Differences in stable isotope compositions of freshwater snails from surface sediments of two Polish shallow lakes

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ABSTRACT

The study reports and discusses the differences in δ^{13}C and δ^{18}O values of shells between several species of freshwater snails. Shells were derived from sediment samples collected from depths of 0.5, 1, 2 and 3 m along transects in two shallow eutrophic lakes located in mid-western Poland. Mean δ^{13}C values of the shells ranged between −7.5 and −3.8‰ in Lake Jarosławieckie and between −8.1 and −5.2‰ in Lake Rosnowskie Duże, whereas mean δ^{18}O values ranged between −2.2 and −0.2‰ and between −2.2 and 0.4‰ respectively in the studied lakes. A similar order of species in terms of shell isotope values, from least to most ^{13}C and ^{18}O-depleted was observed in both lakes and seems to indicate constancy of the factors controlling the stable isotope compositions of snail shells. We postulate that the nearly 4‰ difference in the mean carbon stable isotope values between the species was primarily controlled by the amount of metabolic carbon incorporated into the shells and the δ^{13}C values of the snail food. Different growth cessation temperatures and microhabitats of the species studied result in temporally and spatially varied DIC δ^{13}C values, water δ^{18}O values and water temperature of shell precipitation, and may thus differentiate the δ^{13}C and δ^{18}O values of shells. The range of δ^{13}C and δ^{18}O values of individual shells from a sediment sample (mean 2.35 and 2.15‰, respectively) is interpreted as reflecting an intraspecific variability of isotope compositions in shells from a population and changes of the ambient conditions during the accumulation of the sediment layer. The species-specificity and intraspecific variability in C and O isotopic compositions of shells allow concluding that in palaeolimnological studies, stable isotope analyses should be performed on a set of mono-specific shells representing mean isotope compositions of the species for the interval studied rather than single shells or multispecific bulk shell material.

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1. Introduction

Littoral zones of lakes are areas of intensive biological activity, a site of growth of a variety of aquatic plants and macroalgae and a habitat for molluscs, insects, fishes and many other organisms. Species compositions of this diverse community reflect environmental conditions within the lake littoral zone, including water temperature, chemical composition, pH, trophy and water energy as related to wave action. In the studies of ancient lakes, we can trace back past environments of the littoral zone and use the proxies preserved in the sediments to draw conclusions about changes in climate and environment. Mollusc shells are among the fossils most frequently found in sediments deposited within the littoral zone of lakes and are usually well preserved and abundant. Qualitative and quantitative changes of mollusc assemblages over the length of the sediment sequence reflect changes in habitat during sediment accumulation (Böttger et al., 1998; Kossler, 2010; Alexandrowicz, 2013). Conclusions regarding the climate change are based on thermal limitation of species distribution. Inferences regarding water pH, water trophy and its energy are based on the species tolerance and limits to these environmental variables. Due to the broad environmental tolerance of most aquatic molluscs, palaeoenvironmental interpretation based on changes in species composition and abundance of shells alone provides only limited information and leads to general conclusions. However, the application of molluscs in palaeolacustrine studies is not restricted to reconstructions of the past habitat based solely on the ecological requirements of the species.

Mollusc shells are composed of calcium carbonate, either aragonite or calcite, and thus it is possible to determine their ratios of carbon and oxygen stable isotopes. δ^{13}C and δ^{18}O values of carbonates precipitated in freshwaters have been extensively and successfully used in palaeolacustrine studies. δ^{13}C and δ^{18}O values were measured in authigenic carbonates (Zhao et al., 2010;

Mirosław-Grabowska and Zawisza, 2014), ostracod valves (von Grafenstein et al., 2000; Hodell et al., 2005; Anadón et al., 2006), macrophyte encrustations (Anadón et al., 2000; Becker et al., 2002; Hammarlund et al., 2003) and mollusc shells (Anadón et al., 2008; Apolinarska and Hammarlund, 2009; Escobar et al., 2010; Herzschuh et al., 2010). The application of $\delta^{13}C$ and $\delta^{18}O$ values of carbonates in palaeolimnological studies and the consequent reconstruction of past climatic and environmental conditions requires an understanding of the factors influencing carbon and oxygen stable isotope composition of the carbonates. Broad and detailed discussions of the factors controlling $\delta^{13}C$ and $\delta^{18}O$ values of mollusc shells were provided by numerous authors, including Leng and Marshall (2004), Lorrain et al. (2004), Shanahan et al. (2005), Goewert et al. (2007) and McConnaughey and Gillikin (2008). Below we briefly summarize the most important of these factors.

The primary factor controlling the $\delta^{13}C$ values of mollusc shells is the $\delta^{13}C$ value of the carbon incorporated into the shell. There are two possible sources of carbon to the shells of aquatic invertebrates: ambient DIC (dissolved inorganic carbon) and metabolic carbon derived from the animal food. DIC as the primary source of carbon to the shells of aquatic molluscs has already been suggested in the first experimental studies of the relationship between DIC $\delta^{13}C$ values and the $\delta^{13}C$ values of freshwater gastropod shells (Fritz and Poplawski, 1974). The results of these studies were confirmed by McConnaughey et al. (1997) who modelled the effect of gas exchange physiology on the skeletal incorporation of respired CO_2, and suggested that, for aquatic invertebrates, approximately 90% of carbon built into the shell originates from ambient DIC. Metabolic carbon incorporated into the shells was estimated to be less than 10%, however the exact amount can differ between the species (McConnaughey et al., 1997). The proportion between inorganic and organic carbon incorporation into the shell is important because the $\delta^{13}C$ values of the two carbon sources differ by approximately 20‰ (Leng et al., 2005). It was proposed that in aquatic invertebrates, the incorporation of respired CO_2 reduces shell $\delta^{13}C$ values by <2‰ with respect to equilibrium values (McConnaughey et al., 1997). Freshwater molluscs feed on a variety of sources, including algae, macrophytes, zooplankton, decaying plants and detritus. Because the $\delta^{13}C$ values of each of those sources can be different, the species-specific food preferences will result in different $\delta^{13}C$ values of shells. $\delta^{13}C$ values of the aquatic macrophytes were shown to vary between −50 and −11‰, and the $\delta^{13}C$ values in lacustrine phytoplankton can range between −47 and −12‰ (Leng et al., 2005 and references therein). Such wide ranges are for a compilation of data from different lakes. The $\delta^{13}C$ values of primary producers from one lake can differ by several per mil (Leng and Marshall, 2004). Remains of land plants delivered to the lake, e.g., leaves fallen from trees, are usually within the range of $\delta^{13}C$ values of the phytoplankton and macrophytes, i.e., their $\delta^{13}C$ values are not distinguished from the $\delta^{13}C$ values of aquatic primary producers. Changes in $\delta^{13}C$ values are observed along the food chain. Because each subsequent trophic level is <1‰ ^{13}C-enriched relative to the previous level (DeNiro and Epstein, 1978; Vander Zanden, 2001), the $\delta^{13}C$ values of herbivores can be distinguished from carnivores (Schweizer et al., 2006).

Different $\delta^{13}C$ values were noted in the shells of gill breathing (prosobranch) and lung breathing (pulmonate) snails (McConnaughey et al., 1997, Aucour et al., 2003; Shanahan et al., 2005). Disequilibria from local DIC in prosobranch snails averaged 1.3‰, whereas shells of pulmonate aquatic snails were on average 5.8‰ ^{13}C depleted compared with equilibrium with local DIC (McConnaughey et al., 1997). Decreased $\delta^{13}C$ values in the shells of pulmonate snails are explained by their ability to breath atmospheric air. It was shown that more respired carbon is incorporated into the shells of air-breathing invertebrates compared with

the aquatic animals because of the lower CO_2/O_2 ratio in the air compared with the CO_2/O_2 ratio in water (McConnaughey et al., 1997).

The $\delta^{18}O$ values of mollusc shells are controlled by water $\delta^{18}O$ value and water temperature. The relationships between water temperature, water $\delta^{18}O$ values and $CaCO_3$ $\delta^{18}O$ values are different for calcite (Craig, 1965; Kim and O'Neil, 1997) and aragonite (Grossman and Ku, 1986 modified by Dettman et al., 1999). Thus, in palaeotemperature calculations, mineral compositions of mollusc shells must be determined. According to the equations of Craig (1965), Kim and O'Neil (1997) and Grossman and Ku (1986) modified by Dettman et al. (1999) $\delta^{18}O$ values of calcite and aragonite precipitated in equilibrium with water decrease by 0.2–0.24‰/°C, for temperature range between 3 and 28 °C. The experimental study of Tarutani et al. (1969) showed that the $\delta^{18}O$ values of aragonite precipitated in equilibrium with water was higher by 0.6‰ than the $\delta^{18}O$ values of co-precipitated calcite. Shell mineralogy is also important when discussing the $\delta^{13}C$ values of mollusc shells. A comparison of the $\delta^{13}C$ values of shells with the $\delta^{13}C$ values of DIC must consider the different aragonite-$HCO_3{}^-$ and calcite-$HCO_3{}^-$ enrichment factors. In isotopic equilibrium with DIC, aragonite and calcite are 2.7‰ and 1.0‰ enriched, respectively (Romanek et al., 1992).

Additional processes of possible influence on the stable isotope compositions of shells are kinetic isotope effects occurring during fast $CaCO_3$ precipitation (Goewert et al., 2007). Kinetic isotope effects result in simultaneous ^{18}O and ^{13}C depletion of precipitates associated with fractionation during CO_2 hydration and hydroxylation (McConnaughey, 1989). The faster the precipitation, the more depleted the shells are. However, according to McConnaughey et al. (1997) kinetic effects in mollusc shells are expected to be small.

Following the above information, the $\delta^{13}C$ values of shells of aquatic snails are controlled primarily by the $\delta^{13}C$ value of DIC, and the $\delta^{18}O$ values of shells depends on the $\delta^{18}O$ values of water and water temperature. Because those parameters can be highly variable within a lake, the $\delta^{13}C$ and $\delta^{18}O$ values of the shells are strongly dependant on the snail habitat.

^{13}C-enriched compositions of DIC were measured among macrophyte stands, where intensive photosynthesis leads to ^{13}C-enrichment in DIC, as observed by Pełechaty et al. (2010) in a shallow macrophyte-dominated lake. In contrast, ^{13}C-depleted DIC is found near lake bottoms where the decomposition of organic matter releases increased proportion of ^{12}C relative to ^{13}C (McKenzie, 1985). Oxygen shortage near the lake bottom and in the topmost sediments leads to methanogenesis, the process of anoxic degradation of the organic matter. The formation of ^{13}C-depleted CH_4 is accompanied by generation of ^{13}C-enriched CO_2 (von Grafenstein et al., 1999). Hence, the interpretation of the $\delta^{13}C$ values in shells of benthic molluscs is usually complicated by the $\delta^{13}C$ value of local DIC.

Differences in water $\delta^{18}O$ values in a lake result mainly from the evaporative loss of $H_2{}^{16}O$ from surface waters. As a consequence, molluscs inhabiting shallow littoral zones are ^{18}O-enriched compared with the species from deeper habitats (Jones et al., 2002), i.e., the lake bottom below the thermocline zone where water mixing is absent during the summer stagnation. The evaporative enrichment of ^{18}O in shallow waters is opposed by the already described above, effect of temperature on the $\delta^{18}O$ values of carbonates. Locally, specific water $\delta^{18}O$ values and water temperature in a lake can occur next to river or stream inflows. Inflowing waters usually have lower $\delta^{18}O$ values and lower temperatures, both of which will influence the shell $\delta^{18}O$ values.

Both the $\delta^{13}C$ and $\delta^{18}O$ values of freshwater mollusc shells are influenced by the species life cycle, including its life span and the time during a year when shell is precipitated. In most freshwater snails, the life cycle is restricted to one year or slightly longer