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Age and growth of bigfin reef squid, *Sepioteuthis lessoniana* (Cephalopoda: Loliginidae), in Gulf of Mannar Marine Biosphere Reserve, Indian Ocean

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Abstract

Statolith growth increments were analysed in the bigfin reef squid, *Sepioteuthis lessoniana* lineage B, for estimating the age and growth in the Gulf of Mannar Biosphere Reserve (GOM), southeast coast of India. The identification of *S. lessoniana* lineage B was determined by mitochondrial cytochrome c oxidase I gene sequence. The statolith increment age analysis indicated that the wild-captured squid population of *S. lessoniana* in the study area undergoes rapid growth. The age of *S. lessoniana* in males ranged from 61 (95 mm dorsal mantle length (DML)) to 220 d (390 mm DML), while it was 64 (98 mm DML) to 199 d (340 mm DML) in females. The average daily growth rate in males and females was 1.63 and 1.55 mm DML d^{-1}, respectively. The instantaneous growth rate varied from 0.85 (210 d) to 4.1% (110 d) for males and 0.65 (190 d) to 3.7% (110 d) for females. The age at first maturity was 114 and 120 d for males and females, respectively. Back-calculated hatching dates and the attainment of maturity in females suggested that the reproduction of *S. lessoniana* is year-round, with two distinct spawning peaks during July–August and February months; accordingly, the hatching dates were spread throughout the year, with the presence of two cohorts. Based on the statolith data, it can be concluded that *S. lessoniana* lineage B in the GOM has a potential lifespan of up to 7 months. This finding contradicts the previous growth estimates based on length-frequency data, which underestimated the true growth potential of this species.

Introduction

The bigfin reef squid *Sepioteuthis lessoniana* is a demersal neritic species and one of the most widely distributed loliginid squid of the Indo-West Pacific region (Jereb and Roper, 2010) and it has also been reported from northern Australia, New Zealand, central Japan, the Mediterranean Sea and eastward to the Hawaiian Islands (Lefkaditou *et al.*, 2009; Jereb and Roper, 2010). Given its widespread distribution in the Indo-Pacific region, *S. lessoniana* is an important species in coastal fisheries across many countries (Jereb and Roper, 2010). Moreover, the bigfin squid is utilized for biomedical research and holds commercial value as a mariculture species (Lee *et al.*, 1994; Walsh *et al.*, 2002; Nabhitabhata and Ikeda, 2014).

Most squids exhibit rapid growth and have a short lifespan (Arkhipkin, 2004; Jackson, 2004). Understanding key parameters such as age and growth is essential to comprehend the critical life history patterns necessary for effective management (Jackson, 2004). Age and growth of *S. lessoniana* have been extensively studied using validated daily statolith increments (Jackson, 1990; Jackson *et al.*, 1993; Balgos and Pauly, 1998). Several studies have directly documented the age and growth of *S. lessoniana* in captivity (Lee *et al.*, 1994; Nabhitabhata, 1995, 1996; Forsythe *et al.*, 2001) supporting the growth estimates derived from size-at-age information based on statolith analysis. These captive-rearing studies indicate a lifespan ranging from 115 to 333 d (SEAFDEC, 1975; Nabhitabhata, 1978, 1996; Tsuchiya, 1982; Segawa, 1987; Lee *et al.*, 1994; Walsh *et al.*, 2002). Statolith increment-based age and growth of the *S. lessoniana* were studied in the waters of Tropical Australia, Subtropical Australia, Thailand, the Arabian Sea and Philippines (Jackson, 1990; Balgos and Pauly, 1998; Jackson and Moltschaniwskyj, 2002; Chen *et al.*, 2015; Sajikumar, 2021) that showed a short lifespan with age ranges of 124–260 d.

Recent studies based on both morphological and molecular evidence indicate that *S. lessoniana* may be a species complex (Okutani, 2005; Triantafillos and Adams, 2005). The three lineages (lineage A, B and C) were present in markedly different abundances (Cheng *et al.*, 2014). Lineage C appeared to be most abundant while lineages B and A were less abundant, but co-occurred with lineage C and occasionally each other (Cheng *et al.*, 2014). In Indian seas, both lineages B and C have been reported, with lineage B identified in the Gulf of Mannar (GOM; Cheng *et al.*, 2014).

Sepioteuthis lessoniana accounts for around 7% of the Indian east coast cephalopod landings, all from Palk Bay and the GOM (Jereb and Roper, 2010). The asymptotic models of squid growth curves generated from length-frequency analysis of *S. lessoniana* continue to gain support from Sri Lanka (Charles and Sivashanthini, 2011) and Palk Bay, India (Venkatesan, 2012) and showed a lifespan up to 3.3 years, while age estimation using statoliths has been initiated recently in the Arabian Sea (WIO) suggesting a short life span (Sajikumar, 2021). Significant spatial and temporal variation occurs in the growth rates and maturity of equatorial, tropical and subtropical populations of *S. lessoniana* (Jereb and Roper, 2010). Understanding the specific traits within the *S. lessoniana* species complex in a region is crucial for developing management plans. Therefore, the present study focuses on investigating the age and growth of *S. lessoniana*, particularly the lineage B, by using statolith growth increments, obtained from the Gulf of Mannar Marine Biosphere Reserve, Eastern Indian Ocean (EIO), located in southeast coast of India.

Material and methods

Study area

The GOM in the Indian Ocean is located between 78°08′ E to 79°30′ E and 8°35′ N to 9°25′ N on the Southeast Coast of the Indian Peninsula. It spans a coastline of 365 km, and is bordered by the districts of Kanyakumari, Tirunelveli, Tuticorin and Ramanathapuram in the state of Tamil Nadu, India. The GOM, which encompasses 21 coral islands, is also a Marine Biosphere Reserve, recognized for its rich coastal and marine habitats such as seagrass, seaweeds, mangroves, coral reefs and estuaries, all of which support a diverse array of species (Kumaraguru *et al.*, 2006).

Sampling

The *S. lessoniana* samples included in this analysis were caught using trawls and jigs operated in the GOM during the months of April, May, August–October 2019 and January–December 2020. In the laboratory, the dorsal mantle length (DML) of the squids was measured with an accuracy of ±0.1 mm and the total weight (TW) was recorded to the nearest ±0.01 g. Specimens were dissected to determine sex and maturity. A total of 782 *S. lessoniana* specimens were examined, with males ranging in DML from 59 to 390 mm ($n = 412$) and females ranging from 70 to 349 mm ($n = 370$). Maturity stages for each sex were categorized according to the modified scale proposed by Mangold-Wirz (1963) as I – immature, II – maturing, III – mature and IV – spawning for females and I – immature, II – maturing, III – mature and IV – spent for males.

DNA isolation and PCR reaction

The DNA isolation from the *S. lessoniana* samples was carried out through the conventional phenol-chloroform method and the DNA was stored at −20 °C for further use in PCR reactions (Sambrook *et al.*, 1989). The PCR reaction was performed using a Thermo Scientific™ master mix (Cat. No. K0171) and the primers LCO 1490 and HC02198 (Folmer *et al.*, 1994). The PCR amplification was carried out under normal cyclic conditions of initial denaturation at 94 °C for 180 s, then cycling at 94 °C for 30 s, annealing at 56 °C for 40 s and extension at 72 °C for 40 s for 30 cycles, followed by a final extension of 72 °C for 7 min in the thermal cycler (Agilent sure cycler 8800, USA). The resulting amplified products were cleaned and sequenced at the Genurem Biosciences LLP Sequencing Facility (Applied Biosystems 3730xl DNA Analyzer) in India. The cytochrome c oxidase subunit I gene sequence was blast in the NCBI blast portal and matches with *S. lessoniana* lineage B. The gene sequence was submitted to NCBI and accession number (OP572033.1) was received.

Phylogenetic tree analysis

The phylogenetic tree was constructed using the COI sequences of the current study with the earlier reported individual gene alignments of different lineages (A, B and C) along with out-groups including *Sepioteuthis sepioidea* (AF075392) and *Loligo bleekeri* (AB573754) (Figure 1). The phylogenetic tree was constructed by the maximum likelihood method, Kimura 2-parameter model (Kimura, 1980) using the MEGA 11 program (Tamura *et al.*, 2021) based on the 15 numbers of nucleotide sequences found in the NCBI GenBank database (Table 1). The percentage of trees in which the associated taxa clustered together was depicted next to the branches. A discrete Gamma distribution was used to model evolutionary rate differences among sites (5 categories (+G, parameter = 0.2901)). Codon positions included were 1st + 2nd + 3rd + non-coding.

Statolith collection and processing

Paired statoliths were dissected from fresh specimens, cleaned and preserved in 70% ethanol. The extraction and preparation for counting growth increments were carried out in accordance with Arkhipkin and Shcherbich (2012). The anterior section of the statoliths was mounted on a microscope slide using thermoplastic cement glue (Crystalbond™ 509). The statolith length (SL) was measured to the nearest 1 μm, parallel to the longitudinal axis of the statolith, using a transmitted light microscope (Nikon Eclipse-80i, Japan) and image analysis software and measurements converted to mm for analysis. Statoliths were ground and polished using a 1500-grit fine-lapping film.

Estimation of growth using growth increments

To count growth increments, statolith was observed under a transmitted light microscope (Nikon Eclipse-80i) at a magnification of 600×, and total number of growth increments were determined by averaging the increment counts from three separate observations. The mean count was considered valid if the difference between the first and second counts was below 10%. If the deviation exceeded 10%, the counting process was repeated. The lateral dome of the statolith was used to determine the age, as its daily periodicity has been validated and the daily deposition of statolith increments has been authenticated as daily increments (Jackson, 1990; Jackson *et al.*, 1993). The increments were counted from the hatching ring to the outer edge of the lateral dome, where they were most clearly distinct (Dawe *et al.*, 1985; Villanueva, 1992). In cases where the increments on the lateral dome edges were not clearly recognizable, the number of increments for that section was extrapolated (Natsukari *et al.*, 1988). Extrapolation involved estimating the increment counts in the indistinct area based on the widths of approximately 10 of the most recent countable increments from adjacent areas (Hoving *et al.*, 2007). The images of the statoliths were captured with a transmitted light microscope, Nikon Eclipse-80i, or Leica DM6B with an sCMOS camera.

Daily growth rate

Previous studies have confirmed that the total number of increments in the squid statolith corresponds to the age of an individual in days (Jackson, 1990; Sajikumar, 2021). Therefore, the daily growth rate (DGR) was calculated using the equation provided by Jackson *et al.* (1997):

$$\mathrm{DGR}\ (\mathrm{mm\ d^{-1}}) = \frac{\mathrm{DML\ (mm)\text{-}Hatchling\ size\ (mm)}}{\mathrm{Age\ (days)}}$$

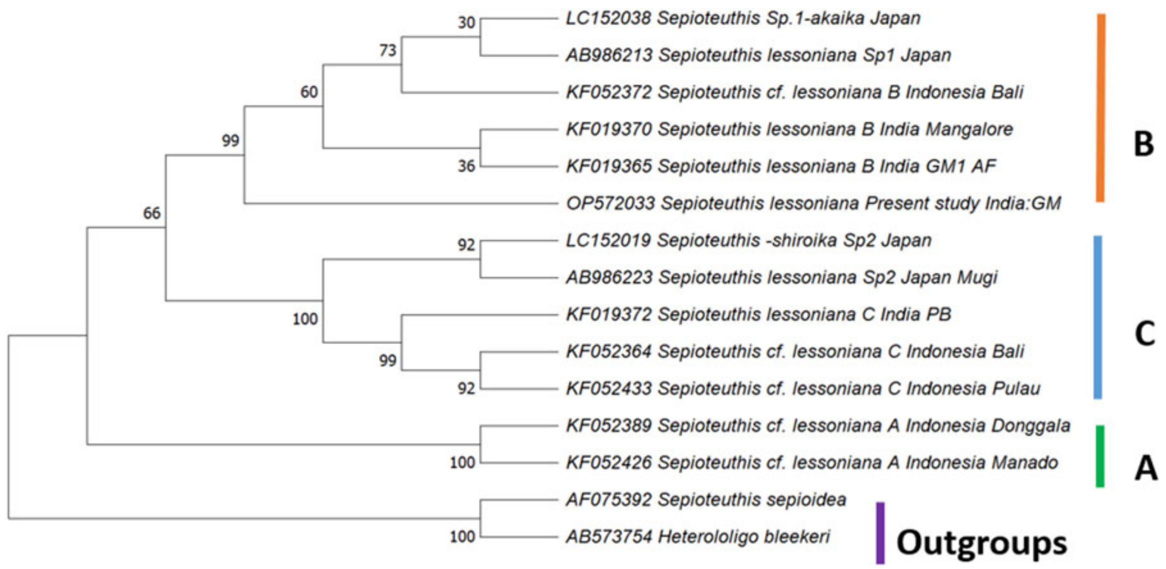

Figure 1. Phylogenetic tree of *Sepioteuthis lessoniana* in this study with the specimens representing distinct lineages. The tree was reconstructed with COI sequences (614 bp) using the Maximum Likelihood method and Kimura 2-parameter model. The lineages marked in the tree were based on the classification of Cheng *et al*. (2014).

Table 1. The details of GenBank accession numbers of COI gene sequences of *Sepioteuthis lessoniana* and its lineage used for phylogenetic tree construction in this study

Species	Location	Lineage/species classification	GenBank accession number	Reference
S. lessoniana	Donggala, Indonesia	A	KF052389	Cheng *et al*. (2014)
S. lessoniana	Manado, Indonesia	A	KF052426	Cheng *et al*. (2014)
S. lessoniana	Bali, Indonesia	B	KF052372	Cheng *et al*. (2014)
S. lessoniana	Mangalore, India	B	KF019370	Cheng *et al*. (2014)
S. lessoniana	Gulf of Mannar, India	B	KF019365	Cheng *et al*. (2014)
S. lessoniana	Bali, Indonesia	C	KF052364	Cheng *et al*. (2014)
S. lessoniana	Pulau, Indonesia	C	KF052433	Cheng *et al*. (2014)
S. lessoniana	Palk Bay, India	C	KF019372	Cheng *et al*. (2014)
S. lessoniana	Japan	sp.1	LC152038	Tomano *et al*. (2015)
S. lessoniana	Japan	sp.1	AB986213	Tomano *et al*. (2015)
S. lessoniana	Japan	sp.2	LC152019	Tomano *et al*. (2015)
S. lessoniana	Mugi, Japan	sp.2	AB986223	Tomano *et al*. (2015)

where hatchling size was 5.0 mm DML (Segawa, 1987), DML = dorsal mantle length

$$\text{DGR (g d}^{-1}) = \frac{\text{TW (g)-Hatchling weight (g)}}{\text{Age (days)}}$$

where the hatchling weight was 0.06 g (Segawa, 1987), TW = total weight.

The power function yielded the best fit for the relationship between DML and DGR (mm DML d^{-1} and g BW d^{-1}) for both sexes.

Statolith length index (SLI)

The statolith length index (SLI) was calculated using the terminology and measurements of statoliths after Clarke (1978):

$$\text{Statolith length index} = \text{SL/DML} \times 100$$

where SL = statolith length (mm), DML = dorsal mantle length.

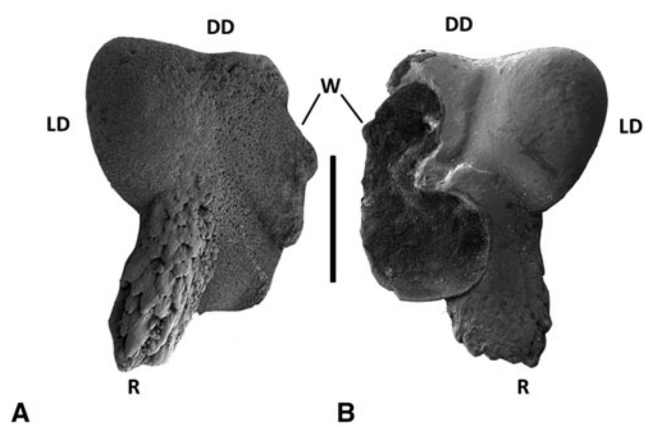

Figure 2. Dorsal (A) and ventral (B) view of the statolith of *Sepioteuthis lessoniana* (212 mm DML) from the Gulf of Mannar. DD, dorsal dome; LD, lateral dome; R, rostrum; W, wing (scale bar = 500 µm).

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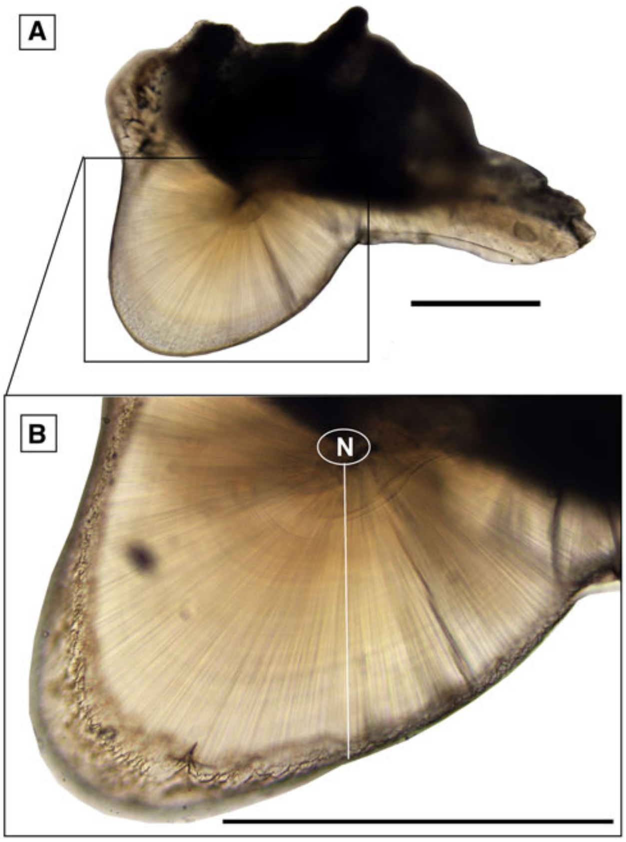

Figure 3. Light micrograph of the ground statolith of *Sepioteuthis lessoniana* adult (male of 225 mm DML) from the Gulf of Mannar (A). Magnified view of the area outlined by the rectangle (B) (scale bar = 500 μm)

Instantaneous relative growth rate (IRG)

The instantaneous relative growth rate (IRG) was calculated in intervals of 20 d for each sex following Forsythe and Van Heukelem (1987) as:

$$IRG = [\ln S2 - \ln S1]/T$$

where S_2 and S_1 are DML at the start and the end of each interval of time (T). Conversion of IRG to the per cent increase in DML d^{-1} was done by multiplying IRG by 100.

Age at maturity

The mean age at which 50% of the squid attained maturity (L_m) was estimated by fitting a logistic function to the proportion of mature squid in the 10 mm size categories (Udupe, 1986).

Hatching date calculation

The hatching date of *S. lessoniana* was estimated by back calculation from the date of capture of the specimen using the age in days estimated from statolith daily growth increments.

Spawning date calculation

The spawning date was estimated by back calculation using the hatching date and the egg incubation period of *S. lessoniana* based on experimental rearing in Thailand by Nabhitabhata (1996). An average egg incubation time of 20 d was used for the calculation.

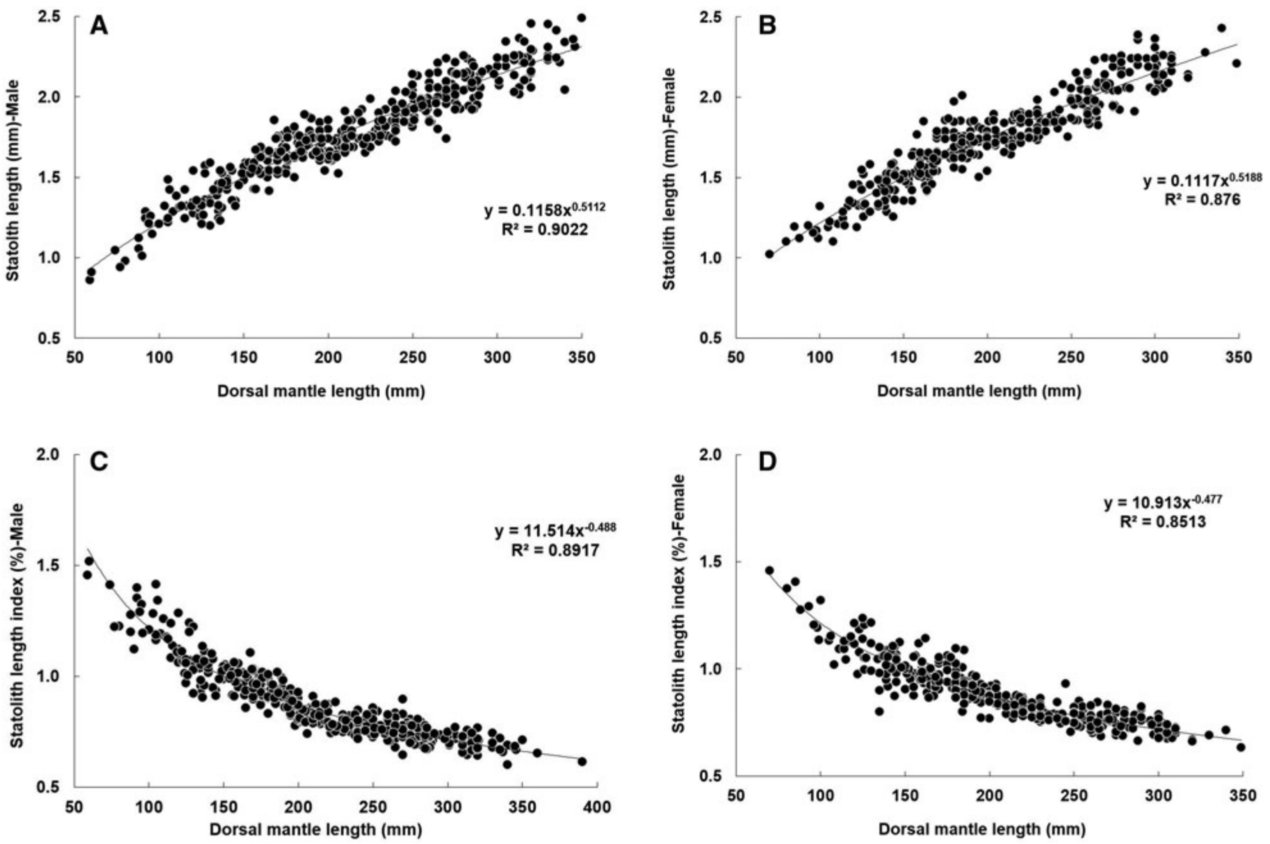

Figure 4. Relationship between dorsal mantle length and statolith length of *Sepioteuthis lessoniana*: (A) males; (B) females; relationship between dorsal mantle length and statolith length index (C) males; (D) females from the Gulf of Mannar

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Data analysis

The data were statistically analysed by statistical package, SPSS version 20 (Carver and Nash, 2008). The difference in DGRs of male and female squids was evaluated using analysis of variance. Student *t*-test was carried out to assess the significant difference between males and females of different length groups at different ages. Comparisons were made at the 5% probability levels and all statements of statistical significance were based on $P < 0.05$

Result

Statolith microstructure

The statolith of *S. lessoniana* is robust and relatively long. It displays a round dorsal dome with a long, thin rostrum and broad wing (Figure 2). The nucleus is located within the central region of the statolith. The growth increments were counted from the lateral dome area, and from the hatching ring towards the statolith edge following the axis with the best visibility (Figure 3). Checks between post-nuclear zone and the peripheral zone were regularly recorded in many statoliths.

Statolith size

In male squid, the length of the statolith (SL) ranged from 0.86 mm (juvenile, 59 mm DML) to 2.45 mm (spent adult, 350 mm DML). The SL in females ranged from 1.02 mm in juvenile (70 mm DML) to 2.43 mm in spawning (340 mm DML) squid. The relationship between DML and SL, and statolith growth index (SI) was best described by the power function. The SL to DML allometric relationship performed by the power function shows negative allometric growth for both males ($b = 0.5112$; $R^2 = 0.902$) and females ($b = 0.518$; $R^2 = 0.876$). The SLI against DML for males reduced from 1.51% (60 mm DML) to 0.60% (340 mm DML) and for females from 1.49% (70 mm DML) to 0.49% (252 mm DML). The SI decreased steadily with increasing DML (Figure 4A–D). The slopes of the relationships between DML and SL, and SI did not differ significantly ($P > 0.05$) between sexes.

Age and growth (hard part ageing)

The age of *S. lessoniana* males ranged from 62 (juvenile, 59 mm DML) to 220 d (spent, 390 mm DML) and in females ranged from 74 (juvenile, 88 mm DML) to 199 d (spawning, 340 mm DML) (Table 2). The most abundant age groups were 120–130 (18.2%) and 130–140 d (19.5%) of males and females, respectively (Figure 5). A comparison of age and DML indicated that the DML of males was greater than that of females above 80 d age group (Figure 6). The size of males between 100 and 160 d age was significantly ($P < 0.05$) larger than females.

Daily growth rate

The DGR (mm d^{-1}) of *S. lessoniana* ranged from 0.87 to 2.33 (mean = 1.63) mm DML d^{-1} for males and 0.86 to 2.07 (mean = 1.55) mm DML d^{-1} for females were observed. The DGR (g d^{-1}) for males ranged from 0.28 to 9.32 g (mean = 3.58 g) d^{-1} and in females it ranged from 0.38 to 9.35 g (mean = 3.37 g) d^{-1}. In both sexes, the DGR (mm d^{-1}) increased with age, reaching a maximum of 121 d in males and 143 d in females. Male *S. lessoniana* recorded a higher DGR than females. The maximum age in *S. lessoniana* was 220 d in males (spent) and 199 d in females (spawning). The relationship between DML and DGR (mm d^{-1}) for both sexes, expressed as a power function, $DML = 0.145 \times Age^{0.452}$ ($r^2 = 0.74$) for males and $DML = 0.151 \times Age^{0.437}$ ($r^2 = 0.72$) for females. The relationship between DML

Table 2. Age, size and growth rate of males and females of *Sepioteuthis lessoniana* from the Gulf of Mannar

Stage	Male					Female				
	N	Age range (d)	DML range (mm)	DGR (mm d^{-1})	DGR (g d^{-1})	*N*	Age range (d)	DML range (mm)	DGR (mm d^{-1})	DGR (g d^{-1})
Immature	39	62–104 (87 ± 10)	59–155 (108 ± 22)	0.87–1.44 (1.17 ± 0.13)	0.28–1.76 (0.88 ± 0.32)	61	74–121 (99 ± 10)	70–198 (136 ± 29)	0.86–1.68 (1.31 ± 0.19)	0.38–3.14 (1.56 ± 0.71)
Maturing	79	86–122 (106 ± 7)	115–208 (154 ± 20)	1.09–1.71 (1.40 ± 0.14)	0.50–3.33 (1.82 ± 0.5)	57	91–136 (113 ± 10)	123–225 (164 ± 23)	1.08–1.81 (1.40 ± 0.14)	0.64–4.24 (2.03 ± 0.64)
Mature	204	95–185 (127 ± 16)	145–337 (226 ± 44)	1.27–2.33 1.73 ± 0.20)	0.89–9.32 (3.88 ± 1.61)	107	102–168 (122 ± 11)	130–280 (194 ± 29)	1.16–2.00 (1.53 ± 0.17)	0.90–5.91 (2.91 ± 1.04)
Spent/spawning	90	126–220 (157 ± 20)	195–390 (285 ± 35)	1.34–2.33 (1.78 ± 0.15)	1.31–9.21 (5.56 ± 1.31)	145	99–199 (150 ± 17)	170–349 (262 ± 33)	1.24–2.07 (1.70 ± 0.13)	1.28–9.35 (5.01 ± 1.29)

DML, dorsal mantle length; DGR, daily growth rate; *N*, number of specimens.
The values given in the parenthesis are arithmetic mean ± SE.

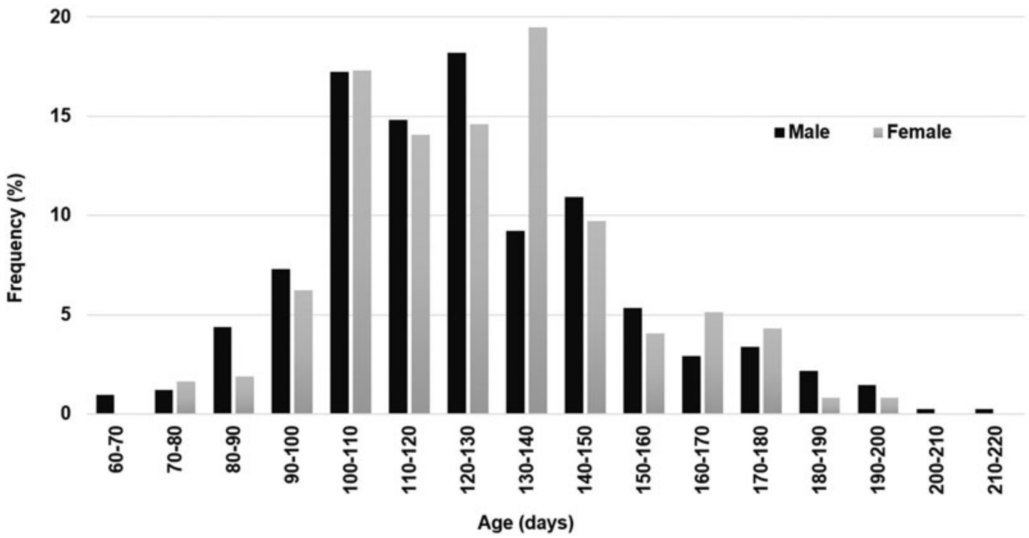

Figure 5. Age distribution of *Sepioteuthis lessoniana* from the Gulf of Mannar

and DGR (g d^{-1}) was BW = 0.0001DML$^{1.885}$ (r^2 = 0.91) for males and BW = 0.0001 DML$^{1.9178}$ (r^2 = 0.92) for females. The relationships between DML and DGR (mm d^{-1}) showed highly significant differences between sexes ($P < 0.0001$), while DML and DGR (g d^{-1}) were not significantly different between male and female squids ($P > 0.05$).

Instantaneous growth rate

The instantaneous growth rate (IGR) ranged from 0.85% (210 d) to 4.1% (110 d) for males and 0.65% (190 d) to 3.7% (110 d) for females (Figure 7). In both sexes, the IGR of DML changed throughout its lifespan. During the initial stage (70 d), the IGR was minimal in both males and females and after 70 d the IRG exhibited a steep increase and reached its maximum between 90 and 110 d beyond which, it decreased continuously. The IGR of males was slightly higher than those of females. The IGR decreased continuously in relation to age. It was very clearly noticed that, before the initial maturity age, both sexes showed higher rates, and as they got closer to maturity, this rate declined.

Maturation

Males attained maturity between 95 and 185 d (145–337 mm DML) and females between 102 and 168 d (130–280 mm DML). The size range of mature females was less than that of mature males, and the youngest mature male was younger (95 d) than the youngest mature female (102 d) (Table 2). According to the present study, the age at first maturity was 114 d for males, 120 d for females and 117 d for sexes combined (Figure 8). Squids older than 122 d for males and 136 d for females were mature (Figure 9). The oldest male was 220 d old at the spent stage, measuring 390 mm DML and weighing 2027 g. The oldest female squid was the age of 199 d in the spawning stage, measuring 340 mm DML and weighing 1450 g.

Hatching and spawning

Back-calculated hatching dates and the attainment of maturity in females suggest that the reproduction of *S. lessoniana* is year-round, with spawning peaks during July (14%), August (11%) and February (16%) months (Figure 10). From the hatching date frequency distribution of *S. lessoniana*, it can be concluded that hatching occurs throughout the year with evident peaks, August (15%)–September (13%) and March (16%) (Figure 11) indicating the two major cohorts. The back-calculated hatching date in the present study suggests that *S. lessoniana* hatched continuously and grows up to the targeted size within 4–5 months after hatching.

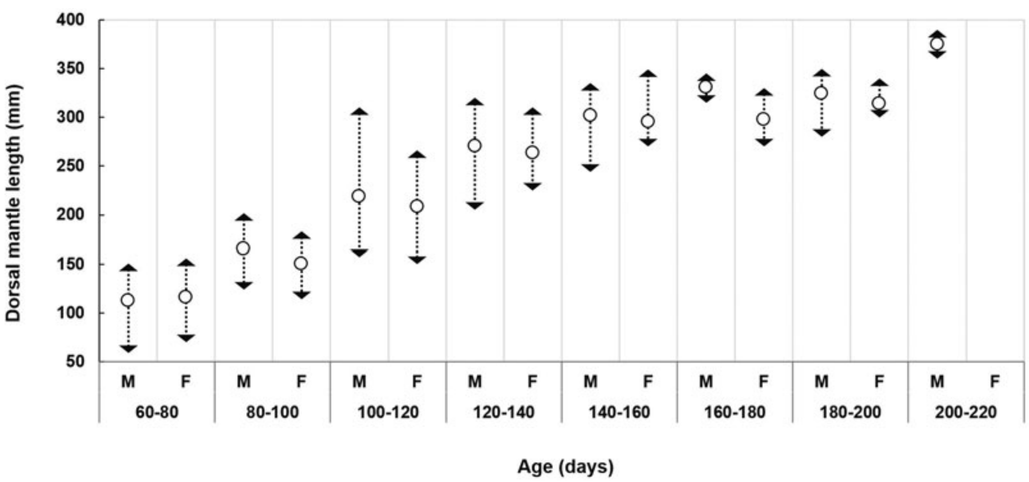

Figure 6. Size range of males and females in the different age groups of *Sepioteuthis lessoniana* from the Gulf of Mannar

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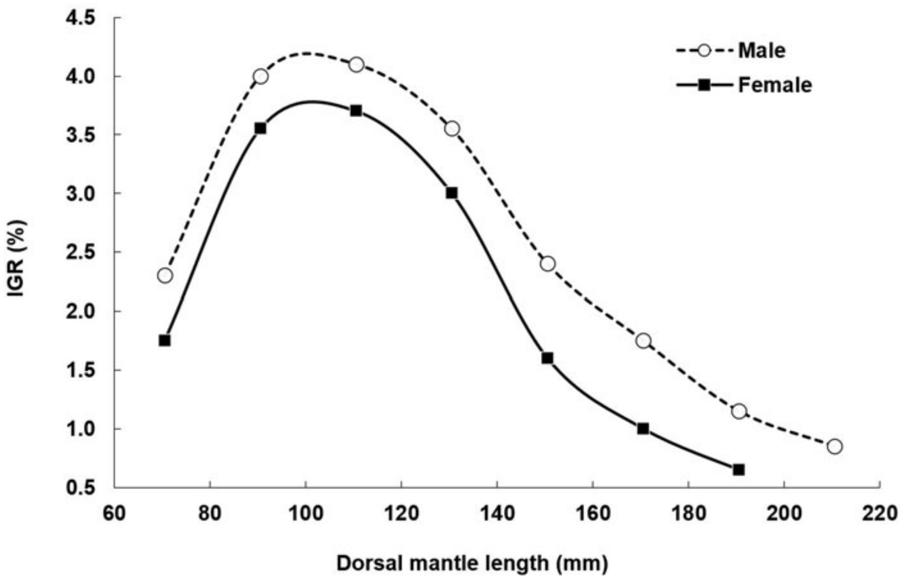

Figure 7. Instantaneous growth rate for males and females of *Sepioteuthis lessoniana* from the Gulf of Mannar

Discussion

Lineage confirmation

Recently *S. lessoniana* has been discriminated using DNA markers such as partial sequences of mitochondrial cytochrome oxidase subunit I (COX1 or COI) for better stock identity, distribution and stock status (Cheng *et al*., 2014; Tomano *et al*., 2015, 2016). Cheng *et al*. (2014) reported that *S. lessoniana* contains lineages A, B and C whereas Tomano *et al*. (2015) classified the *S. lessoniana* into species 1, 2 and 3. In these classifications, it can be equated that lineage A = species 2, B = 1 and C = 3. The phylogenetic tree demonstrated that the *S. lessoniana* samples from this study formed a clade with other lineage B samples. Based on the earlier classifications (Cheng *et al*., 2014; Tomano *et al*., 2015), the DNA barcoding of *S. lessoniana* samples used in this study belonged to lineage B by Cheng *et al*. (2014) that equals to species 1 described by Tomano *et al*. (2015). The genetic difference of *S. lessoniana* among the different lineages showed noticeable differences among them. A similar response was noted by Cheng *et al*. (2014) while studying genetic divergences among the different lineages. In the present study, we adopted the nomenclature/terminology to our samples as lineage B rather than species in line with Cheng *et al*. (2014) whose samples represented similar sequences from our study area.

Statolith microstructure

The statolith of *S. lessoniana* is robust and rather large in length. The statolith pattern and form matched those identified in Australia for this species (Jackson, 1991). The nucleus was surrounded by a distinct hatching ring, and increments observed between the nucleus and the hatching ring may have been the embryonic ring, reflecting statolith growth within the egg (Jackson, 1994; Perez *et al*., 2006). The growth increments were most evident in the region of the lateral dome, while they were difficult to distinguish on the rostrum. The rostrums of species such as *Idiosepius pygmaeus* (Jackson, 1990) and *Uroteuthis (Photololigo) edulis* (Natsukari *et al*., 1988) contain plainly countable clear increments. The size of this hatching ring corresponded closely to the statolith's outer margin of the freshly hatched *S. lessoniana* proving that it is a hatching check. This similar feature has been reported in loliginid squids (Lipinski, 1986; Sajikumar *et al*., 2022) in the *Loligo* spp.

Statolith size

The SL in *S. lessoniana* from GOM is higher than 0.819–1.445 mm, reported by Sajikumar (2021), and 0.239–0.796 mm by

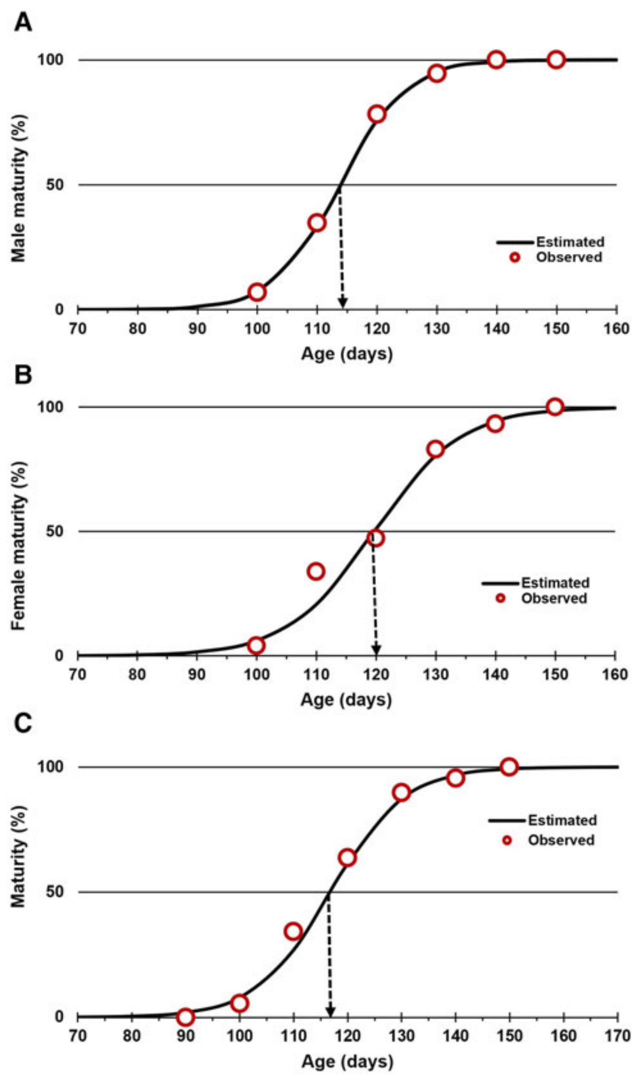

Figure 8. Age at first maturity of *Sepioteuthis lessoniana* from the Gulf of Mannar: males (A), females (B) and pooled sex (C)

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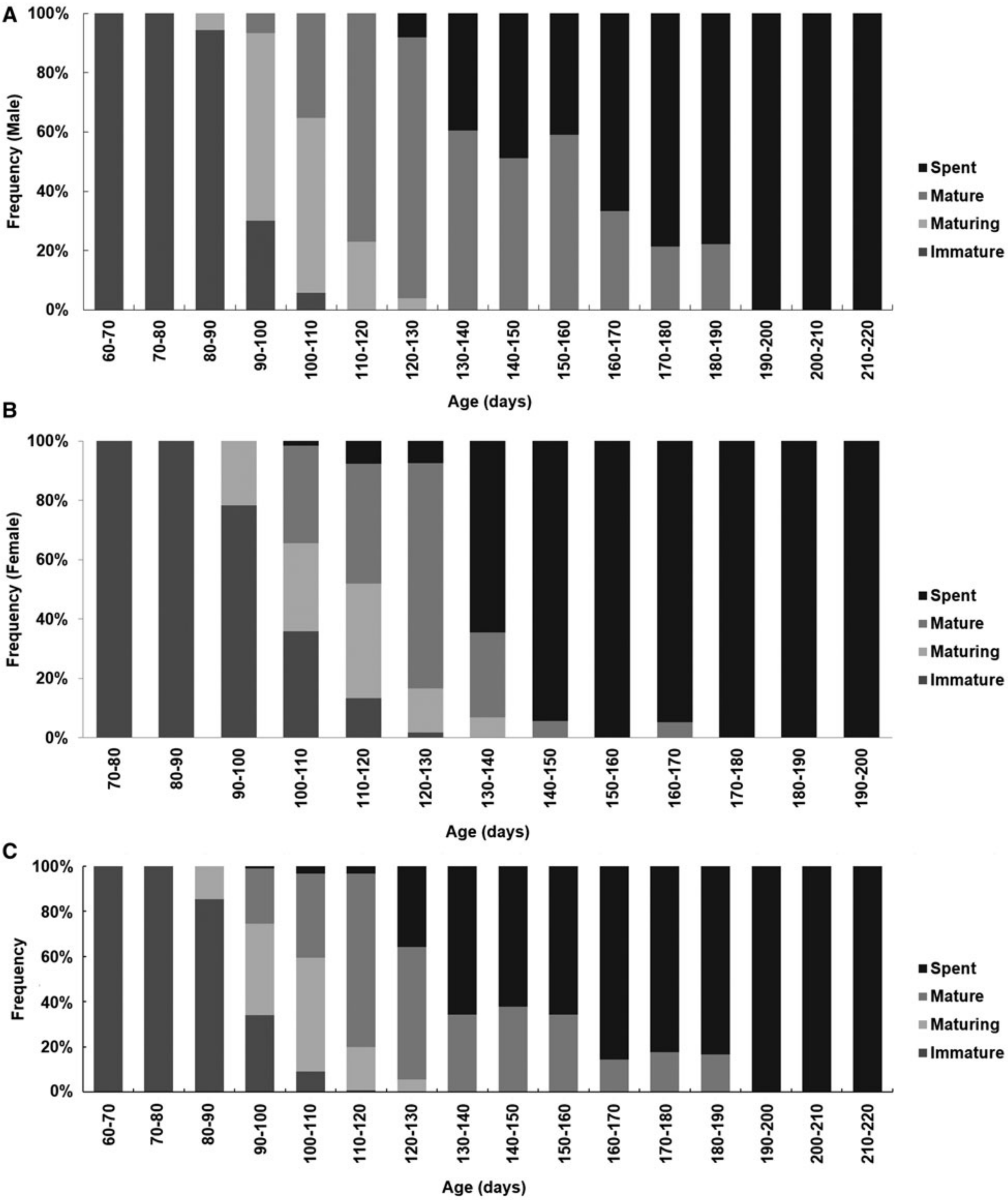

Figure 9. Age-wise proportion of immature, maturing, mature and spent of *Sepioteuthis lessoniana* from the Gulf of Mannar: (A) males; (B) females; (C) pooled

Balgos and Pauly (1998). The allometric relationship of SL to DML indicated negative allometric growth in both males and females, a phenomenon observed in other loliginid squids, including *U. duvaucelii* (Sajikumar *et al*., 2022), *U. edulis* (Wang *et al*., 2010), *L. vulgaris* (Rocha and Guerra, 1999), *Alloteuthis subulata*, *A. africana* (Arkhipkin and Nekludova, 1993) and the mesopelagic squid *Ancistrocherius lesueurii* (Arkhipkin, 1997).

Age and growth

In the GOM region, the maximum lifespan of *S. lessoniana* is likely to be about 7 months. A comparison of age with DML indicates that the DML of male was larger than the female in all age groups, except those between 60 and 80 d. Bat *et al*. (2009) and Huang (2006) have reported that *U. chinensis* and *U. edulis* exhibit a similar pattern. The age and growth of *S. lessoniana* have been previously studied from tropical to sub-tropical waters. Previous research has demonstrated geographic variation in the lifespan of *S. lessoniana*, with a maximum age between 132 and 188 d. The maximum age of 220 d recorded for *S. lessoniana* in this study is greater than the ages previously reported of this species in tropical and subtropical waters [Australia – 188 d (Jackson, 1990); 187 d (Semmens and Moltschaniwskyj, 2000); Philippines – 132 d (Balgos and Pauly, 1998); Taiwan – 192 d

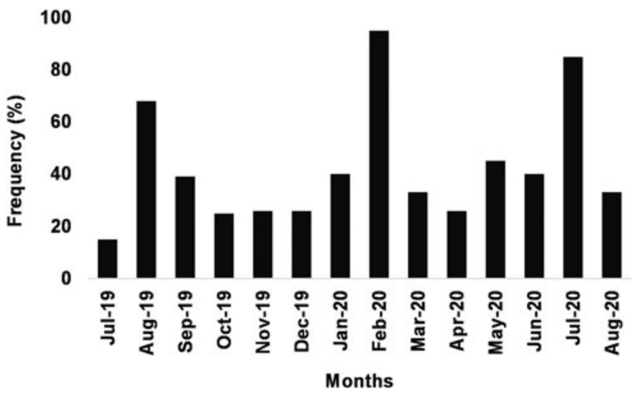

Figure 10. Monthly spawning frequency distribution of *Sepioteuthis lessoniana* from the Gulf of Mannar

(Chiang *et al*., 2020); and India – 156 d (Sajikumar, 2021)]. Chen *et al*. (2015) estimated the age of *S. lessoniana* to be 216 d from Taiwan water, which is more in line with the present study.

Individuals of *S. lessoniana* exhibited extremely varied growth rates, indicative of the plastic growth responses typical of squid (Jackson, 1994). In Japanese waters, *S. lessoniana* was estimated to live for approximately 1 year (Ueta and Jo, 1989). The rearing experiment of *S. lessoniana* from Japan suggests that this species can live for 11 months and reach a maximum size of 350 mm DML (Lee *et al*., 1994), but the largest specimen of *S. lessoniana* (480 mm DML) recorded by Walsh *et al.* (2002) in Japan water had an age of 262 d. Culture studies of *S. lessoniana* from different regions indicate that the maximum age of *S. lessoniana* ranged from 115 to 333 d (Table 3). The length-frequency analysis of *S. lessoniana* published in earlier studies indicates that the age of this species from Indian waters has been overestimated. Venkatesan (2012) reported 3 years for the squid of 300 mm DML and projected a lifespan of about 3.3 years. Rao (1954) similarly modelled a size of 95, 166 and 219 mm DML at the end of the first, second and third years, respectively. Likewise, Charles and Sivashanthini (2011) estimated a lower *K* value of 0.85 year^{-1} for *S. lessoniana* demonstrating a long-life span (>3 years) for this species.

Growth rates

The DGR in length, 1.63 mm DML d^{-1} for males and 1.55 mm DML d^{-1} for females is higher than the previous estimates reported for *S. lessoniana*. Sajikumar (2021) recorded a growth rate of 1.38 mm d^{-1} for males in Indian waters and 1.19 mm d^{-1} for females. According to Jackson (1990), males and females in Australian water grow at a rate of 1.42 and 1.34 mm d^{-1}, respectively. Balgos and Pauly (1998) measured a growth rate of 0.5 mm d^{-1} in water from the Philippines. The estimated DGR in weight (3.58 g d^{-1} for males and 3.37 g d^{-1} females) in the present study is higher than Jackson and Moltschaniwskyj (2002), who reported the DGR of 2.89–3.18 g d^{-1} from the Australian waters and 3.24 g d^{-1} from Thailand waters. According to Jin *et al.* (2019), regional growth rates were notably diverse. A previous study on captive-reared *S. lessoniana* from Thailand revealed a rapid DGR of 1.6 mm and 3.82 g d^{-1} (Nabhitabhata, 1996). In laboratory studies, the majority of loliginid squid species studied exhibited rapid growth rates (Turk *et al*., 1986; Yang *et al*., 1986; Villanueva, 2000; Vidal *et al*., 2014). The DGR increased with age in both sexes, with males having a larger DGR than females, a trait exhibited by loliginid squids (Wang *et al*., 2010), except for the genus *Loliolus* sp. (Sajikumar *et al*., 2019). However, the difference in the DGR between male and female *S. lessoniana* is lesser compared to other loliginid squids, *U. edulis* and *U. singhalensis* (Sajikumar, 2021). In both sexes, the IGR of DML changed during its lifespan. The IGR decreased progressively with age. It was very clearly noticed that, before the initial age of maturity, both sexes showed higher rates, but as they approached maturity, these rates decreased. Certain Ommastrephidae species have also been shown to exhibit a reduction in growth rates with gonadal development (Arkhipkin and Bizikov, 1991).

Maturation

The minimum age of maturity for males and females from the GOM was lower than that reported by Sajikumar (2021), where the youngest mature female was 113 d and the youngest mature male was 102 d of age from the Arabian Sea, Southwest coast of India. Similarly, the age at maturity appears to be variable under captivity, where Nabhitabhata *et al.* (2005) reported 60 d as age at maturity for *S. lessoniana* with a maximum life of 176 d in Thailand waters; Ohshima and Choe (1961) observed 90 d as age at first maturity for this species. In general, cephalopods reach maturity earlier in captive conditions than in the wild (Mangold, 1987) as the constant, relatively high temperature in captivity may accelerate maturation. *Sepioteuthis lessoniana* laboratory cultures have shown that water temperature affects the growth rate and size at maturity (Segawa, 1987; Forsythe *et al*., 2001; Ikeda *et al*., 2009a, 2009b; Amida *et al*., 2019). Such high variation in

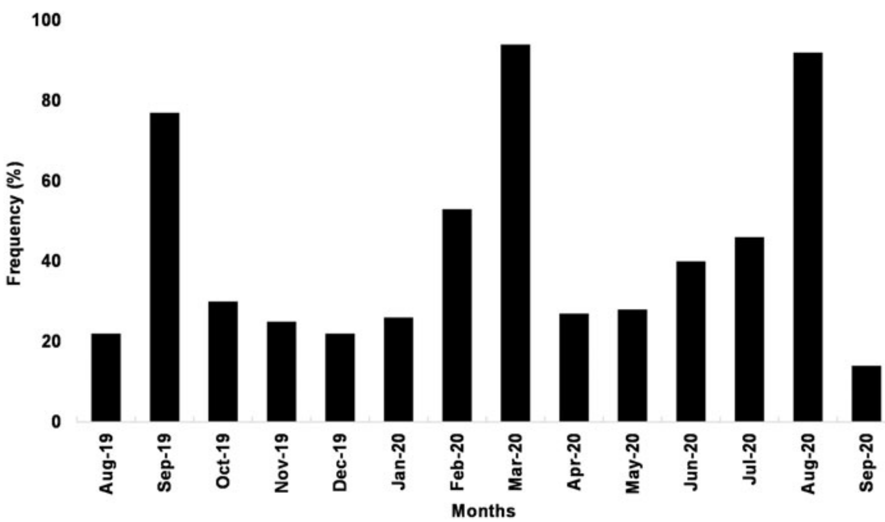

Figure 11. Monthly hatching frequency distribution of *Sepioteuthis lessoniana* from the Gulf of Mannar

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Table 3. Comparison of maximum size and age in *Sepioteuthis lessoniana*

References	Maximum DML (mm)	Maximum age (d)	Sex	Location	Wild/culture
Lee *et al.* (1994)	350	333 (23.3°C)	–	Texas, USA	Culture
Walsh *et al.* (2002)	480	262 (23–24°C)	–	Galveston, USA	Culture
Ikeda *et al.* (2009a)	330	315 (22.8°C)	F	Saitama Prefecture, Japan	Culture
Tsuchiya (1982)	260	306 (24°C)	M	Okinawa, Japan	Culture
Miyazaki *et al.* (2022)	173	259 (23°C)	F	Aichi prefecture, Japan	Culture
Segawa (1987)	–	179 (25°C)	–	Okinawa, Japan	Culture
Nabhitabhata (1996)	252	176 (28°C)	M	Rayong, Thailand	Culture
Nabhitabhata *et al.* (2005)	214	167 (30°C)	F	Rayong, Thailand	Culture
SEAFDEC (1975)	368	115	M	Philippines	Culture
Chen *et al.* (2015)	401	216	F	Northeastern Taiwan	Wild
Chiang *et al.* (2020)	360	192	–	Northeastern Taiwan	Wild
Jackson (1990)	213	188	F	Townsville, Australia	Wild
Semmens and Moltschaniwskyj (2000)	238	187	–	Townsville, Australia	Wild
Jackson and Moltschaniwskyj (2002)	317	224	M	Hervey Bay, Australia	Wild
Sajikumar (2021)	308	156	M	Arabian Sea, India	Wild
Balgos and Pauly (1998)	315	132	F	Luzon, Philippines	Wild
Present study	390	220	M	Gulf of Mannar, India	Wild

DML, dorsal mantle length; M, male; F, female; – indicates sex is not mentioned
The values given in the parenthesis are culture temperature

age-at-maturation of *S. lessoniana* suggested that there may be many intra-annual cohorts that experience various environmental conditions and grow at various rates, which results in a wide range in age at maturity (Pecl, 2001; Moreno *et al.*, 2005).

Hatching and spawning

Different spawning peaks have been reported for *S. lessoniana* from different regions. In GOM, *S. lessoniana* spawning and hatching is year-round, with spawning peaks in the present study observed during July–August and February. Similarly, prolonged breeding was reported by Rao (1954) based on the presence of the egg capsules from January to June on weeds and other objects in the waters of the GOM and the Palk Bay. Venkatesan (2012) also reported a prolonged breeding season of *S. lessoniana* from December to July with a major spawning peak from January to March from Palk Bay, India.

Table 4. Comparison of incubation period and temperature in *Sepioteuthis lessoniana* from culture studies

References	Incubation period (d)	Water temperature (°C)	Location
Choe (1966)	25–28	23.5–24	Tokyo, Japan
Tsuchiya (1982)	23.2 (21–25)	24	Okinawa, Japan
Miyazaki *et al.* (2022)	42	19	Aichi prefecture, Japan
	19	23	
	17	26	
Segawa (1987)	54–55	15	Okinawa, Japan
	33–36	20	
	24–27	25	
	19–23	30	
Nabhitabhata (1996)	20.3 (17–23)	28	Rayong, Thailand

Note: The spawning date was estimated by back calculation using the hatching date and the egg incubation period of *S. lessoniana* based on experimental rearing in Thailand by Nabhitabhata (1996). An average egg incubation time of 20 d was used for the calculation. The water temperature in the hatchery condition in the study location was 27–29°C and the sea water was 27–31°C at various seasons which is similar to the water temperature in the Thailand region.

The hatching rate depends on the biotic and abiotic history during incubation and embryonic development. For *S. lessoniana*, the incubation days varied between 14 and 55 d in different waters (Ohshima and Choe, 1961; SEAFDEC, 1975; Tsuchiya, 1982; Segawa, 1987). The average embryonic period is 20 d (a range of 17–23 d) at about 28 °C (Nabhitabhata, 1978, 1996; Nabhitabhata and Kbinrum, 1981; Nabhitabhata *et al.*, 2005). The duration of the incubation period depends upon the water temperature and is longer at lower temperatures (Table 4). The hatching date frequency distribution of *S. lessoniana* shows hatching occurs throughout the year with evident peaks, August – September and March indicating the two major cohorts. For short-lived species like squids, year-round hatching of intra-annual cohorts, or 'micro-cohorts', leads to continuous recruitment (Caddy, 1991; Boyle and Boletzky, 1996).

Conclusion

Interpretation of the statolith growth increments of *S. lessoniana* estimates a maximum lifespan of 7 months for lineage B with a rapid growth rate. These specific growth traits within the *S. lessoniana* species complex in a region are crucial in the context of conservation and developing management plans for sustainable fisheries. Further, it was found that *S. lessoniana* was likely to show great plasticity in growth as determined by environmental temperature variation along its wide geographical range.

Data availability statement. The data that support the findings of this study are available from the corresponding author upon reasonable request.

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Author contributions. Mookaiah Kavitha: conceptualization, data curation, resources, formal analysis and writing – original draft; Geetha Sasikumar: investigation, methodology and writing – review and editing; Dhanasekaran Linga Prabu: laboratory analysis and barcoding; Pappurajam Laxmilatha: writing – review and editing; Kurichithara K. Sajikumar: software, validation and visualization.

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Competing interests. All authors of this manuscript are declared that no conflict-of-interest present in this manuscript.

Ethical standards. Ethical review and approval were not required for this animal study as no live specimens were involved. The samples used in this study were collected from commercial fishery landings in the Gulf of Mannar Region.

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