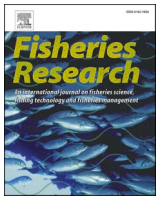
Fisheries Research 248 (2022) 106227

Contents lists available at ScienceDirect

Fisheries Research

journal homepage: www.elsevier.com/locate/fishres



Insight on the reproductive biology of small striped cuttlefish, *Sepia prabahari* in Gulf of Mannar, Indian Ocean and recommendation for a minimum legal size

Mookaiah Kavitha *, Geetha Sasikumar, Jagadis Iyadurai, Ranjith Lakshmanan, Jasmin Felix

ICAR-Central Marine Fisheries Research Institute, P.B.No: 1603, Ernakulam North (PO), Kochi 682 018, Kerala, India

ARTICLE INFO

Handled by B. Morales-Nin

Keywords:
Small striped cuttlefish
MLS
Maturity
Spawning
Reproductive biology

ABSTRACT

This paper provides insight into the size composition and reproductive aspects of small striped cuttlefish *Sepia prabahari* distributed exclusively in the Gulf of Mannar (GoM) Biosphere Reserve, in the Indian Ocean which contributes 11% to the cephalopod catch in this region. The size composition in the fishery varied between 4.6 and 14.6 cm in dorsal mantle length (DML) and the length group between 8.1 and 10 cm dominated the catch (45%). The DML-weight relationship for male, female and for the pooled sexes were 0.5561 $DML^{2.31}$; 0.4821 $DML^{2.39}$ and 0.5214 $DML^{2.34}$ respectively. Observations on maturity stages indicated year-round spawning with two peaks. Maturity indices increased in tandem with the gonadal development in the cuttlefish. Mean GSI in females showed a multi-fold increase from 0.41 in maturing to 2.20 in mature stages, while it increased from 0.51 to 1.35 for the respective stages in males. The minimum legal size (MLS) was set considering the minimum size at maturity of 7.0 cm for the species. The Lm_{50} estimated at 9.2 cm DML for males; 9.7 cm for females and 9.4 cm for the pooled sexes, showed early maturation in males. The size composition indicated that nearly 53.7% of the commercial catch in the fishery is below the Lm_{50}, while 5% of the catch was below MLS. Management measures limiting the fishing pressure on sub-adults are recommended for sustainable exploitation of the resource.

1. Introduction

Cuttlefish are one of the most commercially important and high valued fishery resources, contributing nearly 39% to the total cephalopod production (2,20,844 t) along Indian Seas (CMFRI, 2019). Among the exploited cuttlefish species, *S. prabahari* is described from Gulf of Mannar (GoM) Biosphere Reserve, in the Indian Ocean (Neethiselvan and Venkataramani, 2002). In GoM, *S. prabahari* is a relatively abundant species which is distributed all over the continental shelf (Fig. 1). Neethiselvan and Venkatarmani (2002) described *S. prabahari* as a new species in the targeted cuttlefish trawl fishery from GoM. Morphometrically *S. prabahari* closely resembles the juveniles of *Sepia pharaonis*; with the exception of the arm length, tentacular club, sucker ring size and pattern, dorsal mantle pattern and cuttlebone. Reproductive aspects of commercially important cephalopods in general (see reviews by Pierce et al., 2010; Jereb et al., 2015; Lishchenko et al., 2021) and *Sepia* in particular (Dursun et al., 2013; Salman, 2015; Gras et al., 2016; Sifner et al., 2018; Lin et al., 2019) have been studied in recent years. There is no detailed description on the biology of *S. prabahari* and the only report is on their population characteristics (Singh, 2005). The present paper reports for the first time, on aspects of the biology of *S. prabahari* in GoM, Indian Ocean and attempts to contribute to the knowledge of the reproductive biology of this species in its distributional range.

2. Material and methods

2.1. Study area

Gulf of Mannar in the Indian Ocean extends between 78°08′ E to 79°30′E and 8°35′N to 9°25′N located on the South East Coast of Indian Peninsula. Four districts (Kanyakumari, Tirunelveli, Tuticorin, and Ramanathapuram) with the coastline covering 365 km form the land boundary. Gulf of Mannar, encompassing the 21 coral islands is simultaneously a Marine Biosphere Reserve (GOMMBR), supporting major

* Correspondence to: Molluscan Fisheries Division, ICAR-Central Marine Fisheries Research Institute, P.B. No: 1603, Ernakulam North (PO), Kochi 682 018, Kerala, India.
E-mail address: kavifish@gmail.com (M. Kavitha).

https://doi.org/10.1016/j.fishres.2022.106227
Received 17 October 2021; Received in revised form 4 January 2022; Accepted 6 January 2022
Available online 13 January 2022

coastal and marine habitats *viz.*, seagrass, seaweeds, mangroves, coral reefs and estuaries with rich biodiversity (Kumaraguru et al., 2006).

2.2. Sampling

Sepia prabahari samples were collected fortnightly between January 2016 to December 2017, except in May, due to the seasonal fishing ban commencing from mid-April in this region (Anon, 2017). A total of 2098 specimens (4.6–14.6 DML) were sampled randomly for size composition analysis in the fishery. About 777 males (4.6–14.6 DML) and 671 females (5.0–14.5 DML) were dissected for length-weight data analysis which included 229 males (4.5–13.5 DML) and 224 females (5.0–14.0 DML) subjected to detailed biological studies. They were caught in commercial trawlers throughout the year from 15 to 20 m depth and the dorsal mantle length (DML) (± 0.1 mm) and total body weight (TW) (± 0.01 g) were recorded.

2.3. Length-weight relationship

Log transformed data for the cuttlefish DML-weight relationship of males and females was fitted for the equation, $W=a.DML^b$ (Le Cren, 1951), where W = total weight in gram; DML = Dorsal mantle length in cm; 'a' is the intercept and 'b' is the slope. The parameters a and b were estimated by least-square linear regression. Analysis of covariance (ANCOVA) was used to test the heterogeneity of slopes in males and females and differences between intercepts of regression. The growth component 'b' in males, females and pooled data of sexes was tested by Student t-test to ascertain the deviation of b value from the isometric value (b=3) (Sokal and Rohlf, 1987), using the formula, $t = b\text{-}3/S_b$, where, b = regression coefficient of log-transformed data and S_b = standard error of b.

2.4. Sex-ratio

Sex ratio in *S. prabahari* was calculated monthly and the homogeneity in the distribution of both sexes was tested using the formula, $\chi 2 = : \Sigma(O\text{-}E)^2 / E$ where, O = the observed number of males and females in each month and E = the expected number of males and females in each month.

2.5. Maturity and maturity indices

The specimens were sexed by macroscopic examination of the reproductive organs. The nidamental glands, accessory nidamental glands and the ovary in females; the testis and Needham's sac in males were dissected out and subsequently weighed to the nearest 0.1 g. Maturity stages for each sex were determined by using the scale proposed by Gabr et al. (1998) with modification of female scale in stage III similar to male. The maturity scales for males and females, I - immature, II - maturing, III – fully mature and IV - spawning. Based on the percentage of maturity stages in the monthly samples, the spawning season was calculated. Mean size at which 50% of the cuttlefish attained maturity (Lm_{50}) was estimated by fitting the logistic function to the proportion of mature fish in the 10 mm size categories (King, 1995). Maturity indices were calculated according to (Devlaming et al., 1982).

Gonadosomatic index (GSI) = Gonad weight *100/ Body weight·

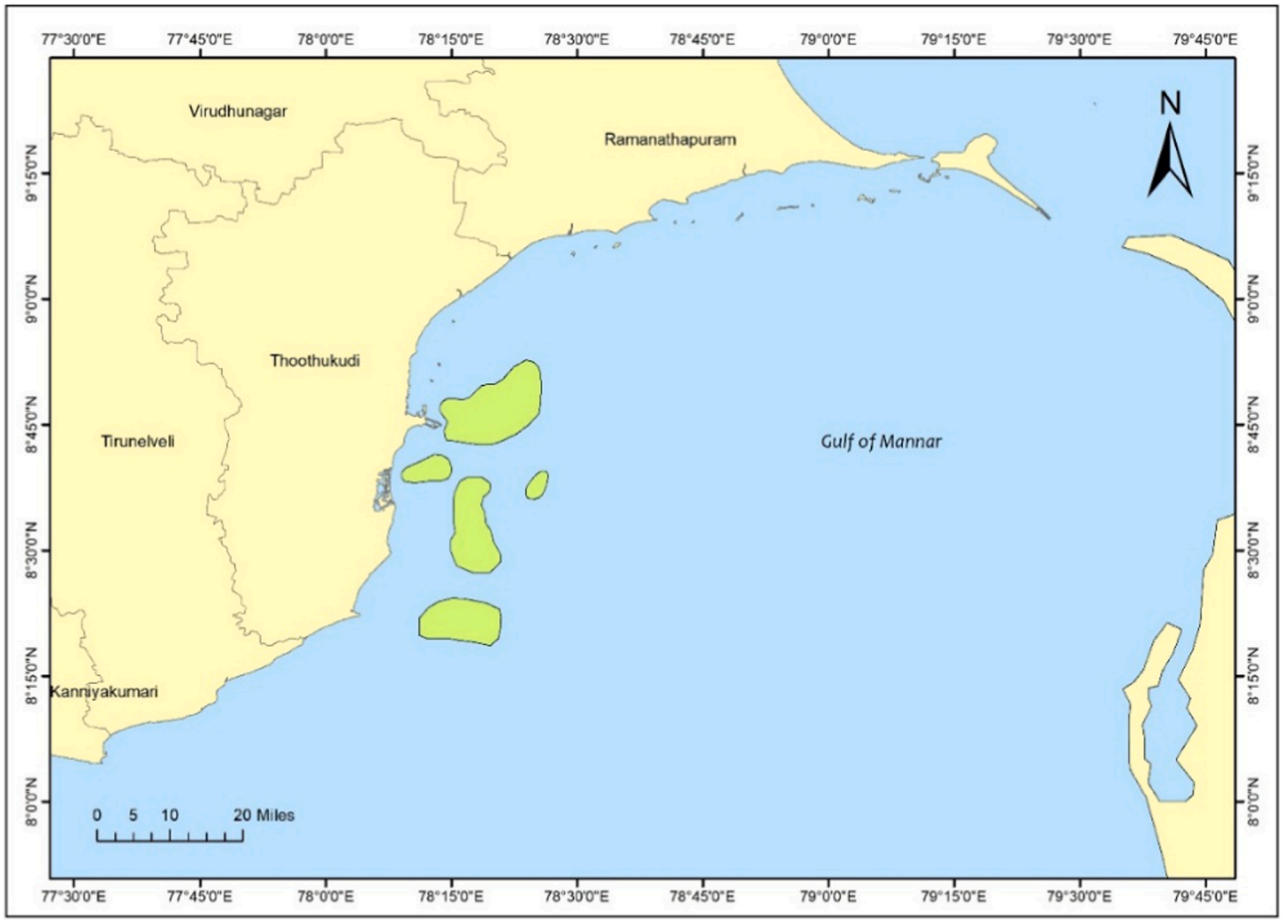


Fig. 1. Map of Gulf of Mannar (GoM) biosphere reserve, in the Indian Ocean illustrating the fishing region.

Nidamental gland index (NGI) = Nidamental gland weight *100/ Body weight·Spermatophoric complex index (SCI)= Spermatophoric complex weight * 100/ Body weight

2.6. Statistical analysis

The correlations of mean maturity indices among the maturity stages were carried out using SPSS version 16.0 and the level of significant difference was indicated * ** ± $P < 0.001$; * * ± $P < 0.01$; * ± $P < 0.05$.

3. Results and discussion

3.1. Size composition distribution

The DML of this species in the fishery varied between 4.6 and 14.6 cm with a mean length of 9.3 ± 1.71 cm. The size range recorded was comparable with the earlier observations by Singh (2005), ranging from 5.2 cm to 13.5 cm. The DML and TW of males ranged from 4.6 to 14.6 cm (mean 9.2 ± 1.9 cm) and 17 – 284 g (mean 100 ± 49.5 g). The DML and TW of females ranged from 5.0 to 14.5 cm (mean 9.2 ± 1.7 cm) and 22 – 282 g (mean 107 ± 46.2 g). The mean length varied between 8.4 and 9.9 cm for different months, with the highest recorded in April and August (Fig. 2), indicating the presence of a greater number of mature cuttlefish in these months, coinciding with the peak spawning season of this species in this region. The length group between 9.1 and 10 cm formed a major catch (24%) in the fishery (Fig. 3) followed by 8.1 – 9.0 cm (21%) during the period.

3.2. Length-weight relationship

The slope 'b' for DML- weight relationship (Figs. 4 and 5) in *S. prabahari* were < 3, showing negative allometric growth in males ($W = 0.5561\ DML^{2.31}$ ($R^2 = 0.9079$)); females ($W = 0.4821\ DML^{2.39}$ ($R^2 = 0.9101$) and in the pooled samples ($TW = 0.5214\ DML^{2.34}$ ($R^2 = 0.9079$)). The regression co-efficient 'b' value obtained for both sexes were significantly different from isometric value 3 (t-test > $t_{0.05}$). This indicated that the growth pattern of male and female *S. prabahari* did not follow the cubic relationship since there was higher growth in length relative to the weight. Similar negative allometric relationships have been described in this species (Singh, 2005) and many cuttlefish species, such as *Sepia officinalis* from Eastern Libya (Razek et al., 2014), Oran Bay (Saddikioui et al., 2017) and Southern Portugal (Vasconcelos et al., 2018); *S. pharaonis* from the Arabian sea (Al-Marzouqi, 2009; Sasikumar et al., 2013); *Sepia aculeata* and *Sepiella inermis* from Bay of Bengal (Siddique et al., 2016).

There were significant differences in the DML-weight relationship between males and females (ANCOVA, $P < 0.05$). The results of the study revealed that females were heavier than males, implying that female *S. prabahari* are relatively heavier at a given length, the feature reported in many cuttlefish. The higher relative weight of the reproductive system in mature females, affects the apparent sexual differences in length weight relationship (Dunn, 1999; Rossetti et al., 2003; Sifner et al., 2018; Vasconcelos et al., 2018).

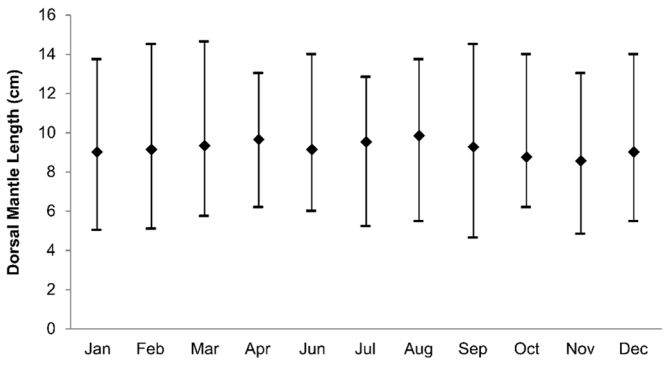


Fig. 2. Seasonal variation in the mean size of *S. prabahari.*

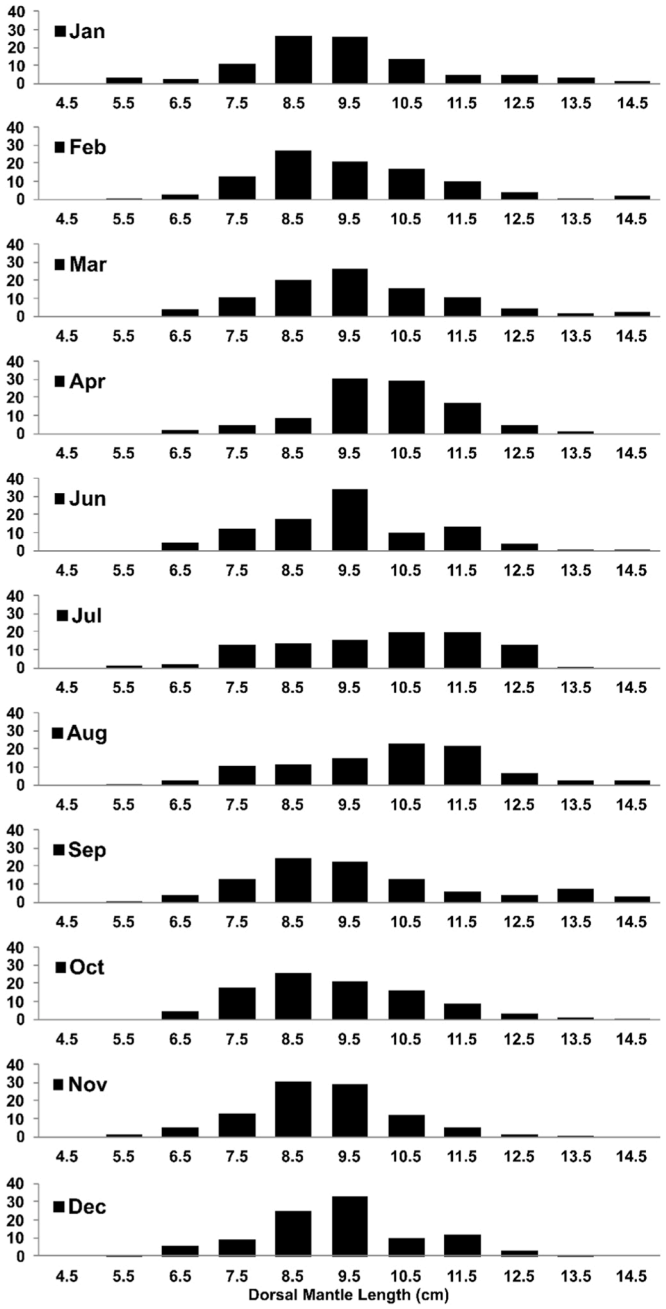


Fig. 3. Seasonal variation in the size composition of *S. prabahari.*

3.3. Sex ratio

The sex ratio fluctuated between 1: 1.4 and 1: 0.4 in November and January respectively. Males were found to be dominant in the fishery with 57% of the total catch. The overall average annual sex-ratio of *S. prabahari* was 1:0.76 (M:F) indicating the dominance of males over females in the population. The χ2-test between sexes showed that males were significantly ($P < 0.05$) dominant during January, April, June, August and October. The skewed sex ratio during most of the months probably reflects behavioral differences associated with continuous

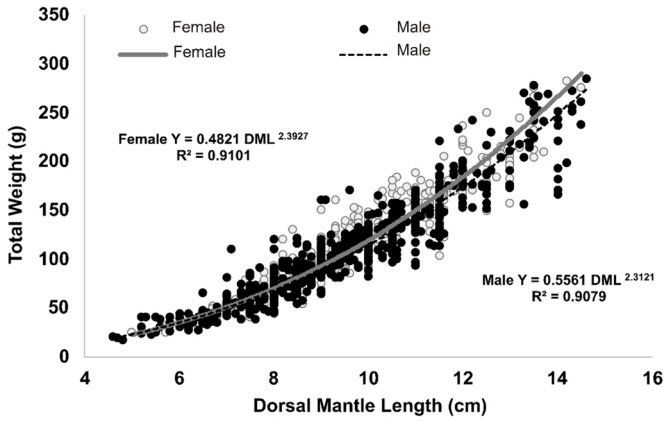


Fig. 4. Dorsal mantle length-weight relationship in male and female *S. prabahari.*

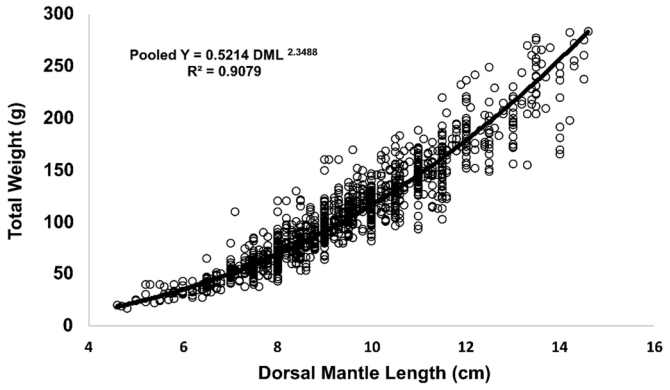


Fig. 5. Dorsal mantle length-weight relationship in *S. prabahari.*

spawning activity in females when they move towards the spawning ground for egg deposition on the underside of rocks or in crevices (Hall and Hanlon, 2002) favouring male predominance. Sexual segregation, where males outnumbering females have been reported in cuttlefish from many areas (*S. pharaonis*, Al-Marzouqi, 2009; *Sepia officinalis,* Akyol et al., 2011; Duysak et al., 2014).

3.4. Size of various maturity stages

Four stages of sexual maturity were classified for both males and females (Table 1) according to the gross morphology of the gonads (Figs. 13 and 14). The mature animal constituted 56% of the male (DML range - 7.0–13.5 cm) and 44% of the female (DML range - 7.5–14 cm)., while the spawning/spent cuttlefishes (stage-IV) were least represented (males-7%; females 4%) in the samples. The dorsal mantle length varied between 4.5 – 8.0 cm for stage-I; 6.5 – 9.0 cm for stage–II; 7.0 – 13.5 for stage–III and 8.0 – 13.0 cm for stage–IV in males; similarly it varied between 5.0 and 8.5 cm for stage–I, 7.5 – 10.0 cm for stage–II, 8.0–14.0 cm for stage-III and 9.0 – 11.0 cm for stage IV) in female (Table 2). The wide size ranges of the matured cuttlefish indicate the continued growth of the cuttlefish after attaining the maturity through incessant feeding until spawning (Chembian, 2013). In general, the proportion of immature and maturing stage specimens were lesser in number compared to mature specimens in both sexes which suggests gonads attain maturity in a short period of time (Gonzalez and Guerra, 1996). The percentage of spent males and females were relatively less compared to other gonadal stages during the study period, attributing to post-spawning exhaustion of cuttlefish. Many cephalopods are semelparous and individuals of all coastal species (eg. *Sepia* sp.) tested for culture die after spawning (Villanueva et al., 2014). Similar incidence

Table 1
Maturity scale of male and female *S. prabahari.*

Developmental stage	Category	Description
Male		
I	**Immature**	Testis very small and thin. Needham's sac small and transparent in color. No sperm in Needham's sac
II	**Maturing/ Developing**	Testis enlarged and thicker. Needham's sac slightly large with visible vas deferens and it contains few visible short spermatophore.
III	**Fully mature**	Testis large and fully developed. Needham's sac full with tightly packed well-developed spermatophores.
IV	**Spawning/ Spent**	Needham's sac flaccid with degenerating spermatophores and appear as white mass Few sperm in Needham's sac.
Female		
I	**Immature**	Nidamental gland and oviducts very small, appear as very fine transparent stripes. The ovary is small, translucent, membranous. No ova apparent.
II	**Maturing/ Developing**	Nidamental glands larger and thicker and slightly oval. Accessory nidamental gland small and creamy white. Oviduct thickened and fully developed. Ovary with clearly visible small – medium sized ova.
III	**Fully mature**	Nidamental gland large, thick and oval. Accessory nidamental gland yellowish to orange in color. Oviduct large with transparent mature eggs. Ovary occupies nearly half the length of mantle cavity with small, medium and large striated egg. The ovary has well defined reticulate pattern on the surface shows the increased number of matured eggs.
IV	**Spawning/ Spent**	Nidamental glands large but soft flabby. Accessory nidamental gland light orange in color. Ovary contains small number of striated loose eggs and few medium to small eggs.

was reported by Aoyama and Nguyen (1989) in *S. pharaonis* where females migrate to deeper water after spawning and most them die, while some males were assumed to survive to the following year later die after participating again in reproductive activity. Mortality is reported in many cephalopods after one or several bouts of spawning (Arnold and Williams-Arnold, 1977; Mangold et al., 1993).

3.5. Size at first maturity (Lm_{50})

The minimum size at maturity in male and female *S. prabahari* was observed at 7.0 and 8.0 cm respectively, while the size at first sexual maturity (Lm_{50}) was observed to be 9.2 cm DML for males and 9.7 cm DML for females, indicating that the males attain maturity earlier than females. Similar observation was made by Saddikioui et al. (2017) in *Sepia officinalis* at Oran Bay, by Al-Marzouqi et al. (2009); in *Sepia pharaonis* at Arabian Sea and Gabr et al. (1998) in *Sepia dollfusi* at Seuz Canal. The combined sex showed Lm_{50} at 9.4 cm DML (Fig. 6). All the males measuring above 10.5 cm of DML and females above 11.5 cm DML were in mature condition. The most exploited size group in the fishery was 8.5–9.5 cm, which was closer to size at first maturity for both males and females. The size frequency distribution indicated that nearly 53.7% of the commercial catch in the fishery is below Lm_{50}, necessitating systematic monitoring. For effective management, the minimum legal size (MLS) for this species is recommended as 7.0 cm DML, considering the size of transitioning from juvenile to adult (Mohamed et al., 2009) *viz.*, the minimum size at maturity observed in this species.

Table 2
Distribution of different maturity stages of *S. prabahari* by length.

DML (cm)	Male Maturity Stages (%)				Total (Nos)	Female Maturity Stages (%)				Total (Nos)
	I	II	III	IV		I	II	III	IV	
4.5	100				1.0					
5	100				1.0	100				1.0
5.5	100				2.0	100				1.0
6	100				5.0	100				4.0
6.5	56	44			9.0	100				6.0
7	50	37	13		16.0	100				17.0
7.5	25	50	25		16.0	92	8			13.0
8	31	36	31	2	42.0	71	24	5		20.0
8.5		43	50	7	14.0	30	52	18		27.0
9		16	72	12	32.0		77	18	5	22.0
9.5			88	12	26.0		37	63	0	27.0
10			73	27	22.0		22	64	14	28.0
10.5			100		14.0			89	11	18.0
11			100		17.0			83	17	12.0
11.5			100		3.0			100		21.0
12			67	33	3.0			100		4.0
12.5			100		3.0			100		1.0
13			50	50	2.0			100		1.0
13.5			100		1.0					
14.0								100		1.0
Total	18	19	56	7	229	28	24	44	4	224

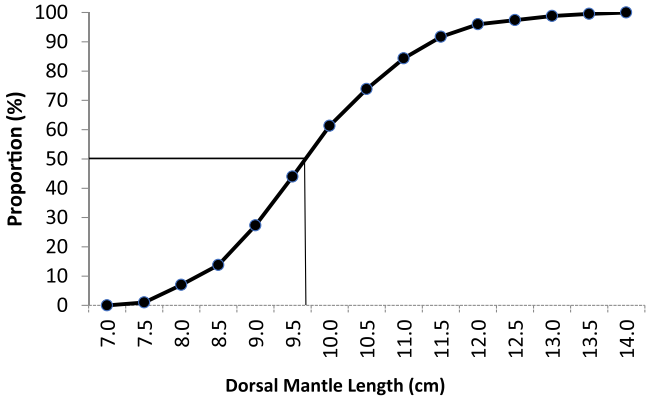


Fig. 6. Length at maturity (Lm_{50}) of *S. prabahari* from Gulf of Mannar.

3.6. Monthly variation in maturity stages

In all months, the matured specimens were higher in number compared to other maturity stages. The monthly percentage composition of the maturity stages of males and females are illustrated in Figs. 7 and 8. The occurrence of a high percentage of mature specimens in the sample throughout the study period indicates a year-round spawning of this species in this region. Similar type of prolonged spawning was

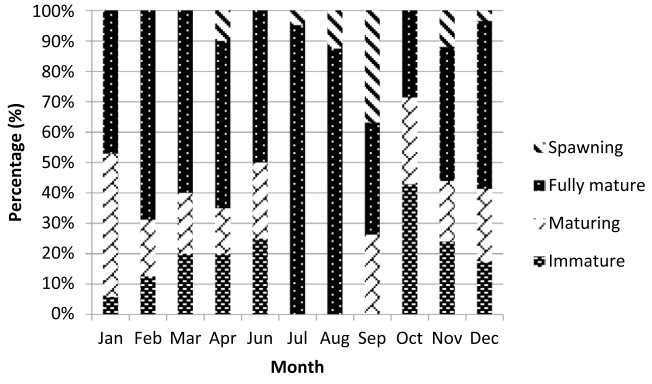


Fig. 7. Monthly percentage of the maturity stages for males of *S. prabahari.*

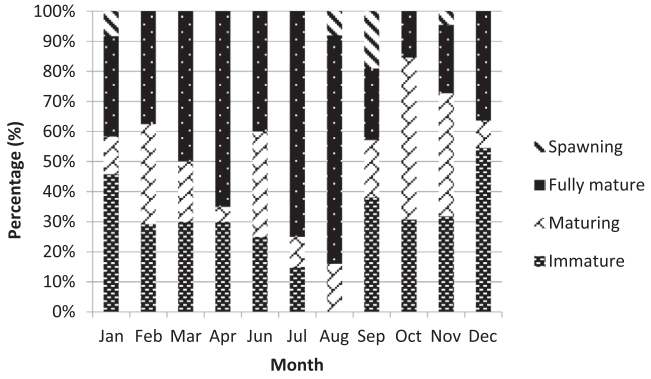


Fig. 8. Monthly percentage of the maturity stages for females of *S. prabahari.*

reported in *S. pharaonis* from the Indian seas (Silas et al., 1985; Nair et al., 1993); *Sepia officinalis* from Iskenderun Bay (Duysak et al., 2014), Aegean Sea (Onsoy and Salman, 2005) and *Doryteuthis (Photololigo) sibogae* from the same study area (Neethiselvan et al., 2001). A high percentage of mature males were observed during most of the months with peak occurrence in July and August. The occurrence of more than 50% of mature males during most of the months further supports continuous spawning. Maturing males were recorded in all the months except in July and August. In females, more percentage of mature specimens were noticed during March to April and July to August, indicating the period of presumed spawning peak of the cuttlefish. Cuttlefish with spawning/spent gonadal stages were not noticed in all the months and only limited numbers recorded in the available months, probably due to post-spawning mortality (Dunn, 1999, 2021).

3.7. Maturity index

For *S. prabahari*, monthly variation in the maturity indices (GSI, NGI, SCI) was estimated for both sexes (Figs. 9 and 10). In male, high GSI and SCI value recorded during July to August coincided with the peak percentage of specimens in fully mature condition. In the male population, the higher GSI value recorded from January to December indicated the availability of a high percentage of mature animals throughout the year. In females, maturity indices (GSI and NGI) started increasing in January and peaked in March, April, July and August which coincided with the

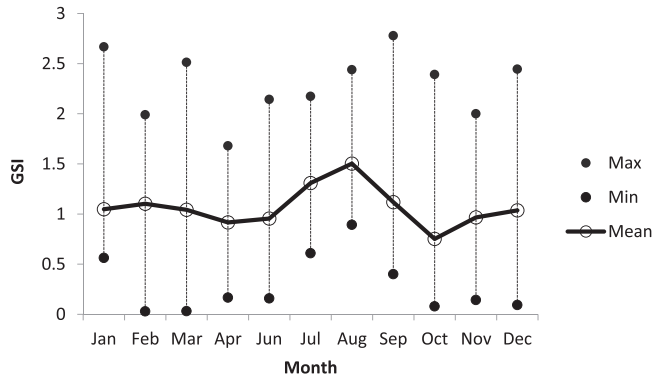


Fig. 9. Monthly variation in mean Gonadosomatic index for male *S. prabahari.*

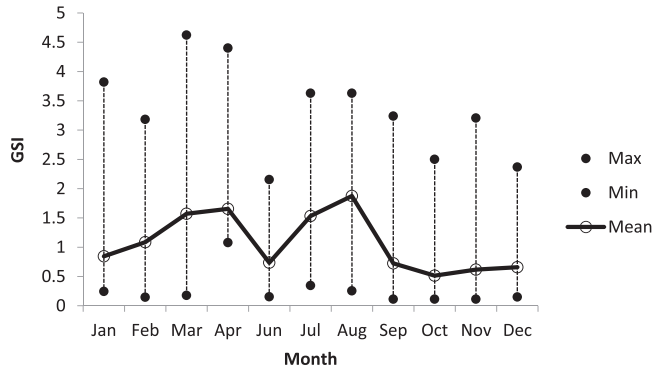


Fig. 10. Monthly variation in mean Gonadosomatic index for female *S. prabahari.*

peak percentage of specimens in spawning condition. Maturation indices declined gradually and reached their lowest values between October and December. There was a significant (Tables 3 and 4) increase in values of all maturity indices along with maturity stage (Figs. 11 and 12). In both sexes, maturity indices show a clear pattern similar to the monthly variation in maturity stages. The maturity indices increased in tandem with the gonadal development of the cuttlefish. There was a multi-fold increase in female GSI from 0.41 in stage II to 2.20 in stage III. The NGI increased more than double from 1.0 in stage II to 2.7 in stage III, which was attributable to the rapid increase in the mature oocytes in ovary and nidamental gland volume (Chembian, 2013). Similar significant increase was noted in male GSI and SCI from stage II to III. In the present study two probable spawning peaks have been identified, one in the month of March-April and another during July-August. This is further strengthened by the female maturity indices GSI and NGI which indicates that the spawning activity is at its peak during the above

Table 3
Correlation of male mean gonadosomatic index (GSI) and Spermatophoric complex index (SCI) with the maturity stages.

Index	Maturity stages	Min	Max	Mean	SD	N	Significance
GSI (%)	I	0.01	0.83	0.11	0.13	40	* **
	II	0.07	1.20	0.51	0.26	44	* **
	III	0.45	3.01	1.35	0.50	129	* **
	IV	0.50	1.91	0.96	0.37	20	
SCI (%)	I	0.09	0.90	0.18	0.14	40	* **
	II	0.14	2.12	0.76	0.41	44	* **
	III	0.49	2.77	1.17	0.16	129	* *
	IV	0.58	1.19	1.01	0.15	20	

Significance levels for comparison of means between maturity stages: * ** ± $p < 0.001$; * * ± $p < 0.01$; * ± $p < 0.05$.

Table 4
Correlation of female mean gonadosomatic index (GSI) and nidamental gland index (NGI) with the maturity stages.

Index	Maturity stages	Min	Max	Mean	SD	N	Significance
GSI (%)	I	0.01	1.20	0.05	0.11	62	* **
	II	0.11	1.28	0.41	0.18	54	* **
	III	0.59	4.62	2.20	0.48	98	* **
	IV	0.52	0.62	0.59	0.03	11	
NGI (%)	I	0.01	1.77	0.40	0.39	64	* **
	II	0.32	2.41	1.00	0.42	51	* **
	III	0.87	5.20	2.70	0.92	98	*
	IV	0.99	3.69	1.93	1.08	12	

Significance levels for comparison of means between maturity stages: * ** ± $p < 0.001$; * * ± $p < 0.01$; * ± $p < 0.05$.

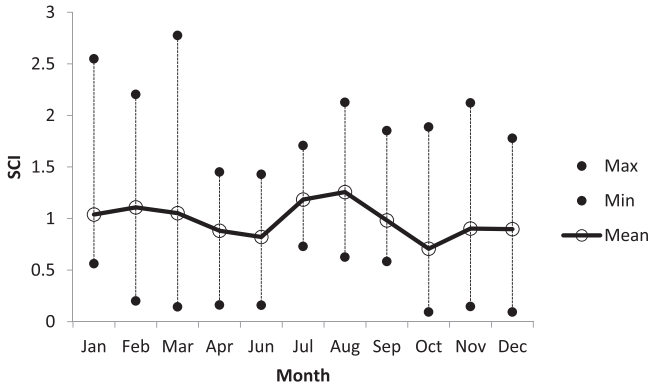


Fig. 11. Monthly variation in mean Spermatophoric complex index for male *S. prabahari.*

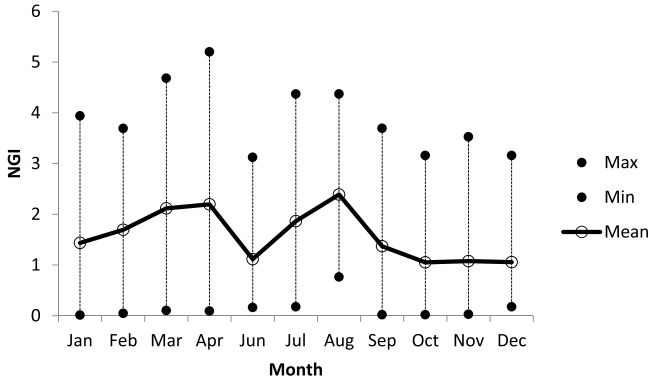


Fig. 12. Monthly variation in mean Nidamental gland index for *S. prabahari.*

months Figs. 13 and 14.

4. Conclusion

Sepia prabahari forms a regular fishery in the Gulf of Mannar region of the Indian coast. Information on reproductive biology is most essential for formulating fishery management measures. This study is the first attempt to investigate the reproductive biology of small striped cuttlefish *S. prabahari* from Indian waters. The size-frequency distribution shows that nearly 53.7% of the commercial catch in the fishery is below the size at first maturity (Lm_{50} - 9.4 cm) and 8.5–9.5 cm is the most exploited size group in the fishery. If exploitation of maturing and matured cuttlefish continues further, the reproductive capacity of this population will be reduced. Hence, the present study would help to formulate effective fishery management measures for a sustainable

Fig. 13. Male reproductive organ (Maturity stage -III) of *S. prabahari.*

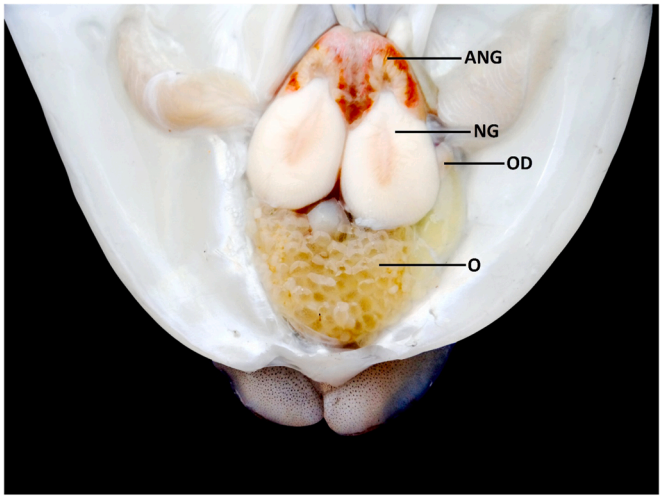


Fig. 14. Female reproductive organ (Maturity stage -III) of *S. prabahari.*

fishery.

Funding Information

This project was supported by funding from Indian Council of Agricultural Research under the inhouse project: Development of Fishery Management Plans for sustaining Marine Fisheries of Tamil Nadu and Puducherry, FISHCMFRISIL 201200800008.

CRediT authorship contribution statement

Kavitha Mookaiah: Conceptualization, Data curation; Resources, Formal analysis, Writing – original draft. **Geetha Sasikumar:** Investigation, Methodology, Writing – review & editing. **Jagadis Iyadurai:** Supervision, Writing – review & editing. **Ranjith Lakshmanan:** Software, Validation, Visualization. **Jasmin Felix:** Methodology, Software, Validation.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data Availability

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

Acknowledgements

The authors are thankful to The Director, ICAR-Central Marine Fisheries Research Institute, Kochi for his support throughout the research work. Further, we are thankful to Scientist-in-Charge, Tuticorin Regional Station of ICAR-Central Marine Fisheries Research Institute, Thoothukudi for facilitating the research work.

References

Akyol, O., Tellibayraktar, B., Ceyhan, T., 2011. Preliminary results on the cuttlefish, *Sepia officinalis*, reproduction in Izmir Bay (Aegean Sea). J. Fish. Sci. Com. 5, 122. https://doi.org/10.3153/jfscom.2011015.

Al-Marzouqi, A., Jayabalan, N., Al-Nahdi, A., 2009. Biology and stock assessment of the pharaoh cuttlefish, *Sepia pharaonis* Ehrenberg, 1831 from the Arabian Sea off Oman. Indian J. Fish. 56, 231–239.

Anon, 2017. Fisheries Policy Note 2017–18. Department of Animal Husbandry, Dairying and Fisheries, Government of Tamil Nadu.

Aoyama, T., Nguyen, T.T., 1989. Stock assessment of cuttlefish off the coast of the People's Democratic Republic of Yemen. J. Shimonoseki Univ. Fish. 37, 61–112.

Arnold, J.M., Williams-Arnold, L.D., 1977. Cephalopoda: decapoda. In: Giese, A.G., Pearse, J.S. (Eds.), Reproduction of Marine Invertebrates. New York, pp. 243–290.

Chembian, J.A., 2013. Studies on the biology, morphometrics and biochemical composition of the Ommastrephid squid, *Sthenoteuthis oualaniensis* (Lesson, 1830) of the south west coast of India. Doctoral thesis. Cochin University of Science and Technology. Kerala, India.

CMFRI, 2019. Annual Report 2019. Central Marine Fisheries Research Institute, Kochi.

Devlaming, V., Grossman, G., Chapman, F., 1982. On the use of the gonodosomatic index. Comp. Biochem. Physiol. Part A Physiol. 73, 31–39. https://doi.org/10.1016/0300-9629(82)90088-3.

Dunn, M.R., 1999. Aspects of the stock dynamics and exploitation of cuttlefish, *Sepia officinalis* (Linnaeus, 1758), in the English Channel. Fish. Res. 40, 277–293. https://doi.org/10.1016/S0165-7836(98)00223-9.

Dursun, D., Eronat, E.G.T., Akalin, M., Salman, M.A., 2013. Reproductive biology of pink cuttlefish *Sepia orbignyana* in the Aegean Sea (eastern Mediterranean). Turk. J. Zool. 37, 576–581. https://doi.org/10.3906/zoo-1209-22.

Duysak, O., Ozcan, G., Cek, S., Tureli, C., 2014. Reproductive biology of the common cuttlefish (*Sepia officinalis* Linnaeus, 1758) in Iskenderun Bay (Northeastern Mediterranean Sea). Indian J. Mar. Sci. 43, 1689–1694.

Gabr, H.R., Hanlon, R.T., Hanafy, M.H., El-Etreby, S.G., 1998. Maturation, fecundity and seasonality of reproduction of two commercially valuable cuttlefish, *Sepia pharaonis* and *S. dollfusi*, in the Suez Canal. Fish. Res. 36, 99–115. https://doi.org/10.1016/S0165-7836%2898%2900107-6.

Gonzalez, A.F., Guerra, A., 1996. Reproductive biology of the short-finned squid *Illex coindetii* (cephalopoda, ommastrephidae) of the northeastern Atlantic. Sarsia 81, 107–118. https://doi.org/10.1080/00364827.1996.10413616.

Gras, M., Safi, G., Lebredonchel, H., Quinquis, J., Foucher, E., Koueta, N., Robin, J.P., 2016. Stock structure of the English Channel common cuttlefish *Sepia officinalis* (Linnaeus, 1758) during the reproduction period. J. Mar. Biol. Assoc. U. K. 96, 167–176 https://doi:10.1017/S0025315415001162.

Guo, B., Lin S., Qi, P., Fan, M., 2021. Proteomic analysis of the spineless cuttlefish *Sepiella japonica*: Exploratory analyses on the phenomenon of death after spawning. Pre-print ⟨10.21203/rs.3.rs-155588/v1⟩.

Hall, K., Hanlon, R., 2002. Principal features of the mating system of a large spawning aggregation of the giant Australian cuttlefish *Sepia apama* (Mollusca: Cephalopoda). Mar. Biol. 140, 533–545.

Jereb, P., Allcock, A.L., Lefkaditou, E., Piatkowski, U., Hastie, L.C., Pierce, G.J., 2015. Cephalopod biology and fisheries in Europe: II. Species Accounts. ICES Cooperative Research Report No. 325, 360 pp.

King, M., 1995. Fisheries biology, assessment and management, Fishing News Books, Oxford, UK.

Kumaraguru, A.K., Joseph, V.E., Marimuthu, N., Wilson, J.J., 2006. Scientific information on Gulf of Mannar-A bibliography, Gulf of Mannar Marine Biosphere Reserve Trust and Centre for Marine and Coastal Studies. Madurai Kamaraj University. Tamil Nadu, India.

Le Cren, E.D., 1951. The length-weight relationship and seasonal cycle in gonad weight and conditions in the perch *Perca fluviatilis*. J. Anim. Ecol. Lond. 20, 201–219.

Lin, D., Xuan, S., Chen, Z., Chen, X., 2019. The ovarian development, fecundity and hypothesis on spawning pattern of common cuttlefish *Sepia officinalis* off Mauritania. Fish. Res. 210, 193–197. https://doi.org/10.1016/j.fishres.2018.08.003.

Lishchenko, F., Perales-Raya, C., Barrett, C., Oesterwind, D., Power, A.M., Larivain, A., Laptikhovsky, V., Karatza, A., Badouva, N., Lishchenko, A., Pierce, G.J., 2021. A review of recent studies on the life history and ecology of European cephalopods with emphasis on species with the greatest commercial fishery and culture potential. Fish. Res. 236, 105847 https://doi.org/10.1016/j.fishres.2020.105847.

Mohamed, K.S., Joseph, M., Alloycious, P.S., Sasikumar, G.P., Laxmilatha, P., Asokan, K., Kripa, V., Venkatesan, V., Thomas, S., Sundaram, S., Rao, G.S., 2009. Quantitative

and qualitative assessment of exploitation of juvenile cephalopods from the Arabian Sea and Bay of Bengal and determination of minimum legal sizes. J. Mar. Biol. Assoc. India 51, 98–106.

Mangold, K.M., Young, R.E., Nixon, M., 1993. Growth versus maturation in cephalopods. In: Okutani, T., Odor, R.K., Kubodera, T. (Eds.), Recent Advances in Cephalopod Fisheries Biology. Tokai. University Press, Tokyo, pp. 697–703.

Nair, K.P., Srinath, M., Meiyappan, M.M., Rao, K.S., Sarvesan, R., Vidyasagar, K., Sundaram, K.S., Rao, G.S., Lipton, A.P., Natarajan, P., Radhakrishnan, G., Mohamed, K.S., Narasimham, K.A., Balan, K., Kripa, V., Sathianandan, T.V., 1993. Stock assessment of the pharaoh cuttlefish *Sepia pharaonis*. Indian J. Fish. 40, 85–94.

Neethiselvan, N., Venkataramani, V.K., 2002. *Sepia prabahari* sp. nov. (Mollusca/Cephalopoda), a new species of Acanthosepion species complex from Tuticorin bay, southeast coast of India. Indian J. Mar. Sci. 31, 45–51.

Neethiselvan, N., Venkataramani, V.K., Srikrishnadhas, B., 2001. Reproductive biology of the siboga squid *Doryteuthis sibogae* (Adam) from Thoothukkudi (Tuticorin) coast, Southeast coast of India. Indian J. Mar. Sci. 30, 257–260.

Onsoy, B., Salman, A., 2005. Reproductive biology of the common cuttlefish *Sepia officinalis* L.(Sepiida: Cephalopoda) in the Aegean Sea. Turk. J. Vet. Anim. Sci. 29, 613–619.

Pierce, G.J., Allcock, L., Bruno, I., Bustamante, P., Gonźalez, A.F., Guerra, A., Jereb, P., Lefkaditou, E., Malham, S., Moreno, A., Pereira, J., Piatkowski, U., Rasero, M., Sánchez, P., Santos, M.B., Santurtún, M., Seixas, S., Sobrino, I., Villanueva, R., 2010. Cephalopod Biology and Fisheries in Europe. Co-Operative Research Report 303, International Council for the Exploration of the Sea, 175 pp. ISBN 978–87-7482–078-079.

Razek, E.A., Ramadan, S.A., Rashad, M.S., Mohammed, E.M., 2014. Molecular phylogeny of cuttlefish (sepiidae) and Morphometeric characterization of *Sepia officinalis* in Ain El-ghazala-Eastern Libya. World J. Zool. 9, 178–183. https://doi.org/10.12692/ijb/10.5.75-84.

Rossetti, P., Sartor, R., Belcari, P., 2003. Length-weight relationship in *Sepia officinalis* L. 1758, (Cephalopoda: Sepioidea) in the eastern Ligurian Sea. Biol. Mar. Mediterr. 10, 895–899.

Saddikioui, L., Mazouz, M., Abi-Ayad, S.M.E.A., 2017. First data on reproduction and growth parameters of the cuttlefish (*Sepia officinalis* L.) in Oran bay (western Algeria coasts). Int. J. Biosci. 10, 75–84. https://doi.org/10.12692/ijb/10.5.75-84.

Salman, A., 2015. Reproductive biology of the elegant cuttlefish (*Sepia elegans*) in the Eastern Mediterranean. Turkish. J. Fish. Aquat. Sci. 15, 265–272. https://doi.org/10.4194/1303-2712-v15_2_08.

Sasikumar, G., Mohamed, K.S., Bhat, U.S., 2013. Inter-cohort growth patterns of pharaoh cuttlefish *Sepia pharaonis* (Sepioidea: Sepiidae) in Eastern Arabian Sea. Rev. Biol. Trop. 61, 1–14.

Siddique, M.A.M., Khan, M.S.K., Habib, A., Bhuiyan, M.K.A., Aftabuddin, S., 2016. Size frequency and length–weight relationships of three semi-tropical cephalopods, Indian squid *Photololigo duvaucelii*, needle cuttlefish *Sepia aculeata*, and spineless cuttlefish *Sepiella inermis* from the coastal waters of Bangladesh, Bay of Bengal. Zool. Ecol. 26, 176–180. https://doi.org/10.1080/21658005.2016.1190523.

Sifner, S., Damjanovic, T., Isajlovic, I., 2018. Distribution, length-weight relationships and reproductive characteristics of *Sepia orbignyana* Ferussac, 1826 in the Northern and Central Adriatic Sea. Cah. Biol. Mar. 59, 43–51.

Silas, E.G., Sarvesan, R., Nair, K.P., Appanasastry, Y., Sreenivasan, P.V., Meiyappan, M. M., Vidyasagar, K., Rao, K.S., Rao, B.N., 1985. Some aspects of the biology of cuttlefishes. CMFRI Bull. 37, 49–70.

Singh, Y.B., 2005. Studies on the population dynamics and stock assessment of *Sepia prabahari*, Neethiselvan & Venkataramani of Thoothukudi coast. Doctoral thesis. Tamil Nadu Veterinary and Animal Sciences University. Tamil Nadu, India.

Sokal, R.R., Rohlf, F.J., 1987. Introduction to Biostatistics, Second ed..,. Freeman Publication, New York.

Vasconcelos, P., Pereira, F., Carvalho, A.N., Gaspar, M.B., 2018. Weight-length relationships and relative growth of the cuttlefish (*Sepia officinalis*): causes and effects of hypoallometry. Thalassas 34, 323–331. https://doi.org/10.1007/s41208-018-0067-0.

Villanueva, R., Sykes, A.V., Vidal, E.A., Rosas, C., Nabhitabhata, J., Fuentes, L., Iglesias, J., 2014. Current status and future challenges in cephalopod culture. In: Iglesias, J., Fuentes, L., Villanueva, R. (Eds.), Cephalopod Culture. Springer, Dordrecht, pp. 479–489.