB5) showed a MAE of 1.9 °C with annual cycle of salinity and of 1.6 °C with constant salinity from the average temperatures measured at Marennes d'Oléron (Fig. 6d). In both cases, the range of the reconstructed temperature amplitude (variables salinities: 5.8–22.4 °C; constant salinity: 8.1–21.7 °C) was slightly broader than the annual reference cycle of temperature (9–20.5 °C) but comparable to initial measurements made in Marennes d'Oléron between 1995–2003 (5.2–24.2 °C).
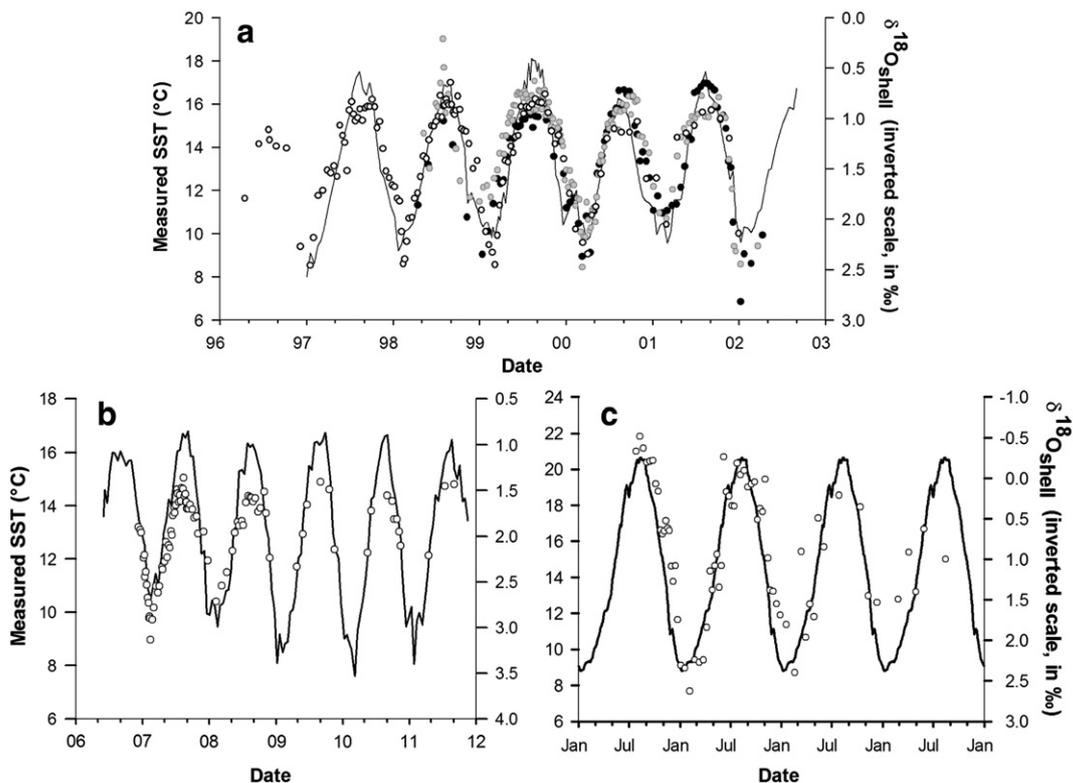

Fig. 5. Redistribution of oxygen isotope samples with the synchronization method: AB1–AB3 (dark, gray and white circles, respectively in part a) and AB4 (white circles in part b) were collected in 2002 and 2012, respectively, and compared with sea surface temperatures (SST) measured at Estacade (dark lines); (c) AB5, the fossilized abalone, was compared with an averaged sea surface temperature measured at Marennes d'Oléron (dark line).

Table 2

Maximum abalone shell length estimates (mm) and annual growth increments (mm) for each winter (W). Three abalones (AB1–AB3) were collected in May 2002 (with mean values ± standard deviation for W1 through W4) and one (AB4) was collected in January 2012 in the northwest part of Brittany; the fossilized abalone (AB5) was collected in the Bay of Biscay. The values indicated in italics were estimated as isotopic samples began at 40 and 30 mm from the apex for AB4 and AB5, respectively.

Winter	W1	W2	W3	W4	W5	W6	Total length
Maximum shell length estimate (mm)							
AB1	5.5	37.9	65.5	88.7			92
AB2	14.2	61.4	97.6	111.7			112
AB3	8.2	44.9	78.3	103.0	112.6	122.6	123
Mean ± s.d. (2002)	9.3 ± 4.5	48.1 ± 12	80.5 ± 16.2	101.1 ± 11.6			
AB4	*15.1*	44.1	66.6	81.8	87.1	93.3	96
AB5	*13.2*	42.1	60.0	69.6			75
Annual growth increment (mm)							
AB1		32.4	27.6	23.2			
AB2		47.2	36.3	14.0			
AB3		36.8	33.4	24.7	9.6	10.0	
Mean ± s.d. (2002)		38.8 ± 7.6	32.4 ± 4.4	20.7 ± 5.8			
AB4		*29.0*	22.5	15.2	5.2	6.2	
AB5		*28.9*	17.9	9.6			

4. Discussion

4.1. Reconstruction of in situ temperatures

The four modern shells used in this study showed clear δ^{18}O oscillations, which reflected the seasonal temperature and salinity cycles in northwest Brittany (France). The paleo-temperature equation of Grossman and Ku (1986) provided temperatures close to the measured water temperatures, in the case of specimen AB4. This finding was consistent with the findings of Gurney et al. (2005) on *Haliotis rubra* whose shells also consist of a mixture of calcite and aragonite. In the study of Gurney et al. (2005), temperature estimates based on the equation of Grossman and Ku (1986) were close to instrumental temperatures, but temperature data derived from the equation of Epstein et al. (1953) did not agree well with the measured SST. The temperature

estimate of AB4 was particularly good for the first two seasonal cycles (Fig. 6b); this confirmed that growth slowed down in winter, but evidently did not stop (Clavier and Richard, 1986; Roussel et al., 2011). For the last two studied seasonal cycles, however, winter temperatures were not captured. This could be explained by (i) a longer and more intense slowdown in growth during adulthood than during the first two years of life and (ii) a decrease in shell growth rate with increasing ontogenetic age. Spatial sampling resolution of such shell portions was likely insufficient to fully capture the lowest winter temperatures.

In contrast, the paleo-temperature equation described by Grossman and Ku (1986) applied to the three abalones collected in 2002 (AB1–AB3) consistently overestimated the actual water temperatures with an estimated offset of 2.5 °C. The different results obtained from AB4 and the remaining three live-collected specimens could not be explained by methodological differences (e.g., equipment, sampling
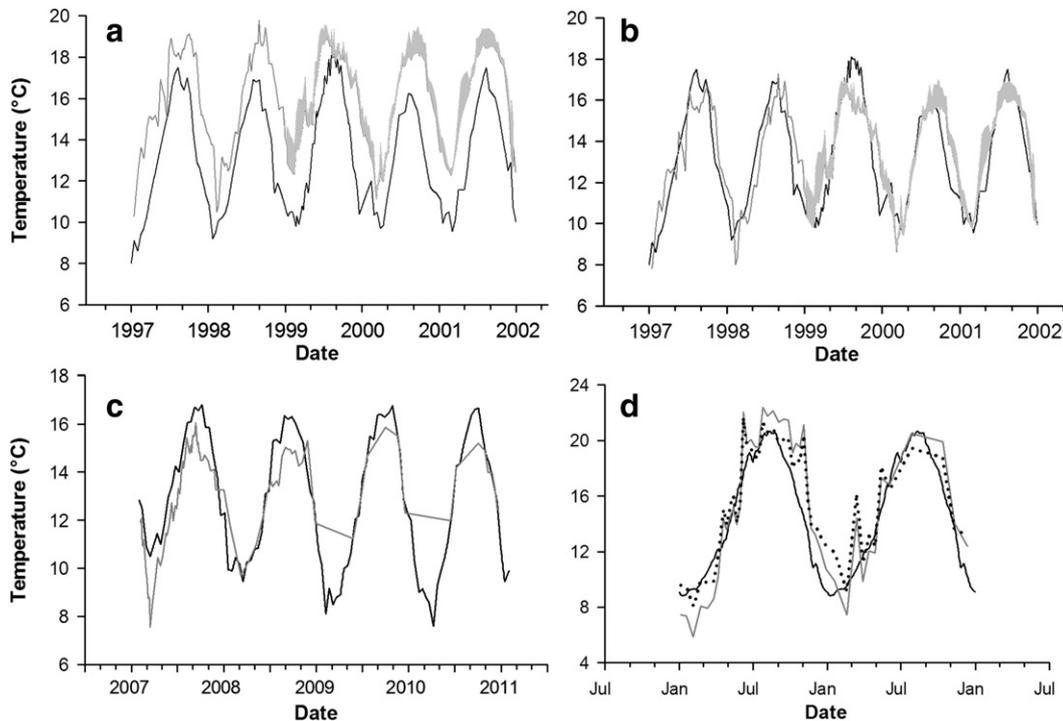

Fig. 6. Temperatures predicted from oxygen isotope samples (gray lines) are compared with measured sea surface temperatures (SST, dark lines). Averaged predictions obtained from the three abalones (AB1–AB3, ± 95% confidence interval) collected in 2002 before (a) and after (b) applying the correction of the vital effect and (c) predictions from the abalone, AB4, collected in 2012 are compared to the SST measured at Estacade in northwest Brittany between 1997 and 2012. (d) Predictions from the fossilized abalone (AB5), calculated either from the annual cycle of salinity (gray line) or from a constant annual salinity (dark dotted line), were compared to the SST measured in Marennes d'Oléron, in the Bay of Biscay, and averaged over the period 1995–2003.

methods). Although the isotope data were measured in different laboratories, the sampled measured in both did not show significant differences. Moreover, this offset did not appear to be due to the sampling method because it was relatively constant according to the periods of fast and slow growth defined by Clavier and Richard (1986). However, other hypotheses can be considered. First, the outer layer composition of the shells may have been different. Second, there may have been substantial uncertainties about the salinity and corresponding $\delta^{18}O_{water}$ values. Third, there may have been kinetic (or vital) fractionation effects.

The first hypothesis concerns the composition of the outer prismatic layer. However, despite its complexity, Raman micro-spectrometry analyses confirmed that it was composed of aragonite as described by Dauphin et al. (2014). Thus, the choice of using the paleo-temperature equation of Grossman and Ku (1986) was appropriate.

The second hypothesis concerns the environmental parameter measurements used in this study. Indeed, the best estimates were obtained for the AB4 abalone, which was collected near the coastal monitoring site, Estacade. The temperatures estimated from the oxygen isotopic samples of specimens AB1–AB3, collected on the other side of Morlaix river estuary (Fig. 1), diverged from temperatures measured at Estacade. Temperature and salinity varied among the different study sites in the estuary. Environmental data acquired at Pen al Lann, a monitoring site at the mouth of the Morlaix river (data from IFREMER, http://www.ifremer.fr/envlit/), showed that the temperatures measured between 1994 and 2003 were comparable to those measured at Estacade, but the salinity showed broad variations (31–35). Salinity is directly correlated to the $\delta^{18}O_{water}$, which in turn, is required to compute temperatures from shell $\delta^{18}O$ values. The measured deviation of 2.5 °C between the temperatures estimated from AB1–AB3 and the measured SST corresponded to $\delta^{18}O$ deviation of 0.53‰, and so to salinity deviation of 3.3 PSU corresponding to annual salinity varying from 29.1 to 33 PSU. However, environmental monitoring performed since 1977 in Pierre Noire, located 2 km away from Primel, showed that environment is comparable to Estacade with the salinity varying between 34 and 35.8, and it only rarely dropped to 33.2 (Dauvin, 1988; Ibanez et al., 1993; Rigal, 2009, E. Thiebaut pers. comm.). Therefore, the hypothesis that salinity might be more variable at Primel than at Estacade did not hold true, and this hypothesis could not explain the different temperature estimates obtained for AB1–AB3.

The last hypothesis concerns the potential effect that significantly faster shell growth rates in specimens AB1–AB3 might have on isotopic fractionation. Indeed, annual growth increment obtained for the three abalones harvested in 2002 appeared 1.5 times higher than growth measured on AB4. This growth was also faster than the H. tuberculata populations living in Guernesey (Forster, 1967) or in Saint-Malo (Clavier and Richard, 1986). Roussel et al. (2011) has explained this difference either by parasitism infecting 70% of the shells living in Guernesey (Forster, 1967), or density and food availability (Day and Fleming, 1992; Huchette, 2003). In the present study, the difference observed between the estimated and measured temperatures was relatively constant throughout the live of the three abalones. This offset could be generally described as a deviation from isotopic equilibrium in biogenic carbonates. This phenomenon is known as "vital effect" (Urey et al., 1951), and it includes a combination of kinetic and metabolic effects (McConnaughey, 1989a,b). The vital effect was previously described in mollusks or gastropods (Wefer and Berger, 1991); it corresponds to the depletion of ^{18}O and ^{13}C that can occur at high calcification rates in the carbonate skeletons of some organisms (McConnaughey, 1989a). In the present study, oxygen isotope values measured on AB1–AB3 were indeed shifted to more negative values than AB4 with a variation range of 0.65–2.37‰ vs. 1.36–3.14‰. When this imbalance occurs, it can be considered relatively constant, and it can be corrected (Wefer and Berger, 1991). In the present study, by applying a correction factor of −0.53‰ (corresponding to the offset of

2.5 °C) on the oxygen isotope values measured on AB1–AB3, the estimated temperature were close to the temperatures measured at Estacade with a mean absolute error of 1 °C (Fig. 6b). This type of vital effect correction was previously suggested for interpreting the oxygen isotope profiles from Haliotis iris (that offset was −1.25‰; Naylor et al., 2007). In the present study, a correction of the "vital effect" could be applied for AB1–AB3 abalones as environmental data were available as well as studies on the growth of Haliotis tuberculata populations living in the Channel (Forster, 1967; Clavier and Richard, 1986). However, for other studies, it can be difficult to detect and estimate this correction without such information. Nevertheless, we can note that the oxygen isotopes from abalone shells could be used to: 1) describe the seasonal temperature and salinity cycles, and 2) estimate temperature amplitude. So, despite the uncertainty on the offset, the Grossman and Ku's paleo-temperature equation, and in particular the slope, works for abalones to estimate changes of temperature as long as $\delta^{18}O_{water}$ did not vary so much.

The results from the present study on H. tuberculata were consistent with those found in other species, including: H. rubra (Gurney et al., 2005) and H. iris (Naylor et al., 2007). Taken together, these studies have demonstrated that stable isotopes measured in the shells of the Haliotis genus represent a good tool for reconstructing sea temperature. The Haliotis genus can be added to gastropods in recognition of a potentially high-resolution environmental archive, this addition will extend the ecosystems that can be studied. Indeed, over the last ten years, numerous studies have demonstrated the utility of gastropod and bivalves shells for reconstructing environments that they inhabited. Thus, shells of Gibbula cineraria and Strombus gigas have been described as highly accurate, precise paleo-thermometers for evaluating their habitats (Schöne et al., 2007; Radermacher et al., 2009). Similarly, the use of Conus shells has provided a novel approach for distinguishing and quantifying seasonal upwellings and freshwater inputs in tropical American coastal environments (Tao et al., 2013).

4.2. Applications

In the present study, results obtained from four modern abalones were associated to the analysis of one fossilized abalone. This fossilized abalone (AB5) was found at Ponthezières in the Bay of Biscay and dated from 6000 cal yr BP (Laporte, 1994; Laporte et al., 1998). Analyses of AB5 showed that the oxygen profile also exhibited seasonal oscillations that reflected both winter and summer temperatures. No corrections were applied to isotopic data of fossilized abalone AB5 because the measured growth rates were comparable to AB4 and to populations living in the Channel. Moreover, to our knowledge, a study describing the growth of modern populations living in the Bay of Biscay to compare with AB5, does not exist. However, the temperatures estimated with an annual cycle of salinity, showed a deviation of 1.9 °C with the annual temperature cycle of Marennes Oléron. This deviation may seem high but i) the comparison was made with an averaged cycle of temperature, and ii) the magnitude of the estimated temperature variations (5.8–22.4 °C) corresponded to temperature variations measured at Marennes Oléron between 1995 and 2003 (5.2–24.2 °C). This stability between actual sea water temperatures and those of Neolithic period was consistent with model estimations of the climate in west-central Europe (Davis et al., 2003).

Haliotids are wide-spread (Geiger, 1999), and they have been collected traditionally in many countries around the world by indigenous communities (Canada: Campbell, 2000; France: Clavier, 1992; Laporte et al., 1998; Oceania: Mannino and Thomas, 2002; South Africa: Volman, 1978). Therefore, living and fossilized specimens of haliotids are present all around the planet in tropical and temperate areas (Geiger and Groves, 1999). All these facts make abalone a very promising tool for contemporary and paleoclimatic studies, as well demonstrated for another gastropod, Patella vulgata (Wang et al., 2011) or for molluscs in general (Thomas, 2015).

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