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Experimental Validation of the Periodicity of Increment Formation in the Statolith of the Bigfin Reef Squid *Sepioteuthis lessoniana* (Cephalopoda: Loliginidae), Lineage C, from the Palk Bay, Indian Ocean

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Abstract

Sepioteuthis lessoniana Lesson, 1831 is a neritic squid that inhabits coral reefs, rocky reefs, seaweed, and seagrass beds within the Indo-Pacific region. Increment validation, which determines the periodicity of increment formation in the squid statolith, is fundamental for age determination and understanding life-history traits; hence, it is critical for fishery management and stock conservation. Egg masses of *S. lessoniana*, Lineage C, were collected from the southeast coast of India and incubated in the hatchery. Post-hatching, the planktonic hatchlings ranged in dorsal mantle length (DML) from 3.9 to 5.49 mm (average 4.98 mm). The size of their statolith (total statolith length) ranged from 318 to 418 μm (average 360 μm). In the nuclear region, the increments formed during embryonic development numbered 9–14 (mean = 12). The first solid increment appeared one day post-hatching. Most of the increment counts (83%) were consistent with the actual age (days) of the squid post-hatching, while 17% of statolith counts were one or two days (increments) older than the actual age of the squid. The early growth rate ranged from 0.07 to 0.24 mm DML/day. The validation data presented here confirm the one-day-one-ring hypothesis in *S. lessoniana*, Lineage C.

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Introduction

S. lessoniana Lesson, 1831 is a demersal neritic squid that inhabits coral and rocky reefs, seaweed, and seagrass beds in the Indo-Pacific regions (Nabhitabhata & Ikeda, 2014). Studies on the embryonic development of the species were conducted in the Gulf of Mannar (Alagarswami, 1966), where hatching was reported on the fifteenth day after egg mass collection from the wild, at a temperature of about 27–29 °C. Similarly, Sivalingam, Ramadoss, Gandhi, and Enose (1993) successfully reared *S. lessoniana* in the hatchery and reported that the squid exhibited fast growth, attaining 55 mm DML at 57 days of age. Its high adaptability to captive conditions allows successful culture through multiple generations (Walsh, Turk, Forsythe, & Lee, 2002; Nabhitabhata & Ikeda, 2014). Sato and Tsuzaki (1984) developed the seed production technique for *S. lessoniana*.

Over the past decade, the interpretation of age using statolith rings has been a major advance in understanding squid population dynamics (Arkhipkin, 2004; Jackson, 2004). Validation of the daily deposition of statolith growth increments enables accurate estimates of age (Jackson, 1998; Jackson, 2004). Studies aimed at validating the periodicity of increment formation in the statolith were conducted in eastern Australia (Jackson, 1990a) and the Philippine waters (Balgos & Pauly, 1998) using tetracycline and alizarin staining methods. However, further validation studies continue to be a priority (Jackson, 2004). Before making a definitive conclusion about squid age, the periodicity of growth increment formation needs to be validated by direct methods such as chemical marking or known-age comparison (Arkhipkin & Shcherbich, 2012). An extensive amount of effort has been concentrated on validating the periodicity of growth increment formation in *S. lessoniana* (Jackson, 1991). Daily periodicity in the increment formation of the statoliths of *S. lessoniana* from Australian and Japanese waters (Jackson, 1990b; Jackson, Arkhipkin, Bizikov, & Hanlon, 1993; Balgos & Pauly, 1998; Jackson & Moltschaniwskyj, 2002) has been validated.

Recent morphological and molecular evidence indicates that *S. lessoniana* is a complex cryptic species (Okutani, 2005; Triantafillos & Adams, 2005). Three lineages (Lineage A, B, and C) have been identified in markedly different abundances (Cheng et al., 2014). Lineage C was predominant throughout most Indonesian sites, southern India, and the central Philippines. In terms of abundance, lineage C was the most commonly sampled, followed by lineage B, whereas lineage A was rare (Cheng et al., 2014). In the Indian seas, both lineages B and C have been reported, with lineage C distributed in the Palk Bay on the east coast of India and lineage B reported from the Gulf of Mannar (Cheng et al., 2014).

Palk Bay squid S*. lessoniana* lineage C is one of the commercially important squid species in Indian waters (Mohamed & Venkatesan, 2017). Several studies on the biology and ecology of S*. lessoniana* lineage C have been conducted in Palk Bay (Rao,1954; Venkatesan & Rajagopal, 2012, 2013). However, information on its early growth and development is lacking.

Daily increment validation in squid is fundamental for understanding statolith microstructure, age determination, and life-history traits, and is therefore useful for species conservation and fishery management. Though squids are dominant components of the marine fauna in Indian waters, such validation studies have never been attempted for tropical Indian squids. The loliginid squid *S. lessoniana* is a very useful species for laboratory experiments due to its hardiness and large size at hatching (Jackson, 2004). However, its age validation based on statolith rings has not been reported from the Indian Seas. Therefore, the present study was carried out to validate daily formation of statolith increments in *S. lessoniana* lineage C, as a representative of tropical loliginid squids in the Indian Seas, by monitoring the growth of hatchery-reared paralarvae under controlled conditions.

Materials and Methods

For attracting *S. lessoniana* (lineage C) for spawning, local fishermen place bundles of tree branches on the bottom of the nearshore waters (9°42′22″ N; 79°12′42″ E) in Palk Bay, Mandapam, India, at a depth of 3 m. The egg masses were collected by SCUBA diving on February 8, 2019, off Vethalai village. They were transported in a plastic bag (1 mm thick, 30 W×75 L cm size) to the marine finfish hatchery at the Mandapam Regional Centre of CMFRI (Tamil Nadu, India) and maintained in an open, aerated, and filtered seawater system with daily renewal of fresh seawater.

The egg masses were graded according to Nabhitabhata and Ikeda (2014), based on their developmental stage. Egg clusters were incubated in seawater (33 PSU) in a 1000 L tank by suspending them near the water surface on a thread while ensuring good aeration between the strands. The water temperature was maintained between 27.8 and 28.6 °C. Hatching typically occurred during the early morning hours (2 to 5 h). Immediately after hatching, the hatchlings were gently transferred to circular tanks (100 L), which were marked with the hatch date. They were fed ad libitum three times daily (08.00 h, 14.00 h and 20.00 h) with mysids, adult *Artemia* sp., and teleost larvae. Each cohort was maintained in a separate tank, and the third cohort (n=62) was selected for the experiment based on the availability of a sufficient number of paralarvae. During the experiment, tanks were checked daily, and dead or weak paralarvae were removed (0-3 individuals/day). Each day, ten squid were sacrificed at 10:00 h, and preserved in 70% ethanol for age estimation. The experiment was conducted over five days to validate the periodicity of statolith growth ring formation.

Extraction of statoliths from squid paralarvae was carried out under a binocular dissecting microscope (Nikon, SMZ25 @10X). The whole head was dissected from each animal and placed in a Petri dish, which was positioned under the dissecting microscope. The dorsal and posterior regions of the head were dissected using a fine surgical blade (No. 11) to expose the entire statocyst (oval sacs) (Fig. 1).

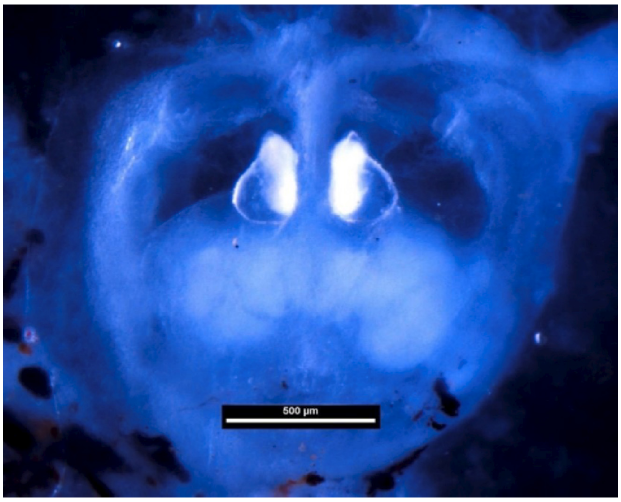

Fig. 1. Opened statocyst of paralarvae (4.3 mm DML) of *Sepioteuthis lessoniana* from Palk Bay, southeast coast of India under a dissecting microscope (Nikon, SMZ25)

The paired statoliths were dissected from the posterior region of the head. The wall of the statocyst sac was punctured using a fine dissecting needle (20 μm diameter tip), and the statoliths were extracted from the cavity along with the statocyst fluid. The statoliths were initially washed in distilled water and gently placed on a microscope slide for mounting. Due to their high transparency, the growth rings in the paralarval statoliths could be counted without polishing and grinding.

The preparation of statoliths for counting growth increments was carried out following Arkhipkin and Shcherbich (2012). The statolith length (SL) was measured to the nearest 1 μm, parallel to the longitudinal axis of the statoliths, using a transmission light microscope (Nikon Eclipse-80i, Japan) and image analysis software. The anterior section of the statoliths was mounted on a microscope slide using thermoplastic cement glue (Crystalbond 509^{TM}). Growth rings were counted under a transmission light microscope (Nikon Eclipse-80i, Japan) at a magnification of 600X. Repeated counts were performed to ensure accurate enumeration. The daily growth rate (DGR) was calculated using the equation provided by Jackson, Forsythe, Hixon, and Hanlon (1997):

$$\text{DGR (mm/day)} = \text{DML (mm)} - \text{Hatchcling size / age (days)}$$

The statolith images were captured with a transmission light microscope (Nikon Eclipse-80i, Japan) or a Leica DM6B microscope with an sCMOS camera.

Results & Discussion

Newly spawned egg clusters were identified by their cylindrical shape (Fig. 2A) and white colour. These egg masses were in the third stage of development. Egg capsules had a finger-like shape, and each egg within the capsule was globular and transparent (Fig. 2B).

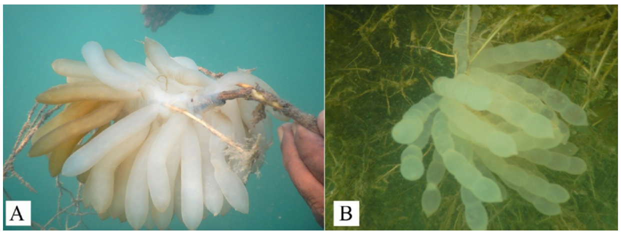

Fig. 2. Egg clusters of *Sepioteuthis lessoniana:* A. Newly laid egg clusters; B. Approximately 8 days old clusters in the wild from Palk Bay, southeast coast of India

The first batch hatched on the 16th day after collection at 05:25 h. After the initiation of hatching, all egg clusters hatched within 6 days (Fig. 3). The hatching rate was 95% (172 hatchlings) at 28.2 °C.

Hatchlings were planktonic, swimming near the surface of the rearing tank. Their mantle length ranged from 3.9 to 5.49 mm (average 4.98 ± 0.55 mm) (Fig. 4A, 4B). They initiated feeding 4-6 h after hatching. The hatchlings were fed three times daily with a combination of live mysids (*Acetes* sp.) collected from the wild, adult Artemia, and larvae of the hatchery-reared teleost silver pompano (*Trachinotus blochii* (Lacepède, 1801)) (1-2 mm size). Because of the rapid feeding rate, mysids were continuously maintained in the tanks with the

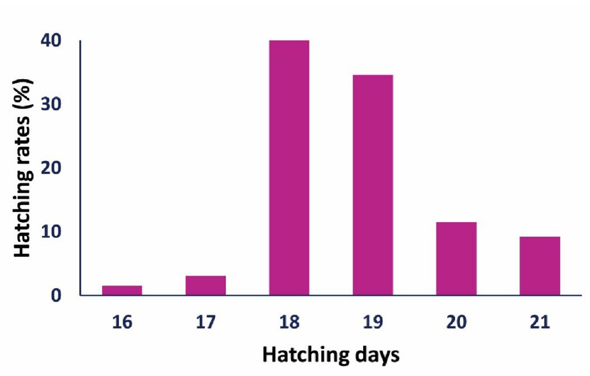

Fig. 3. Daily hatching rate (%) of egg masses of *Sepioteuthis lessoniana* from Palk Bay, under controlled conditions

young squids. The third batch of paralarvae, which hatched after 18 days of incubation (Fig. 4C, 4D), was subjected to validation of the periodicity of growth increment formation. These hatchlings showed an 85% survival rate (excluding sacrificed larvae) after five days.

The hatchlings recorded a growth rate ranging from 0.076 to 0.240 mm DML/day. The first two days showed a comparatively faster growth rate than the subsequent three days (Table 1).

Table 1. Average daily growth rate of paralarvae of *Sepioteuthis lessoniana* from Palk Bay, southeast coast of India

Sl. No.	Age (days)	Average DML (mm)	Average GR (mm DML/day)
1	0	4.98 (± 0.55)	0
2	1	5.22 (± 0.29)	0.24
3	2	5.47 (± 0.24)	0.24
4	3	5.61 (± 0.14)	0.15
5	4	5.69 (± 0.12)	0.08
6	5	5.83 (± 0.23)	0.14

The statoliths of the hatchlings measured between 318 and 418 µm (mean = 360 µm). They were characterised by a well-developed dome, wings, and rostrum (Fig. 5). Very faint increments were observed in the nuclear region of the statoliths of newly hatched paralarvae, ranging from 9 to 14 (mean = 12). The first solid increment was observed one day after hatching (Fig. 6A, 6B). In 83% of the hatchlings, the increment counts were consistent with actual age in days. However, in the remaining 17%, the statolith counts were 1-2 (increments) days older than the actual age of the paralarvae (Table 2). The growth rate during the early stages ranged from 0.07 to 0.24 mm DML/day.

In the present study, hatching of *S. lessoniana* was first observed on the 16th day after collection. Alagarswami (1966) observed a laboratory incubation period of 15 days in *S. lessoniana* at 27–29 °C at Mandapam, southeast coast of India, while it was 21 days at 28–32 °C in the Thai waters (Nabhitabhata & Ikeda, 2014). The loliginid squid *Loligo forbesii* Steenstrup, 1856 required 68 to 75 days to hatch at 12.5 °C in the North Atlantic (Segawa, 1987), and the incubation period of *L. vulgaris* Lamarck, 1798 from the Northwest Mediterranean was 51 days at 12.2 °C (Villanueva, 2000a). Given the uncertainty regarding the exact day of egg-laying in the present instance, the observed incubation period is probably consistent with earlier studies. The average hatchling size of *S. lessoniana* has been reported as 5.3 mm DML (range 3.5-6.4 mm DML) (Lee, Turk, Yang, & Hanlon, 1994) and 5.2 mm DML (Sivalingam et al.,

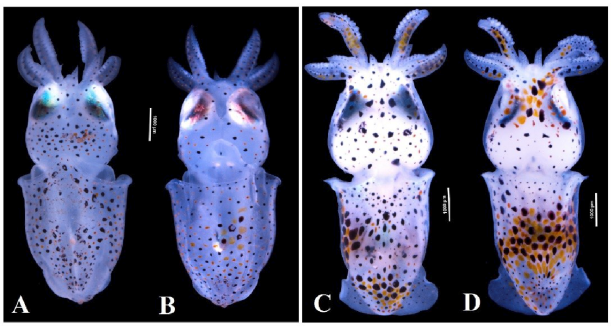

Fig. 4. Dorsal A, C and ventral B, D views of new hatchlings A, B and three days post-hatching C, D of *Sepioteuthis lessoniana* from the Palk Bay, southeast coast of India

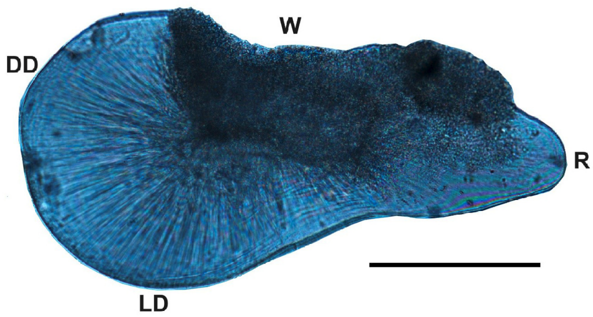

Fig. 5. Statolith of *Sepioteuthis lessoniana* from Palk Bay, southeast coast of India, DD =dorsal dome, LD=lateral dome, R =rostrum and W=wing

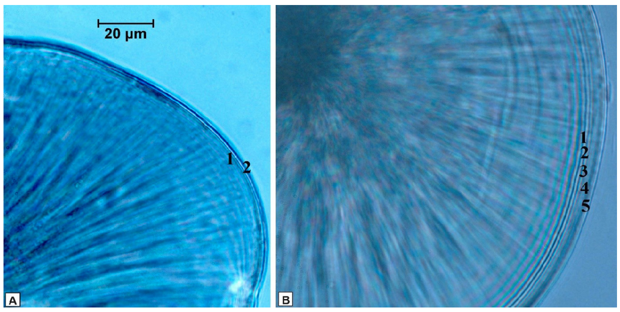

Fig. 6. Statolith micrograph of two-day-old squid with two increments A and a five-day-old squid with five increments B (Scale bar= 150 µm) hatchlings of *Sepioteuthis lessoniana* from Palk Bay, southeast coast of India

Table 2. Relationship between age and number of increments in the statolith of *Sepioteuthis lessoniana* from Palk Bay, southeast coast of India under laboratory conditions.

Sl. No.	Days	Number	Average DML (mm)	Increment (range)	Agreement (%)
1	0	10	4.98 (± 0.55)	0 (0-1)	80
2	1	10	5.22 (± 0.29)	1 (1-2)	80
3	2	10	5.47 (± 0.24)	2 (2-3)	90
4	3	10	5.61 (± 0.14)	3 (3-4)	90
5	4	10	5.69 (± 0.12)	4 (4-5)	80
6	5	10	5.83 (± 0.23)	5 (5-7)	80

1993) in the Pacific waters and the Gulf of Mannar, respectively, corroborating the present findings.

The statoliths of newly hatched *S. lessoniana* exhibited a distinctive ring structure, indicating increment deposition in the statolith from the embryonic stage onwards. This feature has also been recorded in *S. lessoniana* (Jackson, 1990a) from Australian waters and several other loliginid squids, including *Alloteuthis subulata* (Lamarck, 1798) (Lipinski, 1986), *Uroteuthis edulis* (Hoyle, 1885) (Natsukari, Nakanose, & Oda, 1988), and *L. vulgaris* (Villanueva, 2000b). The periodicity of embryonic statolith increment formation varies depending on water temperature (Villanueva, 2000b).

Statolith ageing techniques have helped in understanding the biology of loliginid squids (Jackson, 1998). Validation experiments and quantification of statolith increments in the Palk Bay squid support the one-increment-per-day hypothesis for lineage C of *S. lessoniana* from Indian waters. Increment deposition has also been validated as occurring daily in *S. lessoniana* from Australian waters (Jackson, 1990a; Jackson et al., 1993; Jackson & Moltschaniwskyj, 2001) and the Philippines (Balgos & Pauly, 1998) (Table 3). To date, more than ten statolith increment validation studies have been conducted on loliginid squids (Jackson, 2004), all supporting the one-increment-per-day hypothesis. Furthermore, the 'one increment–one day' relationship was verified for the congeneric southern calamary, *S. australis* Quoy & Gaimard, 1832, in captive-reared hatchlings up to 40 days post-hatching, where the relationship remained stable across the seasonal extremes. However, it was not evident in the chemically marked adults, as inconsistencies of up to 44 days were detected between the number of days elapsed post-staining and the increment count (Hunt, Steer, & Gillanders, 2011).

Several statolith increment validation experiments have previously been conducted on *S. lessoniana* using both chemical marking (Tetracycline and Alizarin) and known-age individuals (Jackson, 1990b; Jackson et al., 1993; Balgos & Pauly, 1998; Jackson & Moltschaniwskyj, 2002) (Table 3). In contrast, validation experiments by Hoving and

Table 3. Summary of statolith increment validation studies of *Sepioteuthis lessoniana*

DML range (mm)	Duration (days)	Number of individuals	Technique	References
5.2-7.3	12-24	5	Alizarin (chemical)	Balgos & Pauly (1998)
12-23	35	11	Tetracycline	Jackson & Moltschaniwskyj (2002)
50-73	9-39	7	Tetracycline	Jackson (1990a)
10-210*	-	39	Known age	Jackson et al. (1993)
3.9-6.05	5	50	Known age	Present study

*Estimated from graph Jackson et al. (1993)

Robinson (2017) on the mesopelagic glass squid *Galiteuthis phyllura* S. S. Berry, 1911 (11 individuals aged up to 11 days) from the Monterey submarine canyon off California showed that daily increment formation was less apparent, and the one-day-one-increment hypothesis was not accepted.

Rings in the statolith can be used as a reliable age marker to determine growth rate and lifespan in other Indian squids, and recently, such growth studies using statoliths have been reported in the Indian squid *Uroteuthis duvaucelii* (A. d'Orbigny, 1835) (Sajikumar et al., 2022). However, the present data did not consistently correspond to the actual age of all the experimental paralarvae. Yang et al. (1986) observed that in cultured 21–71-day-old *Doryteuthis opalescens* (S. S. Berry, 1911), the increment count differed from the actual age by an average of ±4.2 days. Daily increment deposition in *L. vulgaris* from the northwest Mediterranean was confirmed in only 87% of the statoliths (Villanueva 2000a). The differences between the increment number and the days elapsed after marking validation (3 to 42 days) were generally within 0-3 days (Nakamura & Sakurai, 1991). Statoliths are considered the "black boxes" of squids because they can record all events throughout the life cycle, including hatching, stress, ontogenetic shifts, and spawning (Arkhipkin, 2005). The probable stress experienced by squid under captive conditions may contribute to the formation of additional increments in the statolith, potentially intensifying growth increment deposition (Villanueva, 2000a).

Statoliths have been used for age and growth studies of squids in many parts of the world (Jackson, 2004; Arkhipkin, 2004). The present study forms the first validation of daily statolith increment formation in the squid from tropical Indian waters. The first solid increment in the statolith was formed on the first day after hatching. However, the existing data are still modest, and validation of daily statolith increment formation throughout the lifecycle of other tropical squid species remains a priority.

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