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RESEARCH ARTICLE

Stable isotopes (δ^{18}O and δ^{13}C) in *Spirula spirula* shells from three major oceans indicate developmental changes paralleling depth distributions

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Abstract Stable isotopes (δ^{18}O and δ^{13}C) were measured in successive chambers of the aragonitic shells of the small deep-sea squid *Spirula spirula* (Linnaeus 1758) (class Cephalopoda, subclass Coleoidea, order Sepioidea, family Spirulidae) to determine whether their depth distributions change with age. The spiral shells, ranging in diameter from 18 to 23 mm (30–38 chambers), were collected between 2000 and 2006 from beaches in six widely separated locations in three oceans, the Atlantic (Tobago and Canary Islands), Indian (Madagascar, Maldives, and Perth, Australia), and Pacific Oceans (Ulladulla, Australia). The patterns for both isotopes were highly correlated in specimens from all six sites. The δ^{18}O data suggest that after hatching at depths >1,000 m at temperatures of 4–6°C, the squid migrate into shallower, warmer waters at 12–14°C at depths of 400–600 m. Subsequently, the increasing δ^{18}O values suggest a migration back into somewhat cooler, deeper habitats. The δ^{13}C values also revealed three ontogenetic stages in all six specimens, including a major shift from positive to negative values, which probably corresponds to sexual maturation, the initiation of reproduction, and concomitant changes in diet. In three of the six specimens (from Tobago, Canary Islands, and Maldives) a fourth embryonic stage (not detected in the oxygen data) was accompanied by markedly less positive δ^{13}C values in the first few chambers. These data, combined with the scanty life history information from previous studies of *S. spirula*, can be used to compare the habitat requirements of related extant and fossil cephalopod genera.

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Introduction

Knowledge of the ecology and life cycles of recent deep-water organisms is still poor. Among these cephalopods, one tiny cephalopod has proved to be especially elusive: *Spirula spirula* (Decabrachia, suborder Spirulina), the so-called ram's-horn-squid (Clarke 1966; Donovan 1977; Warnke et al. 2003; Lindgren et al. 2004). While *S. spirula* is frequently found on shorelines around the major oceans, information on its habitat and ecology is scarce and imprecise. This species has never been observed or filmed in its actual habitat, the mid- to deep-water zone, largely because of the relative inaccessibility of the deep-sea environment. The ram's-horn-squids are a little-known group of the open subtropic to tropic oceans from about 30°N to 30°S (Clarke 1986) (Fig. 1). Spawning of *S. spirula* apparently takes place in benthic habitats in deep waters over the deepest slopes (1,000–2,000 m), mostly around tropical islands (Bruun 1943; Clarke 1970; Goud 1985;Young et al. 1998). Females are thought to lay eggs on the bottom of the lower continental slope at depths down to 1,750 m. This strategy is comparable to most other cephalopods, although most of them prefer shallower depths.

Adult spirulids are present in high abundance at mesopelagic depths of ~600–800 m, corresponding mostly to the

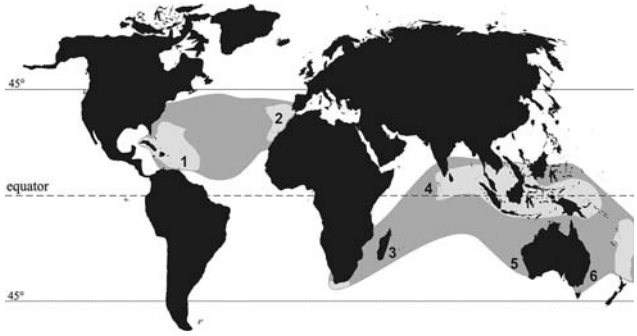

Fig. 1 Distribution of *S. spirula*. *Light-grey* areas indicate live catches., *Dark-grey* regions mark shells found on beaches, by drifting, and fishery bycatch. *Numbers 1–6* correspond to sites in the present study where shells were collected. Distribution map compiled after Bruun (1943), Goud (1985), Schmidt (1922), Norman (2007), and the authors' unpublished data

continental slopes. *Spirula spirula* undertakes vertical day–night migrations, as is characteristic of many planktonic ocean dwellers. Migration distances from 600 m depth at midday to 250 m or less at midnight were reported by Clarke (1969). Details of distribution are best summarized in fishery reports by Bruun (1943) and expedition reports by Joubin (1995). Accordingly, *S. spirula* inhabits the slopes of islands along the margins of the major oceans rather than the open oceans themselves (Fig. 1). Most specimens occurred in depths of 550–1,000 m during the day (peaks at 600–700 m), whereas at night, aggregations were recorded from 100 to 300 m (peaks at 200–300 m) (Clarke 1969). Bruun (1943) stated that the youngest (smallest) specimens were mostly found at depths of 1,000–1,750 m. Clarke (1969) suggested that the latter depth (1,750 m) was the thermocline, which could not be passed by the truly oceanic *S. spirula*.

The ram's-horn squid is important in that it represents another cephalopod with a chambered shell, like the *Nautilus* species. Buoyancy is regulated by the internal aragonitic shell apparatus, as in *Nautilus* spp. and ammonites. The phragmocone of *S. spirula*, connected through a tiny ventral siphuncle, acts as a buoyancy device and can withstand a pressure of at least 200 atmospheres (Clarke 1986).

The name-giving horn-shaped internal shell is positioned at the posterior end of the living squid and, due to its calcareous composition, is suitable for isotopic measurements. Shells consist entirely of pristine aragonite. The outer shell wall is composed of three layers: the outer prismatic, the middle granular and the innermost prismatic layer (Appellöff 1893; Dauphin 1976; Dauphin 2001a, b; Doguzhaeva 1996, 2000; Mutvei 1964; Mutvei and Donovan 2006). The septa consist of four different layers: the dorsal conchiolin, the spherulitic-prismatic, the nacreous and the semi-prismatic layer. Hexagonal aragonite platelets typical for the nacre layer of other cephalopods are absent.

The shell is completely enclosed by the mantle. It is subcutaneous and located in a completely closed shell sac, which adheres to the outer wall of the shell (Chun 1915).

Living *S. spirula* and specimens from fishery by-catch were previously investigated in the late nineteenth century by Appellöff (1893) and Pelseneer (1895), and in the first half of the twentieth century by Chun (1910, 1915), Schmidt (1922), Naef (1922), Böggild 1930, Kerr (1931), Turek (1933) and Bruun (1943). Those detailed anatomical and morphological studies have been more recently complemented by Clarke (1966), Bandel (1982), Dauphin (1976; 2001a, b), Joubin (1995), Lu (1998), Keupp (2000), and Warnke and Keupp (2005).

The open planispirally coiled shell is formed internally within the posterior part of the body and remains covered by the soft tissue during most of the squid's life. Only in fully grown specimens does the internal shell foraminate the mantle on the ventral and dorsal sides. The spiral, chambered shell is a key character in determining the relationships between the genera *Spirula*, *Nautilus*, and the extinct ammonites. Moreover, the *S. spirula* shell provides insight into the autecology of these organisms, the developmental history of each specimen, and the favoured environment of the whole group. The exquisitely preserved shells provide a reliable geochemical archive, which reflects the life-span migration cycle of the ram's-horn-squid.

Comparable investigations on isotope records from cephalopod hard parts have been carried out by Eichler and Ristedt (1966), Cochran et al. (1981), Taylor and Ward (1983), Rexfort and Mutterlose (2006), and Landman et al. (1983, 1994). Isotopes of *Nautilus* spp. shells were measured by Eichler and Ristedt (1966) for *N. pompilius*, Landman et al. (1983, 1994) for *N. belauensis* and Auclair et al. (2004) for *N. macrompahlus*. In most studies the results were compared and correlated with measurements on fossil cephalopods such as belemnites or ammonites. Mutterlose and others focused on the isotopic records of sepiids.

According to the formula $T(°C) = 20.6 - 4.34 (\delta^{18}O_{aragonite} - [\delta^{18}O_{water} - 0.2])$ (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. The ratio can therefore be used to define the relationship between oxygen isotopes and water temperature manifested in aragonitic shells such as those of *S. spirula.* As noted by Cherel and Hobson (2005) and Hobson and Cherel (2006) in cephalopod beaks, $\delta^{13}C$ values can be a valuable tool for reconstructing cephalopod feeding ecology. Food webs and food selection can be determined by testing the incorporated carbon fraction revealed in differentiated $\delta^{13}C$ values.

No specimens of the ram's-horn-squid *S. spirula* have been investigated to reconstruct their life and habitat during ontogeny. Interpretations of the ecology and habitat preferences

of this species are currently based solely on dredging and fishery bycatch data. Here, we used the aragonitic internal shells as a biological proxy to interpret ontogenetically related environmental changes in this model cephalopod.

One of the main objectives of the present study was to determine the possible ontogenetic migrations by analysing the stable isotopes ($\delta^{18}O$, $\delta^{13}C$) and, if such individual changes occur, whether these migrations are similar in different oceans. This approach is a starting point for more detailed isotope analysis in deep-water species combined with investigations of fossil cephalopod material.

Material and methods

Material and sampling sites

Six dead shells of *Spirula spirula* were analysed. They were collected from the western Atlantic (shore deposits of Speyside beach, NE Tobago, 10 km south of Toco; March 2005; site 1), the eastern Atlantic (El Médano beach, SE Tenerife, 20 km east of Los Christianos, Canary Islands; January 2005; site 2), the western Indian Ocean (Manakara beach, 200 km south of Antanarivo, SE Madagascar; April 2000, site 3), the northern Indian Ocean (Kuredu beach, Lhaviyanin Atoll, North Maldives, 100 km north of Malé; February 2006; site 4), the eastern Indian Ocean (Sorrento beach, 13 km N of Perth, Western Australia; July 2006; site 5), and the western Pacific Ocean (Ulladulla Beach, East Australia; June 2002; site 6) (Fig. 1). The distribution map was compiled after Bruun (1943), Goud 1985, Schmidt (1922), Norman (2007), and our own unpublished data. Additional material from the same localities is stored at the Natural History Museum Vienna, Austria (NHMW2007z0095/0001-6). The analysed cephalopod shells ranged from 18 to 23 mm in maximum diameter and represented fully grown adult specimens. The phragmocone of the endogastrically coiled shells displayed 2.5 whorls segmented into 30 to 38 barrel-shaped chambers connected by a ventral siphuncle (Fig. 2a, b). The sex of the measured

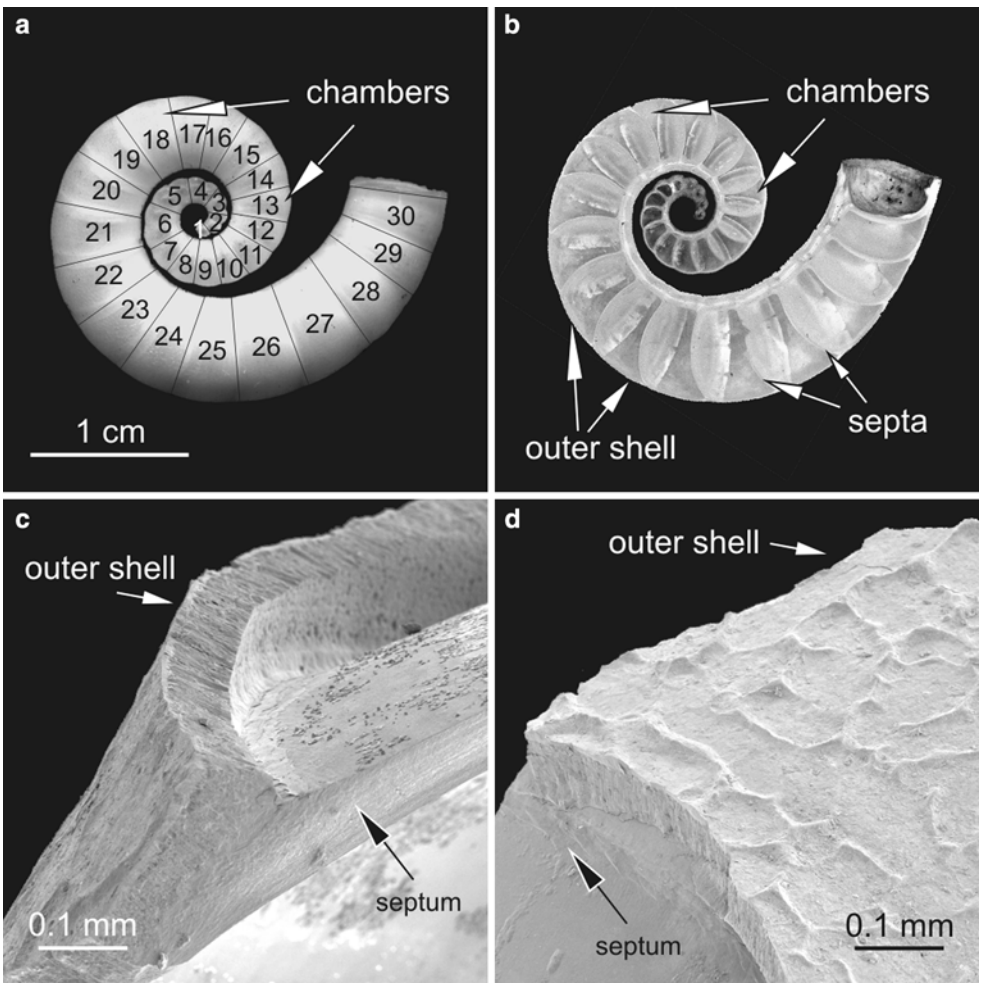

Fig. 2 *S. spirula*: **a** side view with chambers numbered 1–30 in the growth direction; **b** Median section of shell showing chambers separated by septa; **c**, **d** SEM images of aragonitic ultrastructure of shells

specimens is unknown. The isotope measurements were conducted in successive chambers in the growth direction and targeted ontogenetic variations in the life cycle of *S. spirula*.

Data collection and analyses

Six shells of *Spirula spirula* from the tropical Atlantic, Pacific, and Indian Oceans were analysed for their stable isotope (δ^{18}O and δ^{13}C) composition. The ontogenetic trend within the shells was detected by sampling chamber by chamber in the growth direction. No contamination with finer organic or inorganic particles was observable under the light microscope (Leica MZ 6) and SEM (JEOL JSM-6400).

To take into account the possible within-shell variation in isotopic composition [cf. Auclair et al. (2004) in *Nautilus macromphalus*], the within-shell variation of one *S. spirula* was measured. Sub-samples were taken from the septa, sipho, and three areas of the chamber wall: near the sipho, marginally, and opposite the sipho. Standard deviation was <0.08‰ for δ^{18}O and 0.04‰ for δ^{13}C based on repeated measurements (five replicates) of international standards NBS18 and NBS19.

Isotope data were obtained using an automatic Kiel II preparation line and a Finnigan MAT Delta Plus mass spectrometer. Samples were dried and reacted with 100% phosphoric acid at 70°C. The international standards NBS-19, NBS-18, and an internal laboratory standard were analysed at regular intervals for accuracy control. Isotopic data are reported in conventional δ notation relative to the Vienna Peedee belemnite (V-PDB) standard in ‰ units.

Primary aragonite was detected by dry chemical powder measurements with a Siemens D5000 θ–θ powder X-ray diffractometer at 25°C (radiation was Cu–K_α, 2.0 s, 0.01° intervals) at angles of 2°–65°. 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.

Results

The powder X-ray diffraction pattern of the *S. spirula* shell material studied shows unaltered and clean primary aragonite composition of the shell (Fig. 2c, d; supplemtary information). The position, height, and distance of the diffractometer curve-peaks fit perfectly with pristine and primary aragonite. No second mineral phase was present.

The sclerochronological isotope records of all measurements from *Spirula spirula* displayed highly correlated patterns with near-parallel curves (Figs. 3, 4). This indicates a very similar mode of life for all specimens and the same vertical migration patterns in Atlantic, Pacific and Indian

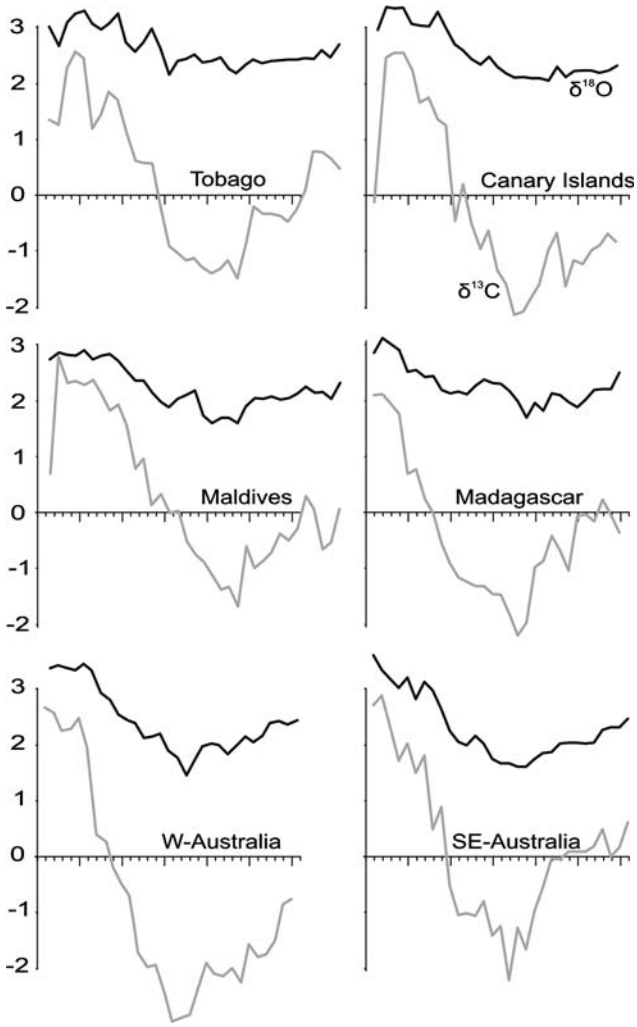

Fig. 3 Isotope data for the deep-water squid *S. spirula* from six sites

Ocean specimens. Both stable isotope records suggest three main phases which correspond to ontogenetically controlled vertical migrations within the water-column: the δ^{18}O values of juvenile shells steadily decrease from c. 3.5–3.0 to 1.7–2.0 and then slightly increase to 2.2–2.6 in adults (Fig. 3). This likely reflects an ontogenetic migration after hatching in deep, cold seawater at temperatures around 4–6°C to shallower, warmer waters at 12–14°C. According to $T(°C) = 20.6 - 4.34\ (\delta^{18}O_{aragonite} - [\delta^{18}O_{water} - 0.2])$, a shift of one per mil in the oxygen isotope ratio corresponds to a temperature change of 4.34°C (Grossman and Ku 1986; McConnaughey et al. 1997; Goodwin et al. 2003). The resulting maximum range of temperature to which the squids are exposed during ontogeny is 9.1°C. This reflects a bathymetric range of 800–1,000 m (LEVITUS 94) for juveniles and a water depth of c. 400–600 m (LEVITUS 94 1994) in later ontogenetic stages (Fig. 5).

δ^{13}C values correlate positively with the δ^{18}O data but have much larger amplitudes. The three main ontogenetic

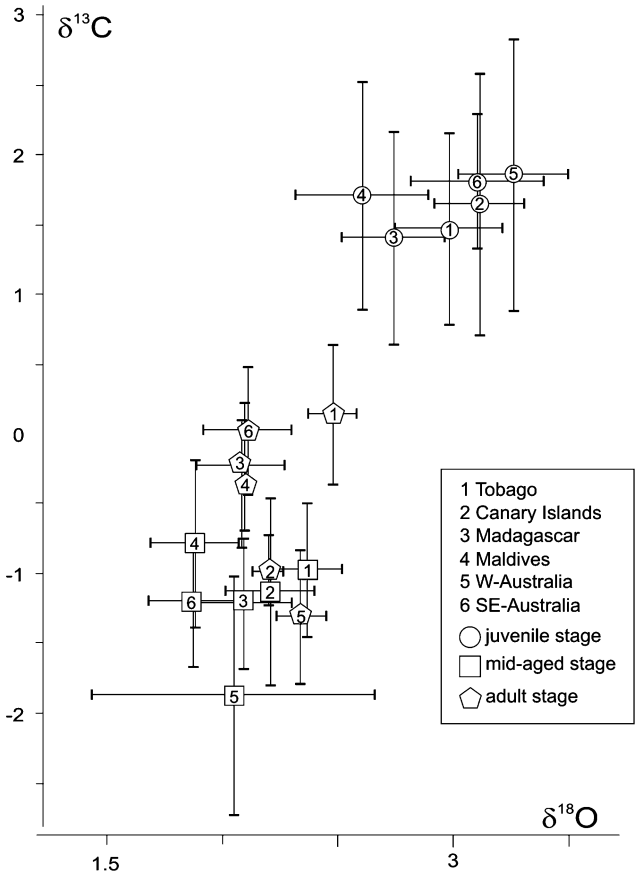

Fig. 4 $\delta^{18}O/\delta^{13}C$ cross plot with mean values and standard deviations for the defined ontogenetic phases (juvenile, mid-aged, adult). Embryonic data were omitted due to their rareness. Clear separation of the juvenile phase is evident

stages are very distinct, as revealed by the oxygen isotopes, and are accompanied by a fourth embryonic one, not reflected in the oxygen data. Three specimens whose initial chambers were preserved showed a striking negative excursion of the $\delta^{13}C$ values in embryonic stages represented by chambers 0 to 2 or 3. This rarely recorded phase represents the pre-hatching stage and has also been documented for *Nautilus pompilius* (Cochran et al. 1981). Then there is a juvenile stage corresponding to positive $\delta^{13}C$ values. This phase is shown by $\delta^{13}C$ values from 2 to 0, but in contrast to the first phase the values decrease rather gradually. The juvenile stage is followed by a mid-aged stage with negative $\delta^{13}C$ values decreasing from 0 to −3 and then increasing to −1. The adult stage is characterized by $\delta^{13}C$ values steadily increasing from about −1 to a final mean of 0 (Fig. 5). This trend was observed in all specimens. A separation of the data into these postulated stages (Fig. 4), plotted in $\delta^{18}O/\delta^{13}C$ cross-plots revealed a clearly separated isotope field comprising the juvenile phase and a moderately separated cluster with the mid-aged and adult stages.

Discussion

The stable isotope records of six *Spirula spirula* shells support the hypothesis that these squid spawn on the sea floor at a water depth >1,000 m. The embryonic stages, however, were reflected only by the carbon signatures in the present study. Our data demonstrate that this cephalopod starts its life cycle in deep bottom waters after hatching. During early growth, migratory behaviour is initiated and the squid move into warmer and shallower waters at about 400–600 m depth (Fig. 3). Diurnal migration into very shallow waters at about 200 m, as documented by fishery data (Clarke 1970), was not reflected in our istope data because the squid apparently reduce biomineralisation during that phase. During mid-life, both isotope signatures showed a peak which may reflect sexual maturity and mating. Then all specimens showed a tendency to migrate back into slightly deeper and cooler habitats, as expressed by the slightly rising $\delta^{18}O$ values. The isotope curves of the Atlantic and Pacific specimens showed identical overall trends. In both oceans, *S. spirula* showed similar temperature profiles and corresponding durations of individual ontogenetic stages. No behavioural vicariance of the disjunct populations was evident in our data.

The $\delta^{18}O$ values support the data obtained from fishery catches of *S. spirula* and strengthen previous suggestions that these squid migrate from deep waters to shallower, warmer waters as they grow and mature. The $\delta^{13}C$ values mark the four phases in ontogeny: embryonic, juvenile, mid-aged, and adult. $\delta^{18}O$ data showed a minimum temperature of 4.3°C in the embryonic stage and an environmental temperature of 13.4°C in a mid-aged specimen. These data indicate that adults, at the age of approximately 1.5 year (Clarke 1970), migrate to somewhat cooler waters at about 9.1°C in their last months of life.

This appearance strengthens also the idea of benthic hatching in *Spirula*. Evidence suggests that larval stages do not migrate after hatching, but that migration takes place after forming the first chambers (Lu 1998). This is supported by the $\delta^{18}O$ data, which show a stable phase during the first month of life in *Spirula* (Fig. 4). Embryos probably stay in cooler waters for the first phase of life. Upward migrations apparently start at around chamber 5. The $\delta^{18}O$ curve shows that the lowest depth and therefore a temperature of at most 13.4°C go hand in hand with reaching sexual maturity; this is also reflected in the $\delta^{13}C$ signature, which shows maximum values around −3.

The same ontogenetic differences were observed by Clarke (1970). He reported three different size-groups in 256 *S. spirula* specimens caught by fishery with different types of nets around Fuerteventura Island (Canaries). The largest individuals were 2.4–4.6 cm in maximal mantle length, with mature females being smaller (abundance peak

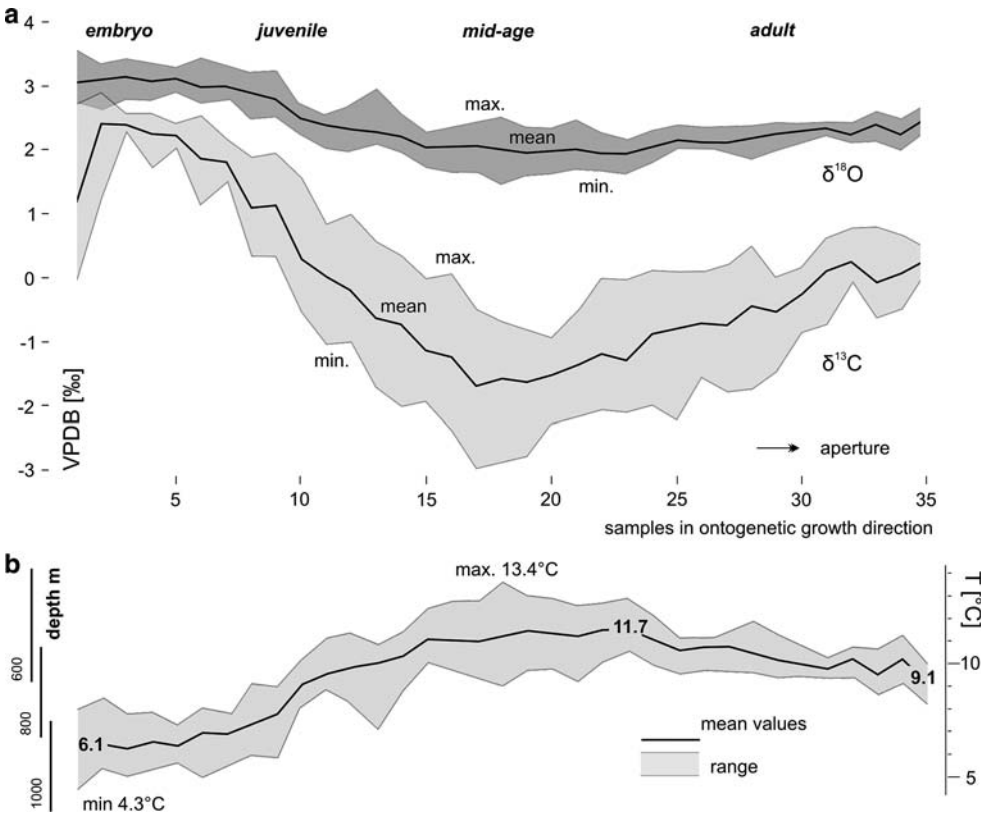

Fig. 5 Distribution and ontogeny in *S. spirula*. **a** δ^{18}O (*dark*) and δ^{13}C (*light*) lines in growth direction. **b** Calculated water temperatures and depth distribution of *S. spirula*

at 3.0 cm mantle length) than mature males (3.6 cm). He supposed the group >2.3 cm to be adults. Based on the numbers of spirulids captured over 1 year, Clarke concluded that hatching probably took place in June to July and the squid grew to maturity after 12–15 months, when mating and egg-laying took place. This suggested a protracted embryonic stage from October to December to the following June or July, and a life span of 18–20 months. The few captures in March indicated a reduced population at this time due to spawning, death, or movement into deeper waters (Clarke 1970). Sea-surface catches of drifting dead *S. spirula* shells were more numerous in March around Fuerteventura, suggesting increased mortality at that time. *Spirula spirula* has a very long breeding season, with a peak during the winter months, and grows for a little more than a year until reaching sexual maturity (Bruun 1943).

The carbon signatures in the present study are clearly related to ontogenetic effects because changes in ambient sea-water chemistry during vertical migration could not account for the large range of values. Moreover, the shift towards negative values coinciding with a vertical migration into shallower water contradicts the expected trend towards positive values (Warnke and Keupp 2005) if carbon signatures of ambient water had been incorporated. Such decoupling from expected water signatures due to ontogenetic effects is also known from *Sepia officinalis* (Rexfort and Mutterlose 2006).

An explanation for such a high-amplitude pattern is that sexual maturation and initiation of reproduction was strongly correlated with the major shift towards negative values. Simultaneously, the ontogenetic vertical migration likely coincides with diet changes, which, in turn, would amplify the δ^{13}C signature. Such feeding- versus sexual-maturation-related changes in the biochemical composition of body tissue are also known from ommastrephid squids (Rosa et al. 2005). The return of adult squid to deeper waters for mating and egg production seems to correlate with a return to early feeding strategies, reflected in comparable δ^{13}C budgets.

New methods for reconstructing cephalopod food webs using isotope data from cephalopod beaks were recently described by Cherel and Hobson (2005) and Hobson and Cherel (2006). Cherel and Hobson (2005) and Hobson and Cherel (2006) showed a direct relationship between the incorporated δ^{13}C and δ^{15}N values and cephalopod diets. Compared to the isotope data from *Sepia officinalis* and other squids, the ontogenetically controlled changes found in the present study in the deep-water squid *S. spirula* are the most dramatic presently known.

At night, *S. spirula* migrates into shallower waters to feed on molluscs and planktonic krill. Nixon and Dilly (1977) reported that spirulids feed on pelagic crustaceans based on the remains found in the stomachs of several specimens and concluded that they are capable of prey selection

(Kerr 1931; Young 1977). *S. spirula* stomachs contained small crustaceans as copepods and ostracods.

Comparing the isotope data set with data obtained from *Nautilus* spp. (Eichler and Ristedt 1966; Cochran et al. 1981; Landman at al. 1983,1994; Taylor and Ward 1983; Auclair et al. 2004) and *Sepia offcinalis* (Rexfort and Mutterlose 2006) shows that the isotope signatures of *S. spirula* allow precise differentiation between the modes of life of these model cephalopod genera. The comparison of Recent *Nautilus*, *Sepia*, and *Spirula* allows quite different modes of life to be deciphered based on stable isotope signatures. Application of these methods to Mesozoic ammonites 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 many paleontological papers attempting to interpret the mode of life of Mesozoic ammonites. Thus, a deeper understanding of this squid's life cycle and the applicability and comparability of our method to fossil shells will be the basis for further studies of fossil cephalopod shells and their ecological interpretations.

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