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Metabolic effects on stable carbon isotopic composition of freshwater bivalve shell *Corbicula fluminea*

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Abstract The stable isotopic composition of the bivalve shell has been widely used to reconstruct the palaeo-climate and palaeo-environment. The climatic and environmental significance of carbon isotopic composition of the bivalve shell is still in dispute, and incorporation of metabolic carbon can obscure carbon isotope records of dissolved inorganic carbon. This study deals with freshwater bivalve, *Corbicula fluminea* aragonite shell. The results indicated that the $\delta^{13}C$ values of bivalve shells deposited out of equilibrium with the host water and showed an ontogenic decrease, indicating that there are metabolic effects and more metabolic carbon is incorporated into larger shells. The proportion of metabolic carbon of shells varies between 19.8% and 26.8%. However, $\delta^{13}C_S$ can still be used as qualitative indicators of $\delta^{13}C_{DIC}$ and environmental processes that occurred during shell growth.

Key words metabolic effect; carbon isotopic composition; bivalve; *Corbicula fluminea*

1 Introduction

The stable isotope geochemistry of biogenic $CaCO_3$ has served as a source of paleo-climatic and paleo-environmental information. The oxygen isotopic signatures of different bivalve shells ($\delta^{18}O_S$) have been used to reconstruct both sea surface temperature and salinity (Jones et al., 1989; Dettman et al., 2004). The stable carbon isotopic composition of bivalve shell ($\delta^{13}C_S$) varies in a more complex manner. Some earlier studies suggested that bivalves shell were deposited in isotopic equilibrium with the dissolved inorganic carbon (DIC) (Mook and Vogel, 1968; Fritz and Poplawski, 1974; Turner et al., 1983); if the $\delta^{13}C_S$ can be used as the proxy to investigate the $\delta^{13}C$ of DIC ($\delta^{13}C_{DIC}$) in ancient water, one can use bivalve shells to obtain the information about paleo-primary production, landuse change, bedrock geology, and paleo-atmospheric CO_2 level (Dettman et al., 1999; Mook, 2000; Gillkin et al., 2009). However, many recent studies have shown that bivalves were not deposited in isotopic equilibrium with DIC, suggesting that both kinetic and metabolic effects play an important role (Keith et al., 1964; Swart, 1983; Tanaka et al., 1986; Klein et al., 1996; McConnaughey et al., 1997; Dettman et al., 1999; Lorrain et al., 2004; Gillikin et al., 2006; Gillikin et al., 2007; Gillikin et al., 2009). Kinetic effects generally influence both $\delta^{18}O_S$ and $\delta^{13}C_S$ and result in a good correlation between them (McConnaughey, 1989). As bivalves generally are precipitated in oxygen isotope equilibrium with their surroundings (Epstein et al., 1953; Wefer and Berger, 1991; Chauvaud et al., 2005), kinetic effects should be minimal and disequilibrium should be mainly due to metabolic effects.

In fact, several authors have found that metabolic carbon can significantly contribute to both marine and freshwater bivalve shell carbonate (Keith et al., 1964; Tanaka et al., 1986; Klein et al., 1996; McConnaughey et al., 1997; Veinott and Cornett, 1998; Dettman et al., 1999; Aucour et al., 2003; Kaandorp et al., 2003; Lorrain et al., 2004; Gillikin et al., 2006; Gillikin et al., 2007; Gillikin et al., 2009; Lartaud et al., 2009). Tanaka et al. (1986) suggested that up to 85% of mollusk-shell carbonate is composed of metabolic carbon, but McConnaughey et al. (1997) found that the previous study overestimated the metabolic contribution partly because it erroneously included the enrichment factor between carbonate and aqueous CO_2. While in most bivalves the amount of metabolic carbon in the shells is typically less than 10%. More recently, Gillikin et al. (2007, 2009) have reported much higher values of 5%–37% for marine bivalve *Mercenaria mercenaria* and of 15%–35% for freshwater mussel

Pyganodon cataracta. Both cases are associated with strong ontogenic decreases in $\delta^{13}C_S$, which is true in many other studies (Krantz et al., 1987; Kennedy et al., 2001; Keller et al., 2002; Elliot et al., 2003; Lorrain et al., 2004). It is believed that it was caused by increased utilization of this metabolic carbon to satisfy carbon requirements for calcification. Furthermore, it is proposed that $\delta^{13}C_{DIC}$ could perhaps be reconstructed from bivalve shells if the metabolic contribution could be accounted for.

In this study, water DIC, shells, and soft tissues were sampled from *Corbicula fluminea* in Guizhou Province, China, to assess the contribution of metabolic carbon to the shell. *Corbicula fluminea* is native to China, Japan and Korea, but now is widespread in many parts of the world (Asia, Europe, North and South America) and it could therefore provide almost "worldwide" paleo-ecological archives (Aucour et al., 2003). Our aim is: (1) to determine whether *Corbicula fluminea* incorporates metabolic carbon and exhibits an ontogenic decrease in $\delta^{13}C_S$; (2) to assess the proportion of metabolic carbon incorporated into the shell.

2 Methods

On August 10, 2007, several living *Corbicula fluminea* samples were collected by hand from the Huaxi River, Guizhou Province, China (26°26′07.99″ N, 106°39′37.42″ E) (Fig. 1). *Corbicula fluminea* is one of the most common and widespread bivalves in the catchment of the Huaxi river. The elevation of the study area is about 1200 m above sea level, the annual precipitation varies from 900 to 1400 mm, and the annual air temperature rangs from 5 to 30℃. The primary type of karst landforms in the Late Paleozoic to Early Mesozoic limestones are common in the Huaxi River confluence basin (Yan Hui et al., 2009).

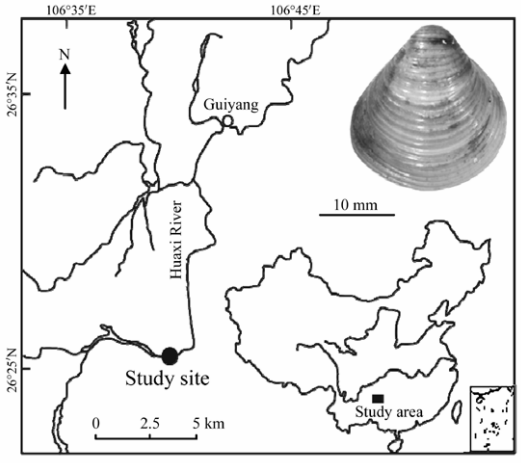

Fig. 1. Location of the study site and the image of *Corbicula fluminea*.

Eighteen shells were selected and shell height was measured by a caliper (shell sizes range from 4.00 to 22.00 mm). The shells were cleaned, their periostracum was removed with a 50℃ hydrogen peroxide solution, followed by demineralized water rinsing and air-drying. Carbonate samples were removed from the shell surface using a scalpel blade and were ground with an agate mortar and pestle; only the most recently formed shell carbonate was sampled. The $\delta^{13}C$ of metabolic carbon can be assumed to approximately match that of soft tissue ($\delta^{13}C_{tissue}$) (McConnaughey et al., 1997), and muscle tissues in bivalves typically have the slowest turnover time (Raikow and Hamilton, 2001; Lorrain et al., 2002), so we used muscle tissue $\delta^{13}C$ as a proxy for $\delta^{13}C$ of the metabolic carbon. Six individual muscle tissue samples were collected, and in order to assess the difference of $\delta^{13}C_{tissue}$ between the individuals, six mixed muscle tissue samples (tissues from several similarly sized individuals) were also collected (Table 1). Each of the tissue samples was prepared for isotopic analysis by drying at 60℃ and grinding with an agate mortar and pestle. One filtered water sample (0.45-μm mesh, $HgCl_2$ added) was collected near the bottom of the water column for isotopic analysis ($\delta^{13}C_{DIC}$) at the same time.

The stable isotopic analysis of shell aragonite, soft tissue and water samples was performed at the State Key Laboratory of Environmental Geochemistry, Institute of Geochemistry, Chinese Academy of Sciences. The $\delta^{13}C_S$ measurement was performed on a Continuous Flow Isotope Ratio Mass Spectrometer. Samples were let to react with 100% orthophosphoric acid at 70℃. The results are reported relative to VPDB by calibration to the reference standards GBW04405 ($\delta^{13}C$=0.57‰), GBW04406 ($\delta^{13}C$ = -10.85‰) and GBW04416 ($\delta^{13}C$=1.613‰). The $\delta^{13}C_{DIC}$ values were measured on a Finnigan MAT-252 Mass Spectrometer after the DIC extraction procedure. Water samples were introduced into the vacutainer tubes, which were pre-loaded with 100% phosphoric acid and magnetic stir bars, using a syringe and the evolved CO_2 was extracted (Atekwana and Krishnamurthy, 1998), at 1σ precision of ~0.1‰ for $\delta^{13}C_S$ and $\delta^{13}C_{DIC}$. The $\delta^{13}C_{tissue}$ values were measured on a Continuous Flow Isotope Ratio Mass Spectrometer. Samples were wrapped in tin cups and were then combusted using an Elemental Analyzer coupled to the IRMS. Standardization was based on IAEA-C3 cellulose ($\delta^{13}C$= -24.91‰) and precision was better than ± 0.05‰.

3 Results

$\delta^{13}C_{tissue}$ values are presented in Table 1. There is no significant difference in $\delta^{13}C_{tissue}$ value between

individual samples and mixed samples.

Table 1 $\delta^{13}C_{tissue}$ of *Corbicula fluminea* (‰, PDB)

Individual		Mixed	
Shell height (mm)	$\delta^{13}C_{tissue}$	Shell range (mm)	$\delta^{13}C_{tissue}$
4.2	-28.49	4.0–5.9	-28.31
6.8	-28.67	6.0–7.9	-28.60
13.0	-28.96	12.0–13.9	-28.89
15.5	-29.00	15.0–16.9	-28.93
18.0	-29.02	17.0–19.9	-28.95
21.0	-28.42	20.0–22.9	-28.33

The measured $\delta^{13}C_S$ values of specimens range from -9.60‰ to -11.27‰, showing a significant negative correlation with shell height (R^2=0.75, Fig. 2). The $\delta^{13}C_S$ values are about 7.04‰ to 8.71‰ more negative than the expected ones based on the equilibrium fractionation (Romanek et al., 1992) and the $\delta^{13}C_{DIC}$ value of the water sample ($\delta^{13}C_{DIC}$= -5.26‰).

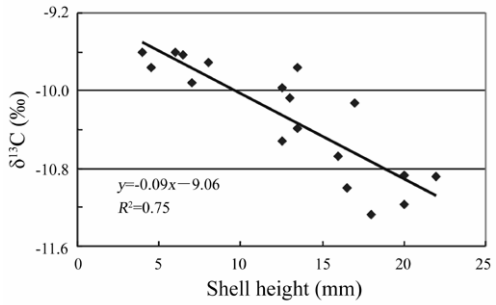

Fig. 2. Carbon isotope plot of *Corbicula fluminea* shell against shell height.

4 Discussion

4.1 $\delta^{13}C$ of soft tissue

It is generally accepted that the $\delta^{13}C_{tissue}$ reflects the $\delta^{13}C$ of diet, so it can be assumed to approximately match the $\delta^{13}C$ value of metabolic carbon (McConnaughey et al., 1997). A change in $\delta^{13}C_{tissue}$ can be caused by food sources with different $\delta^{13}C$ signatures. In this study, $\delta^{13}C_{tissue}$ shows no significant difference between individuals, which are different in size. It is probably illuminated that there was no food change at the time of animal growth. Furthermore, $\delta^{13}C_{tissue}$ values between individual samples and mixed samples are also of no significance. The data showed that there was no difference in $\delta^{13}C_{tissue}$ value between individuals that have the same or similar shell height, so we can use the mixed samples' data to represent the $\delta^{13}C_{tissue}$ values of the samples which fall within the height range.

4.2 $\delta^{13}C$ of shells

Our data clearly show a trend of more negative $\delta^{13}C_S$ through ontogeny in *Corbicula fluminea* shells (Fig. 2). There are several causes for the decrease of $\delta^{13}C_S$. Similarities in $\delta^{13}C_{tissue}$ value between individuals suggest that the diet of *Corbicula fluminea* is similar across different ages, so a change in food as the animal ages is not likely to be the cause of such a $\delta^{13}C$ trend in the shells. Considering that these shells were all collected at the same time and at the same site, thus, changes in environmental conditions and microsite conditions are very unlikely and can be ruled out (Gillikin et al., 2009). The $\delta^{13}C_{DIC}$ values of pore water are expected to be more negative than those of overlying waters and have a strong gradient within the initial 5 cm of sediment due to the remineralization of organic matter (up to -1‰·cm^{-1}; McCorkle et al., 1985). If the clams live at deeper water level in the sediment as they age and utilize a more negative environmental $\delta^{13}C_{DIC}$ source, it also can cause a decrease in $\delta^{13}C_S$ through ontogeny, just as suggested by Keller et al. (2002) and Elliot et al. (2003). However, the case is not always true that older individuals burrow in deeper water in the sediments than the younger ones (Roberts et al., 1989; Gillikin et al., 2009), and it is found that the burial depth of *Corbicula fluminea* in the sediment was independent of clam size (as shown by laboratory cultivated experiments), so it is considered that burial depth is an unlike factor. Kinetic fractionation effects can most definitely be ruled out as bivalves generally are precipitateed in oxygen isotope equilibrium with their surroundings (McConnaughey and Gillikin, 2008).

Therefore, this disequilibrium and trend of more negative $\delta^{13}C_S$ through ontogeny should be mainly due to metabolic effects. Klein et al. (1996) reported that a high metabolic rate resulted in an increase intercellular ratio, and intracellular transport to the extrapallial fluid (EPF) with metabolic carbon that was depleted in ^{13}C, so the higher metabolic rate would lead to a decrease in $\delta^{13}C_S$. Lorrain et al. (2004) showed that the ratio of respired to precipitated carbon, which represents the amount of metabolic carbon (depleted ^{13}C) available relative to the carbon requirements for calcification, tended to increase through ontogeny. This suggests that the decrease of $\delta^{13}C_S$ through ontogeny is actually caused by increased utilization of this metabolic carbon to satisfy carbon requirements for calcification. It is considered that this is also the most rational explanation for an ontogenic decrease in $\delta^{13}C_S$ observed in these *Corbicula fluminea* shells.

4.3 How much metabolic carbon is present in the shells?

The best standing model to calculate the amount of metabolic carbon in the shells is given by McCon-

naughey et al. (1997):

$$M*(\delta^{13}C_R) + (1–M)*\delta^{13}C_{DIC} = \delta^{13}C_S – \varepsilon_{ar\text{-}b} \quad (1)$$

where M is the percentage of metabolic carbon contribution, $\varepsilon_{ar\text{-}b}$ is the enrichment factor between aragonite and bicarbonate (2.7‰ in Romanek et al., 1992), and $\delta^{13}C_R$ is the $\delta^{13}C$ of respiring CO_2 (metabolic carbon) and approximated from $\delta^{13}C_{tissue}$. We used $\delta^{13}C_{tissue}$ of the mixed samples to represent every individual $\delta^{13}C_{tissue}$ value according to the shell height. The $\delta^{13}C_{DIC}$ value of the water sample is -5.26‰, although this $\delta^{13}C_{DIC}$ value can not represent $\delta^{13}C_{DIC}$ information while the shell sample was growing, a rough estimate of the percentage of metabolic carbon in these shells can be calculated (1‰ change in $\delta^{13}C_{DIC}$ will lead to a change in M by 5%, Gillikin et al., 2009).

Using equation (1), we calculated M to be between 19.8% and 26.8% with a strong relationship between shell height (H in mm) and M (Fig. 3; M=0.39×H+17.36; R^2=0.74).

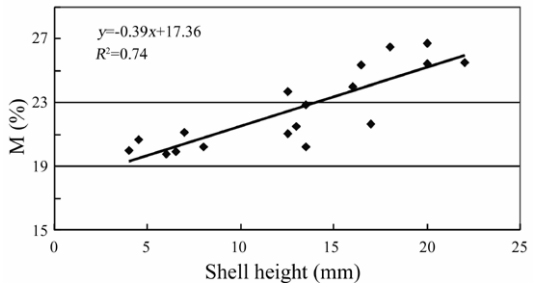

Fig. 3. Estimated percent metabolic carbon (M) for the *Corbicula fluminea* shells [Using the equation of McConnaughey et al. (1997), showing a strong relationship between shell height and M. (M=0.39×H+17.36; R^2=0.74)].

These values are higher than the typical 10% recorded for most aquatic mollusks (McConnaughey and Gillikin, 2008), even when possible errors are taken into consideration (from $\delta^{13}C_{DIC}$ and $\delta^{13}C_{tissue}$ values), but are within the values reported for one marine species (*Mercenaria mercenaria*; 5% to 37%, Gillikin et al., 2007) and one freshwater species (*Pyganodon cataracta*; 21% to 34%, Gillikin et al., 2009).

Gillikin et al. (2007) found that different populations of *Mercenaria mercenaria*, with apparently different metabolic C incorporation, the slopes between M and shell height are similar, with a change in M of +0.19% per mm of shell height. Moreover, despite the significant difference between water chemicals in which animals lived, the slopes between M and shell height are not statistically different between the marine *M. mercenaria* shells and the freshwater *P. cataracta* shells (Fig. 4, Gillikin et al., 2009). This similarity in the slopes suggests that similar mechanisms may be responsible for the ontogenic effect. However, the slope for *Corbicula fluminea* is much different from them, *Corbicula fluminea* is smaller (usually the biggest shell height is about 30 mm) than the species previously studied (Fig. 4), so we argue that the age effect is different among species.

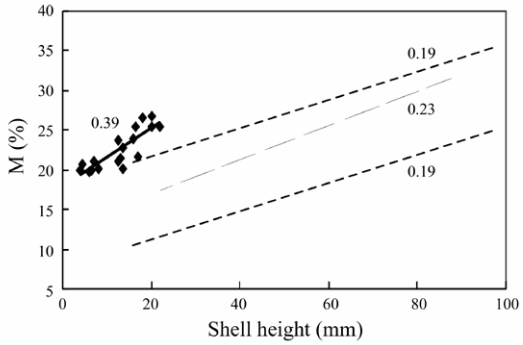

Fig. 4. The slopes between M and shell height for different bivalves. The numbers indicate the slopes; the black symbols and thick line represent freshwater bivalve *Corbicula fluminea* in this study; the thin line indicates freshwater bivalve *P. cataracta* (Gillikin et al., 2009); the dashed lines indicate marine bivalve *M. mercenaria* (Gillikin et al., 2007).

Despite many complexities, $\delta^{13}C_S$ also can reflect environmental conditions. Lorrain et al. (2004) suggested that $\delta^{13}C_S$ may provide information about metabolic rates for different populations of mollusks. Gillikin et al. (2006) found that $\delta^{13}C_S$ showed a shift to a lower value when a mussel was transplanted from a marine into an estuarine environment, which reflects freshwater is input to the ocean and provides a proxy for salinity. Goewert et al. (2007) found that shells had clearly different $\delta^{13}C_S$ values between a corn (C4) -dominated and soybean (C3)-dominated watershed despite metabolic effect is still present and result in an ontogenic decrease in $\delta^{13}C_S$. So this vital effect does not exclude the use of $\delta^{13}C$ aragonite records from freshwater shells as environmental proxies even if it can not provide absolute values of $\delta^{13}C_{DIC}$.

5 Conclusions

This study demonstrates that $\delta^{13}C_S$ values are negative, there is a large amount of metabolic carbon (as much as 19.8%–26.8%) present in freshwater bivalve shell *Corbicula fluminea*, and the percentage of metabolic carbon contribution increases through ontogeny. This ontogenic effect, however, does not exclude $\delta^{13}C_S$ in freshwater mussel shells as useful environmental proxies.

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