Ontogeny and habitat change in Mesozoic cephalopods revealed by stable isotopes ($\delta^{18}$O, $\delta^{13}$C)

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Abstract

Stable isotope ($\delta^{18}$O and $\delta^{13}$C) ratios were measured in successive aragonitic shell sequences of ammonoids (class Cephalopoda) to determine whether their depth distributions changed within ontogeny and whether stable isotope values differ in various morphological groups (e.g. Leiostraca vs. Trachyostraca). We concentrate mainly on $\delta^{18}$O for temperature results and added $\delta^{13}$C data to obtain information on the ontogenetic history, for which full spiral measurements were undertaken for the first time. To obtain valid stable isotope data from ammonoid shells, we measured ontogenetic sequences (full shell) within different genera. Data sets from the Jurassic (Cadoceras) and Cretaceous (Hypacanthoplites, Nowakites) were chosen due to the pure primary aragonitic shell preservation. The study was designed to extract better information on the habitat and life cycle of fossil cephalopods (e.g. ammonoids) in comparison with recent cephalopods (e.g. Nautilus, Spirula, Sepia) possessing equivalent or comparable hard parts. The data from three genera suggest different modes of life in at least two morphological groups. We detected and established two main groups with different ontogenetic strategies based on the $\delta^{18}$O data. The cw-cw-type (warm–cool–warm type) of Cadoceras resembles strategies in Nautilus and Sepia, which migrate from shallow into deeper environments and back in ontogeny (wc-type, warm–cool–type), and the cw-type (cool–warm–type) of Hypacanthoplites resembling the first two migration phases of Spirula (cw-type), which migrates from deeper into shallower and back again into deeper habitats. The main (three) phases revealed by both $\delta^{18}$O and $\delta^{13}$C data sets most probably reflect diet changes in juvenile to mid-aged individuals, followed by a habitat change for spawning adults. In Cadoceras the temperatures range from 21.2 °C for juveniles down to 12.1 °C for mid-aged individuals and back up 16.9 °C in adults. The cw-type strategy of Hypacanthoplites involves a temperature range of 22.8 °C to 28.9 °C. The respective mean values are 24.2 °C (juvenile), 25.8 °C (middle phase) and 27.8 °C (adults). The $\delta^{13}$C values also revealed three ontogenetic stages in Cadoceras and Hypacanthoplites, including two major shifts from positive to negative and from negative to positive values, which probably correspond to sexual maturation, the initiation of reproduction, and concomitant changes in diet. The presented data, combined with previous ontogenetic studies (e.g. stable isotopes) on Spirula, Nautilus and Sepia can be used as proxies to directly correlate the habitats and ontogeny of recent and fossil cephalopods.

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1. Introduction

Ammonoids are an extinct group of cephalopods with an external, primary aragonitic shell. Various morphologies exist, ranging from planispiral to heteromorphic shells, from smooth (leiostracans) to strongly ribbed (trachyostracans) with tubercles or even long spines (Westermann, 1990; 1996). Knowledge of the life cycles, ecology and ontogeny of fossil cephalopods and especially of ammonoids is still poor. While ammonoids are frequently found in Paleozoic and Mesozoic marine sediments worldwide from the tropic–subtropic via boreal to antarctic–arctic zones, information on their habitat and ecology is scarce and imprecise. Their habitat is suggested to be the epipelagic or meso pelagic zones (Westermann, 1990; 1996). The epipelagic or sunlight zone is the uppermost part of the water column from 0–200 m depth, whilst the mesopelagic or twilight zone ranges from 200 to 1000 m (Ott, 1996). Ammonoids are considered to have been nektonic or demersal animals. Nektonic organisms live actively swimming in the pelagic zone, whilst demersal or nektobenthic organisms live actively swimming near or close to the sea bottom (Lincoln et al., 1998). They probably spawned in benthic or even mid-water habitats in the neritic to oceanic zone above the shelf areas and upper slopes within water layers ≤1000 m (Westermann, 1996). Females are thought to have laid 100–1000 eggs on the seafloor (r-strategy), which after hatching as larvae became part of the

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plankton (e.g., Landman et al., 1983; epiplankton after Westermann, 1996). This strategy is comparable to most other cephalopods, except for the K-strategist Nautilus. Ammonoids most probably undertook vertical diel migrations, as is characteristic for many planktonic ocean dwellers such as Spirula spirula (Clarke, 1969; Lukeneder et al., 2008).

The aragonitic composition of the external shells in ammonoids makes them suitable for isotopic measurements. Shells of the herein studied genera Cadoceras, Hypacanthoplites and Nowakites (Fig. 1) consist entirely of pristine aragonite. The planispirally coiled shells were formed gradually during ontogeny and therefore are considered to mirror the paleotemperature of the surrounding seawater (Fig. 2). Thus, the exquisitely preserved shells may provide a reliable geochemical archive that reflects the life-span migration cycle of the ammonoids.

Fractionation and isotopic composition in oxygen and carbon isotopes ($^{18}$O/$^{16}$O and $^{13}$C/$^{12}$C) refers to a change in stable isotope ratios, reflecting chemical and/or physical processes (Hoefs, 2004). Early studies of mollusc shells in respect to stable isotope composition ($^{18}$O and $^{13}$C) already demonstrated that the isotope composition of carbonate shells is a function of seawater-temperature (Urey et al., 1951). Since then, an enormous body of literature has used stable isotopes of bivalve and gastropod shells as environmental proxies (Bandel and Hoefs, 1975; Wefer, 1985). As noted by Rexfort and Mutterlose (2006), isotope thermometry obtained by analyzing hard parts of cephalopods offers valuable information about paleo- and recent seawater temperatures as well. According to the formula

$$T(\degree C) = 20.6 - 4.34 \left( \delta^{18}O_{\text{aragonite}} - \delta^{18}O_{\text{water}} - 0.2 \right)$$

(Grossman and Ku 1986; McConnaughey et al., 1997; Goodwin et al., 2003), a shift of one per mil in the oxygen isotope ratio corresponds to a temperature change of 4.34 °C ($\delta^{18}O_{\text{water}} = -1.0\%$ SMOW for the mean isotopic composition in a nonglacial world in Jurassic to Cretaceous times). The latter equation was extrapolated by Lécuyer et al. (2004) to a more appropriate formula for equatorial or tropical molluscs in marine waters by

$$T(\degree C) = 21.8 - 4.69 \left( \delta^{18}O_{\text{aragonite}} - \delta^{18}O_{\text{water}} \right)$$

assuming that the isotope ratio is strongly related to

$$\delta^{18}O_{\text{water}} = -9.986 + 0.35S$$

(GEOSECS Executive Committee, 1987) when $S$ is the salinity with about 35% at a depth of around 300–500 m according to data by Auclair et al. (2004) and Watanabe et al. (2003). Subsequently, the heavy/light oxygen ratio can be used to define the relationship between oxygen isotopes and water temperature manifested in aragonitic shells such as those of Recent (Spirula, Sepia, Nautilus) and ancient cephalopods (ammonoids, nautiloids belemnoids). Caution must be exercised because nacreous layers in molluscs are $^{18}$O depleted compared to calcite (prismatic layers in cephalopods), which is enriched in $^{18}$O (Tarutani et al., 1969; Grossman and Ku, 1986).

Numerous authors have investigated isotope records from Recent cephalopod hard parts. Sclerochronologic isotope data for Nautilus pompilius, N. belauensis, Nautilus macromphalus and Nautilus sp. were provided by Eichler and Ristedt (1966a,b), Cochran et al. (1981), Taylor and Ward (1983), Wefer (1985), Landman et al. (1983, 1994) and Auclair et al. (2004). Other research groups focused on isotopic

![Fig. 1. Lateral view with numbered samples in ontogenetic direction, growth direction with indicated SEM images of aragonitic ultrastructure, × 500 and × 3700, of (A) Cadoceras, (B) Hypacanthoplites and (C) Nowakites shells.](image-url)
records of sepiids such as Sepia officinalis (Longinelli, 1966; Longinelli and Nuti, 1973; Hewitt and Stait, 1988; Bettencourt and Guerra, 1999; Rexfort and Mutterlose, 2006; Cherel et al., 2009). The stable isotope composition of the deep-water squid S. spirula was investigated by Lukeneder et al. (2008) and Price et al. (2009).


The comparison of Recent Spirula, Sepia, and Nautilus allows quite different modes of life to be deciphered based on stable isotope signatures (Fig. 3). Applying these methods to Mesozoic ammonoids might shed light on the strategies and environmental requirements of fossil cephalopods. Due to its unusual morphology, Spirula is used as a key genus in paleontological papers that attempt to interpret the mode of life of Mesozoic ammonoids (Lukeneder et al., 2008; Price et al., 2009). The life and habitat during full ontogeny have not yet been reconstructed for any ammonoid. Past investigations have examined only parts of shells or used only single-point measurements (one-measurement-per-shell) to calculate paleotemperatures for whole oceans. In contrast, we measured entire ammonoid specimens in spiral direction (from embryonic stages to adult aperture) to gain additional information of the ecology and habitat preferences of various ammonoids. One of the main objectives of the present study is to determine possible ontogenetic migrations in the water column in fossil cephalopod groups based on a comparison with stable isotope data from Recent cephalopods. We concentrated mainly on the $\delta^{18}O$ stable isotope data to detect ontogenetic stages, including shifts in isotope values, corresponding with maturation and concomitant changes in ancient habitats (e.g. water depth).

2. Modern and ancient cephalopods: ontogeny and isotopes

2.1. Recent cephalopods: Spirula, Sepia and Nautilus

2.1.1. Spirula

The $\delta^{18}O$ stable isotope data reported by Lukeneder et al. (2008) for the deep-water squid S. spirula display a steady decrease from $+3.45$ to $+3.00$‰ to $+1.96$ to $+2.04$‰ in juvenile stages and an increase to $+2.17$ to $+2.64$‰ in adults (Fig. 3). $\delta^{13}C$ data also revealed three ontogenetic stages, including a major shift from positive to negative values which corresponds to sexual maturation, the initiation of reproduction, and concomitant changes in diet. A rarely preserved embryonic stage was accompanied by markedly less positive $\delta^{13}C$ values in the first few chambers. These data are related...
to habitat changes during ontogeny: after hatching at depths > 1000 m at approx. 4–6 °C (Young et al., 1998; Lukeneder et al., 2008; Price et al., 2009), the squid migrates into shallower, warmer waters at depths of 400–600 m (12–14 °C). Subsequently, the animals migrate back into somewhat cooler, deeper habitats.

2.1.2. Sepia

*S. officinalis* hatches in warm waters (above 20 °C) at depths of about 1–20 m (Rexfort and Mutterlose, 2006) and descends to greater depths in accordance with a change in life style. Wild-caught specimens displayed δ18O values from −1.28 to +2.98 ‰ during ontogeny, pointing to an experienced temperature of 21 °C in subadult to 5 °C in adult specimens (Fig. 3). This ontogenetic trend of *Sepia* from warm water into deeper and cooler waters was also documented by other isotope studies such as Longinelli and Nuti (1973) and Bettencourt and Guerra (1999). The main difference between *Sepia* and ammonoids is the maximum life-span (see discussion). *Sepia* apparently attains an age of c. 200 days (Rexfort and Mutterlose, 2006), whereas ammonoids might have ranged from 5 to 15 years (Bucher et al., 1996) or even 50–100 years in giant lytoceratids (Westermann, 1996).

2.1.3. Nautilus and fossil allies

Various species of *Nautilus* were measured by Eichler and Ristedt (1966a, b), Cochran et al. (1981), Taylor and Ward (1983), Landman et al. (1983, 1994) and Auclair et al. (2004). *N. macromphalus* needs 5–6 years to reach sexual maturity, with a growth rate of 1 growth line deposited in 2 days and an averaged value of 0.25 mm/day in reared specimens (Martin et al., 1978). Depending on the species, embryonic development takes place at 22–30 °C in a depth of 100–200 m. Typical embryonic δ18O values range roughly around −1.07 to −3.00 ‰. After c. 269 to 362 days (Uchiyama and Tanabe, 1999) hatching takes place and a migration into cooler, deeper waters (150–400 m; 14–16 °C) starts. This is documented by increasing δ18O values of +0.40 to +1.21 ‰ (Fig. 3). The main δ18O shift corresponds with the formation of the 7th to 8th septum, reflecting the hatching after the embryonic stage. Consequently, Taylor and Ward (1983) defined 2 different ontogenetic stages by using isotope data: the embryonic and the free-swimming stage. The embryonic stage with δ18O values below approx. −1.00 ‰ (≤20 °C) and the free-swimming stage showing δ18O values above −1.00 ‰ (>20 °C).

This behaviour seems to be characteristic for *nautilids* at least since Cretaceous times because similar patterns (from lighter to heavier δ18O values after hatching) are observed in fossil *Eutrephoceras* (Landman et al., 1983, Landman, 1988). In *Eutrephoceras*, δ18O shifts occur between septa 2 and 4, with a magnitude of 1.60–2.90 ‰. Earliest stages point to paleo-seawater temperatures of 22–23 °C in the egg and to 14–20 °C after hatching. Afterwards, the nautilid descended into deeper, cooler water of around 14 °C (Landman et al., 1983).

Fig. 3. Stable isotope curves (δ18O in blue and δ13C in black) for the recent cephalopods *Spirula*, *Sepia* and *Nautilus* (Cochran et al., 1981; Landman et al., 1994; Lukeneder et al., 2008; Rexfort and Mutterlose, 2006).
The δ13C variations of −1.35 to +1.52‰ are correlated with changes from the embryonic to juvenile–adult stages and the change in habitat. Hence the δ18O values reveal different stages in early ontogeny of Nautilus, the embryonic followed by the free-swimming stage which correspond to early sexual maturation and concomitant changes in diet and water chemistry due to the “habitat change”. A change of habitat defines in the latter case the pre-hatching and the post-hatching cycles in Nautilus. Hatching from egg-capusle appears after approx. one year.

2.2. Fossil cephalopods: ammonoids

2.2.1. Ammonoids

Stable isotope analyses (δ18O, δ13C) on ammonoids are numerous but contribute little to reconstructing ontogeny. Typically, data were obtained as single-point measurements and lumped with other taxa of coeval strata. These investigations were typically designed to reveal ocean water temperatures at distinct time slices, neglecting the enormous effect on the isotope composition due to migration and habitat change. As δ18O data of single cephalopod shells can range around 2.00‰, spanning almost 8–10 °C these “one-measurement-per-shell-data” are inappropriate for paleotemperature estimations. These ranges are ontogenetically induced and single point measurements will snap-shot ocean water temperatures at a very specific point of development only.

Data exist for the Triassic genera Arcestes, Austroteuthis, Carnites, Rhacophyllites and Sagenites, the Jurassic genera Anomalites, Leicerias, Parkinsonia, Perisphinctes, Phylloceratites, Quenstedtoceras, and Staufenia and the Cretaceous genera Acanthoscaphites, Buculites, Damioceras, Discosphyrites, Euphycadoceras, Gaudryceras, Hauerceras, Hypophyllites, Menutes, Phylloceratites, Polypytchoceras, Scaphites, Sphenodiscus, Tetrarogitites and Yokoyamaoceras (references below).

Stable isotope data (δ18O, δ13C) of Triassic and Jurassic ammonoid shells from the Northern Calcareous Alps have been studied in order to calculate paleotemperatures for these periods (Kaltenegger, 1967; Fabricius et al., 1970; Kaltenegger et al., 1971; Jeletzky and Zapfe, 1976). Cochran et al. (2003) measured different Maastrichtian ammonoids from the Western Interior Sea (North America) to define various depositional settings, paleoenvironments and the corresponding salinity. The Jurassic Leicerias, Staufenia and Quenstedtoceras were studied to estimate the growth rate of ammonoids (Stahl and Jordan; 1969; Jordan and Stahl, 1970). Seasonal variation of about 8–9 °C in the late Middle Jurassic (Callovian) was proposed by these authors for Quenstedtoceras and Staufenia. Similarly, Lécuyer and Buccher (2006) analysed Late Jurassic Perisphinctes from Madagascar (Fig. 4) to obtain seasonal surface water temperatures of the southern hemisphere. Taxa, such as Phylloceratites, display minor variations of 3–4 °C (Jordan and Stahl, 1970) indicating considerable differences in the life styles. Several “ranges”, however, are attributed to variations in calcite–aragonite ratios and thus reflect mere diagenetic effects (e.g. Anomalites in Jordan and Stahl, 1970). Only bactulites have repeatedly been used to decipher ontogenetic changes of these Late Cretaceous heteromorphs (Tourtelot and Rye, 1969; Forester et al., 1977; Whittaker et al., 1987; Fatheree et al., 1998) (Fig. 4).

In addition, the Late Cretaceous heteromorph Polypytchoceras pseudogalatinum from Hokkaido was analysed by Okamoto and Shibata (1997), who concluded either a demersal mode of life almost touching the sea bottom (= nektobentic) or a nektoplanktonic mode in the water column. A corresponding life style was proposed by Moriya et al. (2003) for several taxa from the Late Cretaceous of the North Pacific. The relatively short shell–sections utilized for that study, however, exclude a full record of the ontogenetic shifts and potential migrations.

3. Material and methods

A total of three shells – one each of the ammonoid genera Cadoceras (Callovian, Jurassic; Gorki, Russia), Hypancithoplites (Aptian, Lower Cretaceous; Völhrum, Germany) and Nowakites (Santonian, Upper Cretaceous; Edelbachgraben, Austria) – were analysed for their stable isotope composition (δ18O, δ13C) (Figs. 1 and 2). Additional material from the same localities is stored at the Natural History Museum Vienna, Austria. The analysed shells ranged from 90 to 130 mm in maximum diameter and represented fully grown adult specimens. Morphology varies in the analysed specimens from smooth (e.g. Cadoceras), over weakly ribbed (e.g. Hypancithoplites) to strongly ribbed forms (e.g. Nowakites). The sex of the specimens is unknown. The isotope measurements were conducted in growth direction and targeted ontogenetic variations in the life cycle of the animals.

To take into account possible within-shell variation in isotopic composition (cf. N. macrophalus; Auclair et al., 2004), the within-shell variation of Cadoceras emiliantsevi was measured. Sub-samples were taken from the septa, siphon, and three areas of the chamber wall: near the siphon, marginally, and opposite the siphon. After drilling samples 1–13, the last whorl had to be removed to gain access to inner whorls (Fig. 1). For samples 17–36, a needle was used to remove shell material. Sampling such a specimen with an open umbilicus near the seam has one main advantage – the problem of sampling two whorls at once (external shell of one whorl and internal shell of the next whorl) can be ruled out. No contamination (e.g. organic or inorganic particles) was observed using light microscope and SEM. The standard deviation was < 0.08‰ for δ18O and 0.04‰ for δ13C based on repeated measurements (5 replicates) of international standards NBS18 and NBS19.

Hypancithoplites elegans was sampled in opposite ontogenetic growth direction near the seam (Fig. 1). Special attention was given not to sample the sediment filling of the shells. Nowakites savini was sampled in ontogenetic growth direction (last whorl); only the external part of the shell was used to gain higher resolution (Fig. 1) because early ontogenetic stages are not preserved in this specimen. All three shells showed no alterations (see supplementary information) or dissolution, and primary iridescence was still present in C. emiliantsevi and H. elegans.

Isotopic analysis were performed in the Stable Isotope Laboratory at the Institute of Earth Sciences, Karl-Franzens University Graz, using an automatic Kiel II preparation line and a Finnigan MAT Delta Plus mass spectrometer. Samples for the investigation of isotopic composition were drilled with a 0.3 mm-diameter dental drill. Samples were dried and reacted with 100% phosphoric acid at 70 °C. International standard NBS–18 and an internal laboratory standard were analysed continuously for accuracy control. Standard deviation was less than 0.08‰ for δ18O and 0.04‰ for δ13C. Isotopic data are reported in conventional units relative to the Vienna Pee Dee belemnite (V-PDB) standard in ‰ units and calculating with SMOW (standard mean ocean water). Paleotemperatures were calculated using the equation of Grossman and Ku (1986); Goodwin et al., 2003) according to

\[ T(°C) = 20.6 – 4.34 \left( \delta^{18}O_{\text{aragonite}} - \delta^{18}O_{\text{water}} - 0.2 \right) \]

An aragonite formation in isotopic equilibrium with the Mesozoic seawater is assumed. Ocean water is assumed to be ~1.0‰ (relative to SMOW; standard mean ocean water) for a nonglacial world (Shackleton and Kennett, 1975). Primary aragonite was detected by dry chemical powder measurements with a Siemens D5000 0–60 powder X-ray diffractometer at 25 °C (radiation was Cu-Kα, 2.0 s, 0.01° intervals). About 100 mg of powdered sample was loaded into a flat bed sample holder. Scan range was 2θ of 2–65°, voltage 45 V, and current 25 mA. Position, height, and distance of the diffractometer
curve-peaks fit perfectly with pristine and primary aragonite. Pristine aragonite was additionally detected by geochemical analysis as EDX and SEM (Fig. 1). Quantitative chemical analyses were carried out on a JEOL JSM-6400 scanning electron microscope (operation conditions 15 kV acceleration voltage, ∼1–2 nA sample current). Standardless chemical analyses (normalized to total sum = 100%) were performed using the energy-dispersive system KEVEX Si(Li) detector linked to a VANTAGE EDS system. Ammonoid shells were additionally studied by means of cathodoluminescence. Well preserved microstructure of nacreous layers show primary aragonite tablets (>99% aragonite; supplementary data B). Cathodoluminescence was performed on a TESCAN (Vega TC; Wide Field Optics), voltage 10 kV, at 17 mm distance, at scan rate 7 μs/pixel.

No secondary mineral phase was present. The state of preservation is ideal for a precise geochemical analysis in order to reconstruct past seawater temperatures.

4. Results

4.1. Ammonoid data

4.1.1. Cadoceras emiliantsevi

36 samples (Fig. 1, see Table 1 in supplementary data); δ¹⁸O values range from −1.35% to +0.75%, suggesting an overall temperature change from 21.2 °C to 12.1 °C. The juvenile shell points to a mean temperature of 18.0 °C, which is followed by a middle phase of c. 13.4 °C and a final stage of c. 14.3 °C. δ¹³C values of the juvenile shell (samples 1–7) were inconstant but steadily increase from −1.57 to +0.14‰ up to a middle phase of −0.16 to +0.75‰ and then slightly decrease down to an also unstable phase from −0.36 to +0.60‰ in the adult stage. The δ¹³C values of Cadoceras increase inconstantly during ontogeny and range from −1.57 to +1.14‰. The δ¹³C values of the juvenile shell (samples 1–7) jump markedly from −1.57 to +0.73‰ and then slightly increase to an unstable phase from −0.87 to +1.14‰ (mean +0.14) in adults (Fig. 2). Thus, after hatching at depths of probably less than 100 m at temperatures of 18 °C, Cadoceras migrated into deeper, cooler waters of c. 200–400 m. Subsequently, the decreasing δ¹⁸O values suggest a migration back into somewhat warmer, shallower habitats at 200 m with approx. 14 °C. Near the aperture (samples 33–36), values increase, indicating a temperature rise of about 4–5 °C during mature age. This may be linked to spawning cycles in adults (Fig. 5).

4.1.2. Hypacanthoplites elegans

26 samples (Fig. 1, see Table 1 in supplementary data); δ¹⁸O values were generally negative and range from −3.11% to −1.71%, suggesting that Hypacanthoplites was a warm water dweller living in waters between 23 and 29 °C. δ¹³C values of the juvenile shell (samples 1–10) steadily increase from −2.29 to −1.71‰, followed by a middle phase of −2.57 to −2.26‰ and then a further decrease down to a third phase ranging from −3.11 to −2.73‰ in adults. Three main phases can also be detected in the δ¹³C values of Hypacanthoplites. After hatching at depths of probably less than 100 m at temperatures of c. 24 °C, Hypacanthoplites migrated into even shallower and warmer waters of c. 26 °C at depths of c. 50 m.
Subsequently, the decreasing $\delta^{18}O$ values suggest a second shift into even warmer habitats within the uppermost epipelagic zone with a water temperature of c. 27 °C (Fig. 5). $\delta^{13}C$ values start relatively high during early ontogeny, ranging from +3.73‰ to +4.62‰. A middle phase comprises values between +2.15‰ and +0.41‰ (mean +1.66), during its adult stage, the values increase again, ranging from +2.59‰ to +3.49‰ (mean +3.06) (Fig. 2). The first major decrease seems to mirror a change in habitat and probably also diet as suggested by the oxygen values. The subsequent jump to high values might reflect sexual maturity and mating as documented for Spirula (Lukeneder et al., 2008).

4.1.3. *Nowakites savini*

38 samples (Fig. 1, body whorl only, see Table 1 in supplementary data); $\delta^{18}O$ values range from −0.20%o to −0.10%o and display an overall negative trend. The values of the early last whorl (samples 1–12) steadily decrease from −0.09‰ to −0.47 (mean −0.30). This was followed by an unstable phase, jumping between −0.42‰ and −2.04 (mean−0.83) and then an increase to less negative values in a last phase from −0.64% to −0.30‰ (mean−0.46) in adults. $\delta^{13}C$ values on the last whorl of *Nowakites* are inconsistent. In agreement with the phases detected in $\delta^{18}O$, $\delta^{13}C$ values start relatively high in early stages of the last whorl and range from +2.07‰ to +1.76‰; thereafter, an irregular phase starts, with rapid shifts between +1.73‰ and +0.71‰ (Fig. 2).

5. Discussion

Our stable isotope data point to various ontogenetically controlled types within the ammonoids. $\delta^{18}O$ and $\delta^{13}C$ values mark two to three phases, corresponding to different temperature and habitat levels as observed in modern counterparts. Comparing these fossil patterns with modern analogues requires a short overview of the modern examples *Spirula*, *Sepia* and *Nautilus*. Moreover, own data are compared with the often very spotty data (e.g. one measurement per specimen) on fossil cephalopods. A list of the taxa with isotope data is given in Table 1 (supplementary data).

5.1. Fossil cephalopods: isotopes and ontogeny

5.1.1. *Cadoceras* — a *Nautilus*-*Sepia* equivalent

The observed $\delta^{18}O$ values of *Cadoceras*, ranging from −1.35‰ to +0.75‰, suggest an overall temperature change from 21.2 °C to 12.1 °C. After hatching at depths of probably less than 100 m at temperatures of 18 °C, *Cadoceras* migrated into deeper, cooler waters of up to 13 °C at depths of 200–400 m. Subsequently, the decreasing $\delta^{18}O$ values suggest a migration back into somewhat warmer, shallower habitats at 200 m with approx. 14 °C (cw-type, warm–cool–warm type). Near the aperture (samples 33–36), values increase, indicating a temperature rise of about 4–5 °C during mature age. This may be linked to spawning cycles in adults (Fig. 5). This $\delta^{18}O$ data pattern is reminiscent of that of *Nautilus* (Eichler and Ristedt, 1966a,b; Taylor and Ward, 1983) and *Sepia* (Bettencourt and Guerra, 1999; Rexfort and Mutterlose, 2006). Especially the pattern of *Sepia* is very similar and suggests a start in the epipelagic zone and a main phase in the mesopelagic zone. The tendency of *Cadoceras* to re-appear in the epipelagic zone during latest stages of ontogeny, however, is unparalleled by *Sepia* and *Nautilus* (both cw-type; warm–cool-type).

5.1.2. *Hypacanthoplites* and *Baculites* — inhabitants of the epipelagic zone

Throughout its life, *Hypacanthoplites* was a warm water dweller living in waters between 23 and 29 °C. Nevertheless, slight ontogenetic differences are evident. After hatching at depths of probably less than 100 m at temperatures of c. 24 °C, *Hypacanthoplites* migrated into even shallower and warmer waters of c. 26–29 °C in the upper epipelagic zone (cw-type, cool–warm type; Fig. 5). $\delta^{13}C$ values start relatively high in early ontogeny, jump markedly to +4.62‰, go down to a mean of +1.66‰ during a mid-aged phase and increase again to a mean of +3.06‰ in the adult stage. The first major decrease seems to mirror a change in habitat and probably also diet as suggested by the oxygen values.

No direct parallel trend can be observed in the modern cephalopods listed above. Only the recent deep-water squid *Spirula* displays minor similarities as it also starts in deeper habitats and then migrates into shallower areas (Lukeneder et al., 2008). The starting points, however, are completely different because *Spirula* hatches at depths of more than 1000 m at low temperatures of 4–6 °C (Fig. 5). Moreover, the last phase is different in *Spirula* and *Hypacanthoplites*. Mature *Spirula* migrates back into deep and cool habitats, whereas *Hypacanthoplites* apparently stays in surface waters. The general trend to inhabit shallower environments after hatching, however, is common to both taxa. In contrast, the three-phased $\delta^{13}C$ patterns of *Spirula* and *Hypacanthoplites* are strikingly similar. This suggests a strong change in diet at the transition from the juvenile to the mid-aged animal.
Stable isotope data of Baculites were provided by Fatherree et al. (1998) from the Western Interior Seaway (Late Campanian). The oxygen data (Fig. 4) suggest a seawater-temperature variation of about 10.0 °C, from 19.7 °C to 29.7 °C. Although the data set is incomplete, it appears that the investigated specimen changed into shallower waters after reaching maturity (Fatherree et al., 1998). In contrast to the pure surface water dweller Huypancunctholipites, it thus did change its depth preference and seems to have started as a juvenile in the lower epipelagic zone (Fig. 5).

5.1.3. Nowakites — a migrant between epi- and mesopelagic zones

The $\delta^{18}O$ values (−2.04% to −1.0%) suggest an overall temperature range from 24.2 to 15.8 °C. The trend within the last whorl of Nowakites indicates a general migration history from cooler and deeper waters of 15.8 °C at depths of 200–300 m into somewhat warmer, shallower habitats with approx. 19 °C (Fig. 5). Close to the aperture (samples 32–38), oxygen values increase by about 1.5‰, pointing to a distinct temperature decrease that might reflect a retreat to the mesopelagic zone in latest ontogenetic stages. This general trend is accompanied by a very rapid fluctuation causing a serrated pattern of the oxygen isotope curve. This regular serration could indicate frequent migration from the deeper and cooler mesopelagic zone into the shallow and warm epipelagic zone. The serration of the $\delta^{13}C$ curve supports this interpretation.

5.1.4. Perisphinctes — same habitat but different prey

Data on Perisphinctes have been provided by Lécuyer and Bucher (2006), although they did not cover the earliest ontogenetic stages. A threefold post-embryonic development is signaled by the oxygen values, which point to a shallow and warm late juvenile to mid-aged phase with c. 23–24 °C opposing slightly cooler and deeper juvenile and adult stages with 20–21 °C (Fig. 5). This pattern is somewhat similar to that of Spirula although the deep mesopelagic environment of Spirula (Lukeneder et al., 2008; Price et al., 2009) clearly differs from the epipelagic environment of Perisphinctes. The carbon pattern of the latter, however, has little in common with the former but is strongly reminiscent of that of Nautilus (very low embryonic and early juvenile values and a considerable shift towards positive values thereafter). As this shift is not reflected in the $\delta^{18}O$ values, it is likely that a major change in diet or the onset of sexual maturity caused the $\delta^{13}C$ shift without a marked change in habitat. The animals probably changed their prey preference after attaining a certain size.

5.2. Mode of life

The main difference between ammonoids and Recent cephalopods such as Spirula and Sepia is the maximum life-span. Sepia apparently attains an age of c. 200 days (Rexfort and Mutterlose, 2006), Spirula with lives approx. 2 years (Lukeneder et al., 2008) whereas ammonoids might have lived 5–100 years (Bucher et al., 1996; Westermann, 1996). Most estimates are based on proxy data derived from epifauna such as serpulids and bivalves (Seilacher, 1960; Meischner, 1968) and range between 1 and 15 years. Similar ages are suggested based on growth rate estimates based on growth line counting (Bucher et al., 1996). Calculations, based on growth rate comparisons with Nautilus achieved similar results with individual ages of 1–2 years for small, shallow water ammonites and 5–10 years for most pelagic taxa, comparable to those studied herein. Exceptions are the giant tyloceratids which seem to have grown 50 to 100 years (Westermann, 1996). Different growth rates in shallow water and deeper basinal environments, however, may complicate the calculations (Elmi and Benshli, 1987). Due to these uncertainties, we will not discuss the individual ages of the studied ammonites but focus on the clear ontogenetic trends.

Most ammonoids are supposed to have lived in the epipelagic and mesopelagic zones (Westermann, 1990; 1996). An epicontinental ocean with deeper immersed basins, with epi- and mesopelagic depth areas, is also assumed for deposition for all investigated specimens. In our reconstruction of depth, we use a model of an epicontinental ocean comparable to a gently sloping continental shelf with a steep continental slope. Different morphologies in ammonite shells (plesiomorphic to heteromorphic) and the variety of shell coiling (cadicone, ancylocercone etc.) were discussed as a reflection of differences in the mode of life (Cecca, 1997). Based on shell shape, septal, siphuncle and suture morphology, accompanied by investigations of co-occurring biofacies, Westermann (1990; 1996) proposed different life styles of certain ammonoids: juveniles of several pelagic ammonoids in the open ocean seem to have lived in deeper zones than the adults (e.g.: scaphitids or ancyloceratids). Nevertheless, Westermann (1996) suggested that about 50% of the pelagic ammonoids did not migrate within the water column. The pelagic type was opposed by taxa which seem to have changed from nektic to a demersal life style (e.g.: cadicone Fagesia, heteromorph Baculites). A nektobenthic mode of life for several taxa was also proposed by Wiedmann (1973), Vašíček and Wiedmann (1994) and Lukeneder (2003; 2005). Ebel (1992) suggested also a benthic, more gastropod like, life style for heteromorphs.

Further proxies for the mode of life are shell strength and morphology such as ribbing and whorl cross-section reflected in groups such as the Leiostraca (smooth shells, in deeper water) and the Trachyostraca (sculptured with ribbing, in shallow water) (Westermann, 1996). The stable isotope data, now, confirm this scenario. Hence, the $\delta^{18}O$ values of the trachyostracan representatives such as Hypacantholipites, Nowakites and Perisphinctes reveal them as inhabitants of the epipelagic zone. Hypacantholipites (Deshayesitidae, with moderately coarse ribbing, discocone) is interpreted to be an inhabitant of the photic zone of the uppermost 100 to 50 m in the water column with a planktic to nektic, mobile life style. Nowakites (Pachydiscidae with strong ribbing, platycone–discocone) seem to have preferred the transition from the epipelagic to mesopelagic zone, with a mobile to sluggish mode of life and strong vertical migrations. Heteromorphs, at least Baculites, apparently preferred a similar water depth. In contrast, the much more positive $\delta^{18}O$ values of the leiostracan Cadoceras indicate the cooler and deeper mesopelagic zone as the preferred environment. Based on this still low number of species, the general rule of thumb that Trachyostraca dominated in the neritic epipelagic zone <100 m water depth, whereas Leiostraca dominated in the deeper oceanic mesopelagic zone, seems to be valid.

A major difference in the modes of life of many ammonites compared to the modern cephalopods Spirula, Sepia and Nautilus is observed in their latest adult stage of ontogeny. All extant examples tend to retreat into the deepest environments as mature adult animals (Spirula, Sepia) or at least to remain there throughout their post-juvenile phase (Nautilus). In contrast, all measured ammonites except for Perisphinctes display a clear tendency to migrate into shallower environments in their latest ontogenetic stage (Fig. 5).

5.3. Cretaceous seawater temperatures: proxies from Hypacantholipites

Maximum $\delta^{18}O$ values in Hypacantholipites are −3.11% and correspond to temperatures of at least 28.9 °C. This paleotemperature corresponds with Mid-Cretaceous sea-surface temperature estimates of about 30–34°C (Mutterlose and Immenhauser, 2007). Similar values of 35 °C in the tropical zone and high-latitude temperatures of c. 20 °C have been proposed by Bornemann et al. (2008) for the Late Cretaceous. Stable isotope data on Atlantic sediments suggest a synchronous shift of $\delta^{18}O$ values in surface and deep ocean waters during the Middle and Late Cretaceous (Frakes, 1999; Fassell and Bralower, 1999; Bornemann et al., 2008) caused by an extreme greenhouse climate (supergreenhouse in Bornemann et al., 2008). Numerous papers discuss atmospheric conditions and ocean-atmosphere coupling during this Mid-Cretaceous climate-optimum (Caldeira and Rampino, 1991; Wilson and Norris, 2001; Donnadieu et al., 2006; Wagner et al., 2008). The unstratified
Jurassic and Cretaceous oceans allowed a warming of bathyal waters of up to 20 °C during the Cenomanian (Huber et al., 2002) and caused a strong heat flux from the tropic zone into high latitudes (Hay and DeConto, 1999; Mutterlose and Immenhauser, 2007). This explains the high paleotemperatures in the “boreal realm”, as indicated by Hypacanthoplites from northern Germany. Moreover, the compilation of δ¹⁸O literature data (Figs. 6 and 7) reveals an excellent fit of our Aptian Hypacanthoplites and Santonian Nowokites with expected greenhouse climate values. A comparable “hot” period was detected only during the Triassic (Figs. 6 and 7). Therefore, the estimated narrow migratory range of these taxa as reflected by oxygen values might be distinctly underestimated due to the buffering effect of an insignificant thermocline (Barrera and Johnson, 1999).

6. Conclusions

Both stable isotope records suggest separated main phases which correspond to ontogenetically controlled vertical migrations within the water column. δ¹⁸O and δ¹³C values mark three to four phases in ontogeny: embryonic, juvenile, mid-aged, and adult. The data demonstrate that the ammonoids started their life cycles in different environments (e.g. depth). This difference in strategies is detected in both stable isotope signatures (δ¹⁸O, δ¹³C), reflecting changes in diet, sexual maturity and mating to spawning phase.

The ontogenetic series of stable isotope records of the different ammonoid groups (Cadoceratidae, Deshayesitidae, Pachydiscidae) displayed highly divergent oxygen and carbon curves. This indicates

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Fig. 6. Cluster analysis after Bray–Curtis of the estimated temperature data set obtained by stable isotope data (δ¹⁸O). Calculated temperatures for Cadoceras, Hypacanthoplites and Nowokites perfectly cluster in the groups of same age estimated from literature data.
juxtapose different modes of life for the measured genera reflected in different migration patterns.

Stable isotope records ($\delta^{18}$O, $\delta^{13}$C) in Cadoceras and Hypacanthoplites suggest three main phases which correspond to ontogenetically controlled, vertical, long-time migrations within the water column. The $\delta^{18}$O values of juvenile Cadoceras shells steadily decrease from the juvenile −2.29‰ to an adult value of −2.80‰, with a mid-aged minimum of −3.11‰. This reflects an ontogenetic migration of Hypacanthoplites from shallow, warm marine environments to even warmer environments (27–28 °C). The $\delta^{13}$C values of juvenile Cadoceras shells steadily increase from juvenile (−0.93‰) to adult (+0.39‰), with a juvenile minimum of −1.35‰ and a mid-aged minimum of −0.75‰. This points to a shallow, c. 21 °C warm marine habitat of juvenile Cadoceras. Later, the mid-aged animal preferred slightly cooler and deeper environments (12–16 °C). Finally, the adult Cadoceras migrated back to slightly warmer and shallower environments (c. 17 °C).

The resulting maximum range of temperature to which the ammonoids were exposed during ontogeny is about 10 °C in Cadoceras and 6 °C in Hypacanthoplites. If compared to recent seawater temperatures [LEVITUS 94], this would suggest a bathymetric range of 50–700 m in Cadoceras and of up to 60 m in Hypacanthoplites. In respect to the unstratified ocean system during the Jurassic and Cretaceous, however, the observed data might point to even much larger ranges.

From the results we postulate at least two main ontogenetic strategies for the two morphological ammonoid groups Leiostraca and Trachystraca:

1. The cw-type (warm–cool–warm type) of Cadoceras resembles the strategy (wc-type, e.g. first two phases) and patterns represented by Nautilus and Sepia, which start in warm shallow waters as juveniles and migrate into deeper and cooler waters in later stages of ontogeny. In Cadoceras the temperatures decrease from 21.2 °C for juveniles down to 12.1 °C for mid-aged individuals and back up 16.9 °C in adults.

2. The cw-type (cool–warm type) of Hypacanthoplites, represented in a somewhat “modified” strategy in modern cephalopods by the first two ontogenetical phases in Sepia, migrated from deeper into shallower and back again in deeper (cw-type) habitats. The latter trend is slightly modified in Hypacanthoplites by reaching a higher temperature plateau. But during this higher level (e.g. adult phase) a slightly decreasing temperature is notable (28.9 °C down to aperture with 27.5 °C). Isotope data of Hypacanthoplites support the idea of a Mid-Cretaceous greenhouse with warm waters even in high latitudes.

Cadoceras exhibits a maximum temperature range of 10 °C, and $\delta^{18}$O values point to a temperature range of 6 °C in Hypacanthoplites, reflecting a bathymetric range in Cadoceras of 50–700 m and a water depth for Hypacanthoplites of approx. 10–60 m in ontogeny.

Ammonoids differ from Recent cephalopods as Spirula, Sepia and Nautilus by their increasing $\delta^{18}$O data of their last stage in ontogeny. All measured ammonoids except for Perisphinctes display a clear tendency to migrate into shallower environments during their latest ontogenetic stage. The impulse for the ontogenetic migrations in all groups is most probably the same as in modern cephalopods: firstly, the change in diets and secondly the mating–spawning phase in mid-aged to adult ammonoids.

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Appendix A. Supplementary data

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References


