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Population Biology of Sbour *Tenualosa ilisha* (Hamilton-Buchanan) in Kuwait

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Abstract

Tenualosa ilisha (=*Hilsa ilisha*), locally known as sbour, is one of the most important target species in the Kuwaiti drift-net fishery. Average annual landings in 1981-89 amounted to 152 t, and constituted about 2.5% of Kuwait's total commercial fish landing (6,000 $t \cdot year^{-1}$). This study provides information on the biology, growth and mortality of *T. ilisha* in this fishery.

Specimens of *T. ilisha* ranged in size from 14 to 57 cm, and in age from 1 to 5 years. The length-weight relationship was $W = 0.011\ L^{2.983}$ for males and $W = 0.007\ L^{3.104}$ for females. Von Bertalanffy growth equations estimated for both sexes from Gulland's (1964) and Allen's (1966) methods are

$$\text{Gulland: } L_t = 52.70\ (1 - e^{-0.28\ [t + 0.26]})$$
$$\text{Allen: } L_t = 52.50\ (1 - e^{-0.36\ [t + 0.07]})$$

The average total mortality (Z) was calculated to be 1.3 ± 0.1 (95% confidence limits) $year^{-1}$. Natural and fishing mortality were estimated to be 0.5 and 0.8 per year, respectively.

Length at maturity ($L_{50\%}$) for females was estimated as 41.5 ± 3.5 cm (95% confidence limit). Seasonal changes in the ovarian weight of mature females were used to determine when the spawning season takes place through the relationship between ovary and carcass weight for February-July 1990. It was found that *T. ilisha* may spawn from May to July with a peak in June.

Introduction

The fisheries of Kuwait, though small by world standards, are diverse with many distinct types of vessels - speedboats, dhows (traditional wooden-hulled boats) and steel shrimp trawlers - and types of gears used to catch a large number of species, of which only 15-20 contribute significantly to the landings.

Tenualosa ilisha (=*Hilsa ilisha*), known as sbour, belong to the sub-family Alosinae of the family Clupeidae, and is one of the most important target species in the drift-net (operated from small fiberglass speedboats of 12-22 feet in length fitted with outboard engines) and fixed stake-net (hadrah) fishery.

T. ilisha is an anadromous pelagic species which migrates from the sea to freshwater (rivers and estuaries) to spawn. The fishing grounds for *T. ilisha* are usually around Failakah and Oha islands, and they are caught in small quantities on the northern side of Kuwait Bay (Fig. 1).

The average annual landings of this species in 1981-89 was 152 t and constituted about 2.5% of Kuwait's total commercial fish landings (6,000 t·year^{-1}). In addition, 96% of the *T. ilisha* catch comes from the gill-net fishery and 4% from the fixed stake-net fishery (Baddar and Morgan 1983; KISR 1988; Baddar et al. 1990; Lee et al. 1990a). *T. ilisha* landings exhibit clear seasonal variations with lowest catches during May-July.

Many studies on the biology and population dynamics of *T. ilisha* have been done in India, Pakistan and the Bay of Bengal (Pillay 1958; Pillay and Rao 1963; Islam and Talbot 1968; Ramakrishnaiah 1972; Shafi et al. 1978; Quddus et al. 1984a, 1984b; Gupta 1989). The present study provides information on the biology, growth and mortality of *T. ilisha* in Kuwait waters.

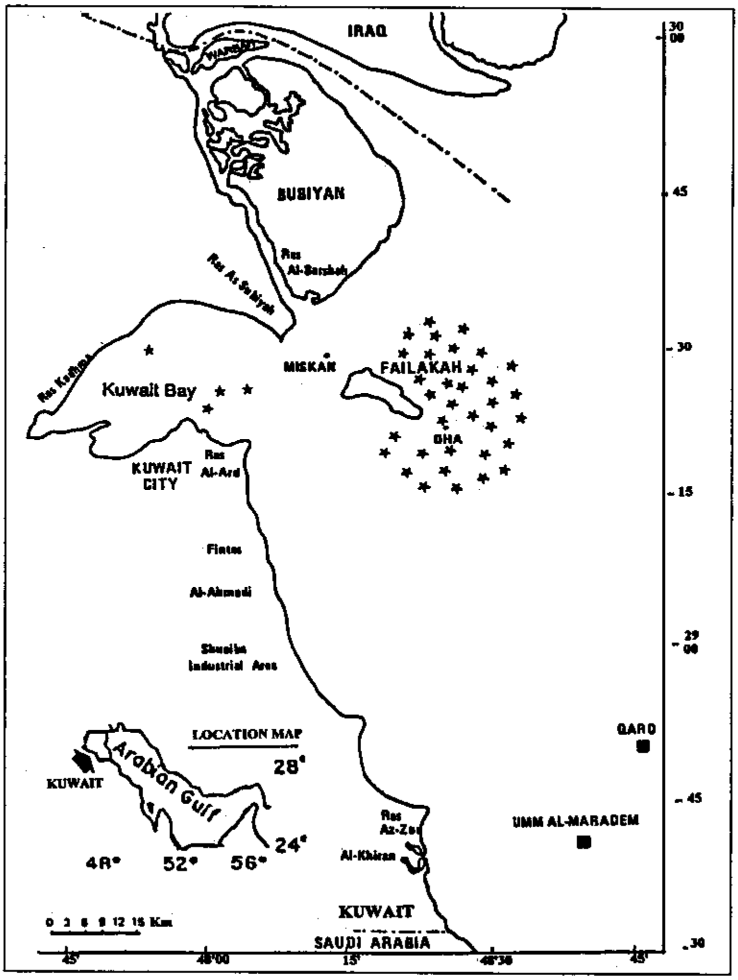

Fig. 1. Map of Kuwait showing the fishing grounds of *T. ilisha* (*), and a location map for Kuwait.

Materials and Methods

The length-frequency data of *T. ilisha* were measured from catches landed by gill-net and fixed stake-net (hadrah) at Kuwait fish markets during 1989-90 and 1992. The lengths were truncated to the nearest centimeter. Representative samples of 50-500 fish were collected on a monthly basis. A total of 4,376 fish were measured during the study period.

In addition, a random sub-sample of 50-100 fish were purchased monthly from March 1989 to July 1990. Along with total length, total body weight (to the nearest 1.0 g) of each fish was also measured. The fish were sexed, and gonad weight and gonadal maturity determined. The gonadal phase was classified to eight stages according to the method of Laevastu (1965).

Total length (L) and body weight (W) were used to calculate the length-weight relationship by fitting the function:

$$W = aL^b$$

where W is total body weight in g, and L is total length in cm, and a and b are regression parameters. Analysis of covariance was applied to explore any difference between the slope of the length-weight curve for both sexes.

The age of *T. ilisha* was determined by immersing the whole sagittal otolith in water in a black petri dish under a stereo-microscope. The von Bertalanffy growth equation was applied to the data obtained from age determination as follows:

$$L_t = L_\infty\left(1-e^{-K[t-t_0]}\right) \qquad ...1)$$

where L_∞ is the asymptotic length, or average maximum length a fish reaches with infinite time; K, a growth parameter, is a measure of the rate at which the growth curve approaches the asymptote; and t_0 is the time, equivalent to the (hypothetical) starting time at which the fish would have zero length according to (1). The von Bertalanffy growth parameters were estimated using Gulland's (1964) graphical method and Allen's (1966) least squares method.

Total mortality (Z) was estimated according to the following methods:

1) Wetherall et al. (1987):

The coefficients of mortality and growth (Z/K) in steady-state fish stocks were estimated along with the asymptotic length (L_∞) from length-frequency data which were collected during 1989-90 and 1992. By plotting ($\bar{L}$-L') against cutoff length (L'), where $\bar{L}$ is defined as the length computed from L' upward; and L' is the limit of the first length class used in computing a mean length $\bar{L}$. In addition, the cutoff length L' can take any value equal to and above the smallest length under full exploitation. Z/K and L_∞ were estimated as follows:

$$\frac{Z}{K} = \frac{1+b}{-b}$$

$$L\infty = \frac{-b}{a}$$

where a and b are the regression coefficients.

2) Srinath (1986):

Using length-frequency data and growth parameters (L_∞, K), Z was calculated for each pair of length classes according to the following equation:

$$Z = -\left(\frac{1}{dt}\right)\mathrm{Ln}\left(1 - q_{t,\ t+dt}\right)$$

$$\text{and } dt = \left(\frac{1}{K}\right)\mathrm{Ln}\left(\frac{L_\infty - L_t}{L_\infty - L_{t,\ t+dt}}\right)$$

$$\text{where, } q_{t',\ t+dt} = \frac{C_{t,\ t+dt}}{\sum C_t}$$

$C_{t,t+dt}$ are the numbers of fish caught in the interval (t,t+dt); ΣC_t is the cumulative catch from the largest length group to size at first capture (L_c), L_t + dt are the length at ages t and t+dt, respectively, and L_∞ and K are the von Bertalanffy growth parameters.

Natural mortality (M) was estimated using the indirect method of Pauly (1980) on the basis of the relationship between M, von Bertalanffy growth parameters (L_∞ and K) and the mean annual water temperature (T°C) as follows:

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

Pauly (1980) suggests that in the case of clupeid fishes, the predicted M should be reduced by 30% because of schooling behavior which is strongly developed in the Clupeidae group, and also to estimate unaffected M by the taxonomic or ecological affinities of a stock.

The size at maturity ($L_{50\%}$) was predicted by plotting the cumulative maturity percentage of *T. ilisha* female against total length (L) from data collected in 1989-90.

Depending on the gonad and total body weight collected during February-July 1990 from the monthly sub-samples, the relationship between gonad weight and carcass body weight (total body weight - gonad weight) was plotted for each month to calculate the function,

$$GWt = a + b\ CWt \qquad ...2)$$

where GWt is gonad weight (g), CWt is carcass weight (g); and a and b are the regression coefficients. Seasonal changes in gonad weight were traced by plotting the expected gonad weight (g) for each month using (2).

Results

Length-Frequency Distribution

The length composition of *T. ilisha* ranged from 14 to 57 cm, with majority of the fish landed in the market ranging from 35 to 45 cm. Fish from 14-22 cm, 16-31 cm and 30-57 cm are caught by mullet (locally known as maid) gill-net, fixed stake-net (hadrah) and *T. ilisha* (sbour) drift-net, respectively. Small *T. ilisha* fish (14-22 cm) caught as a bycatch in Kuwait Bay by speedboats gill-net fishing for mullet in November are usually landed in small quantities. They are usually used as fish bait. The length range 14-30 cm was not fully sampled by mullet gill-net and hadrah because their catch was not usually landed in the Kuwaiti market.

Fig. 2 shows the length-frequency distribution for different months of the study. *The only sample series which might indicate when recruitment occurs is* for November 1989 - July 1990. Small fish were reported in the 40 mm gill-nets

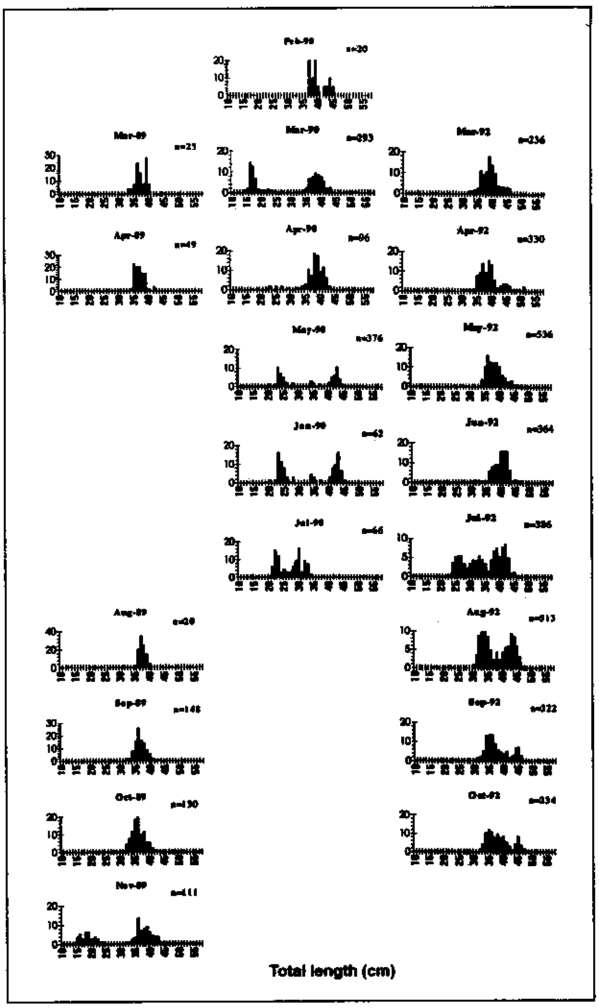

Fig. 2. The length-frequency (percentage) distribution of *T. ilisha* at different months during 1989-90 and 1992.

in November 1989. Similar sized fish were detected again in March 1990 and could be followed until July 1990. If only a single annual recruitment of young *T. ilisha* occurred, then these fish would have shown little growth from November to March. Alternatively, there could be several recruitment periods per year, but this sample series could not identify this. Modal progressions were not clearly established and this may be due to the use of gill-nets with different mesh sizes in the fishery. As a result of a pause in fishing operations for about 2 years due to the invasion of Kuwait on 2 August 1990, the maximum length of *T. ilisha* in the Kuwait fishery increased by about 24% of the maximum length measured in 1990 (46 cm), reaching 57 cm in June 1992.

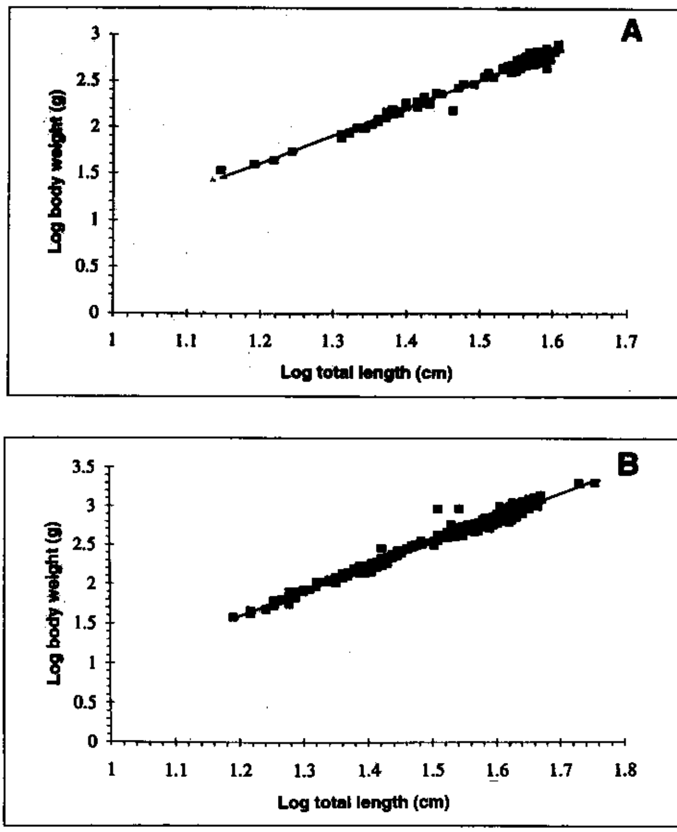

Fig. 3. The logarithmic relationship between length and weight for (A) males and (B) females.

Length-Weight Relationship

The relationship between length and weight for males and females was derived by plotting $Log_{10}(L)$ against $Log_{10}(W)$ (Fig. 3a and 3b, respectively). The relations were

$$\text{Male}: W = 0.011\ L^{2.983}$$
$$\text{Female}: W = 0.007\ L^{3.104}$$

Table 1. Analysis of covariance for simple linear regression analysis of $Log_{10}W Vs Log_{10}L$ (A) Male (B) Female (C) Comparison of regression line between male and female.

Source	SS	df	Ms	F	F0.025
(A) Male ANCOVAR					
Regression	12.128	1	12.128	8,124.65	5.02
Residual	0.252	168	0.002		
Total	12.381	169			
(B) Female ANCOVAR					
Regression	51.180	1	51.180	23,944.9	5.02
Residual	0.938	439	0.002		
Total	52.118	440			
(C) Combines sexes ANCOVAR					
Combined regression	63.514	1	63.514	32,405.10	5.02
Between coefficients	0.0016	1	0.016	8.16	5.02
Between constants	0.043	1	0.043	21.94	5.02
Residual	1.190	607	0.002		
Total	64.762	610			

Males ranged in size from 14 to 40.5 cm; and females from 15.5 to 57 cm. To compare the regression lines of both sexes of *T. ilisha*, covariance analysis was carried out according to Minitab software to test the homogeneity of the regression coefficients for each sex, and it was found that both slope and intercept were significantly different (Table 1). Therefore, no single regression will adequately describe the length-weight relationship for both sexes of *T. ilisha*.

Age and Growth

The age composition based on otoliths of *T. ilisha* is shown in Fig. 4. The lengths of the fish that were aged varied from 14 to 48 cm, and their ages ranged from 1 to 5 years. The fish were fully recruited to the fishery at 3 years of age. The zero age class did not occur in the fishery. The mean length and mean weight for each age group were calculated (Fig. 5 and 6, respectively)

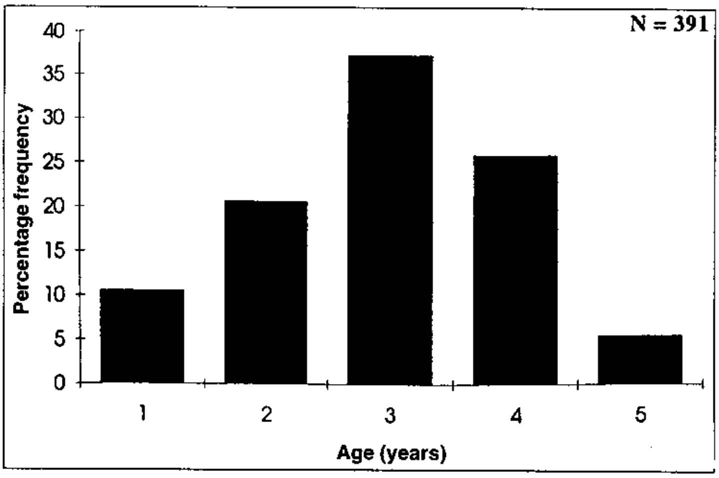

Fig. 4. The *T. ilisha* age histogram for ages 1-5.

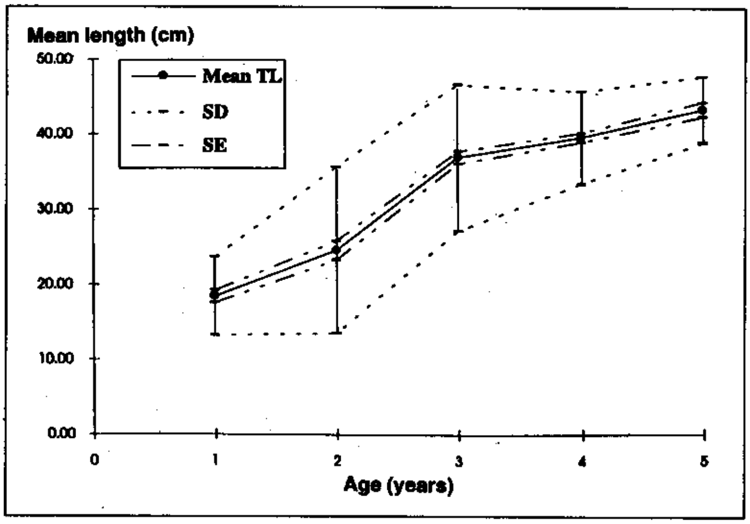

Fig. 5. The empirical plot for growth-in-length of *T. ilisha*. The 95% confidence limits of standard deviation (SD) and standard error (SE) shown.

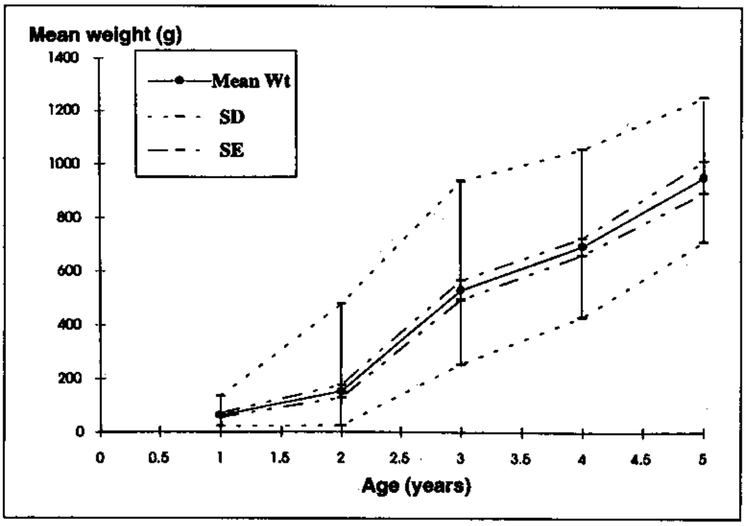

Fig. 6. The empirical plot for growth-in-weight of *T. ilisha*. The 95% confidence limits of standard deviation (SD) and standard error (SE) shown.

and it appeared that *T. ilisha* usually grows faster during the first 2 years than during the ages of 3-5 years when growth rate is nearly constant.

Gulland's method (1964) was applied to length-at-age data by plotting the increase in length (L_{t+1}-L_t) against mean length (L_t). The von Bertalanffy growth parameters were estimated to be L_∞ = 52.70 cm and K = 0.28 year^{-1}. Hence, K and L_∞ were estimated and the value of t_0, -0.26 year, was obtained by plotting Ln(L_∞-L_t) versus age.

When Allen's method (1966) was applied to the same length-at-age data by using the VONBER computer program, a part of the package of Length-Based Fish Stock Assessment Programs (LFSA) (Sparre 1987), the growth parameters (95% confidence limit) were estimated to be:

$$L_\infty = 52.50 \pm 4.59$$
$$K = 0.36 \pm 0.08$$
$$t_0 = 0.07 \pm 0.19.$$

The asymptotic length (L_∞) from Gulland's method was within the confidence limits of the L_∞ value predicted by Allen's method. Fig. 7 shows the von Bertalanffy growth curves of *T. ilisha* predicted by Gulland and Allen's methods fitted to the length-at-age data. The mean length-at-age from Allen's method for ages 2-5 years was higher than those from Gulland's method. The difference in mean length-at-age might be caused by the smaller number of younger fishes being caught by mullet gill-net and not representatively landed at Kuwait fish markets, giving an underestimation of growth rate for the first age class.

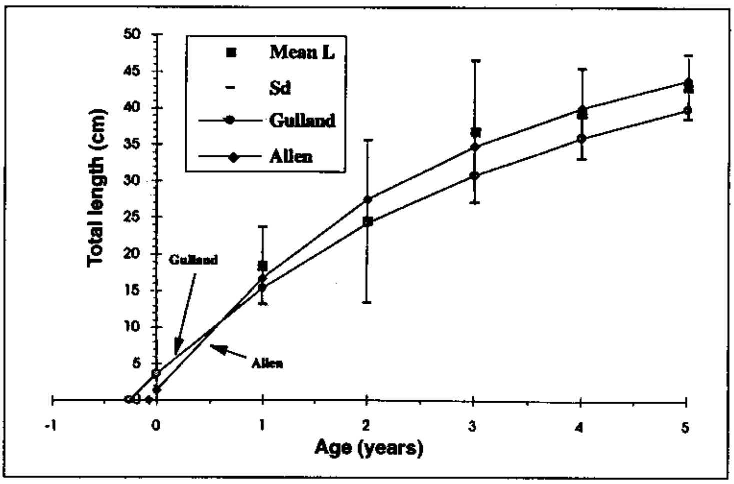

Fig. 7. von Bertalanffy growth curves of *T. ilisha*, predicted by Gulland (1964): $L_t = 52.69\ (1\text{-}e^{-0.276[t + 0.259]})$ and Allen (1966): $L_t = 52.496\ (1\text{-}e^{-0.357[t + 0.074]})$. The mean length-at-age and 95% confidence limits shown.

Mortality

Wetherall et al.'s (1987) method was used to estimate total mortality (Fig. 8) using pooled length-frequency data collected during the study period, grouped into 2 cm intervals. The range of 38-46 cm (where 38 cm is the smallest length under full exploitation) was used to estimate Z/K (3.42) and L_∞(52.61 cm). Annual total mortality (Z) was estimated to be 1.2 using the K value from Allen's method (K = 0.36). When Srinath's (1986) method was used with the same data (length of 38-46 cm) the Z/K and Z (± standard error) were estimated as 3.877 ± 0.002 and 1.384 ± 0.001 year^{-1}, respectively. Average total mortality (Z) from both methods was 1.30 ± 0.13 (95% confidence limits) year^{-1}.

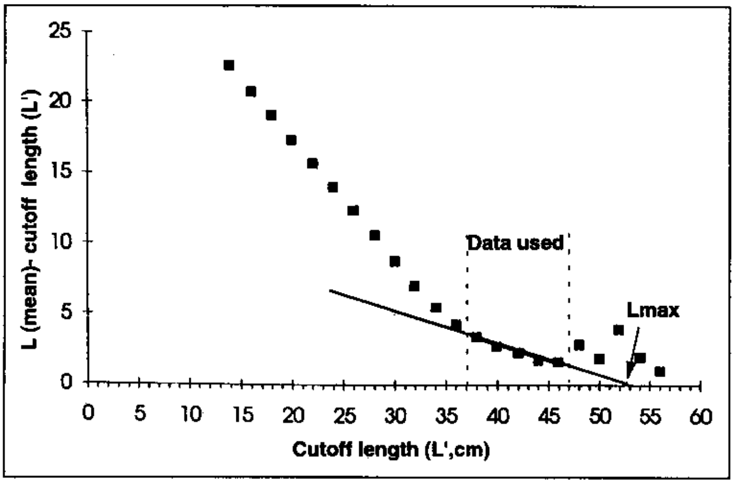

Fig. 8. Wetherall plot of L(mean) - L' (cutoff length) against cutoff length (L', cm). The straight line cutting the X-axis at point equal to L_∞ = 52.61 cm and Z/K calculated to be 3.42.

The value of M was multiplied by a conversion factor of 0.7, as suggested by Pauly (1980) and was found to be 0.5 year^{-1} when using L_∞ = 52.50 cm and K = 0.36 year^{-1}. The observed mean annual water temperature (T = 23.4°C) for Kuwait waters in 1989 was used (Lee et al. 1990b). Fishing mortality (F) was calculated to be 0.8 year^{-1} from the relation F = Z-M.

Sex Ratio

During 1989-90, 580 specimens of *T. ilisha* were examined, ranging from 14 to 46.5 cm. The numbers of juveniles, males and females were 41 (7.07%), 158 (27.24%) and 381 (65.69%), respectively. The size range of juveniles, males and females were 14.5-26 cm, 14-40.5 cm and 15.5-46.5 cm, respectively. Females dominated throughout almost the entire year. Male to female ratio was 1:2.4.

Size at Maturity

The data for analysis of the percentage of mature female *T. ilisha* for different size groups were collected from 1989 to 1990. The smallest mature female observed in the Kuwait fishery was 34.4 cm. The length at which 50% of the fish are sexually mature was estimated to be 41.5 cm ± 3.5 (95% confidence limits) (Fig. 9).

The size at maturity of males could not be judged easily because no mature males (stages IV-VII) were observed in the fishery.

Spawning Season

Using data from mature females collected during February-July 1990, a linear relationship was plotted between ovarian weight in mature females and

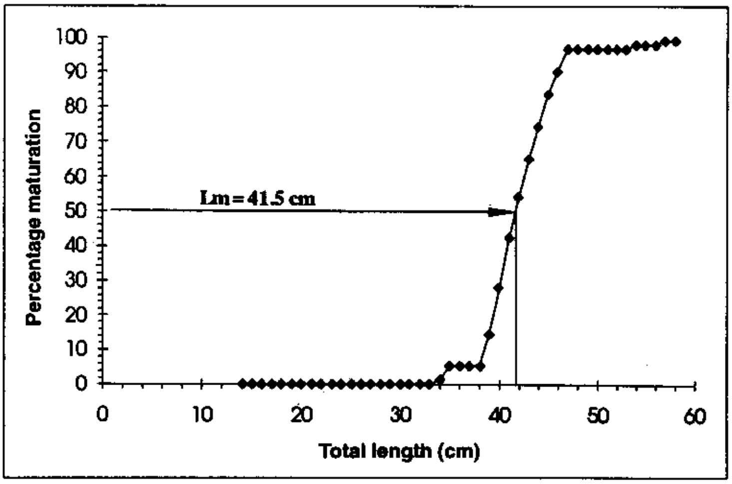

Fig. 9. The maturation ogive plot of the cumulative maturity percentage against total length (cm). The $L_{50\%}$ = 41.5 cm.

carcass weight for each month to trace seasonal changes in ovarian weight and to indicate when the spawning season takes place. The smallest mature body weight was 500 g.

The regression coefficients for the different months are listed in Table 2. The regression coefficient (b) for February-July 1990 gradually increased as gonad:carcass-weight ratio increased from February (3.6%) until gonad weight peaked at about 11% of carcass weight in June, then declined again in July (6.5%). The predicted ovary weight, converted from carcass weight, for mature females in relation to length (36-50 cm) for different months was plotted (Fig. 10). The highest gonad weight occurs in May-July. Therefore, the available data indicates that *T. ilisha* probably spawns between May and July with a peak in June.

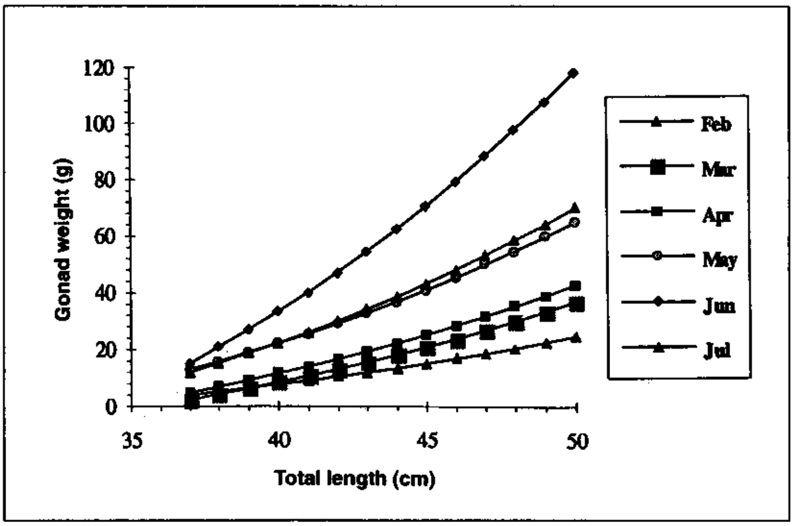

Fig. 10. The expected gonad weight (g) plotted against total length (cm) for the months of February to July.

Table 2. The regression parameter values of the logarithmic relationship between the gonad weight (G.Wt) and carcass weight (C.Wt) at different months in 1990.

Month	a	b ± SE	n	r	P
Feb	-9.3624	0.02438 ± 0.00935	10	0.91	0.0005
Mar	-20.0669	0.04003 ± 0.00991	37	0.81	<0.0001
Apr	-19.6479	0.04371 ± 0.01312	12	0.92	0.0427
May	-20.7262	0.05914 ± 0.07415	23	0.34	0.1120
Jun	-51.5438	0.11138 ± 0.03962	20	0.81	0.0004
Jul	-25.4475	0.06545 ± 0.00537	13	0.56	0.0013

Discussion

The monthly length-frequency of *T. ilisha* during the study period (1989-90 and 1992) does not show any clear seasonal fluctuation as a result of gill-net selectivity. The small sizes (14-22 cm) and middle sizes (16-33 cm) were not landed in reasonable quantities throughout the year because the fishing gears used to harvest these size groups suffer from seasonal changes in availability, whereas, for example, the fixed stake-net (hadrah) catches the middle sizes of *T. ilisha* in winter. Therefore, a smaller mesh size (<80 mm) would better catch the middle size of *T. ilisha.*

In the present study, recruitment to the fishable stock may take place once a year in November and extend to March, or perhaps twice a year, in November and March; whichever is the case cannot be decided because of insufficient data from the survey. Pandit and Hora (1951) observed in the Bay of Bengal that younger fish return to the sea or estuarine areas in larger numbers during October-November with the return gradually diminishing until February.

The regression coefficient (b) of the length-weight relationship of *T. ilisha* in the Kuwaiti fishery lies between 2.983 and 3.104 which Martin (1949) suggested are reasonable values for this stock. Studies in Bangladesh and India (Ramakrishnaiah 1972; Shafi and Quddus 1974; Quddus et al. 1984b) found the regression coefficients of *T. ilisha* to be in the range 2.768-3.125. These values are similar to those obtained for Kuwaiti fish. The small change could be due to the different environmental conditions in which the two populations live.

The maximum age of *T. ilisha* in the present was 5 years, in comparison to the Bay of Bengal, where Prashad et al. (1940), Pillay (1958), Pillay and Rao (1963) and Quddus et al. (1984b) estimated it to be 5-7 years, 5 years, +6 years and 5 years, respectively.

The asymptotic lengths of 52.5 and 52.7 cm estimated by Allen's and Gulland's methods are similar to the value obtained by the Wetherall method (52.6 cm). The estimated asymptotic length for the present study is lower than estimated values from the Bay of Bengal which ranged between 58 and 68 cm (Quddus et al. 1984b; Van der Knaap et al. 1987; Gupta 1989). Ricker (1979) notes that many fish tend to grow larger in the cooler parts of their temperature range, which may explain the difference in asymptotic length between the areas, as fishes in the Bay of Bengal grow in a narrow temperature range (24.9-29.4°C), while those in Kuwait grow in a wide temperature range (14-32°C).

The estimated mean lengths for ages 1-5 years from this study are lower than the values given by Van der Knaap et al. (1987) and Gupta (1989). Some factors have been suggested to explain this variation in growth rate of fish in the wild between different populations. Different temperatures may affect food supply or the appetite and growth efficiency of fish (Brett 1979).

Experience in Kuwait suggests that 300-500 fish need to be sampled, if reliable growth curves are to be obtained (Samuel and Mathews 1987). Due to the lower numbers of fish, length-at-age data were not analyzed and computed separately by sex. When enough data are available for younger and older fish of different sexes, sexual dimorphism in growth can be analyzed more accurately.

The average total mortality of *T. ilisha* estimated in this study differs from the results of Van der Knaap et al. (1987) and Gupta (1989) for the Bay of Bengal. This may be a result of sampling different regions and different rates of exploitation of *T. ilisha*. The values found here were 1.30 ± 0.13 (± 95% confidence limits) $year^{1}$, while Van der Knaap et al. (1987) and Gupta (1989) found values of 1.9 and 1.89 $year^{1}$, respectively.

The estimated natural mortality in the present study is lower, but has the same pattern as total mortality in the Bay of Bengal values. This may be due to the difference in population growth parameters as well as temperature. Natural mortality, when multiplied by 0.7 as suggested by Pauly (1980) was 0.50, while data from Van der Knaap et al. (1987) and Gupta (1989) when calculated for clupeids would be 0.889 and 0.924, respectively.

Contradictory views have been expressed by previous workers on the sex ratio of *T. ilisha* populations. Jones and Menon (1951) reported that the ratio of males to females in the Hooghly is generally constant, with a preponderance of males at the commencement of the breeding season, and of females during the spawning period. David (1954) recorded a striking preponderance of males in catches from the Hooghly at Barrackpore throughout the year. Pillay (1958) did not find any significant deviation from the expected ratio of 1:1 in the monsoon run of the fish, and he was of the opinion that the predominance of males in winter catches is attributable to selective fishing. In Bangladesh, Quddus et al. (1984a) studied the biology of two populations of *T. ilisha* in the rivers Padma and Meghna and found that the sex ratio of type B did not significantly differ throughout the year for both sexes. In the case of type A, females were predominant in October and December, whereas males predominated in June.

In the present study, monthly samples showed great variations in sex ratio. Females were the predominant sex throughout the year. This variation may be caused by males and females often moving in separate shoals (Pillay 1958). Wanner (1972) suggested several reasons for the unequal sex ratios. These include differences in mortality, growth and longevity, sex reversal, sex differences in activity, and migration in and out of the sampling area. There is no evidence for sex reversal in this species, but evidence exists to support the idea that the sexes of *T. ilisha* are different in size and growth (Chacko and Ganapati 1949; Shafi et al. 1977). Beverton (1964) noted that in terms of catchability, size, growth and longevity, the sexes behave almost like two different species.

The minimum size of female *T. ilisha* at first maturity was 34.4 cm which is similar to observations from the Bay of Bengal (Chacko and Ganapati 1949; Jones and Menon 1951; Shafi et al. 1978; De 1980), and female *T. ilisha* appear to attain 50% maturity at a greater length ($L_{50\%}$ = 41.5 ± 3.5 cm) than those from the Ganga (35 cm) (Mathur 1964). The variations in size or age at first sexual maturity for a given species in different geographical areas are generally manifestations of the environmental conditions to which a population is exposed. Purdom (1979) in his review suggested that the timing of the age at which fish mature must be under genetic control in that individual fish species have a characteristic age at first maturity. He concluded that the time of first maturity, the season of spawning, fecundity and egg size are influenced both by genetic and environmental factors. Wootton (1990) found wide interspecific variation in the age at first maturity, and that within a species there may be considerable inter- and intrapopulation variations, reflecting genetic and environmental influences.

Different spawning periods have been observed for *T. ilisha*. This study found that *T. ilisha* spawns in May-July with a peak in June. Unpublished data from the Mariculture and Fisheries Department, Kuwait Institute for Scientific Research, from a *T. ilisha* survey in the Shatt al-Arab shows that this species spawns during May-August with a spawning peak in May-June, while no spawning activity was noticed beyond October when the mature fish migrate to the sea. Small immature fish (9-17 cm) are observed in October-December. So this observation supports our conclusion regarding the spawning period for the Kuwaiti fishery.

In contrast, it has been reported that *T. ilisha* of the Hooghly (Hora and Nair 1940; Hora 1941; Pillay 1958) and Ganga (Mathur 1964) spawn several times during the breeding season, while other authors found this species breeds only once, during the monsoon in July-September (Chacko and Ganapati 1949; Chandra 1962; Pillay and Rao 1963; Islam and Talbot 1968; Ramakrishnaiah 1972). These differences in the spawning periods of populations in different areas may be due to genetics and environmental factors as mentioned before. It will also be relevant to determine whether the population found in different rivers of India, Pakistan and Bangladesh are from the same population or from different and isolated populations. This study can be extended to Kuwaiti fish also. This can be done through genetic fingerprinting, mitochondrial DNA analysis, or by studying specific gene loci by electrophoresis (isozyme analysis).

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