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RESEARCH

Variations of the stable isotope ratios of carbon and oxygen of the *Patella vulgata* (Linnæus, 1758) shells according to the vertical zonation of collect

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Abstract

Isotopic investigations performed on carbonated shells from anthropogenic middens provide information about past environments and cultural practices of the human populations who left these vestiges. *Patella vulgata*, an intertidal gastropod that inhabits northwest Atlantic rocky shores, is commonly occurring as shells in European shell middens, constituting therefore a good candidate for isotopic studies. However, high tidal ranges characterize most of European Atlantic coastlines, and species largely distributed upper to lower foreshore, as *Patella* sp., may encounter pronounced variations in immersion time depending on their elevation in the intertidal zone, which could affect their shell stable isotopic ratios. In this study, we compared carbon and oxygen stable isotopes of *Patella vulgata* shells collected in the same station at three different cotidal levels. Isotopic measurements are analyzed in terms of individual growth and aim to characterize the cotidal origin of the specimens. Our results demonstrate the absence of a significant link between the cotidal level on the shore and the growth and $\delta^{18}O$ profiles of the shell, as high shore and low shore shells show the highest similitude while medium shore shells had a reduced growth with a higher heterogeneity. Consequently, the SST reconstructions were not significantly different. Thus, the use of the $\delta^{18}O$ of archaeological shells as an SST proxy appears unaffected by the cotidal origin of the specimens. In contrast, the $\delta^{13}C$ scales from the high shore (lower $\delta^{13}C$ values) to the low shore (higher $\delta^{13}C$), constituting a promising new proxy for determining the precise elevation in the intertidal zone where the shells were collected.

Introduction

The link between $\delta^{18}O$ of marine mollusk shells and the sea surface temperature (SST) in which they grew is well established for several decades (Epstein et al. 1953; Grossman and Ku 1986) for a wide diversity of marine and estuarine habitats (Burchell et al. 2014; Lavaud et al. 2013) and for a growing number of mollusk species, whether bivalves (Chauvaud et al. 2005; Hallmann et al. 2009; Wanamaker 2007) or gastropods (Colonese et al. 2012; Gutiérrez-Zugasti et al. 2015; Jolivet et al. 2015; Parker et al. 2017). The $\delta^{13}C$ signal of carbonated shells (measured together with $\delta^{18}O$) is more complex to interpret. It is in fact notably affected by several factors, including the variations of the $\delta^{13}C$ from inorganic dissolved carbon ($\delta^{13}C_{DIC}$; Killingley and Berger 1979; Mook and Vogel 1968) and from the incorporation of the metabolic carbon (Klein et al. 1996; Lorrain et al. 2004). The relative proportion of the sources depends on the age, size, metabolism, season, sources of food, and geographic area of the specimens (Beirne et al. 2012; McConnaughey 1989a, 1989b; Poulain et al. 2010). These isotopic signals, preserved in the shells accumulated in shell middens produced by humans all along the world's coasts, are a useful source of information about the past environments as well as about the relationships the human populations had with the marine resources (Andrus 2011; Gutiérrez-Zugasti et al. 2011; Milano et al. 2022). Intertidal species, accessible by foot, are the most abundant in these middens. In the West-European middens and more specifically for the Iroise Sea shell middens, the limpet *Patella vulgata* is largely a preeminent species of marine mollusks (Bailey and Craighead 2003; Mougne 2015, 2019). However, interpreting these carbonate archives relies upon reliable information about

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the way these shells records environmental signals. Up to now, *Patella vulgata* is still under-studied as an environmental archive because of its important inter-individual growth heterogeneity and the absence of a general growth pattern, within a population (Bailey et al. 1983; Ballantine 1961; Blackmore 1969; Cudennec and Paulet 2021a, b; Jenkins and Hartnoll 2001) or along the biogeographic distribution of the species (Ambrose et al. 2016; Gutiérrez-Zugasti et al. 2017; Surge et al. 2013).

Different works have confirmed the feasibility of palaeoclimatic studies based on stable oxygen isotope analysis of modern and archaeological limpet shells (*Patella vulgata*: Fenger et al. 2007, Gutiérrez-Zugasti et al. 2017, Surge and Barrett 2012, Wang et al. 2012; *Patella caerulea*: Prendergast and Schöne 2017; *Patella candei*: Parker et al. 2017). However, these studies did not extensively investigate the impact of the intertidal level on the isotopic signature (both δ^{18}O and δ^{13}C). This lack of investigation might induce a bias on the interpretation of archaeological palaeothermometry data. The different areas of the intertidal zone are characterized by differences in aerial exposure and immersion durations, which can lead to differences in the calcification rates, a process considered to take place underwater only (Jazwa et al. 2020; Marin et al. 2012), this being confirmed in *Patella vulgata* (Tagliarolo et al. 2013). The fidelity of the oxygen isotopic profiles to the annual temperature records is mainly controlled by the growth rhythm of the shells (Goodwin et al. 2003). We tested here the hypothesis of a potential influence of the altitudinal position of an individual on its δ^{18}O signature. If this is true, the palaeo-environmental reconstructions based on intertidal shells need to be reconsidered in terms of collect levels on the shore, and the shells could be considered as a proxy of elevation on the intertidal zone of collect rather than an accurate palaeo-thermometer. If it is not, the limpet shells found in anthropogenic shell middens could be considered as a reliable archive for past SST. We also investigate δ^{13}C to detect a potential effect of the vertical zonation on the shore, to infer the level of collection and thus the habits of past human populations.

Materials and methods

The study site where animals were collected (48°20′45.4″N 4°51′21.2″W) is situated on the shore of Beniguet Island (Finistère, France: Figure 1). There are no freshwater sources on the island, which is considered under oceanic conditions, as δ^{18}O of the shells covaries with temperature and δ^{18}O of the seawater, the latter being mainly influenced by salinity (Andrus and Crowe 2000; Andrus and Thompson 2012; Burchell et al. 2014; Epstein et al. 1953). In absence of salinity variations, δ^{18}O is thus considered as a proxy for SST only.

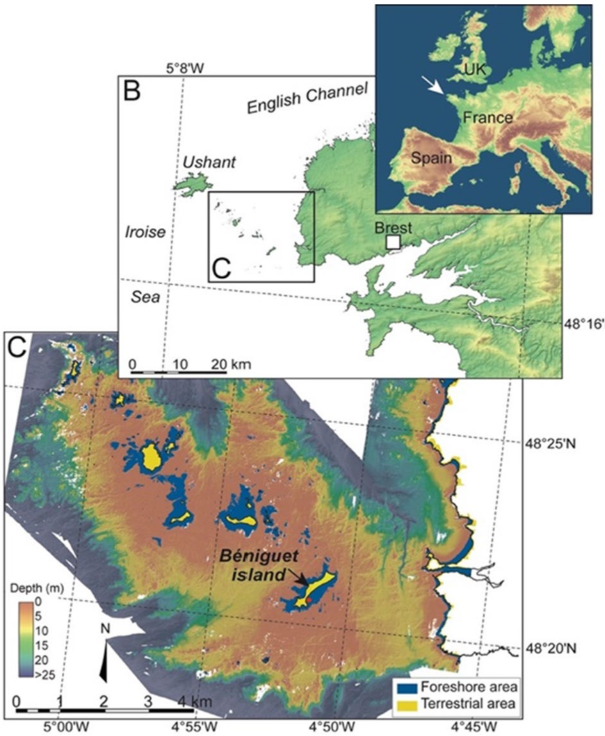

Fig. 1 Geographic location of Iroise Sea and Béniguet Island. Sampling took place in a sheltered area on the southwest shore of the Island

Temperature records

Two Hobo Ware U24 sensors were deployed on the shore of Beniguet Island at the mid-tide level (40 cm above the mid-tide level) from January 2017 to May 2018 recording data every 10 min. Due to semi-diurnal tides, half of the records were aerial. Thus, only temperatures from 10 min before to 10 min after the high tide at Le Conquet (which is the closest tidal reference area) were kept in order to get the best approximation of the seawater conditions in which the limpets precipitate their shells (under the assumption of underwater growth only). These records aim to check the accuracy of temperature reconstructions from δ^{18}O data, and to test the offset from isotopic equilibrium determined by Fenger et al. (2007) on our geographic area.

Shell collection

The studied limpet shells from Beniguet Island shore were collected on 02/15/2018. Three different shore levels were determined according to the algal communities. The high intertidal level (HIL) is aerially exposed most of the time, and *Pelvetia canaliculata* is the predominant algal species. The medium intertidal level (MIL), dominated by *Ascophyllum nodosum* and *Fucus vesiculosus* is half-time underwater and half-time in the open air. The limpets of this level were collected less than two meters from the sensors (see the "Temperature records" section for more details). The lower intertidal level (LIL), characterized by *Laminaria digitata* and *Himanthalia elongata* cover, is exposed only during low tides and remains underwater during neap tides.

Three shells for each intertidal level were selected with regular shape and no marks of recalcifications or repair (O'Neil et al. 2018). As growth is one of the major factors influencing the isotopic profiles, shells were selected in a narrow size spectrum of 40 ± 0.2 mm, despite the complexity of the size/age relationship for this species (see Ballantine 1961; Choquet 1968; Cudennec and Paulet 2021a, b; Jenkins and Hartnoll 2001; Lewis and Bowman 1975 for more details about *P. vulgata* growth heterogeneity). The large shell of the oldest individuals is supposed to have a slowed growth, reducing the time step represented by each carbonate sample, while a small shell is fragile, and the number of carbonate samples (which is the same for every shell) may not cover a full year of growth. In the absence of clear annual growth checks on the shells in our study area (Ballantine 1961; Choquet 1968; Surge et al. 2013), it is not possible to estimate the regularity of growth and the age of each specimen before having access to the isotopic data. Shells were cleaned, included in Araldite 2020 epoxy resin, cut along the longest growth axis through the apex in 1.2-mm slices, and fixed to microscope slides.

Stable isotope analysis

On each shell, 35 carbonate samples were collected along the growth axis, from the margin toward the apex with a New-Wave Research MicroMill equipped with a 300-µm-wide drill bit. The samples were collected in the crossed-foliated m+2 and radial crossed-foliated m+3 layers, both being calcitic. For a detailed description of the different shell structures of the *Patella vulgata* shells, see Fenger et al. (2007) and MacClintock (1967). Each powder sample weighted 60 ± 20 µg. The step between two drilling points was 200 µm: overlapping two successive 300-µm-wide drills allows a better temporal resolution on the final profile. The samples were analyzed at the Stable Isotope Platform of the European Institute for Marine Science (University of Western Brittany) using a MAT-253 (Thermo Scientific) stable isotope ratio mass spectrometer coupled with a KIEL IV Carbonate Device (Thermo Scientific). The standard deviation was calculated using an in-house homogeneous carbonate standard. It was ± 0.03‰ for $\delta^{18}O$ and ± 0.01‰ for $\delta^{13}C$ for this range of masses (30–100 µg). To formulate the values in the V-PDB scale, all samples were calibrated using two international carbonate standards: NBS-19 ($\delta^{18}O=-2.20$ ‰ and $\delta^{13}C=+1.95$ ‰) and NBS-18 ($\delta^{18}O=-23.38$ ‰ and $\delta^{13}C=-5.01$ ‰). As the island is mainly under oceanic conditions and with no fresh water sources, the $\delta^{18}O_{water}$ was considered constant (0.276) considering a salinity of 34.5 PSU (practical salinity unit). Salinity was measured along the T°C data. The calcite-water relationship is defined by O'Neil et al. (1969)

$$(1)\ SST\ (^{\circ}C) = 16.9 - 4.38\ (\delta_{calcite} - \delta_{water)} + 0.1\ (\delta_{calcite} - \delta_{water})$$

According to Fenger et al. (2007), *Patella vulgata* does not precipitate its shell in isotopic equilibrium with surrounding waters, and a 1.01‰ positive offset needs to be applied to the raw data before transforming into SST. $\delta^{13}C$ data were used directly without any transformation.

Results

Annual temperature records

Aerial temperatures were removed, and only the high tide temperature data were kept, according to Le Conquet tide charts. A biweekly oscillation overlaps with the seasonal cyclicity, corresponding to the tidal cycles, with periods of day or night high tides. The recorded SST curve was smoothed with a moving average covering 2 days (4 tides) on each step to be more representative of the isotopic profiles, under the assumption of constant growth of shells across the year (Figure 2).

$\delta^{18}O$ annual variations and SST reconstructions

The $\delta^{18}O$ and $\delta^{13}C$ profiles obtained from systematic carbonate sampling along the growth axis of *Patella vulgata* shells are presented in Figure 3. All shells show clear variations

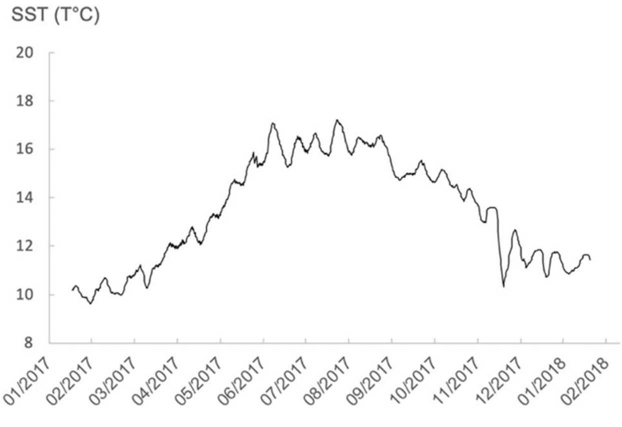

Fig. 2 Annual variations of seawater temperature recorded at high tide on the shore of Beniguet Island, from 01/26/2017 to 01/24/2018

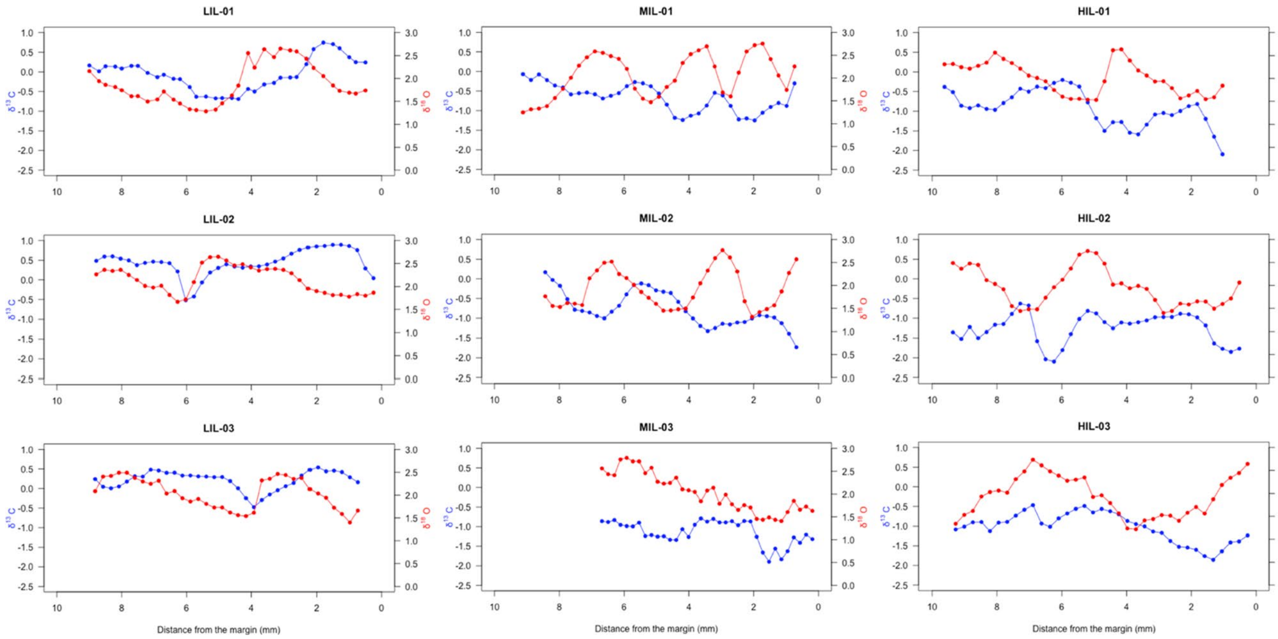

Fig. 3 $\delta^{18}O$ (red) and $\delta^{13}C$ (blue) variations of the three shells from each intertidal level (low intertidal level (LIL); medium intertidal level (MIL); and high intertidal level (HIL)). Each shell was sampled from the margin (right) toward the apex (left). Isotopic ratios are expressed in ‰ relative to the VPDB carbonate standard

of $\delta^{18}O$, except the shell MIL-03. These variations can be linked to annual variations in temperature, and the differences from one shell to another can be interpreted in terms of growth rate variabilities between individuals. A shorter annual cycle is the result of reduced annual growth, while smooth variations running over a longer distance of shell represent a higher growth rate. The $\delta^{18}O$ values range from 1.28 to 2.65‰ for the low intertidal shells, from 1.25 to 2.79‰ for the medium intertidal level, and from 1.22 to 1.53‰ for the high intertidal level. Once converted in SST, the range of each level is 11.67–16.20°C for the low intertidal level, 10.54–16.87°C for the medium intertidal level, and 10.82–16.60 °C for the high intertidal level. The range of reconstructed temperatures is less extensive than the recorded temperatures, and none of the reconstructed SST is out of the recorded SST range. The overall minimum temperature, considered the average of all minimal SST from shells of all levels, is 11.0 ± 0.6 °C and the maximal is 16.6 ± 0.3 °C. The reconstructed SST profile for each of the nine studied shells is presented together in Figure 4. The shells from the high and low intertidal level have similar growth: for every shell, the sampling distance is about 8 to 10 mm and represents 1.5 years of growth. A smaller number of annual $\delta^{18}O$ cycle on the same length of the shell suggest a faster growth. Annual growth (mm year^{-1}) has been determined as a complete cycle from the last $\delta^{18}O$ sample on the margin. The low intertidal level (LIL-01: 5.0 mm, LIL-02: 5.6 mm, and LIL-03: 6.0 mm) and the high intertidal (HIL-01: 4.2 mm, HIL-02: 4.4 mm, HIL-03: 5.0 mm) have similar growth (Student's *t*-test, *p*-value = 0.08). The medium intertidal shells show reduced and more variable marginal growth compared to the previous groups: 1.4mm for MIL-01 and 2.2mm for MIL-02 (Wilcoxon's test, *p*-value = 0.006). MIL-03 shows no cycle at all. It is indeed impossible to extract information about the annual growth of this particular shell.

$\delta^{13}C$ variations

Figure 3 presents the $\delta^{13}C$ profiles of each of the nine studied shells together with oxygen isotope values. Examination of individual profiles shows a recurrent oscillatory pattern, partially in phase with the $\delta^{18}O$ profiles. If annual variations are considered as a temporal reference (with minimal $\delta^{18}O$ during summer and maximal $\delta^{18}O$ in winter), the carbon isotopes variations can be summarized with a maximum during the thermal decreasing (autumn), constantly occurring before the winter minimum temperatures, and a minimum $\delta^{13}C$ value is observed when temperatures are rising, but always before the summer thermal maximum. The $\delta^{13}C$ values are scaling according to the shore level: the LIL shells' $\delta^{13}C$ values are higher (from −0.69 to 0.89 ‰) than MIL shells (from −1.90 to 0.17 ‰), which are themselves above HIL shells $\delta^{13}C$ values (from −2.10 to −0.20 ‰). Each level was determined as significantly different from the others through a Wilcoxon's test (*p*-value < 0.05). The $\delta^{13}C$ profiles show reduced variations compared to the $\delta^{18}O$. The $\delta^{13}C$ data as annual means and deviation of each shell are

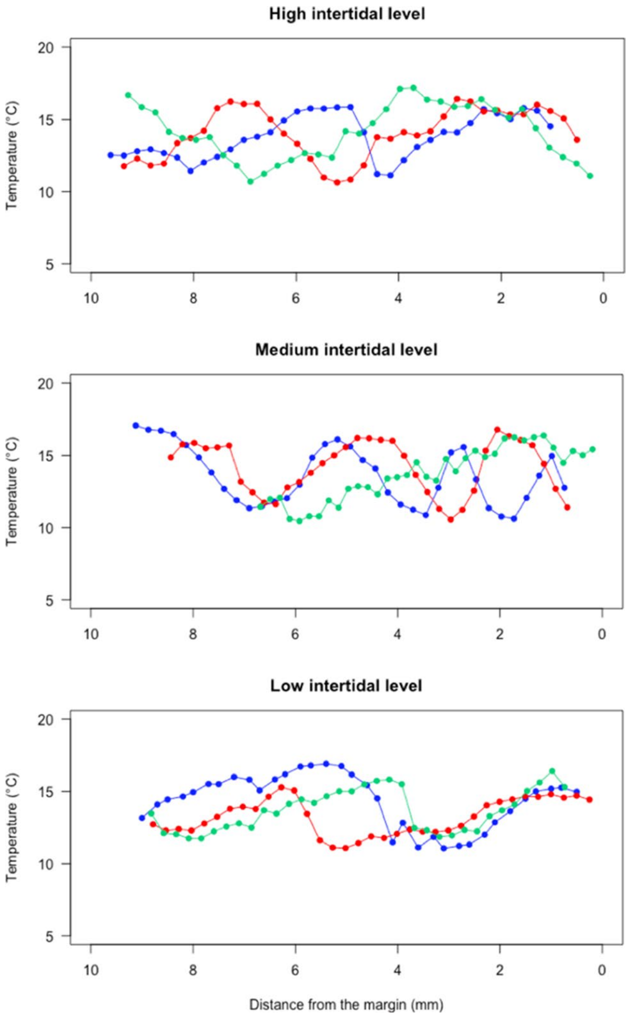

Fig. 4 Reconstructed SST profiles based on $\delta^{18}O$ corrected with an offset to the equilibrium of 1.01‰. Each intertidal level is represented by three shells. The n°1 is in blue, the n°2 in red, and the n°3 in green

summarized in Figure 5, which illustrates the $\delta^{13}C$ scaling from low intertidal to high intertidal.

Discussion

Is it possible to detect an effect of the cotidal level of collect on the $\delta^{18}O$ profiles?

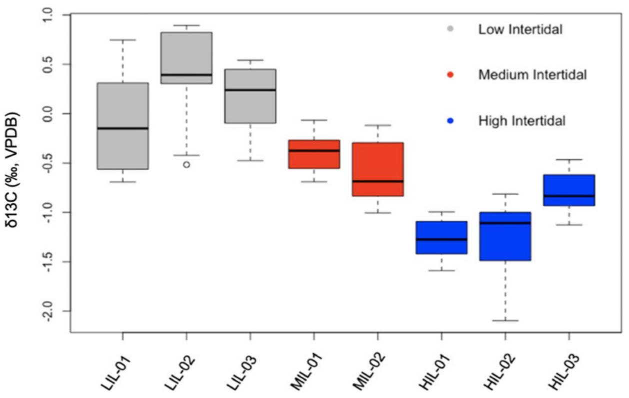

Fig. 5 Cotidal scaling of $\delta^{13}C$ values from the high intertidal to the low intertidal. Each box represents one shell. The colored portion represents the interquartile range of the data (25th–75th percentiles). The horizontal bar represents the mean of each shell and the tails represent the minimum and maximum. The shell MIL-03 is not displayed here as the absence of annual variation in $\delta^{18}O$ casts doubt on the interpretations of isotopic data

The isotopic records in the shells are impacted by the differences in growth rates throughout the year, particularly if the growth stops, resulting in an interruption of records. Those variations and interruptions are caused by environmental thermal conditions in most of the ectotherms organisms. The growth interruptions occur when the heat exceeds the metabolic tolerance in summer, eventually causing heat shock or even coma and death (Chapperon et al. 2016) or during the winter when the temperature is too low. For Blackmore (1969), the growth interruption occurs in winter for the British islands while Surge et al. (2013) detected summer stops along the Spanish coasts. In the Channel Sea, the situation seems to be more complex, as the previous study detected a mixed pattern with some shells having winter interruptions and others having summer stops. According to Choquet (1968), still in the Channel Sea, a complete interruption of growth of *Patella vulgata* shells only occurs in winter, and only for the older specimens. For Ballantine (1961), "there is no way of distinguishing year groups in limpet populations (at least in the larger sizes), nor do the limpets in Britain have recognizable annual growth rings in their shells." The shells studied here showed only one clear annual growth check on the MIL-02 shell. This mark corresponds to low $\delta^{18}O$ values (summer conditions). At the medium intertidal level, for similar environmental conditions, the growth rates and the conditions in which an annual growth check forms differ from one shell to another, and the age of the animal seems to be a more determining factor compared to the temperatures. This issue is discussed in Cudennec and Paulet (2021a, b), which analyzed the growth heterogeneity of *Patella vulgata* through a calcein experiment in the same area. During the investigated period, the overall sensor recorded temperature (including aerial data) ranges from −3.78 °C (02/28/2018) to 40.13 °C (06/26/2017). Averaging aerial and underwater temperatures would result in differences according to the elevation, as the exposure period is shorter for lower individuals (and no aerial exposure during neap tides), and these differences cannot be detected on the profiles. The differences between the maximal and minimal temperatures reconstructed from shells of different cotidal levels are weak, so the calcification and growth process is arguably occurring when the limpets are underwater.

The small-sized limpets only inhabit the middle and low shore (Blackmore 1969; personnal observations) as the larvae cannot settle at higher shore level as the underwater/exposed ratio is not suitable for their survival. Thus, the high shore limpets must migrate from lower levels, and this kind of movement has been observed by Lewis (1954). Intuitively, one might think that the high intertidal level is the one with the higher variability in terms of growth rates, and lowest growth in general, each specimen encountered on the high shore is supposed to have a different arrival period in this area, and with a shorter underwater period per tide (inducing a shorter growing window per tide). The low intertidal level was supposed to show reduced variability and higher growth rates, as the underwater limpets were supposed to take advantage of a buffered environment and wider growth window at each tide and even continuous growth during the neap tide, as suggested by Antoine and Quemerais-Pencreac'h (1980). However, our results contradict this idea as the growth of the high shore specimens is a bit slower but close to the growth of low shore limpets, and the medium intertidal level is the one with the slowest growth and highest variability. This variability is congruent with the high inter-individual growth variability observed over a few weeks of growth at the same location by calcein marking experiments (Cudennec and Paulet 2021a, b), but the lack of variability at the other levels on the shores remains unexplained. The absence of the extreme recorded temperatures on the isotopic results may come from the carbonate sampling. A punctual climatic event can be "diluted" in more mild conditions within the same sample of carbonates. For the low shore shells, the array of reconstructed temperatures for the last year before death (2017) were:

- LIL-01: 11.6–16.9°C
- LIL-02: 11.0–15.3 °C
- LIL-03: 11.85–16.4 °C

For the same year, the mean instrumental recorded temperatures were 9.5°C in winter and 16.5 in summer. Depending on the growth rate of the shell, each sample can represent a few days when the growth is fast or a few weeks when growth is reduced. This resolution of the SST reconstruction does not allow to get punctual climatic events, but there is a good correspondence between the recorded and reconstructed summer temperature. On the other side, there is an offset of approximately 2°C between the winter recorded temperatures and winter reconstructed temperatures. This is probably caused by the reduced growth in winter, provoking an underrepresentation of this period in the profile. A similar offset is observed by Gutiérrez-Zugasti et al. (2017), except that it occurs in summer, in an area (Spain) where *Patella vulgata* is supposed to form annual growth check in summer. In our data set, the lowest reconstructed temperature ranges from 10.45°C (MIL-03) to 11.74°C (LIL-03), which might lead to the conclusion that *Patella vulgata* stop growing under 10°C. This thermal tolerance threshold does not seem to be constant among the biogeographic distribution of this species, as other studies on *Patella vulgata* in colder regions (the North Sea for Fenger et al. (2007); the Orkney Islands for Wang et al. (2012)) allow to get colder SST from $\delta^{18}O$ data, around 6°C. This threshold value can depend on other drivers than SST, like food availability or the age of the shell (Goodwin et al. 2003). An older specimen will grow slower and stop growing during longer periods, inducing a reduced $\delta^{18}O$ array in the shell. This is observable on the MIL-01 shell, which is the shell with the longest record, with more than three annual cycles represented on the profile. The thermal maximum of 2014 is 17.1°C. The maximum for 2015 is 16.1°C, 15.6°C in 2016, and finally 15.0°C for 2017. In the same way, the shell length produced between the 2014 and 2015 thermal maxima is 4.4mm, 2.3 mm between 2015 and 2016, and 1.9 between 2016 and 2017. The decreasing of the maximal recorded SST and the decrease of the produced shell length over the year can be explained by the reduction of growth with the age, each carbonate sample covers longer periods of growth, reducing drastically the resolution of the profile. The reconstructed SST thus gets closer to the optimal growing conditions, during spring and late summer. The extreme temperatures of winter and summer are less represented in younger parts of the shell. When summer and winter are well represented on the profile, with smooth variations of the $\delta^{18}O$ (like for the shells LIL-01, LIL-02, and LIL-03), it is possible to argue that the shell kept growing all year long. On the opposite, if the winter and summer conditions are poorly represented on the SST profile, with abrupt variations of SST and peak aspect (like for the shell MIL-01), is possible to consider that the growth stopped or at least was significantly reduced. The fact that none of the reconstructed SST is out of the recorded SST range confirms that the 1.01‰ offset from isotopic equilibrium proposed by Fenger et al. (2007) allows getting reliable SST from $\delta^{18}O$ data of the shells. However, it would be more rigorous to determine a specific offset for the Iroise Sea. A site-specific calibration seems to be necessary to obtain robust palaeo-climatic data. The different studies about the genus *Patella* in Europe have used different offsets depending on their geographic area:

- Fenger et al. (2007) are defining an average 1.01‰ offset for the North Sea, which is also used by Surge and Barrett (2012) on *Patella vulgata* shells from the Orkney Islands.
- Gutiérrez-Zugasti et al. (2017) use an offset of 0.36‰ on *Patella vulgata* shells from northern Spain.

- Prendergast and Schöne (2017) have used an offset to the isotopic equilibrium of 0.72‰ for the Mediterranean Sea, on *Patella caerulea*.
- Parker et al. (2017) have determined a 1.3‰ offset for *Patella candei* shells from Canary Islands.

Given the differences between different areas for the same species, it seems that this offset depends on the environmental conditions, in particular the range of SST in which the limpets grow, yet this SST is specifically what is looked for on archaeological shells for palaeoenvironmental studies. Thus, the reconstructed SST from archaeological shells, on the basis of an offset determined upon modern shells, may induce a bias, as the environmental conditions could be significantly different in the past. Another bias could come from the $\delta^{18}O_{seawater}$ used in the temperature reconstruction. In this study, $\delta^{18}O_{seawater}$ is considered constant (along with a constant salinity). In comparison, Fenger et al. (2007) used two different $\delta^{18}O_{seawater}$ values, one measured in October–November and another one measured in April–July.

Due to the variability observed between the MIL shells and the similarities of the profiles from high and low intertidal levels, the $\delta^{18}O$ does not seem to be impacted by the elevation of collect, i.e., following the gradient of aerial exposure. One of the hypotheses was that the growth rates depended on the time spent underwater as the growth occurs only when the animal is submerged. Thus, the high intertidal shells were supposed to grow slowly compared to medium intertidal shells, which will themselves grow slower than low intertidal shells. This scheme is not observed in our data, as the medium intertidal shells show the slowest growth rates. The fact that high intertidal shells show high growth rates remains unexplained. These animals may keep growing when they are emerged, even though aerial temperatures are not represented in the reconstructed SST, or that shells grow much faster in a reduced submerged period. This latter hypothesis could be tested by investigating the intra-specific competitive interactions (Boaventura et al. 2002), the availability of microphytobenthos, the feeding behavior of this species, and the altitudinal differences in activity rhythm of *Patella vulgata* (Jenkins and Hartnoll 2001; Lorenzen 2007; Santini et al. 2019; Schaal and Grall 2015). Consequently, it is not possible at the moment to determine the shore level of the collect (and thus the foraging behaviors of these populations, and eventually overexploitation patterns) just from the analysis of $\delta^{18}O$ profiles. However, from a palaeo-environmental perspective, this absence of altitudinal variations of $\delta^{18}O$ reinforces the reliability of SST reconstructions. Past human populations could collect limpets from anywhere along the aerial exposure gradient on the shore the shells still can be used for palaeothermometry studies.

Interpreting the variations of $\delta^{13}C$ profiles of the shells

Despite the reduced number of analyzed shells, the $\delta^{13}C$ provided here information about the cotidal level where the animal lived. On the other hand, the $\delta^{18}O$ was not significantly impacted by the intertidal level. However, it is necessary to clarify the different sources of carbon that contribute to this isotopic signature and the seasonal process involved in the annual variations of the $\delta^{13}C$ in the shells. These processes seem to be relatively close as the same pattern is observed on all the shells regardless of the shore level, even if the array of $\delta^{13}C$ is different for each level. Historically, the authors working on marine mollusk carbonates have interpreted the $\delta^{13}C$ variations as reflecting the dissolved inorganic carbon of the seawater (Mook and Vogel 1968). However, using these variations as a proxy for productivity and heterotrophy for modern and past environments faced the accumulation of results blurring the simplicity of this simple transfer function. The lack of correlation between $\delta^{13}C$ of the shells and the DIC has been interpreted by the influence of numerous mechanisms, including the metabolic activity, the food sources, ontogeny, or the ethology of the organisms. By coupling high-resolution sclerochronological, stable isotopes, in situ monitoring, and laboratory experimentations on *Pecten maximus*, Lorrain et al. (2004), Chauvaud et al. (2011), and Marchais et al. (2015) provided an interpretation framework which remains the most complete so far. There is no reason to think that the DIC of the seawater would be different between the low and the high tide. The different array of $\delta^{13}C$ observed from one shore level to another may be caused by differences in food sources, as *Patella vulgata* mostly feed on the locally available food sources, as demonstrated on soft tissues by Schaal and Grall (2015) who emphasize the importance of small spatial scale. The regular distribution of the $\delta^{13}C$ values, more negative from the low shore toward the high shore, could also be caused by the incorporation of aerial CO_2 during exposure, even if the Patellid limpets are not pulmonates gastropods. A study focused on *Mytilus californianus* (a species with no aerial respiration and closed valves when aerially exposed) did not find such a correlation between $\delta^{13}C$ and intertidal levels (Jazwa et al. 2020). This is also supported by the fact that atmospheric $\delta^{13}C$ is about −7‰ while the $\delta^{13}C$ of marine carbonates is about 0‰ (Kendall and McDonnell 1998). Other studies about *M. galloprovincialis* (Milano et al. 2020, 2022) showed a $\delta^{13}C$ distribution along an estuarine (and thus a salinity) gradient, even if the salinity is considered constant in our study area (a marine island without freshwater sources on it). The $\delta^{18}O$ does not show signs of aerial precipitation of the shell which is contradictory to the idea of aerial breathing and growing. The incorporation of atmospheric $\delta^{13}C$ would thus be indirect, through the diet. The $\delta^{13}C$ of the food is strongly different from one level to another, and feeding on microphytobenthos on the high shore and macroalgae propagules on the low shore would result in zonation of $\delta^{13}C$ along the cotidal gradient.

Conclusion

This study aimed to determine the impact of the intertidal level of collect of *Patella vulgata* shells on the carbon and oxygen stable isotope signatures. Our results suggest that the $\delta^{18}O$ cannot be used to replace the shell on an altitudinal gradient, as high intertidal and low intertidal shells are closer to each other than medium intertidal shells. Consequently, the level of collect does not seem to cause any problems in interpreting the archaeological $\delta^{18}O$ for palaeothermometry purposes. In opposition, the carbon profiles show a gradation in $\delta^{13}C$ values, the shells being more and more depleted in ^{13}C toward the high shore. That's the first time that such a phenomenon is described for *Patella vulgata*. This phenomenon is not supported by a detailed explicative model for the moment, but we can assume that the taxonomic and isotopic composition of the biofilm grazed by the limpets and the eventual incorporation of breathed atmospheric carbon play a crucial role in the formation of this $\delta^{13}C$ gradient. Further investigations and quantifications of this phenomenon, eventually coupled with morphometric analysis, could lead to a reliable attribution of archaeological shells on the aerial exposure gradient and thus exploring the foraging practice of past human coastal populations.

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Data availability The datasets generated during and/or analyzed during the current study are available from the corresponding author Jean-François Cudennec on reasonable request.

Declarations

Competing interests The authors declare no competing interests.

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