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The role of biogeography and ecology on the isotope signature of cuttlefishes (Cephalopoda, Sepiidae) and the impact on belemnite studies

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ABSTRACT

Calcitic belemnite guards are often used for temperature reconstructions of ancient seawater by using oxygen isotope thermometry. These geochemical studies discuss diagenesis and vital effects but neglect ecological or biogeographic effects on the isotope signature. To estimate the impact of seasonal temperature variations, short-term salinity changes and biogeography on the isotope signals we compare the $\delta^{18}O$ and $\delta^{13}C$ signals of ten cuttlebones with local water temperatures. The cuttlebones (aragonitic internal shells) come from five different species of recent cuttlefish (Sepiidae, *Sepia* sp.) from seven different regions (North Sea, Baltic Sea, Mediterranean, Red Sea, Angola, North Australia and Tasmania). All analysed specimens reflect the temperature-characteristics of their habitat perfectly. The $\delta^{18}O$ signal and calculated temperatures follow annual temperature changes of up to 15 °C. The $\delta^{13}C$ values show no clear pattern and are thought to be controlled by vital effects. Freshwater influence is recognizable in the negative $\delta^{18}O$ and $\delta^{13}C$ values of the Baltic Sea specimen, although sudden short-term salinity changes are not reflected by the signatures.

1. Introduction

One of the major problems in interpreting the stable isotope composition of fossil belemnite guards is the almost complete lack of understanding of belemnite ontogeny and ecology. According to previous palaeobiologic studies belemnites show allometric growth with a length-dominated early ontogenetic growth stage (Schulz, 1979; Mutterlose, 1983) but not much else is known about the ontogeny. The resemblance between belemnite reconstructions (i.e. Naef, 1922; Stevens, 1965; Monks, et al., 1996) and present-day pelagic "teuthids" leads to the assumption that belemnites were fast surface swimmers. This comparison is, however, based on superficial analogies rather than on actual data. It is arguable that belemnite genera with differently shaped guards had different modes of life (nektonic versus nektobenthic). Specimens with short, thick guards (e.g. *Acroteuthis*) would perhaps suggest a more nektobenthic mode of life, while slender and elongated forms (e.g. *Hibolithes*) may have been fast swimmers and taxa with extremely laterally flattened guards (e.g. *Duvalia*) may have had a benthic mode of life. These interpretations, which are based on the morphology alone, are nevertheless highly speculative.

Arm hooks found with preserved soft bodies (Reitner and Urlichs, 1983; Riegraf and Hauff, 1983) indicate that belemnites lived as active predators of large prey with soft bodies such as fish. This type of predation is today often associated with an active, swimming mode of life. The occurrence of a buoyancy mechanism in the form of a gas-filled phragmocone supports the inference that belemnites were active swimmers. Modern "teuthids", who have a reduced keratinous gladius, possess an enlarged and muscular mantle cavity making them fast and permanent swimmers. Several authors (Anderson et al., 1994; Mitchell, 2005; Wierzbowski and Joachimski, 2007) propose a bottom-dwelling mode of life for belemnites on the basis of oxygen isotope thermometry. They interpreted the oxygen thermometry results as bottom water signals. This mode of life would be similar to that of modern sepiids which show a nektobenthic mode of life. This is, however, contradicted by the occurrence of various belemnite genera recorded from black shales that lack any benthic or nektobenthic organisms due to anoxic bottom waters. The early Jurassic Posidonienschiefer of Holzmaden, for example, yields well preserved belemnite guards including the genera *Acrocoelites*, *Parapassaloteuthis* and *Passaloteuthis* (Hauff and Hauff, 1981; Seilacher et al., 1985; Oschmann et al., 1999). Allochthonous deposition is unlikely because of the fine and undisturbed lamination of these shales. TOC-rich sediments of Barremian age (Blätterton of northwest Germany) lack any benthic organisms but contain a rich nektonic fauna including fishes, reptiles, teuthids and belemnite guards (*Aulacoteuthis* [Mutterlose, 1983]). These findings clearly support the view that belemnites in general, or at least certain belemnite genera, had a nektonic mode of life. On the other hand, Martill et al. (1994) interpret the late appearance of Jurassic belemnites in transgressive sequences as evidence for a deeper habitat.

The calcitic belemnite guards are considered as a reliable source of Jurassic and Cretaceous isotope data by geochemists and geologists.

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These datasets are widely used for the reconstruction of palaeoclimate and temperature conditions (e.g. van de Schootbrugge et al., 2000; Price and Mutterlose, 2004; Rosales et al., 2004; van de Schootbrugge et al., 2005; Zakharov et al., 2006; McArthur et al., 2007b; Mutterlose et al., 2009) as well as ice-volume estimations (e.g. McArthur et al., 2007a) and reconstructions of entire palaeoenvironments (Wierzbowski and Joachimski, 2007).

The lack of knowledge of belemnite biology, however, makes the interpretation of these isotope data difficult. In modern species isotope datasets can provide useful insights when the ecological background is known (e.g. Rexfort and Mutterlose, 2006; Lukeneder et al., 2008).

Sessile organisms, which are limited to certain restricted habitats and use a well known mode of shell precipitation such as corals (e.g. Kuhnert et al., 2000) or rudists (e.g. Steuber, 1999; Steuber et al., 2005) serve as good environmental archives. Deducing environmental factors, however, from non-sessile organisms whose ecology is unknown includes the danger of circular reasoning. It is unclear whether the isotope data derived from belemnites reflect a surface or deeper water signal nor do we know whether the mode of life of belemnites changed during ontogeny. Provincialism in Jurassic and Cretaceous belemnites is well known (Stevens, 1963; Mutterlose et al., 1983) but it is unclear whether the populations remained in one relatively restricted area or whether they migrated seasonally. All these biological factors, which do control the isotope signature substantially have a profound impact upon palaeoclimatic interpretations.

To avoid circular reasoning we have used recent coleoids, with a well known ecology and life habits, for isotope studies in order to obtain an insight into the role of ecology in biological precipitation in coleoids. The Sepioidea are the only remaining group of coleoids that possess an aragonitic shell (cuttlebone in *Sepia* sp. and the ram's horn in *Spirula spirula*) and *Sepia* sp. is a biologically and ecologically well known genus. Recent studies show the absence of oxygen biofractionation in *Sepia officinalis* (Rexfort and Mutterlose, 2006) but reveal a strong seasonal influence. We try to expand this knowledge by analysing different species of *Sepia* from different biogeographic settings for their stable isotope signals (δ^{18}O, δ^{13}C). This may in turn shed light on stable isotope signatures of belemnites and their potential way of life.

2. Geochemical background

The concept of isotope studies on calcareous shells of marine invertebrates goes back to the empirical studies of Urey (1947) and Epstein et al. (1951, 1953) who showed the temperature dependence of the oxygen isotope composition of biogenic calcium carbonate. In the carbonate shells of marine invertebrates these isotope imprints are supposed to show a direct quantitative relationship to ecological factors with respect to the isotope signal of the ambient seawater. The two most often used parameters are the ^{18}O/^{16}O oxygen isotope ratio (δ^{18}O), and the ^{13}C/^{12}C carbon isotope ratio (δ^{13}C). The unbiased usage of δ^{18}O as a proxy for water temperature is limited by two factors. I) The pH of seawater can influence the isotope signal, although this has not been examined for mollusc shells. II) Oxygen also fractionates heavily during evaporation and freezing (e.g. Craig and Gordon, 1965). Changes in salinity due to freshwater input or evaporation therefore have a strong influence on the oxygen isotope composition. The carbon isotope ratios of carbonate shells may record the carbon isotope composition of dissolved inorganic carbon and the metabolic activity of the organism (e.g. Scholle and Arthur, 1980). Overall, δ^{13}C varies significantly throughout the ecosphere due to fractionation by enrichment of ^{12}C during fixation by photosynthesis, varying air–sea exchange and water circulation (e.g. Hudson, 1977).

Both δ^{18}O and δ^{13}C enable the reconstruction fossil environments to a very precise degree in regard to the size and growth of the organism. Additional factors which have to be considered include an alteration of the isotope signature. This may have occurred during the life of the organism, reflecting a biological and/or environmental control, or subsequently during fossilization and diagenesis. These factors may render the isotope datasets useless by producing severe shifts in the isotope equilibrium from the original seawater composition. During the lifetime of the animal biofractionation occurs when metabolic functions favour one isotope over the other due to kinetic effects or biochemistry (McConnaughey and Whelan, 1997; McConnaughey, 1989a,b). This implies that the shell calcite is not precipitated in equilibrium with the surrounding seawater. Oxygen fractionation is normally not influenced by biofractionation, while δ^{13}C is often prone to biofractionation, especially in fast-growing organisms, an effect discovered e.g. in *Sepia officinalis* (Rexfort and Mutterlose, 2006). A second obstacle in fossil material is the potential diagenetic overprint. The original seawater signature is overprinted during fossilization by a secondary signature due to solution, recrystallisation rendering the samples useless.

3. Biological background

As summarized well by Strugnell et al. (2009), the systematic classification of the Cephalopoda and especially the subclass Coleoidea is problematic and has been under discussion for a long time (Mangold and Young, 1998; Sweeney and Roper, 1998) because of contradictory morphological and molecular evidence (e.g. Roper et al., 1969; Strugnell et al., 2006; Lindgren and Daly, 2007). Of the modern coleoid cephalopods, however, only some species of the Sepioidea (containing the Sepiidae and the Spirulidae) have not reduced their shell. In the Sepiidae the biology and ecology of the species are mostly well studied and understood. All sepiids are primarily nektobenthic species which inhabit near-shore and continental shelf zones in warm and temperate waters. They can be found in shallow waters (0–20 m) at the coastline down to about 200 m depths, being most abundant in the upper 100 m. Although excellent swimmers, they generally are bottom dwellers. Habitats range from rocky, sandy and muddy bottoms to seaweed beds and coral reefs. The distribution patterns depend for some species on ontogenetic migration and an annual vertical migration. In warmer waters (>10 °C during winter) mating can occur all year round, usually with a maximum in spring, when the first, large specimens ascend from deeper waters, followed by a second wave of smaller individuals a few months later. In colder waters, such as the German North Sea and the Baltic Sea, water temperatures determine the start of the mating season. Mating starts when the water temperature increases above 12 to 13 °C. Mating occurs in shallow areas, where the eggs are attached to hard substrates in 1–10 m water depths. Most females lay eggs approximately one year after hatching and die shortly afterwards; males can live for a further year and take part in a second mating season (von Boletzky, 1983). Young sepiids hatch in shallow waters, where they stay for a period of two to three months, after which they wander down the shelf slope to deeper waters. Throughout the year the body size increases steadily. They return to shallow waters in the next mating season, resulting in a one-year migration cycle. This seasonal life cycle has been observed in nearly all populations even tropical assemblages with little annual climate variation (Roper et al., 1984).

The cuttlebone of the sepiids (Fig. 1) represents the phragmocone of the belemnite shell and is likewise made of aragonite. The guard, which is calcitic in belemnites, has lost its function as a counterweight in sepiids and has been reduced to a small, solely organic appendix of the shell. The cuttlebone is composed of thin parallel aragonitic septa with narrow chambers of about 0.2 mm wide between them. The individual septa are separated by aragonitic walls and columns. Buoyancy is managed by osmotic mechanisms which move fluid from/into the chambers along the porous siphuncular zone by changing the osmolarity of the chamber fluids. Higher osmolarity results in water flow into the chambers, reducing the gas volume and making the animal heavier; lower osmolarity results in water leaving