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RESEARCH ARTICLE

Food effects on statolith composition of the common cuttlefish (*Sepia officinalis*)

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Abstract The concentration of trace elements within cephalopod statoliths can provide a record of the environmental characteristics at the time of calcification. To reconstruct accurately the environmental characteristics at the time of calcification, it is important to understand the influence of as many factors as possible. To test the hypothesis that the elemental composition of cuttlefish statoliths could be influenced by diet, juvenile *Sepia officinalis* were fed either shrimp *Crangon* sp. or fish *Clupea harengus* under equal temperature and salinity regimes in laboratory experiments. Element concentrations in different regions of the statoliths (core–lateral dome–rostrum) were determined using laser ablation inductively coupled plasma mass spectrometry (LA- ICPMS). The ratios of Sr/Ca, Ba/Ca, Mn/Ca and Y/Ca in the statolith's lateral dome of shrimp-fed cuttlefish were significantly higher than in the statolith's lateral dome of fish-fed cuttlefish. Moreover, significant differences between statolith regions were found for all analysed elements. The fact that diet adds a considerable variation especially to Sr/Ca and Ba/Ca must be taken into account in future micro-chemical statolith studies targeting cephalopod's life history.

Introduction

Statoliths, the earstones of cephalopods, are composed mostly of calcium carbonate (aragonite form) but also include protein and minor and trace elements. The concentrations of elements in statoliths can provide substantial information for the reconstruction of cephalopod's environmental histories (Ikeda et al. 2003). Furthermore, stock separations based on statolith microchemistry appear to be possible (Arkhipkin et al. 2004).

Statolith composition studies generally assume that element incorporation into the statolith is mainly influenced by chemical and physical parameters of the surrounding water (Yatsu et al. 1998). However, strontium is also incorporated into the statolith matrix via the cephalopod's diet (Hurley et al. 1985). In their study, artificially enriched diet (shrimp soaked in strontium chloride solution) was used to chemically mark distinct statolith regions. Therefore a positive effect of Sr in the diet on the statolith Sr/Ca was revealed, but a quantification of this influence has not been shown yet. Furthermore, strontium is the only element tested for a dietary effect up to now.

Research on the structurally similar fish otoliths has shown that many factors can affect otolith chemistry (for a detailed review, see Campana 1999). In addition to temperature and salinity, growth rate (Sadovy and Severin 1992; Mugiya and Satoh 1997), gonad development (Kalish 1991), stress (Kalish 1991; Townsend et al. 1992) and diet (Limburg 1995; Gallahar and Kingsford 1996; Buckel et al. 2004) are all thought to influence incorporation of elements into otoliths. The

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magnitude of the effect of these factors on cephalopod statoliths, and how precisely they can be analysed, will be important in determining how reliable statoliths can be used in recording environmental history.

The general effect of diet on fish otolith chemistry is still being debated; of the six studies that have addressed this question (reviewed by Buckel et al. 2004), three have found a dietary effect on otolith Sr/Ca (Limburg 1995; Gallahar and Kingsford 1996) or Sr/Ca and Ba/Ca (Buckel et al. 2004). Three other studies on different species, however, found no effect of artificially enriched diet on otolith composition (Hoff and Fuiman 1995; Farrell and Campana 1996; Milton and Chenery 2001).

For spatially resolved microchemical analyses of statoliths, the evaluation of the elemental composition in different statolith regions like core, rostrum and lateral dome is essential. Considerable spatial variations in strontium contents, but not in magnesium were found in statoliths of squid and cuttlefish (Durholtz et al. 1997; Bettencourt and Guerra 2000). Distributions of other elements, however, have not been investigated systematically up to now.

Cuttlefish are among the most important cephalopod resources in European waters (Denis and Robin 2001). Official statistics for this species indicate an average production of 41,000 tons per year (1993–2003) almost equally coming from the Atlantic and the Mediterranean (FAO 2005). As well as representing an important fisheries resource, cuttlefish have a potentially important ecological role both as predators on shrimp and fish (Castro and Guerra 1990) and as prey (e.g. Clarke and Pascoe 1985). Since cuttlefish is rather unproblematic in rearing experiments, compared to other cephalopods, this species is regularly used as a model organism for cephalopod studies. Thus, cuttlefish provide an opportunity to examine the effect of natural prey types such as fish and shrimp on statolith chemistry. The dietary effect of natural prey types, a crucial question for micro-analytical statolith studies targeting cephalopod's life history, has never been investigated before. The aim of this study therefore was to (1) test the null hypothesis that statolith chemistry of cuttlefish is independent of diet, and (2) to quantify and compare the elemental composition in different regions of *S. officinalis* statoliths, independent from the diet.

Materials and methods

Rearing experiments

Cuttlefish eggs were collected in coastal waters of Normandy, France in July 2005 and transported to the aquarium at IFM-GEOMAR, Kiel, Germany. Hatching took place in the aquarium in a common tank in running water from the main aquarium water circuit (salinity: 28, temperature 19°C). Hatchlings were initially fed with live mysid shrimps for the first 20 days. After that time they were randomly distributed among six experimental tanks and were fed either shrimp (*Crangon* sp.) or fish (*Clupea harengus*) over a 60-day period. For each food treatment three replicate tanks with a stocking of three specimens each were used. The light:dark cycle was 12:12 h for the duration of the experiment. Both prey types were caught in the North Sea and stored frozen. The temperature during the experiments was maintained at 21.3°C (standard deviation 0.6), salinity was 28.4 (standard deviation 0.4). Both temperature and salinity were controlled daily. At the end of the experiment, the animals were killed and statoliths were removed immediately.

Statolith processing

One statolith from each cuttlefish was used, i.e. altogether 18 statoliths were analysed. Statoliths were attached concave side up onto a microscopic glass slide with thermoplastic resin (Buehler®) and were ground on one side with wet waterproof lapping film (3 M®; 30, 15, 3 μm) until the ground surface extended to the edge (i.e. the most extended point) of the dorsal dome and the focus could be seen just beneath the ground surface. Ground statoliths were observed under a Leitz Laborlux^K microscope (250× magnification) to locate the analytical regions.

Statolith analyses

The polished statoliths used for element analysis were triple-rinsed in MilliQ water. Eight analytical points were placed on each statolith (Fig. 1). One point was placed into the core, i.e. the region laid down before hatching. Four points were placed into the outer lateral dome and three points were placed into the rostrum, both regions representing the time of experiments with different feeding.

The analyses were carried out by laser ablation-inductively coupled plasma-mass spectrometry (LA-ICP-MS) at the Institute of Geosciences, University of Bremen, using a 266 nm frequency-quadrupled Nd:YAG laser (Finnigan UV LaserProbe) coupled to a ThermoFinnigan Element2. Helium was used as sample gas in the ablation cell (0.4 l min^{-1}) and Argon was subsequently added (0.8 l min^{-1}) to the gas flow. Ablation parameters included a laser energy of 2–2.5 mJ (Q-switched mode) and a pulse rate of 5 Hz resulting in crater sizes of 60–80 μm. This analytical setup provided

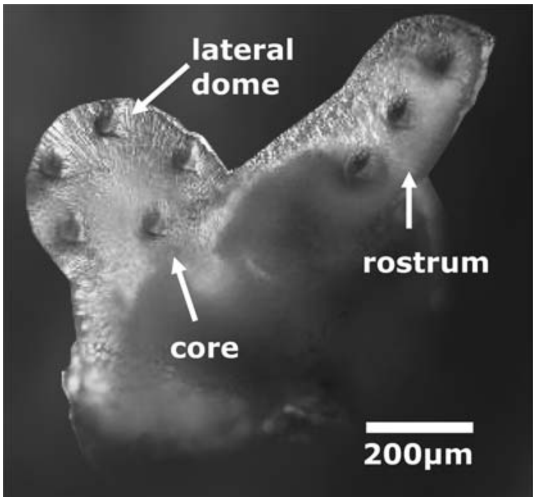

Fig. 1 *Sepia officinalis.* Ground statolith showing the location of analytical points as laser ablation craters

the determination of eleven isotopes, recorded during 90 s with five samples near the center of each peak and a total dwell time of 50 ms per isotope. Owing to the lack of matrix-matched standards, we used the glass reference materials NIST610 (for ^{23}Na, ^{43}Ca, ^{88}Sr) and NIST612 (for ^{23}Na, ^{25}Mg, ^{43}Ca, ^{55}Mn, ^{64}Zn, ^{89}Y, ^{90}Zr, ^{93}Nb, ^{138}Ba, ^{238}U) for external calibration taking the accepted concentrations of Pearce et al. (1997). Both standards were analysed and a new calibration line established after every 5–11 data points (standard bracketing) to compensate for any instrumental drift.

We used the GeoPro™ software to define a blank of 8–20 s duration and a stable signal period of 15–50 s duration following a pre-ablation period of 5–13 s for each measured point. For quantification the blank was subtracted and Ca was used as internal standard element with an assumed stoichiometric concentration of 40% of wt. We preferred single-point over two-point calibration because the two differently coloured NIST standards show distinct ablation behaviour and element fractionation at 266 nm laser wavelength (Guillong et al. 2003). The external analytical precision was determined through replicate analyses of the homogeneous standard reference materials NIST612 and GOR128G (basaltic glass; Jochum et al. 2000). Our data indicate a precision of better than 3% for concentrations above 0.5–1 µg g^{-1} and up to 13% for concentrations above 0.01 µg g^{-1}.

Prey and water analyses

Bulk analyses of prey and water were carried out by solution ICP-MS at the Institute of Geosciences, University of Bremen, using a ThermoFinnigan Element2™. Prior to analysis, water samples from each experiment tank were diluted 1:200 for Ca, Mg and Sr, and 1:20 for all other elements. Samples of whole shrimp and fish pieces as used for the feeding were freeze-dried and hackled. The dry samples were weighted (between 146 and 368 mg) and mixed with 5 ml of concentrated ultrapure nitric acid in teflon beakers for more than a day at room temperature. For subsequent pressure digestion the samples were heated in about 10 min to 210°C in a MLS Ethos™ microwave and the temperature held for further 10 min. The solutions were diluted and spiked with indium as internal standard with the final analyte solutions containing 0.29–0.74 mg ml^{-1} of total dissolved solids.

For sample introduction we used a PEEK cyclonic spray chamber with a micro-flow nebulizer operating in self-aspirating mode. In order to avoid mass interferences, Mg, Mn, Ni and Zn were measured at medium resolution (4,000) and all other elements at low (300) resolution. Internal precision as expressed by the relative standard deviation of nine analytical passes was typically 1–7% for most elements and increased for concentrations below 0.01 ng ml^{-1}.

Statistical analyses

Molar element/Ca ratios were calculated and values per statolith region were averaged by specimen. We compared statolith element/Ca ratios using a nested ANOVA to test for the hypotheses of no overall effect of diet on element incorporation into statolith aragonite. For comparisons between statolith locations a one-way analysis of variance (ANOVA) and post hoc Tukey multiple comparisons were used to test for significant differences in element/Ca ratios among the core, the lateral dome and the rostrum. The assumptions of ANOVA were met: the data were normally distributed and variances were homogeneous among factor levels.

Results

Water chemistry

Element/Ca ratios in the water did not differ significantly between treatments or between replicates for all analysed elements (*P* values between 0.08 and 0.87). The elemental composition of the rearing water is listed in Table 1.

Prey composition

The concentrations of all analysed elements except from U differed between the two prey types (Table 2). Shrimp prey contained significantly more Ca, Sr, Ba,

Table 1 Mean ± SD element concentrations in rearing water determined by ICP-MS

Elements	Tank water fish diet	Tank water shrimp diet
Sr/Ca (mmol mol^{-1})	17.0±0.9	16.3±0.4
Y/Ca (nmol mol^{-1})	134.6±3.0	147.9±32.4
Zr/Ca (nmol mol^{-1})	968.8±125.6	916.5±73.1
Nb/Ca (nmol mol^{-1})	15.5±1.6	18.3± .9
Ba/Ca (μmol mol^{-1})	96.5±8.4	87.4±6.9
U/Ca (nmol mol^{-1})	782.3±23.2	644.6±79.3
Mg/Ca (mol mol^{-1})	11.1±0.1	11.2±0.4
Mn/Ca (μmol mol^{-1})	1.55±0.27	1.1±0.35
Zn/Ca (μmol mol^{-1})	2.61±0.39	7.28±4.96

Table 2 Mean ± SD element concentrations for fish (*Clupea harengus*) and shrimp (*Crangon* sp.) prey

Element	Fish	Shrimp
Ca	1184±162 μg g^{-1}	1,570±271 μg g^{-1}
Mg	83.5±10.8 μg g^{-1}	148.5±10.8 μg g^{-1}
Mn	0.45±0.14 μg g^{-1}	1.23±0.22 μg g^{-1}
Zn	6.4±1.0 μg g^{-1}	2.8±0.3 μg g^{-1}
Sr	3.1±0.4 μg g^{-1}	42.1±7.6 μg g^{-1}
Y	0.14±0.05 ng g^{-1}	3.3±2.7 ng g^{-1}
Zr	0.86±0.65 ng g^{-1}	9.6±4.4 ng g^{-1}
Nb	<0.02 ng g^{-1}	0.86±0.4 ng g^{-1}
Ba	59±14 ng g^{-1}	300±60 ng g^{-1}
U	0.86±0.23 ng g^{-1}	0.76±0.4 ng g^{-1}

Mg, Mn, Y, Zr, Nb and less Zn than fish prey (*t*-test, $P < 0.05$).

Statolith analyses

Dietary effect

Sr/Ca, Ba/Ca, Mn/Ca, and Y/Ca are significantly higher in the statolith's lateral dome of shrimp-fed cuttlefish compared to fish-fed cuttlefish (Fig. 2). Though statistically significant, the absolute differences are comparably low, ranging between 5 and 15%. However, no significant difference between treatments could be found in the rostrum and in the core for any element (Table 3). When averaging the elemental composition over the whole statolith, i.e. all analytical points from all regions, again no significant difference between treatments was observed.

Spatial variations

Significant differences in element/Ca ratios between the three distinguished statolith regions (core–lateral dome–rostrum) are observed for all determined elements (Table 4). Element/Ca ratios in the core are significantly higher than in both the lateral dome and the rostrum for Sr, Mg, Y, U and Mn (Fig. 2). Na/Ca ratios in the core and in the rostrum are significantly higher than in the lateral dome. Ba/Ca ratios are significantly lower in the core compared to the lateral dome and the rostrum. For Zn/Ca, Zr/Ca and Nb/Ca, only a significant difference between the core and the lateral dome was found. Their element/Ca ratios in the lateral dome and in the rostrum are not significantly different.

Discussion

Dietary effects

Our data show that the hypothesis that statolith chemistry is independent of diet can be rejected for cuttlefish. Especially Sr and Ba, elements that are almost routinely used as proxy for salinity or temperature of the surrounding water for fish, corals and bivalves, should be viewed with some caution because their amounts vary with diet types, thus potentially masking the influences of environmental factors. Our data suggest that the dietary influence on barium incorporation into the statolith seems to be rather small compared to environmental influences, e.g. the temperature effect on Ba concentration (around − 5% per °C, Zumholz 2005; Zumholz et al., submitted). The dietary effect on statolith Ba/Ca as indicated by our data ranges around 10% for completely different diets with Ba values being one order of magnitude higher in shrimps than in fish. Therefore a complete diet shift from crustaceans to fish would result in an inaccuracy of around 2°C when using Ba as a temperature proxy.

In contrast to Ba/Ca, the Sr/Ca ratio in *S. officinalis* statoliths is apparently not affected by both temperature and salinity (Zumholz 2005; Zumholz et al., submitted). Thus, the dietary effect on Sr/Ca (which is up to 10% in our study) can be an important proxy of varying feeding habits even under changing water conditions. For many cephalopod species including *S. officinalis*, a distinct shift in feeding habits due to ontogenetic development is reported (e.g. Castro and Guerra 1990). The present results suggest that a shift from crustacean to fish diet can be detected with modern microanalytical methods in cuttlefish statoliths by their Sr contents. Combined with optical ageing, based on statolith growth increments, feeding habits may be assigned to the individual age.

Yttrium, though present in very low concentrations, was significantly influenced by the diet. However, as it also varies with both temperature and salinity in *S. officinalis* statoliths (Zumholz 2005; Zumholz et al., submitted), we consider it not to be an appropriate proxy for dietary signals.

Fig. 2 *Sepia officinalis.* Element/Ca ratios measured by LA-ICPMS in different regions of statoliths from shrimp-fed (*filled squares*) and fish-fed (*open circles*) specimens. Each point represents the mean of measurements in nine statoliths; error bars indicate 95% confidence intervals

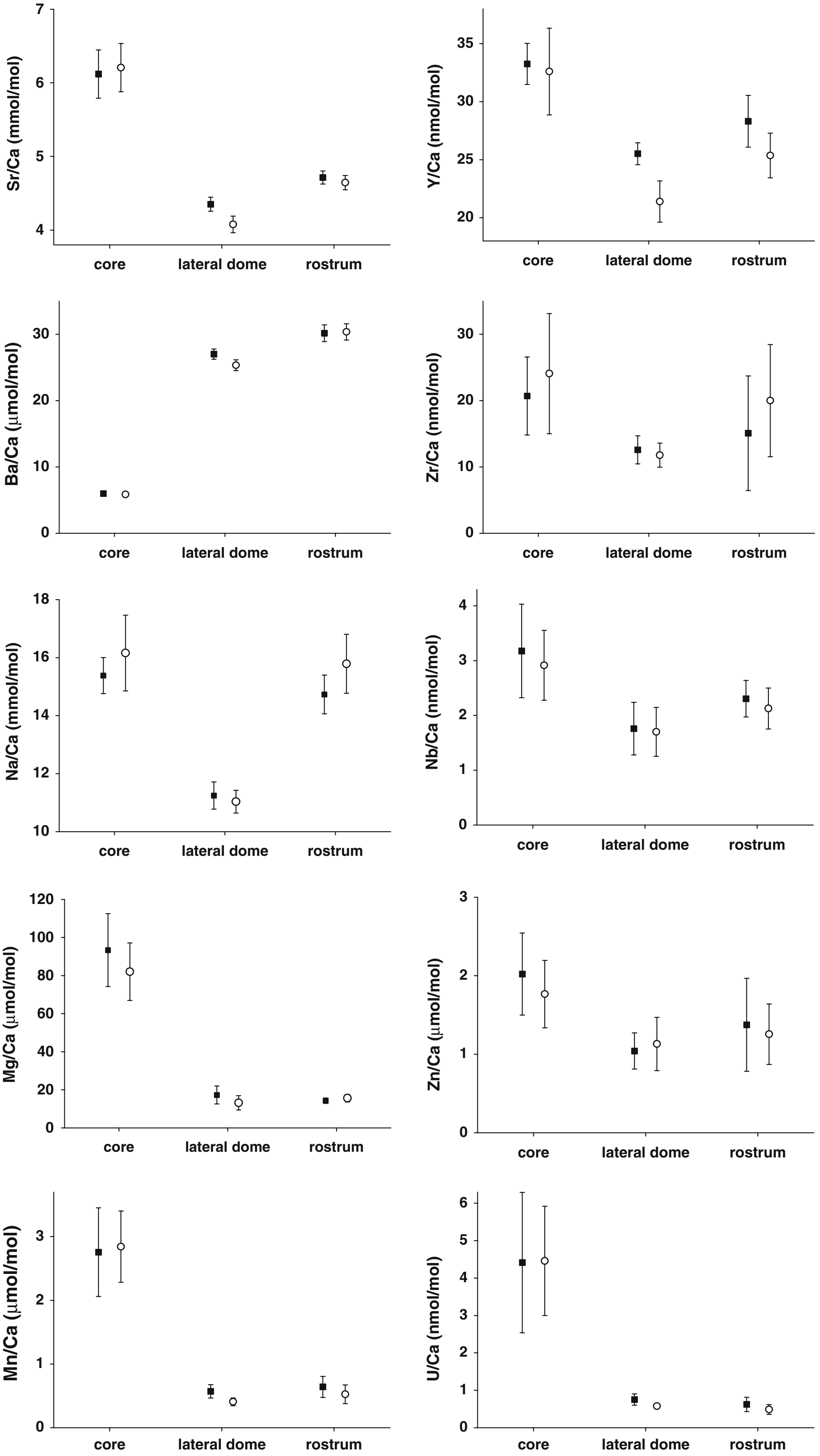

Table 3 Analyses of Variances (ANOVA) table summarizing the dietary effect (*P*-values for shrimp-fed vs. fish-fed specimens) on the element/Ca ratios in different statolith regions

Element/Ca	Core	Lateral dome	Rostrum
Sr/Ca	0.36	0.0006	0.22
Ba/Ca	0.31	0.005	0.82
Mg/Ca	0.85	0.42	0.24
Na/Ca	0.18	0.43	0.065
Mn/Ca	0.26	0.004	0.25
Y/Ca	0.68	0.00004	0.064
U/Ca	0.69	0.059	0.24
Zr/Ca	0.83	0.41	0.43
Nb/Ca	0.21	0.84	0.40
Zn/Ca	0.22	0.63	0.70

Table 4 Analysis of variance (ANOVA) table summarizing the effect of statolith location on element/Ca ratios

Element	Df	Anova between core–LD–rostrum		Post hoc Tukey-multiple comparison		
		F	*P*	Core vs. LD (*P*)	Core vs. RO (*P*)	LD vs. RO (*P*)
Strontium	2	248.41	<0.0001	0.0001	0.0001	0.0001
Barium	2	2099.1	<0.0001	0.001	0.001	0.001
Magnesium	2	108.39	<0.0001	0.0001	0.0001	0.99
Sodium	2	96.34	<0.0001	0.0001	0.35	0.0001
Manganese	2	51.09	<0.0001	0.0001	0.0001	0.95
Zinc	2	4.26	0.019	0.031	0.114	0.83
Yttrium	2	40.56	<0.0001	0.0001	0.0001	0.007
Zirconium	2	3.79	0.029	0.017	0.135	0.64
Uranium	2	27.30	<0.0001	0.0001	0.0001	0.99
Niobium	2	7.76	0.001	0.002	0.01	0.80

All 18 statoliths from both food treatments were pooled in this analysis

Spatial variations

The spatial variation of elemental composition independent fom the diet has substantial relevance for further studies. Solution-based methods generate a pooled signal of the elemental composition over the whole statolith and do not differentiate between regions. This means that spatial variations add a considerable source of variation.

The Sr/Ca values determined in this study are higher in the rostrum than in the lateral dome. Further, the wing is reported to contain more Sr than the lateral dome (Bettencourt and Guerra 2000). Both our results and the results from Bettencourt and Guerra (2000) are different from the concept by Lipinski (1993), who suggested that good increment visibility in cephalopod statoliths is associated with high Sr contents. This hypothesis was confirmed for statolith of the chokka squid *Loligo vulgaris reynaudii* (Durholtz et al. 1997), but at least in *S. officinalis* statoliths, increments are best visible in the lateral dome and almost indistinguishable in the wing and the rostrum. Sr incorporation into coral skeletons is inversely correlated with the rate of calcification (Cohen et al. 2001; Ferrier-Pages et al. 2002). Bettencourt and Guerra (2000) proposed that good increment visibility is associated with high organic matter contents. Combining these points with our results, we suggest that enhanced calcification rates, related to higher organic matter incorporation, are somehow associated with better increment visibility in *S. officinalis* statoliths.

The observation that Mg/Ca did not vary significantly outside the core region is in accordance with the results from Bettencourt and Guerra (2000), who compared the Mg/Ca ratios in the wing and the lateral dome. While Mg is considered to be the key factor in statolith calcification (Morris 1991), hypotheses on statolith deposition are still controversial (Arkhipkin 2005) and convincing evidence has not been supplied yet.

Core composition

The core regions, laid down during embryo development inside the egg showed no differences in the elemental composition between treatments during the experiments. This confirms that material deposited into the statolith is metabolically inert after deposition and not influenced by later processes. The strongly different elemental composition in the statolith core region compared to the regions deposited after hatching may be related to the transfer of almost completely developed eggs from the Atlantic to experimental tanks in Kiel. However, the capsule of cuttlefish eggs is known to act as a shield to protect embryos against influx of elements such as zinc and cadmium (Bustamante et al. 2002). The extremely low Ba concentrations in the core suggest a similar protection against this element. U concentrations, however, are significantly higher in the core than in the outer regions, suggesting that this shield does not protect against U. If the same protection would be active against U, our results would indicate substantially higher U concentrations in the cuttlefish's spawning sites. However, these mechanisms have to be experimentally tested, before distinct assumptions are possible.

Sr contents in the core were significantly higher than in outer regions. While there is evidence that the yolk composition likely influences Sr concentrations in fish otoliths more than the surrounding water (Kalish 1990), there is also evidence that environmental conditions, specifically temperature, can affect Sr contents in statoliths of encapsulated marine neogastropod larvae (Zacherl et al. 2003). For further evaluation it would be desirable to analyse the elemental composition of the liquid inside the eggs, its dependence on the surrounding water composition and temperature and its influence on the statolith composition.

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