

What's Hiding Behind Ontogenetic $\delta^{13}\text{C}$ Variations in Mollusk Shells? New Insights from the Great Scallop (*Pecten maximus*)

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Received: 13 November 2009 / Revised: 23 December 2009 / Accepted: 9 January 2010 / Published online: 9 March 2010
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Abstract Mollusk shells contain geochemical information about environmental conditions that prevailed at the time of formation. We investigated ontogenetic and seasonal variations of $\delta^{13}\text{C}$ in calcitic shells of *Pecten maximus*. Ontogenetic variations of $\delta^{13}\text{C}_{\text{shell}}$ in three large specimens collected in Norway, France, and Spain exhibited a similar linear decrease with increasing shell height. We removed this linear drift (detrending). These three residual time series displayed variations that could be linked to environmental fluctuations. To check it, we reanalyzed the isotopic datasets of Lorrain et al. (Journal of Experimental Marine Biology and Ecology 275:47–61, 2002, Geochimica et Cosmochimica Acta 68:3509–3519, 2004), who worked on three scallops harvested in 2000 in the bay of Brest (France), a well-monitored ecosystem. Lowest values of $\delta^{13}\text{C}_{\text{shell detrended}}$ were recorded in all shells in late spring–early summer, most likely reflecting corresponding variations in food availability. Our results indicate that ontogenetic and seasonal variations of $\delta^{13}\text{C}_{\text{shell}}$ cannot be used as a proxy for past $\delta^{13}\text{C}_{\text{DIC}}$ variations but should be considered as promising tools for ecophysiological studies.

Keywords Scallop shells · Carbon isotopes · Phytoplankton · Ontogeny · Proxy

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Introduction

Bivalve shells grow by accretion of calcium carbonate crystals, in the form of either calcite, aragonite, or both, depending on the species (Marin and Luquet 2004). Shell growth, however, does not occur continuously over a day or over a year; instead, growth ceases periodically (Schöne 2008). These growth stops result in the formation of so-called growth lines, which are enriched in organic matter and separate growth increments that represent equal time slices. Periodic growth lines can therefore be used to assign precise calendar dates to each successive increment of accreted shell material. Accordingly, bivalve shells have been used increasingly over the past six decades as high-resolution archives of environmental conditions and as archives of the animal's biology. Several publications have demonstrated that the geochemical composition of bivalve shell carbonates can be used as a reliable proxy for seawater temperature (Goodwin et al. 2003; Chauvaud et al. 2005), phytoplankton dynamics (Elliot et al. 2009; Thébault et al. 2009a), oceanic circulation (Müller-Lupp and Bauch 2005; Wanamaker et al. 2008a), climatic oscillations (Schöne et al. 2003; Carré et al. 2005), river discharge and salinity (Dettman et al. 2004), and pollution (Gillikin et al. 2005; Barats et al. 2008). Moreover, many life-history traits have been extracted from shells; e.g., longevity (Garcia-March and Márquez-Aliaga 2007; Wanamaker et al. 2008b), metabolism (Lorrain et al. 2004), calcification rate (Lorrain et al. 2005; Thébault et al. 2009b), growth seasons (Ivany et al. 2003; Grefsrud et al. 2008), and recruitment periods (Richardson et al. 2004).

Oxygen and carbon isotope compositions of biogenic carbonates are the geochemical proxies that are most often studied in the framework of paleoclimatic and paleoenvironmental reconstructions. For example, the skeletal oxygen

isotope composition ($\delta^{18}\text{O}$; isotope data are expressed in the conventional delta (δ) notation expressed in ‰) of many taxa (including bivalves such as scallops, mussels, and clams) has been used widely since the pioneering work of Urey et al. (1951) to infer paleotemperature variations, sometimes with an accuracy of less than 1°C (Chauvaud et al. 2005; Thébault et al. 2007). In contrast to $\delta^{18}\text{O}$, factors controlling variations of $\delta^{13}\text{C}$ in marine biogenic carbonates, especially bivalve shells, are numerous and far more complex (Romanek et al. 1987).

Early authors have suggested that $\delta^{13}\text{C}$ variations in shells are mainly caused by variations in dissolved inorganic carbon ($\delta^{13}\text{C}_{\text{DIC}}$; Mook and Vogel 1968; Mook 1971; Fritz and Poplawski 1974). If so, analysis of ancient shells would provide useful biogeochemical information about past aquatic ecosystem metabolism (respiration, primary production, and calcification), nutrient loading, bedrock geology, and atmospheric CO_2 levels. However, <10% of the carbon used for shell calcification comes from respiratory CO_2 stemming from food metabolism (McConnaughey 2003; McConnaughey and Gillikin 2008). Recently, McConnaughey and Gillikin (2008) stated in a review that $\delta^{13}\text{C}$ in mollusk shell carbonate is typically a few parts per thousand lower than the ambient dissolved inorganic carbon (DIC) and often decreases with increasing shell size.

Hypothetical reasons for this ontogenetic $\delta^{13}\text{C}$ decrease include a change in diet, kinetic effects, the Suess effect, a deepening of the bivalve in the sediment, and an increasing metabolic carbon contribution to shell carbonate with age (see McConnaughey and Gillikin 2008 for a review). In the Great Scallop *Pecten maximus*, Lorrain et al. (2004) observed and modeled the increasing contribution of respiratory CO_2 on $\delta^{13}\text{C}_{\text{shell}}$ throughout ontogeny in specimens of different sizes and from different sites in Western Brittany (France). Surprisingly, to our knowledge, no one has ever tried to remove the ontogenetic trend and to investigate the worth of ecological information recorded behind the observed linear decrease.

In the present study, we focused on the carbon isotope composition of shells of *P. maximus* (Bivalvia: Pectinidae). This species is ubiquitous, ranging from Spain to Norway and from 0 to 500 m depth. Its biology is well understood in terms of growth rate (Chauvaud et al. 1998; Lorrain et al. 2000; Chauvaud et al. 2005), reproduction (Paulet et al. 1988; Strand and Nylund 1991; Paulet et al. 1997; Strohmeier et al. 2000; Magnesen and Christophersen 2008), and energy allocation (Saout et al. 1999; Lorrain et al. 2002). Moreover, striae, easily discernable on the shell external surface, are formed on a daily basis (Chauvaud et al. 1998; Chauvaud et al. 2005). This allows for estimation of daily growth rates and of the exact date of formation of each part of the shell. Our primary goals were (1) to check the ubiquity of the metabolic ontogenetic drift in large *P.*

maximus specimens collected in contrasted ecosystems all along the European Atlantic coasts (Norway, France, and Spain), (2) to remove this trend in order to highlight residual $\delta^{13}\text{C}$ variations in the shells of these three large specimens, (3) to reanalyze previously published isotopic datasets (Lorrain et al. 2002, 2004) obtained from three juvenile *P. maximus* shells sampled in an ecosystem (bay of Brest, France) where an extensive environmental survey was conducted, and (4) to compare the detrended $\delta^{13}\text{C}$ time series of these juveniles with environmental data ($\delta^{13}\text{C}$ of dissolved inorganic carbon and particulate organic carbon [POC]). We hypothesized that our data analysis would reveal seasonal $\delta^{13}\text{C}_{\text{shell}}$ variations related to carbon cycling (DIC, primary production, or both).

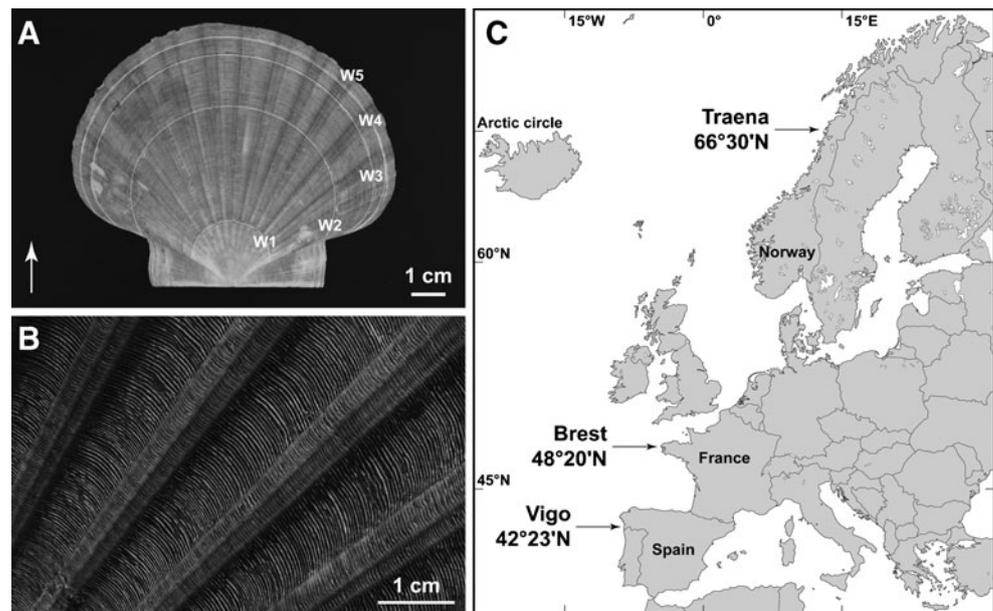
Materials and Methods

Shells of *P. maximus* were collected from three different study sites spread within the distribution area of the species and reflecting contrasted environments (Fig. 1). From north to south, three large specimens were harvested alive by scuba diving (1) in September 2001 at 20 m depth in the archipelago of Træna (Norway; $66^\circ30'$ N; shell height=135.8 mm), (2) in February 2002 at 25 m depth in the Bay of Brest (France; $48^\circ20'$ N; shell height=124.6 mm), and (3) in April 2003 at 20 m depth within the Ria of Vigo (Spain; $42^\circ23'$ N; shell height=110.9 mm).

Daily growth rates were determined by measuring distances between successive daily growth striae on the left valve using the image analysis method described by Chauvaud et al. (1998). On the basis of the daily rhythm of striae formation, absolute dates of precipitation were assigned to each stria by backdating from the last deposited stria at the day of collection (see Chauvaud et al. 2005 for elaboration).

Once growth measurements were performed, the shells were sampled for isotopic analyses. Shell surfaces were cleaned using Milli-Q water, and consecutive shell samples were collected from the outer calcitic layer of the flat valve (Roux et al. 1990) along the axis of maximum growth (the dorso (umbo)-ventral axis) using a 300- μm drill bit. We drilled 116, 111, and 90 samples from the scallop shells harvested from the archipelago Træna, the bay of Brest, and the Ria of Vigo, respectively. Aliquots of shell calcite used for mass spectrometry weighed on average 80 μg ($n=317$) and represented 1–5 days of shell growth. Calcite powder samples were acidified in 100% phosphoric acid at 70°C for 470 s and analyzed at Stanford University using an automated Finnigan MAT Kiel III carbonate device coupled to a Finnigan MAT 252 Isotope Ratio Mass Spectrometer. Shell isotopic data are expressed in conventional delta (δ) notation (Epstein et al. 1953) relative to the Vienna Pee Dee

Fig. 1 **a** Surface of the left valve of *Pecten maximus*. “Winter marks” (W_1 – W_5) deposited during spring growth restart allow for unambiguous aging. **b** In this species, daily growth increments can be observed without any treatment aside from surface cleaning (see Chauvaud et al. [1998, 2005] for details). **c** Map showing location of sampling sites along the European Atlantic coast



Belemnite (VPDB) standard. A total of 44 samples of the international isotopic reference standard NBS-19 (National Institute of Standards and Technology, NIST SRM 8544) and 22 samples of the Stanford Isotope Lab Standard SLS-1 were analyzed with the scallops and yielded a reproducibility (1σ) of 0.057‰ VPDB (NBS-19) and 0.058‰ VPDB (SLS-1) for $\delta^{18}\text{O}$ and 0.030‰ VPDB (NBS-19) and 0.020‰ VPDB (SLS-1) for $\delta^{13}\text{C}$.

A linear decrease in $\delta^{13}\text{C}_{\text{shell}}$ was observed from youth to adult portions of the shells (i.e., from umbo towards the ventral margin). Detrending (i.e., removal of this linear drift) was performed for each specimen (1) by computing the least-squares fit of a straight line to each individual dataset and subsequently (2) by subtracting the resulting function from the data. This residual time series is hereafter referred to as $\delta^{13}\text{C}_{\text{shell detrended}}$.

Results

Scallop Shell Growth and Isotopic Composition

Shell daily growth exhibited clear seasonal variations, allowing age determination in all specimens studied (Fig. 2). Eight, three, and five annual growth cycles were present in the scallops from Træna (Fig. 2a), Brest (Fig. 2b), and Vigo (Fig. 2c), respectively. The maximum daily growth rate was 350–400 $\mu\text{m day}^{-1}$ and occurred during the second and third years of growth at all locations. In contrast to the growth rate, seasonal variations in the oxygen isotope composition of the shells ($\delta^{18}\text{O}_{\text{shell}}$) were only observed in the scallops from Træna and Brest. Based

on the well-established association of $\delta^{18}\text{O}_{\text{shell}}$ with $\delta^{18}\text{O}_{\text{water}}$ and temperature (Chauvaud et al. 2005), our data revealed that shell growth variations were not linked to seawater temperature annual cycles in the Ria of Vigo.

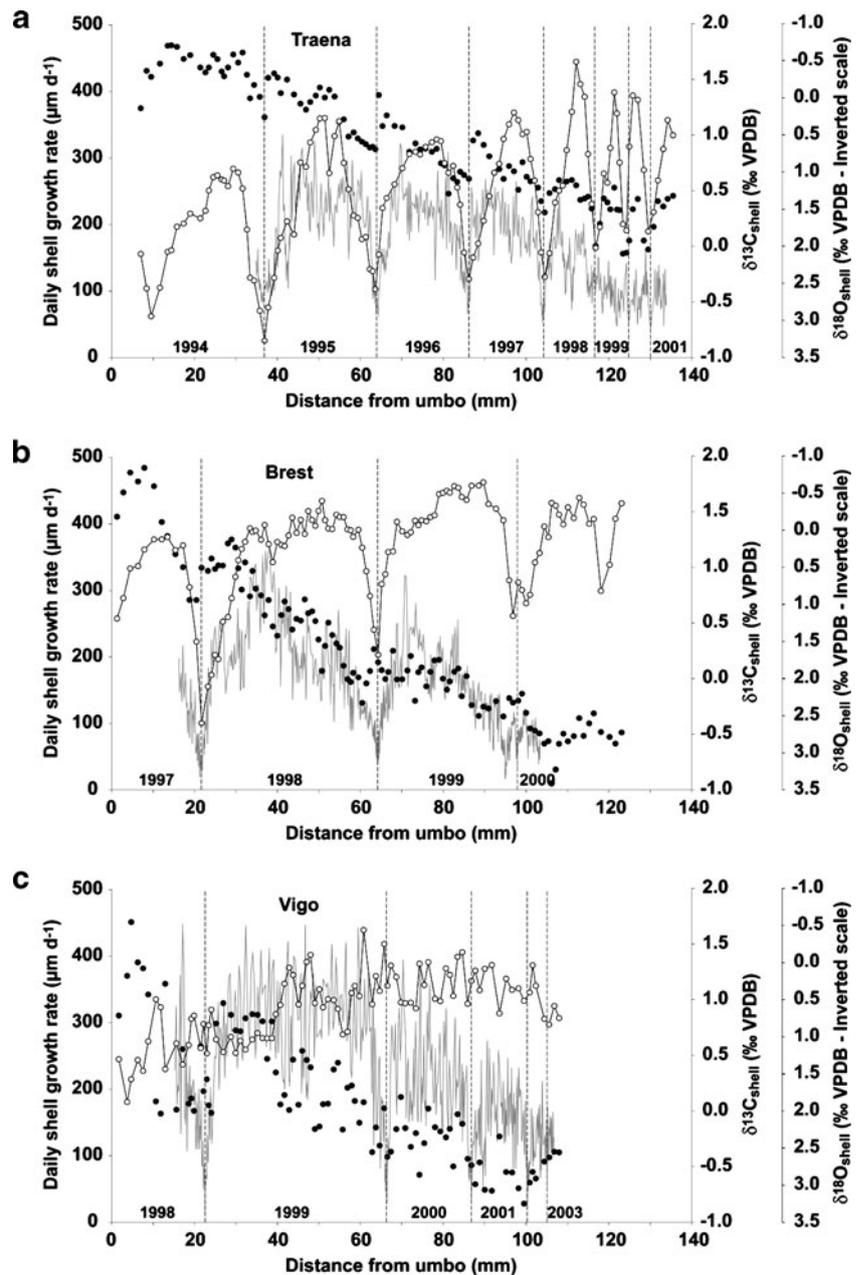
The shell calcite $\delta^{13}\text{C}_{\text{shell}}$ values of the scallops ranged between 1.81‰ (near the umbo) and -0.07 ‰ (at the ventral margin) in Norway, between 1.89‰ and -0.94 ‰ in France, and between 1.70‰ and -0.83 ‰ in Spain (Figs. 2 and 3). There was a strong and statistically significant linear decrease in $\delta^{13}\text{C}_{\text{shell}}$ with increasing shell height ($0.66 < r^2 < 0.90$; $p < 0.01$) in all of the specimens. The slopes of these linear regressions were roughly similar in all of the specimens, ranging from -0.018‰mm^{-1} to -0.013‰mm^{-1} (Fig. 3). Oscillations ranging from 0.1‰ to 0.5‰ can be seen behind this linear decrease in Fig. 3.

Detrended $\delta^{13}\text{C}_{\text{shell}}$ Time Series: Behind the Ontogenetic Trend

Once detrended, the $\delta^{13}\text{C}_{\text{shell}}$ time series of shells collected in Træna, Brest, and Vigo revealed important variations (Fig. 4). In Træna (Fig. 4a) and Brest (Fig. 4b), $\delta^{13}\text{C}_{\text{shell detrended}}$ annual minima roughly coincided with $\delta^{18}\text{O}_{\text{shell}}$ annual maxima, i.e., with winter conditions. Annual ranges of $\delta^{13}\text{C}_{\text{shell detrended}}$ varied from 0.38‰ to 0.82‰ in Træna, from 0.48‰ to 0.99‰ in Brest, and from 0.24‰ to 1.75‰ in Vigo (Fig. 4c).

To thoroughly investigate the factors behind this ontogenetic trend and to relate $\delta^{13}\text{C}_{\text{shell}}$ residual variations to environmental parameters, we reexamined two datasets previously published by Lorrain et al. (2002, 2004). Lorrain et al. (2004) analyzed the skeletal carbon isotope compo-

Fig. 2 Comparison of daily growth increments (gray continuous line), $\delta^{13}\text{C}_{\text{shell}}$ (black dots), and $\delta^{18}\text{O}_{\text{shell}}$ (open circles) profiles in shells sampled in **a** Træna (Norway), **b** Brest (France), and **c** Vigo (Spain). Gray dotted vertical lines represent winter growth cessations



sition of three juvenile specimens of *P. maximus* (2 years old) collected by dredging at 30 m depth in the Bay of Brest in December 2000 (hereafter referred as to shell A, shell B, and shell C; Fig. 5a). $\delta^{13}\text{C}_{\text{shell}}$ was measured only during their second year of life, i.e., after the first winter (April 2000 to November 2000). Weekly variations of $\delta^{13}\text{C}_{\text{DIC}}$ (Fig. 5c) were also measured in the bay of Brest by these authors in 2000. Lorrain et al. (2002) also measured weekly variations in the isotopic composition of POC ($\delta^{13}\text{C}_{\text{POC}}$; Fig. 5d) in 2000. Both environmental surveys were conducted 1 m above the sediment, exactly at the place where the three juvenile scallops were harvested.

Seasonal variations of $\delta^{13}\text{C}_{\text{shell}}$ were similar among these three specimens (Fig. 5a). After winter growth cessation and during growth restart (beginning of April 2000), $\delta^{13}\text{C}_{\text{shell}}$ values were high (0.7–1.1‰), close to spring $\delta^{13}\text{C}_{\text{DIC}}$ values. From that point onward, $\delta^{13}\text{C}_{\text{shell}}$ decreased linearly to approximately -0.2‰ at the beginning of November 2000. Furthermore, $\delta^{13}\text{C}_{\text{shell}}$ was almost always lower than $\delta^{13}\text{C}_{\text{DIC}}$ and was much higher than $\delta^{13}\text{C}_{\text{POC}}$ (values between -26.4‰ and -19.9‰). Finally, $\delta^{13}\text{C}_{\text{shell}}$ values did not covary with seawater temperature (data provided by Service d’Observation en Milieu Littoral [SOMLIT] Institut National des Sciences de l’Univers,

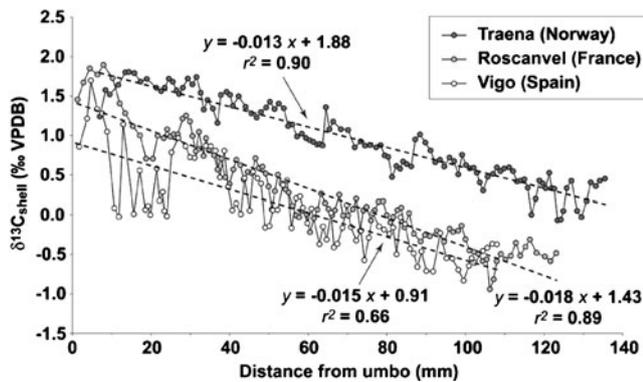


Fig. 3 Comparison of ontogenetic linear decreases in $\delta^{13}\text{C}_{\text{shell}}$ versus shell height (distance from umbo) in specimens sampled in Træna (Norway), Brest (France), and Vigo (Spain). Linear regressions are denoted by black dotted lines. Equations and determination coefficients of these relationships are also shown

station de Brest; available at: http://www.domino.u-bordeaux.fr/somlit_bdd/).

When the linear decrease was removed from the $\delta^{13}\text{C}_{\text{shell}}$ time series, the resulting variations of $\delta^{13}\text{C}_{\text{shell}}$ detrended revealed a clear seasonal pattern in shells A, B, and C, with the lowest values recorded in late spring–early summer (Fig. 5b). These low values occurred at the same time (early May to mid-July) as maximum food availability (POC concentration; Lorrain et al. 2002). In addition, until July, $\delta^{13}\text{C}_{\text{shell}}$ detrended values tended to decrease when both $\delta^{13}\text{C}_{\text{DIC}}$ and $\delta^{13}\text{C}_{\text{POC}}$ increased.

In summary, variations of $\delta^{13}\text{C}_{\text{shell}}$ during a given year of growth could be separated into two distinct components: a linear ontogenetic decrease and a seasonal oscillation. These two components did not correlate with either seawater temperature or $\delta^{13}\text{C}_{\text{DIC}}$.

Discussion

$\delta^{18}\text{O}_{\text{shell}}$ Time Series and Daily Shell Growth

One of the most interesting findings of this study was that large seasonal cycles in shell growth rates stay in the same range throughout the distribution area. In *P. maximus*, it was previously suggested that shell extension rates are at least partially controlled by variations of seawater temperature (Chauvaud et al. 1998). Furthermore, in coastal ecosystems displaying small variations of salinity, $\delta^{18}\text{O}_{\text{shell}}$ variations can be considered to be an excellent proxy for seawater temperature (Chauvaud et al. 2005).

No seasonal $\delta^{18}\text{O}_{\text{shell}}$ oscillations were discernable in the specimen harvested in the Ria of Vigo, indicating that bottom-water temperature variations are modest during the growth season (<1°C because of recurrent upwelling

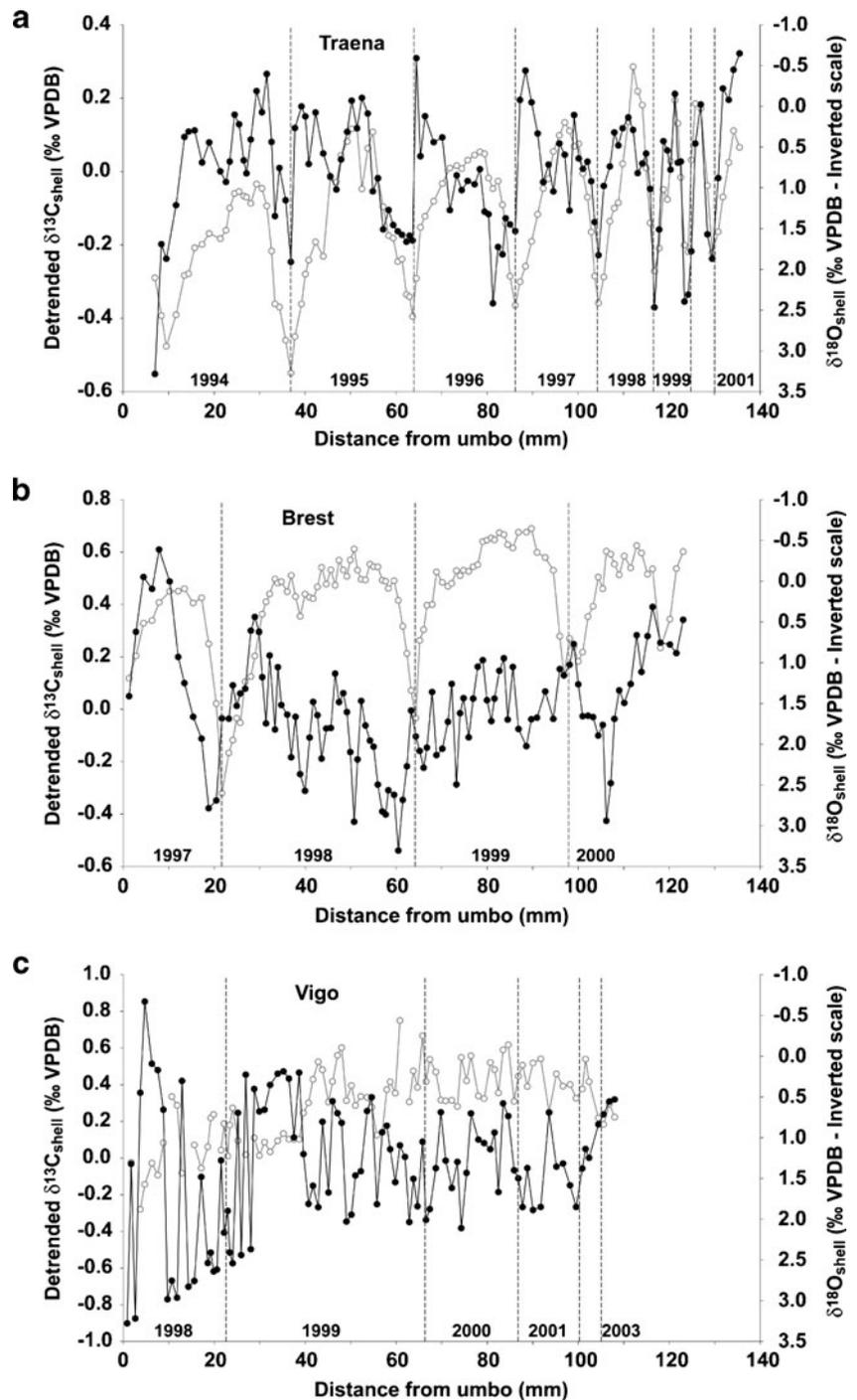
conditions; Nogueira et al. 1997). However, important variations of shell growth rates were measured in shells of this ecosystem (Patry et al., submitted for publication). To our knowledge, our study is the first one to demonstrate that seawater temperature is not always the main regulator of daily shell growth. This is in contradiction with the conclusion of Chauvaud et al. (1998), who worked within a single population of *P. maximus* in the middle of its distribution area.

As was previously done in different mollusk species (Wefer and Killingley 1980; Kobashi and Grossman 2003; Chauvaud et al. 2005; Schöne et al. 2007; Radermacher et al. 2009), we showed that the life span of scallops from Traena and Brest can be inferred using the number of $\delta^{18}\text{O}$ temperature-like cycles. In the three contrasted ecosystems studied here, *P. maximus* always exhibits large seasonal growth variations even when seasonal variations of temperature are very weak. Therefore, we conclude that age determination using shell daily growth cycles is more reliable than the isotopic method.

Detrended $\delta^{13}\text{C}_{\text{shell}}$

The first objective of this study was to check the ubiquity of the $\delta^{13}\text{C}_{\text{shell}}$ ontogenetic decrease regardless of the population of *P. maximus* we sampled. All of the shells sampled along Atlantic European coasts exhibited nearly the same linear decreases in $\delta^{13}\text{C}_{\text{shell}}$ with increasing shell height. These results, obtained on a wide spatial scale, are in agreement with the observations of Owen et al. (2002) and Lorrain et al. (2004), who worked on a local scale (English Channel and Iroise Sea, respectively). Carbon used for biomineralization is derived from both dissolved inorganic carbon and respiratory CO_2 stemming from food metabolism (Tanaka et al. 1986; McConnaughey 2003; Gillikin et al. 2007; McConnaughey and Gillikin 2008; Gillikin et al. 2009). Lorrain et al. (2004) showed that in *P. maximus*, 10–30% of the carbon used to build the shell comes from respiration. This internal carbon source has a very negative $\delta^{13}\text{C}$ value compared to the external inorganic pool ($0\text{‰} < \delta^{13}\text{C}_{\text{DIC}} < 1.5\text{‰}$ in the Bay of Brest). This is because particulate organic matter consumed by this suspension feeder (particularly phytoplankton blooms) is strongly enriched in ^{12}C ($-26\text{‰} < \delta^{13}\text{C}_{\text{POC}} < -20\text{‰}$; Lorrain et al. 2002). Lorrain et al. (2004) proposed that the ratio of the total amount of respired carbon to the total carbon required for shell construction dictated the amount of metabolic carbon incorporated into calcium carbonates during growth. This ratio increases with increasing shell height. Because the ontogenetic $\delta^{13}\text{C}_{\text{shell}}$ linear decrease is ubiquitous and similar regardless of the ecosystem, we propose that this theory, which emerged from a single population in the bay of Brest, is valid in all populations

Fig. 4 Comparison of $\delta^{13}\text{C}_{\text{shell}}$ detrended (black dots) and $\delta^{18}\text{O}_{\text{shell}}$ (open circles) profiles in shells sampled in **a** Træna (Norway), **b** Brest (France), and **c** Vigo (Spain). Gray dotted vertical lines represent winter growth cessations



along the Atlantic coasts and does not depend upon environmental conditions nor upon shell growth rate. The larger the shell, the “lighter” the $\delta^{13}\text{C}_{\text{shell}}$: this observation is prevailing and can be considered a rule.

The second objective of our study was to examine the factors influencing this ontogenetic trend. For the first time, to our knowledge, our study demonstrated that once detrended, seasonal variations of $\delta^{13}\text{C}_{\text{shell}}$ highlighted a

clear seasonal pattern with very little interindividual variability. To date, interpreting carbon isotope records in shells was complicated by the contribution of the metabolic carbon (Gillikin et al. 2009). We show that this so-called “vital effect” can be removed easily.

To test the environmental origin of $\delta^{13}\text{C}_{\text{shell}}$ detrended variations, we reanalyzed the isotopic datasets obtained on three juvenile specimens from the bay of Brest to take

Fig. 5 Bay of Brest (year 2000; data from Lorrain et al. 2002, 2004). **a** $\delta^{13}\text{C}_{\text{shell}}$ variations in three juvenile scallops. **b** Same dataset detrended using a linear regression. **c** Weekly variations of $\delta^{13}\text{C}_{\text{DIC}}$ (measured at 1 m above the sediment). **d** Weekly variations of concentration POC and its isotopic composition (measured at 1 m above the sediment)

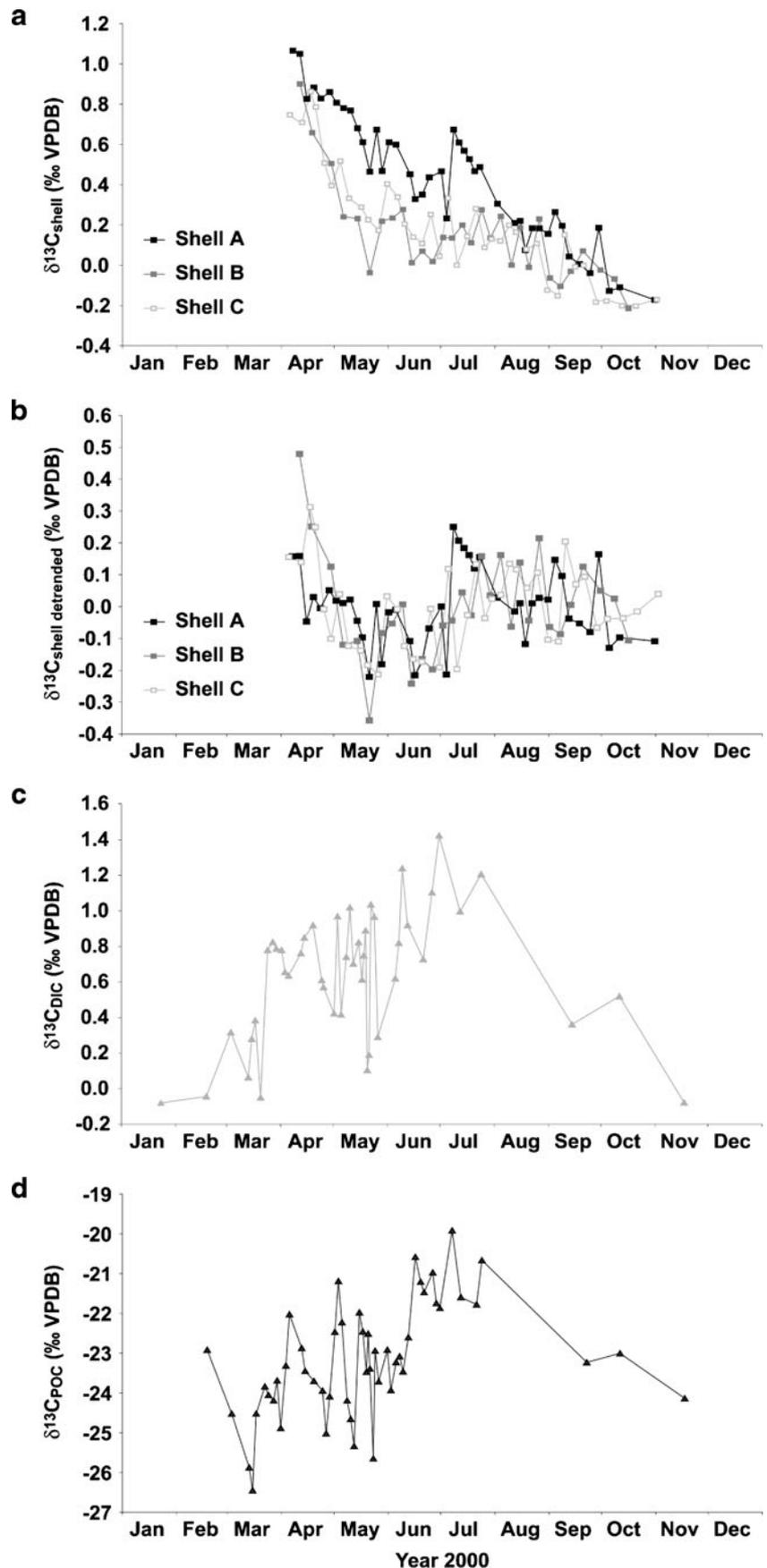
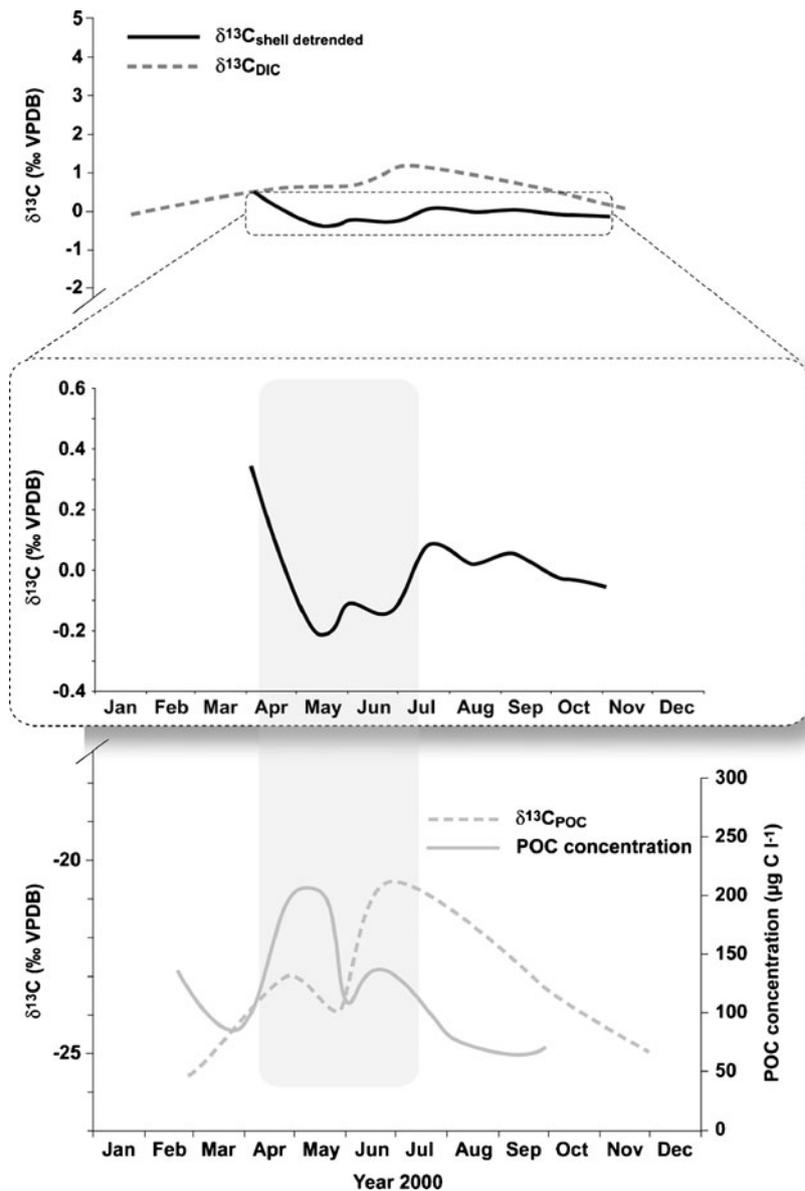


Fig. 6 Illustration of the postulated model for $\delta^{13}\text{C}_{\text{shell}}$ variations after removal of the ontogenetic linear decrease (detrending). In temperate coastal ecosystems, the isotopic signature of POC is at least 20‰ lower than the $\delta^{13}\text{C}$ of scallop shells. Because scallops eat POC and use it to build their shell, $\delta^{13}\text{C}_{\text{shell detrended}}$ variations are likely induced by seasonal variations of food availability (POC concentration). Although seawater DIC is the main source of carbon for shell biomineralization, we postulate that metabolic carbon alone drives $\delta^{13}\text{C}_{\text{shell}}$ variations (i.e., ontogenetic decrease and seasonal oscillations); an increase in the concentration of isotopically light metabolic carbon observed during phytoplankton blooms and its subsequent use as food by scallops is sufficient to decrease $\delta^{13}\text{C}_{\text{shell detrended}}$. This is particularly apparent from early April to mid-July (*light gray area*). Indeed, the carbon isotope composition of the food is different enough from $\delta^{13}\text{C}_{\text{DIC}}$ to mask the influence of weak $\delta^{13}\text{C}_{\text{DIC}}$ seasonal variations in the precipitating calcite crystals. In the proposed paradigm, $\delta^{13}\text{C}_{\text{DIC}}$ seasonal variations are too weak to compensate for the huge offset between $\delta^{13}\text{C}_{\text{shell}}$ and $\delta^{13}\text{C}_{\text{POC}}$



advantage of the extensive environmental survey conducted at exactly the site of scallop collection (Lorrain et al. 2002, 2004). Once detrended, the seasonal variations of $\delta^{13}\text{C}_{\text{shell}}$ revealed a clear seasonal pattern in all specimens, with the lowest values recorded in late spring–early summer. $\delta^{13}\text{C}_{\text{shell detrended}}$ decreased when $\delta^{13}\text{C}_{\text{DIC}}$ increased. Moreover, $\delta^{13}\text{C}_{\text{DIC}}$ was always higher than $\delta^{13}\text{C}_{\text{shell}}$. These two findings confirm that seasonal variations of $\delta^{13}\text{C}_{\text{DIC}}$ do not explain seasonal variations of $\delta^{13}\text{C}_{\text{shell detrended}}$. Therefore, neither $\delta^{13}\text{C}_{\text{shell detrended}}$ nor $\delta^{13}\text{C}_{\text{shell}}$ should be considered to be proxies for $\delta^{13}\text{C}_{\text{DIC}}$. Seawater DIC is incorporated into the shell, but the small variations (annual range=1.5‰) in its carbon isotope composition are not discernable in $\delta^{13}\text{C}_{\text{shell detrended}}$ variations.

Conversely, $\delta^{13}\text{C}_{\text{shell detrended}}$ may reflect seasonal variations in food availability (Fig. 6). Scallops are

suspension feeders; they eat and respire POC; in the bay of Brest, this is mainly pelagic and benthic diatoms (Chauvaud et al. 2000). In the bay of Brest, phytoplankton blooms occur during spring and summer, i.e., the scallop growth season. Regardless of the time of year, $\Delta\delta^{13}\text{C}$ (shell minus POC) is always higher than 20‰ (Figs. 5 and 6). Consequently, the incorporation of a small amount of this light carbon would result in a decrease in $\delta^{13}\text{C}_{\text{shell}}$, masking the seasonal signal derived from water $\delta^{13}\text{C}_{\text{DIC}}$. Moreover, given that food availability (i.e., POC concentration) increases with day length (photosynthesis), this ^{12}C -enriched pool of carbon would lead to decreased $\delta^{13}\text{C}_{\text{shell}}$ in late spring–early summer (Fig. 6); i.e., when the photophase is at its annual maximum. Our detrended $\delta^{13}\text{C}_{\text{shell}}$ data strongly support this hypothesis. Indeed, the increase in food availability observed in the bay of Brest in

April–May 2000 is synchronous with an important decrease in $\delta^{13}\text{C}_{\text{shell detrended}}$ (Fig. 6).

Ontogenetic and seasonal variations of $\delta^{13}\text{C}_{\text{shell}}$ can therefore not be used as a proxy for past variations of $\delta^{13}\text{C}_{\text{DIC}}$; however, they should be considered as promising tools for ecophysiological studies.

Acknowledgments Laurent Chauvaud gratefully acknowledges the EU program “Training and mobility Researchers” (Large Scale Facilities and “Marie Curie” research training grants) for the award of a postdoctoral fellowship. We are grateful to Robert B. Dunbar and David A. Mucciarone (Stanford University, CA, USA) for isotopic analyses of *P. maximus* shells and to Jacques Guillou for providing the SOMLIT data. Special thanks are due to Nolwenn Coïc for her help with the figures. This manuscript has benefited from helpful comments by Anthony Robson. This study was partly supported by the EU program “Marie Curie” and the French program ANR-Blanc (Agence Nationale de la Recherche—CHIVAS project).

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