Seasonal growth, stock-recruitment relationship and predictive yield of the Indian squid *Loligo duvauceli* (Orbigny) exploited off Karnataka coast

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ABSTRACT

A seasonally oscillating version of the von Bertalanffy growth function was fitted to explain growth in the Indian squid *Loligo duvauceli* (Orbigny) exploited from the Arabian Sea off Karnataka State. The parameters estimated were $L_\infty = 371$ mm; $K=1.4$ yr$^{-1}$; $C=0.5$ and $W_F=0.56$, considering that the $\Delta T$ ($5^\circ$C) in annual mean seawater temperature is sufficient to induce small but significant oscillations in the growth pattern. A retrospective analysis of the data on squid fishery for 1983-95 was done using length-structured virtual population analysis (VPA) and this indicated that the mean number of survivors was on an average 10 times more than the numbers caught. Further, nearly 6% of the stock died due to natural causes annually, Ricker's stock-recruitment curve could adequately ($R^2=0.45$) explain the variation in recruitment with respect to spawning stock biomass (SSB). The study indicated that squid SSB is a reasonably good predictor of its recruitment. Predictive yields were assessed using the Thompson and Bell model and it indicated an MSY level of 6,065 t and MSE of Rs. 270.3 million, while the present average catch (1990-94) amounted to 5,157 t valued at Rs. 234.9 million. The MSY and MSE can be attained by reducing trawl effort to 44% of the present effort.

Introduction

Cephalopods constitute about 4% of the total marine fish catch along the Karnataka coast, and of this more than 90% is comprised of the Indian squid *Loligo duvauceli* (Orbigny). Trawl is the principal gear used to exploit this neritic species. The trawl fishery along Karnataka coast is carried out by two types of fleets (Zacharia *et al.*, 1996), the single day fleet (SDF), which form the majority, consisting of small coastal trawlers and the multi-day (MDF) consisting of larger boats which undertake fishing trips up to seven days in depths ranging from 25 to 100 m. About 98% of the squid catch from Karnataka is realised by the MDF.

From the late 1980s the rapid development of MDF resulted in steep
increase in cephalopod catches in Karnataka (Mohamed and Nagaraja, 1997). So much so, cephalopods contribute a significant 26 % of the MDF fishery revenue at Mangalore port (Mohamed and Zacharia, 1996). During the early 1980s the annual average cephalopod catch in Karnataka was less than 500 tonnes (t), while presently it is more than 5,000 t. Such a steep increase (10 times) within a span of 15 years indicates the need for study and management of the resource.

Some aspects of the biology and fishery of *L. duvauceli* from Mangalore was studied by Rao (1988); later Mohamed (1993) reported on the spawning congregations and nonsemelparous reproduction of this squid along the Mangalore-Malpe coast. Recently, Mohamed (1996) fitted the generalised von Bertalanffy Growth Function (VBGF) and applied the yield per recruit (YPR) model to derive the maximum sustainable yield (MSY) for the Mangalore population of *L. duvauceli*. This study showed the need for regulation of the fishery by raising the age at first capture and reduction of the effort by 35 %. Considering that the YPR model is not a very appropriate one (all assumptions cannot be met) for tropical species, the present study was designed to apply the more pertinent length-based Thompson and Bell predictive model to the squid fishery of Karnataka coast. Further, a retrospective analysis of the fishery using virtual population analysis (VPA) technique was carried out and the relationship between spawning stock and recruitment of squids was examined in order to assess the productivity of the population in terms of recruitment.

**Materials and methods**

A multistage stratified random sampling design developed by the Central Marine Fisheries Research Institute (CMFRI), Cochin (Banerji and Chakraborty, 1972) was used for estimating the catch of squids and effort by trawlers (in fishing hours) in the State.

Biweekly observations were made from the principal fishing port at Mangalore in Karnataka (1983 to 1995). This port accounts for 25 to 50 % (average 35 %) of the State's squid catch (Fig. 1). On every observation day, the dorsal mantle length (DML) and weight of at least 50 squids of each sex were recorded. The length-frequency data from Mangalore was utilised to get estimates for Karnataka State. Although it is known that growth of male and female *L. duvauceli* is significantly different (Mohamed, 1996), pooled data were used for this study for the sake of ease and brevity and hence all estimates made here refer to an average for male and female squids. The length-weight relationship parameters used in the study were:

- \( a = 0.0025331 \)
- \( b = 2.10526 \)

For estimation of growth parameters, weighted (by catch) length-frequency data of *L. duvauceli* collected from Mangalore for the period 1990-'91 to 1993-'94 fishing seasons (4 seasons) was the basic input. The frequencies were grouped into 10 mm class intervals and later pooled monthwise. Age, growth and mortality parameters were worked out using the computer software FISAT (FAO-ICLARM Stock Assessment Tools; version 1.0; Gayanilo et al., 1996). With the growth and mortality parameters as input, the length structured virtual population analysis (VPA) was carried
out and later the same package was utilised to find the long-term predictive yield and biomass using the length-based Thompson and Bell analysis (Thompson and Bell, 1934).

**Analysis of data:** A rough estimate of the growth parameter \( (L_n) \) was initially made using the modified Wetherall plot (Wetherall et al., 1987). Based on this the automatic search routine and response surface analyses were run to get the best estimates of \( L_n \) and \( K \). This, however, resulted in poor goodness of fit and hence the modes in the size-frequency were separated using the Bhattacharya method (Bhattacharya, 1967) and then the modes were linked and the VBGF parameters were estimated using the Gulland and Holt plot (Gulland and Holt, 1959).

**Seasonal growth:** To further improve the growth parameters estimates, the seasonally oscillating version of VBGF of the following form was used as suggested by Pauly (1985).

\[
L = L_n \left[ 1 + \exp \left( - \frac{K}{C} \sin \left( \frac{2\pi}{2} \left( t - t^* \right) \right) \right) \right]
\]

where \( L_n, L_s, K \) and \( t^* \) are the same parameters as in the normal VBGF, \( C \) is a constant expressing the amplitude of growth oscillations and \( t^* \) is the onset of sinusoid oscillations with respect to \( t = 0 \). Seasonal oscillations in growth are caused by temperature fluctuations, and slight seasonal fluctuations of temperature such as that occurring in the tropics are sufficient to generate seasonally oscillating growth curves (Pauly, 1982). Along the Karnataka coast the mean monthly temperature range (unpublished data from hydrography records for Mangalore coast available at the RC of CMFRI, Mangalore) has a \( \Delta T \) (difference between the highest and lowest average mean monthly temperature to which the animals are exposed in the course of the year) of 5°C.

**Correction for gear selection:** Depending on the mesh size, the trawl gear allows the small sized squids to escape, and this affects the growth parameter estimates (by reducing \( K \) estimates). The length-frequency data can be corrected to take into account the squids that would have been caught had it not been for the effect of incomplete selection and/or recruitment (Pauly, 1987). The selection factors (\( L_{50}=77 \) mm, \( L_{75}=88 \) mm) were obtained from the catch curve. This approach was used here to estimate the approximate probabilities of capture, correct the length-frequencies, and re-estimate the growth parameters.

The \( L_n \) and \( K \) values thus obtained were used to estimate total mortality (\( Z \)), following the catch curve method.

Table 1: Stock-recruitment functions used in the study. All models were fitted by linear least squares regression on linearised equation

<table>
<thead>
<tr>
<th>Model</th>
<th>Equation</th>
<th>Linearised equation</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ricker</td>
<td>( R = S \exp(a - bS) )</td>
<td>( \ln(R/S) = \ln(a) - bS )</td>
</tr>
<tr>
<td>Beverton-Holt</td>
<td>( R = \frac{1}{a + bS} )</td>
<td>( 1/R = a + bS )</td>
</tr>
<tr>
<td>Simple Linear</td>
<td>( R = a + bS )</td>
<td></td>
</tr>
</tbody>
</table>
The natural mortality coefficient (M) was estimated by applying Pauly's (1980) empirical formula using 29.5°C as the temperature input. The fishing mortality coefficient (F) was estimated indirectly as the difference between Z and M, and directly from the length-structured VPA, based on the annual length-frequency data for the years 1983-95 and by using 5 as an estimate of F (terminal fishing mortality). This analysis provided estimates of mean annual F, F/Z, and length classwise fishing mortality.

**Stock-recruitment relationship:** Estimates of spawning stocks (S) and recruits (R) were derived from length-structured VPA. Considering that 110 mm was the mean size at first maturity for males and females (Rao, 1988; Mohamed, 1993), the population in a certain year above this size were regarded as spawners and the population below this size in the following year (t+1) were deemed as corresponding recruits. To relate recruitment to spawning stock, the Ricker (1954), Beverton and Holt (1975) and a simple linear model were fitted as stock-recruitment functions. The models and the equations used are given in Table 1.

**Results and discussion**

**Production and effort**

The average annual squid production from Karnataka State during 1983-95 was estimated as 2,900 t. Until 1986 commercial catches were low, much below the 1,000 t mark. From 1986 to the early nineties catches hovered between 1,000 and 3,000 t. In 1993 the squid catches increased steeply to cross 8,000 t and since then the catches dropped steadily and in 1995 it was a little more than 5,500 t (Fig. 1). The estimated fishing effort in actual trawling hours for the MDF in Karnataka showed rapid increase during the period. The average annual effort during the eighties was only 0.35 million hours, while in the nineties it quadrupled to 1.5 million hours. In 1994 the effort crossed the 2 million hr mark and increased further in 1995. Increase in MDF effort during the last few years has been particularly steep due to rapid rise in fleet strength at Mangalore and Malpe mainly because of the high rate of returns earned by the MDF boats (Zacharia et al., 1996).

**Age and growth**

The Wetherall Plot gave lower estimates of \( L_m \) than other methods (Table 2). After separation of modes using Bhattacharya method, fitting of the Gulland and Holt Plot resulted in low \( L_m \) and high K estimates. Using ELEFAN I with seasonality resulted in better estimate of \( L_m \), but low K value. These estimates were further improved by correcting the frequencies for gear selection. Analysis of the length-frequency data (size range: 30-340 mm DML) showed that the best fit (higher...
Population dynamics of Loligo duvauceli from Karnataka

...goodness of fit values) for $L_\infty$ and $K$ was obtained by adjusting the length frequencies for selection and by using the seasonally oscillating model of VBGF (Table 2). Pauly (1985) advocates use of VBGF model with seasonal oscillations as a means of standardising growth estimates for different squid species allowing comparative studies to be made. The WP (winter point) values obtained presently correspond to July when peak minimal temperatures occur along the southeastern Arabian Sea.

The restructured length-frequency data with growth curves fitted for $L_\infty = 371$, $K=1.4$, $C=0.5$ and $WP=0.56$ is shown in Fig. 2. The longevity of L. duvauceli as per these estimates is a little more than two years. The phi prime ($\phi'$) index for the above equation was 3.28. The age-length key using the above equation is given in Table 3. An earlier study (Mohamed, 1996) on growth of squids exploited from Mangalore indicated that females grew faster than males, but the latter reached larger ultimate sizes. Similar sex-wise differences in growth has also been noted by Meiyappan and Srinath (1989) and Meiyappan et al., (1993) in L. duvauceli exploited from the west coast of India. In this study, however, the length data of both males and females have been pooled and therefore the present estimates are an average for both sexes.

The use of a seasonally oscillating version of VBGF has not been reported earlier for any other tropical Indian marine species. Its use seems appropriate considering that between 12 and 15° latitude there exists a $\Delta T$ of 5°C in mean seawater temperature. This is sufficient to induce a small but significant oscillations in the growth patterns (Pauly, 1987).

**Mortality and exploitation**

The total mortality coefficient ($Z$) derived from catch curve analysis (annual mean = 6.31 ± 1.49) and VPA (annual mean = 5.74 ± 1.26) were almost identical, although the former gave higher estimates in most years (Table 4). Estimates derived from VPA were used for further analysis as this technique gives mortality values of smaller length classes more accurately. High mortality rates were observed in

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**Table 2. Results of length-frequency data analysis using FiSAT**

<table>
<thead>
<tr>
<th>$L_\infty$ (mm)</th>
<th>$K$ ($r^1$)</th>
<th>$C$ (Amplitude)</th>
<th>WP (Winter point)</th>
<th>Method</th>
</tr>
</thead>
<tbody>
<tr>
<td>376</td>
<td>1.25</td>
<td>--</td>
<td>--</td>
<td>ELEFAN I</td>
</tr>
<tr>
<td>368</td>
<td>1.32</td>
<td>--</td>
<td>--</td>
<td>Bhattacharya and G&amp;H plot</td>
</tr>
<tr>
<td>375</td>
<td>1.10</td>
<td>0.5</td>
<td>0.66</td>
<td>ELEFAN I with seasonality</td>
</tr>
<tr>
<td>371</td>
<td>1.40</td>
<td>0.5</td>
<td>0.66</td>
<td>After correction for gear selection</td>
</tr>
</tbody>
</table>

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**Table 3. Age-length key for Karnataka population of L. duvauceli**

<table>
<thead>
<tr>
<th>Age (years)</th>
<th>Length (mm)</th>
</tr>
</thead>
<tbody>
<tr>
<td>0.25</td>
<td>110</td>
</tr>
<tr>
<td>0.50</td>
<td>187</td>
</tr>
<tr>
<td>0.75</td>
<td>241</td>
</tr>
<tr>
<td>1.00</td>
<td>280</td>
</tr>
<tr>
<td>1.50</td>
<td>326</td>
</tr>
<tr>
<td>2.00</td>
<td>346</td>
</tr>
</tbody>
</table>
TABLE 4. Estimated mortality rates for Karnataka population of L. duvauceli

<table>
<thead>
<tr>
<th>Year</th>
<th>Mean Z (from VPA using M constant at 2.149)</th>
<th>Z (from catch curve)</th>
<th>Mean F</th>
<th>Exploitation rate (F/Z=E)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1983</td>
<td>7.101</td>
<td>7.80</td>
<td>4.952</td>
<td>0.70</td>
</tr>
<tr>
<td>1984</td>
<td>2.586</td>
<td>2.54</td>
<td>0.437</td>
<td>0.17</td>
</tr>
<tr>
<td>1985</td>
<td>6.491</td>
<td>7.19</td>
<td>4.342</td>
<td>0.67</td>
</tr>
<tr>
<td>1986</td>
<td>5.898</td>
<td>6.84</td>
<td>3.749</td>
<td>0.64</td>
</tr>
<tr>
<td>1987</td>
<td>7.577</td>
<td>8.41</td>
<td>5.425</td>
<td>0.72</td>
</tr>
<tr>
<td>1988</td>
<td>7.420</td>
<td>8.25</td>
<td>5.271</td>
<td>0.71</td>
</tr>
<tr>
<td>1989</td>
<td>5.534</td>
<td>6.15</td>
<td>3.358</td>
<td>0.61</td>
</tr>
<tr>
<td>1990</td>
<td>5.676</td>
<td>6.46</td>
<td>3.527</td>
<td>0.62</td>
</tr>
<tr>
<td>1991</td>
<td>4.404</td>
<td>5.05</td>
<td>2.255</td>
<td>0.51</td>
</tr>
<tr>
<td>1992</td>
<td>5.288</td>
<td>5.56</td>
<td>3.139</td>
<td>0.59</td>
</tr>
<tr>
<td>1993</td>
<td>5.552</td>
<td>5.58</td>
<td>3.403</td>
<td>0.61</td>
</tr>
<tr>
<td>1994</td>
<td>5.648</td>
<td>6.81</td>
<td>3.499</td>
<td>0.62</td>
</tr>
<tr>
<td>1995</td>
<td>5.671</td>
<td>5.30</td>
<td>3.322</td>
<td>0.61</td>
</tr>
</tbody>
</table>

1983, 1985, 1987 and 1988. High Z values were also observed by Mohamed (1996) for Mangalore population of L. duvauceli during 1987-88 after which the mortality rates decreased. After 1991, Z values appeared to have stabilised around 5. The lowest Z value was observed in 1984 when catch and effort were also low.

The natural mortality coefficient (M) was estimated as 2.149 at a mean annual sea water temperature of 29.5°C. Using M as a constant over the years, the F value varied from 0.44 in 1984 to 5.43 in 1987 with mean F at 3.593 ± 1.26 (Table 4). The exploitation ratio (E) varied from 0.17 in 1984 to more than 0.7 in 1993, 1987 and 1988. During the other years the E was near the mean E value of 0.63 which is above the E_in of 0.5.

A plot of annual mean length on F showed that the parameters were significantly inversely correlated (Fig. 3, inset). The relationship ($R^2 = 0.89$) indicated indirectly the robustness of the estimated F values. The mean length varied between 99 mm in 1987 and 158 mm in 1984 when the mean F values were the highest and the lowest respectively. After 1992 the mean length appeared to stabilise around 110-115 mm which is close to the mean size at first maturity (110 mm). Thus at least 50 % of the squids would appear to have an opportunity to reproduce.

**Virtual population analysis**

The length-structured VPA is a powerful tool for stock assessment by which the size of each cohort is estimated along with the annual mortality caused by fishing. The technique picturises the past situation by estimating more precisely the mortality of smaller length classes. VPA results indicated that maximum number of squids are caught between 85 and 165 mm with values of F exceeding 8 in the mid-length 135 mm. Another peak of F is observed at 285 and 295 mm mid-lengths in some years. This is probably due to the heavy virtual population analysis

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![Fig. 3. Annual mean lengths of Loligo duvauceli and estimated F per year. Inset shows relationship between F and mean length ($R^2 = 0.89$).](image-url)
exploitation of large squids during September-October period of some years (Mohamed, 1993).

Results of the retrospective assessment of squid population of Karnataka using VPA is shown in Fig. 4. Squid stock numbers in the sea were very low in 1983 and 1985 and very high from 1993. The numbers caught and survivors showed a dramatic increase in 1993 and thereafter remained at reasonably high levels indicating a declining trend. The numbers dying naturally were more than 90 million in 1993 and on an average they represented nearly 6 % of the total stock except in 1984 when it was 8 %. The mean number of survivors was on an average 10 times more than the numbers caught. In 1984, the natural mortality was much larger than the estimated F (Table 4) and consequently the number of natural deaths was much larger than catches. From 1988 there has been a slow but steady increase in the squid spawning stock biomass (Fig. 5) and this could explain the increased abundance of squid stocks in the 90's. Besides, large scale spawning congregations of squids were reported in some areas off Karnataka coast during 1990 and 1991 (Mohamed, 1993) and this would have helped to increase the squid stocks in subsequent years.

Stock-recruitment relationship

The relationship between spawning stock biomass (SSB) and recruitment (R) is highly variable, but is a central problem of fish population dynamics, since it represents nature's regulation of population size. One of the chief goals of fisheries management is that recruitment over fishing must be prevented and adequate spawning stock be maintained to ensure future productivity of the stock.

Annual estimates of squid spawning stock biomass and recruits in the following year are shown in Fig. 5. The mean SSB was very variable, at 64.4±103.1 million numbers and the mean recruitment level was 506.4±461.1 million. Except for 1984 when an unusually high level of SSB did not result in a correspondingly high number of recruits, the levels of squid SSB and R in the subse-
quent year followed a close trend. This indicates that squid SSB is a reasonably good predictor of its recruitment. The causes for the recruitment failure in 1984 are not clear but they may be attributed to environmental effects or ecological competitors.

The S-R plot for Karnataka squid population is shown in Fig. 6. The year 1992 showed high levels of recruitment at reasonably low levels of SSB while in 1991 and 1984, low levels of R at high SSB levels were seen. This could be due to density-dependent mortality. However, the years 1993 and 1994 showed high levels of recruitment at high levels of SSB. The S-R relationships (Table 5) using both the Beverton-Holt model and the simple linear model showed poor goodness of fit ($R^2 = 0.1$). In the B-H model which is an asymptotic curve, squid recruitment number appeared to be independent of SSB over a very wide range of stock sizes. The reproductive curve that applies for the squid population of Karnataka appears to be of the Ricker type ($R^2 = 0.45$). Using the Ricker curve, the replacement size of the parental generation was 303 million and the SSB which produces maximum recruits was 120 million. This indicates that the management of the squid stock in Karnataka should aim at a target SSB near 120 million if maximising the yield is the goal.

S-R models are normally used as part of an age-structured assessment of fish populations in temperate waters. However, it is generally agreed that the S-R relationships in tropical stocks are also similar (Murphy, 1982). Indeed, in annual squid species in which adults spawn only once and the following year's stocks will consist almost entirely of new recruits, the S-R relationships, however, weak provide the only means of predicting stock sizes from previous years data (Pierce and Guerra, 1994). Assessment of the Todarodes pacificus fishery in the Sea of Japan has been attempted based on S-R relationship with considerable success (Okutani and Watanabe, 1983). The present results indicate that the Ricker model can reasonably explain the squid recruitment in the Arabian Sea off Karnataka. After high levels of SSB and R in 1992 and 1993 (Fig. 5), they dropped in 1994 and this has reflected in the squid catch of 1995 (Fig. 1) and 1996 (4,017 t, not shown in Fig.).

Fig. 6. Relationship between squid SSB and R using linear, Ricker and Beverton-Holt models.

<table>
<thead>
<tr>
<th>Model</th>
<th>Equation</th>
<th>Goodness of fit ($R^2$)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Beverton-Holt</td>
<td>$R = 1(2.24E-03 + 2.55E-05/S)$</td>
<td>0.11</td>
</tr>
<tr>
<td>Ricker</td>
<td>$R = S \exp 2.5311 (1-S/303.25)$</td>
<td>0.45</td>
</tr>
<tr>
<td>Simple Linear</td>
<td>$R = 345.034 + 1.239 S$</td>
<td>0.10</td>
</tr>
</tbody>
</table>
Predictive yield of squids

Unlike VPA and cohort analysis which analyse the history of a fishery, prediction models like the Thompson and Bell model (1934) can be used to predict the future yields and biomass at different levels of fishing effort. The ultimate aim in using such models is to provide those agencies responsible for the management of fishery resources with information on the biological and/or economical effect of fishing on the stock (Sparre and Venema, 1992).

Using the length-based Thompson and Bell model the annual MSY for squids exploited from Karnataka was estimated as 6,059 t at an \( F_{\text{key}} \) of 0.44 times the present \( F \) (Fig. 7). The MSE was determined as Rs. 270.3 million at 0.44 \( F \). The biomass MSY and MSE were similar at 2,599 t. However, the average catch (1990-'94 period) amounted to 5,157 t which was about 900 t less than the MSY. Similarly, the average value of the catch was Rs. 234.9 million which was Rs. 35.4 million less than the MSE. Such a scenario indicates that a 56 \% decrease in trawl effort could increase the rate of *L. duvauceli* catch in Karnataka by 17 \% and value by a significant 16 \%. The earlier study using the YPR model (Mohamed, 1996) also advocated decrease in effort by 35 \% and mesh size of trawl net by 58 \%. Further, Meiyappan *et al.* (1993) based on data from west coast of India for 1984-'89 and using Thompson and Bell model suggested maintaining the effort at the 1989 level throughout the west coast of India. Among various long-term fishery management measures generally used such as mesh size regulations, size limits, seasonal area closures and effort limitation, Rosenberg *et al.*, (1990) suggest that the most effective means of managing squid fisheries is by regulating fishing effort.

It is very difficult at present to set out clear management options based on the VPA, S-R plot and Thompson and Bell model as the trawl fishery in Karnataka is multispecies in character and squid is only one of the components, albeit major. Moreover the trawl fishery is very dynamic in nature particularly with year to year expansion in trawling grounds and decreasing mesh sizes (Zacharia *et al.*, 1996). Nonetheless a reduction in trawl fishing effort is warranted as the past studies and the present one also indicate such a necessity. Further, considering that squids are an important revenue earner for the multiday trawl fleet in Karnataka any decrease in effort could significantly boost per boat profits.

Acknowledgments

We are grateful to Mr. D. Nagaraja for technical and field assistance. We are thankful to M/s. C. Muthiah,
K.K. Sukumaran, P.U. Zacharia, M. Srinath and T.V. Sathianandan of CMFR Institute for critical comments and statistical help. Data on seawater temperatures were provided by G.S. Bhat, RC of CMFRI, Managalore. We also thank the Director, CMFRI, Cochin for facilities and encouragement.

References


