Population Dynamics of Hilsa Shad (*Tenualosa ilisha*, Clupeidae) in Bangladesh Waters

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Abstract

The hilsa shad (*Tenualosa ilisha*, Clupeidae) is an important migratory species in the Indo-Pak subcontinent and the Persian Gulf region, especially in Bangladesh and India. The population dynamics of the species collected from river and marine environments were studied using length-based methods. The estimated von Bertalanffy growth parameters, \(L_\infty\) and \(K\) were 588 mm and 0.82 yr\(^{-1}\) for river and 610 mm and 0.80 yr\(^{-1}\), for marine populations, respectively. Growth performance indices (\(\phi\)) were 3.45 for the river and 3.47 for the marine populations. The estimated \(Z\), \(M\) and \(F\) values were 2.38, 1.00 and 1.38 and 2.30, 0.98 and 1.32 yr\(^{-1}\), for river and marine environments, respectively. Optimum length of hilsa at first capture (\(L_c = L_{50}\)) was 329 mm TL, and the optimum mesh size for gillnets was 80 mm. The recruitment patterns for both river and marine populations were more or less continuous, but with two major pulses. Present exploitation levels for the hilsa fishery in the river and marine habitats were 0.58 and 0.57, respectively. The hilsa populations in the rivers exhibit tendencies towards overexploitation.

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Introduction

Length-based methods (Munro 1983; Morgan 1984; Pauly 1984a; Sparre et al. 1989; Venema and van Zalinge 1989) are being increasingly used in tropical fish stock assessment, both where age information is unavailable (Morgan 1987), and also where age data can be easily collected. The rationale behind the latter is that the assessment based on easily collected length composition samples is more cost effective than those based on more tedious and time-consuming methods of fish ageing from hard structures (Morgan 1987).

The hilsa shad, *Tenualosa ilisha* (clupeid, commonly known as hilsa) is an important migratory alosine species in the Indo-Pak subcontinent and the Persian Gulf region, especially in Bangladesh and India. Bangladesh shares about 87% of the world catch (223,177 t) of the species and India about 7% (Rahman 2001). The species is an extremely popular food fish for the people of Bangladesh where it contributes about 20% of the country’s total fish production of $1.2 \times 10^6$ t (Rahman 2001). Some preliminary work on the population dynamics of hilsa based on length-frequency data were conducted in Bangladesh waters by BOBP (1987), BFRI/RS (1994), Miah et al. (1997), Rahman et al. (1999) and Rahman et al. (2000). Gupta (1989) used length-frequency distribution to study growth and mortality of hilsa population in Indian waters. However, no studies corrected the length-frequency for the gear selectivity nor validated the results by length-at-age data, so understanding of the population dynamics remains problematic and a more comprehensive study in this important field is urgently needed. The present study on the dynamics of the hilsa stocks was run in parallel with work on stock discrimination and ageing of the species (Rahman 2001). The aim of this paper is to overcome some of the limitations of the previous studies. This allowed comparison of age and growth data determined from hard structures for improving the analysis and interpretation of length-based methods.

Materials and Methods

Sampling

Two sets of length-frequency data for hilsa were collected from Bangladesh waters. One sample was representative of river hilsa and the
other representative of the marine population. Approximately 200 adult hilsa were randomly selected from commercial gillnet catches from each of the environments each month in 1998 and measured (TL, mm). As the samples were caught by gillnets, the bias due to the gear were corrected using probability of capture (Gayanilo et al. 1996). To estimate the probability of capture, 400 specimens were collected from each of 76, 102 and 127 mm mesh nets and measured (Table 1) to test selectivity of different mesh sizes. These three mesh sizes were selected for analysis because, they are the sizes mostly used in commercial fishery.

Table 1. Length-frequency distribution of hilsa shad (*Tenualosa ilisha*) captured by three different meshed gillnets in Bangladesh waters

<table>
<thead>
<tr>
<th>Class midlength (TL in mm)</th>
<th>Catch in number by each mesh size</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>76 mm</td>
</tr>
<tr>
<td>270</td>
<td>3</td>
</tr>
<tr>
<td>290</td>
<td>8</td>
</tr>
<tr>
<td>310</td>
<td>35</td>
</tr>
<tr>
<td>330</td>
<td>80</td>
</tr>
<tr>
<td>350</td>
<td>93</td>
</tr>
<tr>
<td>370</td>
<td>84</td>
</tr>
<tr>
<td>390</td>
<td>45</td>
</tr>
<tr>
<td>410</td>
<td>24</td>
</tr>
<tr>
<td>430</td>
<td>10</td>
</tr>
<tr>
<td>450</td>
<td>11</td>
</tr>
<tr>
<td>470</td>
<td>3</td>
</tr>
<tr>
<td>490</td>
<td>3</td>
</tr>
<tr>
<td>510</td>
<td>1</td>
</tr>
<tr>
<td>530</td>
<td></td>
</tr>
<tr>
<td>550</td>
<td></td>
</tr>
<tr>
<td>570</td>
<td></td>
</tr>
<tr>
<td>590</td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>400</td>
</tr>
</tbody>
</table>

* One data was missing

Gillnet selectivity

Using the length-frequency distribution of hilsa caught by the three gillnets (Table 1), the probability of capture was estimated applying equations 1 and 2 (Baranov and Holt method) (Sparre et al. 1989; Gayanilo et al. 1996; Braimah 2001).

\[
P_A, L = \exp \left[-\frac{(L - L_A)^2}{2 s^2}\right] \quad \text{(equation 1)}
\]

\[
P_B, L = \exp \left[-\frac{(L - L_B)^2}{2 s^2}\right] \quad \text{(equation 2)}
\]
where, \( L \) = total length of hilsa (TL, mm) for which probability of capture to be estimated; \( P_A \) = probability of capture of hilsa of size \( L \), by the smaller meshed gillnet (\( m_A \), e.g. 76 mm meshed net); \( P_B \) = probability of capture of hilsa of size \( L \), by the larger meshed gillnet (\( m_B \), e.g. 102 mm meshed net); \( L_A \) = optimum length of hilsa for capture by the smaller meshed gillnet; \( L_B \) = optimum length of hilsa for capture by the larger meshed gillnet; \( s \) = common standard deviation assumed equal for both mesh sizes.

The \( L_A \) and \( L_B \) (the optimum length for mesh sizes \( m_A \) and \( m_B \), respectively) were estimated by equations 3 and 4:

\[
L_A = SF \times m_A \quad \text{(equation 3)}
\]

\[
L_B = SF \times m_B \quad \text{(equation 4)}
\]

where \( SF \) is the selection factor computed from equation 5:

\[
SF = \frac{-2a}{b(m_A + m_B)} \quad \text{(equation 5)}
\]

where \( a \) & \( b \) are the intercept and slope of the regression equation 6:

\[
\ln \left( \frac{C_iB}{C_iA} \right) = a + b L_i \quad \text{(equation 6)}
\]

where the index ‘\( i \)’ denotes length classes, and \( C_iA \) and \( C_iB \) are the observed catches (in numbers) for class \( i \) of gillnets \( A \) (smaller meshed one) and \( B \) (larger meshed one), respectively.

Finally, the standard deviation (\( s \)) was computed from equation 7:

\[
s = \left[ \frac{2a (m_A - m_B)}{b (m_A + m_B)} \right]^{0.5} \quad \text{(equation 7)}
\]

where, \( a \) & \( b \) are the intercept and slope of the regression equation 6.

To estimate the probability of capture using the three mesh sizes together (Holt’s method for multiple mesh sizes), an overall selection factor and a common standard deviation were obtained from the results of each pair of successive mesh sizes, following the same procedures as for the two mesh sizes described above (Sparre et al. 1989).

\[
-2 \frac{a_i}{b_i} = SF \times m_i + m_{i+1} \quad \text{(equation 8)}
\]

where, \( y_i = -2 \frac{a_i}{b_i} \) is the dependent variable and \( m_i + m_{i+1} \) is the independent variable and the slope then becomes the selection factor (\( SF \)). The optimum length for mesh size \( i \) was finally obtained from equation 9:
\[ L_{mi} = SF \times m_i \]  

(equation 9)

The overall standard deviation was obtained by taking the mean of the standard deviation estimated from mesh pair comparisons (Braimah 2001); and finally the overall probability of capture of hilsa using multi-meshed gillnets were obtained from equation 10:

\[ P = \exp \left[ - \frac{(L - L_{mi})^2}{(2 \sigma^2)} \right] \]  

(equation 10)

where \( \sigma \) was the overall standard deviation.

**Growth parameters**

To estimate growth parameters, the von Bertalanffy growth equation was used, which expresses the length, \( L \) as a function of age of the fish, \( t \), in the form (equation 11):

\[ L_t = L_\infty [1 - e^{(-K(t-t_0))}] \]  

(equation 11)

where \( L_\infty \) is the mean length of infinitely old fish (asymptotic length), \( K \) is a curvature parameter, which determines how fast the fish approaches \( L_\infty \), and \( t_0 \) (sometimes called the initial condition parameter), determines the point in time when the fish has zero length.

The asymptotic length \( (L_\infty) \) and growth constant \( (K) \) were estimated by the ELEFAN I (electronic length-frequency analysis) routine of the FiSAT (FAO-ICLARM Stock Assessment Tools) package (Gayanilo et al. 1996) that was applied on the length frequency distributions of the catches.

Having estimated the growth parameters, the growth performance index ‘Munro’s phi prime (\( \phi' \))’ (Munro and Pauly 1983; Pauly and Munro 1984) was estimated using equation 12:

\[ \phi' = \log K + 2 \log L_\infty \]  

(equation 12)

where, \( K \) and \( L_\infty \) were the same as in equation 11.

The estimated growth parameters were tested for reliability by comparing the estimated \( \phi' \) values.

**Mortality and exploitation**

Total mortality \( (Z) \) was estimated using the linearised length-converted catch curve method as provided in the FiSAT package (Gayanilo et al. 1996), with the von Bertalanffy growth parameters as input data. This model is discussed in Pauly (1983b; 1984b; 1984c). The slope \( (b) \) of the
curve is \(-Z\). Thus, from the length frequency data, together with the estimated growth parameters, \(K\) and \(L_\infty\), the total mortality, \(Z\) was estimated.

The natural mortality (\(M\)) was estimated using Pauly’s empirical formula (equation 13) based on growth parameters (\(L_\infty\) and \(K\)) and mean annual temperature (\(T = 26^\circ\text{C}\)).

\[
\ln M = -0.0152 - 0.279 \ln L_\infty + 0.6543 \ln K + 0.463 \ln T \quad \text{(equation 13)}
\]

Pauly (1983a) suggested a correction factor for clupeids or other schooling fish by multiplying the estimated \(M\) by 0.8, so that for schooling species the estimate becomes 20% lower. Therefore, the final estimate \(M\) was obtained after correcting by the schooling factor.

Taking the estimated \(Z\) and \(M\), the fishing mortality, \(F\) was estimated as \(F = Z - M\) and the exploitation level, \(E\) as \(E = F/Z\).

**Recruitment pattern and relative yield per recruit (\(Y'/R\))**

The recruitment pattern was determined by plotting the number of recruits in each month using the corrected length-frequency data in FiSAT. This routine of FiSAT reconstructs the recruitment pulses from a time series of length-frequency data to determine the number of recruitment pulses per year and the relative strength of each pulse. The relative yield per recruit (\(Y'/R\)) used in the analysis is based on the Beverton and Holt model, as modified by Pauly and Soriano (1986). The model produces a \(Y'/R\) vs \(E (=F/Z)\) and a relative biomass per recruit (\(B'/R\)) vs \(E\), from which \(E_{\text{max}}\) (exploitation rate which produces maximum yield), \(E_{0.1}\) (exploitation rate at which the marginal increase of \(Y'/R\) is 1/10th of its value at \(E=0\)) and \(E_{0.5}\) (value of \(E\) under which the stock has been reduced to 50% of its unexploited biomass) are also estimated.

**Results**

**Gillnet selectivity**

The standard deviations (\(s\)), selection factors (\(SF\)) and optimum lengths of fish estimated from the pair-wise and multiple comparisons are shown in table 2. The mean optimum length and mean selection factors obtained from the pair-wise comparison gave similar results to those from the multiple comparisons (Table 2). The plots of probability of capture
against lengths for all mesh sizes showed three different selection ranges and formed typical bell-shaped curves (Fig. 1).

Table 2. Regression parameters ($a$ & $b$), standard deviation ($s$), selection factor ($SF$) and Optimum length ($L_{mi}$) estimated from the gillnets selectivity studies of hilsa shad ($Tenualosa ilisha$)

<table>
<thead>
<tr>
<th>Comparison</th>
<th>Parameters estimated</th>
<th>Optimum length (TL mm) for each mesh size</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>$a$</td>
<td>$b$</td>
</tr>
<tr>
<td>Pair of comparison</td>
<td></td>
<td></td>
</tr>
<tr>
<td>76 and 102 mm mesh</td>
<td>-5.570</td>
<td>0.015</td>
</tr>
<tr>
<td>76 and 127 mm mesh</td>
<td>-10.510</td>
<td>0.025</td>
</tr>
<tr>
<td>102 and 127 mm mesh</td>
<td>-6.380</td>
<td>0.014</td>
</tr>
<tr>
<td>Mean</td>
<td>-7.487</td>
<td>0.018</td>
</tr>
<tr>
<td>Multiple comparison</td>
<td></td>
<td></td>
</tr>
<tr>
<td>76, 102 and 127 mm mesh</td>
<td>0</td>
<td>4.082</td>
</tr>
</tbody>
</table>

Fig. 1. Selection curves for gillnets of hilsa shad ($Tenualosa ilisha$) fishery in Bangladesh.

Finally, a relationship between the optimum length of hilsa and mesh size of gillnets was established and described by

$$L_{mi} = 17.36 + 3.92 \, m$$

where, $L_{mi}$ is the optimum length (TL in mm) of hilsa to be caught by the gillnets with mesh size, $m$ (mm).
From this relationship, the optimum mesh size to catch a particular size of hilsa (e.g. size at first capture) can be calculated and vice versa.

**Growth**

The estimated von Bertalanffy growth parameters, $L_\infty$ and $K$ were 588 mm and 0.82 yr$^{-1}$ for rivers and 610 mm and 0.80 yr$^{-1}$, for marine population, respectively (Table 3). The growth curves superimposed on the length-frequency samples are presented in figure 2. Although the asymptotic length for marine population was found to be slightly longer than that of river populations, the resultant growth curves showed little difference between the environments. The growth performance index ($\phi'$) were 3.45 for the river and 3.47 for the marine population (Table 3).

Table 3. Growth parameters, mortality parameters, exploitation levels and optimum lengths at first capture ($L_c$) of hilsa shad (*Tenualosa ilisha*) population in Bangladesh

<table>
<thead>
<tr>
<th>Parameters estimated</th>
<th>Hilsa population</th>
<th>Marine</th>
<th>Mean</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Growth parameters</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Asymptotic total length, $L_\infty$ (mm)</td>
<td>588</td>
<td>610</td>
<td>599</td>
</tr>
<tr>
<td>Curvature parameter, $K$ (yr$^{-1}$)</td>
<td>0.82</td>
<td>0.80</td>
<td>0.81</td>
</tr>
<tr>
<td>Growth performance index, $\phi'$</td>
<td>3.45</td>
<td>3.47</td>
<td>3.46</td>
</tr>
<tr>
<td><strong>Mortality parameters</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total mortality, $Z$ (yr$^{-1}$)</td>
<td>2.38</td>
<td>2.30</td>
<td>2.34</td>
</tr>
<tr>
<td>Natural mortality, $M$ (yr$^{-1}$)</td>
<td>1.00</td>
<td>0.98</td>
<td>0.99</td>
</tr>
<tr>
<td>Fishing mortality, $F$ (yr$^{-1}$)</td>
<td>1.38</td>
<td>1.32</td>
<td>1.35</td>
</tr>
<tr>
<td><strong>Exploitation level, $E$</strong></td>
<td>0.58</td>
<td>0.57</td>
<td>0.58</td>
</tr>
<tr>
<td>$E_{\text{max}}$</td>
<td>0.61</td>
<td>0.65</td>
<td>0.63</td>
</tr>
<tr>
<td>$E_{0.1}$</td>
<td>0.55</td>
<td>0.62</td>
<td>0.59</td>
</tr>
<tr>
<td>$E_{0.5}$</td>
<td>0.36</td>
<td>0.36</td>
<td>0.36</td>
</tr>
<tr>
<td><strong>Probability of capture</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>$L_{25}$ (TL in mm)</td>
<td>309</td>
<td>324</td>
<td>317</td>
</tr>
<tr>
<td>$L_{50}$ (= $L_c$) (TL in mm)</td>
<td>322</td>
<td>335</td>
<td>329</td>
</tr>
<tr>
<td>$L_{75}$ (TL in mm)</td>
<td>332</td>
<td>344</td>
<td>338</td>
</tr>
<tr>
<td><strong>Optimum mesh size (mm) to catch $L_{50}$ (= $L_c$)</strong></td>
<td>78.0</td>
<td>81.0</td>
<td>80.0</td>
</tr>
</tbody>
</table>

**Mortality**

The estimated $Z$, $M$ and $F$ values were 2.38, 1.00 and 1.38, and 2.30, 0.98 and 1.32 yr$^{-1}$, for river and marine environments, respectively (Table 3). The linearised length converted catch curve analysis to estimate total mortality, $Z$ is presented in figure 3. No remarkable differences were found among the mortality parameters between the samples. However, the fishing mortality for the river population was higher than that of marine population (Table 3).
Fig. 2. Growth curves superimposed on the length-frequency distribution of hilsa shad (*Tenualosa ilisha*) in Bangladesh; a) river ($L_\infty = 588$ mm, $K = 0.82$ yr$^{-1}$, $R_n = 0.136$) and b) marine ($L_\infty = 610$ mm, $K = 0.80$ yr$^{-1}$, $R_n = 0.132$).

Fig. 3. Linearised length converted catch curve analysis to estimate total mortality, $Z$ from the length-frequency distribution of hilsa shad (*Tenualosa ilisha*) in Bangladesh; a) river ($L_\infty = 588$ mm, $K = 0.82$ yr$^{-1}$) and b) marine ($L_\infty = 610$ mm, $K = 0.80$ yr$^{-1}$).
**Optimum length at first capture (Lc)**

From the probability of capture analysis using selection curves (Fig. 4), the estimated optimum length of hilsa (TL, mm) at first capture ($L_c = L_{50}$) were 322 and 335 mm, TL, respectively for river and marine populations (Table 3). The estimated optimum mesh size for gillnets to catch the size at first capture ($L_c$), using the mesh size-fish length relationship (equation 16) were 78 and 81 mm for river and marine stocks, respectively (Table 3).

![Fig. 4. Plot of probability of capture against length classes of hilsa shad (Tenualosa ilisha) to estimate length at first capture ($L_c = L_{50}$) in Bangladesh waters; a) river ($L_\infty = 588$ mm, $K = 0.82$ yr$^{-1}$) and b) marine ($L_\infty = 610$ mm, $K = 0.80$ yr$^{-1}$).](image)

**Recruitment pattern**

The recruitment pattern for both rivers and marine population was more or less continuous, with two major pulses, of which one was found to be distinctively larger than the other (Fig. 5). For the rivers, the larger pulse was between March and May and the second pulse was between November and January. In the marine environment, the pulses were relatively shorter, having the larger pulse during March-April and the shorter pulse during January-February (Fig. 5).

**Exploitation level (E) and relative yield per recruit (Y'/R)**

Present exploitation levels for the hilsa fishery in the river and marine habitats were 0.58 and 0.57, respectively (Table 3). From the relative yield per recruit analysis (Fig. 6), the estimated $E_{\text{max}}$, $E_{0.1}$ and $E_{0.5}$ values were 0.61, 0.55 & 0.36 and 0.65, 0.62 & 0.36, for river and marine populations, respectively (Table 3). The river population indicated slight over-exploitation ($E = 0.58$, instead of $E = E_{0.1} = 0.55$), whilst, the marine population showed slight under-exploitation ($E = 0.57$, instead of $E = E_{0.1} = 0.62$).
Fig. 5. Recruitment pattern of hilsa shad (*Tenualosa ilisha*) in Bangladesh; a) river ($L_\infty = 588$ mm, $K = 0.86$ yr$^{-1}$, $t_0 = 0.003$ yr) and b) marine ($L_\infty = 610$ mm, $K = 0.80$ yr$^{-1}$, $t_0 = 0.003$ yr).

Fig. 6. Relative yield per recruit ($Y'_R$) and relative biomass per recruit ($B'_R$) analyses of hilsa shad (*Tenualosa ilisha*) in Bangladesh; a) river ($L_\infty = 588$ mm, $M/K=1.22$) and b) marine ($L_\infty = 610$ mm, $M/K=1.23$).
Both the populations are, however, still under the maximum acceptable limit ($E = E_{\text{max}} = 0.61$ and 0.65, for river and marine populations, respectively), at which the fishery might obtain maximum yield (Table 3).

The $Y/R$ analysis showed that maximum yield could be obtained from the hilsa fishery at the exploitation level, $E=0.61$ for the river population and $E=0.65$ for marine population (Fig. 6). The 50% level of the biomass could be obtained at the exploitation level, $E=0.36$ for both river and marine populations (Fig. 6). The biologically optimum yield following the principle of $E_{0.1}$ could be obtained at the exploitation level $E=0.55$ for the river and $E=0.62$ for the marine population.

**Discussion**

The growth parameters of hilsa populations from other studies in Bangladesh waters varied widely (BOBP 1987; BFRI/RS 1994; Miah et al. 1997; Rahman et al. 1999; Rahman et al. 2000). Asymptotic length ($L_\infty$) varied between 520 and 615 mm and the $K$ varied between 0.6 and 1.1 yr$^{-1}$. Although the present findings (Table 3) are well within the range of the previously published ones, it is unwise to compare the present results to the previous results, because, previous studies did not correct the length-frequency data for the gear selectivity and no validation was carried out with the length at age data by counting daily rings in otoliths. In the present study the length-frequency data were corrected for gear selectivity which minimised the bias due to gillnet used to catch the fish. Moreover, the growth parameters obtained from the length-frequency data are comparable with the parameters obtained from the length-at-age data based on otolith studies ($L_\infty = 580$ mm, $K= 0.77$ yr$^{-1}$ for combined sexes) (Rahman 2001).

Another test is the so-called ‘Munro’s phi prime test’ (Munro and Pauly 1983; Pauly and Munro 1984) estimated from both length-frequency data ($\phi^\text{'} =3.45$) and length-at-age data ($\phi^\text{'} =3.41$). The data were found to be well within the clupeid fish values, which indicate the reliability of the estimated parameters.

Growth parameters differ from species to species, but they may also vary from stock to stock within the same species, i.e. growth parameters of a particular species may take different values in different parts of its range. Furthermore, successive cohorts may grow differently depending on envi-
ronmental conditions. Growth parameters also often have different values for the two sexes, as found in the otolith study (Rahman 2001). If there are pronounced differences between the sexes in their growth parameters, the input data should be separated by sex and values of $K$ and $L_\infty$ should be estimated for each sex separately (Sparre et al. 1989). Nonetheless, sexed length-frequency data could provide more reliable information. Moreover, inclusion of missing size classes, especially the younger fish, may provide more realistic growth parameters.

Fish species with a high $K$-value generally have a high natural mortality ($M$) value, and vice versa (Sparre et al. 1989). For the hilsa populations, the $M$ and $K$ values were moderate (Table 3). From the ageing study (Rahman 2001) using both length-frequency data and otolith’s microstructure reading, there were at least seven age groups present in the commercial fishery, indicating hilsa live to at least 7 years.

The natural mortality estimated in this study ($M=1.00$ and 0.98 yr$^{-1}$ for river and marine hilsa, respectively) was lower than the values ($M=1.28$ - 1.32 yr$^{-1}$) estimated by other workers (Gupta 1989; Rahman et al. 2000). Other workers did not correct the estimated $M$, by multiplying with the schooling factor (0.8), which might be the reason of higher estimate (Gupta 1989; Rahman et al. 2000).

The mean fishing mortality obtained in this study (1.35 yr$^{-1}$) (Table 3) was higher than that obtained by BFRI/RS (1994) (1.25 yr$^{-1}$) and Miah et al. (1998) (1.14 yr$^{-1}$). This indicated that the fishing pressure in the hilsa fishery in Bangladesh is increasing and due to this increasing exploitation the fishery is moving towards overexploitation.

The mean optimum length for hilsa obtained in this study was 329 mm (Table 3), which was lower than the value (350 mm) obtained by BFRI/RS (1994). This may be an indication that the number of large size fish is decreasing, which ultimately indicates that the fishery is heading towards overexploitation. Therefore, any hilsa smaller than 325 mm TL must not be captured.

The recruitment pattern of hilsa, as obtained in this study was continuous with one major pulse (March-May) and one minor pulse (November-January). BFRI/RS (1994) also obtained similar results but did not determine the months where the pulses occurred. The two pulses most probably associated with the two peaks in spawning seasons (Rahman 2001). The offspring born during the peak spawning period (September-October) probably recruited in the fishery during March-May, forming the
main recruitment pulse. Similarly, the offspring born during the second peak spawning period (January-February) probably recruited to the fishery during November-January, forming the second pulse in the recruitment pattern.

The present exploitation level ($E = 0.58$) indicates that the fishery is moving towards overexploitation. Other workers also found overexploitation of the hilsa fishery in Bangladesh, e.g. $E = 0.56$ (Miah et al. 1997), $E = 0.66$ (Rahman et al. 1999) and $E = 0.60$ (Rahman et al. 2000). This trend towards overexploitation possibly reflects a recent drastic fall in hilsa catch in some regions in Bangladesh, as reported in the media (Talukder 2000; Khan 2000). However, according to the present study, there is further possibility to increase yield by increasing the exploitation level up to $E = 0.61$ ($E_{\text{max}} = 0.61$) for the rivers and $E = 0.65$ ($E_{\text{max}} = 0.65$) for the marine environment, the fishery should maintain the biologically optimum exploitation level by following the $E_{0.1}$ principle which is approximately $E = 0.55$ for rivers and $E = 0.62$ for marine population (Table 3). The question is how the fishery could be regulated to maintain the desirable level. The most obvious answer might be the regulation of fishing pressure, especially in the rivers where fishing mortality is high (Table 3). To maintain a large exploited fishery, a sound management plan linked to the socio-economic conditions of the fishing communities and other parties involved is necessary. However, the implementation of a management plan for a large fishery, especially for an artisanal fishery like hilsa, is problematic. Consequently, a management plan for the hilsa fishery has been formulated (Rahman 2001).

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References


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