

Abrupt changes in distance between succeeding septa at the hatching time in modern coleoids *Sepiella japonica* and *Spirula spirula*

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Abstract Analyses of distances between succeeding septa throughout ontogeny of modern coleoids *Sepiella japonica* and *Spirula spirula* reveal that the first several septa (until ca. 6th–8th septa in *Sepiella japonica* and until ca. 2nd–3rd septa in *Spirula spirula*) have relatively larger septal distances than the following septa and then the distances between succeeding septa abruptly decrease at the time of hatching for both species, which are known from previous rearing observations and stable isotopic analyses. If this relationship holds in fossil cephalopods preserving internal shells, their paleo-hatching timings could be reconstructed through the ontogenetic analyses of their septal distances.

Keywords Septa · Hatching · Ontogenetic change · *Sepiella japonica* · *Spirula spirula*

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Introduction

Some modern coleoids, such as those found in the families Sepiidae and Spirulidae, have internal shells that function as buoyancy devices (Denton and Gilpin-Brown 1964, 1971; Denton et al. 1967). These internal shells have septa, which divide the shells into phragmocones used to regulate buoyancy. As coleoids grow, new septa are formed within their internal shells, thus generating a record of ontogenetic growth. In cephalopods with external shells (e.g., modern and fossil nautiloids and ammonoids), the external shells also have septa that delineate air chambers. Numerous studies have been dedicated to the ontogenetic analysis of the septate external shells of cephalopods to reconstruct ontogenetic growth in modern nautiloids (Landman et al. 1983; Collins and Ward 1987; Tanabe and Tsukahara 1987; Landman 1988; Klug 2004; Chirat et al. 2008; Klug et al. 2008), fossil nautiloids (Ruzhencev and Shimansky 1954; Davis and Mohorter 1973; Landman et al. 1983; Landman 1988; Chirat and Rioult 1998; Chirat 2001; Wani and Ayyasami 2009; Wani and Mapes 2010) and ammonoids (Kulicki 1974; Doguzhaeva 1982; Checa 1987; Landman 1987; Dommergues 1988; Bucher et al. 1996; Okamoto and Shibata 1997; Korn and Titus 2006; Ebbighausen and Korn 2007; Kraft et al. 2008; Arai and Wani 2012). However, little attention has been devoted to the study of internal cephalopod shells and their ontogenetic analysis (but see Hewitt and Stait 1988). If there is any common feature in the ontogenetic patterns of septal distances among cephalopods, similarities in septal distances are expected to be seen in those with internal shells. In this study, two representatives of modern coleoids with internal shells were analysed, especially focusing on hatching time. These analyses were used to identify patterns of ontogenetic growth, with implications for fossil cephalopod growth analysis.

Materials and methods

Source of specimens

Eleven cuttlebones of *Sepiella japonica* Sasaki, 1929 and 12 shells of *Spirula spirula* (Linnaeus, 1758) were used for the analyses of septal distance in this study (Fig. 1; Tables 1, 2; deposited in the Mikasa City Museum, Hokkaido, MCM.A.1741–1763). Entire specimens of *Sepiella japonica* with soft parts were obtained from a fish market. These specimens were caught from the Seto Inland Sea, Japan (Fig. 2a). The environmental information (e.g., seawater temperature, depth) of the area where these animals lived is unknown. An attempt was made to sex the specimens by examination of sex organs (the presence of

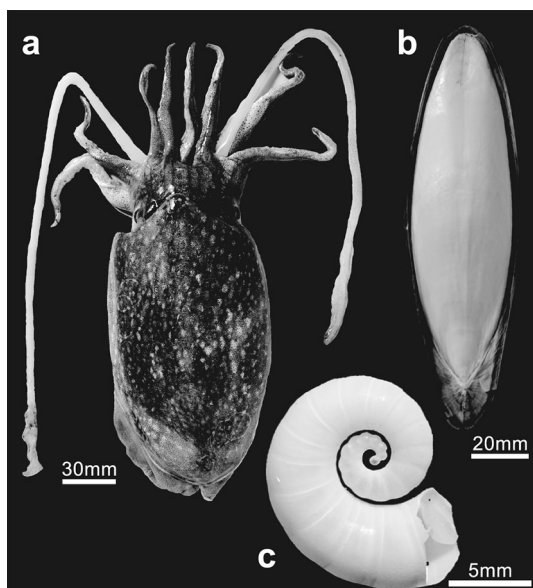


Fig. 1 Photographs of the examined coleoid species. **a** *Sepiella japonica*, including soft parts. **b** Cuttlebone of *Sepiella japonica*. **c** Shell of *Spirula spirula*

spermary or ovary). Five out of 11 specimens were successfully sexed, and these were all female.

Among the examined specimens of *Spirula spirula*, nine shells were obtained as beached shells at Taemaro Bay, New Zealand (Fig. 2b), and three shells were obtained at a shell market. These market shells were collected as beached shells at Lanzarote Island of the Canary Islands (Fig. 2c). The exact beach locations and environmental information where these specimens were collected is unknown.

Specimen analysis

The cuttlebones of *Sepiella japonica* were first embedded in transparent epoxy resin to avoid damage to the thin septa and then the cuttlebones were cut along the median line. Cuttlebone longitudinal sections were examined under a digital microscope (Keyence, VHX-900, with magnification of 25–175 \times) and distances between succeeding septa were measured to the nearest 0.01 mm from the median point of the septa, perpendicularly to the previous septum (Fig. 3a).

The morphology of *Spirula spirula* shells approximates a logarithmic spiral. Thus, the septal distances between succeeding septa were defined by the septal rotational angle at the position of attachment between the septa and the shell whorl (Fig. 3b). This is the same method commonly used to examine the septal angles of ammonoids and nautiloids (Wani and Mapes 2010; Arai and Wani 2012, and references therein). The centre of the rotational angles was approximated as the centre of the logarithmic shell spiral approximating the shell whorls (see Arai and Wani 2012 for detailed methods to determine the spiral's centre). The septal distances between succeeding septa were measured using a digital microscope (Keyence, VHX-900, with magnification of 25–175 \times). This septal distance is defined as the rotational angle of two succeeding septa (i.e., septum numbers N and $N-1$) at the positions of attachment between the septum and the shell whorl (Fig. 3b).

Table 1 Examined specimens of *Sepiella japonica*, from the Seto Inland Sea, Japan

Specimen no.	Repository no.	Sex	Cuttlebone length (mm)	No. of septa
SJ1-3	MCM.A.1741	–	140.5	137
SJ1-7	MCM.A.1742	–	157.5	147
SJ1-10	MCM.A.1743	–	147.6	136
SJ2-1	MCM.A.1744	–	156.0	127
SJ2-2	MCM.A.1745	–	157.4	140
SJ2-3	MCM.A.1746	–	152.7	143
SJ2-4	MCM.A.1747	F	145.3	116
SJ2-5	MCM.A.1748	F	158.0	143
SJ2-6	MCM.A.1749	F	145.1	141
SJ2-7	MCM.A.1750	F	143.8	149
SJ2-9	MCM.A.1751	F	143.1	142

– Sex was not recorded

Table 2 Examined specimens of *Spirula spirula*, from Taemaro Bay, New Zealand and the Canary Islands

Specimen no.	Repository no.	Locality	Shell diameter (mm)	No. of septa
SS7	MCM.A.1752	Taemaro Bay, NZ	19.0	32
SS12	MCM.A.1753	Taemaro Bay, NZ	20.0	30
SS14	MCM.A.1754	Taemaro Bay, NZ	15.7	27
SS15	MCM.A.1755	Taemaro Bay, NZ	20.6	31
SS16	MCM.A.1756	Taemaro Bay, NZ	19.7	32
SS21	MCM.A.1757	Taemaro Bay, NZ	20.0	30
SS22	MCM.A.1758	Taemaro Bay, NZ	19.3	32
SS23	MCM.A.1759	Taemaro Bay, NZ	18.7	30
SS24	MCM.A.1760	Taemaro Bay, NZ	17.2	29
SS17	MCM.A.1761	Canary Is., NW Africa	13.5	26
SS18	MCM.A.1762	Canary Is., NW Africa	14.3	25
SS19	MCM.A.1763	Canary Is., NW Africa	13.4	25

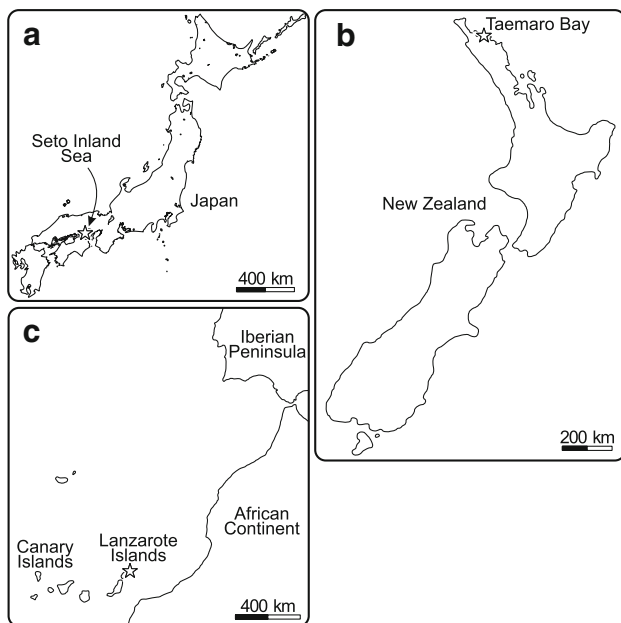


Fig. 2 Maps showing the localities of the examined specimens. **a** The Seto Inland Sea, Japan, where the specimens of *Sepiella japonica* (11 specimens) were caught. **b** Taemaro Bay, New Zealand, where some of the specimens of *Spirula spirula* (nine specimens) were collected. **c** The Canary Islands, northward of Africa, where the remaining specimens of *Spirula spirula* (three specimens) were collected

Results

Sepiella japonica

The septal distances for *Sepiella japonica* are shown in Fig. 4 and Supplementary Material 1. The results show that the distances between septa follow a general decrease in their means (\pm SD) from the first septum (0.29 ± 0.14 mm) to the 8th septum (0.13 ± 0.06 mm), and a subsequent linear increase in mean from the 9th septum (0.16 ± 0.06 mm) to the 42nd septum (0.45 ± 0.17 mm).

The measurements between septa from the 42nd to the 139th septum are maintained between 0.43 and 0.50 mm, followed by a decline to a single measurement of 0.19 mm on the last 149th septum. It is notable that the standard deviations of measurements between septa decrease dramatically from the first septum to the 8th septum and then increase gradually toward the point at which measurements level off (around the 40th septum). Large standard deviations are observed until about the 130th septum where variations decrease. These variations were closely linked to growth patterns that separated specimens into two groups with larger (specimen nos., SJ2-2, SJ2-3, SJ2-4, SJ2-6) and smaller (specimen nos., SJ1-3, SJ1-7, SJ1-10, SJ2-1, SJ2-5, SJ2-7, SJ2-9) septal distances (Fig. 4a). These differences were particularly evident in the middle of the ontogenetic growth between the 20th and 135th septum.

Spirula spirula

Spirula spirula specimens from two different localities across the globe had similar patterns in septal distances (Fig. 5; Supplementary Material 2). Results show that the first septum has the greatest distance with a mean (\pm SD) angle of $50.29^\circ \pm 11.92^\circ$, followed by a sharp decrease to about 3rd septum. A gradual decrease in distances was observed for subsequent measurements. There also was an indication of a slight increase or peak in septal distances at around the 10th septum, and another low but broad peak from the 20th to the last septum.

Discussion

Septal distances in *Sepiella japonica*

Septal distances for *Sepiella japonica* show a clear decrease in mean distance and variation among

Fig. 3 Measurements of septal distance and angle. **a** Schematic diagram of the cross section of *Sepiella japonica*. **b** Septal angles in *Spirula spirula*

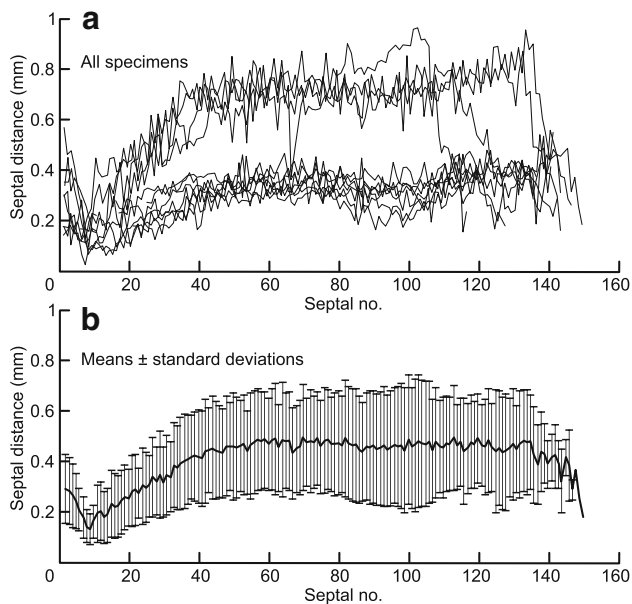
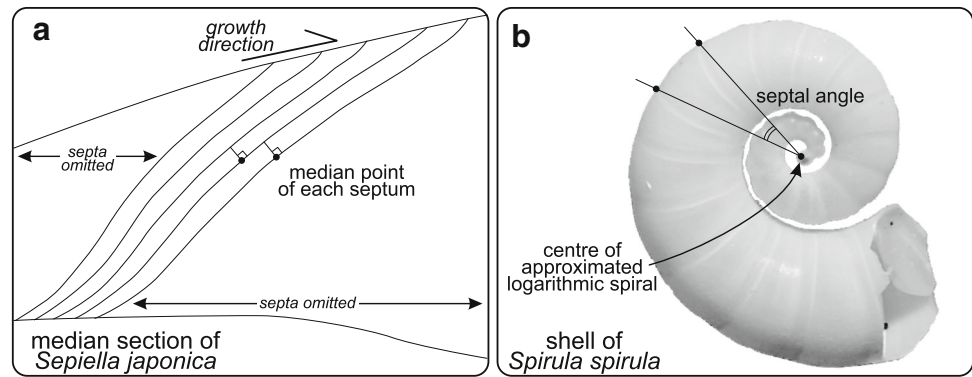


Fig. 4 Septal distances in *Sepiella japonica*. **a** The septal distance of all specimens, which were superimposed for comparison. **b** The mean septal distances with bars of standard deviations

measurements at the 8th septum. Previous rearing studies of *Sepiella japonica* have shown that this species has 7–9 septa when they hatch (Oshima and Choe 1961; Choe 1962), which suggests that the sharp decrease in septal distance observed in this study at the 8th septum is associated with hatching. Furthermore, based on the results of this study, we estimate that *Sepiella japonica* attains maturity when septal distances dramatically decrease after about 135th septum. These decreasing trends of septal distances at hatching and maturity have been similarly observed in modern and fossil nautiloids (Wani and Ayyasami 2009; Wani and Mapes 2010; and references therein).

The results of the septal distances in *Sepiella japonica* clearly indicate that the specimens can be clustered into two groups, although both groups share common features including (1) the transition of the septal distances at about

the 8th septum, and (2) decreasing septal distances in the last several septa. These patterns in mean distances were closely associated with differences in standard deviations along the life cycle, suggesting that hatching time and maturity at the end of shell growth are constrained events common to both groups. Two possible explanations for the separate growth clusters include habitat differences and sexual differences. Unfortunately, the environmental conditions (e.g., seawater temperature, water depth) of these animals' habitats are unknown. However, it has been reported that *Sepiella japonica* is very sensitive to environmental changes (e.g., water temperature and salinity), which may result in physiological stress (Zheng et al. 2014) and potential differences in growth rates. The species is also known to swim in schools (Oshima and Choe 1961; Boyle and Rodhouse 2005). Therefore, different schools may adapt slightly differently to environmental conditions, which possibly reflects differences in growth patterns. Further studies with specimens collected from distinct locations with known environmental conditions will be needed to identify potential growth differences due to environmental conditions.

Differences in septal distances in the middle of the ontogenetic growth for this species are unlikely to be due to sexual dimorphism since the specimens that were clearly identified to be females (the presence of ovary) had septal distance patterns that fell within both groups. Unfortunately, it was not possible to identify any males in the specimens obtained for this study.

Septal distances in *Spirula spirula*

While the evidence for the hatching time for *Spirula spirula* is poor, the sharp decrease in septal distance from the first to the third septum in this species is likely to also be associated with hatching. Although the life cycle of this deep-water organism has been studied (Bruun 1943; Denton and Gilpin-Brown 1964, 1971; Denton et al. 1967; Clarke 1969, 1970; Lukeneder et al. 2008; Price et al. 2009), there is limited direct observation of the hatching

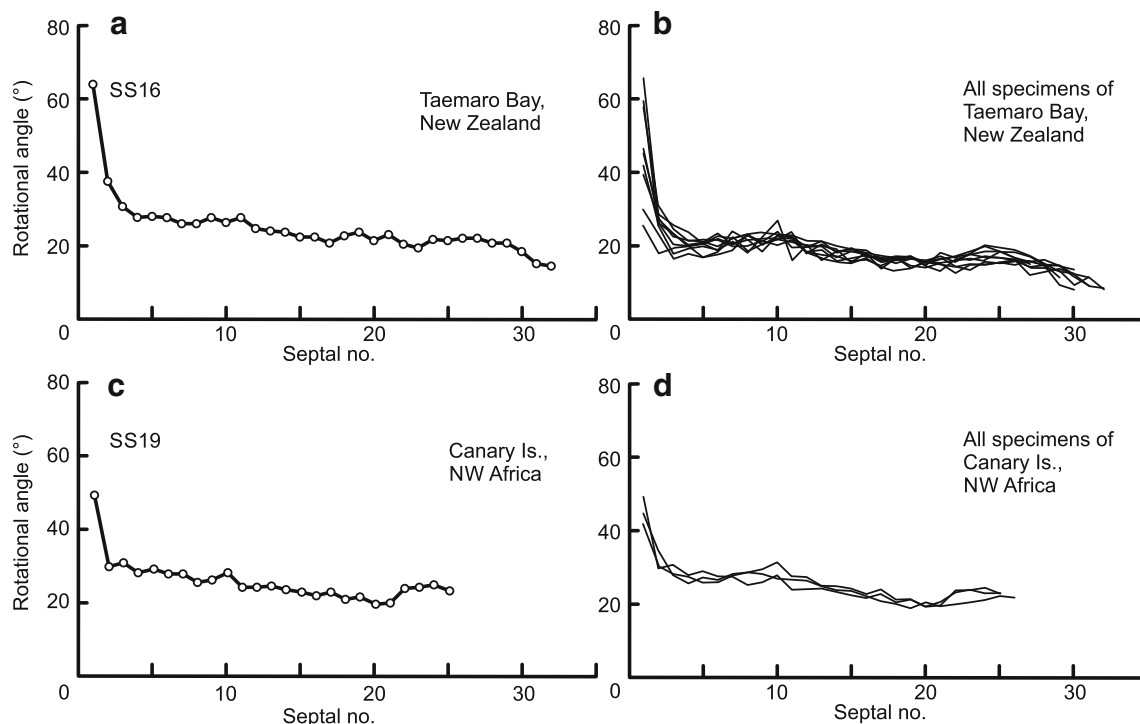


Fig. 5 Septal distances in *Spirula spirula*. **a, b** For specimens from Taemaro Bay, New Zealand. **c, d** For specimens from Lanzarote Island of the Canary Islands

process. However, based on isotopic analyses of *Spirula spirula* shells, Lukeneder et al. (2008) reported that the first 2–3 septa of this species were accompanied by markedly less positive $\delta^{13}\text{C}$ values. The relationship between the less positive $\delta^{13}\text{C}$ values of pre-hatching shell material has been documented in modern *Nautilus pompilius* (Cochran et al. 1981). Based on this information, Lukeneder et al. (2008) concluded that *Spirula spirula* has 2–3 septa when it hatches.

The reason for the slight peaks in *Spirula spirula* septal distances is neither known, nor is it evident if these angular increases are biologically significant. It is possible that the decreasing trends after the 25th septum may indicate maturity. Indeed, maturity for this species has been suggested to be at a growth stage of ca. 28 chambers (Schmidt 1922; Price et al. 2009). Similarly, in modern nautili, the lower septal interval between the last two or three septa is known to be indicative of maturity (Collins and Ward 1987; Klug 2004; Klug et al. 2007; Chirat et al. 2008).

Implications for fossil cephalopods

Septal distances have been ontogenetically analysed in cephalopods with external shells, such as ammonoids and nautiloids. However, analyses of the septal distances in cephalopods with internal shells (e.g., coleoids) are limited (e.g., Hewitt and Stait 1988). As a consequence, there is

much uncertainty about the ontogenetic reasons for septal distances and their implications for shell growth. In the present contribution, we have suggested that septal distances and angles can be used to identify hatching events in *Sepiella japonica* and *Spirula spirula*. If the relationship between the sharp decrease of septal distances at the first several septa and the hatching timings is held in fossil cephalopods with internal shells, their hatching timings could be reconstructed through the ontogenetic analyses of the septal distances. Similarly, in fossil nautiloids, the hatching timings have been reconstructed (e.g., Landman 1988; Wani and Mapes 2010; and references therein). For fossil cephalopods with internal shells, there is little information regarding hatching time and it is possible that septal distances may be used not only to identify hatching events, but to better understand their reproductive strategies and evolutionary changes, which may then be compared to fossil cephalopods with external shells (e.g., Landman et al. 1996; Wani 2011).

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