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Population dynamics of two squid species, *Uroteuthis duvaucelii* (D'Orbigny, 1835) and *U. singhalensis* (Ortmann, 1891) (Family: Loliginidae) in the Trincomalee bay, Sri Lanka

N.B. Prasada Punyadewa[1], K.L.R.C. Wijayasinghe[1] and Upali S. Amarasinghe[2*]

[1]*National Aquatic Resources Research and Development Agency, Crow Island, Colombo 15, Sri Lanka*
[2]*Department of Zoology and Environmental Management, University of Kelaniya, Kelaniya 11600, Sri Lanka*

*Corresponding author (zoousa@kln.ac.lk)

ORCID : https://orcid.org/0000-0002-0465-6950

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Abstract In the Trincomalee bay of Sri Lanka, two species of squids, *Uroteuthis duvaucelii* and *U. singhalensis*, support profitable small-scale fisheries. The present study is an attempt to assess the fisheries of these two squid species using length-based stock assessment methodologies. Length frequency data collected from the landings of two species, collected during the fishing season from May to October 2003 were analyzed using FiSAT II software package. The asymptotic length (mantle length) and growth constant of *U. duvaucelii* were 31.8 cm and 0.90 yr^{-1} respectively and of *U. singhalensis* were 31.2 cm and 0.72 yr^{-1} respectively. Using the mortality coefficient estimates based on these growth parameters, exploitation rates (E) of *U. duvaucelii* and *U. singhalensis* during the study period were found to be 0.55 and 0.44 respectively. Optimal fishing strategies determined by relative yield-per-recruit (Y'/R) analyses of two squad species indicated that the sizes of first capture (L_c) and E were at sub-optimal levels. As both squid species are exploited by the same fishing gear, optimal E values predicted by Y'/R analyses cannot be achieved. This analysis indicates that levels of exploitation during the study period having L_c of 15.8 cm for *U. duvaucelii* at E = 0.55 and 14.3 cm at E = 0.44 for *U. singhalensis* be maintained. It is therefore concluded that fishing effort and the sizes of the first capture of the two squid species in the Trincomalee bay do not require adjustments through fishery regulations for the sustainability of their fisheries.

Keywords: cephalopod fisheries, Indian squid, length-based stock assessment, long barrel squid, small-scale fisheries

INTRODUCTION

In the world fisheries, compared to finfish capture fisheries squids make a rather small contribution, but over the last decade, the proportion has increased steadily over, with some signs of recent leveling off (Arkhipkin *et al.* 2015). One of the crucial factors contributing to the increase of squid stocks worldwide is assumed to be due to their considerable flexibility in life-history traits, which make them adapt successfully to environmental changes (Doubleday *et al.* 2016; Pang *et al.* 2022). In various squid species, considerable differences in life-history traits have been observed. For example, squids in warmer geographical regions grow faster and mature earlier than those in colder regions (Jackson and Moltschaniwskyi 2002; Moreno *et al.* 2007; Chemshirova *et al.* 2021).

In terms of the flesh quality of squids for human consumption, negatively buoyant species possess favourable characteristics having muscular mantles. The neutrally buoyant squid species having flesh with an ammoniacal flavour and flaccid texture are generally unacceptable for human consumption. The commercially viable squid fisheries therefore should essentially target aggregations near the surface at least for part of their lifecycles (Arkhipkin *et al.* 2015). The squid and cuttlefish species occurring in the coastal sea areas around Sri Lanka are mainly caught by commercial-scale fisheries targeting large-scale aggregation during spawning season, or as by-catch in trawl fisheries (De Bruin *et al.* 1994). Squid stocks are known to be capable of recovering from low biomass levels, which may occur due to unfavourable environmental conditions, and as a result, overfishing generally does not take place (Arkhipkin *et al*. 2015). However, stock depletion is likely when heavy fishing pressure coincides with unfavourable environmental conditions. Rodhouse (2001) has stated that in squid populations, recruitment variability is driven by the environment, presenting a challenge to the management of squid fisheries.

Apart from food value for humans, squids are widely used as baits in pelagic longline fisheries (Coelho *et al.* 2012; Gilman *et al.* 2020) targeting tunas, 'tuna-like' (Scombroidei) and billfishes (Xiphioidei). There are, however, environmental concerns about the use of squids as baits in the pelagic longline fisheries because sea turtles (Gilman *et al.* 2006) and seabirds (Ryan *et al.* 2002) are caught incidentally in the pelagic longlines with squid baits. Presently, several bait types including imported squid baits are used in pelagic longline fisheries off Sri Lanka. Gunasekara and Haputhanthri (2020) advocated that instead of imported squid baits, locally available bait types including squids should be used.

In Sri Lanka, studies on the fisheries of cephalopods are restricted to taxonomic descriptions (Perera 1976), fisheries (Dayaratne 1978), and population dynamics of big fin squid, *Sepioteuthis lessoniana* from the Northern Coast of Sri Lanka. In the database of www.sealifebase.org (Palemares and Pauly 2022), information about the population dynamics of squids is available only for three species. However, some studies on the population dynamics of squids are reported elsewhere (e.g., Ding *et al.* 2019; Arkhipkin *et al.* 2021). Pierce and Guerra (1994), who reviewed stock assessment methods used for cephalopod fisheries mentioned that such assessment methods include stock-recruitment relationships (e.g. the Japanese *Todarodes pacificus* stock), recruitment indices (e.g. Saharan Bank cephalopod stocks), swept-area biomass estimates (e.g. Northwest Atlantic stocks of the squids *Loligo pealei* and *Illex illecebrosus*), production models (e.g. Saharan Bank cephalopod stocks), cohort analysis (e.g. *Illex argentinus* in the Falkland islands), yield-per-recruit models (e.g. Northwest Atlantic squid stocks), length-based cohort analysis (e.g., *Dosidicus gigas* in the Gulf of California), and depletion estimates of stock size (e.g. *Illex argentinus* in the Falkland islands). Pierce and Guerra (194) further mentioned that despite the widespread application of assessment methods, available management options are constrained by the nature of the fisheries and the generally poor quality of available data. As information about the status of squid fisheries off Sri Lanka is scanty, strategies for sustainable management of the resources are difficult to be defined under the future scenarios of exploitation for human consumption, for supporting hoteliers associated with the tourist industry and for potential uses as baits in the pelagic longline fisheries. Globally, the management of cephalopod fisheries is challenging and complex interactions between squid fisheries and marine ecosystems are not fully understood (Arkhipkin *et al.* 2015). In this context, the holistic understanding of marine ecosystems and the role of squids in them in developing squid fishery management protocols according to the principles of the ecosystem approach to fisheries is highlighted (Arkhipkin *et al.* 2015). Under the fisheries regulatory measures in Sri Lanka, no specific management interventions have been reported. In the present study, an attempt is made to assess the fisheries of two squid species, *Uroteuthis duvaucelii* and *U. singhalensis* caught in the Trincomalee bay of Sri Lanka using length-based stock assessment methodologies.

MATERIALS AND METHODS

The fishery

Of the two kinds of cephalopods (cuttlefish and squids), in the mid-1970s, cuttlefish were reported to contribute approximately 17% of their total production in waters around Sri Lanka (Dayaratne 1978). Perera (1976) reported the occurrence of two species of cuttlefish and four species of squids in Sri Lankan waters. Squids aggregate in large schools for mating and spawning (De Bruin *et al.* 1994) and these aggregations appear to support profitable small-scale fisheries in many parts of the coastal waters off Sri Lanka. In Trincomalee bay (Fig. 1), there is a seasonal fishery for squids (Siriwardane-de Zoysa 2018). During the season when squid stocks are plentiful (May-October), daily fishing cycles generally commence at sunset and end in the early morning. There are three squid fishing methods in the study area, i.e., fishing with light attraction, scoop netting and stick-held dip netting (SHDN), and all three methods involve the use of luring lamps to attract squids. Unfortunately, information about the fishing effort of the three fishing methods, the number of fishermen engaged, the number of boat trips in a given period, etc., was not available.

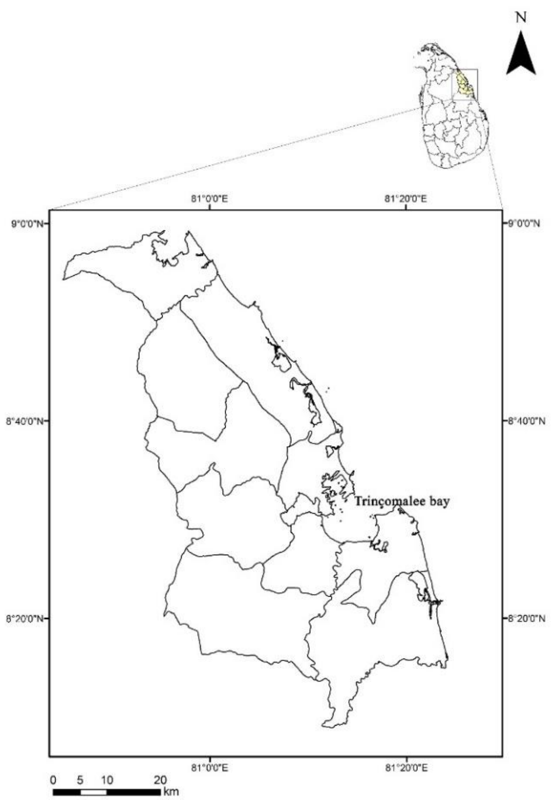

Fig 1 Squid fishing area in Trincomalee bay. The inset shows the location of the Trincomalee district in Sri Lanka.

(a) Fishing with light attraction (LA):

Two fishing boats are engaged in this fishery one of the fishing boats is anchored in the appropriate fishing location where the squids are available. The squid luring lamps are illuminated before sunset. Lights are illuminated for several hours to attract squids around the boat. When plenty of squids are gathered, an encircling fishing net of mesh sizes 26 mm – 38 mm is set on the deck of the other boat and gradually pulled into the sea and encircle the fishing net around the squids attracted to the boat. After completing the encircling, the net is pursed using a purse line and the net is hauled to the boat with the squids.

(b) Scoop netting (SN)

The fishing boat is anchored and squid luring lamps are illuminated for several hours commencing before the sunset, to attract squids around the boat. Fishing is done with a luminous coloured squid jig attached to the end of the fishing line and is gradually jerked. Information about the number of lines used by each boat is, however, not available. Squids attracted to the jig get entangled. Then entangled squids are taken to the boat with the help of a scoop net. The operation is done on either side of the boat in order to make the operation easier and more convenient.

(c) Stick-held dip netting (SHDN) (Punyadewa *et al.* 2004)

The fishing boat is anchored and the squid luring lamps are illuminated before sunset and is a nighttime operation to attract them for catching. The net (mesh size: 26 mm – 38 mm) is set on the deck of the boat and gradually pulled in the sea to allow the net to drift away parallel to the boat. The operation is done on either side of the boat, which is convenient. When the squids get aggregated near the sea surface, fishermen pull hauling lines until the front part of the net is hauled up to the sea surface to prevent squid from escaping. With the help of bamboo poles, the net is pulled towards the boat to make it easier to scoop the squid being caught. During the study period, the number of fishing trips per month ranged from 3 to 15.

In the squid fishery in Trincomalee bay, the dominant species caught are Indian squid, *Uroteuthis duvaucelii* (D'Orbigny, 1835), and long-barrel squid, *U. singhalensis* (Ortmann, 1891). The two species are caught simultaneously in the three fishing methods, and as such, the fishery can be treated as a multi-species (two species in this case) fishery.

Length frequency data collection

Mantle lengths of *U. duvaucelii* and *U. singhalensis* landed from the fisheries of LA, SN, and SDN in the

Trincomalee bay from May to October 2003 were measured to the nearest cm below the actual lengths of individual squids. Monthly sample sizes ranged from 300 in May 2003 to 8,040 in August 2003 for *U. duvaucelii*, and from 6,964 in May 2003 to 14,000 in August 2003 for *U. singhalensis*. Length frequency data (LFD) of the two squid species were grouped separately into 1 cm length classes.

Data analysis

For the monthly distribution of LFD of two squid species, the von Bertalanffy growth formula (VBGF) for non-seasonalised growth described by the following equation, was fitted separately.

$$L_t = L_\infty[1 - \exp\{-K(t - t_o\}] \qquad (1)$$

where L_t is the mean mantle length of squid at age t, L_∞ is the asymptotic mantle length, K is the growth constant and t_o is the theoretical age they would have at zero body length. The analysis was performed using ELEFAN II (version 1.2.2) software (Gayanilo *et al.* 2006). For fitting VBGF using the ELEFAN I routine of FiSAT II, initial estimates of L_∞ of the two squid species were obtained using the Powell-Wetherall method (Powell 1979; Wetherall 1986; Pauly 1986a; Gayanilo and Pauly 1997), which were essentially based on the exploited phase of a given fish stock.

Since L_∞ and K are not species-specific but are inversely proportional, the following growth performance index (φ'), which is constant for a species (Moreau *et al.* 1986), was used to compare growth parameters of taxonomically similar squid species in different localities.

$$\varphi' = 2\,\mathrm{Log}_{10}L_\infty + \mathrm{Log}_{10}K \qquad (2)$$

The φ' index is sensitive to the units of measurement of L_∞ and K and the expression of L_∞ (mantle length in cm in the present study), so that comparable units and expressions of growth parameters were used in calculating φ'.

Total mortality (Z) was calculated using original LFD by the length-converted catch curve method (Pauly 1983), as implemented in FiSAT II software. In this method, t_o was assumed zero and the slope of the following linear regression line fitted to the right-hand descending part of the catch curve, starting from the second highest data point, gives an estimate of Z.

$$\mathrm{Ln}\,\frac{C_i}{\Delta t} = a - Zt_i \qquad (3)$$

where, C_i = Catch in numbers in i[th] length class, $\Delta t = \frac{1}{K}\ln[\frac{(L_\infty - L_i)}{(L_\infty - L_{i+1})}$, and t_i = relative age of the mid-point of i[th] length class (i.e., $t - t_o$).

As squids were caught in three types of fishing gear in which larger sized classes were retained, perhaps except for possible escapees causing 'behavioural selection', descending part of the catch curve was considered to represent the exponential decay curve of the exploited phase of the fish stock. Natural mortality was estimated using the following empirical equation derived by Pauly (1980).

$$\mathrm{Log}_{10}M = -0.0066 - 0.279\,\mathrm{Log}_{10}L_\infty + 0.6543\,\mathrm{Log}_{10}K + 0.4634\,\mathrm{Log}_{10}T \qquad (4)$$

where T is the mean habitat temperature in degrees Celsius, which in the present analysis was considered as 28° C. Fishing mortality (F) was estimated by subtracting Natural mortality coefficients (M) from Z and the exploitation rate (E) was estimated as F/ (M + F).

Through a detailed analysis of the ascending part of the length-converted catch curve (Pauly 1986b), probabilities of capture of smaller size classes were determined, and from a plot of probabilities of capture against mantle length, mean mantle length at first capture (L_c) (i.e., length at 50% retention) was determined. Recruitment pulses per year and their relative strength were determined from the routine implemented in FiSAT II software, which involves backward projection of length frequencies onto the time axis based on growth parameters. Relative yield-per-recruit (Y'/R) analysis was carried out incorporating probabilities of capture (Pauly and Soriano 1986; Gayanilo and Pauly 1997) determined as above. As fishers generally tend to increase the efficiency of fishing gear, to leave a provision for such trends, the E value which corresponds to 10% of the maximum rate of Y'/R increase with increasing E, defined as $E_{0.1}$ was also determined as an index of assessing the status of the fishery (Gayanilo and Pauly 1997).

RESULTS

The size ranges were 7.5 cm to 28.5 cm for *U. duvaucelii*, and from 6.5 cm to 28.5 cm for *U. singhalensis*. As mentioned above, the two species are jointly caught in the three fishing methods, and as such, the estimates of the optimal fishing strategies essentially require a trade-off for them. The overall LFD of the samples of two squid species during the study period are shown in Figure 2. Monthly LFD of both squid species are available from the corresponding author upon request. The fully exploited phases in the length ranges of the two squid species can be clearly noticed from the Powell-Wetherall plots (Figure 3), from which L_∞ and Z/K could be estimated (Table 1).

The non-seasonalised VBGF growth curves of *U. duvaucelii* and *U. singhalensis* determined by means of ELEFAN I and superimposed on monthly LFD and restricted LFD are shown in Figure 4, having sensible fits with the peaks of data. When the estimated VBGF parameters (L_∞ and K) were compared with those available in www.sealifebase.org (Palemares and Pauly 2022) and other literature, based on the φ' values (Table 2), the estimates of VBGF parameters of *U. duvaucelii* and *U. singhalensis* were biologically reasonable.

Total mortality (Z) estimated from length converted catch curves of *U. duvaucelii* (Figure 5A) and *U. singhalensis* (Figure 5B) was 3.67 yr^{-1} and 2.56 yr^{-1} respectively (Table 3). Natural mortality coefficients (M) of the two squid species estimated from Pauly's (1980) function, assuming mean habitat temperature as 28°C, were 1.64 yr^{-1} for *U. duvaucelii* and 1.43 yr^{-1} for *U. singhalensis*. Accordingly, fishing mortalities were estimated to be 2.03 yr^{-1} for *U. duvaucelii* and 1.14 yr^{-1} for *U. singhalensis*. As exploitation rates (E) were 0.55 and 0.44 for *U. duvaucelii* and *U. singhalensis* respectively, during the period of study, the two squid stocks appeared to be optimally exploited (Table 3). It must be noted that the estimated E_{opt} of 0.7 from the relative yield-per-recruit analysis was not used as the reference point for fisheries management but $E_{0.1}$ (for the explanation, see above).

The probabilities of the capture of the two squid species represented sigmoid selection curves (Figures 6A and 6B), and the lengths at 50% retention that were treated as the length at first capture (L_c), were 15.9 cm for *U. duvaucelii* and 14.3 cm for *U. singhalensis* (Table 3).

Both species of squids exhibited recruitment patterns having a single peak (Figures 7A and 7B). From the relative yield-per-recruit (Y'/R) curves expressed as functions of exploitation rates for *U. duvaucelii* (Figure 8A) and *U. singhalensis* (Figure 8B), optimal fishing strategies were determined as optimal lengths at first capture ($L_{c(opt)}$), exploitation rates producing long-term Y'/R (E_{max}), and exploitation rates which correspond to 10% of the maximum rate of Y'/R increase with increasing E ($E_{0.1}$). Accordingly, $L_{c(opt)}$ was 13.8 cm for *U. duvaucelii* and 14.7 cm for *U. singhalensis*. Also, E_{max} and $E_{0.1}$ were 0.70 and 0.56 respectively for *U. duvaucelii*. For *U. singhalensis*, E_{max} was 0.70 and $E_{0.1}$ was 0.57 (Table 3). These results indicate that the optimal fishing strategies for the long-term sustainability of the fishery were by and large identical for both squid species, which are simultaneously exploited using similar fishing techniques.

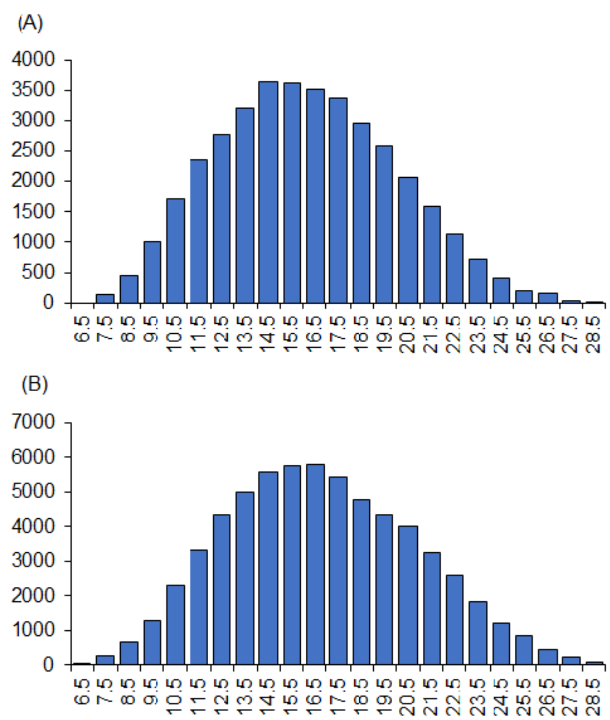

Fig 2 Overall length frequency distribution (mantle length in cm) of (A) *U. duvaucelii* (n = 6.306) and (B) *U. singhalensis* (n = 63,485) during the study period.

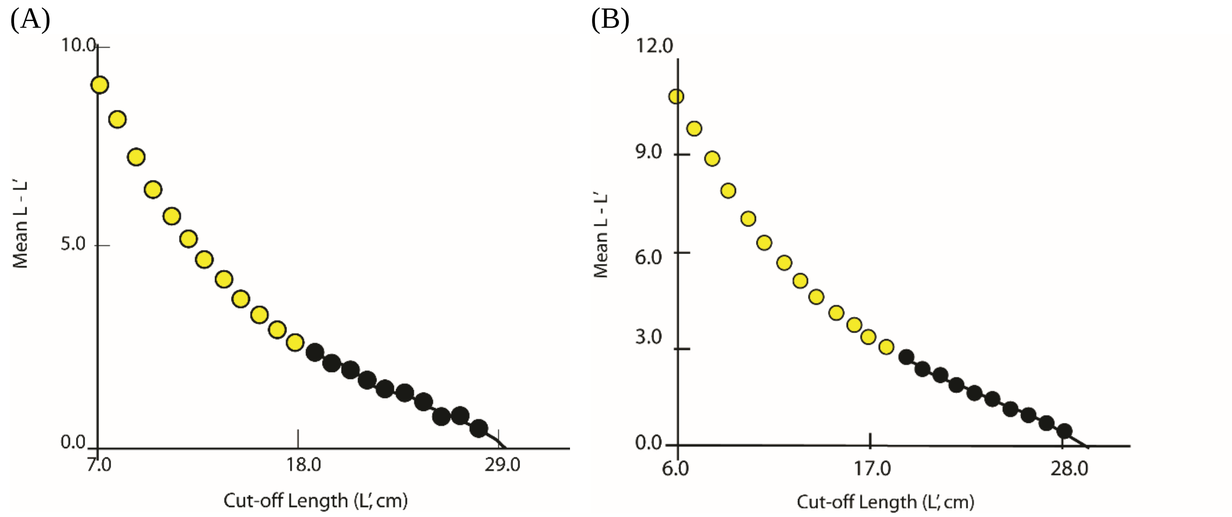

Fig 3. Powell-Wetherall plots of (A) *U. duvaucelii* and (B) *U. singhalensis*. Lighter colour circles representing incomplete selection were not used in the regression analysis, and only dark circles were used.

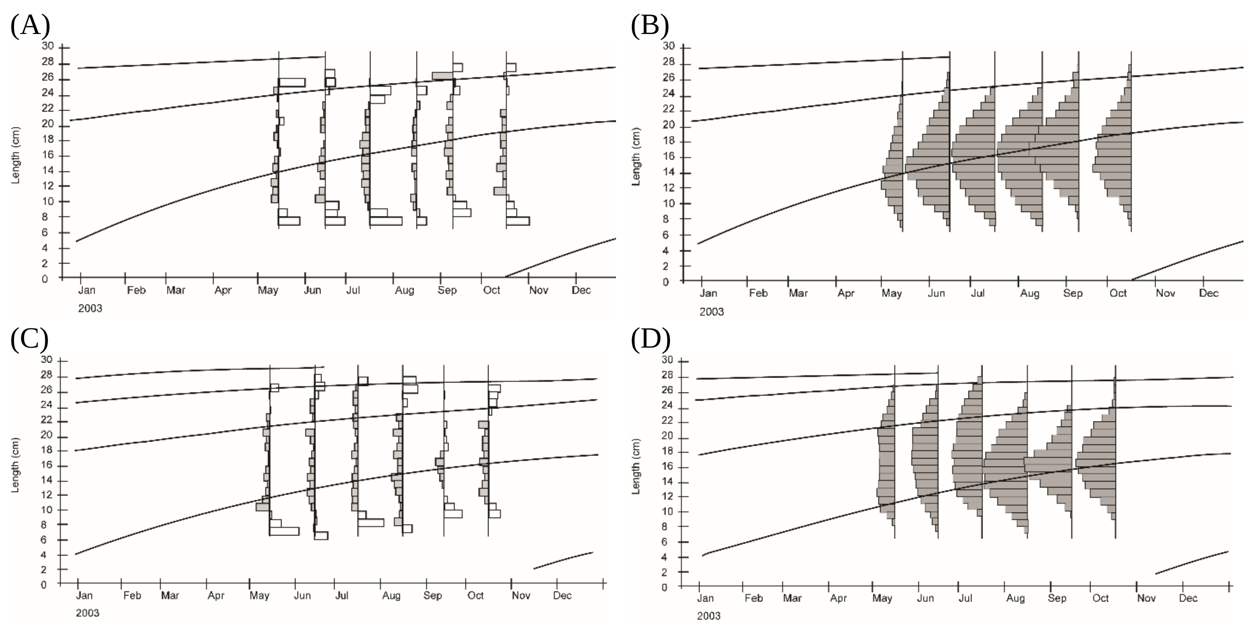

Fig 4 Growth curves of *U. duvaucelii* superimposed on (A) restructured LFD, (B) original LFD and those of *U. singhalensis* superimposed on (C) restructured LFD, (D) original LFD.

Table 1 Growth parameters of *U. duvaucelii* and *U. singhalensis*

	U. duvaucelii	*U. singhalensis*
Powell-Wetherall method		
Asymptotic length (L_∞) ML in cm	29.6	29.5
Z/K	3.628	2.873
ELEFAN I		
Asymptotic length (L_∞) ML in cm	31.8	31.2
K (yr^{-1})	0.90	0.72

Table 2 von Bertalanffy growth parameters and growth performance indices (φ') of several squid species and those of *U. duvaucelii* and *U. singhalensis* estimated in the present study

Species	L_∞ (Mantle length in cm)	K (yr^{-1})	φ'	Source
Uroteuthis chinensis (3 populations)	40.9 – 44.1	0.49 -.1.73	3.30 (range: 2.91 – 3.53)	Palemares and Pauly 2022
U. duaucelii (28 populations)	20.5 – 42.1	0.49 – 2.25	2.98 (range: 2.64 – 3.29)	Palemares and Pauly 2022
U. duaucelii (16 populations)	20.5 – 38.5	0.61 – 1.43	2.90 (range: 2.64 – 3.23)	Chhandaprajnadarsini *et al.* 2020
U. singhalensis (2 populations)	31.8 – 33.8	0.50 – 0.91	2.84 (range: 2.70 – 3.02)	Palemares and Pauly 2022
Sepioteuthis lessoniana	31.1	0.85	2.92	Charles and Sivashanthini 2011
U. duaucelii	31.8	0.90	2.96	Present study
U. singhalensis	31.2	0.72	2.85	Present study

(A) (B)

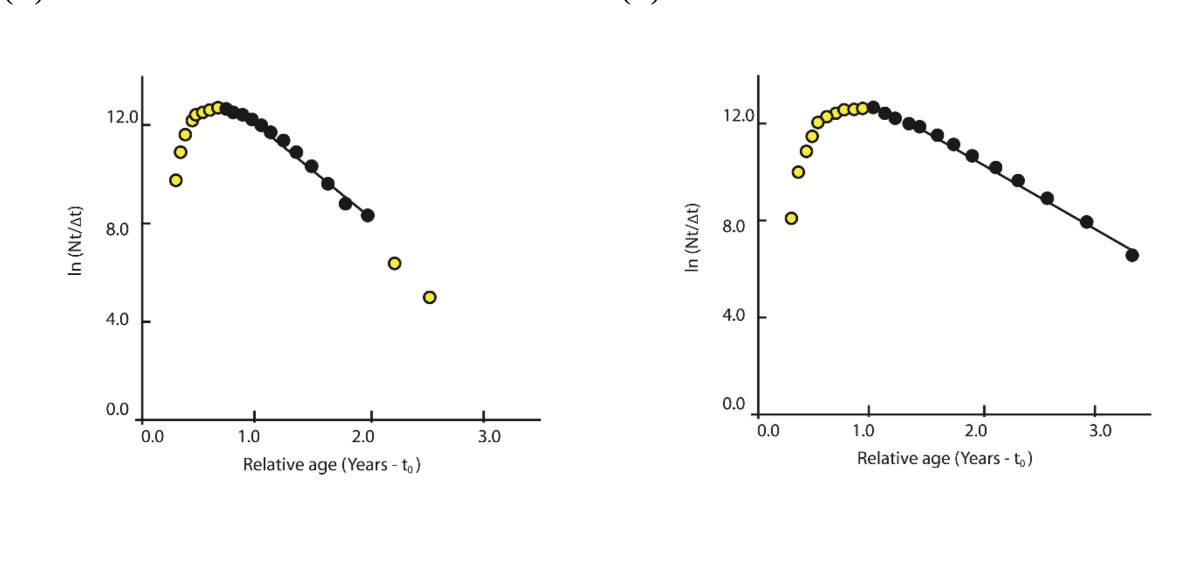

Fig 5 Length converted catch curves of (A) *U. duvaucelii* and (B) *U. singhalensis*. Lighter colour circles representing incomplete selection (and outliers in in Figure A) were not used in the regression analysis, and only dark circles were used.

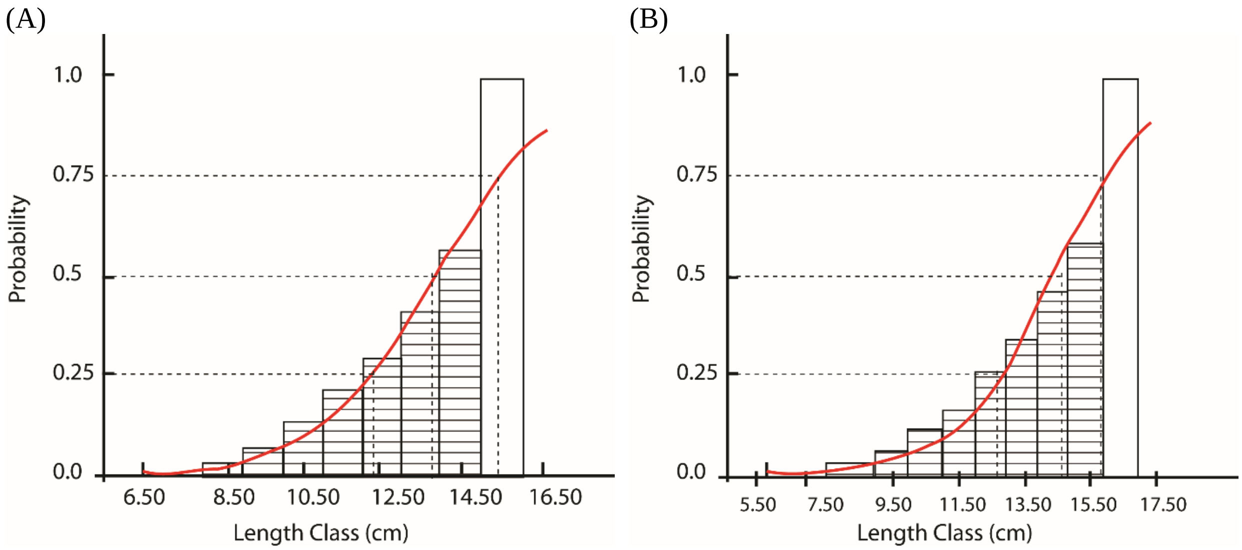

Fig 6 Probabilities of capture of (A) *U. duvaucelii* and (B) *U. singhalensis*. Broken lines indicate lengths at 25% (L_{25}), 50% (L_{50}) and 75% (L_{75}) probabilities of retention. In this analysis, L_{50} of each species was treated as the mean length at first capture (L_c).

Table 3 Mortality rates, exploitation rates (current), lengths at first capture (current), and optimal exploitation rates and optimal lengths at first capture of *U. duvaucelii* and *U. singhalensis*

	U. duvaucelii	*U. singhalensis*
Total mortality (yr^{-1})	3.67	2.56
Natural mortality at 28°C (yr^{-1})	1.64	1.43
Fishing mortality (yr^{-1})	2.03	1.14
Exploitation rate (E) (current)	0.55	0.44
Optimal E (E_{max})	0.70	0.70
$E_{0.1}$	0.56	0.57
Length at first capture (L_C) (current)	15.90	14.30
Optimal length at first capture ($L_{C(opt)}$)	13.80	14.70

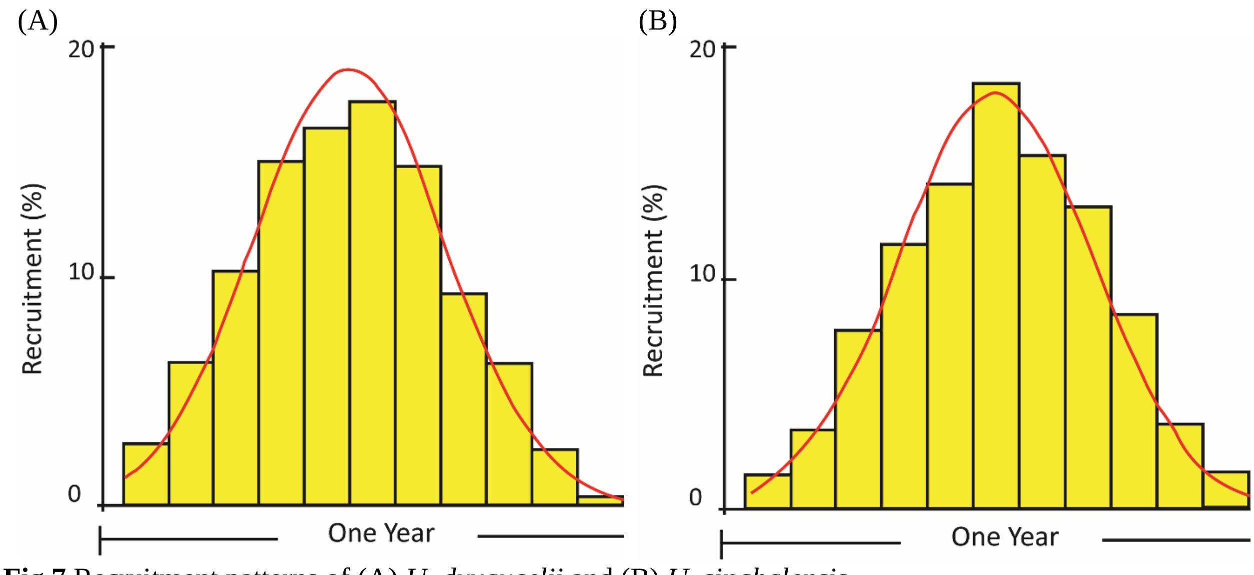

Fig 7 Recruitment patterns of (A) *U. duvaucelii* and (B) *U. singhalensis*.

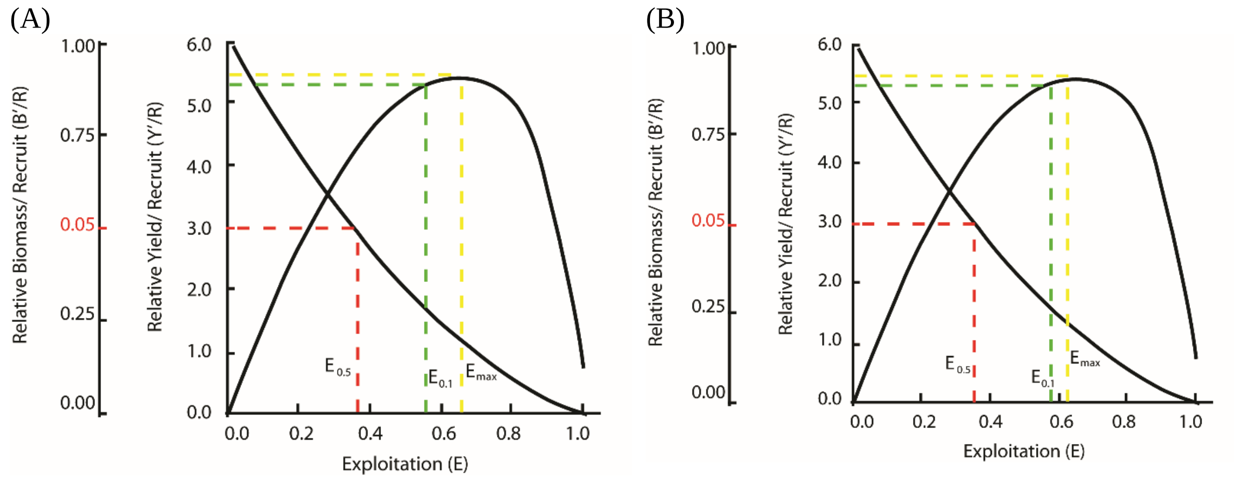

Fig 8 Relative yield-per-recruit (Y'/R) and relative biomass-per-recruit (B'/R) (in arbitrary units) as functions of exploitation rates of (A) *U. duvaucelii* and (B) *U. singhalensis.* Yellow broken lines indicate E_{max} corresponding to maximum Y'/R, red broken lines show $E_{0.1}$, and green broken lines indicate the E values corresponding to 50% of B'/R.

DISCUSSION

Although this analysis is based on the LFD collected in 2003, the fishing methods, seasons, and other fishery-related characteristics remained almost similar at least until 2022 (personal observations). As such, the management recommendations based on the present analysis are thought to be not outdated. The squid fisheries in the coastal waters of Sri Lanka, including *U. duvaucelii* and *U. singhalensis*, are targeted for spawning aggregations (De Bruin *et al.* 1994), and as such, obviously, juveniles do not occur in the fishing grounds. Consequently, the landings from which LFD were collected, consisted of the size ranges of adults. As LFD were corrected for gear selection within the length range of exploitation, based on the procedure proposed by Pauly (1986), it is thought that the possible bias arising due to the non-availability of LFD of juveniles did not make a significant impact on the estimation of growth parameters. Independent estimates of L_∞ and Z/K from Powell-Wetherall method (Table 1) were also in close agreement with those estimated from ELEFAN I. Phi-prime values of the two squid species were similar to those reported in the literature. As such, estimates of VBGF parameters of the two squid species are considered to be realistic.

Determination of mortality coefficients and recruitment patterns were essentially based on the estimated VBGF parameters and as such, the analyses conformed to the scientific assumptions behind the length-based stock assessment methodologies (Pauly 1984). In the length-converted catch curves (Figure 5), while the data points in the descending fall on a straight line for *U. singhalensis*, there were two outliers in the tail end of the descending arm of the catch curve of *U. duvaucelii*. This may be due to the possible escape of large individuals from fishing gear. The bias caused by this likely 'behavioural selection' could be avoided in the present analysis by selecting the rest of the data points in the descending part of the curve. Exploitation rates estimated for the period of study were around 0.5 for both squid species. As mentioned by Gulland (1971), one reference point for fisheries management (which is actually a rule-of-thumb) is to treat the E = 0.5 as optimum, i.e., the level at which fishing mortality is equal to natural mortality (F_{opt} = M). Also, in Y'/R analysis, generally the E_{opt}, which is 0.7 in the present analysis, is taken as the E value corresponding to optimal L_c producing the maximum Y'/R. However, in small-scale fisheries, as there is a general characteristic that the exploitation rates would increase as a result of increasing the efficiencies of fishing strategies, E_{opt} cannot be treated as a reasonable reference point for fisheries management. As such, in the present analysis, $E_{0.1}$, which leaves a provision to increase E, through fishermen's behaviour, beyond the optimal E is taken as the appropriate level of exploitation.

Present analysis revealed that the annual recruitment pattern had a single peak for both squid stocks. Generally, spawning seasons in tropical fish stocks are longer than those in the temperate regions but encounter a 'survival window' that is open only during a short period (Bakun *et al.* 1982; Pauly and Navaluna 1983), which may result in sharply peaked recruitment pulses. Despite the fact that the information about recruitment seasonality in squid stocks is scanty, they are known to exhibit considerable flexibility in life-history traits, which make them to adapt successfully to environmental changes (Doubleday *et al.* 2016; Pang *et al.* 2022). Recruitment patterns of the two squid species in the present study having a single peak can therefore be assumed to be due to such flexibility. Seasonality in fishing allows a natural closure of the fishery. Ni and Sandal (2019) have shown that fishing seasonality offers a natural moratorium supporting sustainability.

Although Sajikumar *et al.* (2022) reported that the maximum lifespan of *U. duvaucelii* in the southeastern Arabian sea was 6 months, according to Chhandaprajnadarsini *et al.* (2020), lifespan of the same species ranged from 2.5 to 3.53 years among 8 populations in Indian waters. The latter appears to be consistent with the value of lifespan that can be deduced from the estimates of K in the present study (i.e., Lifespan (≈ 3/K) of *U. duvaucelli* was 3.3 years; and of *U. singhalensis* was 4.2 years).

Relative yield-per-recruit (Y'/R) analysis indicated that the fishery *U. duvaucelii* could be optimized by decreasing L_c from 15.9 cm during the study period to 13.8 cm, while L_c of *U. singhalensis* could be slightly increased from 14.3 cm to 14.7 cm. However, as squids are caught in nets and in gigging lines in the same pattern that finfish species are caught, it is practically impossible to control L_c through mesh regulations or hook size regulations. Instead, the practicable means of regulating the exploitation levels of squids is apparently through the amount of fishing. The optimal exploitation rates of both squid species could be achieved by increasing E from 0.55 for *U. duvaucelii* and 0.44 for *U. singhalensis* to 0.70. As in many small-scale fisheries, there is a tendency of increasing fishing mortality of exploited stocks through fishers' behaviour to increase efficiencies of fishing techniques. As such, for managing the fisheries of the two squid species, it is advisable to maintain the fishing mortality, hence the exploitation rate, at a sub-optimal level. As such, in the present study, $E_{0.1}$ was considered the appropriate reference point for fisheries management. From Y'/R analysis, it is evident that the $E_{0.1}$ values of *U. duvaucelii* and *U. singhalensis* were 0.56 and 0.57 respectively (Table 3), slightly higher than the E values of the two species during the period of study. As both squid species are exploited by the same fishing gear in the Trincomalee bay, having E values of 0.55 for *U. duvaucelii* and 0.44 for *U. singhalensis*, it is not practicable to achieve similar E values for both species in order to optimize fishing strategies. The fishing strategies for the two squid species in Trincomalee bay are observed to remain more or less similar to those of the study period in the present analysis. It is therefore recommended that the current levels (i.e., levels of exploitation during the study period) having L_c of 15.8 cm for *U. duvaucelii* at E = 0.55 and 14.3 cm at E = 0.44 for *U. singhalensis* be maintained. As such, for the fisheries of two squid species in Trincomalee bay, it is not necessary to introduce management interventions.

The present analysis is based on the analysis of the LFD of two squid species by means of the FiSAT approach. However, a new analytical toolbox specifically designed for data-limited fisheries analysis using LFD, known as TropFishR (Mildenberger *et al.* 2017) is now available. This R package contains powerful algorithms to optimize L_∞ and K. As squids are known to exhibit considerable flexibility in life-history traits, updating future assessment of their fisheries based on improved approaches of LFD analyses such as TropFishR is advocated.

Squid fisheries production in Sri Lanka is destined for local human consumption and tourist hotels. Squids are also popular as tuna baits in longline fisheries but in Sri Lanka, imported squid baits are used in tuna longline fisheries. However, these imported squid baits are not meant for human consumption and as such, there is no market competition between locally produced squids and imported 'bait squids.' However, with the prospects of using locally available bait types for tuna longlines (Gunasekara and Haputhanthri 2020), there would be possibilities to increase exploitation levels in squid fisheries. Nevertheless, such trends may essentially be governed by market demand for locally produced squids, which are generally known to be fetched at higher prices (personal observations; NBPP). Hence, their future trends in production and marketing are needed to be monitored for effective management.

CONCLUSION

The stocks of two squid species in the Trincomalee bay, *Uroteuthis duvaucelii* and *U. singhalensis*, support productive small-scale fisheries and fishers use three squid fishing methods, i.e., fishing with light attraction, scoop netting and stick-held dip netting. This fishery is seasonal and generally lasts from May to October of the year. Monthly length frequency data collected during the fishing season in 2003 were analysed using FiSAT II software package. A length-based stock assessment was found to be reliable and applied for assessing optimal fishing strategies. The von Bertalanffy growth parameters estimated were found to be biologically reasonable as growth performance indices of the two species fall within the range of values reported elsewhere. Both species exhibited recruitment patterns with a single annual mode, perhaps due to spawning aggregations during a particular period of the year supporting seasonal fisheries. According to relative yield-per-recruit (Y'/R) analyses, it was evident that the fisheries production could be optimized through slight adjustment of sizes at first capture and exploitation rates of the two squid species. The fishing strategies during the study period were evidently at sub-optimal levels (i.e., exploitation levels lower than E_{opt}). In small-scale fisheries, there is a general tendency that catch efficiencies of fishing gear would increase resulting unprecedented increase in fishing pressure. As it is difficult, if not impossible, to optimize fisheries of two species that are exploited simultaneously by the same fishing gear, it is advocated to maintain the levels of exploitation below the biologically optimal levels as determined by Y'/R analyses. It is therefore concluded that fishing effort and the sizes of the first capture of the two squid species in Trincomalee bay do not require adjustments through fishery regulations for the sustainability of their fisheries.

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