Journal of Fisheries
Volume 13 Issue 3 December 2025
Peer Reviewed | Open Access

eISSN 2311-3111
pISSN 2311-729X

DOI: https://doi.org/10.17017/j.fish.1000

Original Article

Spawning dynamics and maturity patterns of the Indian squid, *Uroteuthis* (*Photololigo*) *duvaucelii* (A. d'Orbigny, 1835), along the southeastern coast of India

R. John Peter • A. John Chembian • K. Silambarasan • A. Tiburtius

Fishery Survey of India, Royapuram, Chennai, Tamil Nadu 600 013, India

Correspondence
R. John Peter; Fishery Survey of India, Royapuram, Chennai, Tamil Nadu Post code, India
rjohnpeter004@gmail.com

Manuscript history
Received 30 May 2025 | Accepted 8 October 2025 | Published online 20 October 2025

Citation
John Peter R, John Chembian A, Silambarasan K, Tiburtius A (2025) Spawning dynamics and maturity patterns of the Indian squid, *Uroteuthis* (*Photololigo*) *duvaucelii* (A. d'Orbigny, 1835), along the southeastern coast of India. Journal of Fisheries 13(3): 133210. DOI: 10.17017/j.fish.1000

Abstract
Uroteuthis (*Photololigo*) *duvaucelii* (A. d'Orbigny, 1835), is an economically important squid species along the southeastern coast of India. This study presents a comprehensive analysis of its reproductive biology, based on the specimens collected during an exploratory fishery resources survey in the region. The results provide valuable insights into the reproductive patterns of this important fishery resource. The overall sex ratio was 0.9:1 (Male:Female), indicating a predominance of females over males. The length at 50% maturity (L_{50}) was estimated at 138 mm dorsal mantle length (DML) for Males, and 118 mm for females, showing that females tend to mature earlier. Observation of maturity stages revealed that sexually mature (stage V) males and females were found throughout the year, with a reproductive peak in April, though no spent individuals were observed during the study. The maximum number of total eggs recorded in the ovary was 69,629 with 841 mature ova. Potential fecundity ranged from 544 to 20,865 eggs, with an average of 9,114. Relative fecundity (RF) value ranged from 8 to 115, while potential reproductive investment (PRI) values ranged from 0.01 to 0.196. The maximum egg weight was observed between 1.6 and 1.7 mg. Histological examination of the ovary and oviduct (stages IV and V) confirmed that this species follows an iteroparous spawning strategy, characterised by multiple spawning events throughout the year.

Keywords: cephalopods; fecundity; Indian squid; maturity; multiple spawners; sex ratio; *Uroteuthis duvaucelii*

1 | INTRODUCTION

With the intensifying exploitation of fin fish resources and the alarming depletion of several major fish stocks that have historically supported large-scale industrial fisheries, the focus has shifted towards alternative fishery resources. These resources, often termed "unconventional fishery resources," encompass a variety of marine species that were previously under-utilised. Among these, cephalopods—such as squids, cuttlefish, and octopuses—have gained prominence due to their ecological roles and commercial importance. This shift underscores the urgent need to diversify fisheries and alleviate pressure on over-exploited fin fish populations (Jereb and Roper 2010).

Squids, belonging to the class Cephalopoda, subclass Coleoidea, and order Teuthida, have emerged as valuable fishery resources, contributing significantly to global cephalopod landings. In India, cephalopods account for 1.18% of total production, with a reported 4.814 million tonnes harvested along Indian waters (DoF 2023). The Indian squid, *Uroteuthis duvaucelii* (family Loliginidae), is an abundant and economically important species in this context, especially along the southeastern coast of Tamil

Nadu. While primarily landed as bycatch in the region's multi-gear, multi-species trawl fisheries, it contributes significantly to commercial catches and plays a critical ecological role as both predator and prey in the marine food web (Navarro *et al.* 2013).

Understanding the reproductive biology of *U. duvaucelii* is vital for its sustainable fisheries management. Reproductive studies provide essential insights into key population parameters, including spawning seasons, size at maturity, reproductive capacity and fecundity. These parameters are critical for developing effective management strategies, such as suggesting seasonal fishing bans, implementing size limits, or closed and open fishing zones. Additionally, cephalopods exhibit diverse spawning patterns influenced by environmental factors and rapid life cycles, which make them highly sensitive to changing environmental conditions (Pierce *et al.* 2008). Thus, studying their reproductive biology not only informs fishery management but also provides valuable data on ecosystem dynamics.

Research on the reproductive biology of *U. duvaucelii* has been conducted across its distribution range, including the Indian Ocean, Pakistan, the Gulf of Thailand, the Eastern Indian Ocean, and the China Seas (Supongpan *et al.* 1992; Mohamed 1993; Sukramongkol *et al.* 2007; Kilada and Riad 2010; Wang *et al.* 2015). However, studies at both national and regional levels remain scarce, despite the species' economic and ecological importance in Indian waters. Understanding the reproductive biology of *U. duvaucelii* is critical due to its significant contribution to commercial fisheries and its role in marine ecosystems across the Indian Ocean region.

To address this knowledge gap, the present study investigates the reproductive biology of *U. duvaucelii* along the southeastern coast of India. Specifically, it examines key reproductive parameters, including sex ratios, size at maturity, gonadosomatic index, fecundity and histological validation. By providing a comprehensive understanding of the maturation and spawning mechanisms of *U. duvaucelii*, this study aims to generate valuable data to support sustainable fishery management and conservation strategies in the region.

2 | METHODOLOGY

2.1 Study area and sample collection

The present study was conducted as an exploratory fishery resources survey by the departmental survey vessel MFV Samudrika (OAL: 28.8 m), attached to the Chennai Base of Fishery Survey of India, Govt. of India, Ministry of Fisheries, Animal Husbandry and Dairying, Department of Fisheries. The survey was conducted from November 2018 to October 2020, covering the area between 10 – 16°N and 80 – 86°E off the southeastern coast of India within a depth range of 30 – 50 m and 50 – 100 m (Figure 1). During the study, a total of 786 specimens were collected. The samples were stored onboard at –20°C to preserve them for further analysis. Subsequently, the samples were transported to the shore laboratory for detailed examination and studies.

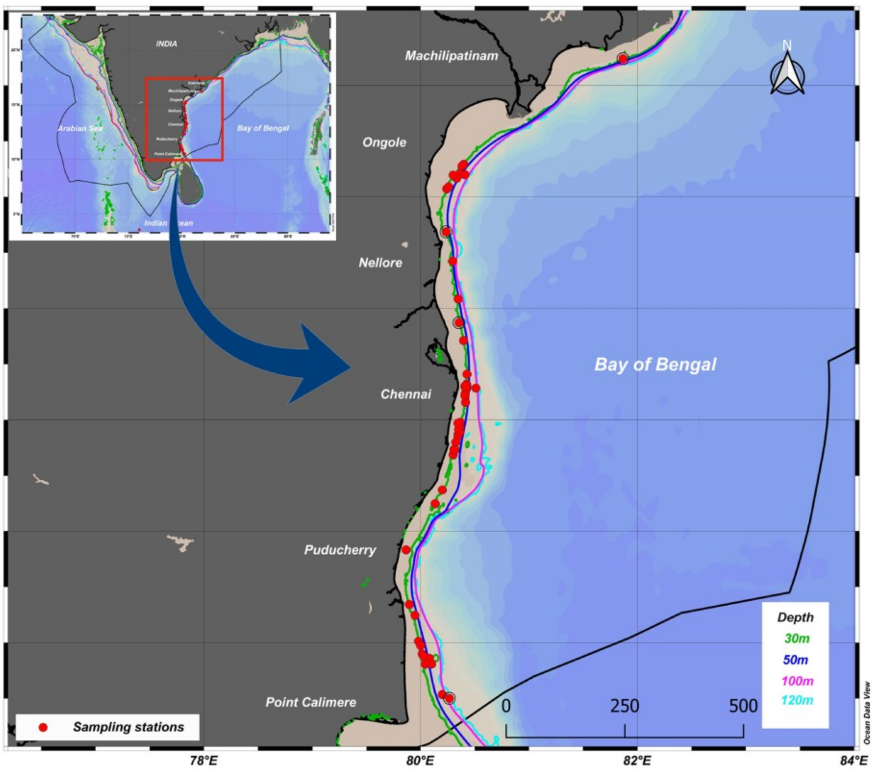

FIGURE 1 Map showing sampling stations of *Uroteuthis duvaucelii* along the southeast coast of India. Source: Ocean Data View (Schlitzer 2024)

2.2 Study of gonad maturation

A total of 786 specimens were collected of which 415 were females and 371 males whose maturity stages (gonads) were identified using the universal maturity scale (Lipinski 1979). The length at first sexual maturity (L_{50} or L_{95}) was studied in both the sexes i.e. the length at which 50% or 95% of squid population reach their sexual maturity was estimated by fitting the percentage of maturity against mid-lengths. The L_{50} or L_{95} was estimated as the point on X-axis corresponding to a 50 or 95 point on Y-axis (Gewida *et al.* 2021). Similarly, sex ratio (M:F) was analysed month-wise to identify the availability range between both sexes. The Chi-square (χ^2) test was employed to examine deviations from the expected 1:1 ratio using the formula: $\chi^2 = \Sigma^*(Oi - Ei)^2 / Ei$; where χ^2 = Chi-square value, O_i = observed value, and E_i = expected value. This method follows standard statistical procedures described by Zar (1999).

To study the maturity indices of both sexes, the reproductive parts were weighed to the nearest 0.1 g. The reproductive parts of females consist of the oviductal complex (OC) [including ovary (O), oviduct (OD), and oviductal gland (ODG)], ovary and oviduct (OVD), nidamental gland (NG) (both left and right) and accessory nidamental gland (ANG). Whereas, male reproductive parts comprise of testis (T) and spermatophoric complex (SPC) (including vas deferens, spermatophoric organ, spermatophoric duct, Needham's sac and penis). The maturity indices of these reproductive parts were studied following standard method (Markaida and Sosa-Nishizaki 2001; Chembian 2013) with slight modifications as follows:

In females: accessory nidamental gland weight index (ANGWI), nidamental gland weight index (NGWI) ovary weight index (OWI), oviductal complex weight index (OCWI), reproductive system weight index (RSWI) [including ovary weight, oviductal complex weight, nidamental gland weight)] and in males: testis weight index (TWI), spermatophoric complex weight index (SPCWI) were employed to study maturity indices and calculated as follows,

For females:

Accessory Nidamental Gland Weight Index (ANGWI) = Accessory Nidamental Gland Weight (ANGW) × 100 / Body Weight – Nidamental Gland Weight (BW – ANGW)

Nidamental Gland Weight Index (NGWI) = Nidamental Gland Weight (NGW) × 100 /Body Weight – Nidamental Gland Weight (BW – NGW)

Ovary Weight Index (OWI) = Ovary Weight (OW) × 100 / Body Weight – Ovary weight (BW – OW)

Oviductal Complex Weight Index (OCWI) = Oviductal Complex Weight (OC) × 100 /Body Weight – Oviductal Complex Weight (BW – OCW)

Reproductive system Weight Index (RSWI) = (Ovary Weight + Oviductal Complex Weight + Nidamental Gland Weight) × 100 / (Body Weight – Ovary Weight – Oviductal Complex Weight – Nidamental Gland Weight)

For males:

Testis Weight Index (TWI) = Testis Weight (TW) × 100 / Body Weight – Testis weight (BW – TW)

Spermatophoric Complex Weight Index (SPCWI) = Spermatophoric Complex Weight (SPCW) × 100 / Body Weight – Spermatophoric Complex Weight (BW – SPCW)

The maturity indices were analyzed month-wise and for different maturity stages to find out the changes or variations in the maturity indices as per month wise and stages.

2.3 Study of ova and fecundity

Ovary and oviduct were analyzed in matured specimens (*n* = 73) with maturity stages IV and V. The different types of ova in ovary and the matured ova in oviduct were weighed and counted by implying steps provided by Chembian (2013). The different stages of ova in the ovary were identified based on microscopically determined stages of *Loligo reynaudii* (Sauer and Lipiński 1990; Lipinski and Underhill 1995), with a slight modification. For instance, in the present study stage I and II (primary oogonia round and primary oogonia cuboidal) were named opaque ova (OP), Stage III (follicular epithelium invading the oocyte) as small reticulate ova (SR), stage IV (displacement of follicular folds) as large reticulate ova (LR) and stage V (oocyte ready to be freed) as matured ova (MO).

After the identification of ova type, the diameter of the ova in the ovary and oviduct was measured using a light microscope with an ocular scale by taking the longest axis of the egg as egg length (in mm) and the weight of the matured ova to the nearest value of 0.0001 g. After measurement, the diameter of different types of ova in the ovary value was plotted against the dorsal mantle length (DML) of the female specimen to identify the range of different ova sizes.

Potential fecundity (PF) was calculated as the sum of the total oocyte number in the ovary and egg number in the oviducts. Then relative fecundity (RF) was estimated as the ratio of PF to Total weight or body weight. An index of potential reproductive investment (PRI) was calculated as the product of RF and the weight of an individual ripe egg (Laptikhovsky and Nigmatullin 1993, 1999; Laptikhovsky 1999). Later, the linear relationship between the variables: DML, number of mature ova in the ovary (NMOO), number of ova in the oviduct (NOOOD), potential fecundity (PF), relative fecundity (RF), index of potential reproductive investment (PRI), total weight (TW) and ovary weight (OW) were studied using the simple linear regression equation. The histological validation of reproductive parts of the males (testis) and females (ovary and oviduct) were studied by implying method proposed by Sauer and Lipiński (1990).

2.4 Data analysis

Data obtained during the study were analysed using specific software tools. Microsoft Excel 2016 was used to perform the Chi-square test, analyse dorsal mantle length, determine the month-wise distribution of the species, and calculate the gonadosomatic index. Sampling stations were mapped using Ocean Data View, version 5.7.2 (Schlitzer 2024), while other graphical representations and statistical analyses, including descriptive statistics and correlation analyses, were conducted using R statistical software (R Core Team 2015).

3 | RESULTS

3.1 Study of gonads

3.1.1 Dorsal mantle length (DML) and monthly distribution: The distribution of different maturity stages across DML was analysed for both sexes. In females, Stage I was observed within the DML range of 51 to 120 mm, Stage II between 61 and 140 mm, Stage III from 71 to 150 mm, Stage IV from 71 to 160 mm and Stage V from 81 to 190 mm, with 100% of the population maturing above 161 mm. Similarly, in males, Stage I was observed within the DML range of 51 to 110 mm, Stage II from 51 to 130 mm, Stage III from 71 to 160 mm, Stage IV from 71 to 180 mm, and Stage V from 91 to 210 mm, with 100% of the population maturing above 181 mm (Figure 2). Overlapping gonadal maturation stages were observed within the same DML size groups for both sexes. Additionally, the monthly distribution of maturity stages showed that all stages were present throughout the study period (Figure 3). However, Stage V (mature) individuals peaked in April 2019, with the highest proportion observed in females (69.2%), followed by males (71.1%) along the southeastern coast of India.

3.1.2 Sex ratio and size at maturity: The overall sex ratio was 0.9:1 (Male:Female), with males comprising 47.2% and females 52.8%, showing monthly variation in the ratios. While females dominated the overall sex ratio, males exhibited a higher ratio (1.5:1) during the peak spawning period in April. The Chi-square test (χ^2) revealed no significant variations between the months (Table 1).

The observed sizes of mature females (Stage V) ranged from 78 mm to 184 mm, while mature males ranged from 93 mm to 217 mm DML. The L_{50} for females, indicating the size at which 50% attain maturity, was 118 mm DML, whereas for males, it was 138 mm DML. The L_{95} for females, marking the size at which 95% reach maturity, was above 144 mm DML, and for males, it was 172 mm DML along the southeastern coast of India (Figure 4).

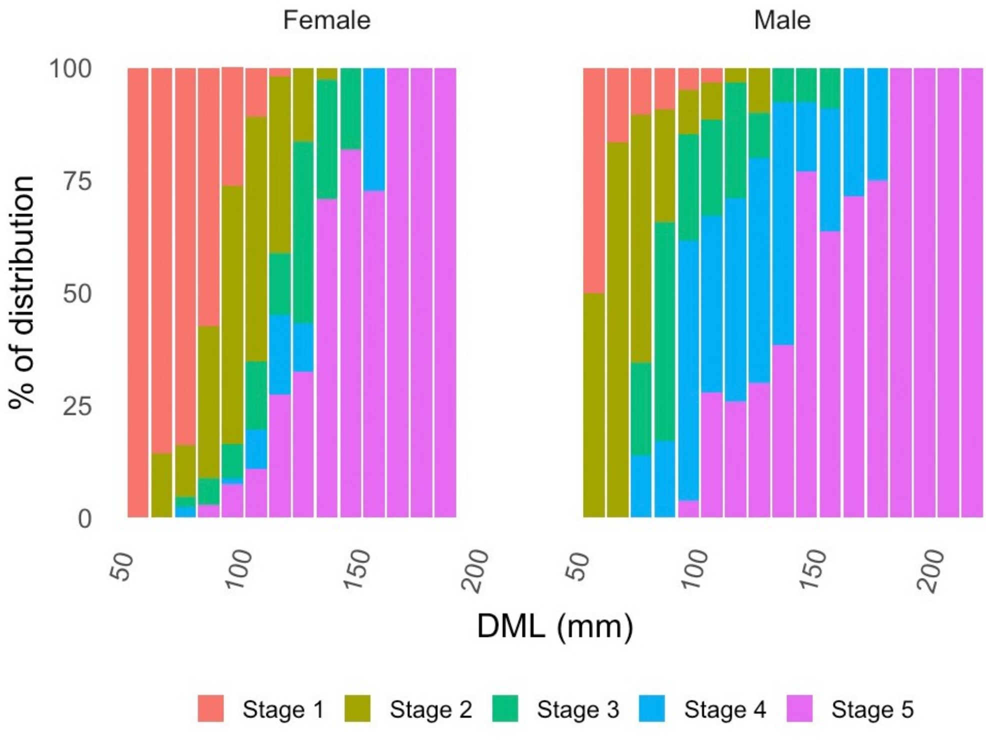

FIGURE 2 Dorsal mantle length (DML) wise distribution of different maturity stages for females and males of *Uroteuthis duvaucelii*.

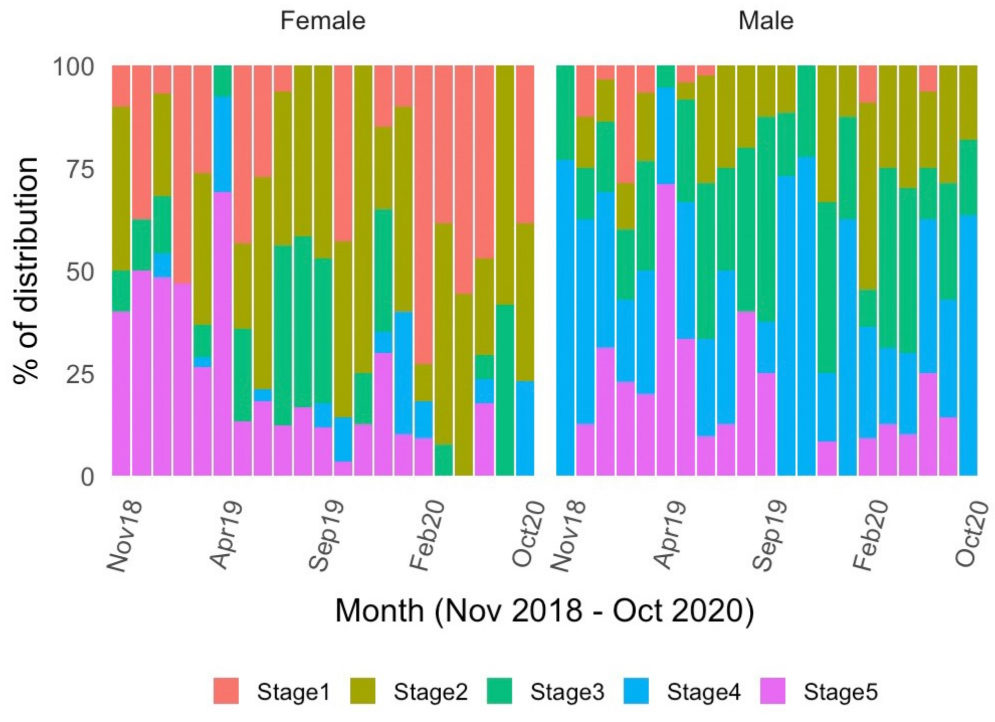

FIGURE 3 Month wise distribution of different maturity stages for females and males of *Uroteuthis duvaucelii*.

TABLE 1 Sex ratio and chi square test estimated for male and female of *Uroteuthis duvaucelii*.

Month	Total	Sex ratio (M:F)	Male		Female		χ^2-values	*p*-values	Significance
			n	%	*n*	%			
18-Nov	23	1.3:1	13	56.5	10	43.5	0.39	0.53	N
18-Dec	16	1:1	8	50.0	8	50.0	0.00	1.00	N
19-Jan	58	1:1	29	50.0	29	50.0	0.00	1.00	N
19-Feb	67	1.1:1	35	52.2	32	47.8	0.13	0.71	N
19-Mar	68	0.8:1	30	44.1	38	55.9	0.94	0.33	N
19-Apr	64	1.5:1	38	59.4	26	40.6	2.25	0.13	N
19-May	77	0.5:1	24	31.2	53	68.8	10.9	0.00	S
19-Jun	75	1.3:1	42	56.0	33	44.0	1.08	0.30	N
19-Jul	24	0.5:1	8	33.3	16	66.7	2.67	0.10	N
19-Aug	23	0.8:1	10	45.5	13	54.5	0.39	0.53	N
19-Sep	25	0.5:1	8	32.0	17	68.0	3.24	0.07	N
19-Oct	54	0.9:1	26	48.1	28	51.9	0.07	0.79	N
19-Nov	17	1.1:1	9	52.9	8	47.1	0.06	0.81	N
19-Dec	32	0.6:1	12	37.5	20	62.5	2.00	0.16	N
20-Jan	18	0.8:1	8	44.4	10	55.6	0.22	0.64	N
20-Feb	22	1:1	11	50.0	11	50.0	0.00	1.00	N
20-Jun	29	1.2:1	16	55.2	13	44.8	0.31	0.58	N
20-Jul	19	1.1:1	10	52.6	9	47.4	0.05	0.82	N
20-Aug	33	0.9:1	16	48.5	17	51.5	0.03	0.86	N
20-Sep	19	0.6:1	7	36.8	12	63.2	1.32	0.25	N
20-Oct	24	0.8:1	11	45.8	13	54.2	0.17	0.68	N
Total	**786**	**0.9:1**	**371**	**47.2**	**415**	**52.8**	--	--	--

χ^2 - Chi square value; N - insignificant, S - significant

3.1.3 Maturity indices and maturity stages: Weight indices were calculated for different maturity stages (Table S1). In females, reproductive organs gained weight as DML and maturity stages increased, except for the accessory nidamental gland, which was absent in Stage I. Similarly, in males, the testis and spermatophoric complex also grew from low to high weight indices as the maturity stages increased, with the absence of spent individuals in both sexes during the study period.

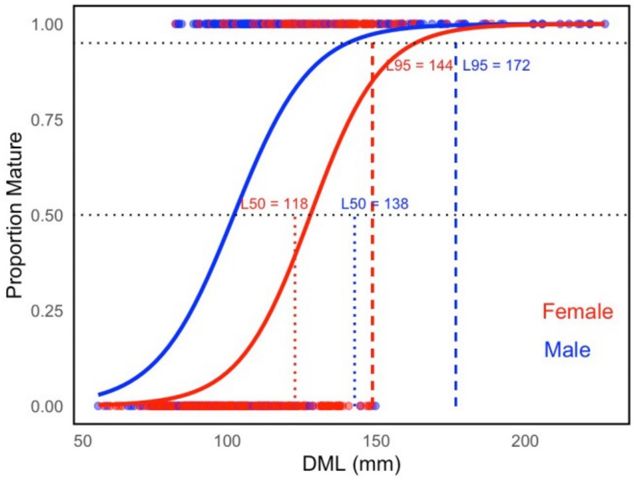

FIGURE 4 Size at maturity estimation for females and males of *Uroteuthis duvaucelii*.

3.1.4 Relationship between DML and reproductive somatic weight index (RSWI) in females: In females, the reproductive parts became distinctly visible and easier to weigh beyond a DML of 65 mm. At this point, the average RSWI entered a lag phase, followed by a logarithmic or exponential growth phase between 91 mm and 150 mm. Beyond 150 mm, the RSWI gradually stabilised, entering a stationary phase (Table S2).

3.1.5 Monthly maturity indices: The maturity index for both sexes was examined on a monthly basis and is tabulated in Table S3. For females, the reproductive parts weight index (RSWI) was highest in January, February and April, indicating a preparatory phase for spawning. The percentage of mature females was highest in April, suggesting that April is the peak spawning month for females along the southeastern coast of India. In males, Testis Weight Index (TWI) and Spermatophoric Complex Weight Index (SPCWI) were examined both across size classes (Table S2) and on a monthly basis (Table S3). In size-wise data, TWI increased with body size, peaking at DML: 151 – 170 mm, while SPCWI generally increased but showed minor fluctuations, reflecting the transfer of spermatophores from the testis to the spermatophoric complex. Month-wise data showed TWI peaks in April 2019 and January 2020, corresponding to periods of active male reproduction, while SPCWI peaked in November 2019, reflecting storage of mature spermatophores for mating. Pearson correlation analysis of month-wise mean revealed a significant positive relationship between TWI and SPCWI (r = 0.62, p < 0.01), indicating that spermatophore production generally increases with testis growth, although short-term differences occur due to organ-specific transfer dynamics. Together, these patterns confirm that TWI and SPCWI reflect sequential stages of male reproductive activity.

3.2 Study of ova

3.2.1 Size and percentage of different stages of ova in the ovary: The diameter of the different stages of ova in the ovary (Stage V) ranged from 0.21 mm to 1.4 mm, with the smallest ova being opaque ova (OP), averaging 0.35 mm, followed by small reticulate ova (SR) with an average size of 0.74 mm, large reticulate ova (LR) averaging 1.15 mm, and the largest being matured ova (MO) with an average size of 1.19 mm and a maximum size of 1.4 mm (Figure 5). The percentage availability of different stages of ova in the ovary was analyzed within the DML range of 111 mm to 190 mm (Table 2).

TABLE 2 Summary of Percentage of different stages of ova in ovary.

DML	Percentage (%)			
	OP	SR	LR	MO
111-130	63.9	9.5	25.9	0.6
131-150	59.1	11.2	28.6	1.0
151-170	58.6	13.0	27.6	0.7
171-190	56.6	10.4	32.6	1.0

DML - dorsal mantle length, OP - opaque ova, SR - small reticulate ova, LR - large reticulate ova, MO - matured ova

3.2.2 Ova relation to DML: The total number of eggs (in various stages) in the ovary increased with DML size. For instance, the average number of eggs in the ovary for DML sizes of 101 to 130 mm was 26,698 ± 11,125, followed by 30,793 ± 11,376 for DML sizes of 131 to 160 mm. The maximum number of eggs observed was 69,629 in the DML range of 161 to 190 mm, with a mean of 57,964 ± 13,930 (Table 3). The linear relationship between the number of mature ova in the ovary (NMOO) and DML was analysed, showing a positive correlation, with a minimum of 30 and a maximum of 841 mature ova observed (Figure S1B).

TABLE 3 Mean dorsal mantle length (DML) against the mean of total number of eggs in ovary, number of mature ova in ovary (NMOO), ovary weight and oviduct weight.

DML	Total number of eggs in ovary		NMOO		Ovary weight (g)		Oviduct weight (g)	
	Range	Mean±SD	Range	Mean±SD	Range	Mean±SD	Range	Mean± SD
101–130	11586–42158	26698±11125	30–323	162±93	0.77–6.67	4.00±1.8	0.23–5.82	2.25±2.06
131–160	14821–61179	30793±11376	43–752	263±200	2.87–10.95	6.08±1.8	0.22–8.57	3.41±1.95
161–190	41646–69629	57964±13930	675–841	758±117	7.27–10.39	8.92±1.4	6.94–11.88	9.35±2.47

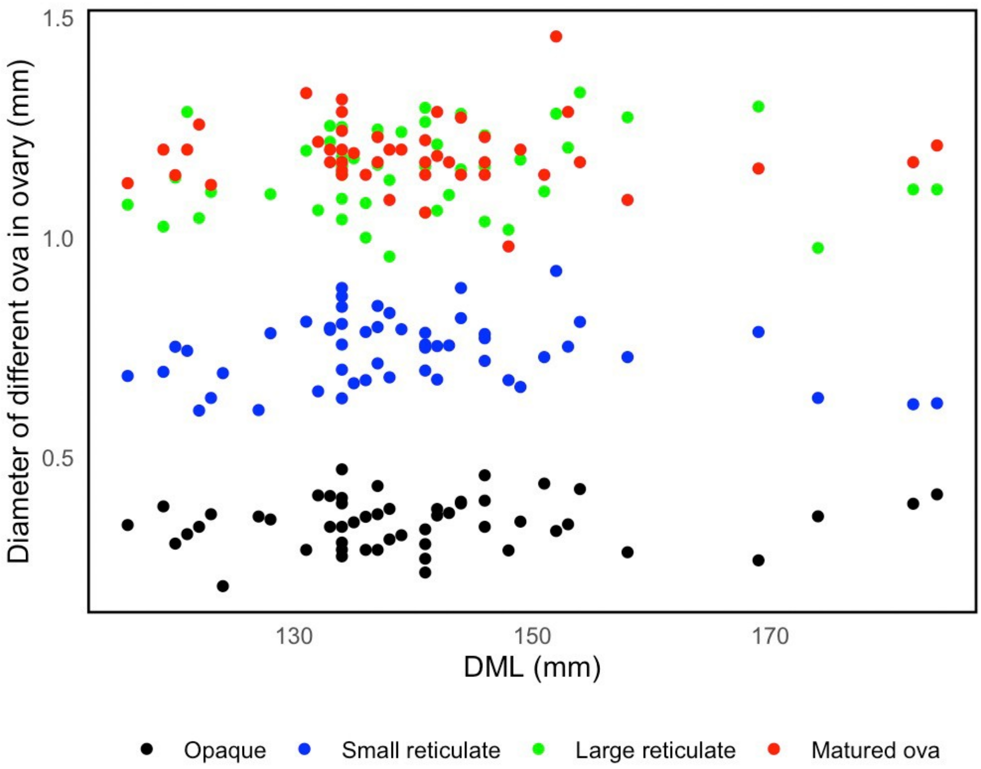

FIGURE 5 Size of different types of ova in ovary against dorsal mantle length (DML).

3.2.3 Linear relationship of ovary and oviduct weights with ova: The total number of eggs in the ovary was examined in relation to the ovary weight of the collected specimens (Table 3). The analysis revealed a clear trend: as the ovary weight increased, so did the total number of eggs in the ovary (Figure S1C). Similarly, the relationship between the total number of mature ova in the oviduct and oviduct weight (OVD) was analysed (Table 3).

3.3 Fecundity

3.3.1 Potential fecundity (PF), relative fecundity (RF), and index of potential reproductive investment (PRI): The PF of *U. duvaucelii* along the southeastern coast of India ranged from 544 to 20,865, with an average of 9,114 (Table 4). The linear relationship between DML and potential fecundity showed a positive correlation (Figure S2A). The RF ranged from 8 to 115, while the PRI ranged from 0.01 to 0.196 along the southeastern coast of India.

3.3.2 Potential fecundity (PF) and other variables: The PF values were examined against variables such as total body weight, oviduct (OD) weight, and OVD (ovary + oviduct) weight. The lowest PF value of 544 was observed in a specimen with a total body weight of 54.8 g, oviduct weight of 0.23 g and OVD weight of 3.15 g. The highest PF value of 20,865 was observed in a specimen with a total body weight of 184 g, oviduct weight of 11.88 g and OVD weight of 21.82 g (Table S4). All three variables showed a positive linear growth in relation to potential fecundity, with R^2 values ranging from 0.5 to 0.9 (Figure S3A–C).

TABLE 4 Summary of potential fecundity (PF), relative fecundity (RF), index of potential reproductive investment (PRI) against dorsal mantle length (DML).

DML (mm)	Mean DML (mm)	Potential fecundity (PF)		Relative fecundity (RF)		PRI		Egg weight (mg)
		Range	Mean±SD	Range	Mean±SD	Range	Mean±SD	
111–130	121	544–11128	4343±3837	8–135	64±49.5	0.01–0.255	0.119±0.09	1.6–1.7
131–150	139	1210–11810	5270±2527	16–131	67±26.6	0.012–0.227	0.130±0.05	
151–170	156	473–16063	9714±5879	4–114	72±23.3	0.007–0.213	0.145±0.07	
171–190	183	13128–20865	16997±5470	71–115	93±31	0.135–0.196	0.165±0.04	

3.4 Histological study of reproductive parts: The ovaries and oviducts of mature female *U. duvaucelii* (Stages IV and V) were subjected to histological study (Figure 6). The ovary at Stage IV consisted of OP, SR, and LR ova, but no MO ova were present (Figure 6A). In Stage V, all four types of ova were present in the ovary, and mature ova were observed in the oviduct (Figure 6B).

The testis of males from maturity stages III to V were subjected to histological observation to understand the formation of spermatophores. In Stage III, spermatocytes

(SC) were observed at the corners of the lobules (LO), with developing spermatids (ST) present at the center in lower abundance (Figure 7A). In Stage V, the testis contained well-developed spermatozoa (SO) and developing spermatids, with fully formed lobules (Figure 7B).

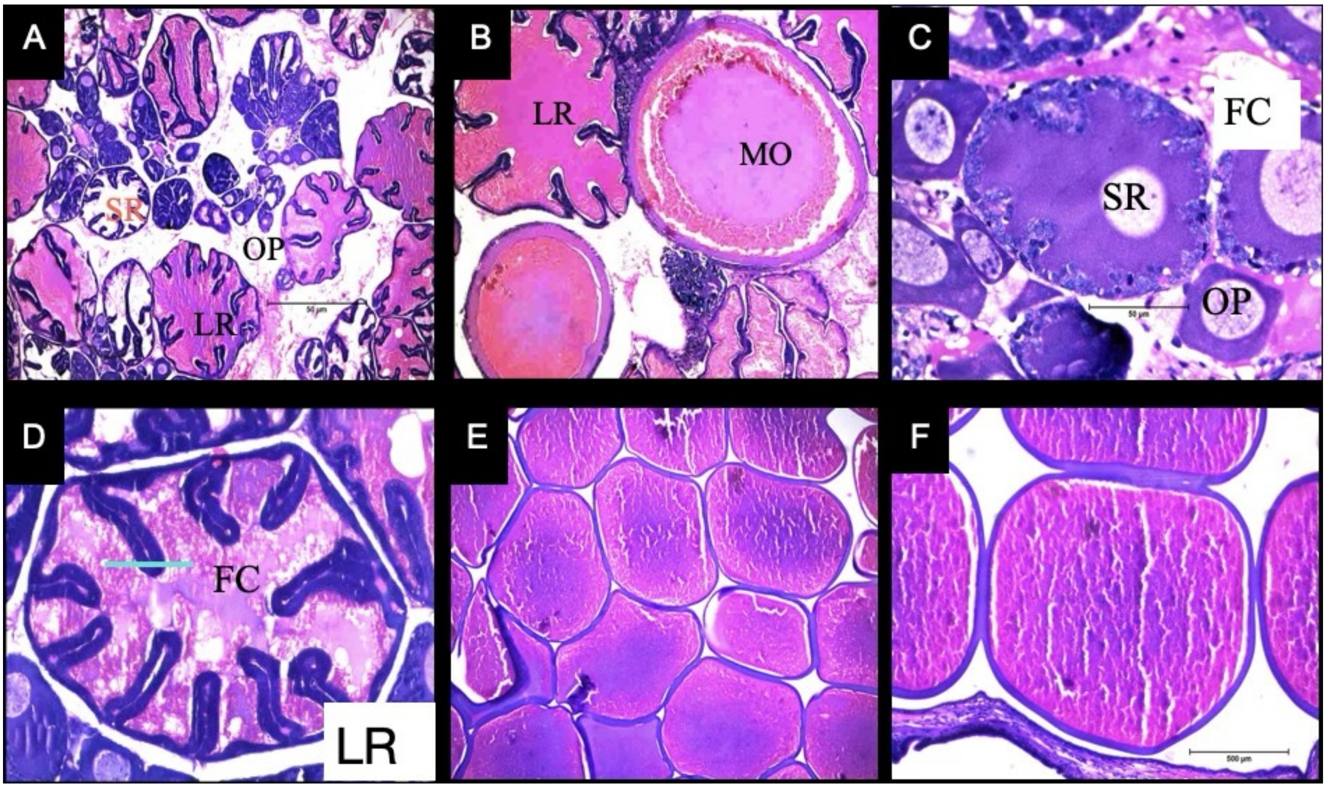

FIGURE 6 Histological slides: **(A)** section of ovary Stage IV opaque ova (OP), small reticulate ova (SR), larger reticulate ova (LR) and matured ova (MO); **(B)** section of ovary Stage V; **(C)** section of OP and SR with follicle cells (FC); **(d)** section of LR; and **(E–F)** section of matured ova in oviduct.

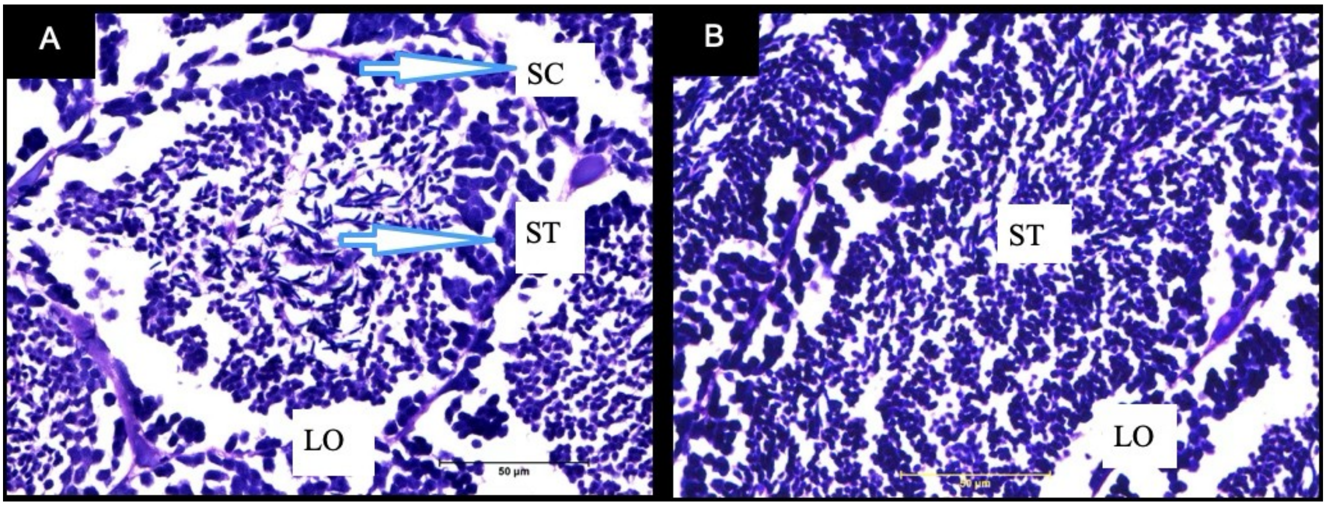

FIGURE 7 Histological slides: **(A)** section of testis Stage III, Spermatocytes (SC), lobules (LO) and spermatids (ST); and **(B)** section of testis Stage V.

4 | DISCUSSION

Supporting the monthly distribution of maturity stages of this study, Chhandaprajnadarsini *et al.* (2020) in south-western Bay of Bengal, along with Gewida *et al.* (2021) and Elsayed *et al.* (2021) in Suez has also reported the highest percentage of matured females in April. Similarly, observed the matured stages of *U. duvaucelii* throughout the year. Arkhipkin *et al.* (2015) documented similar findings in the eastern Indian ocean, with peak maturity seasons ranging from January to June, and August to December. These observations suggest that both sexes reach maturity for spawning in April, making it as a peak spawning period. Maturity stages were compared against size ranges to identify variations at each stage and monthly groupings were analysed to track changes in abundance. This approach helped in understanding seasonal fluctuations in various maturity stages, providing insights into the reproductive biology and spawning patterns of the species (Chembian 2013).

The sex ratio observed in this study was 0.9:1 (male to female), contrasting with findings from other regions. Gewida *et al.* (2021) observed a sex ratio of *U. duvaucelii* in the Gulf of Suez as 1.6:1.0 (M: F), and Elsayed *et al.* (2021) reported a ratio of 1.7:1 in the same region, with males were dominant in both cases. In contrast, Arkhipkin *et al.* (2015) observed a ratio of 1:1.3 on the east coast of India and Petsut and Kulabtong (2012) reported a ratio of 1:2, where females were dominant. These findings suggest that the sex ratio may vary based on population adaptations, reproductive behaviour, food availability, environmental conditions, habitat preferences, migration patterns or behavioural differences between sexes. Additionally, one sex may be more easily caught due to size differences or specific fishing methods, such as jigs, which might contribute to catch bias rather than reflecting the actual population structure (Chembian 2013; Mohamed *et al.* 2014; Elsayed *et al.* 2021).

In terms of size at maturity (L_{50}), the current study showed females attaining maturity at 118 mm DML and males at 138 mm DML, consistent with previous findings. For instance, Elsayed *et al.* (2021) reported that the size at maturity of females in Suez was above 100 mm and 135 mm for males. According to Jereb and Roper (2006), females ranged from 90 – 130 mm DML and males from 70 – 150 mm DML. Similarly, Naik *et al.* (2017) observed females attained maturity at 70 – 90 mm DML, while males matured at 90 – 110 mm in the southwest coast of India. In comparison with previous studies, the present study indicates that both sexes continue to grow in DML size even after reaching maturity. This demonstrates that somatic growth persists during the spawning period or maturation time. Moreover, females mature earlier than males, with relatively slower growth. For instance, females reached L_{50} at 118 mm DML, and males at 138 mm, while the maximum observed sizes were 184 mm for females and 217 mm for males. This observation supported by Mohamed *et al.* (2014), who stated that animals maturing at smaller sizes exhibit slower growth rates compared to those maturing at large sizes, despite being of equivalent ages.

The weight indices of reproductive organs in both sexes increased with maturity stages, indicating resource allocation toward reproduction. According to Chembian (2013), the highest weight indices of the reproductive parts were observed mainly in individuals ready for spawning. Also, the weight of the nidamental gland increases due to the accumulation of nidamental gland secretions and in the ovary, it is due to the formation of yolk oocytes from immature ova while, oviductal complex weight increases due to the presence of matured oocytes in both the ovary and oviduct. In males, the presence of spermatophore increases the weight indices of the testis, and the spermatophoric complex weight index increases due to the presence of matured sperm in Needham's sac and penis. Though, the weight index increases with the increase in maturity stages which results in the overlapping of different weight index among the same DML size. The RSWI values for individuals above 150 mm indicate that reproductive organs do not grow further once fully mature, consistent with size at maturity results (100% mature above 151 mm). A methodological limitation of this study is that the decline (spent) phase was not observed, as no spent animals were collected during sampling, which may introduce a potential bias in interpreting the complete reproductive cycle.

The reproductive cycle for females showed higher weight indices in January, February and April, indicating preparation for spawning. The highest percentage of mature females in April underscores its importance as a peak spawning month. In males, the testis weight index (TWI) peaked in April, while the spermatophoric complex weight index (SPCWI) also increased, reflecting the sequential transfer of spermatophores from the testis to the spermatophoric complex. Pearson correlation analysis revealed a significant positive relationship between TWI and SPCWI (r = 0.62, p < 0.01), indicating that spermatophore production generally increases with testis growth, although short-term differences occur due to organ-specific transfer dynamics. These results are consistent with reproductive strategies observed in many marine species, where males and females exhibit distinct patterns of gonadal development in preparation for a synchronised spawning event.

The size of mature ova in this study (up to 1.4 mm) is consistent with Naik *et al.* (2017), who reported sizes ranging from 1.26 to 1.6 mm. In case of the percentage of ova in ovary, opaque ova (OP) was highest among the other, followed by large reticulate ova (LR), small reticulate ova (SR) and matured ova (MO). MO was the least found ova in the ovary, because after ova maturation it moves into the oviduct storage and gets stored there until released for spawning. Also, its graphical representation of linear relationship between mean DML and average total number of eggs shows positive relationship. Similarly, the percentage of different ova in ovary is independent of its DML size, because it’s mainly based on their maturation process. The positive correlation between DML and the number of matured ova in ovary (NMOO) supports previous findings by Mohamed *et al.* (2014), who observed matured ova in ovary of 480 to 4671 eggs with the

DML size ranging from 145 mm to 185 mm, which evidently supports that the NMOO was directly proportional to the DML size. Incase of ovary and oviduct weight in relational to DML, the finding indicates that ovary weight is directly proportional to the total number of eggs in it and the oviduct weight is directly proportional to the number of matured ova present. These observations highlight the strong correlation between reproductive organ weight and the reproductive potential of the specimens.

Potential fecundity (PF) values were aligned with findings by Naik *et al.* (2017), who observed in *U. duvaucelii* ranged from 1,545 to 13,585 with an average of 7,554 eggs from the SW coast of India and Sundaram and Mane (2019) range from 1,080 to 15,570 in the north-west coast of India. From the overall studies, the potential fecundity of *U. duvaucelii* in Indian waters ranges less than 20,000. Similar to the potential fecundity, the relative fecundity (RF) and index of potential reproductive investment (PRI) value also get increased against the increase of DML size, which supports the statement, RF value and PRI value was directly proportional to the DML size.

The PF values were examined against variables such as total body weight, oviduct (OD) weight and OVD (ovary + oviduct) weight. All three variables showed a positive linear relationship with potential fecundity, with R^2 values ranging from 0.5 to 0.9. Similar results for the relationship between total weight and potential fecundity were reported by Mohamed *et al.* (2014) ($Y = -1056.1 + 33.987X$, $R^2 = 0.4702$) and Naik *et al.* (2017) ($Y = 0.9942 + 1.5332X$) in *U. duvaucelii*, both of which demonstrated a positive linear correlation.

The histological analysis revealed that the production of ova in ovary was synchronous ovulation and the matured ova in oviduct were released as batch (spawn more than once) in the southeast coast of India. Which can be supported by the previous study led by Elsayed *et al.* (2021) who observed the gonadal development of *U. duvaucelii* in Suez Gulf by histological study and concluded that, females are iteroparous and spawns partially throughout the year. In addition, Jereb and Roper (2010) and Petsut and Kulabtong (2012) reported that *U. duvaucelii* exhibited partial spawning or extended reproductive phase within the life cycle. Hence, it can be concluded that *U. duvaucelii* exhibit iteroparous spawning in the southeast coast of India. The presence of spermatids in male testis and spermatophores in Needham's sac indicates synchronous reproductive development, further supporting the iteroparous spawning pattern.

The spawning pattern of *U. duvaucelii* from the southeast coast of India was elucidated through detailed analysis of size at maturity (L_{95}) and reproductive organ development. The results indicated that the population reaches maturity at a dorsal mantle length (DML) exceeding 144 mm in females. Notably, somatic growth continued even after reaching full maturity, suggesting that body growth occurs alongside the spawning process. This finding is consistent with histological observations of Stage V ovaries and oviducts, where the oviducts were stocked with mature ova, while primordial, follicular, and mature ova coexisted in the ovary. Such observations imply synchronous ovulation and batch spawning in the species. Females exhibit synchronous ovulation and batch spawning, accompanied by somatic growth during each spawning cycle. These findings align with the categorization proposed by Rocha *et al.* (2001), who described such a spawning pattern as iteroparity—characterized by multiple spawning events during the species lifetime. Similar observations were reported by Mohamed (1993) and Sajikumar *et al.* (2022) for *U. duvaucelii* populations along the west coast of India, who also classified the species as a multiple spawner. Additionally, Silas *et al.* (1985) noted that *U. duvaucelii* does not die after a single spawning event, further supporting its iteroparous nature.

The current study confirms that *U. duvaucelii* in the southeast coast of India demonstrates multiple spawning behavior, a finding supported by both histological and reproductive biology analyses. However, despite these insights into the reproductive strategies of the species, there remains a gap in understanding the development of ova into juveniles in this region. Future studies focusing on post-spawning development and juvenile stages could provide a comprehensive understanding of the species life cycle. This knowledge would be invaluable for the management and conservation of *U. duvaucelii* populations in Indian waters.

ACKNOWLEDGEMENTS
The authors express their gratitude to the Ministry of Fisheries, Animal Husbandry and Dairying, Department of Fisheries, Government of India, for providing the necessary support and facilities. They extend their grateful to the Director General, Fishery Survey of India and Shri A. Tiburtius, Zonal Director, Chennai base of Fishery Survey of India for their unwavering support and facilitation throughout the study. The authors also thank the crew members of the MFV Samudrika for their assistance during sample collection. The first authors extended his sincere thanks to Shri Ashish P Jacob, Young Professional, Chennai base of Fishery Survey of India for his technical support.

CONFLICT OF INTEREST
The author declares no conflict of interest.

AUTHORS' CONTRIBUTION
RJP: Conceptualisation, Data curation, Formal analysis, Investigation, Methodology, Software, Writing – original draft. AJC: Supervision, Validation, Visualisation and Writ-

ing – review and editing. KS: Writing – review and editing. AT: Supervision.

DATA AVAILABILITY STATEMENT

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

REFERENCES

Arkhipkin AI, Rodhouse PGK, Pierce GJ, Sauer W, Sakai M, ... Chen CS (2015) World squid fisheries. Reviews in Fisheries Science & Aquaculture 23(2): 92–252.

Chembian AJ (2013) Studies on the biology, morphometrics and biochemical composition of the ommastrephid squid, *Sthenoteuthis oualaniensis* (Lesson, 1830) of the south-west coast of India. PhD thesis, Cochin University of Science and Technology, Cochin, India.

Chhandaprajnadarsini EM, Rudramurthy N, Sethi SN, Kizhakudan SJ, Sivadas M (2020) Stock assessment of Indian squid, *Uroteuthis* (*Photololigo*) *duvaucelii* (d'Orbigny, 1835) from south-western Bay of Bengal. Indian Journal of Geo-Marine Sciences 49(11): 1750–1757.

DoF (2023) Annual reports 2022–2023. Department of Fisheries Ministry of Fisheries, Animal Husbandry and Dairying, Government of India, New Delhi, 142 pp.

Elsayed E, Abdel-Khalek A, Mohamed KS (2021) Reproductive dynamics of Indian squid, *Uroteuthis duvaucelii* (Cephalopoda: Loliginidae) of the Suez Gulf, Red Sea, Egypt. Egyptian Journal of Aquatic Biology and Fisheries 25(4): 573–589.

Gewida H, Khalil M, El-Desouky H (2021) Some reproductive aspects of the Indian squid *Loligo duvauceli* in the Gulf of Suez, Egypt. Egyptian Journal of Aquatic Biology and Fisheries 25(4): 367–382.

Jereb P, Roper CFE (2006) Cephalopods of the world: an annotated and illustrated catalogue of cephalopod species known to date, volume 3: octopods and vampire squids. FAO Species Catalogue for Fishery Purposes No. 4, Vol. 3. FAO, Rome.

Jereb P, Roper CFE (2010) Cephalopods of the world: an annotated and illustrated catalogue of cephalopod species known to date, volume 2: Myopsid and Oegopsid Squids. FAO, Rome.

Kilada R, Riad R (2010) Seasonal reproduction biology of *Uroteuthis duvauceli* (Cephalopoda: Loliginidae) in northern Red Sea, Egypt. Journal of Shellfish Research 29(3): 781–791.

Laptikhovsky VV (1999) Fecundity and spawning in squid of families Enoploteuthidae and Ancistrocheiridae (Cephalopoda: Oegopsida). Scientia Marina 63(1): 1–7.

Laptikhovsky VV, Nigmatullin CM (1993) Egg size, fecundity, and spawning in females of the genus *Illex* (Cephalopoda: Ommastrephidae). ICES Journal of Marine Science 50(3): 393–403.

Laptikhovsky VV, Nigmatullin CM (1999) Egg size and fecundity in females of the subfamilies Todaropsinae and Todarodinae (Cephalopoda: Ommastrephidae). Journal of the Marine Biological Association of the United Kingdom 79(3): 569–570.

Lipinski MR (1979) Universal maturity scale for the commercially important squids. The results of maturity classification of the *Illex illecebrosus* (Lesueur, 1821) population for the years 1973–77. International Commission for the Northwest Atlantic Fisheries Research Document. 79: 40 pp.

Lipinski MR, Underhill LG (1995) Sexual maturation in squid: quantum or continuum? South African Journal of Marine Science 15: 207–223

Markaida U, Sosa-Nishizaki O (2001) Reproductive biology of jumbo squid *Dosidicus gigas* in the Gulf of California, 1995–1997. Fisheries Research 54(1): 63–82.

Mohamed KS (1993) Spawning congregations of Indian squid *Loligo duvauceli* (Cephalopoda: Loliginidae) in the Arabian Sea off Mangalore and Malpe. Indian Journal of Marine Sciences 22(3): 172–175.

Mohamed Y, Ghobashy AF, Gabr H, Tantawy H (2014) Maturation, fecundity and seasonality of reproduction of the squid *Uroteuthis duvaucelii* (Cephalopoda: Loliginidae) in the Suez Canal. Catrina International Journal of Environmental Sciences 9(1): 33–39.

Naik NR, Shivaprakash SM, Anjaneyappa HN, Somasekhara SR, Naik J, Benakappa S (2017) Reproductive biology of the commercially important Indian squid *Uroteuthis* (*Photololigo*) *duvaucelii* (d'Orbigny, 1835) off Mangalore, south-west coast of India. Indian Journal of Fisheries 64(2): 75–79.

Navarro J, Coll M, Somes CJ, Olson RJ (2013) Trophic niche of squids: insights from isotopic data in marine systems worldwide. Deep-Sea Research Part II: Topical Studies in Oceanography 95: 93–102.

Petsut N, Kulabtong S (2012) Biology of Indian squid, *Loligo duvauceli* in Thailand. Veridian E-Journal 6(1): 19–33.

Pierce GJ, Valavanis VD, Guerra A, Jereb P, Orsi-Relini L, ... Sobrino I (2008) A review of cephalopod–environment interactions in European seas. Hydrobiologia 612(1): 49–70.

R Core Team (2015) R: a language and environment for statistical computing. R Foundation for Statistical Computing. https://www.R-project.org/

Rocha F, Guerra Á, González ÁF (2001) A review of reproductive strategies in cephalopods. Biological Reviews 76(3): 291–304.

Sajikumar KK, Sasikumar G, Jayasankar J, Bharti V, Venkatesan V, ... Mohamed KS (2022) Dynamics of growth and spawning in the Indian squid *Uroteuthis duvaucelii* (Cephalopoda: Loliginidae) from the tropical Arabian Sea. Regional Studies in Marine Science. 52: 102324.

Sauer WH; Lipiński MR (1990) Histological validation of morphological stages of sexual maturity in chokker squid *Loligo vulgaris reynaudii* D'Orb (Cephalopoda: Loliginidae). South African Journal of Marine Science 9(1): 189–200.

Schlitzer R (2024) Ocean data view. Available at: https://odv.awi.de

Silas EG, Rao KS, Sarvesan R, Nair KP, Vidyasagar K, ... Rao BN (1985) Some aspects of the biology of squids. CMFRI Bulletin 37: 38–48.

Sukramongkol N, Tsuchiya K, Segawa S (2007) Age and maturation of *Loligo duvauceli* and *L. chinensis* from the Andaman Sea of Thailand. Reviews in Fish Biology and Fisheries 17: 237–246.

Sundaram S, Mane S (2019) Species diversity and basic biology of squids from Maharashtra waters, northwest coast of India. International Journal of Life Sciences 7: 43–50.

Supongpan M, Boongerd S (1992) Catch analysis of Indian squid *Loligo duvauceli* by light luring fishing in the Gulf of Thailand. Nippon Suisan Gakkaishi. 58: 439–444.

Wang J, Yu W, Chen X, Lei L, Chen Y (2015) Detection of potential fishing zones for neon flying squid based on remote-sensing data in the Northwest Pacific Ocean using an artificial neural network. International Journal of Remote Sensing 36: 3317–3330.

Zar JH (1999) Biostatistical analysis. Prentice-Hall, New Jersey. 620 pp.

R John Peter http://orcid.org/0009-0004-7936-2545
A John Chembian http://orcid.org/0009-0001-7538-4024
K Silambarasan https://orcid.org/0000-0001-5805-1562