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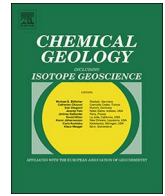
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Contrasting shell growth strategies in two Mediterranean bivalves revealed by oxygen-isotope ratio geochemistry: The case of *Pecten jacobaeus* and *Glycymeris pilosa*

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ABSTRACT

High-resolution stable-isotope ratio data ($\delta^{18}\text{O}$, $\delta^{13}\text{C}$) were used to study growth strategies of two bivalve species, *Pecten jacobaeus* (calcitic shell) and *Glycymeris pilosa* (aragonitic shell) from the North Adriatic Sea. The principal objectives of this study were to identify the period of the year when the growth line is formed in the shell of two target species, to identify the main growing season of these two species, to identify the environmental drivers of shell growth, and to evaluate the potential applicability of $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ values for the reconstruction of environmental variability. Samples were collected from the North Adriatic Sea by commercial bean trawl (*P. jacobaeus*, December 2013 and January 2014, N = 4) and SCUBA diver (*Glycymeris pilosa*, March 2016, N = 3). Samples for the oxygen ($\delta^{18}\text{O}$) and carbon ($\delta^{13}\text{C}$) isotope composition of the calcium carbonate were collected by drilling the outer shell layer across several annual cycles. Temporal and spatial temperature and salinity values inside the investigated area were simulated using the 3D numerical ocean model - ROMS. The $\delta^{18}\text{O}$ cycles corresponded to the number of seasonal growth marks observed on the external shell surface of both target species, thereby confirming the annual periodicity of these growth patterns. In February 2012, extreme cooling of the water column accompanied by dense water formation occurred in the Adriatic Sea - an event recorded by *P. jacobaeus* shells. This study indicates that *P. jacobaeus* and *G. pilosa* have contrasting shell growth strategies. *Pecten jacobaeus* grows during winter and slows shell growth during the warmest part of the year, and thereby may be an interesting archive for winter conditions. Due to its longevity and continuous growth during the warmest part of the year, *G. pilosa* is a promising archive for the reconstruction of summer seawater temperatures.

1. Introduction

Over the past decade, the field of sclerochronology has been rapidly developing by investigating structural elements, as well as the geochemical composition of bivalve shells, with the objective of obtaining information on environmental conditions archived during the lifetime of an organism (Schöne and Gillikin, 2013). Analysis of oxygen-isotope ratios ($\delta^{18}\text{O}$) of mollusk shell carbonates has become a key tool for paleoclimate reconstruction as this data can be used to estimate the temperature of the ambient water at the time of shell formation, when $\delta^{18}\text{O}_{\text{water}}$ is known (Urey, 1947; Epstein et al., 1953; Grossman and Ku,

1986; Schöne and Surge, 2005; Gröcke and Gillikin, 2008; Oschmann, 2009; Wanamaker et al., 2011; Schöne and Gillikin, 2013; Butler and Schöne, 2017; Prendergast et al., 2017). Although the interpretation of $\delta^{13}\text{C}$ data is often less straightforward because of species-specific metabolic effects (Chauvaud et al., 2011; Marchais et al., 2015), stable carbon-isotope ratio signatures of mollusk shells may provide data on salinity and $\delta^{13}\text{C}_{\text{DIC}}$ values in estuarine environments (Gillikin et al., 2006; McConnaughey and Gillikin, 2008). These records can range from daily to sub-seasonal time-scales, depending on growth rate and longevity of the studied species, and can provide data for recent years and decades, as well as past centuries (e.g. Black et al., 2009; Butler

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et al., 2013; Schöne, 2013; Reynolds et al., 2016).

Despite having the analytical capabilities for isotope ratios and the tools for milling/drilling shells readily available, only a few studies have investigated the isotopic geochemistry of Mediterranean bivalve shells. Richardson et al. (2004), Bušelić et al. (2015) and Peharda et al. (2015) applied stable-isotope ratio analyses for the validation of periodicity of growth line formation in Adriatic Sea bivalves *Pinna nobilis*, *Glycymeris bimaculata*, and *Lithophaga lithophaga*, respectively. Purroy Albet (2017) used oxygen isotopes for the identification of the main growing season of *Callista chione* and *Glycymeris bimaculata* in the Adriatic. In a recent study, Crippa et al. (2016) performed stable isotope analysis of fossil shells of several bivalve species from the lower Pleistocene Arda river marine succession (northern Italy). To the best of our knowledge, the only studies on the potential of stable-isotope ratios in recent bivalve shells in the Mediterranean for paleoclimate reconstruction are that of Maier and Titschack (2010) on *Spondylus gaederopus* and García-March et al. (2011) on *Pinna nobilis*.

According to a number of studies, the Mediterranean Sea might be an especially vulnerable region to global climate change (e.g. Giorgi and Lionello, 2008; Adloff et al., 2015; Mariotti et al., 2015). These studies agree that Mediterranean region is expected to become substantially drier and warmer during the twenty-first century, especially in the warm season. In the context of possible ecological and environmental changes, understanding drivers of growth in marine organisms is crucial to forecast the impact of climate change on marine biota, and marine bivalve shells present an excellent archive for this purpose. This study comparatively analyzes two bivalve species with different life strategies (as detailed below), the commercially important Mediterranean scallop *Pecten jacobaeus* (Peharda et al., 2003) and the long living bittersweet clam *Glycymeris pilosa* (> 50 years, Peharda et al., 2016).

Due to their fast growth rates and high commercial value associated with fishing, as well as aquaculture activities, scallops have been subject of numerous studies. Shell oxygen-isotope ratios were successfully applied to determine the ontogenetic age of several Pectinidae species (e.g. Krantz et al., 1984; Dare and Deith, 1990; Lasta et al., 2001; Heilmayer et al., 2003; Chute et al., 2012). Besides ageing, the application of oxygen-isotope ratios for (paleo-) environmental reconstructions has been evaluated (e.g. Hickson et al., 1999; Chauvaud et al., 2005; Thébaud et al., 2007; Trevisol et al., 2012; Jolivet et al., 2015).

Pecten jacobaeus is the largest scallop inhabiting the Mediterranean Sea and can attain a shell length of up to 140–160 mm (Marguš et al., 1992; Onofri and Marguš, 1995; Peharda et al., 2003). This species lives at depths ranging from 25 to 250 m, on sand, mud and gravel substrates (Poppe and Goto, 2000). Although it is present throughout the Mediterranean coastal waters, it occurs in exploitable quantities only in the Northern Adriatic (Mattei and Pelizzato, 1996). Significant variation in the biomass of *P. jacobaeus* fished in the North Adriatic occurred over the last four decades. During 1970 to 2000, the annual landing at the Chioggia fish market (Italy), the main port for scallop fishing in the Adriatic, varied between 105 and 1172 tons (mean \pm standard deviation = 551 \pm 326 tons), with a subsequent significant decrease, with average annual landings of only 56 \pm 19 tons (Mazzoldi et al., 2014; Clodia database, 2015). Although overfishing is probably the main reason behind the decrease in landings, it is possible that environmental factors, such as seawater temperature, salinity, oxygen saturation and food availability, might have also negatively affected growth as well as other biological processes in *P. jacobaeus*.

The second target species, *G. pilosa*, a longlived bivalve (maximum of about 70 years) that was recently proposed as a potential environmental archive to investigate the relationship between climate and biology in the Mediterranean (Peharda et al., 2016). Species of *Glycymeris* were previously identified as targets for sclerochronological research and chronologies spanning several decades have been constructed using *G. glycymeris* from the North-East Atlantic (Brocas et al., 2013; Reynolds et al., 2013; Royer et al., 2013). According to Reynolds et al. (2013), maximum longevity of *G. glycymeris* is ~200 years,

whereas Peharda et al. (2016) estimated the maximum longevity of *G. pilosa* at ~70 years. Although it was previously thought that *G. glycymeris* inhabits the Mediterranean and Adriatic Seas, a recent study by Purroy et al. (2016) identified this species as *G. pilosa* raising the need for a better understanding of the ecology and shell growth of this species. Because of distinct annual growth lines (Peharda et al., 2016), *G. pilosa* has a great potential for paleoclimate reconstructions, but there is the need for understanding the timing of growth line formation, as well as the rate of seasonal growth, in order to properly interpret chronologies in terms of environmental variations in the Mediterranean Sea.

The principal objectives of this study were to: i) identify the period of the year when the growth line is formed in the shell of two target species, *P. jacobaeus* (calcitic shell) and *G. pilosa* (aragonitic shell); ii) identify the main grow season of these two species; iii) identify the environmental drivers of shell growth; and iv) evaluate the potential applicability of $\delta^{18}\text{O}$ values for the reconstruction of environmental variability.

2. Materials and methods

2.1. Environmental variables

Daily mean temperature and salinity fields inside the investigated area (offshore of West Istria) were modeled using the 3D numerical model ROMS with a spatial resolution of 2 km and 20 “s” level coordinates in the vertical (Janeković et al., 2014). In this study we used results only at the bottom for temperature and salinity parameters, computed previously within the Adriatic Sea ROMS modelling study. The model was integrated for 6 years starting from 2008 till the end of 2014 and was validated in many studies with available observations (e.g. CTD profiles and satellite SST in Janeković et al., 2010, 2014; Vilibić et al., 2016). During the period 2009–2014, the model used realistic atmospheric forcing, lateral boundary conditions, and freshwater input from 41 rivers providing accurate estimates for all model state variables in the whole water column (from which we used only temperature and salinity subsets closest to the bottom). Separate models were computed for the different sample localities (Fig. 1), water depths and time periods for *P. jacobaeus* (25–30 m, 2009–2013) and *G. pilosa* (10 m, 2011–2014).

2.2. Sample collection

Pecten jacobaeus specimens were collected by the commercial beam trawl type “Rapido” along the western coast of the Istrian peninsula (North Adriatic) in December 2013 and January 2014 (Fig. 1). Sampling was conducted within latitudes 45°08'57.76"–45°23'07.55"N, and longitudes 13°17'04.99"–13°54'04.07"E at depths between 25 and 30 m and haul duration varied between 20 and 30 min. Specimens were transported to the laboratory, soft tissues carefully removed, and shells washed and stored dry at the Institute of Oceanography and Fisheries in Split.

Isotope-ratio analyses focused on three shells collected in December 2013 (PJ12-5, PJ12-8 and PJ12-16) and one shell collected in January 2014 (PJ1-3). Shell length (anterior-posterior axis) and height (dorso-ventral axis) of each scallop were measured with vernier calipers to the nearest 0.1 mm. Prior to laboratory analysis, left valves were gently brushed to remove most of the epibionts as well as sediment trapped between striae, and washed in a 10 vol% acetic acid bath for 30 s followed by rinsing in water (Thébaud and Chauvaud, 2013).

Glycymeris pilosa samples were collected by SCUBA diver in March 2016 at 10–11 m depth from a coastal locality in the North Adriatic Sea (44°59'7.47"N, 13°44'19.22"E; WGS84). Upon collection specimens were frozen and transported to our laboratory where they were thawed, soft tissues carefully removed, and shells washed and air dried. Three shells of similar size were selected for analyses (S3P67, S3P91 and



Fig. 1. Map of the study area indicating the location at which *Pecten jacobaeus* was collected by the commercial fishing beam trawl (dark grey) and the SCUBA diving locality at which *Glycymeris pilosa* was collected (black empty circle). The four black filled dots off Istria Peninsula represent the stations where Stenni et al. (1995) sampled water for $\delta^{18}\text{O}_{\text{w-SMOW}}$ and salinity analyses.

S3P106). Prior to collection of samples for stable-isotope ratio analysis, the periostracum was physically removed with grinding paper.

2.3. Stable isotope analysis

Samples for the shell calcium carbonate oxygen ($\delta^{18}\text{O}$) and carbon ($\delta^{13}\text{C}$) isotope-ratio analysis were collected by milling narrow sample swaths from the shells by hand under a stereo microscope using a DREMEL Fortiflex drill equipped with a 300 μm tungsten carbide drill bit. Estimating milling depth was $\sim 100 \mu\text{m}$. For *P. jacobaeus*, shallow milling was completed parallel to the growth striae, each sample extending over 1–3 striae (Fig. 2). In total, 308 samples were collected: 61 from shell PJ12-5, 79 from shell PJ12-8, 68 from shell PJ12-16 and 100 from shell PJ1-3. Shells were photographed and distances between samples were measured using Image Pro Premier software. For *G. pilosa*, shallow milling was done parallel to the growth lines covering two growth increments, as well as several samples before and after these two growth increments. Growth increments were chosen on the basis of their width in order to obtain a sufficient number of samples (> 9) per growth increment. Mean distance between samples was $\sim 193 \pm 40 \mu\text{m}$. In total 93 samples were analyzed: 29 from shell S3P67, 35 from shell S3P91 and 29 from shell S3P106. During milling, detailed notes were taken on position of samples in relation to growth lines visible on the external shell surface.

Isotope-ratio analyses was performed at the University of Mainz, Germany, on a Thermo Finnigan MAT 253 continuous flow – isotope ratio mass spectrometer, equipped with a GasBench II. Samples were measured against an in-house Carrara marble ($\delta^{18}\text{O} = +2.01\text{‰}$; $\delta^{13}\text{C} = -1.91\text{‰}$) calibrated against the international isotopic reference standard NBS-19. Results are expressed as parts per thousand with respect to the Vienna Pee Dee Belemnite standard (‰ V-PDB). Long-term (1.5 years) reproducibility (= accuracy, 1 sigma) of the mass spectrometer is 0.04 ‰ for $\delta^{18}\text{O}$ and 0.03 ‰ for $\delta^{13}\text{C}$ based on 421 blind measurements of NBS-19. The average 1 sigma internal precision error (eight injections per sample) is 0.04 ‰ for $\delta^{18}\text{O}$ and 0.03 ‰ for $\delta^{13}\text{C}$.

To enable temporal alignment of obtained $\delta^{18}\text{O}_{\text{shell}}$ values, daily modeled seawater salinity and temperature data were used for reconstructing theoretical variations of $\delta^{18}\text{O}_{\text{shell}}$. Kim and O'Neil (1997) equation for calcite was applied to the *P. jacobaeus* dataset:

$$1000 \ln \alpha_{\text{calcite-water}} = 18.03(10^3 T^{-1}) - 32.42 \quad (1)$$

For the aragonite *G. pilosa* dataset the Kim et al. (2007) equation of

was applied:

$$1000 \ln \alpha_{\text{aragonite-water}} = 17.88(10^3 T^{-1}) - 31.14 \quad (2)$$

Because $\delta^{18}\text{O}_{\text{w-SMOW}}$ of the water was not monitored over the life-span of the studied specimens, we reconstructed $\delta^{18}\text{O}_{\text{w-SMOW}}$ values from modeled salinity data (S) using the equation derived from Stenni et al. (1995) data for $\delta^{18}\text{O}_{\text{w-SMOW}}$ and salinity at transect B (black filled dots on Fig. 1):

$$\delta^{18}\text{O}_{\text{w-SMOW}} = 0.366^\circ\text{S} - 12.568 \quad (r^2 = 0.964) \quad (3)$$

To convert $\delta^{18}\text{O}$ values from the V-PDB to V-SMOW (Vienna Standard Mean Ocean Water) scale, and vice versa, the equation of Coplen et al. (1983) was used. $\delta^{13}\text{C}_{\text{shell}}$ values for *P. jacobaeus* were detrended, as previously done for *Pecten maximus* by Chauvaud et al. (2011). Presence of ontogenic trends in $\delta^{13}\text{C}_{\text{shell}}$ values can mask the seasonal signal of this parameter and its detrending enables comparison with $\delta^{18}\text{O}_{\text{shell}}$ values (Chauvaud et al., 2011). The least-squares fit of a straight line was calculated separately for each analyzed individual. Subsequently, these values were subtracted from measured $\delta^{13}\text{C}_{\text{shell}}$ data. The residual time-series is referred to as $\delta^{13}\text{C}_{\text{shell det}}$. Spearman correlation was applied for testing relationship between $\delta^{18}\text{O}_{\text{shell}}$ and $\delta^{13}\text{C}_{\text{shell}}$.

Temporal aligning of measured $\delta^{18}\text{O}_{\text{shell}}$ values was conducted manually in Excel by assigning each data point calendar date that placed that measured data point on graph closest to modeled $\delta^{18}\text{O}_{\text{shell}}$ values. Final graphs were prepared in Sigma Plot 13.0 software.

3. Results

3.1. Environmental variables

For the area where *P. jacobaeus* specimens were collected, the modeled values for seawater bottom temperature (25–30 m) showed pronounced seasonal patterns, with minimum values ($\sim 10^\circ\text{C}$ or lower) occurring between January and April, and maximum values ($\sim 19^\circ\text{C}$ or higher) from July to October (Fig. 3). The overall lowest and highest monthly temperatures of 7.8°C and 20.6°C occurred in March 2012 and October 2009, respectively. Modeled monthly values of bottom salinity ranged from 37.0 (November 2013) to 38.4 (February 2013). Between 2009 and 2013, mean salinity \pm one standard deviation was 37.9 ± 0.3 . Most variable intra-annual values were noted during 2013, when the lowest values were also obtained through the ROMS

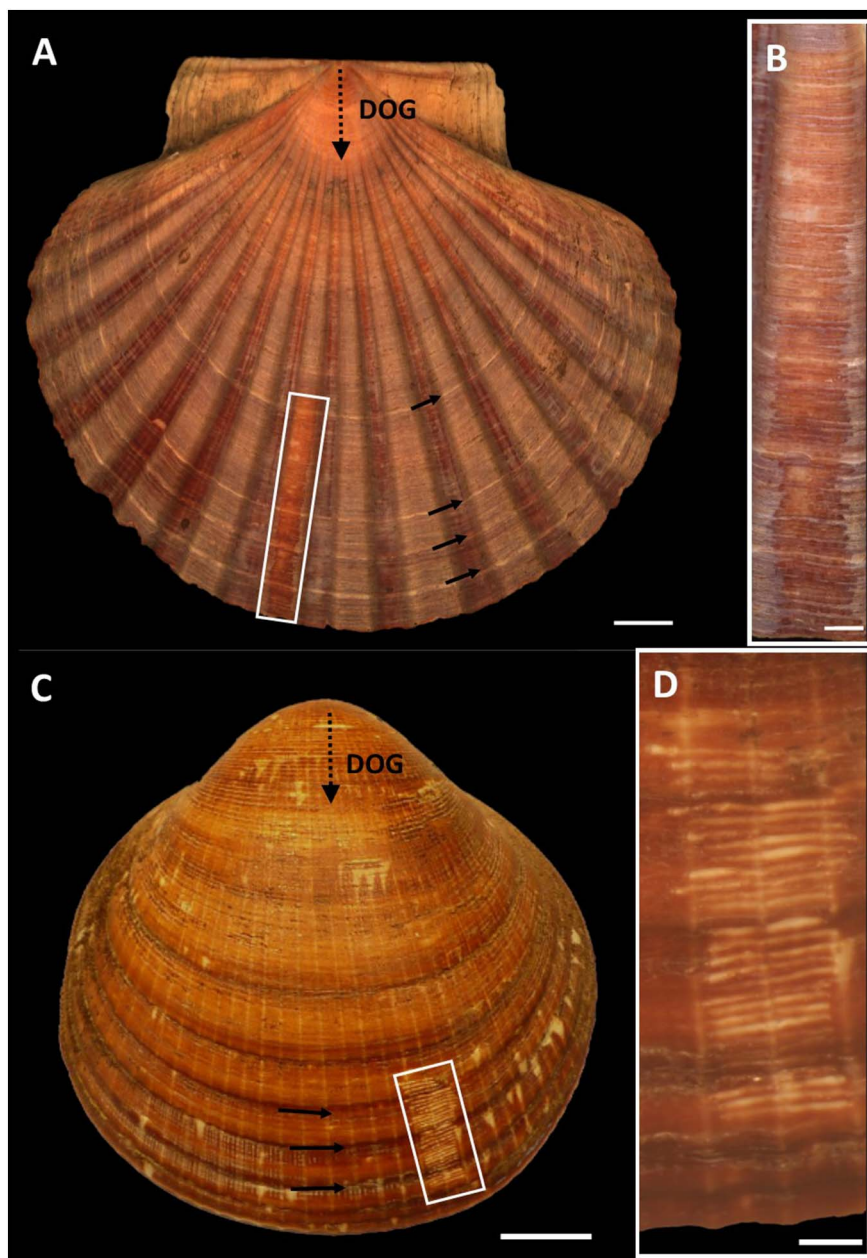


Fig. 2. A. Left valve of *Pecten jacobaeus* shell PJ 12-8 showing bright annual growth rings (black arrows) and milling swaths (within white rectangle) for isotope-ratio analyses. B. Close-up of milling swaths on the surface of *P. jacobaeus*. C. *Glycymeris pilosa* shell S3P106 showing dark growth rings (black arrows) and milling swaths (within white rectangle) for isotope analysis. D. Close-up of milling swaths on the surface of *G. pilosa*. Direction of shell growth (DOG) indicated with dashed arrows. Scale bars represent 1 cm in A and C, and 2 mm in B and D.

simulation for the second half of the year. Overall, the time interval between October and December was characterized by higher variations in bottom salinity.

At the shallow coastal locality (10–11 m depth) where *G. pilosa* was collected, modeled values for seawater bottom temperature ranged from 7.7 °C (February 2012) to 25.7 °C (August 2014). Annual minimum values (~13 °C or lower) occurred from January to April, while annual maximum values (~20 °C or higher) were characteristic for the months of June to September. Large seawater temperature variations sometimes occurred within days. Furthermore, pronounced variations in lowest modeled seawater temperatures between years are clearly evident, e.g., high winter seawater temperatures corresponding to the beginning of year 2014. Between the beginning of year 2011 and June 2014 salinity values ranged between 35.9 (September 2013) and 38.5 (April 2012), with an average of 37.7 ± 0.4 (1 SD). Modeled salinity showed considerable variability within and between years. With the exception of 2011, higher salinity was observed during the first half of the calendar year (January to June), whereas lower and more variable salinities were characteristic for the July to November

period.

Modeled temperatures for two studied areas clearly show that temperature maxima were lower in deeper water (for *P. jacobaeus*) and occurred later during the year (Fig. 3C). Winter temperature minima were very similar between two studied locations as the water column is well mixed during this season. Salinity was in general lower in shallower water and more variable on daily to weekly time scales.

3.2. *Pecten jacobaeus* shell geochemistry

Shell lengths of analyzed *P. jacobaeus* ranged from 98.3 mm (PJ12-16) to 116.5 mm (PJ12-8). Shells PJ1-3 and PJ12-5 had intermediate lengths of 113.0 and 116.0 mm, respectively. The $\delta^{13}\text{C}_{\text{shell calcite}}$ values of *P. jacobaeus* shells ranged from -1.64 to $+0.40\text{‰}$ ($N = 308$, $\bar{x} = -0.52 \pm 0.45\text{‰}$, 1 SD), and showed an ontogenetic decline as shell height increased (Fig. 4). The $\delta^{18}\text{O}_{\text{shell calcite}}$ values ranged from $+0.01$ to $+3.08\text{‰}$ ($N = 308$, $\bar{x} = 1.40 \pm 0.64\text{‰}$, Fig. 5). Observed cyclicity in the $\delta^{18}\text{O}_{\text{shell calcite}}$ values corresponded to the number of lightly colored growth rings observed on the external shell surface of *P.*

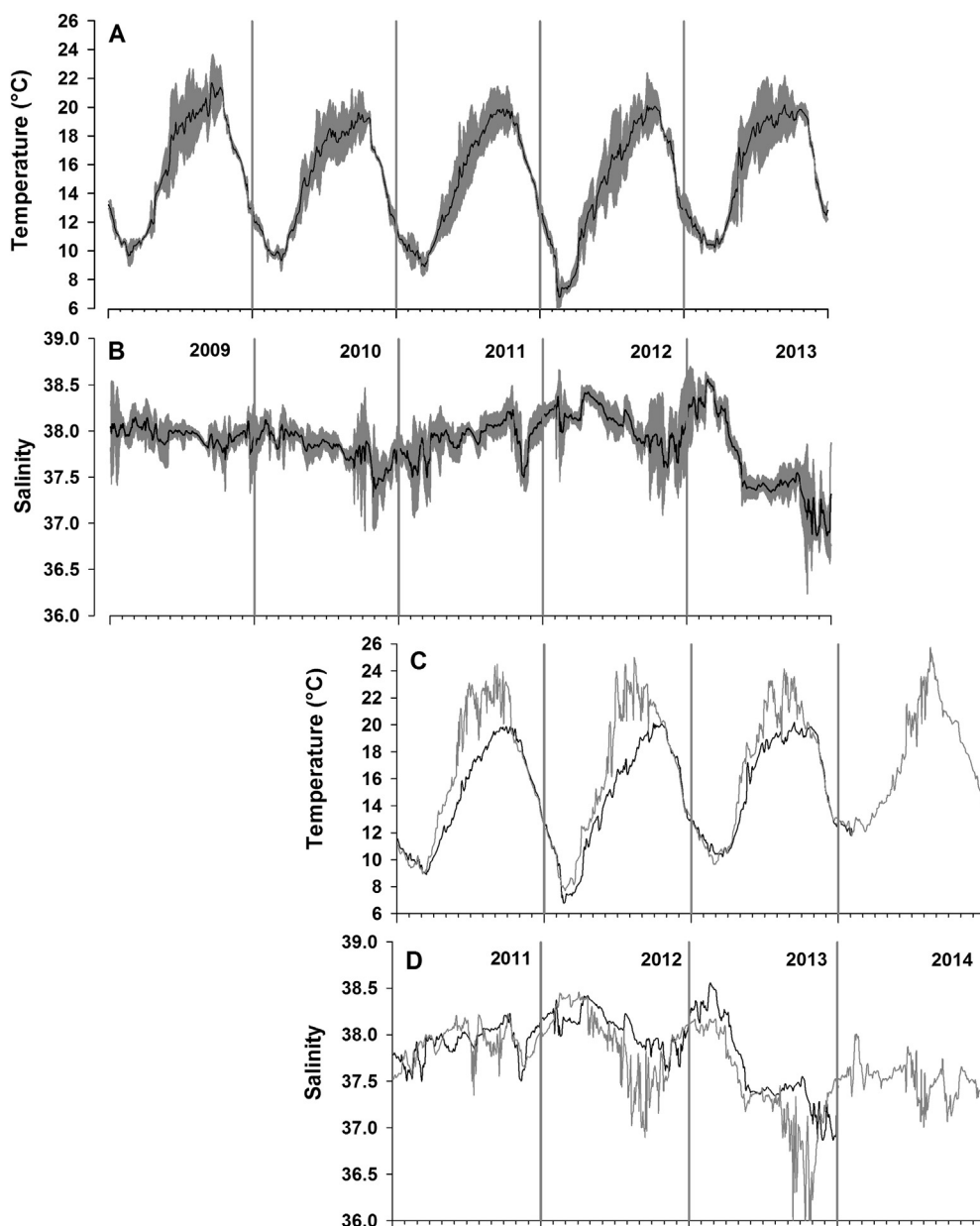


Fig. 3. Modeled seawater temperature (A) and salinity (B) curves for the *Pecten jacobaeus* sampling area. Black lines indicate daily average values, grey areas ± 2 SD. Modeled temperature (C) and salinity curves (D) for the sampling sites of *P. jacobaeus* (black, sampling depth 25–30 m) and *Glycymeris pilosa* (dark grey, sampling depth 10–11 m).

jacobaeus, thereby validating the annual periodicity of these bands. Stable isotope values corresponded to the time interval from 2009 to 2013. Detrending of $\delta^{13}\text{C}_{\text{shell}}$ values enabled the analysis of seasonal variations and comparison of $\delta^{13}\text{C}_{\text{shell det}}$ and $\delta^{18}\text{O}_{\text{shell calcite}}$ values (Fig. 5). A certain degree of cyclicity was observed in $\delta^{13}\text{C}_{\text{shell det}}$ with higher values coinciding with the highest $\delta^{18}\text{O}_{\text{shell calcite}}$ values (coldest part) of each year, whereas lower $\delta^{13}\text{C}_{\text{shell det}}$ values coincided with lower $\delta^{18}\text{O}_{\text{shell calcite}}$ values (warmest part of the year). There was a statistically significant, albeit weak, positive correlation between $\delta^{18}\text{O}_{\text{shell calcite}}$ values and $\delta^{13}\text{C}_{\text{shell det}}$ values in shells PJ12-8 (Spearman $r^2 = 0.40$, $p < 0.001$), PJ12-16 ($r^2 = 0.80$, $p < 0.001$), and PJ1-3 ($r^2 = 0.43$, $p < 0.001$), but no such significant correlation occurred in shell PJ12-5 ($r^2 = 0.16$, $p = 0.211$).

Comparison of $\delta^{18}\text{O}_{\text{shell calcite}}$ values of the four studied *P. jacobaeus* shells and $\delta^{18}\text{O}_{\text{shell calcite}}$ values reconstructed on the basis of the ROMS output and the local freshwater mixing line are shown in Fig. 6. Major growth rings visible on the external shell surface of the left valve coincided with $\delta^{18}\text{O}_{\text{shell calcite}}$ minima. This suggests that cessation and/or slowdown of shell growth occurred during the warmest part of the year. In all shells, growth resumes in December, at the latest. In most years,

no or very little shell growth occurred during a period of almost 5 months, between July and November. Some shell growth variations were observed between years and specimens, and it appears that the shell growth slowdown periods were absent or shorter during early ontogeny (Fig. 6C). Besides seasonal shell growth cessation, there were time intervals of faster growth, as indicated by shell portions during which reconstructed temperatures barely changed. Shells appear to have grown faster during the periods December–January and April–June. The lowest $\delta^{18}\text{O}_{\text{shell calcite}}$ values were related to Summer 2009 (PJ1-3). Three of the studied shells showed $\delta^{18}\text{O}_{\text{shell calcite}}$ maxima of $\sim 3\text{‰}$ during early 2012, which is consistent with the lowest modeled temperature for this period.

3.3. *Glycymeris pilosa* shell geochemistry

Lengths of analyzed *G. pilosa* shells were 56.4 (S3P67), 58.9 (S3P91) and 58.6 mm (S3P106). In case of this species, $\delta^{13}\text{C}_{\text{shell aragonite}}$ values for the three studied specimens ranged from $+0.80$ to $+1.97\text{‰}$ ($N = 93$, $\bar{x} = +1.33 \pm 0.23\text{‰}$), whereas the $\delta^{18}\text{O}_{\text{shell aragonite}}$ values ranged from -0.36 to $+2.64\text{‰}$ ($N = 93$, $\bar{x} = -1.04 \pm 0.81\text{‰}$)

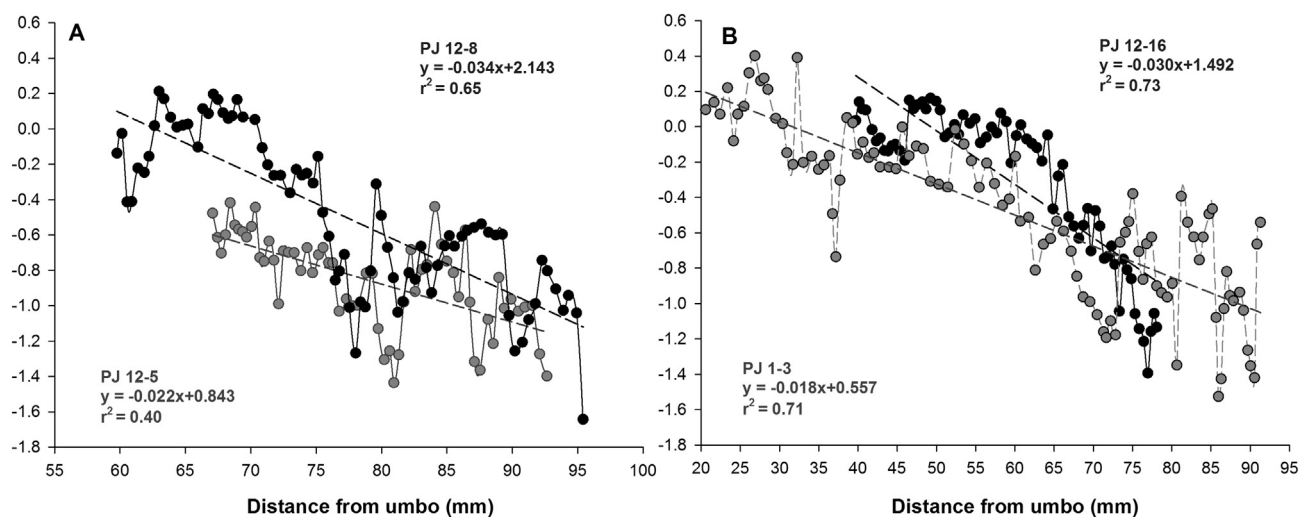


Fig. 4. Ontogenetic linear decrease in $\delta^{13}\text{C}_{\text{shell calcite}}$ values versus shell height (distance from umbo) in *Pecten jacobaeus* A. specimens PJ 12-5 (dark grey) and PJ 12-8 (black), B. Specimens PJ 12-16 (black) and PJ 1-3 (dark grey). Linear regression lines, equations and determination coefficients shown in corresponding graphs.

(Fig. 7). Observed $\delta^{18}\text{O}_{\text{shell aragonite}}$ values correspond to the number of increments on the external shell surface confirming that growth lines were formed annually and measured values correspond to the time interval of Spring 2011 to Winter 2013/2014. A statistically significant, albeit weak, positive correlation was found between $\delta^{13}\text{C}_{\text{shell aragonite}}$ and $\delta^{18}\text{O}_{\text{shell aragonite}}$ values for shells S3P67 ($r^2 = 0.42$, $p = 0.022$) and S3P106 ($r^2 = 0.41$, $p = 0.002$). There was no significant relationship between these two parameters in case of shell S3P91 ($r^2 = -0.23$, $p = 0.188$).

Temporally aligned $\delta^{18}\text{O}_{\text{shell aragonite}}$ values reconstructed on the basis of the ROMS output and the local freshwater mixing line, as well as $\delta^{18}\text{O}_{\text{shell aragonite}}$ values of the three studied *G. pilosa* shells, are shown in Fig. 8. Growth lines coincided with $\delta^{18}\text{O}_{\text{shell aragonite}}$ minima or periods when values started to increase (~September). According to these data, *G. pilosa* did not show a pronounced shell growth slowdown or cessation during the summer period. Highest reconstructed $\delta^{18}\text{O}_{\text{shell aragonite}}$ values were 3.37‰ (February 20th 2012), which is 0.73‰ higher than the highest measured $\delta^{18}\text{O}_{\text{shell aragonite}}$ value (2.64‰, specimen S3P67), indicating that shell growth slowed down or was halted during the coldest period of the year. Specimens S3P91 and S3P106 had even lower maximum $\delta^{18}\text{O}_{\text{shell aragonite}}$ values, 2.33 and 2.50‰, respectively. Based on these values, shells did not grow between January and March, or even longer. Temporal distances between measured $\delta^{18}\text{O}_{\text{shell aragonite}}$ values indicate fastest shell growth occurred during October–November period, i.e., after the growth line formation. Seasonal differences in growth slowdown/cessation between the two studied species are evident from the data presented in Fig. 9. Whereas *G. pilosa* slowed shell growth during coldest part of the year, shell slowdown/cessation in *P. jacobaeus* occurred during warmest part of the year.

4. Discussion

4.1. Periodicity of growth line formation and environmental conditions

Strong inter-annual variations in $\delta^{18}\text{O}_{\text{shell}}$ values of both studied bivalve species, *P. jacobaeus* and *G. pilosa*, as well as reconstructed and modeled seawater temperature and salinity values were observed. Highest $\delta^{18}\text{O}_{\text{shell calcite}}$ values recorded by *P. jacobaeus* shells, corresponding to lowest seawater temperatures, occurred during February 2012. This coincided with extreme cooling of seawater and dense water formation in the Adriatic Sea (Janežević et al., 2014). Unlike *P. maximus* from the Atlantic which forms winter growth lines (Chauvaud et al., 1998, 2005, 2012; Owen et al., 2002), *P. jacobaeus* from the

North Adriatic seem to be able to deposit shell even at lowest winter seawater temperatures. It is interesting to note that seawater temperatures lower than 8 °C, as those that occurred during the extreme cold event in February 2012, are extremely rare. Despite variations between years and specimens, this study clearly indicate that a *P. jacobaeus* shell growth slowdown and/or cessation occurred during the warmest part of the year.

Unlike *P. jacobaeus*, this study clearly indicates that *G. pilosa* cannot be used to reconstruct seasonal seawater temperature minima. Highest reconstructed $\delta^{18}\text{O}_{\text{shell aragonite}}$ values (corresponding to minimum seawater temperatures) were significantly higher than $\delta^{18}\text{O}_{\text{shell aragonite}}$ values obtained from the shell, indicating a slowdown/cessation of shell growth of *G. pilosa* from the North Adriatic during winter at seawater temperatures below ~12 °C. The same was found for a related species, *Glycymeris bimaculata*, from two localities in the eastern Adriatic – Pag Bay and Cetina river estuary (Purroy Albret, 2017). According to this study, *G. bimaculata* did not deposit new shell between January and April when seawater temperatures dropped below ~12 °C in Pag bay and below ~14 °C in Cetina river estuary. Walliser et al. (2015) evaluated the potential of fossil bivalve *Glycymeris planicostalis* for high-resolution reconstructions of seawater temperatures during the Early Oligocene (30 Ma) and found that shells grew uninterruptedly and have therefore, in their opinion, recorded the entire seasonal seawater temperature range at that time. Certain caution is needed when applying these findings to other species and locations, since Early Oligocene seawater parameters are not readily available. However, seawater temperature values reconstructed from these fossils ranged from 12.3 to 22.0 °C, i.e., lowest winter temperature exceeded the shutdown temperature of modern glycymerids in the Adriatic Sea. Caution needs to be applied when using *G. planicostalis* as a seawater temperature archive in deep time, because shells may have stopped growing below the lower seawater temperature threshold of 12 °C observed in recent glycymerids. A careful analysis of subannual shell growth patterns is advised prior to interpreting seawater temperature data of fossil bivalves. A growth slowdown below 12 °C has also been observed in *G. glycymeris* from Brittany, northwest France (Royer et al., 2013).

All studies cited in the paragraph above indicate the high potential of glycymerids for the reconstruction of summer seawater temperatures. In *G. pilosa* from the North Adriatic the annual growth line is formed in September, i.e. at the end of summer, but there was no pronounced slowdown in shell growth during the warm season of the year, because minimum $\delta^{18}\text{O}_{\text{shell aragonite}}$ values obtained from the studied shells coincided well with the lowest reconstructed $\delta^{18}\text{O}_{\text{shell aragonite}}$ values.

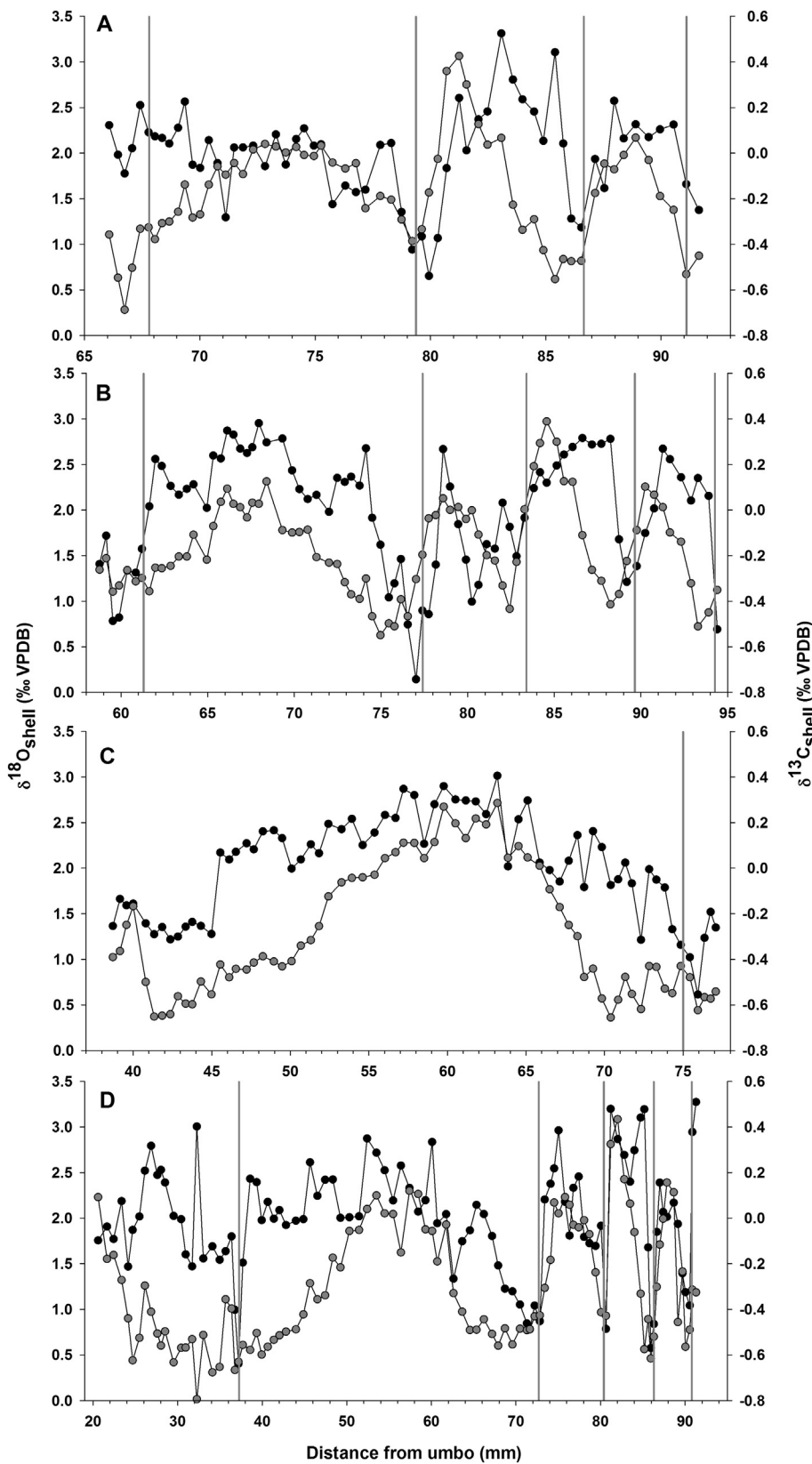


Fig. 5. Relationship between $\delta^{18}\text{O}_{\text{shell calcite}}$ (Y₁ axis, dark grey) vs. $\delta^{13}\text{C}_{\text{shell det}}$ (Y₂ axis, black) for the four studied *Pecten jacobaeus* shells. A. PJ 12-5, B. PJ 12-8, C. PJ 12-16, D. PJ 1-3. Vertical bars identify annual growth lines observed on the outer shell surface.

Other factors besides seawater temperature can also influence shell growth rate and growth line formation. According to a recent experimental study on gaping activity of long lived bivalve *Arctica islandica* conducted in the Northern Norway, gaping activity was related to interaction of several environmental variables including Chlorophyll *a*,

temperature and photoperiod (Ballestra-Artero et al., 2017). In an earlier paper, Witbaard et al. (2003) demonstrated that *A. islandica* growth in the northern North Sea is mainly influenced by the abundance of copepods. According to this study, copepods intercept downward flux of food particles what might lead to depression of shell

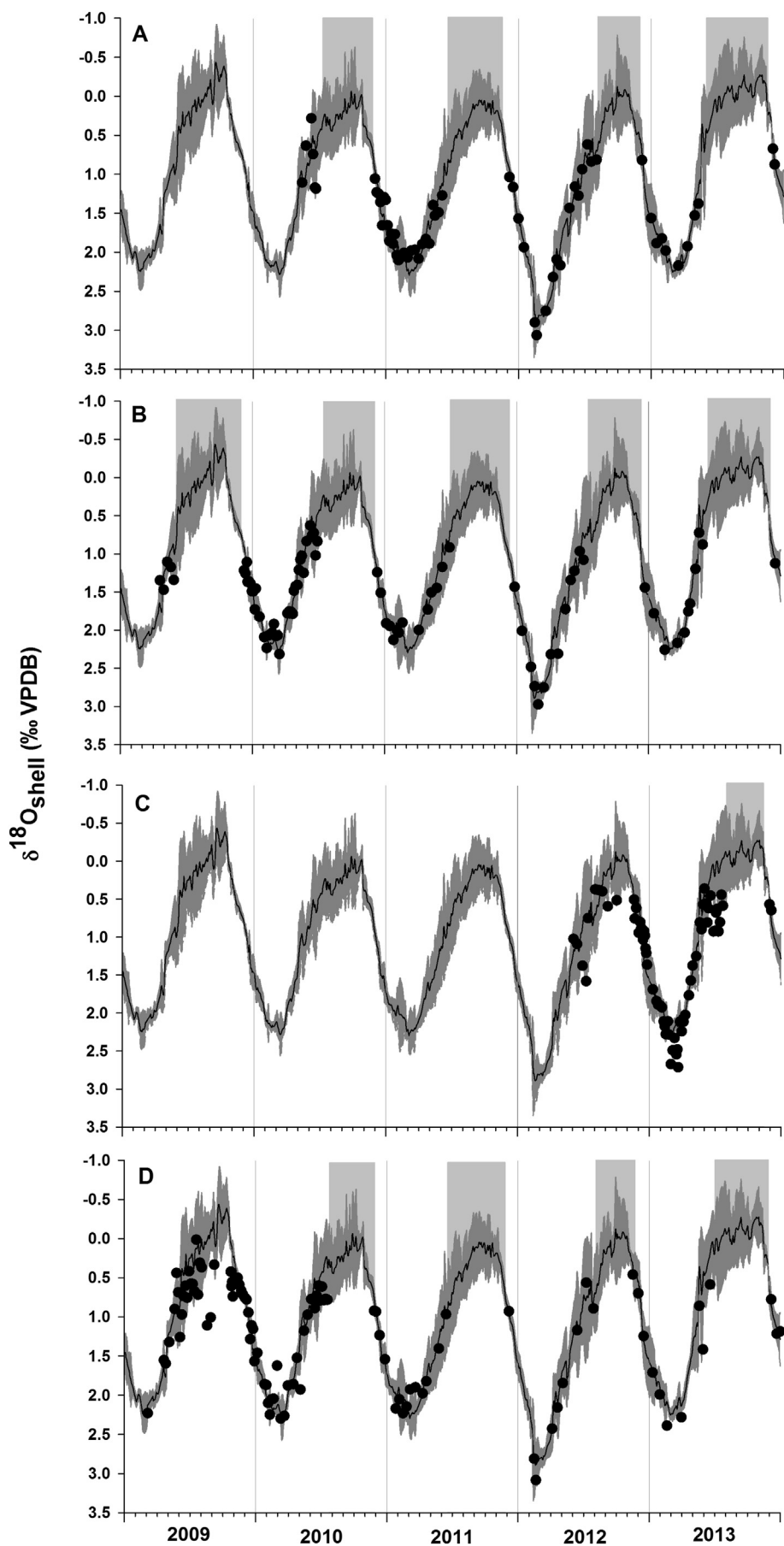


Fig. 6. Temporally aligned modeled $\delta^{18}\text{O}_{\text{shell calcite}}$ values (black line = daily averages, grey areas ± 2 SD) and measured $\delta^{18}\text{O}_{\text{shell calcite}}$ values of *Pecten jacobaeus* shells (inverted scale). Missing reconstructed data denote slow-down or cessation of shell growth (grey shading). Vertical grey lines indicate calendar years. A. PJ 12-5, B. PJ 12-8, C. PJ 12-16, D. PJ 1-3.

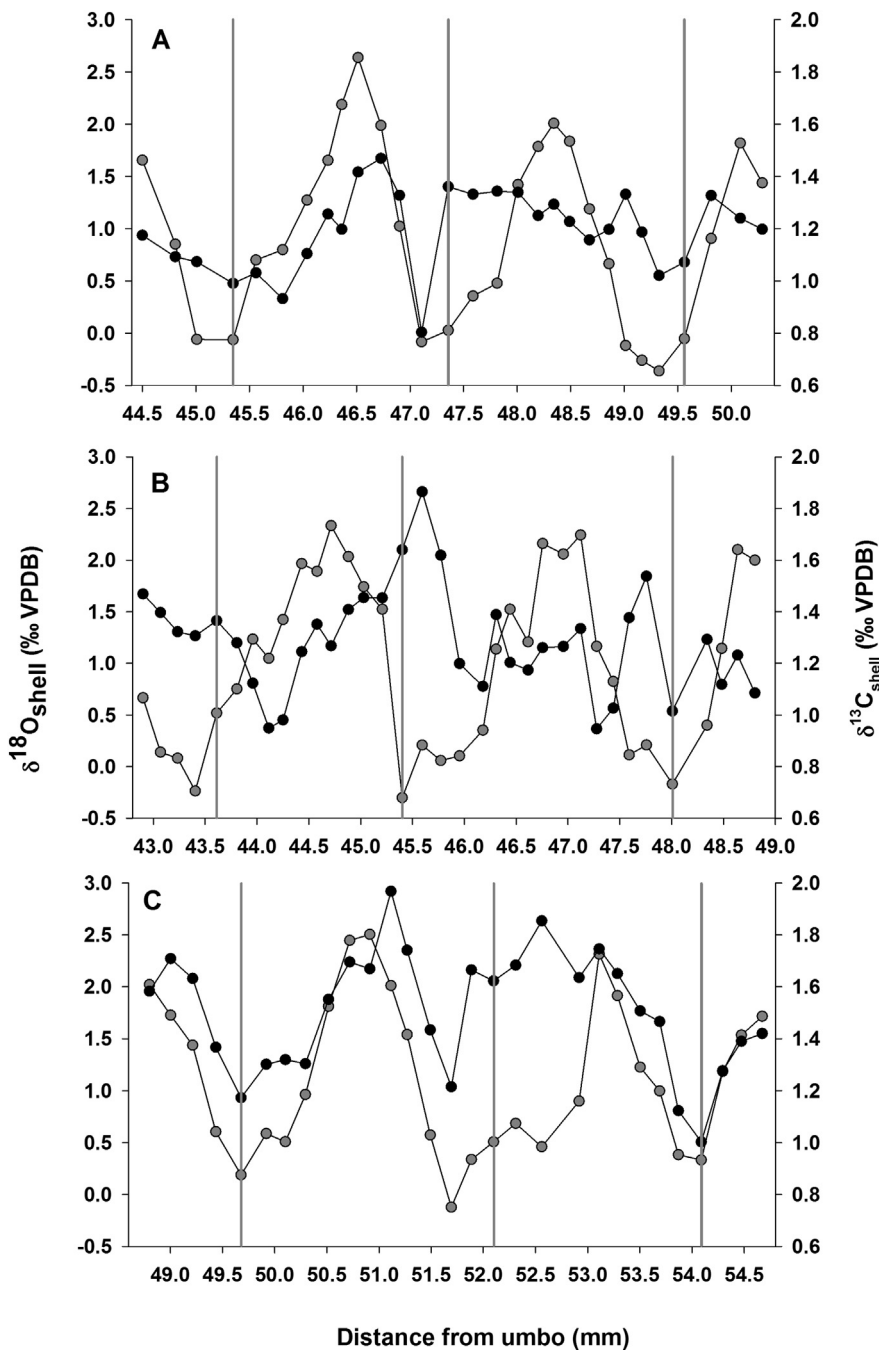


Fig. 7. Relationship between $\delta^{18}\text{O}_{\text{shell}}$ aragonite (Y_1 axis, grey) vs. $\delta^{13}\text{C}_{\text{shell}}$ aragonite (Y_2 axis, black) for three studied *Glycymeris pilosa* shells. A. S3P67, B. S3P91, C. S3P106. Vertical bars identify annual growth lines observed on the outer shell surface.

growth due to food shortage. An opposite relationship was reported by Wanamaker et al. (2009) in the western Gulf of Maine, where a significant positive correlation was determined between shell growth of *A. islandica* and relative abundance of copepod *Calanus finmarchicus*, indicating complex and environmentally specific relationships.

It has been demonstrated for several bivalve species that survival, metabolism and shell growth are reduced when animals are exposed to concurrent low dissolved oxygen and low pH conditions (Gobler and Baumann, 2016). Gobler et al. (2014) analyzed the effects of hypoxia and acidification on early life stages of bivalves and found that shell growth was significantly reduced when both conditions occurred simultaneously. According to Djakovac et al. (2015), hypoxia events occurred frequently in the north Adriatic Sea between mid-summer and mid-fall. Low pH conditions occurred in the Gulf of Trieste (North Adriatic Sea) during August and September (Cantoni et al., 2012). Unfortunately, there is no sufficient data available to evaluate whether

hypoxia is an annual event of similar intensity between years, since data collection efforts in the area vary between years. Mid-fall period coincided with the annual growth line formation of both species, possibly indicating that growth line is formed as a response to low DO and low pH. Recent expansion of low oxygen zones in coastal ecosystems, a trend that may accelerate with climate warming (Gobler et al., 2014), will likely have negative effects on bivalve growth.

4.2. Trends in $\delta^{13}\text{C}_{\text{shell}}$ and $\delta^{18}\text{O}_{\text{shell}}$ values

An ontogenetic trend of $\delta^{13}\text{C}_{\text{shell}}$ to lower values has previously been observed for many bivalve species (for review see McConnaughey and Gillikin, 2008). Examples of some recent studies include the great scallop, *P. maximus* from the Atlantic (Chauvaud et al., 2011), the thorny oyster, *Spondylus gaederopus* from the Mediterranean (Maier and Titschack, 2010) and the date shell, *Lithophaga lithophaga* from the

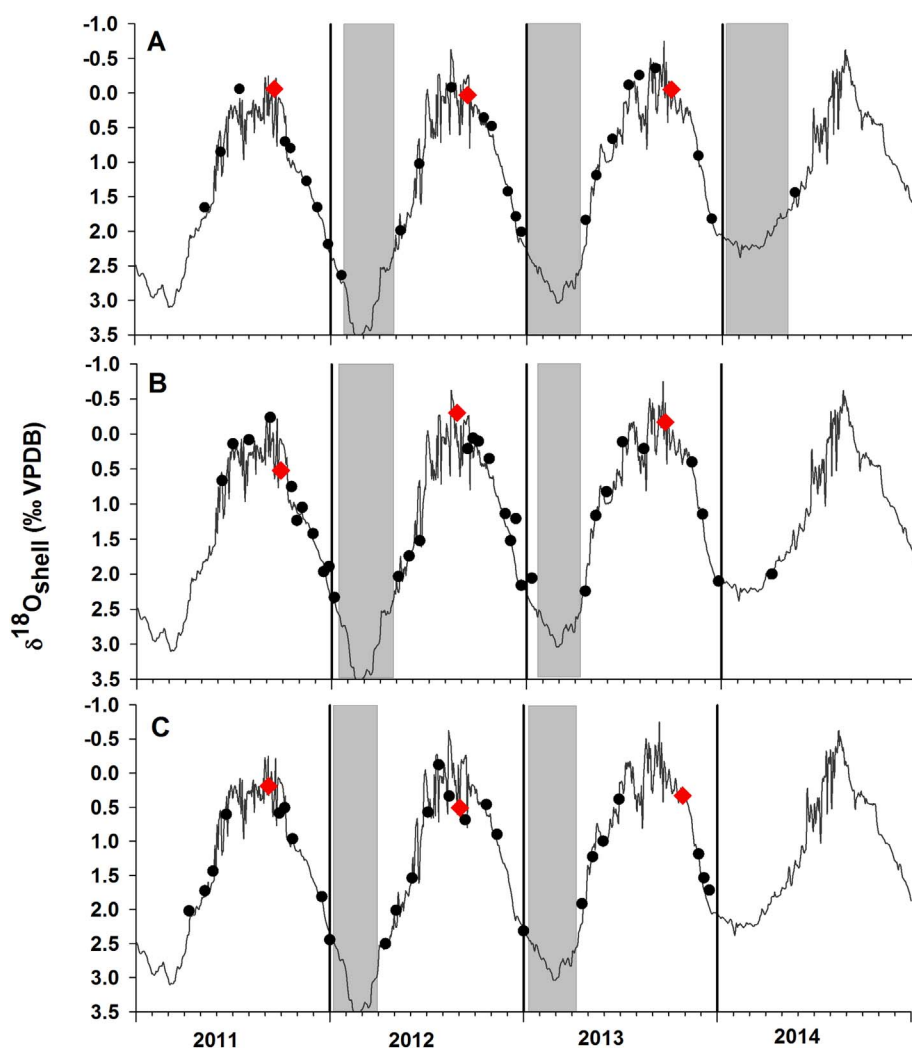


Fig. 8. Temporally aligned modeled $\delta^{18}\text{O}_{\text{shell aragonite}}$ values and measured $\delta^{18}\text{O}_{\text{shell aragonite}}$ values of *Glycymeris pilosa* shells (inverted scale). Absence of reconstructed data indicates slowdown or stop of shell growth. Vertical black lines indicate calendar years, red data points indicate position of growth lines, grey areas indicate periods of shell growth slowdown. A. S3P67, B. S3P91, C. S3P106.

coastal middle Adriatic (Peharda et al., 2015). Observed decrease in $\delta^{13}\text{C}_{\text{shell}}$ values with age might also be related to marine Suess effect, as was previously observed for *Arctica islandica* (Schöne et al., 2011). Presence of strong ontogenetic trends can mask the seasonal signal, and therefore, Chauvaud et al. (2011) suggested detrending $\delta^{13}\text{C}_{\text{shell}}$ values of species that show age-related trends in order to enable an analysis of seasonal variations.

P. maximus from the Bay of Brest had lowest values of $\delta^{13}\text{C}_{\text{shell det}}$ in late spring/early summer, most likely reflecting corresponding variations in food availability (Chauvaud et al., 2011). In our study, in *P. jacobaeus*, low $\delta^{13}\text{C}_{\text{shell det}}$ values coincided with $\delta^{18}\text{O}_{\text{shell}}$ values corresponding to spring. In case of *G. pilosa*, $\delta^{13}\text{C}_{\text{shell}}$ values varied among specimens and between years, but in general lowest $\delta^{13}\text{C}_{\text{shell det}}$ values occurred in the summer. Similar findings were reported for the thorny oyster, *S. gaederopus* from the Mediterranean Sea with lowest $\delta^{13}\text{C}_{\text{shell}}$ values attained in May/June, whereas phytoplankton blooms regularly occurred in January/February (Maier and Titschack, 2010). Highest stable carbon isotope values in young *Arctica islandica* occurred during summer, i.e., during maximum primary productivity (Schöne et al., 2005). Due to observed inter-specimen variations in $\delta^{13}\text{C}_{\text{shell}}$ values, future studies should analyze this parameter before it can be fully evaluated and applied for the reconstruction of environmental variability.

Changing relationships between $\delta^{13}\text{C}_{\text{shell}}$ and $\delta^{18}\text{O}_{\text{shell}}$ in coeval specimens from the same habitat have been noticed in previous studies and were interpreted as reflecting variable biological controls on the incorporation of carbon isotopes into the shell (Lorrain et al., 2004). In this study, such variations were observed for both studied bivalves, *P.*

jacobaeus and *G. pilosa*. A statistically significant positive correlation between these two variables was observed in three out of four studied *P. jacobaeus* shells, and in two out of three studied *G. pilosa* specimens. Overall, $\delta^{13}\text{C}_{\text{shell}}$ values for *G. pilosa* were significantly higher ($\bar{x} = +1.33\text{‰}$) than those for *P. jacobaeus* ($\bar{x} = -0.52\text{‰}$; Mann Whitney test $z = -14.62$, $p < 0.0001$). It is interesting to note that $\delta^{13}\text{C}_{\text{shell det}}$ values of *P. jacobaeus* in the present study (-1.64 to 0.40‰) are lower than those measured by Chauvaud et al. (2011) in the closely related species *P. maximus* (-0.94 to 1.89‰). Stable carbon isotope-ratio values of *G. pilosa* (0.80 to 1.97‰), however, were almost identical to those previously determined in *G. bimaculata* from the Pag bay, middle Adriatic Sea (0.81 to 2.03‰ , Bušelić et al., 2015). Lower $\delta^{13}\text{C}_{\text{shell}}$ values in *G. bimaculata* were recently obtained for shells collected from Pag bay and Cetina river estuary (-0.52 to 1.77‰ ; Purroy Albet, 2017), indicating differences possibly related to site and year. Future studies should analyze carbon isotope-ratio values from same species across different sampling sites characterized by different environmental conditions, as well as from different species collected at the same size in order to gain a better understanding of $\delta^{13}\text{C}_{\text{shell}}$ potential as an environmental proxy. Such studies should include detailed analysis of environmental variables.

4.3. Chemical sclerochronology and bivalve ecology

In order to fully understand these marine bivalve mollusk archives, future studies should address the ecology of the studied species including reproduction, feeding ecology and growth rate of soft tissues.

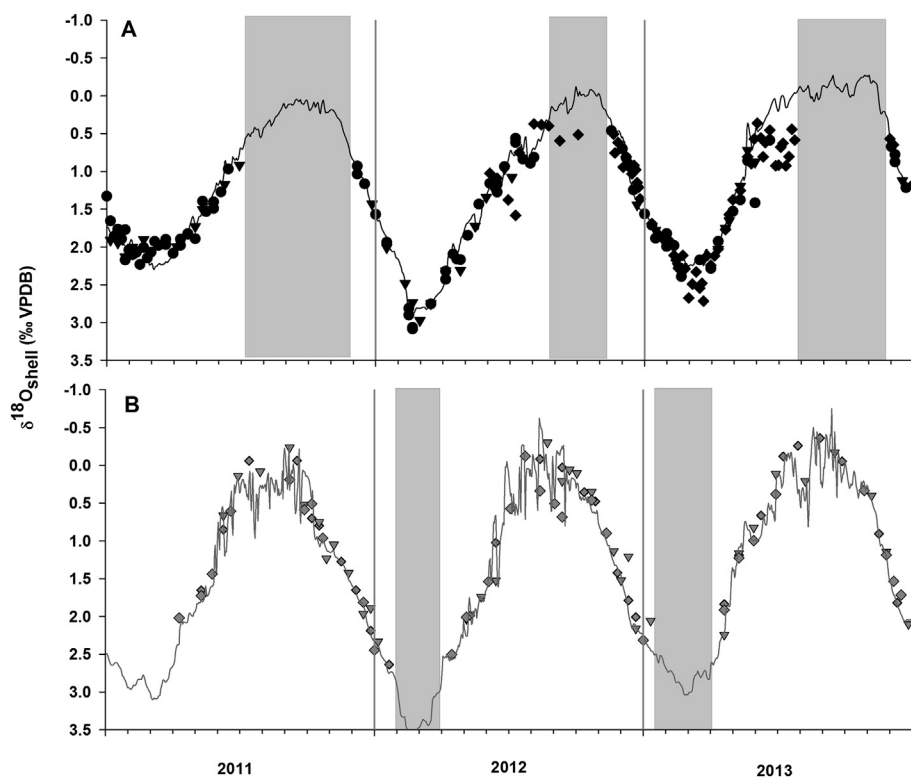


Fig. 9. Comparison between modeled $\delta^{18}\text{O}_{\text{shell}}$ values (line) and temporally aligned $\delta^{18}\text{O}_{\text{shell}}$ values (symbols). A. *Pecten jacobaeus*, B. *Glycymeris pilosa*. Different individuals shown in different symbols. Grey areas indicate periods of shell growth slowdown or cessation.

As yet, only reproduction data were published for a *P. jacobaeus* population from the Krka River estuary, middle Adriatic (Marguš et al., 1993). According to this study, the highest gonad index was attained in February followed by a strong decrease in April and May. Low gonad indices were observed during summer and minimum values in September. According to the recent work of Ezgeta-Balić (unpublished data), full gonads were developed in *P. jacobaeus* from the North Adriatic during January to April, and a decrease in gonad mass was observed in early May. In this study, shell growth was fastest between April and June indicating that *P. jacobaeus* redirected its energy resources to growth as soon as spawning was over. The main shell growth slowdown overlapped with the low gonad index, possibly indicating unfavorable environmental conditions. To date, there is no study on feeding ecology of this species. According to Chauvaud et al. (2011), seasonal and ontogenetic variations of $\delta^{13}\text{C}_{\text{shell}}$ in *P. maximus* shells can be considered as a possible tool for ecophysiological studies, and the same potential for *P. jacobaeus* shells should be explored in future field and laboratory studies.

The reproductive cycle of *Glycymeris pilosa* was recently analyzed by Purroy Albet (2017) on specimens collected from the Pašman channel, middle Adriatic Sea. From October to December most gonads were inactive. Gametogenesis started in December and early and late active stages extended into June when ~20% of the population had ripe gonads, while others had gonads that were in late stage of development. Spawning took place between July and October. There is no other study on the reproductive cycle of this species. Periods of inactive gonads found by Purroy Albet (2017) coincided with times of faster shell growth in the North Adriatic *G. pilosa* population. Furthermore, the winter shell growth slowdown coincided with the early and late development of gonads, indicating that during this period of the year *G. pilosa* was redirecting its energy resources to reproduction.

The only available data on *G. pilosa* feeding ecology are those for populations from Pag bay and Pašman channel, Middle Adriatic Sea (Purroy Albet, 2017). According to this study, significant differences in $\delta^{13}\text{C}_{\text{digestive gland}} (\text{‰})$, $\delta^{15}\text{N}_{\text{digestive gland}} (\text{‰})$ and the C:N molar ratio occurred between sites, with significantly higher values at Pašman.

Since these two sites are geographically positioned relatively closely (~50 km), isotopic variations clearly indicate that results cannot be used to interpret the feeding ecology of populations at other sites. Therefore, future studies should analyze variations in feeding ecology of *G. pilosa* along latitudinal, longitudinal and environmental gradients in order to identify possible relationships between food supply and growth.

5. Conclusions

Seasonal shell formation rates vary between bivalve species. Growth slowdown of the Mediterranean scallop *P. jacobaeus* from the North Adriatic Sea occurred during summer, whereas the bittersweet clam *G. pilosa* from the same area grew at slowest rates, or not at all, during winter. Both species formed distinct annual growth lines in September to November period, indicating that other factors, besides seawater temperature, are important drivers of shell growth. Possible drivers include low dissolved oxygen concentration and low pH conditions that co-occur in the North Adriatic during late summer/early fall (Cantoni et al., 2012; Djakovac et al., 2015). It is hypothesized here that climate change-induced variations of these parameters could negatively influence shell growth, especially in the case of *P. jacobaeus*.

In relation to further sclerochronological research, *G. pilosa* is an important target species for studies looking at variations in annual growth increments in the Adriatic and Mediterranean Seas (Peharda et al., 2016). Since *G. pilosa* forms annual growth lines in September, the annual shell growth increment covers certain periods of two calendar years. This needs to be taken into account when shell chronologies are constructed and annual shell increment width data are compared to environmental data. Furthermore, due to its longevity and continuous growth during the warmest part of the year, *G. pilosa* is an interesting archive for the reconstruction of seawater temperatures during summer.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.chemgeo.2017.09.029>.

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