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Age, growth and maturation in the mesopelagic squid *Abralia andamanica* (Cephalopoda: Enoploteuthidae) from the Arabian Sea

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Summary: Age, growth and maturation in the mesopelagic squid *Abralia andamanica* (Cephalopoda: Enoploteuthidae) were studied in 140 individuals of 15-60 mm dorsal mantle length (DML) captured from open waters in the southeast Arabian Sea. The length-weight relationship was estimated as $W=0.278\ DML^{1.884}$ (R^2=0.93). Age estimates based on statolith increment counts ranged from 79 to 177 days, suggesting a short (<200-day) lifespan. Growth in length was best described by a linear function for males and a power function for females. Growth in weight was best described by a power function for both sexes. Growth rates of the DML ranged from 0.16 to 0.30 (mean=0.24) mm/day in males and from 0.23 to 0.43 (mean=0.33) mm/day in females. The hatching season extended from June to August (monsoon season).

Keywords: *Abralia andamanica*; statolith; age; growth rate; lifespan; hatching; tropical.

Edad, crecimiento y maduración en el calamar mesopelágico *Abralia andamanica* (Cephalopoda: Enoploteuthidae) del mar de Arabia

Resumen: El patrón de crecimiento del calamar mesopelágico *Abralia andamanica* se estudió a partir de 140 ejemplares de 15-60 mm de longitud dorsal del manto (LDM) capturados en aguas oceánicas del sureste del mar de Arabia. La relación entre LDM y peso (P) de ambos sexos combinados se estimó como: $P = 0.278\ LMD^{1.884}$ ($R^2 = 0.93$). La edad de A. andamanica se estimó mediante contaje de incrementos de crecimiento de sus estatolitos, oscilando entre 79 y 177 días, lo que evidencia que *A. andamanica* tiene un ciclo de vida breve (<200 días). El crecimiento en longitud se describió mediante una función lineal para machos y potencial para hembras. El crecimiento en peso para cada sexo se describió mediante una función potencial. El dimorfismo sexual mostró una tasa de crecimiento que osciló entre 0.16 y 0.30 (media = 0.24) mm LDM/día en los machos y entre 0.23 y 0.43 (media = 0.33) mm LMD/día en las hembras. La época de puesta se extendió entre junio y agosto (época de monzones) en el sureste del mar de Arabia.

Palabras clave: *Abralia andamanica;* estatolito; edad; tasa de crecimiento; esperanza de vida; eclosión; tropical.

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INTRODUCTION

Cephalopods are common components of the mesopelagic zones of the world oceans and occupy crucial roles in marine ecosystems both as predators and as prey (Clarke 1996, Piatkowski et al. 2001, Boyle and Rodhouse 2005). Enoploteuthid squids, known as "myctophid fishes" of the squid world (Young and Harman 1985), generally occur at middle depths and occasionally on continental shelves (Norman 2003). The genus *Abralia* comprises small species associated with shallow bottoms on steep slopes, which as such are members of the mesopelagic-boundary fauna (Reid et al. 1991, Roper and Jereb 2010). The genus contains 20 nominal species (Young and Tsuchiya 2018).

Abralia andamanica Goodrich, 1896 is a small (mantle length up to 60 mm) mesopelagic-boundary species distributed in the Indo-West Pacific, the Arabian Sea, the Seychelles, the Yellow Sea, Japan, Hawaii, and off Australia's northwest shelf (Wood and Day 1998, Roper and Jereb 2010). A detailed study in the Arabian Sea showed that it is distributed along the continental shelf edge (Silas 1968). Its body morphology has been described, and its distribution is known, but little is known about its ecology and nothing about its age, growth or maturation. Enoploteuthids are an important component of the Arabian Sea ecosystem (Silas 1968, Varghese et al. 2013). According to the IUCN Red List of threatened species, it is as a species of Least-Concern and further research is recommended to better understand its population dynamics, life history, ecology and potential threats affecting it (Barratt and Allcock 2014).

Statolith growth increment analysis is a specialized method used for age and growth studies of squids (Arkhipkin 2004, Jackson 2004). Life-cycle characteristics of squids include rapid growth and a relatively short lifespan (Arkhipkin 2004). However, there have been few studies of age and growth using statoliths in squids from the Arabian Sea (Sajikumar et al. 2019a, 2020). Furthermore, little is known about the biology, length-weight relationships and growth of mesopelagic squids from the Arabian Sea in general and of *A. andamanica* in particular. Though the family Enoploteuthidae comprises 41 species globally, only five have had their age and growth studied using statoliths: *Abralia trigonura* Berry, 1913, *Abraliopsis atlantica* Nesis, 1982, *Abraliposis morisii* Verany, 1839, *Enoploteuthis leptura* Leach, 1817 and *Pterygioteuthis gemmata* Chun, 1908 (Arkhipkin and Murzov 1990, Bigelow 1992, Young and Mangold 1994, Arkhipkin 1994, 1996a, 1997). These species are slow-growing, have a short lifespan, and mature at 3-4 months.

The biology of *A. andamanica* is poorly known, and nothing is known about the age and growth of enoploteuthids from the Arabian Sea. The objective of the present study was to determine the age and growth of *A. andamanica* from the tropical Arabian Sea based on statolith increment analysis.

MATERIALS AND METHODS

Sampling

Individuals of *A. andamanica* were collected from commercial bottom trawls towed at 300 m depth in the Arabian Sea off Kollam (8°45'N; 73°52'E) on 26 December 2019. The squid were caught in trawls targeting the deep-sea shrimp *Aristeus alcocki* Ramadan, 1938 and were identified as *A. andamanica* based on the key provided by Tsuchiya (2009). The species was identified based on the structure of five photophores (two large terminal opaque organs and three intermediate silvery organs) on the ventral side of the eyeball (Fig. 1B). In this species, the mantle is conical and wide at the anterior margin (Fig. 1A), and tapers in the posterior half forming a long mantle apex (tail). The arm formula is 4<2<3<1.

A total of 140 specimens comprising 119 females and 21 males were examined. The samples were preserved in ice immediately after capture and transported to the laboratory, where the dorsal mantle length (DML) of each specimen was measured to the nearest mm, as defined by Roper and Voss (1983), and sexual maturity was assessed using the scale described in Lipinski (1979). Body weights of thawed specimens were determined using an electronic balance.

Length-weight relationship

The relationship between DML and total weight was determined by fitting the equation $W = aDML^b$ for males and females, where W is total weight (g), DML is dorsal mantle length (cm), 'a' is intercept and 'b' is slope. An analysis of covariance (ANCOVA) was performed to test for significant differences in 'b' values in males and females following the method of Snedecor and Cochran (1967) using Excel® 2016.

To determine the deviation of the b-value from the isometric value of 3, a Student t-test was applied (Sokal and Rohlf 1987) using the formula $t = b\text{-}3/S_b$, where b is the regression coefficient of log-transformed data and S_b is standard error of b.

Age and growth

Age was estimated from statolith increment counts as per Arkhipkin and Shcherbich (2012). Terminology and measurements of statoliths used were after Clarke (1978). Statolith increments form daily in the congener *A. trigonura* (Bigelow 1992) and were assumed to also form daily in *A. andamanica*. One statolith from each pair was used for age determination. Each statolith was attached to a microscopic slide with the anterior (concave) side on top with a crystal bond mounting medium. After drying (usually 5 minutes), the statolith was ground with wet waterproof sandpaper (1000 grade) and polished with fine sandpaper

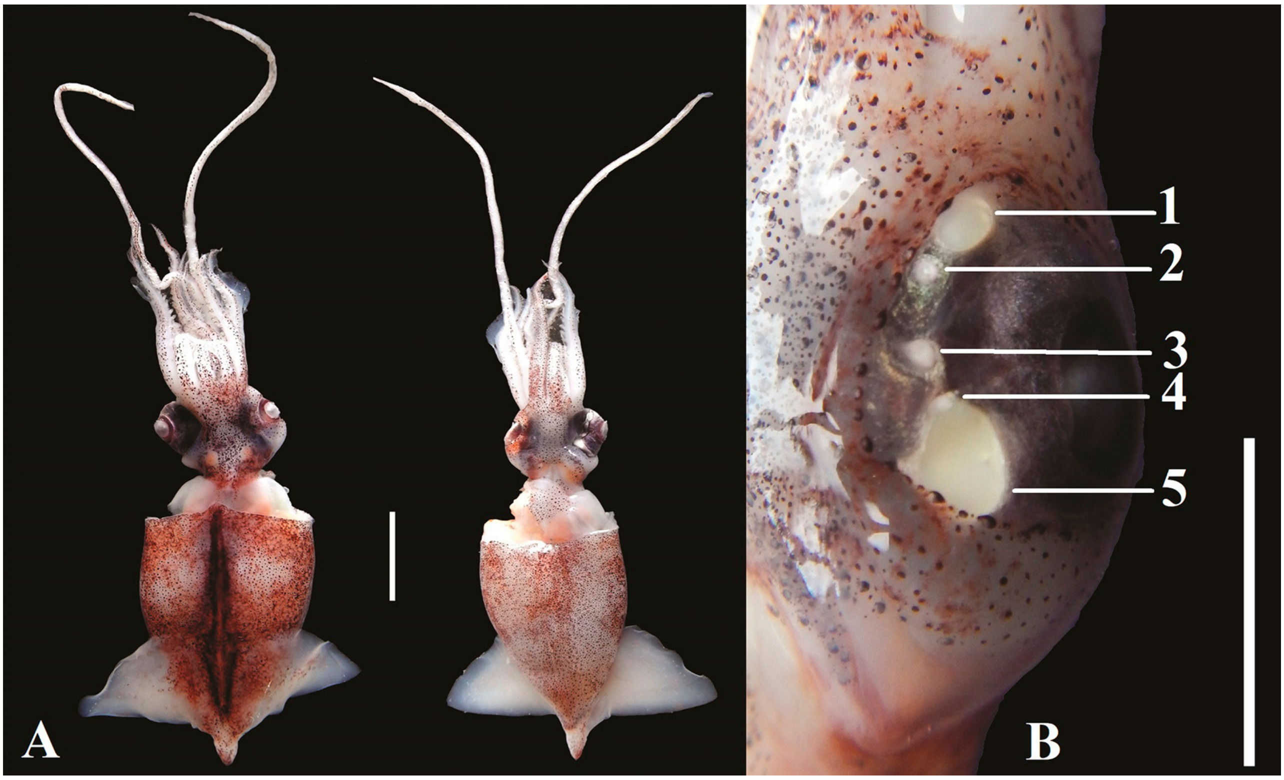

Fig. 1. – Dorsal and ventral view of *Abralia andamanica* collected from Arabian Sea (scale bar=2 cm) (A); view of ocular photophore in the ventral region of the eyeball (scale bar=1 cm) (B).

(1500 grade). Growth increments in *A. trigonura* statoliths start forming outside of the nucleus just after hatching (Bigelow 1992), so the increments were examined and counted from the nucleus to the first dorsal dome checkmark, and from the checkmark increments were counted to the rostrum. However, in 4 of the 140 cases (3%) it was necessary to extrapolate (based on the increment widths of approximately 10 of the last countable increments) from adjacent areas to resolve increment counts in local unclear areas (Hoving et al. 2007). The number of increments in each statolith was counted by averaging three counts. Estimated hatch dates were back-calculated from age data (hatch date: sampling date-age estimated in days).

The daily growth rate (DGR) was calculated using the following equation from Jackson et al. (1997):

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

The size at hatching of *A. andamanica* is not known, so we assumed it has the same hatching size as *A. trigonura* (1 mm DML, Young and Harman 1985), a closely related congener. The hatching size in *A. trigonura* was determined from hatchlings reared in captivity (Young and Harman 1985).

Age at length and age at weight data were fitted to a linear ($Y = a + bX$), power ($Y = aX^b$), exponential ($Y = ae^{Xb}$) and logistic ($Y = 1 + e^{-k(x-x0)}$) model. The curve of best fit was determined by the least coefficient of variance of the curve parameters (highest R^2).

Maturity and fecundity

Oviducal oocyte counts were made on preserved specimens. The oviducts were removed, and oocytes were counted. Oocyte diameters (n=30) were measured using a stereo zoom microscope (Nikon, SMZ-25, Japan). The gonadosomatic index (GSI) was calculated as given by Laptikhovsky and Nigmatullin (1993):

$$\mathrm{GSI} = (\mathrm{GW}/\mathrm{BW}) \times 100$$

where GW is gonad weight and BW is body weight.

RESULTS

Length-weight relationship

DMLs ranged from 15 to 26 mm (mean=22 mm, SD±5.6) in males and 23 to 60 mm (mean=31 mm, SD±7.7) in females. Body weights ranged from 0.58 to 2.1 g (mean=1.28 g, SD±0.61) in males and 1.5 to 5.7 g (mean=2.9, SD±1.4 g) in females. The length-weight relationship was $BW = 0.313\ DML^{1.808}$ for females and $BW = 0.308\ DML^{1.718}$ for males (Fig. 2). The coefficient of determination (R^2) was 0.88 for females and 0.85 for males. The ANCOVA showed no significant difference between the sexes (P=0.354). Therefore, the length-weight relationship of pooled samples (combined sexes) was determined as $W = 0.278\ DML^{1.884}$ ($R^2 = 0.93$). Negative allometric growth was observed for males, for females and for the pooled data. The value of the exponent, b, was significantly different from 3 (P<0.01).

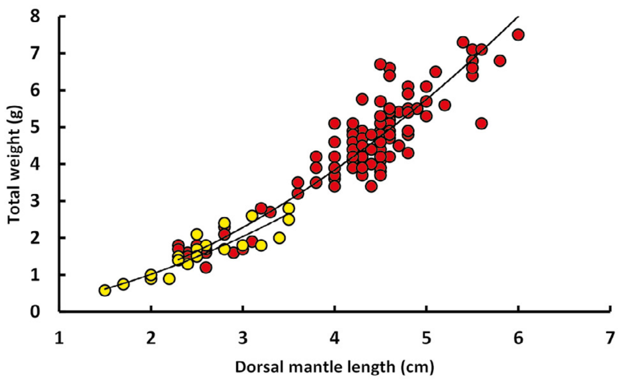

Fig. 2. – Length-weight relationship of *Abralia andamanica* males (yellow circle) and females (red circle) from the Arabian Sea.

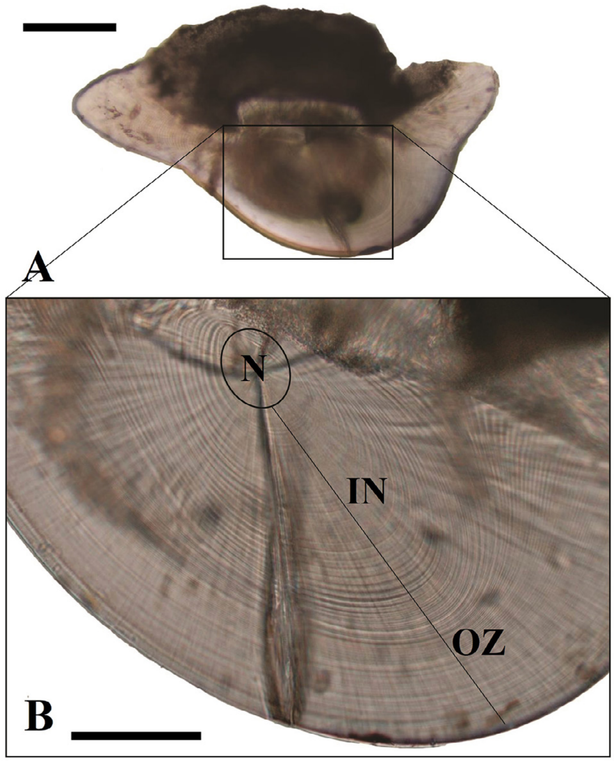

Fig. 3. – Light micrograph of the statolith of *Abralia andamanica* (DML=38 mm) (A) and lateral dome region of statolith with increments (B). N, nucleus; IN, inner zone; and OZ, outer zone of the statolith (scale bar, A=200 µm; B=100 µm).

Age and growth

The total lengths of statoliths ranged from 815 to 960 µm (mean= 876 µm, SD±31). The statolith shape has a round lateral dome, with a straight rostrum and a dorsal dome and a large wing (Fig. 3A). Growth increments were observed in all statoliths. They were deposited around an oval-shaped nucleus with a diameter ranging from 14.26 to 18.46 µm (mean=15.46 µm, SD±4.1). Growth increments were grouped into two zones based on the increment width (Fig. 3B). The first 30-40 increments from the outside of the nucleus (inner zone) had an average width of 2.63 µm. Towards the margin (outer zone), increment widths gradually decreased (mean= 0.70 µm) (Fig. 3B).

Based on the increment counts, ages ranged from 83 to 125 (mean =99, SD±12) days in males and 79 to 177 (mean=126, SD±18) days in females (Fig. 4A). The youngest (79 days) was a maturing female with a DML of 24 mm, and the oldest (177 days) was a mature female of 60 mm DML. The smallest female measured had a DML of 23 mm and was 82 days old, while the smallest male measured was 15 mm DML and was 83 days old.

The growth rate in body weight ranged from 0.006 to 0.02 g/day in males and 0.01 to 0.05 g/day in females (Fig. 4B). The maximum growth rate recorded was 0.05 g/day in a female of 43 mm DML at an age of 106 days. The daily growth rate in length ranged from 0.16 to 0.30 mm (mean=0.24, SD±0.03) in males and from 0.23 to 0.43 mm (mean=0.33, SD±0.04) in females (Fig. 5). For both sexes, the relationship between DML and growth rate was best described as a power function (Fig. 5).

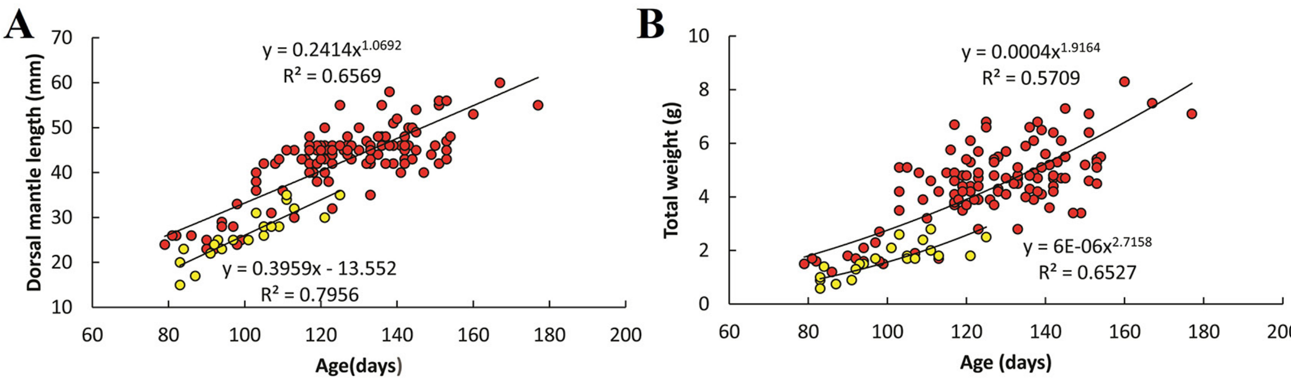

Fig.4. – Relationship between age with dorsal mantle length (A) and total weight (B) of males (yellow circles) and females (red circles) *Abralia andamanica* from the Arabian Sea.

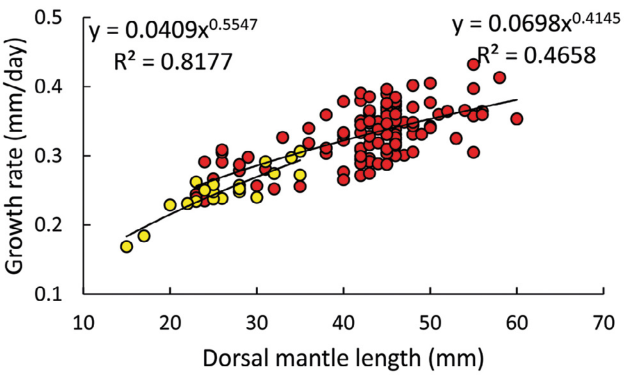

Fig. 5. – Relationship between dorsal mantle length and growth rate of males (yellow circles) and females (red circles) *Abralia andamanica* from the Arabian Sea.

The length (DML) at age data were described by a linear function for males and a power function for females (Table.1). The relationship between DML and age was expressed as DML=0.395+13.552AGE (R^2=0.79) for males and DML=0.241AGE$^{1.069}$ (R^2=0.65) for females. The relationship between BW and age was expressed as a power function for both sexes: BW=6E-06AGE$^{2.715}$ (R^2=0.65) for males and BW=0.0004AGE$^{1.916}$ (R^2=0.57) for females. The correlation coefficient (R^2) was higher for males than for females for both the DML and BW age relationships.

Maturity and fecundity

Mature females were larger (both in DML and weight) than males. A total of 83 mature (33-60 mm DML), and 36 maturing (23-45 mm DML) females were observed. The weight of the reproductive system (ovary and oviducal gland) varied from 18.5% to 33.3% (mean=23.6%, SD±5) of body weight in mature females. There were 158 to 648 (mean=274, SD±101) oocytes in the oviducts of mature females. The diameter of ripe oocytes varied from 0.81 to 0.92 mm (mean=0.87, SD±39).

DISCUSSION

This report of *A. andamanica* from the southeast Arabian Sea was made after a 50-year hiatus. Silas (1968) recorded *A. andamanica* from the southeast Arabian Sea in all months of 1967 except January, September and October during the *Varuna* expedition. The individuals in the present study were caught from continental shelf waters, and earlier findings (Silas 1968) showed that *A. andamanica* is a member of the mesopelagic boundary community like its closely related congener *A. trigonura* from Hawaiian waters (Bower et al. 1999).

There were no apparent differences between males and females in the dorsal mantle length - body weight relationship. The exponent (b) of the DML-BW relationship was significantly lower than 3, showing allometric growth. This general change in body shape with growth, in which the mantle length increases allometrically as juveniles develop into slender, more streamlined adults, has been previously recorded in other squid species (Coelho et al. 1994, Sifner and Vrgoc 2004).

Statoliths of *A. andamanica* are similar to those of other species of the genus *Abralia* (Young and Mangold 1994, Sajikumar et al. 2019b). Characteristic morphological features include the short rostrum and well-developed dorsal dome, as well as the broad wing. The statolith increments are well resolved, unambiguous and similar to those in *A. trigonura* (Young and Mangold 1994).

The average diameter of the statolith nucleus of *A. andamanica* is larger than that of *A. trigonura* (12.7 µm) from Hawaiian waters (Bigelow 1992). The two growth zones of the statolith indicate slow and fast statolith growth corresponding to two life-history phases. *A. trigonura* paralarvae occur at 15-30 m during the night and 50-70 m during the day (Young and Harman 1985), while adults are epipelagic (<200 m during the night) to mesopelagic (~600 m during the night). The early stages of the enoploteuthids occur in pelagic warm waters, later start their vertical migrations ascending the epipelagic zone at night and plunge during the day into mesopelagic waters (Arkhipkin and Schetinnikov 1989), where the temperature is normally much lower than in surface waters. Bigelow (1992) and Arkhipkin (1996a) hypothesized a sharp decrease in the growth rate during

Table 1. – Models of growth curves fitted to the male and female *Abralia andamanica* from the Arabian Sea (bold type face indicates best fit model).

		DML/number of increments			BW/number of increments		
Sex	Function	a	b	R^2	a	b	R^2
Male	**Linear**	**0.395**	**13.552**	**0.79**	0.0386	2.198	0.622
	Power	0.016	1.594	0.78	**6E-06**	**2.715**	**0.650**
	Exponential	5.261	0.016	0.76	0.107e	0.026	0.625
Female	Linear	0.323	2.055	0.601	0.0538	2.288	0.490
	Power	**0.241**	**1.069**	**0.656**	**0.0004**	**1.916**	**0.570**
	Exponential	14.221	0.0086162	0.609	0.605e	0.015	0.526

the transition from holopelagic to mesopelagic lifestyle seems to be similar for all enoploteuthids.

Females grew faster than males. Earlier, length at age data were described as a linear function in *P. gemmata* from the central-east Atlantic (Arkhipkin 1997). The relationship between body mass and age was best described by an exponential and linear growth curve for females and males, respectively, in *A. andamanica* from the Arabian Sea.

The oldest mature female was 177 days old, suggesting that *A. andamanica* may have a lifespan of about 6 months in the tropical Arabian Sea, which is similar to that reported for *A. trigonura* from the Hawaiian waters (Young and Mangold 1994). A mature female individual of *Abralia siedleckyi* Lipinski, 1983 (29 mm DML) from the Arabian Sea had an age of 93 days with a daily growth rate of 0.31 mm DML/day (Sajikumar et al. 2019b). It has been found that enoploteuthids including *Abraliopsis atlantica*, *Abraliopsis morisii* and *Enoploteuthis leptura* grow slowly and have short lifespans (Arkhipkin and Murzov 1990, Arkhipkin 1994, 1996a). However, the lifespan is longer than that of the smallest enoploteuthid squid, *P. gemmata,* which has a lifespan of 2.5 months (Arkhipkin 1997). The short lifespan is a characteristic feature of squids of tropical waters. A six-month life span has also been described for many ommastrephids in oceanic tropical waters (Arkhipkin 1996b, Arkhipkin et al. 1998) and nearshore loliginid squids in the tropical waters (Jackson 2004, Jin et al. 2019, Sajikumar et al. 2019a). Sexual dimorphism is also reflected in age and growth rates. Females of the enoploteuthid squid *Abraliopsis atlantica* live 1 to 1.5 months longer than males (Arkhipkin and Murzov 1990). The biological reasons for the sexual dimorphism in the age of *A. andamanica* is unclear.

The age versus DML data could be explained by a linear function for males and a power function for females. Previous studies in *A. trigonura* from Hawaiian waters showed a logistic model for females and a Gompertz model for males, while a linear function was reported in *P. gemmata* from the central-east Atlantic (Arkhipkin 1997). The congener *A. trigonura* is characterized by exponential growth in the paralarval stage, followed by a slower growth stage, which is evident from a length of 16 mm ML onwards (Bigelow 1992). In *A. andamanica*, females grew faster than males, but the lack of individuals below 15 mm DML and the limited number of samples prevented us from the constructing a growth curve.

The relative weight of the reproductive system (mean=23.6%) was the same as that of enoploteuthids from the Atlantic (Laptikhovsky 1999). However, the GSI was higher than in *A. trigonura* (GSI=9.7%) from Hawaiian waters (Young and Mangold 1994). The oocytes were small (mean=0.87 mm), as in all enoploteuthids studied (Laptikhovsky 1999). The oviducal fecundity of enoploteuthid squids reaches 400 in *Abraliopsis atlantica* and *A. trigonura*, and a maximum number of 2800 oocytes were observed in *Enoploteuthis anapsis* Roper, 1964 (Young and Mangold 1994, Laptikhovsky 1999). The absolute fecundity of *Abralia andamanica* from the Arabian Sea was estimated to range from 2400 to 3200 oocytes (Amelekhina 1983). The mean oocyte number was 251 in the oviducts of *Abralia verany* Rüppell, 1844 from the eastern Mediterranean Sea (Salman and Laptikhovsky 2005), and 284 in *A. siedleckyi* from the Arabian Sea (Sajikumar et al. 2019b), figures which are comparable to our estimated mean of 274 oocytes. Young and Mangold (1994) indicated that *A. trigonura* is a multiple spawner, and Laptikhovsky (1999) showed that spawning is prolonged and intermittent for enoploteuthids.

The present study provides information on the age and growth of *A. andamanica*, a mesopelagic squid from the tropical Arabian Sea, which reveals a short lifespan, slow growth and sexual dimorphism.

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