



Growth and mortality of the oceanic squid *Sthenoteuthis oualaniensis* (Lesson, 1830) off south-west coast of India

A. JOHN CHEMBIAN AND SALEENA MATHEW*

Chennai Base of Fishery Survey of India, Fishing Harbour Complex, Royapuram, Chennai - 600 013
Tamil Nadu, India

*School of Industrial Fisheries, Cochin University of Science and Technology, Fine Arts Avenue
Kochi - 682 016, Kerala, India

e-mail : johnchembian@yahoo.co.in

ABSTRACT

The study attempted to understand the difference in growth and mortality rate, between two phenotypic variants of the oceanic squid *Sthenoteuthis oualaniensis*. Specimens (1015 nos.) of the species collected off the south-west coast of India (lat. 07 to 11°N; long. 74 to 77° E) at a depth range of 180-2601 m were used in this study. Data on dorsal mantle length (DML) of dwarf and medium forms of the species were collected and analysed using the length-based FiSAT routine. L_{∞} varied from 17.37 to 18.05 cm with an average of 17.89 cm for the dwarf and 29.5 to 30.49 cm with an average of 30.08 cm for medium form. Dwarf forms had a higher average K value (3.65 cm y⁻¹) with π of 3.06, whereas, medium form had a lower average K value (2.38 cm y⁻¹) with π of 3.33. Growth curve and longevity study indicated longer than a year life span for medium forms (461 days) with growth rate of 13.3 cm DML in three months (91 days), 20.8 cm in six months (182 days) and 25.0 cm in nine months (273 days). Dwarf form attained maximum length in ten months (302 days) with a growth of 10.5 cm in three months (91 days), 14.9 cm in six months (182 days) and 16.7 cm DML in nine months (274 days). The average total instantaneous mortality (Z) was estimated as 4.58 y⁻¹ for dwarf and 6.03 y⁻¹ for medium form. As there was no commercial fishing for this species, fishing mortality was considered nil. Therefore, total mortality rate Z was considered equivalent to natural mortality.

Keywords: Dwarf form, Growth, Medium form, Mortality, Purple back squid, *Sthenoteuthis oualaniensis*

Introduction

Existing studies on the growth function of cephalopods are not consistent and mostly indicate exponential, linear and asymptotic phases, with or without seasonal oscillation (Miyahara *et al.*, 2006). However, the peculiar life history of squids and the impact of environment on its growth may prove otherwise. The linear or quasi-linear growth indicated in many studies may be attributed to the cephalopod paedomorphic life history (Yatsu, 2000) and the overestimation of its growth rate based on statolith ring (Hatfield, 2000). These rings are dark and proteinaceous, formed in response to feeding activity that often has a regular dial basis (Radtke, 1983). Therefore, factors such as temperature (Villanueva, 2000; Chung and Lu, 2005), age (Bettencourt and Guerra, 2001), body size (Hussy, 2008a), activity level, pH (Morris, 1991) and feeding level (Hussy, 2008b) are all known to influence the accretion process of statoliths and thereby its legibility. Besides, oxygen limitation also leads to blurred areas without rings towards the margins of the statoliths of older squid. Indeed, this may be the very reason why "linear" growth

curves often emerge from size at age data based on age readings presumed to be daily.

In addition to that, the elimination of many older specimens from the population due to strong post-spawning mortality also contributes to the postulation of the initial linear or log-linear segments of growth curves as the total growth curve of the squid. As a consequence, a serious underestimation of the real age (Pauly, 1998) and overestimation of the growth rate of the squid is done. Moreover, this is in contrast with the growth curves of cephalopods raised in captivity (Forsythe and Van Heukelem, 1987), where the increase in the growth rate mimic logarithmic growth during the juvenile phase of the squid, which then decline as it approaches asymptotic. However, this second phase is often not visible in wild, perhaps due to mortality and possibly due to paedomorphosis and the aging bias indicated earlier. The asymptotic growth model on the contrary, is an ideal prediction model for the growth, as it is the net result of a volume to surface relation (von Bertalanffy, 1951) and constructs the growth curve by length modal progression analyses (MPA). Verrill

(1882) first used this modal analysis method for estimating growth rates of cephalopods.

Mortality in this species is entirely by natural cause, due to the non-existence of directed fishing. Hence, natural mortality (N) is considered equivalent to total mortality rate (Z) *i.e.*, $Z = M$ (Sinclair, 2001). Predation is probably the most important cause for natural mortality as indicated by the prevalence of this species in the diet of many large fishes, marine mammals and many sea birds that forage within its habitat. Clarke (1983) estimated that sperm whales alone consume >100 million t of squid annually. Besides predation, squids meet one third of their maintenance food requirement by cannibalism. It is generally assumed that post-spawning mortality in cephalopods is very high and occurs due to flaccid mantle. Roper *et al.* (1984) also reported that many species die after spawning, but the phenomenon is apparently not universal.

In Indian waters, apart from a study on its phenotypic variants in the south-west coast of India (Chembian and Mathews, 2014) and a preliminary estimate by Mohamed *et al.* (2006), no published works are available on the growth and mortality of *Sthenoteuthis oualaniensis*. In view of the above facts, this study has been attempted through the available methods of the length based routine of FiSAT software.

Materials and methods

Specimens of *S. oualaniensis* were collected from the south-west coast of India (lat. 07 to 11° N; long. 74 to 77° E) in the depth range of 180-2601 m (Fig. 1)

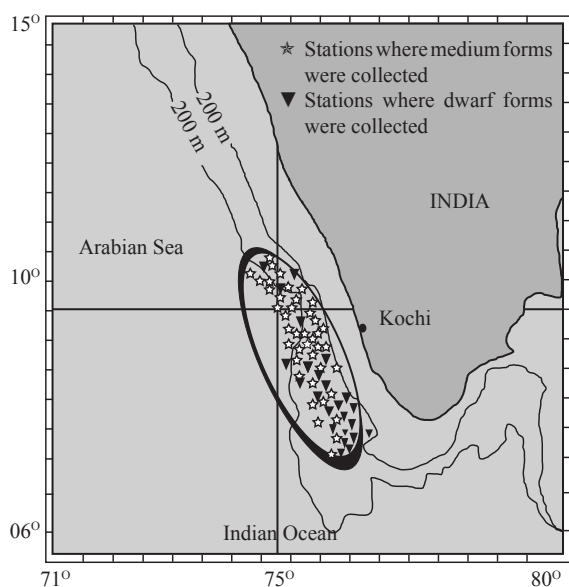


Fig. 1. Map of the south-west coast of India showing the oceanic squid sampling area during the study period.

during January 2007-December 2008. *Matsya Sugundhi* (31.5 m OAL, 245.8 GRT and 650 BHP), a long liner-cum-squid jigger of the Fishery Survey of India (FSI) and the 44-60 feet gill netters/tuna longliners of the Cochin based Colachal fishing fleet were the prime source for collection of samples. *Matsya Sugundhi* employed an automatic squid jigging machine, while the fishing boats employed handline with jigs to collect samples. No sampling was done during July, due to the 45 days fishing ban from June 15th to July 30th for mechanised fishing vessels, along the west coast of India.

A total of 1015 specimens were collected during the study. On the basis of the description provided by Nesis (1993), two forms of *S. oualaniensis* were identified from the samples, medium form with dorsal mantle length (DML) ranging from 9.8 to 27 cm and dwarf form with the DML in the range of 9.1 to 16.5 cm. Out of the 1015 specimens collected, 565 were of the medium and 450 were of the dwarf form. Specimens were thawed and measured for DML, from the tip of dorso-posterior end to the tip of the dorso-anterior end of the squid mantle. Measurements were made separately to the nearest millimeter for the dwarf and medium forms. Though *S. oualaniensis* are sexually dimorphic (Chembian and Mathews, 2014), with females growing larger than males, due to the poor representation of males in the sample, sex-wise analyses could not be done and only indicative study on the growth of the dwarf and medium forms were conducted with the available samples. In some of the months, sufficient samples could not be collected due to the non-availability of species in the fishing area. In view of that, data collected during 2007 and 2008 were merged month-wise to increase the sample strength for meaningful study. It was then analysed by length based software, FiSAT II, as has been done by Chakraborty *et al.* (2013) and Mehanna and El-Gammal (2010) on other cephalopod species.

The output of the monthly data analysed employing Bhattacharya's method (Bhattacharya, 1967) was saved as the "mean and standard deviation" file for further analyses in the FiSAT routine. The mean lengths of the components obtained were plotted against the sampling months and the mean lengths believed to be of the same cohort were linked to create growth increment file (GIN) and length at age file (LAA). As the linking process was highly subjective, previous knowledge on the growth pattern of the squid was helpful in performing the analysis. The GIN file created by linking of means was used as input for the Gulland and Holt, Munro's and Fabens routines of FiSAT to calculate the K value and the L_{∞} . The asymptotic length (L_{∞}) and Z/K ($Z = \text{total}$

mortality; K = growth coefficient) was estimated using the Powell-Wetherall method of FiSAT. The length at age (LAA) file was used as input in the FiSAT routine to study the age at length. Growth parameters were estimated using different methodology and compared to arrive at an acceptable mean value of these parameters separately for the dwarf and medium forms. The L_{∞} and the K value of the Gulland and Holt plot were taken as standard due to its proximity to the average and used as the input in the von Bertalanffy's growth equation

$$L_t = L_{\infty}(1 - \exp^{-k(t-t_0)})$$

The results were used to generate the VBGF plot of the FiSAT routine with the oscillation parameter (C) and winter point assumed to be 0 due to its tropical nature. Growth performance index (π) was computed using the equation (Pauly, 1984):

$$\pi = \log_{10}K + 2 \log_{10}L_{\infty}$$

and Longevity from the following equation:

$$t_{max} = t_0 + 3/K$$

where t_{max} is the approximate maximum age of the squid in a given population.

The total instantaneous mortality coefficient (Z) was estimated using length-converted catch curve analysis, Jones & van Zalinge plot, Beverton & Holt and Ault & Ehrhardt routine of the FiSAT software. However, for the dwarf form, the length-converted catch curve analysis was not applied for estimating Z due to insufficient data. As there was no commercial fishing done for this species, fishing mortality was considered nil. As a result, the total mortality rate Z was considered equivalent to natural mortality (M).

Results and discussion

Asymptotic length (L_{∞})

The L_{∞} of the dwarf form was estimated as 17.62 cm DML by the Powell - Wetherall method (Fig. 2a) with the cut-off length (L^1) ranging from 12.5 to 15.5 cm and mean $L - L^1$ (mean length – cut-off length) ranging from 0.5 - 1.21 cm. The regression equation for the dwarf was of $Y = 4.18 - 0.237 X$ with highly negatively correlated mean $L - L^1$ and L^1 ($r^2 = -1.00$). Medium form L_{∞} was 29.5 cm with L^1 ranging from 13.5 to 26.50 cm and mean $L - L^1$ ranging from 0.50 - 3.68 cm. Regression equation for the medium form was $Y = 7.04 - 0.239x$ with mean $L - L^1$ and the L^1 being highly negatively correlated similar to that of the dwarf form ($r^2 = -0.951$) (Fig 2b). L_{∞} arrived by other methods varied from 17.37 to 18.05 cm DML with the average of 17.89 cm for the dwarf and 29.65 to 30.49 cm with the average of 30.08 cm for medium form as stated in Table 1.

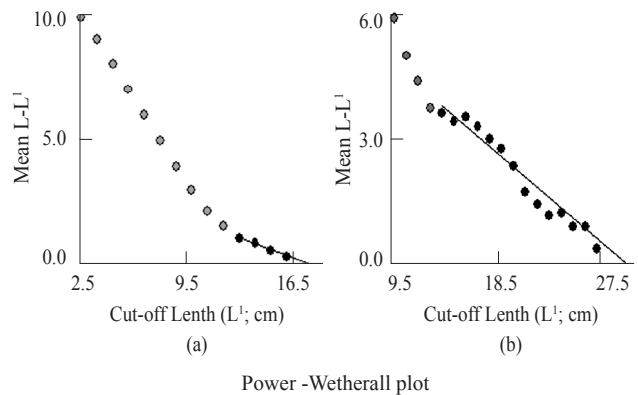


Fig. 2. L_{∞} estimation for *Sthenoteuthis oualaniensis* using (a) Dwarf form, (b) Medium form

Table 1. Growth parameters estimated for *Sthenoteuthis oualaniensis* of south-west coast of India

Forms	Parameters	Models					Average
		Powell Wetherall	Gulland and Holt	Faben	Munro	Analysis of length at age	
Dwarf	L_{∞} (cm)	17.62	18.05	18.05	18.37	17.37	17.89
	K year ⁻¹		3.48	4.07	3.24	3.82	3.65
	ϕ		3.05	3.12	3.04	3.06	3.06
	t_0		0.0	0.0	0.0	0.0	0.0
	t_{max} (days)			314	269	337	286
Medium	L_{∞} (cm)	29.50	30.2	30.2	29.65	30.49	30.08
	K year ⁻¹		2.33	2.68	2.35	2.19	2.38
	ϕ		3.33	3.39	3.3	3.3	3.33
	t_0		0.0	0.0	0.0	0.0	0.0
	t_{max} (days)			470	408	465	500

Results are in conformity with the previous results from Western Indian Ocean, wherein, the DML ranged from 9.0-18.0 (dwarf form) and 8.0-27.0 cm (medium form) (Trotsenko and Pinchukov, 1994). However, according to Nesis (1993), medium form had a maximum model size of 25 cm DML and dwarf with a maximum model size of only 15 cm DML. It was also suggested that the dwarf form could be a separate species and could be identified only as an adult (Xinjun *et al.*, 2007). Meanwhile, attempts were also made to describe these forms as separate species (Clarke, 1965; Wormuth, 1976). A study based on RAPD (Random Amplified Polymorphic DNA) analysis done also indicates large variations in biology among the groups (Xinjun *et al.*, 2007).

Growth parameters

Growth coefficient (K value) computed using various methods stated in the methodology indicated that dwarf and medium forms have different range of K values.

Dwarf form

The growth coefficient (K value) of the dwarf form was computed as 3.48 y^{-1} employing Gulland and Holt plot method with an L_{∞} of 18.05 cm DML. The computed K and L_{∞} values for the dwarf form by the Fabens and Munro methods were 4.07 y^{-1} , 18.05 and 3.24 y^{-1} and 18.37 respectively. The K and L_{∞} were also estimated with the length at age routine of FiSAT. This indicated a similar trend with K value as 3.82 y^{-1} and L_{∞} as 17.37 cm. The average L_{∞} of all the five methods was 17.89 cm and the average K value was 3.65 cm y^{-1} . The high growth rate of the species observed in this study is similar to that indicated by the other studies (Nesis, 1977; Zuev *et al.*, 1985; Xinjun *et al.*, 2007). Sparre and Venema (1996) indicated that higher K is related to the higher metabolic rate of the species. The metabolic rate is also a function of temperature and tropical species have higher K values than cold-water species. Growth performance index (π) ranged from 3.04-3.12 with an average of 3.06 and the t_{max} ranged from 269-337 days with an average of 302 days. The growth performance index (π) obtained from different methods were compared and it showed slight variation ranging from 3.04-3.12 for the dwarf form. The growth performance index of 2.58-3.28 calculated for *Loligo duvaucelii* by Mohamed (1996) off south-west coast of India and the present study are indications of the high growth rate in squid along the south-west coast of India.

The von Bertalanffy's growth equation of $L_t = 18.05 (1 - \exp[-3.48(t - t_0)])$ for dwarf and the VBGF plotted (Fig. 3) along with the Faben's growth curve (Fig. 4.) indicates that, dwarf form may attain L_{∞} in around ten months. This corroborate the results obtained from the

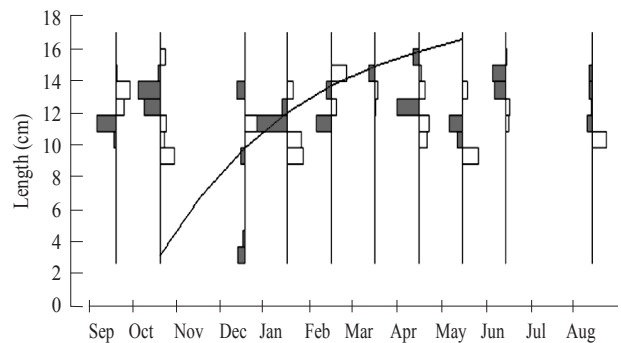


Fig. 3. von Bertalanffy growth curve for *S. oualaniensis* dwarf form with superimposed histograms. The dark and white bars are positive and negative deviations from the weighed model classes representing pseudo cohorts (Months have been rearranged to get the model curve)

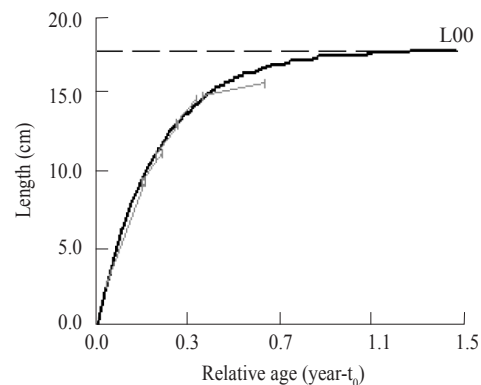


Fig. 4. Fabens growth curve for *S. oualaniensis* dwarf form

t_{max} method, where the average longevity obtained was of ten months (302 days) with the average K value of 3.48 y^{-1} . In total, longevity of the dwarf form varied from 269-337 days among the four methods applied (Table 1). Zuyev *et al.* (1985), noted that the growth parameters estimated through von Bertalanffy's growth equation for the small, early-maturing form of genus *Sthenoteuthis* indicates its life span to be 1 year. Other studies also support the view that *S. oualaniensis* had its life span less than 1 year (Nesis, 1993; Trotsenko and Pinchukov, 1994). However the study based on the gladius micro structure indicates that the duration of life cycle in the dwarf early-maturing equatorial form of *S. oualaniensis* was only about 6 months (Zuyev *et al.*, 2002).

From the growth curve it is evident that growth is faster in the first half of life when compared to the second half, as 75% of the growth is achieved in the first five months time. However, it takes another four months to achieve the remaining 25% of the growth indicating a slower growth rate in the later phase. Growth rate of the dwarf form computed from Gulland and Holt plot was 0.11 for the mean length of 6.34 cm, 0.061 for the mean

length of 10.61 cm, 0.058 for the mean length of 12.42 cm, 0.055 for the mean length of 14.55 and 0.011 for the mean length of 15.50 cm. This indicates a decreasing rate of growth from the juvenile to adult. Lipinsky and Roeleveld (1990) says that squid displays a form of asymptotic growth, well represented by the standard von Bertalanffy model with growth rates that declined linearly with length. It is estimated that dwarf grows approximately 10.5 cm in DML in three months (91 days), 14.9 cm in six months (182 days) and 16.7 cm in nine months (274 days). Zaidi bin Zakaria (2000) determined the age of the smallest oceanic squid *S. oualaniensis* of 10.7 cm as 102 day old. However, Zaidi bin Zakaria (2000) determined growth curves for both sexes and reported a female of 12.0 cm DML at 51 days of age. This suggests that environmental conditions such as temperature and food availability are the main factors influencing the growth rates, lifespan, and fluctuations of relative gonad investment.

Medium form

Growth coefficient of medium form was computed using Gulland and Holt plot as of 2.33 y^{-1} with the L_{∞} as 30.20 cm DML. Similarly, the K and L_{∞} value computed in Fabens and Munro methods for the medium form were 2.68 y^{-1} , 30.20 cm and 2.35 y^{-1} , 29.65 cm DML respectively. The K and L_{∞} computed using the length at age routine of the FiSAT were 2.19 y^{-1} and 30.49 cm DML. The average L_{∞} of all the five methods was 30.08 cm DML with the average K value of 2.38 y^{-1} from the four methods. Growth performance index (π) ranged from 3.3-3.39 with an average of 3.33 and the t_{max} ranged from 408-500 days among the four methods with an average of 461 days. The t_{max} was substantiated by the growth curve generated in the VBGF plot (Fig. 5) from the equation:

$$L_t = 30.2 (1 - \exp(-2.33 (t - t_0)))$$

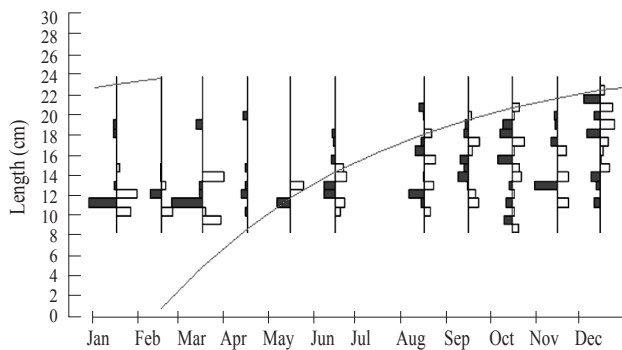


Fig. 5. von Bertalanffy growth curve for *S. oualaniensis* medium form with superimposed histograms. The dark and white bars are positive and negative deviations from the weighed model classes representing pseudo-cohorts

Fabens curve (Fig. 6.), indicated a slightly longer than a year life span for medium forms to attain L_{∞} . Zuyev *et al.* (1985) estimated the life span for the large, late-maturing form as 2 years using the von Bertalanffy growth equation. However, the study based on the gladius microstructure indicates that the duration of life cycle of middle-sized tropical, Red Sea and Arabian Sea forms are about 1 year (Zuyev *et al.*, 2002).

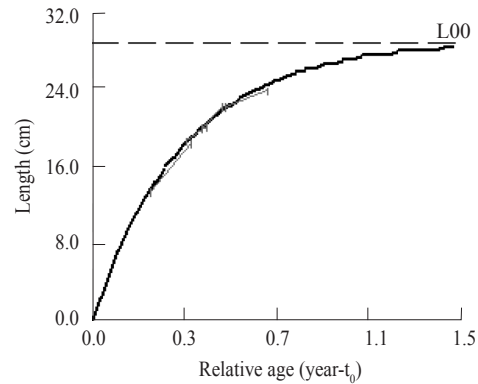


Fig. 6. Fabens growth curve for *S. oualaniensis* medium form

It is inferred from the growth curve that the growth is faster in the first half of the life when compared to the second half, as 63% of the growth is achieved in the first seven months time. However, it takes another seven months to achieve the remaining 37% of the growth indicating a slower later phase of growth. Medium form approximately grows to 13.3 cm DML in three months (91 days), 20.8 cm in six months (182 days) and 25.0 cm in nine months (273 days). Zaidi bin Zakaria (2000) estimated that female *S. oualaniensis* of 21.7 cm DML was 275 day old and male of 16.1 cm DML was 259 day old. Growth rate of the medium form computed from Gulland and Holt plot was 0.083 for the mean length of 16.89 cm, 0.068 for mean length of 20.32 cm, 0.057 for mean length of 22.23 cm and 0.029 for mean length of 24.13 cm. This indicates a decreasing rate of growth from the juvenile to adult.

Mortality parameters

The total instantaneous mortality (Z) of the dwarf form was estimated as of 4.010 y^{-1} (confidence interval of $Z = 3.445 - 4.57$; standard deviation of the slope = 0.131; $r = 0.99$) by the Jones and van Zalinge method (Fig. 7 and Table 2). However, Beverton & Holt and Ault and Ehrhardt methods estimated the same as 5.419 and 4.299 y^{-1} respectively. The average total mortality was computed as 4.57 y^{-1} .

In the medium form, total mortality coefficient (Z) was estimated as 6.80 y^{-1} using length-converted catch curve (Fig. 8) (confidence interval of $Z = 5.0-8.6$; standard

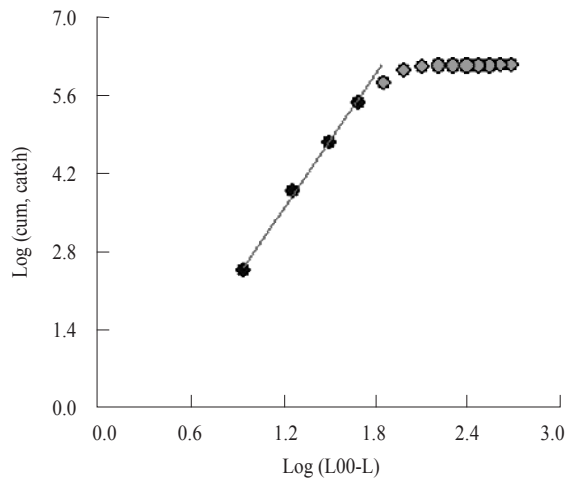


Fig. 7. Length based Jones and van Zalinga plot of *Sthenoteuthis oualaniensis* dwarf form for estimating total mortality

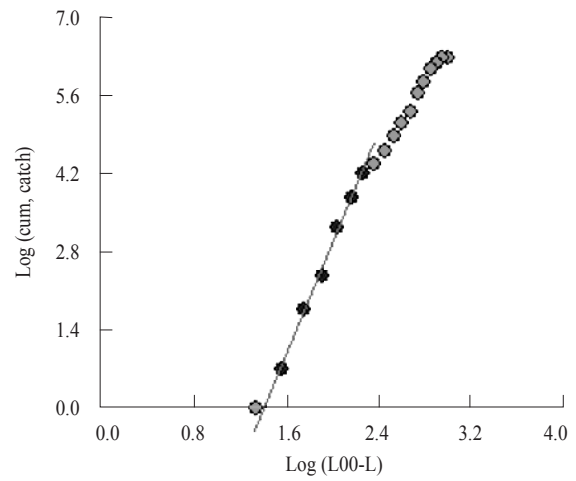


Fig. 9. Length based Jones and van Zalinga plot of *Sthenoteuthis oualaniensis* medium form for estimating total mortality

Table 2. Mortality parameters estimated for *Sthenoteuthis oualaniensis* of south-west coast of India

Forms	Parameters	Models					Average
		Powell Wetherall	Length converted catch curve	Jones & van Zalinge	Beverton & Holt	Ault & Ehrhardt	
Dwarf	Z/ year	-	-	4.010	5.419	4.299	4.576
	Z / K	3.215	-	-	-	-	-
Medium	Z/year	-	6.80	4.906	6.227	6.177	6.027
	Z / K	3.191	-	-	-	-	-

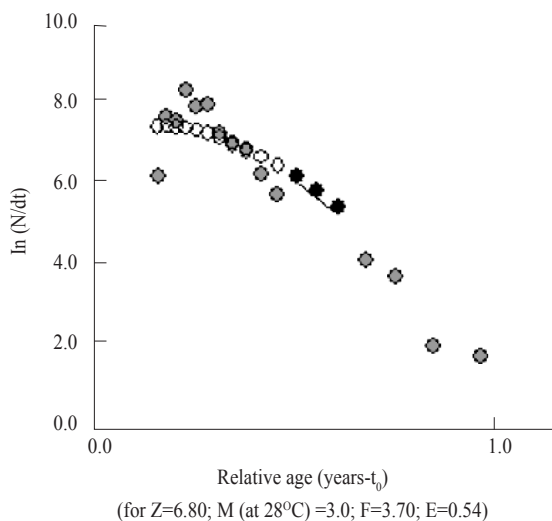


Fig. 8. Length converted catch curve of *Sthenoteuthis oualaniensis* medium form

deviation of the slope = 0.142; $r = 0.99$). While the total mortality coefficient computed by Jones and van Zalinge method (Fig. 9.) was 4.906 y^{-1} (confidence interval of $Z = 4.48\text{-}5.33$; standard deviation of the slope = 0.153;

$r = 0.99$) and by Beverton & Holt and Ault and Ehrhardt was 6.227 and 6.177 y^{-1} respectively. The average total mortality rate was 6.02 y^{-1} . High rate of mortality in the short-lived species such as squids are quite natural (Caddy, 1983). Meiyappan and Srinath (1989) reported the total mortality of the Indian squid *Loligo duvaucelli* as high as 10.6 y^{-1} at Cochin based on length converted catch curve method. The high mortality rate could be possibly due to faster growth, short life span, high level of cannibalism and possibly higher post-spawning mortality in *S. oualaniensis*.

From the present study it is evident that the growth, size and mortality parameters of the dwarf forms are clearly distinguishable from the medium forms of *S. oualaniensis* caught off the south-west coast of India.

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