Spawning times and early life history of
*Hilsa ilisha* in Bangladesh

by

Md. Mokammel Hossain

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We accept this thesis as conforming to the
required standard

The University of British Columbia

April 1985

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Department of  Zoology

The University of British Columbia
1956 Main Mall
Vancouver, Canada
V6T 1Y3

Date  April 22, 1985
ABSTRACT

Sexual condition of female *Hilsa* was sampled from October 1983 to August 1984 from freshwater, estuarine and marine localities in Bangladesh. At Chandpur, on the River Meghna, changes in gonadosomatic index showed that early monsoon (June), late monsoon (October), and winter (February) are the major spawning periods. Ages of juvenile *Hilsa* were determined up to six months old (12 cm long) by counting daily growth rings of otoliths. Hatching dates of juveniles collected in different months were back calculated from otolith readings, and confirmed the existence of the three spawning peaks. Migratory movements of juvenile *Hilsa* in the River Meghna were studied from samples obtained by experimental beach seining, by experimental drift gill netting, and by fishermen's gear. Length-frequency analysis of fish from beach seines and from fishermen's catch indicated juveniles less than 8 cm in total length inhabit shore and shallow river areas (<10 ft depth). When juveniles attain a larger size (>7 cm) they migrate to the deeper river (>10 ft depth) in January. After reaching 12 cm, all disappeared from the deeper river in May. Their migration from the river towards the sea was indicated by the direction of gilling in experimental nets, and by mean length analysis of juveniles collected in the upper and downstream areas of the River Meghna.
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1. INTRODUCTION

*Hilsa ilisha* (Hamilton), currently known as *Hilsa* or *Hilsa shad* (Fig. 1), belongs to the subfamily Alosinae of the Family Clupeidae. *Hilsa* occurs in foreshore areas, estuaries, brackish water lakes and freshwater rivers, in the western division of the Indo-Pacific faunistic region. It is held to be anadromous by most authorities but some authors argue that it is not truly anadromous (Raja 1984). Its marine range extends from Iran and Iraq on the Persian Gulf, along the west coast of India in the Arabian sea, and in the Bay of Bengal. It has also been reported (perhaps erroneously) from the coastal waters of Srilanka, and from Cochin China (Vietnam) (Pillay and Rosa 1963). The commonest life history pattern is believed to be that the adults (about 35.6 cm to 54.0 cm in length) shed large numbers of small demersal eggs in rivers; the young go to sea after some weeks in freshwater. *Hilsa* have many long gill rakers, and all stages subsist on small food particles.

In Bangladesh, *Hilsa* is an immensely important source of protein. The Ganges-Brahmaputra forms in Bangladesh the largest delta in the world, occupying 25,000 square miles in a country of 55,000 square miles. The population of 90,000,000 persons is heavily dependent on fish. *Hilsa* is by far the most important species, contributing perhaps 33% of the total catch while no other single species contributes over 5% (Lindsey 1981). Of the three countries in the Upper Bay of Bengal region, where *Hilsa* forms a commercial fishery, Bangladesh is reported to take the largest share of something over 100,000 tonnes. In India the landings may account to 25,000 tonnes, and in Burma about 4,000 to 5,000 tonnes (Raja 1984).
FIGURE 1. *Hilsa ilisha* in different size groups taken from Barisal Fish landing centre, April 15, 1984. The smaller fish are about 14 cm long and about 7 months old. The largest on the left is about 53 cm long and is probably a mature adult.
The present problems of managing the *Hilsa* fishery are daunting, partly because of the lack of knowledge of the life history, and partly because of the scarcity of means of implementing any control measures. With a view to solving some of these problems, a *Hilsa* fishery development and management project of the Government of Bangladesh, assisted by the International Development Research Centre, is planned to be implemented in the fiscal year 1985-1986. Basic biological information on spawning, migration, population structure and age of the fish is to be acquired as a basis for a sound management program. A review of the literature shows that extensive work on this species has been done in India, but in Bangladesh the information is limited.

The principal goals of the present research were 1) to determine the spawning times of *Hilsa* in different habitats in Bangladesh (marine, estuarine, and the Meghna River) as indicated by sexual condition of females; 2) to determine the age of young *Hilsa* by examining their otoliths, and thereby back-calculate their hatching dates as an independent check of spawning times, and 3) to study, from samples obtained by beach seining, by experimental drift gill netting, and by fishermens’s gear, the migratory movements of young *Hilsa* from shallow to deep parts of the river and from there towards the sea.
2. MATERIALS AND METHODS

2.1 Samples of adults

To procure specimens for the study of gonad size, sampling of adult *Hilsa* was started in October 1983 and continued to August 1984. During this period the monsoon rains ended in November 1983 and commenced again in May 1984. The sampling stations, such as Chandpur, Barisal and Chittagong, are shown in Fig. 2. Samples from Chandpur, Barisal and Chittagong, represented catches from the Meghna River, the estuarine and the marine (Bay of Bengal) habitats respectively. Samples were taken monthly in Chittagong and Barisal, and twice monthly at Chandpur. In each sampling, 25 fish were taken at random from the commercial catch at landing stations and were immediately preserved in ice in a special insulated box and transported to the laboratory.

In the laboratory, the total length of each specimen was measured on a standard fish measuring board, from the anterior tip of the premaxilla to the end of either lobe of the tail, whichever was longer, without stretching the fish in any way. In the present study, total length was chosen because of its common use in the Indo-Bangladesh region. The total weight was taken on a Sauter balance sensitive to 0.01 gm. The specimen was then cut open and the gonads were removed, and their weight noted to the nearest gram. A total of 939 specimens from the three sampling stations were examined; of these 411 were females. Sex of the specimens were determined by visual
FIGURE 2. Map of Bangladesh showing the different sampling stations.
observation of gonads, or, in the case of immature gonads, by microscopic observation.

The body weight and gonad weight of female *Hilsa* in all the habitats were recorded each month. Gonadosomatic index was calculated from the formula:

\[
GSI = \frac{\text{Gonad weight}}{\text{Body weight}} \times 100
\]

2.2 Experimental seining

To determine the migratory movements of young *Hilsa*, sampling by beach seine was started in December 1983 and continued to August 1984. The Meghna River between Tarpachandi and Chirarchar of North Chandpur, shown in the Figure 2, was selected as the study area. Fortnightly seining was conducted except in the months of April, May and June, when seining was only monthly due to rough weather. An experimental beach seine (150 ft x 20 ft x 1.8" mesh) was employed to collect samples. Generally, more than one haul was made to obtain samples. Each haul involved stretching the net perpendicular to the shore using a speed boat with outboard engine. The net was then turned and pulled in the direction of river flow by the boat for a few minutes, and was then drawn by the boat in an arc towards the shore as shown in Figure 3.

Fish captured by this method were placed in a plastic bag, packed on ice, and transported to the laboratory to separate the *Hilsa* from other species. Juvenile *Hilsa* was distinguished from the river clupeid *Gadusia chapra* on the basis of five dark spots along the lateral band and larger scales in *Hilsa*. Furthermore, to confirm the
identification of the species *Hilsa ilisha*, meristic counts (lateral line scales, dorsal fin rays, pectoral fin rays, and number of scutes) of a few specimens in each sampling were taken before starting to count and measure specimens. Total lengths of young *Hilsa* were measured to the nearest millimeter, using the same methods followed for adult *Hilsa*.

2.3 Fishermen samples of juveniles

During winter months (December to April) there is a commercial fishery for juvenile *Hilsa* (called "jatka") in Bangladesh rivers. Fishing occurs in water depths greater than 10 feet, beyond the limits of the experimental beach seining. Samples of commercially caught Jatka were procured from the market at Chandpur and from the catches of fishermen's gear in the Meghna River of North Chandpur. To minimize bias from gear selectivity the collections were made from the different gears such as gill net, boat seine net, and encircling seine net. The types of gear are shown in Figs. 4 and 5. Juveniles were also procured during the peak seasons (March-April; July-August) from the fish markets of Barisal, Paksey and Rajshahi shown in Fig. 2. The samples of Barisal represented the juveniles in downstream areas, while the samples of Paksey and Rajshahi represented the fish in upper areas in Bangladesh. The samples obtained by purchase from fishermen were preserved in plastic bottles with 10% formalin. In the laboratory, all collected samples were measured and weighed as described in the previous chapter.
FIGURE 5. Fishermen operating encircling seine in the Meghna River of North Chandpur, April 25, 1984.
2.4 Experimental gill netting

To obtain information on size distribution of juveniles, in addition to the results obtained from analysis of fishermen's catch, experimental drift gill net sampling was conducted in the Meghna River of North Chandpur. The study area was between Chandpur and Nilkamal as shown in Fig. 2. Nets were set fortnightly, starting in October 1983 and continuing to August 1984. The multifilament drift gill net had a total length of 630 ft and consisted of nine panels ranged in ascending order of mesh sizes from 1 inch to 5 inches diamond stretch, fastened together. The length of the panels was 45 feet for the 1 to 2 1/2 inch nets, and 90 feet for the 3 to 5 inch nets, with a constant depth of 12 feet. The net was set in the river off Chandpur from the 16 foot outboard speed boat, and drifted with the current for two hours. Direction of movement was tide-dependent. The net was set in the river in the period of both high and low tide. Catch of the net was preserved in an ice box, and brought to the laboratory for length and weight measurements. To study the direction (downstream or upstream) of migration, gilling direction of juvenile Hilsa in the experimental drift gill net was recorded.

2.5 Otolith interpretation

To determine the age and hatching date of juvenile Hilsa, sagittal otoliths were removed from 495 juvenile Hilsa collected from the Meghna River in Bangladesh. A sharp stiff-bladed knife was used to split open the head and expose the cavities in which they were located. Under a binocular dissecting microscope sagittal otoliths
were removed from the cavities with forceps. Prior to removing the otoliths, *Hilsa* were measured to the nearest millimeter. Sizes ranged from 2.1 cm to 17.5 cm. Both otoliths (left and right) of all specimens were prepared for examination as described by Neilson and Geen (1981). Otoliths were measured, and growth rings counted, with a compound binocular microscope using transmitted light at a magnification of 400x. Of the 495 otoliths examined, 113 otoliths were discarded as unreadable. Otolith length was measured from the centre of the nuclear area to the tip of the postrostrum with a calibrated ocular micrometer.

Both direct and indirect counts (Ralston and Miyamoto 1983) were employed to estimate age of juvenile *Hilsa*. Following the method of Ralston and Miyamoto, readings on otoliths were made at selected points along the postrostral axis wherever increments or rings were clearly viewed. The average width of increments in the readable areas was calculated, and also the proportion of the otolith radius with readable and unreadable zones; these were used to estimate the total number of rings present in the whole otolith. To find out the difference between direct and indirect counts, paired t-test comparisons were made. To determine the date of hatching, the method of Townsend and Graham (1981) was followed.

To validate the age determinations by otolith readings, the progression of modal lengths were analyzed by the Peterson Polygon method based on 1214 specimens. In addition, two validation experiments, (Figs. 6,7) as described by Campana *et al.* (1982) were carried out to determine whether the growth increments in otoliths of *Hilsa*
FIGURE 6. Intraperitoneal tetracycline inoculation of juvenile Hilsa.
FIGURE 7. Saline/tetracycline immersion experiments of juvenile Hilsa.
are daily or not. One involved injection of tetracycline, the other immersion in saline/tetracycline solution. Also, wild juveniles from the Meghna River were reared in a pond at the Fisheries Research Station at Chandpur for the same purpose.
3. RESULTS

3.1 Spawning time as indicated by female sexual condition

Gonadosomatic indices of female *Hilsa* in the Meghna River, estuarine and marine habitats, were calculated for each month and are depicted in Fig. 8. The gonad index values of Meghna River *Hilsa* indicate three peaks: in October (11.9), February (8.9), and June (8.0). The index values of estuarine *Hilsa* show two peaks; one in March (9.8) and another in June (6.9). On the other hand, the values of marine *Hilsa* exhibit a rise in the value starting in June and reaching a peak in August (7.9). A small ascent of value was also noted in February (0.8) with a fall in March (0.4).

In Bangladesh, winter starts in December and ends in April, and the monsoon period commences in May and terminates in November. The three peaks in the Meghna River habitat suggest that there are three major spawning times of *Hilsa*. The February peak indicated many *Hilsa* spawn in winter season, while the peaks in June and October revealed *Hilsa* also spawn two times in the monsoon season.

Based on 8 months data, in estuarine samples there was evidence of only two spawning periods per year, in March which was denoted as winter spawning, then another in June that was considered as the monsoon spawning. There was no September, October and November sampling of estuarine habitat. However, as the rise and fall of index values showed a similar pattern in estuarine habitats and in the Meghna River, the possibility of a third spawning in the estuaries could be postulated. Further, although early monsoon spawning (June)
FIGURE 8. Seasonal fluctuations of Gonadosomatic Index (with standard error) of female Hilsa in three habitats (River Meghna, estuarine and marine).
occurs in both the habitats, winter spawning was earlier in the Meghna River (February) than in estuaries (March). This indicates that mature estuarine fish were not all moving up to spawn later in Meghna.

The index values of marine *Hilsa* resulted in a different picture from the values of estuarine and Meghna River habitats. There were no data in September; August showed a peak in maturation of marine *Hilsa*. There is a possibility that no spawning occurs in the sea, and all the fish which mature there make trips into rivers or estuaries to release eggs.

3.2 Hatching date and early growth based on otoliths

Until now, no work has been done by any fishery scientist in India or in Bangladesh to determine the age of juvenile *Hilsa* by counting the daily growth rings in otoliths. Daily growth rings have now been used successfully to determine the age of larval and juvenile fish of other species (Campana 1983). The discovery of daily rings in otoliths by Pannella (1971) increases the resolution and precision of age determination, and promises to provide fishery biologists with new levels of information (Radtke and Dean 1982).

In the present study, an attempt has been made to determine the age, and hence the hatching date, of juvenile *Hilsa* of the Meghna River in Bangladesh by counting daily growth rings in otoliths. This information will be compared with data previously presented on spawning time as indicated by sexual condition of the adults.
3.2.1 Otolith development

Figure 9 indicates different stages in the development of *Hilsa* otoliths of fish ranging from 2.1 cm to 9.3 cm total length. The otolith of the smallest *Hilsa* examined was ellipsoidal in shape, with a convex distal side and flat proximal side. In this size group of fish, the beginning of the formation of the antirostrum can be seen (Fig. 9a). The position of excisura major was also evident in the otoliths of this size group. Otoliths of 3.2 cm (Fig. 9b) had a well developed rostrum and antirostrum. In the 4.1 cm length group (Fig. 9c), the otoliths had attained the typical shape of *Hilsa* with a well developed antirostrum, pararostrum and post-rostrum, and also a serrated edge. On the distal side, a slight depression, presumably the nucleus, can be seen at certain angles of reflected light. Inside the nucleus, the focus or primordium can be seen (Fig. 10).

Rarely, there are two primordia in *Hilsa* (Fig. 11). Variable primordia in fish otoliths were first described by Neilson (1984) in *Salmo gairdneri* and *Oncorhynchus tshawytscha*, but this is the first discovery of two primordia in *Hilsa* otoliths.

3.2.2 Age of juvenile *Hilsa*

As *Hilsa* is a fish of the tropical environment, the growth rings in otoliths are faint in comparison to those from temperate fishes. Nevertheless, they form clearly countable series,
FIGURE 9. Outlines of *Hilsa* otoliths showing their development. Respective total lengths of fish were: A, 2.1 cm; B 3.2 cm; C, 4.1 cm; D, 5.3 cm; E, 6.1 cm; F, 7.1 cm; G, 8.4 cm; and H, 9.3 cm. All outlines same magnification; otolith H is 112 um maximum length. Otolith of Fig. 9 a: i=antirostrum, ii=excisura major; b: i=rostrum, ii=antirostrum; c: i=rostrum, ii=antirostrum, iii=pararostrum, iv=postrostrum, v=serrated edge.
FIGURE 10. Ground and polished sagittal otolith from Meghna River juvenile *Hilsa* (4.3 cm) showing primordium. (magnification 410x).
FIGURE 11. Central area of ground and polished sagittal otolith from Meghna River juvenile *Hilsa* (6.1 cm) showing a double primordium (magnification 410x)
particularly in the central region of the otoliths (Figs. 12 and 13). The counts of rings within otoliths are summarized in Table 1 and Fig. 14; these combine direct and indirect counts. By assuming the increments were formed daily, the fish are aged as shown. Up to a length of 12 cm there was a steady increase of 2 cm in length for every 30 rings (i.e., approximately 1 month). In this study, the smallest *Hilsa* collected, 2.1 cm in total length, showed 33 rings, and hence was probably just over one month old. The growth rings of *Hilsa* otoliths can probably be used to estimate age fairly reliably up to 171 days (approximately 6 months old) and lengths of 12 cm.

At lengths over 12 cm rings become more difficult to count. If the counts in Fig. 14 are correct, they suggest an increase in growth rate after length of 12 cm, which is the size at which, as described in a later section, the young migrate towards the sea.

A pairwise t-test was used to test for differences between the direct and indirect ages. For this purpose some otoliths in which a complete series of increments could be counted (direct count) were also subjected to estimates by the indirect method, (by counting increments only over measured subdivisions of the whole series). The difference between ages arrived at by the two methods was not significant (p=0.1943, n=25). It was therefore assumed that the estimation of age by the indirect method in older fish (<12 cm) may be reasonably accurate, but it becomes progressively harder at larger sizes.
FIGURE 12. Ground and polished sagittal otolith from Meghna River juvenile *Hilsa* (3.7 cm) showing the growth rings (Bar = μm 2.5).
FIGURE 13. Ground and polished sagittal otolith of juvenile *Hilsa* (11.1 cm) from Meghna River showing the growth rings (Bar = μm 2.5).
FIGURE 14. Number of daily rings in otoliths of juvenile *Hilsa* of different sizes. Circles are means, vertical lines are ranges. Data in Table 1. Line fitted by eye to lengths up to 12 cm.

<table>
<thead>
<tr>
<th>Total Length - cm.</th>
<th>Ring Counts</th>
<th>Estimated Age</th>
<th>Sample Size</th>
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<td></td>
<td>Mean Class</td>
<td>Mean</td>
<td>Days</td>
</tr>
<tr>
<td></td>
<td>Intervals</td>
<td>Range</td>
<td></td>
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<td>2.1-3.0</td>
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<td>3.1-5.0</td>
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<tr>
<td>5.93</td>
<td>5.1-7.0</td>
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<td>7.1-9.0</td>
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A direct count was possible in otoliths up to 295 \( \mu \)m long, coming from fish of the 4.9 cm size group. Of all direct counted otoliths \((n=25)\), 75% were under 190 \( \mu \)m long and came from fish below 4 cm in total length, so aging in this study was based on both direct and indirect counts.

### 3.2.3 Validation of age determinations (tetracycline, saline, Peterson)

Attempts were made to validate otolith interpretations by various treatments of wild-caught juvenile *Hilsa* held in experimental ponds at Chandpur. Juveniles proved very sensitive to handling. Juvenile *Hilsa* were treated with tetracycline through intraperitoneal injection \((100 \text{ mg/kg body wt})\). The injected juveniles which ranged from 7.5 to 17.5 cm in length, died within 15-20 minutes of injection. In a separate experiment, juvenile *Hilsa* were immersed in .01% NaCl solution to which had been added approximately .005% tetracycline. Saline immersed juveniles \(<7 \text{ cm}\) survived only up to 30-60 minutes. In a third experiment, samples were collected from a pond containing young *Hilsa*, but variation in size of the original fish placed in the pond coupled with high mortality and small sample sizes precluded their use in validating otolith interpretation. This was however the first time that any young *Hilsa* had been held in captivity, and there is some hope of future success.

An independent method of age validation was more successful, namely the Peterson Polygon method which attempts to
follow the growth of a cohort of fish identifiable as a mode in
length frequency plots. Figure 15 shows the length frequency
distribution of juvenile Hilsa collected from the Meghna River
at Chandpur. The first mode at 5.0 cm was seen in December
which shifted to 7.0 cm in January and to 9.0 cm in February.
Up to February, the progression of modal values was at the rate
of 2.0 cm in each month. A 1.0 cm progression of modal values
was observed in between February (9.0) and March (10.0). The
modal value progressed to 12.0 cm in April. Overall, the
progression of modal values suggests that the fish grow about
2.0 cm in 30 days. In the previous section it was observed
that the otoliths of the 2.0 cm size group Hilsa had 30 growth
rings, which is consistent with the subsequent shift in modal
values at 2.0 cm per 30 days. Thus, it can be concluded that
the growth rings in otoliths of juvenile Hilsa are usually
formed daily and that the determined ages of young fish are
probably valid.

3.2.4 Hatching dates

The hatching date (or more correctly the date when the
first growth ring was formed) was back-calculated for each
specimen by subtracting the number of growth rings in the
otoliths from the date of capture. Figure 16 shows the age
structure, so calculated, of juvenile Hilsa which were captured
in different months in the Meghna River of North Chandpur. The
fish hatched between early August and early November were first
FIGURE 16. Date of formation of the first otolith growth ring (horizontal axis) in juveniles collected in different months indicated at left.
captured in December. The progeny of late October spawning were dominant in the months of December and January. November hatchers appeared in peak abundance in February, but their disappearance was observed in March. In April, both the progeny of late monsoon and winter spawning were abundant, but in May they completely disappeared from the river. After their disappearance, the progeny of post-winter and early monsoon occupied the same habitat in May to August.

The bottom panel of Fig. 16 indicates the trimodal age distribution of juvenile *Hilsa* from all the samples. From this it becomes clear that *Hilsa* spawn three times on a large scale in the Meghna River: early monsoon (June), late monsoon (October), and winter (January and March). Besides, the extended hatching date (August 1983 - July 1984) clearly indicates that some *Hilsa* also spawn on a small scale throughout the year in the Meghna River of North Chandpur in Bangladesh.

3.3 Migratory movements of juveniles

Because knowledge about migratory movements of juvenile *Hilsa* as well as of adult *Hilsa* is necessary for intelligent management (since both stages sustain a commercial fishery), an attempt has been made to study the migration of juveniles on the basis of research fishing (experimental seine and gillnet), as well as by examination of the catch in fishermen's gear, with special emphasis on the Meghna River of North Chandpur.
3.3.1 Length frequency analysis of experimental beach seine and fishermen's gear

Monthly samples of beach seine and fishermen's gear were examined for a nine month period. The total number of fish measured was 1439, of which 757 and 682 were from beach seine and fishermen's gear respectively. The fish were grouped in 1.0 cm intervals, and their percentage frequencies calculated, as shown in Fig. 17. The beach seine data represented juvenile *Hilsa* inhabiting less than 10 ft depths, while the samples of fishermen's gear represented the *Hilsa* in deeper water (>10 ft).

Length-frequency distributions of beach-seined fish had a single modal peak in December (5.0), March (8.0), May (4.0), June (4.0), July (5.0), and August (5.0), but were bimodal in January (4.0 and 6.0), February (4.0 and 8.0) and April (3.0 and 6.0). All size groups from 3.0 to 8.0 cm were represented in the catches of beach seine. Evidently young *Hilsa* (<8.0 cm) are the inhabitants of shore and shallow areas in the Meghna River.

Again, monthly length frequency data of fishermen's gear exhibited bimodal peaks in April (7.0 and 12.0) and a single modal peak in January (7.0), February (9.0), and March (10.0). The range of modal values was 7.0 cm to 12.0 cm which indicates the juveniles in deeper river are larger than those in the shore and shallow areas. Boat seine nets as shown in Fig. 4, which are generally operated in the middle of the river in
BEACH SEINE CATCH FROM RIVER AREAS (<10ft. DEPTH)

FISHERMEN'S CATCH FROM RIVER AREAS (>10ft. DEPTH)
deeper water, have a small mesh size (1/2-1")]. The mode in January at 7.0 cm perhaps indicates the size of immigration to deeper water. In January, the progeny of late monsoon immigrated to deeper water from the shore area, while in April the progeny of winter spawning showed their appearance in deeper water. The shifting of mode from January (7.0) to April (12.0) indicate the river residence growth. The non-availability of juveniles in May documented the migration of older juveniles out of the river. As the fish disappeared in May, the modal peak at 12.0 cm in April may indicate the size at migration from the river.

Prior to the present observations, the availability of juvenile *Hilsa* in December was unknown to fishery biologists and fishermen in Bangladesh. The availability of fish to the fishermen's gear in January clearly indicate the migratory movements of juvenile *Hilsa*; in December there was no evidence of the occurrence of juveniles in the catches of fishermen's gear. Evidently juvenile *Hilsa* below 8.0 cm prefer shore and shallow river areas, perhaps to avoid the strong currents of the deeper river.

The fish hatched in late monsoon and in the beginning of winter all moved into deeper water of the river and remained there (supporting the Jatka fishery) until they reached a size of about 12 cm before they migrated to sea in May. A few smaller sized fish may also migrate from the deeper river due to high downward flow in May. On the contrary, the fish
hatched in late winter and early monsoon were caught only inshore and at small sizes; possibly when they move into deeper water, which at that time of year is very swift, they do not remain there but are carried downstream to the sea.

3.3.2 Experimental gillnet sampling

Length frequency of juvenile *Hilsa* in the deeper water (>25 ft depth) in the Meghna River of North Chandpur, taken by experimental drift gillnets, are shown in Fig. 18. The first appearance of juveniles (10.0 cm) in the deeper river was recorded in February. Juveniles were abundant in April, and thereafter they suddenly disappeared. This corresponded with the cessation of commercial fishing for "Jatka" which also occurred in April (Fig. 17). Prior to the experiment, the assumptions of the author was that during the monsoon season (May-October) fishermen do not operate the young *Hilsa* catching net because the river is flooded and the currents are strong. This might have accounted for why juveniles in the monsoon have not been recorded by any author in Bangladesh. Now however, it is clear from experimental netting and also from personal communication with the fishermen that juvenile *Hilsa* are not available in the deeper river early in the season; the fishermen know this, and consequently, they do not operate their nets then. Experimental gill netting in deeper water therefore supports the conclusion that the juveniles migrate at that time from the river Meghna to other areas. As the season advances
the fishermen use clap nets, gill nets, and seine nets of bigger mesh sizes for catching adult Hilsa.

3.3.3 Gilling direction

To examine whether juvenile Hilsa migrate downstream or upstream, the gilling direction of fish taken in 7th April experimental drift net was recorded. From Fig. 19 it is evident that the fish ranging from 13 - 17 cm in total length were facing downstream, while the juveniles less than 11 cm (9.0-11.0 cm) were facing upstream. This finding coincides with the suggestion of the previous section that juvenile which had reached more than 11.0 cm started to migrate downstream. The fish under 12.0 cm, facing upstream, may have been holding position; the larger fish, facing downstream, can not have been doing so.

3.3.4 Juvenile sizes in different regions of River Meghna

As a further check on their direction of migration, juveniles were sampled from the upper, middle and downstream areas in Bangladesh, in each of four months during the peak season of Jatka availability. Monthwise mean total lengths are shown in Fig. 20. From the figure, a gradual increase of mean lengths of older juveniles was observed from upper to downstream areas in the samples of March and April. On the other hand, a gradual decline of mean lengths of small juveniles was observed in the samples of July and August. The gradual increments of mean length from upper to downstream areas indicates the congre
FIGURE 19. Gilling direction of juvenile *Hilsa* caught by experimental gillnet in the Meghna River on April 7, 1984. Boat was drifting downstream during sampling period.
FIGURE 20. Mean total length of juvenile Hilsa in the different areas. Upper areas - fish from the River Padma, collected from Paksey and Rajshahi; middle areas - fish from the River Meghna, collected from Chandpur; lower areas - fish from the estuary, collected from Barisal.
The diagram shows the total length (cm) of fish by area and time from March to August. The data is represented for three areas: Upper, Middle, and Lower, with each area indicated by different symbols. The y-axis represents the total length in centimeters, ranging from 1.0 to 13.0 cm. The x-axis represents time in months: March, April, July, and August. The sample size, N = 743, is indicated on the graph.
gation of larger juveniles in the downstream areas, which may be the result of migration of juvenile *Hilsa* from the Meghna and Padma Rivers. In addition, the non-availability of larger juveniles in the samples of July and August from the upper area showed that although the smaller-sized juvenile were facing upstream when gilled (Fig. 19), their net movement over time was downriver. Also, the larger size gradient of smaller juvenile may be the evidence of early winter spawning in the upper river.
4. DISCUSSION

4.1 Spawning periods

Day (1873) was the first to attempt to determine the spawning grounds and breeding season of *Hilsa ilisha* in the Indian region. Since then, much attention has been focussed on the study of breeding and bionomics of this fish, both by Indian and Bangladeshi authors. In Bangladesh, based on the studies of ova maturity and gonad size index, Shafi *et al.* (1978) and Quddus *et al.* (1984) attempted to determine the spawning seasons of *Hilsa ilisha*. Similarly, in India, based on gonad size index and ova maturity studies, several authors (Pillay 1958, Nair 1958, Pillay 1963, Mathur 1964, Ramakrishnaiah 1972, and De 1980) studied the spawning seasons of the species. In India, many authors, such as Nair (1939), Hora and Nair (1940), Jones and Menon (1950, 1951), Chandra (1962), and Bhanot (1973), also tried to estimate the extent of the spawning seasons based on occurrence of eggs or juvenile *Hilsa*. Until now, no attempt has been made by any author, either in India or in Bangladesh, to study the spawning activities of *Hilsa* in different habitats (marine, estuarine and river) during the same period of time.

Based on gonad size index and ova maturation studies in India, Motwani *et al.* (1957) reported that the breeding of *Hilsa* in the Ganges would appear to commence with the onset of the monsoon season in July, with peak breeding from September to December. Pillay (1958) has described the breeding season in the Hooghly as from the beginning of the southwest monsoon to November and again from January to
February or March. Mathur (1964) observed two spawning seasons in the upper stretches of the Ganges, the first commencing in February and lasting until April with a peak during March. The second spawning was found to start in August and to terminate in November with a peak in October. Again, in Narbada in India, Karamchandani (1961) found that the main spawning season commences in June-July and continues up to September, the peak being in August. For the Ganga-Hooghly system, Pillay and Rosa (1963) suggested that there may be two distinct spawning seasons with a period of time between: one which begins at the start of the southwest monsoon (June) and continues through to November, and a second which occurs from January to March. In Bangladesh, Shafi et al. (1978) concluded that there are two spawning seasons: one from January to March and the other from July to October. Quddus et al. (1984) observed that Hilsa breeds at two different times, June to October with a peak in September and December to March with a peak in February.

In the present study, based on the gonad indices, two distinct spawning seasons, with a period of time between, were considered. Monsoon breeding started in the beginning of the season (June) and continued to November with peaks in June and October, and winter breeding began in the winter (January) and terminated in April with peak period in February and March. The present findings not only corroborated the results of Indian authors but also supported the observations of Shafi et al. (1978) and Quddus et al. (1984) in Bangladesh regarding the establishment of two distinct spawning seasons of Hilsa. About the peak time period of spawning, a slight
difference was noted between their works and the present. Both of their studies were confined to different river systems in the upper stretches in Bangladesh (Meghna and Padma River). On the other hand, in the present study, samples were taken from three habitats (marine, estuarine, and Meghna River) with an aim to determine the spawning time of *Hilsa* in different habitats. From the results, it was clear that riverine and estuarine habitats represented two spawning seasons with three major time periods, while the marine habitat showed a peak period of maturation. In winter spawning, a slight difference was noted between the Meghna River *Hilsa* and the estuarine *Hilsa*; those in the Meghna River spawn in February whereas those in estuaries spawn in March. Hence, it may be that, like the Fraser River sockeye salmon (Ricker 1950) and Ganges *Hilsa* (Ghos and Nagpal 1970), there are also populations which spawn in the upper stretches and in the lower stretches in the Bangladesh waters during late winter months. These findings support the opinion of Job (1942) that the breeding period is slightly variable from place to place, due to different ecological conditions. Recently, similar suggestions were made by Melvin (1984) in Bangladesh, who stated that the spawning season of *Hilsa* has been reported to vary from a few months to year-round, depending on the river and author. For instance, Kulkarni (1950) and Islam and Talbot (1958) observed in the rivers Godavari (India) and Indus (Pakistan), a single breeding season instead of two seasons.

Winter breeding of *Hilsa ilisha* in the Gangetic system has for a long time been a controversial issue. Some authors rejected the possibility of winter breeding, while others disagreed in their
opinion as to the time of spawning. Ghos and Nagpal (1970), based on their collection of pre- and post-larvae in the Ganga River system, surmised that Hilsa breeds there in the winter season. In addition, a systematic larval survey conducted by the Central Inland Fisheries Research Institute during the years 1965 and 1966 revealed the presence of post-larvae in the collections during the month of March, thereby indicating the possibility of winter spawning of this species. Both Shafi et al. (1978) and Quddus et al. (1984) reported the existence of winter breeding in Bangladesh waters. On the contrary, Jones and Menon (1951), based on scarcity of the pre- and post-larvae of the species in routine plankton hauls, concluded that the breeding in the Hooghly is very restricted if not at a standstill during the winter months of December and January. Again, from studies on the distribution and abundance of fish larvae in the Hooghly estuary, Chandra (1962) inferred that there is no winter spawning of this species. The present findings in winter breeding, based on the study of gonad size index, the availability of young Hilsa (Fig. 21) and back-calculations of hatching date, clearly showed the existence of winter breeding in the Bangladesh areas.

Whether Hilsa spawns in the sea is still a controversial issue in the Indo-Bangladesh region. Pillay (1963), the only author who reported the Hilsa breeding in the sea on the Saurastra coast in India, probably based her opinion on the presence there of maturing, mature and spent fish. In the present study, the evidence of both ripe and spent Hilsa in the habitat (Table 2) suggests that spawning may occur there, unless the fish are making brief trips into nearby
FIGURE 21. Diagrammatic summary of seasonal timing of adult maturity (G.S.I. = Gonadosomatic Index), hatching, growth and movement of young. Peak hatching times indicated by triangles, extent of principal hatching periods by horizontal bars. Open circles are mean lengths from experimental seining inshore; solid circles are mean lengths from fishermen's catch offshore; vertical lines are size ranges. Diagonal lines suggest boundaries for offspring from different principal spawning periods.

<table>
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<tr>
<th>Month of Sampling</th>
<th>Maturing</th>
<th>Mature</th>
<th>Spent</th>
<th>Sample Size</th>
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<td>21</td>
<td>4</td>
<td>24</td>
</tr>
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<td>12</td>
<td>25</td>
</tr>
<tr>
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<td>46</td>
<td>0</td>
<td>54</td>
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</tr>
<tr>
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<td>67</td>
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<td>33</td>
<td>24</td>
</tr>
<tr>
<td>March</td>
<td>4</td>
<td>0</td>
<td>96</td>
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</tr>
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</tr>
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<td>32</td>
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</tr>
<tr>
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<td>24</td>
<td>68</td>
<td>8</td>
<td>25</td>
</tr>
</tbody>
</table>
estuaries or rivers to release their eggs. (Comparable data on spawning condition for Meghna River and estuarine Hilsa are shown in the Appendix). However, as there is as yet no evidence of availability of eggs and larvae in the marine habitat, the question of whether spawning actually occurs there must remain open at present.

Difference in breeding behaviour with respect to salinity is not unusual among fishes of the genus Hilsa. Hilsa toli, which breeds in the sea on the Indian coast (Chacko-Krishnamurthy 1949), is known to breed in freshwater rivers in Thailand (Smith 1945). In shad as a group variation in behaviour of this type has also been observed. Though the European and American shads (genus Alosa) breed in freshwater, the West African shad, Ethmalosa dorsalis, has been found to breed near shallow offshore banks in the Sea of Sierra Leone (Bainbridge 1961). Gras (1958) has reported that the stock of this shad in Lake Nokone (Dahomy) breeds in the lake (lagoon) itself, unlike the marine stocks, which are known to breed only in the sea.

It has yet to be determined whether Hilsa spawning at different seasons in the Meghna River represent different races with distinctive morphometric or other characteristics. Guddus et al. (1984) have reported that there are two races separable on the basis of relative body depth. However, our own preliminary investigations, not reported here, suggest that body depth varies considerably with sexual conditions of the fish, and is not strictly isometric, so its use as a racial indicator requires further study.
4.2 Early growth and hatching date

One of the major handicaps in the study of Hilsa biology has been the lack of a suitable method for age determination. A review of literature shows that many workers, especially in India (Hora and Nair 1940), Chacko et al. (1948), Raj (1951), Jones and Menon (1951), Menon (1953), Pillay (1958)), have tried to determine the age of Hilsa by the scale method. However, seasonal annulus formation does not take place in the scale. They also tried to interpret spawning marks on the scales, but the results have not been encouraging so far. In addition, Pillay (1958), Pillay and Rao (1962), and Rajyalakshmi (1973) tried to determine the age of Hilsa by using length-frequency polygons. The method has not been reliable because the analysis is often confounded by extended hatching periods, and sometimes by size selective sampling.

That the use of otoliths in aging Hilsa fish might be possible was first suggested by Shafi et al. (1976) in Bangladesh. Later, Guddus et al. (1984) determined the age of adult Hilsa through the readings of annuli in otoliths. According to them, the annulus was formed in otoliths at the time of spawning. Recently, Raja (1984) in India reported that hard parts like scales and otoliths have been tried, but that the results have not been encouraging or that they require confirmation. However, even in the absence of annuli, the growth rings in otoliths may be useful to age fish. The use of daily growth rings in aging fish is a well-established technique in temperate and a few tropical areas, but the present study is the first
attempt in the Indo-Bangladesh region to estimate age of juvenile *Hilsa* by using growth rings in the otoliths.

Crecco *et al.* (1982) suggested that in Connecticut shad larvae the first growth ring was deposited shortly after hatching. Daily ring deposition was validated by many authors using larvae of known age (Taubert and Coble 1977, Barkman 1978, Neilson and Geen 1982, Wilson and Larkin 1982), by rearing wild fish in enclosures (Wilson and Larkin 1980), or by the incorporation of time markers (Campana and Neilson 1982, Neilson and Geen 1984). In many cases, the ring deposition rate was assumed to be constant for the entire larval period over a wide range of environmental conditions (Geffen 1982). Taubert and Coble (1977) and Methot and Kramer (1979), however, reported that ring deposition ceased under severe conditions of starvation or low temperature but indicated that as long as growth continues, larvae will deposit one ring per day.

Although tetracycline and saline immersion experiments were unsuccessful in the present study to validate the daily formation of rings in *Hilsa* otoliths, the agreement of the Peterson method with age as determined by growth rings suggested that the rings were formed at the rate of one per day, and that the first ring may be formed just after hatching.

The otoliths of the smaller size group of *Hilsa* showed clear rings in the whole otolith, but in older *Hilsa* the growth rings were not clearly visible in all areas. The direct and indirect methods of counting did not give any significant differences in size groups up to 4.9 cm. Therefore in this study, although it was not possible to
extend direct counts to older size groups (>5.0 cm), it was assumed that age determination in older size groups by the Ralston method (indirect) might be reliable. The 2.0 cm size group *Hilsa* showed 30 rings, which was consistent with the month-wise progression of modal values of 2.0 cm found by the Peterson method. Growth rings could be counted in juvenile *Hilsa* 12.0 cm long, which showed 171 rings and so were approximately 6 months old. Hence, it is suggested that age determination through otolith-growth rings is possible in order to age *Hilsa* juveniles up to about 12 cm (approximately 6 months old). These findings agree with Brothers (1979) who reported that growth rings often become unclear after about 200 days. Uchiyama and Struhasker (1981) reported that counting rings in whole mounted otoliths of skipjack and yellowfin tuna becomes progressively more difficult with increasing specimen size. Recently, Campana and Neilson (unpublished MS) reported that the utility of otolith microstructure examination for age determination beyond one year is questionable, particularly in species found in temperate zones.

Information on hatching date can be determined from the examination of otolith rings. Many authors, such as Ralston (1976), Struhasker and Uchiyama (1976), Townsend and Graham (1981), Steffensen (1980), and Lough et al. (1982), have used the otolith microstructure to determine the hatching date of fishes. In the present study, the hatching time of juvenile *Hilsa* was determined by the same method. The observed trimodal peaks in hatching time indicate that there are three major spawning times for *Hilsa*. These findings supported the
evidence for three spawning times of *Hilsa ilisha* in the Meghna River of Bangladesh based on gonad size index (Fig. 21).

4.3 Migratory movements of juveniles

A review of literature on migratory movements of *Hilsa ilisha* revealed that much attention has been paid to migration of adults, but migratory information on juvenile *Hilsa* is scanty and conflicting. The migratory behaviour of *Hilsa* described by many workers, has been based almost entirely on catches by commercial fishing equipment. The information on migratory movements of juvenile *Hilsa* obtained in the present study are based on experimental gill and seine nets, length data analysis of fishermen's catch, and collected samples of juvenile *Hilsa* in the different areas in Bangladesh. This is the first attempt undertaken specifically to provide a picture of juvenile *Hilsa* migration.

Based on the results of experimental beach seining (Fig. 21), it was observed that juvenile *Hilsa* less than 8.0 cm in total length live in the shore and shallow areas (<10 ft. depth) in the river. When they attain larger size, they migrate to the deeper river, and sustain a fishery there. Based on length data analysis of fishermen's gear catch, (Fig. 21) January was the time of congregation of juvenile *Hilsa* in deeper river (>10 ft. depth). May was the month for total migration of these fish from the river. A mean length of 7.0 cm in January corresponded to the immigration size to the deeper river; a mean length of 12.0 cm in April corresponded to the migration size from the river (Fig. 21). The total disappearance of juveniles in May
from the deeper water in the river Meghna of North Chandpur clearly suggested the migration of juveniles from the river.

These findings are in general agreement with those by other workers on related species, or on *Hilsa ilisha* in other waters. According to Jones and Menon (1951), eggs and larvae of *Hilsa ilisha* were present in larger numbers near the bank than in the middle or the river where the current was stronger. Regarding the distribution of *Hilsa* larvae in different water zones, Ghos and Nagpal (1970) concluded that the larvae prefer marginal waters in the regions where the total depth does not exceed approximately 1.3 m (4.3 ft.); practically no larvae occur in the deeper layers. Marcy (1976) noted that ova of American shad (*Alosa sapidissima*) are semi-buoyant and drift along the river bottom. Newly hatched American shad larvae also remain near the bottom until the yolk is nearly gone, after which they swim near shore and become susceptible to seine sampling.

Concerning the timing of the fishery for juvenile *Hilsa*, in India Sujansinghani (1957) concluded based on length data analysis of fishermen's catch that juveniles are generally abundant in the cold season from November to January; there is a marked decrease in numbers from February onwards, with practically no young *Hilsa* in the catches towards the end of March. Rao (1969) said that in the lower reaches of Godavari estuary in India the juvenile fishery extends from January to June with a peak period from February to April. He also reported that most of the fish from the catches ranged from 9 cm to 15 cm, and only a few are bigger from 16 cm to 19 cm. In Bangladesh, Melvin (1984) reported that the Jatka (young *Hilsa*) fishery begins around
January and continues until April when the fish suddenly vanish. In the present study, based on experimental gill netting, February was observed to be the time of appearance of juvenile Hilsa in the deeper river, and May was the time of disappearance from the river. These findings corroborate the observations on length data analysis of fishermen’s gear data discussed above.

The disappearance of young Hilsa from the river indicated the migration of the juveniles. Which direction they migrate becomes an essential matter of the discussion. A review of the literature showed that conflicting opinions were expressed by many authors. Their conclusions were based on the analysis of fishermen's catch. In favour of downward migration, Hora (1938) based on the collection of young specimen at Nowabganj in India during November-February, concluded that the young fish do not reside in the river but pass down to the estuaries. Sujansinghani (1957) said that there is a large-scale downward movement of fish commencing about January-February. Pillay (1958) observed that spent Hilsa as well as their progeny migrate down the rivers and the lower estuaries, and that the coastal areas form the habitat of the species. Ramakrishnaiah (1972) based on observation of catches of fixed purse nets in November-January concluded that larger juveniles moved downward into foreshore areas. On the other hand, Pandit and Hora (1951) believed that in March-April the young, known as Jatka, enter East Bengal (Bangladesh) waters in large swarms for feeding and form an independent fishery. According to Hora and Nair (1940), the Jatka caught in East Bengal rivers are five months old and are migrating up from the estuaries for feeding.
It has, however, been shown by Pillay (1958) that these fish are mature and migrate upriver for spawning. According to Pillay (1952) and Pillay et al. (1963) the range of migration of *Hilsa* is probably not as great as was originally believed, and the fisheries of the Gangetic River system depend on more than one stock. In the present study, the analysis of gilling direction of fish in the experimental gillnet sampling in the Meghna River during the period October-August, and the recorded information of gradual increments of mean length downstream, strongly support the existence of a downstream migration of juvenile *Hilsa* in Bangladesh waters.

The downstream migration is also supported by reports of older juvenile *Hilsa* in the estuary and the sea. With reference to *Hilsa* in South India rivers, Raj (1937) stated that the fish spends the first year of its life in the lower reaches of the rivers, and goes to the sea in the third year. Naidu (1939) reported that shoals of small-sized *Hilsa* of 9"-10" begin to make their appearance in October-November every year along the foreshore of the Bay of Bengal, even south to Cox's Bazar (Bangladesh), and in the mouths of rivers including the Hooghly (India). Mozumder (1939) refers to the presence of *Hilsa* 9"-10" long along the Chittagong Coast in Bangladesh. Prashad et al. (1940) stated that the fish migrates into the sea during the first year of its life, where it moves along the foreshore and does not go far out into the sea. The appearance of young *Hilsa* (21-24.0 cm) in the coastal areas in Bangladesh in October and November was reported by Raja (1984). On the other hand, no literature is available to suggest of the appearance of shoals of young
Hilsa in the upper areas, either in India or in Bangladesh. Hence, it seems fairly certain that young Hilsa migrate downstream.

The factors triggering the downstream migration of juvenile Hilsa are still unknown. Only the author Melvin (1984) surmised that rising temperatures might serve to trigger the young Hilsa to leave the rivers. In contrast, extensive work on the subject has been done by many authors in North America on juvenile American shad. The timing of the emigration of juveniles from the rivers, like that of the spring spawning migration of the adults, is closely linked to changes in water temperature (Sykes and Lehman 1957, Chittenden 1969, Leggett and Whitney 1972) and occurs sequentially. The downstream migration of juvenile shad occurs when water temperature falls below 15.5°C. Marcy (1976) noted that the time of the emigration of juvenile shad from the Connecticut River was also partially length-dependent, the fastest growing and hence largest juveniles leaving the river first. The length-dependence may be related to the swimming ability of juvenile shad to meet the requirements of the marine migration. The final emigration from the river is associated with the high river flows and low temperatures of the late autumn. Leggett (1977) stated that these findings support the hypothesis of Foerster (1954) and Burgner (1962) that size and emigration may serve as an important density-dependent regulator of survival in shad, just as it does in salmon. In the present study, it is possible that a length-dependent factor is responsible for the emigration of juvenile Hilsa from the deeper river along with other associated factors, such as rising temperature and high river flows during the monsoon. It is notable
(Fig. 21) that young hatched from late monsoon spawners remain in the river and grow large enough there to support an offshore Jatka fishery during the low discharge winter periods. On the other hand, young hatched from winter spawners do not reach a size large enough to move offshore until after the monsoon floods begin; they support no Jatka fishery, and may in fact be swept downstream at a smaller size than that of their late monsoon counterparts.
LITERATURE CITED


Neilson, J.D. and G.H. Geen. 1982. Otoliths of Chinook salmon (*Oncorhynchus tshawytscha*): daily growth increments and factors


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