Spawning seasonality of hilsa (*Tenualosa ilisha*) in Myanmar's Ayeyarwady Delta

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The hilsa is a critically important species for small-scale fishing communities in Myanmar's Ayeyarwady Delta and Rakhine State. Yet current fishing regulations are inadequate and exploitation rates are well beyond sustainable levels. This study analyses key parameters underlying hilsa biology, comparing them across different ecological zones of the hilsa's range in Myanmar and across time. It provides evidence of major spawning activity between July and September in the freshwater zone, particularly in September. We recommend that policymakers restrict access to fishing in freshwater areas at least during the month of September; promote and enforce measures to protect juvenile hilsa; establish marine protected areas to conserve spawning stock biomass; and ensure effective, adaptive fisheries management throughout migratory routes.

Contents

Summary

The hilsa is a crucially important resource for small-scale fishing communities in Myanmar's Ayeyarwady Delta and adjacent Rakhine State. Yet current fishing regulations are inadequate and rates of exploitation are well beyond sustainable levels. In Bangladesh, the effective enforcement of fishing restrictions to protect spawning hilsa and the creation of sanctuaries in nursery grounds are thought to have contributed to an increase in hilsa production of more than 100% over the last 15 years.

To be effective, fishing restrictions must be based on an understanding of the reproductive biology of hilsa, particularly their size at first maturity, the onset and duration of spawning seasons, and the location of spawning grounds. Any restrictions must not only coincide with the main spawning season, but also last long enough to allow sufficient spawning. This study analyses key parameters of hilsa biology across the species' migration route, in order to develop a more detailed picture of hilsa reproduction in Myanmar and to determine the optimum timing for fishing restrictions.

From November 2017 to November 2018 (inclusive), samples of hilsa were taken on a monthly basis from sites in the three ecological zones: fresh water, brackish water and saline water. We assessed seasonal and spatial patterns in the length–weight relationship, gonadosomatic index (a measure of reproductive capacity), sex ratio, and maturity of the hilsa. Together these parameters were used to assess spawning behaviour and provide a robust basis for effective fishery management.

The hilsa specimens caught in fresh water were significantly smaller and lighter than those caught in brackish and saline water. This indicates that hilsa spawn in the freshwater zone, which also provides a nursery area for juveniles before they migrate towards the coast, where they reach maturity. The females caught in brackish and saline water were heavier and larger than other specimens, indicating that they migrate from the saline zone through the brackish zone to fresh water, where they release their eggs (resulting in significant weight loss). In these areas, females were heavier than males, owing to their greater gonad weight. Negative allometric growth (exponent parameter $b < 3$) was observed in September, indicating that fish had released their gonad products at this time. This suggests that September is a significant month for spawning.

The gonadosomatic index (GSI) represents the relative weight of the gonad to body weight. This study focused on female fish, which have a larger gonad size and greater variation in gonad weight over the course of the reproductive cycle. Mean female GSI values varied most in the freshwater zone, indicating that more brood fish congregate and release their eggs in this zone. Peaks in mean GSI values (indicating a larger number of fish with ripe gonads) were observed in the freshwater zone in July, April, and November 2018, probably suggesting more than one spawning season. A steep dip in the mean freshwater GSI values between the highest peak in July to the lowest trough in September, combined with a parallel drop in length–weight relationship parameter b, indicates that August–September is the main spawning season. In brackish water, mean GSI values peaked in June and November 2018, indicating that gonads have grown as fish migrate upstream for spawning in freshwater. Mean female GSI values were least variable in the saline zone, with peaks in February and November 2018, which could be an indication that gonads have begun to grow with the initiation of spawning migration.

Within the saline zone, mature fish (80%) were much more abundant than immature fish, whereas in fresh water, immature fish predominated (77%). This highlights the importance of fresh water as a favourable habitat for spawning and as nursery grounds for immature hilsa before they migrate downstream through brackish waters to reach maturity in coastal waters. Across all ecological zones, the percentage abundance of immature hilsa peaked in December (59%) and November 2018 (55%), and was lowest in June (6%), which is consistent with major spawning activity occurring in August–September. In the freshwater zone, where most spawning activity occurs, immature hilsa were most abundant in August (93%) and September (94%), declining to a low of 27% in April. This could be evidence of additional spawning seasons in January–February and April–May. In brackish water, the percentage abundance of immature hilsa peaked in November 2018, probably reflecting their migration path towards the sea after spawning in August and September.

The sex ratio of hilsa samples can provide an indication of where and when male and female hilsa gather together. Overall, and in fresh water, females predominate over males, while in brackish and saline

waters, sex ratios are more equal. Among immature hilsa, females predominate over males, whereas the ratio is closer to 1:1 for mature hilsa. This could reflect a difference in growth rates between males and females, or some form of hermaphroditism. The sex ratio divergence observed in fresh water probably reflects the divergence seen among immature specimens, supporting other evidence from this study that the freshwater zone is an important spawning area and nursery area for immature hilsa. Fluctuations in sex ratio by month indicate that males and females congregate for spawning in July, September, and March–April, but larger sample sizes would be required to draw robust conclusions.

Our findings demonstrate when and where spawning hilsa most require protection and highlight the need for different management strategies in different ecological zones. Specifically, we offer the following conclusions and recommendations:

- **Current fishing restrictions do not coincide with main hilsa spawning season.** Monthly patterns in GSI and length–weight relationship clearly support the existence of a peak spawning season in September. Myanmar's current fishing restrictions between May and August therefore do not adequately protect hilsa during its main spawning season. We recommend that access to fishing be restricted in freshwater areas during the month of September.
- **Freshwater nursery grounds require year-round protection.** The spatial distribution of fish size and maturity across zones clearly shows that the freshwater zone holds both spawning grounds and nursery grounds. It is therefore important to introduce measures here for the protection of juvenile hilsa, such as mesh-size regulations and sanctuaries where fishing is restricted throughout the year, or at least for long enough after the main spawning season to allow time for recruitment.
- **Marine protected areas could support spawning stock.** We recommend the creation of no-take marine protected areas to protect mature hilsa, which we have shown spend time predominantly in the saline zone.
- **Migratory routes must be maintained.** The success of these management measures depends upon the maintenance of upstream and downstream migration routes. Effective enforcement of current fishing restrictions may protect hilsa on their upstream migrations, but this study suggests that June may be the most critical month during which to focus restrictions. More research is required further assess migratory routes and timings.
- **Management should be adaptive.** It is important that the spatial and temporal aspects of each of these management measures are flexible and adaptable enough to keep pace with environmental change. Inter-annual variation in the length and timing of spawning seasons, and the environmental factors which underpin it, should therefore be monitored over the long term if fishing restrictions are to be effective into the future.
- **Research gaps:** There is evidence of more than one spawning season in Myanmar, but we cannot establish with certainty when or where additional spawning periods occur without further investigation through analysis of gonad histology or otolith microchemistry. Until such research findings are available, we recommend focusing management measures to protect spawning hilsa in the period in which we can say with certainty that large numbers of hilsa spawn, namely August and, particularly, September.

1

Introduction

The hilsa shad (*Tenualosa ilisha*, locally known in Myanmar as *Nga Tha Lauk*) is a member of the ray-finned Clupeidae family, which also includes herrings and sardines. As a euryhaline clupeid, the hilsa tolerates a wide range of salinity and is distributed throughout freshwater, estuarine, and coastal regions of South Asia, from Kuwait in the Persian Gulf eastwards to Myanmar in the Bay of Bengal (Whitehead, 1985). Hilsa supports important commercial fisheries, particularly in Bangladesh, Myanmar, and India. It is fast growing, reaching sexual maturity within six to 12 months and living for up to six or more years (Milton, 2009; Rahman and Cowx, 2008).

The hilsa is typically understood to be anadromous, migrating from marine to freshwater for spawning, but it also demonstrates amphidromy, whereby immature fish migrate between fresh and marine waters for non-spawning purposes (Rahman et al., 2018). Spawning migration is thought to take place in large numbers with the onset of the southwest monsoon (mid-May to late October) and associated flooding, when water depth, current velocity, and temperature are favourable (Ahsan et al., 2014; Bhaumik, 2015a). However, movements are complex and varied, and some permanent (ie non-migrating) freshwater and marine stocks have also been observed (Bhaumik, 2015a). Within the Bay of Bengal, scientific techniques, such as the analysis of otolith microchemistry and allozyme variation, provide evidence of substantial gene flow between groups of hilsa, indicating that fish in Myanmar may also have spawned in India or Bangladesh and vice versa (Milton and Chenery, 2001; Salini et al., 2004).

In Myanmar, the hilsa is distributed throughout the Ayeyarwady region and adjacent Rakhine State, migrating between inland rivers and the coastal zone (Baran et al., 2015). Owing to its relatively high value (DoF, 2018), it is the main target species in these areas and a major source of income for vulnerable fishing communities (Khaing et al., 2019). Yet there is evidence that overfishing and habitat destruction are threatening the sustainability of Myanmar's hilsa fishery. Exploitation rates (the proportion of mortality caused by fishing) have been found to reach 0.7 in the Ayeyarwady region, well beyond the sustainable threshold of 0.5 (BOBLME, 2015). Hilsa are often targeted in Myanmar during spawning runs and juveniles are caught when fishing nets with small mesh are used, reducing recruitment (Baran et al., 2015; Khaing et al., 2019).

Under Myanmar's *Freshwater Fisheries Law* (1991), all open-access inland and inshore marine fisheries are closed from May to July to protect the spawning and recruitment of commercial fish species (not only hilsa). Specific timings vary between locations depending on the time at which local target species are expected to spawn. The catch and captivity of freshwater juveniles, spawning fish, and fish ready to spawn are also banned from May to August. These regulations were developed on the basis of research by organisations including the World Wide Fund for Nature (WWF), the International Union for Conservation of Nature (IUCN), Fauna and Flora International, WorldFish, and bilateral and multilateral donors under the Myanmar Fisheries Partnership (Akester, 2019). However, they were not designed specifically with the spawning and migratory behaviour of hilsa in mind and fishery closures are rarely enforced (Soe et al., 2018; Tezzo et al., 2019).

Previous studies of hilsa throughout the Indo-Pacific have called for the protection of spawning and nursery grounds, a reduction in juvenile catches, and regulatory compliance to rebuild depleted stocks (Ahsan et al., 2015; BOBLME, 2012). The government of Bangladesh has implemented fishing-access restrictions for the protection of spawning hilsa during the month of October (spawning is thought to take place in September and October) (Islam et al., 2016a). Monitoring and enforcement of a 22-day ban on fishing is targeted to areas thought to hold important spawning grounds. Although not all fishers comply and there are still improvements to be made, there is evidence to suggest that the restrictions have contributed to an increase in hilsa production of more than 100% over the last 15 years (Bladon et al., 2016; DoF, 2017; Islam et al., 2016b). Sanctuaries in hilsa nursery grounds are also thought to have contributed to the increase in catches in Bangladesh (Islam et al., 2016b; Islam et al., 2018).

To be effective, spatial and temporal fishery closures must be based on an understanding of the reproductive biology of hilsa, particularly size at first maturity, the onset and duration of spawning seasons, and the location of spawning grounds. Any closure must not only coincide with the main spawning season(s), but also be long enough to allow sufficient spawning. A great deal of research has been conducted on hilsa reproduction, particularly in Bangladesh and India (Amin et al., 2008; Ahsan et al., 2014; Haldar and Amin, 2005; Rahman and Cowx, 2008). However, the spawning behaviour of hilsa varies throughout its range and over time, according to fluctuations in rainfall, upstream runoff, sediment input, and variation in habitat types (Hossain et al., 2019). It is therefore essential that spawning behaviour is assessed – and monitored over the long term – within Myanmar.

Studies in Myanmar have used local ecological knowledge from fishers to identify migration routes and spawning sites of hilsa (Baran et al., 2015; Ko Ko et al., 2016). Baran et al. (2015) identified spawning sites in 15 out of 32 locations surveyed, with the largest and most important found in the Hinthada Township area, which is located 230 to 310km from the sea. Local knowledge indicated that spawning takes place during March–April in the majority of spawning sites identified, but further investigation was recommended. In another study, over 50% of household survey respondents placed the main spawning season in April or May (Khain et al., 2018).

The aim of this paper is to interrogate the existing understanding of spawning seasonality in hilsa, in order to determine the optimum timing for fishing restrictions. We assess seasonal and spatial patterns in the length–weight relationship, gonadosomatic index (a measure of reproductive capacity), maturity, and sex ratio of hilsa. Analysed together, these parameters can be used to assess spawning behaviour and provide a robust basis for effective fishery management.

The paper is structured as follows: first we describe the methods used for sampling the fish and collecting and analysing their data (Section 2), then we present and discuss the results (Section 3), before providing conclusions and policy recommendations (Section 4).

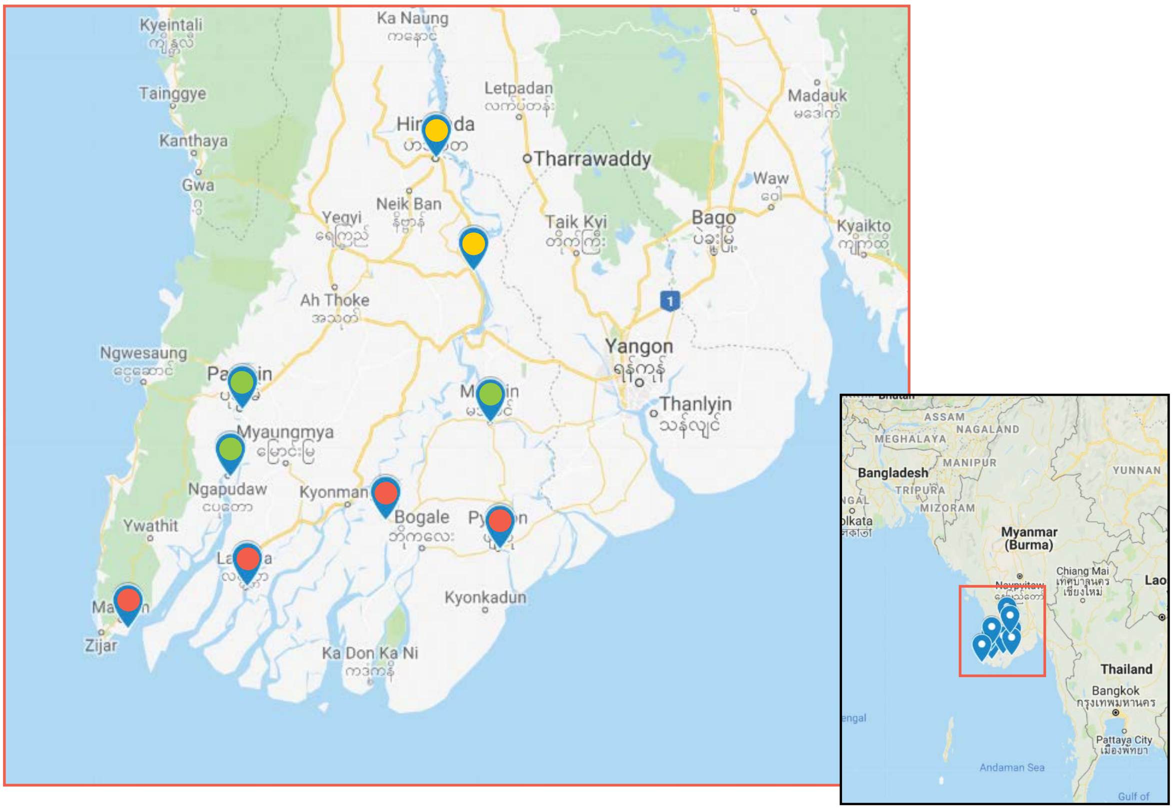
2

Methods

2.1 Study sites

Through consultation with township-level fisheries managers from the Department of Fisheries (DoF) of the Ministry of Agriculture Livestock and Irrigation (MoALI) of Myanmar, we selected nine study sites from the Ayeyarwady region on the basis of their importance as habitats for hilsa and the accessibility of their landing sites (see Fig. 1). Although there are seasonal variations during dry and wet seasons, each of these sites falls within one of three ecological zones: fresh water, brackish water, or saline water.

Figure 1. Map of study sites in different ecological zones in the Ayeyarwady Delta region: Hainggyi, Labutta, Mawlamyinegyun and Pyapon townships (saline sites in red); Maubin, Ngapudaw, and Pathein townships (brackish sites in green); and Danuphyu and Hinthada townships (freshwater sites in yellow).



Two freshwater sites were selected from the Ayeyarwady River system in Hinthada and Danuphyu townships. Although there is anecdotal evidence that hilsa have been seen as far upriver as the Chindwin-Ayeyarwady River intersection at latitude 21.5^{0}, local fishers tend to view these townships as the northern-most hilsa fishing sites. Hinthada was described as a shallow, seasonally flooded nursery area for hilsa and an important seed collection site for commercial inland aquaculture. Three brackish water sites were selected from Ngapudaw, Pathein and Maubin townships. These are areas with large and small rivers connected to the Ayeyarwady River that experience tides and saltwater intrusion. Maubin is thought to be important for spawning hilsa, owing to the convergence of the Maubin, Yangon, and Toe Rivers. Four sites were selected from the coastal saline zone in Hainggyi, Labutta, Mawlamyinegyun, and Pyapon townships. These are important fishing grounds for hilsa all year round.

2.2 Sampling and dissection

A team of fisheries scientists from the University of Yangon took monthly samples, totalling 8,793 hilsa fish, from catch landed by fishers from November 2017 to November 2018 (inclusive), with a sample average of 676 fish per month (see Table 1). They sampled the fish at approximately equal intervals during the last week of each month. Weight and length measurements were recorded for each specimen. Of these samples, 982 (an average of 75 specimens per month) were randomly selected and dissected to determine their sex. For most of these specimens (a sub-sample of 943), weight and length of the gonad (reproductive gland) were also recorded. Of the specimens selected for dissection, 519 were purchased, washed, stored on ice (with a fish-to-ice ratio of 1:2 by weight), and transported to the laboratory of the University of Yangon's Zoology Department within a 36-hour period. On arrival at the laboratory, each fish was dried with a paper towel before being weighed, measured and dissected. Owing to budget restrictions, the rest of the specimens were examined at the collection site, before returning to sellers.

The team measured the total length (TL) and standard length (SL) (excluding the tail fin) of each fish using a vinyl measuring sheet, calibrated in centimetres (cm) (Fig. 2). They measured whole body weight using a digital balance (Electronic Compact Scale SF-400A), accurate to 1 gram (g). For the fish that were dissected, their sex was determined according to the location and appearance of gonads. The gonads were removed and weighed using a microbalance (CAMRY) with a digital scale accurate to 0.001g. A measuring tape was used to measure the length of the gonads in millimetres (mm).

Table 1. Location of study sites, sample sizes, and sub-sample sizes. Sub sample included only specimens which were dissected for gonad examination.

STUDY SITE	RIVER SYSTEM	SAMPLE SIZE	SUB-SAMPLE SIZE
Freshwater zone			
Danuphyu	Ayeyarwady	1010	127
Hinthada	Ayeyarwady	868	113
Brackish water zone			
Ngapudaw	Nghat Pauk / Thet kae thoung	970	91
Pathein	Nga Won / Thet kae thoung	1075	94
Maubin	Toe River	913	115
Coastal zone			
Hainggyi	Nga Won / Thet kae thoung	1004	109
Labutta	Ywae / Pyan ma lut	908	103
Mawlamyinegyun	Hlaing Phone	1083	94
Pyapon	Pyapon	962	97
Totals		8793	943

Figure 2. Hilsa specimens on measuring sheet.

2.3 Length and weight

The relationship between length and weight of a fish sheds light on its pattern of growth. The length–weight relationship (LWR) for the hilsa in this study was established using a logarithmic form of the equation $W=aL^b$ (Le Cren, 1951), where W is the body weight of the fish (g), L is the total length of the fish (cm), 'a' is the coefficient describing rate of change of weight as the fish grows in length, and 'b' is the exponent describing change in form or shape of the fish as it grows.

When the value of b is equal to three, this indicates isometric growth (ie the body shape does not change as the fish grows), and when the value of b is more or less than three, this indicates (positive or negative) allometric growth (ie the fish becomes more or less rotund as the length increases). Exponent parameter b is a good indicator of conditions for growth and of possible changes in patterns of energy investment (for instance, females tend to focus their energy in different ways prior to spawning), and can therefore complement other parameters that describe the reproductive cycle (Freitas et al., 2011).

Following Froese (2006), we detected and excluded outliers through the visual inspection of plots of log-transformed[1] weight and length data. Log transformations linearise LWRs and correct for the increase in variation with length. Outlier removal is important because, in most fish, early juveniles have not yet attained an adult body shape and very old specimens often have distorted body forms with unusually high proportions of fat (Froese, 2006). Similarly, specimens that are unusually thin, stunted, or otherwise distorted should not be included. After excluding outliers, we estimated LWR parameters a and b using the linear regression of the log-transformed equation: $\log(W) = \log(a) + b\log(L)$, where a represents the intercept and b represents the slope of the relationship. Additionally, we estimated 95% confidence limits of a and b, and the coefficient of determination (R^2) (ie the proportion of variance explained by a model).

It should be noted that because the samples used in this study were not caught using the same type of fishing gear, and because the type of gear that was used is unknown, some bias may have been introduced

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[1] Throughout this paper, 'log' refers to the natural logarithm.

to our estimation of length–weight relationships (Froese, 2006).

2.4 Gonadosomatic index

The gonadosomatic index (GSI) is a metric that represents the relative weight of the gonad to body weight. A high GSI value indicates a heavier gonad relative to body weight, and vice versa. Changes in GSI are mostly determined by variations in yolk concentration during different stages of oocyte (immature ovum) development, so the index provides information about gonad development and maturity (Wallace and Selman, 1981; West, 1990). Inexpensive and easy to calculate, GSI has been widely used to evaluate reproductive timing in fish (eg Lowerre-Barbieri et al., 2011), especially when direct inspection of gonad maturity through macroscopic or histological analysis is not possible. In a plot of GSI values over time, very high GSI values followed by very low GSI values indicate a period over which fish spawn (ie release their gonads).

GSI values for the hilsa in this study were calculated using the equation $GSI = (GW / BW) \times 100$, where GW is gonad weight (g) and BW is body weight (g). To examine seasonal variation in spawning activity and reproductive readiness, we plotted GSI values by month. We used analysis of variance (ANOVA) to test for statistically significant differences between the means of fish sampled in different months and from different ecological zones. To meet the assumptions of ANOVA (normality and homoscedasticity), we used log transformations of GSI values. We focused our GSI analysis on females because, as in many species, the gonads of female hilsa tend to be much larger than those of males and vary much more in size according to maturity (Almukhtar et al., 2016).

2.5 Maturity

Owing to time and resource constraints, neither histological staging – the most accurate method for determining maturity stage in fish (West, 1990) – nor macroscopic staging were possible in this study. Instead, we performed hierarchical agglomerative clustering on GSI and length to roughly divide specimens into two classes, which can be assumed to represent immature and mature fish. Using GSI and length to estimate maturity reduces the risk of mistaking immature fish for spent or recovering fish, which have a reduced body weight due to loss of gonad weight.

We used the Hierarchical Clustering on Principle Components (HCPC) function in R package FactoMineR (Lê et al., 2008). Rather than visually identifying arbitrary cut-off points from plots between the variables, this method uses Ward's criterion and Euclidian distance to cluster the specimens according to selected continuous variables. We performed the analysis using both total length (TL) and standard length (SL). Clustering was significantly different for each ($P < 0.0001$, where the p-value indicates the significance of results). We opted to use the classifications based on SL, because it excludes tail length, which grows at a different rate to the body. We conducted the analysis on all specimens as a group and repeated it for females and males separately.

2.6 Sex ratio

The sex ratio was calculated as total number of males/total number of females, and divergence from the expected value of 1:1 was assessed. For instance if there were 30 males and 35 females in a sample, then the sex ratio would be $30/35 = 0.86$. This is usually written 0.86:1 (0.86 males per female). The sex ratio was calculated for the overall sample and for sample groups relating to ecological zone, maturity and month of sampling. Sex ratios were also compared between sample groups.

2.7 Data analysis

We removed outliers more than 1.5 times the interquartile range above the third quartile and below the first quartile for all variables analysed (Crawley, 2012). We used ANOVA with Tukey's honest significant difference (HSD) test to compare mean lengths, weights, and GSI between sample groups. We used linear regression to examine relationships between log transformations of weight and length. We used analysis of covariance (ANCOVA) to test for statistically significant differences between regression relationships. A t-test was used to determine significant differences of LWR parameter b from the isometric value of $b = 3$ (ie positive or negative allometric growth). Chi-squared tests were used to identify divergence from the expected sex ratio of 1:1 (female:male), and to compare sex ratios and maturity counts between sample groups. A Spearman's rank test was used to check correlations between GSI and length. All statistical analyses were performed using the software environment R 3.5.2 (R Development Core Team, 2018) and were considered significant at 5% ($P < 0.05$).

Owing to time and resource constraints, we were unable to control for township-level variation in the data collected for this study, or to provide a fine-grain spatial analysis of spawning seasonality.

3

Results

In order to determine when and where spawning hilsa most require protection, we sought primarily to describe the reproductive biology of hilsa as they migrate through different ecological zones. To do this, we focused on four key parameters: the length–weight relationships of sampled fish (Section 3.1); the gonadosomatic index (GSI) (Section 3.2); the maturity of sampled fish (Section 3.3); and their sex ratios (Section 3.4).

3.1 Length and weight

Measurement of the length and weight of hilsa specimens sampled from different ecological zones can provide an indication of when and where the hilsa spawn. Mature fish are expected to be longer in length and immature fish shorter, while fish are expected to be heavier relative to their size the closer they are to spawning, and lighter for their size immediately after spawning.

Excluding outliers, sampled fish ranged in total length (TL) from 10.4cm to 62.7cm, with a mean (± standard error) of 36.6cm (± 0.1). Body weight (BW) ranged from 0.4g to 1.8kg, with a mean of 598.5g (± 4.4). These estimates roughly correspond to previously published maximum and common lengths and weights for hilsa (Amin et al., 2005; BFRI, 2000; Haldar and Amin, 2005; Froese and Pauly, 2019). This indicates that the data gathered in this study are reliable.

We found significant interactions between sex and ecological zone in their effects on length and weight (see Appendices, Table A1). As found in previous studies of hilsa and most other fish species, our results indicate that females tend to grow bigger and heavier than males (Amin et al., 2005; Pauly, 2019). Females also develop much larger gonads than males do, which contributes to their greater body weight (see Section 3.2).

Post-hoc testing revealed that – on average – females were significantly longer in length than males within the brackish zone, but not within the saline or freshwater zones (see Table 2). Females were also significantly heavier than males within brackish and saline zones, but not within the freshwater zone (Table 2). On average, females collected from brackish water were significantly longer than other fish, apart from those collected from saline water. Females collected from saline water were significantly heavier than all other fish, apart from females collected from brackish water. Both male and female fish collected from the freshwater zone were significantly smaller and lighter than all other fish.

These interactions between sex and zone are probably a reflection of the hilsa's migratory route, as well as the variation in gonad size between sexes (Section 3.2) and between females at different stages of their life cycle (Section 3.3). The results indicate that mature fish migrate upstream to spawn in fresh water, which provides a nursery area for juveniles until they migrate towards the coast, where they grow larger and heavier before migrating back upstream. Similar patterns have been observed in other countries including Bangladesh, India and Iraq (Almukhtar et al., 2016; Bhaumik 2015a).

Large females, like those found mainly in the saline and brackish waters, are often referred to as mega-spawners and have long been recognised for their importance to healthy fish stocks. Not only are longer females more fecund, but also their eggs tend to be larger and hatch larvae with a greater chance of survival (Froese, 2004).

Table 2. Mean total length (TL) (cm) and body weight (BW) (g) of hilsa sampled from the Ayeyarwady Delta (November 2017 to November 2018) and dissected to identify sex.

	BRACKISH ZONE		FRESHWATER ZONE		SALINE ZONE	
	FEMALES	MALES	FEMALES	MALES	FEMALES	MALES
TL						
n	174	166	165	78	195	202
Min TL	19.2	19.0	12.4	15.8	21.4	21.2
Max TL	52.4	49.0	50.8	47.5	51.8	51.2
Mean TL	38.1	34.4	30.4	30.1	39.7	37.3
SE	0.6^{a}	0.6^{b}	0.8^{c}	0.9^{c}	0.4^{a}	0.4^{a}
BW						
n	173	165	164	78	195	202
Min BW	78.0	8.8	10.23	38.0	54.0	65.5
Max BW	1787	1315	1426	992	1545	1463
Mean BW	713.8	498.8	382.9	335.25	783.10	602.1
SE	27.1^{ab}	23.0^{c}	27.6^{d}	28.4^{d}	23.1^{a}	17.6^{b}

TL, total length (cm); BW, body weight (g); n, sample size; Min, minimum; Max, maximum; SE, standard error.

$^{a, b, c, d}$ Similar superscript letters indicate no significant difference in mean values between sample groups according to analysis of variance (ANOVA) results and Tukey's HSD test when TL and BW were log transformed.

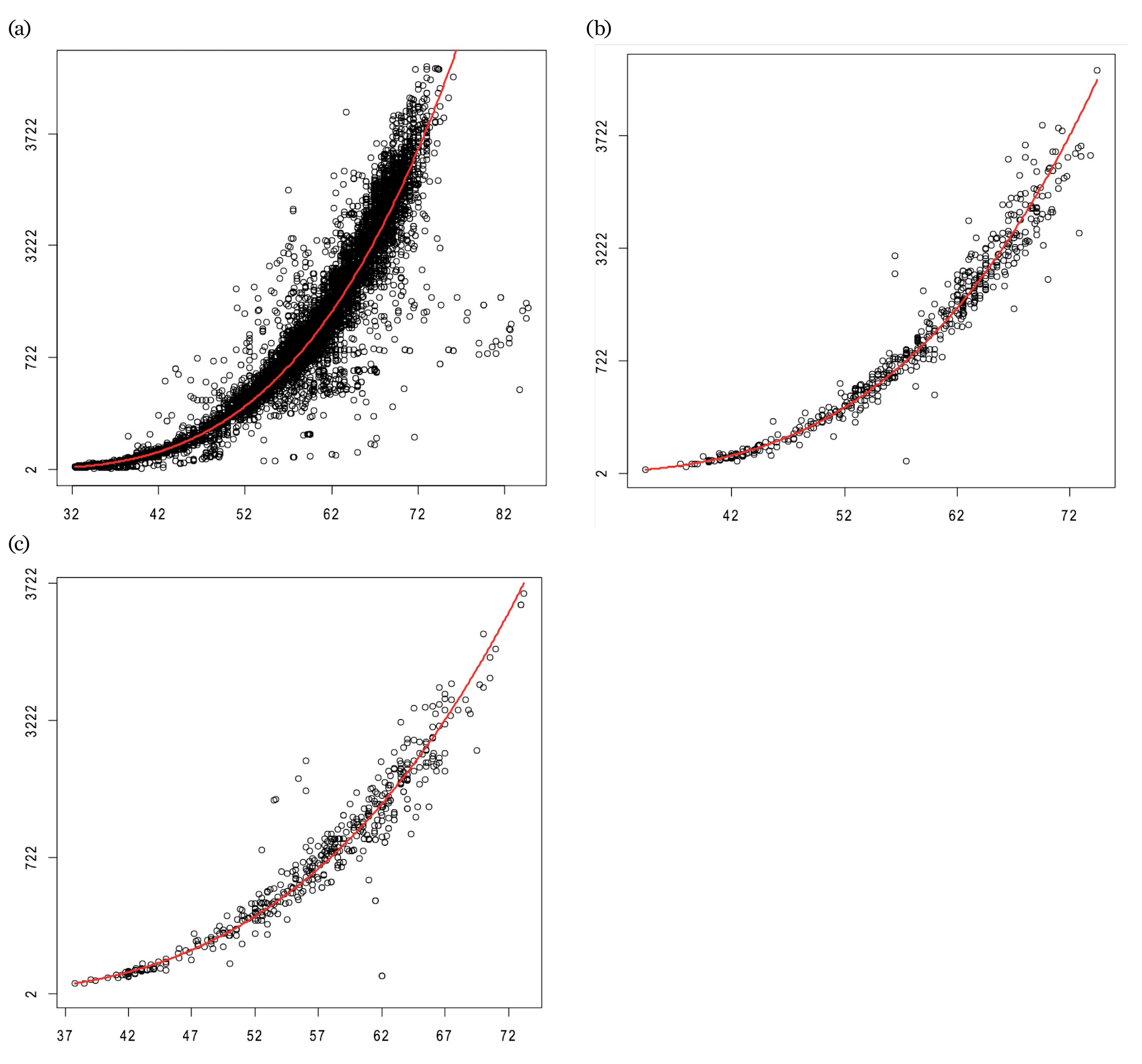
Best-fit regression models indicated significant relationships between TL and BW when log transformed. The values of the slopes (length–weight relationship parameter b, which represents the change in shape of a fish as it grows) indicated positive allometric growth for all samples, as well as for females and males individually (see Figs 3a, b and c). These positive allometric relationships imply that hilsa become relatively fatter or deeper-bodied as they increase in length.

All regression models exhibited a tight fit to the data, with the exception of a few individuals ($R^2 > 0.95$). The mean b value (3.18 ± 0.01) falls within the range of values previously identified for hilsa. For example, Dutta et al. (2012) found a mean b value of 3.11 in hilsa landed in West Bengal, and Amin et al. (2005) found a slightly higher b value of 3.38 in hilsa from Bangladeshi waters. The consistency in b values with what was expected provides evidence of the strength of our sampling protocol and the validity of results.

ANCOVA revealed significant interactions between length and zone and between sex and zone in their effects on weight (see Appendices, Table A2). Comparison of b values between ecological zones revealed statistical differences between saline and brackish zones, and between saline and freshwater zones (saline = 2.95 ± 0.04, brackish = 3.10 ± 0.03, freshwater = 3.15 ± 0.03). This indicates that fish collected from fresh water and brackish water are becoming fatter as they increase in length, compared to those collected from saline water, primarily due to gonad growth as fish migrate upstream to spawn. The slightly negative allometric growth observed in saline specimens indicates that the gonads of mature specimens were largely 'spent', that is, they had released their sperm or eggs, leading to weight loss, before returning downstream.

Comparison of estimated marginal means confirmed that female fish tend to grow faster than male fish, except within the freshwater zone. The difference between marginal means for brackish and freshwater fish was much higher for females (0.11) than males (0.02). The effect of sex is as expected in hilsa (Amin et al., 2005; Rahman and Cowx 2008) and can be attributed to the difference in gonad size between male and female specimens. Variability in this effect between zones can be attributed to the variability in gonad size that is expected between ecological zones, according to sexual maturity. In the freshwater zone, where most immature fish were found (see Section 3.3), differences in male and female gonad sizes (and therefore body weight) are not observable, compared with further downstream where most fish mature and female gonads become larger relative to those of the male.

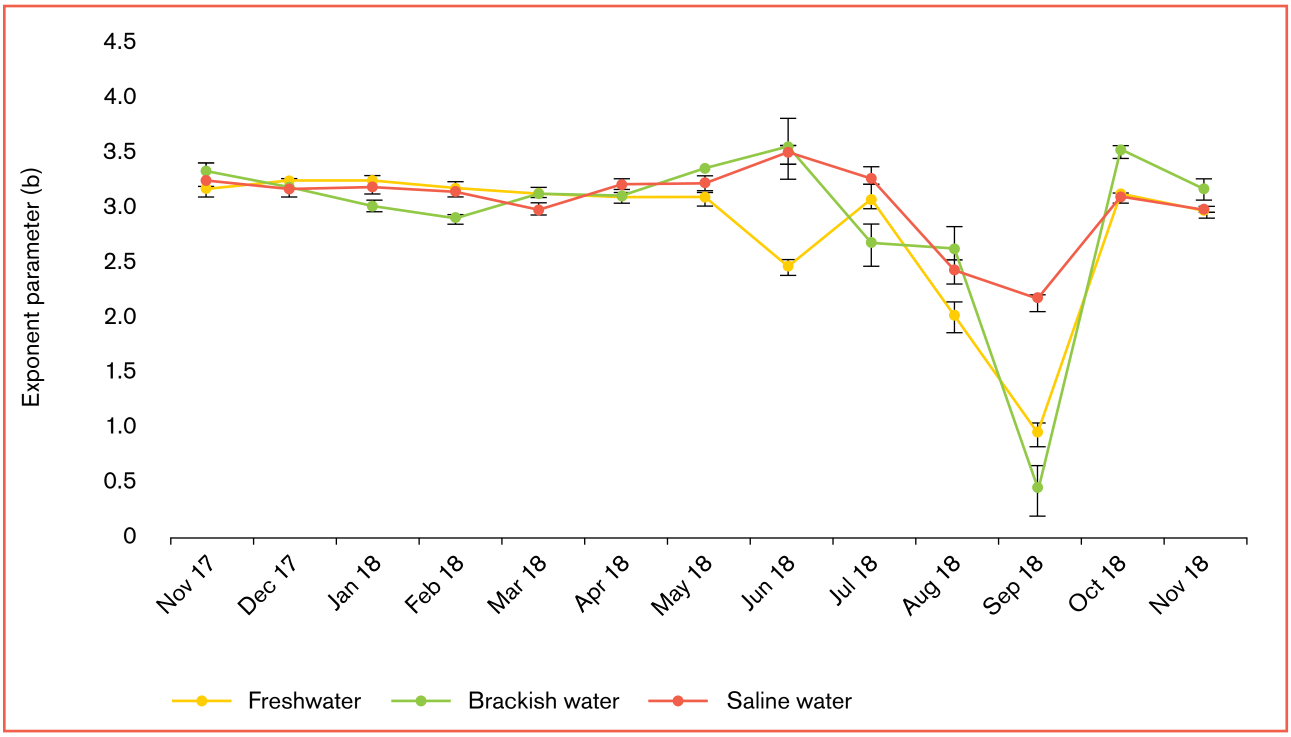
Figure 3. Total length and body weight of (a) all hilsa (n = 8091) with regression line (BW = 0.00559 x $TL^{3.18}$, R^2 = 0.96, 95% CL of a = 0.00530-0.00589, 95% CL of b =3.17-3.20); (b) female hilsa (n = 530) with regression line (BW = 0.00539 x $TL^{3.20}$, R^2 = 0.98, 95% CL of a = 0.00467-0.00621, 95% CL of b =3.17-3.24); and (c) male hilsa (n = 444) with regression line (BW = 0.00702 x $TL^{3.12}$, R^2 = 0.96, 95% CL of a = 0.00568-0.00868, 95% CL of b =3.06-3.18), collected from the Ayeyarwady region in 2017-2018.



For ease of interpretation, specimens were pooled by sex and separated by ecological zone before testing for differences between regression relationships by month. In each zone, ANCOVA revealed a significant interaction between the length of the fish and the month they were caught (see Appendices, Tables A3 and A4), with b values reaching their lowest in September (see Fig. 4). In the freshwater zone, b values were significantly lower in September (0.94 ± 0.22) than in any other month, and significantly lower in August (2.01 ± 0.21) than in most other months. In brackish water, b values were significantly lower in September (0.43 ± 0.11) than in all other months, whereas in May, June and October they were significantly higher than in any other month (ranging from 3.33 ± 0.06 to 3.53 ± 0.07). In the saline zone, b values were again significantly lower in August and September than all other months (2.13 ± 0.08 and 2.40 ± 0.11 respectively).

The negative allometric growth observed in August and, particularly, September can be attributed to spawning activities. Given the patterns observed in monthly GSI values (Section 3.2), which also reach their lowest point in September, it is probable that the lowest b values reflect the loss of gonad mass that would occur once a female fish has released its eggs. The drop in freshwater b values during June could be due to a change in some aspect of feeding ecology causing the fish to become less fat with increasing length. During their spawning migration, female hilsa tend to reduce or cease feeding

Figure 4. Monthly variation in mean values of exponent parameter (b) (ie change in shape of a fish as it grows) for length-weight relationship of hilsa collected from freshwater (n = 1499), brackish water (n = 2791) and saline water (n = 3724). Error bars represent standard error.



activities and take energy from reserve carbohydrates (Bhaumik and Sharma, 2012). At the same time, they withdraw lipids from muscle tissue and invest them in gonad development.

The main findings from the length and weight analysis are as follows:

- The male and female hilsa specimens caught in fresh water were significantly smaller and lighter than those caught in brackish and saline water, indicating that hilsa spawn in fresh water, which provides a nursery area for juveniles before they migrate towards the coast, where they grow larger.
- On average, fish caught in brackish and saline water were heavier and larger, indicating that they migrate from the saline zone through the brackish zone to fresh water where they spawn (resulting in significant weight loss). In these areas, females were heavier than males, owing to their greater gonad weight.
- On average, the lowest values for length–weight relationship parameter b were observed in September, followed by August. In both months they showed negative allometric growth, indicating a loss of gonad mass after the female fish have released their eggs and the male fish have released their sperm. This suggests that August–September is the main spawning season, with September being the most critical month.

3.2 Gonadosomatic Index

The Gonadosomatic Index (GSI) represents the relative weight of the gonad (reproductive gland) to body weight in both males and females. As described in Section 2.4, a high GSI value indicates a greater gonad weight (GW) relative to body weight (BS), where GSI = (GW/BW) x 100. A major drop from high to low GSI is an indication of spawning activity, and so the GSI is a useful way to evaluate reproductive timing in fish. It is especially relevant for females, whose gonads tend to be much larger than those of males and vary much more in size according to maturity and the reproductive cycle. One would expect female GSI values to be highest immediately prior to the release of eggs and to decrease afterwards to a significantly lower level.

Mean male GSI values were lower and less variable than mean female GSI values throughout the year (ranging from 0.30 ± 0.04 in May to 0.77 ± 0.28 in July) (see Fig. 5). Female GSI values were consistently much higher than male GSI values, as would be expected given the relatively large size of female gonads in hilsa (mean 33.1g as opposed to 2.9g in males). The range of GSI values observed correspond roughly to those reported in previous studies of hilsa GSI, for example, in Iraq and Bangladesh (Almukhtar et al., 2016; Flura et al., 2015; Hossain, 1985). The difference between male and female GSI values was similar to that found in Iran, apart from in the months following spawning, where male and female GSI values were more similar to one another in some waters (Roomiani et al., 2014).

The much higher level of seasonal variation in the GSI values of female hilsa, compared to that in the values of the male, reflects the seasonal variation in the size of female gonads as they develop and release their eggs. It may also indicate a difference in energy budget variation between the sexes, although it should be noted that this study did not directly assess energy budgets. While females mobilise energy for reproduction by withdrawing muscle tissue lipids, males do not have so much need to do so (Bhaumik and Sharma, 2012). We focused the GSI analysis on female specimens, given the limited variation in male GSI and the significant difference in GSI values between the sexes (see Appendices, Table A7).

Peaks and troughs in mean female GSI values were visible throughout the year, indicating that there may be more than one spawning season (see Fig. 5). The highest peak occurred in November 2018 (8.61 ± 0.71). This is notable because it was significantly higher than mean values in the three preceding months (see Appendices, Tables A5 and A6), while values dropped in January. This could indicate the presence of many female fish with ripe gonads in November, and which release their eggs over the period December to January. However, given that the peak in November 2017 was less pronounced (6.64 ± 0.81), further research would be required to confirm the existence and timing of a winter spawning period. Similarly, the peak in April (6.69 ± 0.71) and trough in May (3.40 ± 0.56) could indicate major spawning activity in May (noting that samples were taken during the last week of each month). However, the lowest mean female GSI values were seen in September (2.75 ± 0.50). Since this observation coincides with the timing of the lowest b values ($b < 3$, see Section 3.1), which is probably a reflection of the loss of gonad mass that would occur once a female fish has released its eggs, September is likely to be the most critical month for spawning.

When broken down by ecological zone, the GSI picture becomes more complex (see Fig. 6). ANOVA revealed a significant effect of the interaction between zone and month on GSI (see Appendices, Tables A8 and A9).

Female GSI values were the most variable in the freshwater zone, with higher peaks than other zones, indicating that more brood fish congregate in fresh water than in other zones and release their eggs in this zone, particularly in July (10.82 ± 0.92), April (10.53 ± 1.51), and November 2018 (10.64 ± 2.30). Freshwater GSI values dropped from one of their highest points in July to their lowest in September (2.00 ± 1.05), indicating declines in body weight due to fish releasing eggs during this time. Given the clear dip in length–weight relationship exponent b (negative allometric growth) that also occurs in August–September (Section 3.1), we can assume that this is the main spawning season, with September being the main spawning month. Two further freshwater peaks and troughs occurred in April–May and November–February, which could indicate additional spawning periods with May and January–February being the main spawning

Figure 5. Mean monthly gonadosomatic index (GSI) values for male hilsa (n = 448) and female hilsa (n = 534) collected from Myanmar's Ayeyarwady Delta from November 2017 through November 2018. Error bars represent standard error.

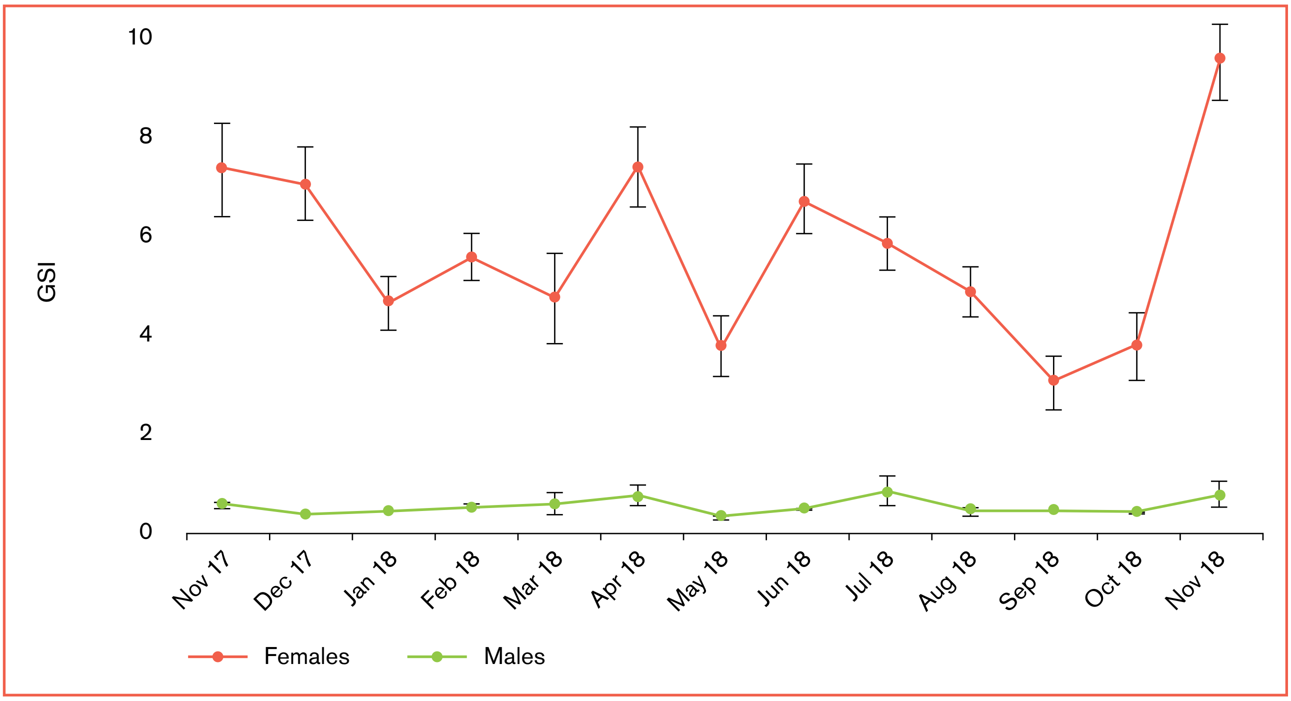
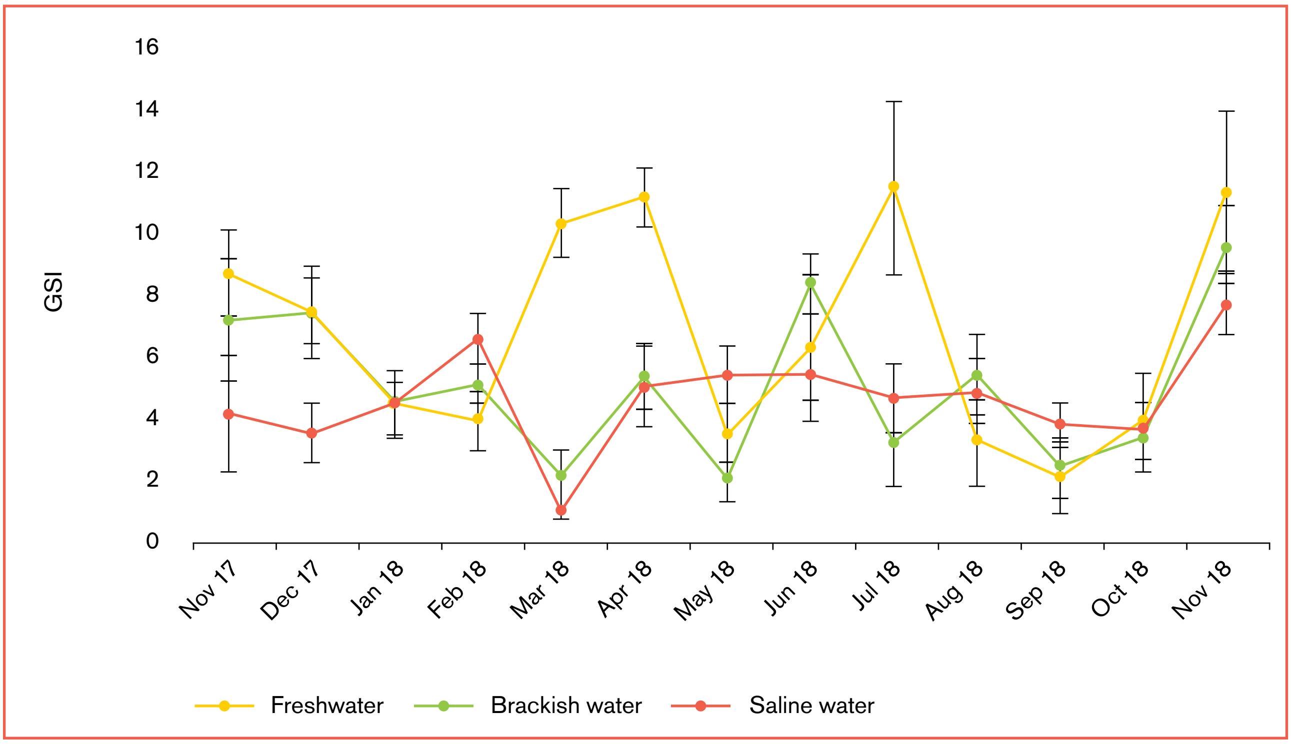


Figure 6. Mean monthly gonadosomatic index (GSI) for female hilsa collected from the brackish zone (n = 174), freshwater zone (n = 165), and saline zone (n = 195) of Myanmar's Ayeyarwady Delta over 13 months from 2017-2018. Error bars represent standard error.



months. Khain et al. (2018) also found that over 50% of survey respondents in the Ayeyarwady delta perceived spawning activity to take place in April and May. However, more evidence would be required to establish the importance of these periods for spawning.

The pattern of GSI values in brackish water bears some similarity to that of fresh water (see Fig. 6). Brackish water values peaked in November 2018 (9.05 ± 0.35), June (7.90 ± 0.45), and November 2017 (6.75 ± 1.60), suggesting that fish with ripening gonads might migrate upstream at these times for spawning in freshwater. The brackish water peak in June supports the hypothesis that major spawning takes place in fresh water during August and September, since fish with ripe gonads appear to begin releasing eggs at the end of July and stop doing so at the end of September. But while GSI values peaked during March–April and July in fresh water, those in brackish water dropped. The troughs in March (2.04 ± 0.77), May (1.89 ± 0.57) and July (3.05 ± 0.84) highlight the complexity of migrations through brackish water; while some mature fish with ripening gonads may be migrating upstream for spawning, others may be passing back downstream having released their eggs.

Female GSI values were least variable in the saline zone, peaking in February (6.26 ± 0.76) and November 2018 (7.29 ± 0.97), with a trough in March (0.94 ± 0.28). The peaks could be an indication that gonads have begun to grow with the initiation of spawning migration. The decline from February to March could be evidence of spawning activity occurring in saline waters, but more research would be required to confirm this.

In the Meghna River of Bangladesh, GSI studies have slightly different results, indicating that the main spawning season is September–October, with the main month being October, and with smaller spawning periods observed in June–July and January–March (Ahsan et al., 2014; Hossain, 1985; Quddus 1982; Rahman et al., 2012). In riverine and estuarine environments in Iraq, Almukhtar et al. (2016) found an extended spawning season with two major periods in March–June and August–October. And in the Khouzestan Province of Iran, Roomiani et al. (2014) found GSI values to indicate a main spawning season from May to August. These differences in spawning seasonality of populations in different areas may be due to a range of genetic and environmental factors.

The different levels and times at which GSI values peak within each ecological zone support the prevalent understanding that hilsa feed and grow in coastal and estuarine zones, before migrating upstream to spawn (Bhaumik, 2015a). Hossain et al. (2014) found that the most suitable areas for spawning are in inland rivers, while estuarine and nearshore water bodies are less appropriate, and offshore deep waters least suitable. Nevertheless, those estuarine and nearshore water bodies are essential corridors for hilsa migrating upstream from waters further offshore.

It should be noted that GSI is not only an indicator of spawning seasonality. It is affected by any changes in body weight, which can be driven by multiple different factors, including nutrient flows, food availability, genetics, and fishing-related mortality. For example, the relatively high mean GSI value seen among saline specimens in February, followed by the significant dip in March (in both saline and brackish waters), could reflect a loss in body weight due to unfavourable environmental conditions, such as lack of nutrients, rather than any change in gonad size. These interpretations are beyond the scope of this study.

Focusing on the GSI values of female hilsa fish, the main findings are as follows:

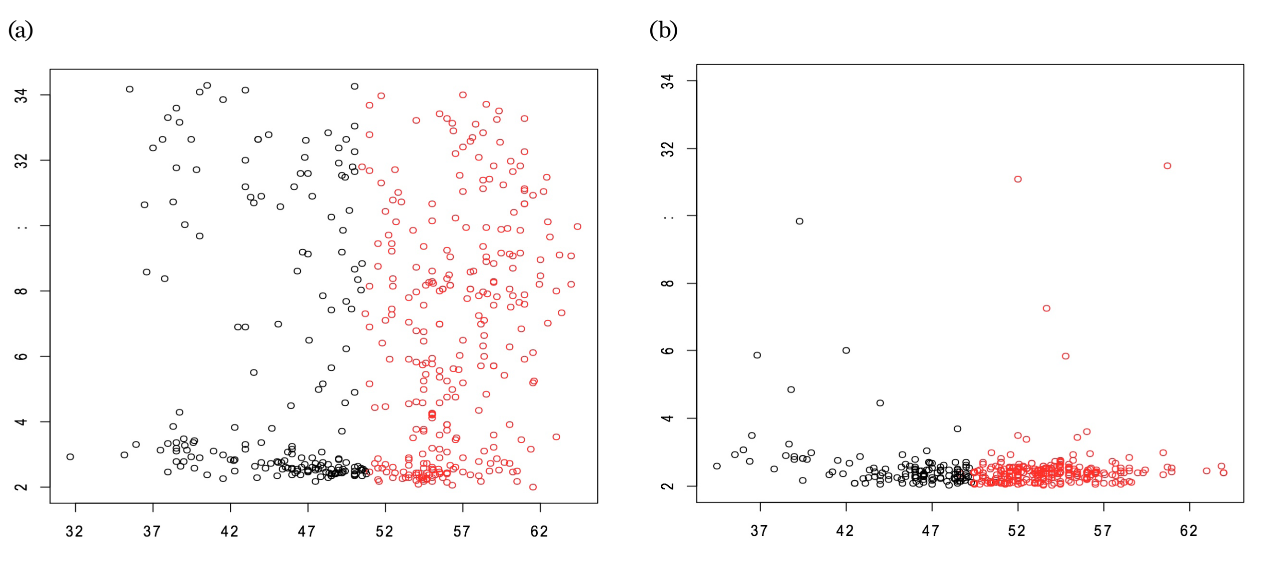
- Multiple peaks and troughs in mean GSI values were visible, indicating that there may be more than one spawning season.
- Mean female GSI values varied most in the freshwater zone, indicating that more brood fish congregate in fresh water than in other zones and release their eggs in this zone; the main spawning seasons appear to be during the periods July–September, November–February, and April–May.
- The steep dip in mean freshwater GSI values between the highest peak in July to the lowest trough in September, combined with a parallel observed decline in length–weight relationship exponent b, indicates that August–September is the main spawning season, and that September is the main spawning month.
- In brackish water, mean GSI values peaked in June and November 2018, indicating that gonads have grown as fish migrate upstream for spawning in freshwater.
- Mean female GSI values were least variable in the saline zone, with peaks in February and November 2018, which could be an indication that gonads have begun to grow with the initiation of spawning migration.

3.3 Maturity

An assessment of when mature and immature hilsa tend to be caught, and in which ecological zones, providing further evidence to describe when and where hilsa spawn. It also sheds light on migratory behaviour and the preferred habitats of hilsa at different life stages.

The results of cluster analysis on GSI values (which indicate the relationship between gonad weight and body weight) and standard length (SL) were similar for the whole group and for females alone, but significantly different between male and female samples ($\chi^2 = 4.54$, df = 1, $P < 0.05$), and so we analysed the sexes individually (Fig. 7a and b). Cluster analysis separated female fish into SL < 28.5cm and ≥ 28.5cm, and male fish into SL < 27.4cm and SL ≥ 27.4cm. These results suggest that sexual maturity occurs at an SL of about 27.4cm in male hilsa and 28.5cm in female hilsa. Published estimates of size at first maturity

Figure 7. Relationship between Gonadosomatic Index (GSI) and standard length (SL) for (a) female fish and (b) male fish. Plots are colour coded according to cluster analysis: black represents immature fish (< 28.5cm for females and < 27.4cm for males) and red represents mature fish (≥ 28.5cm for females and (≥ 27.4cm for males).



range from 16–25cm for male hilsa and 19–37cm for females (Bhaumik, 2015b). Although our estimates fall comfortably within that range, size at maturity is typically found to be at least 4cm less for males than females (Bhaumik, 2015b), and so, within our samples, the length of male and female specimens differed less than might be expected.

Although we found no significant relationship between GSI and SL when all samples were combined, correlations between GSI and SL within the two maturity stages were significant. In mature hilsa, the correlations were positive (males: $r_s = 0.15$, $P < 0.05$; females: $r_s = 0.25$, $P < 0.0001$), indicating that both body length and the body-weight-to-gonad-weight ratio were increasing, as would be expected. This correlation was most significant for females, due to their relatively large gonads compared with males. For immature hilsa, the correlations were negative (males: $r_s = -0.35$, $P < 0.0001$; females: $r_s = -0.32$, $P < 0.01$) because although the bodies of these fish will be growing, their gonads are not yet growing. The larger immature fish therefore tend to have lower GSI values than both the mature fish and the smaller immature fish.

Maturity was significantly associated with ecological zone for both females (χ^2 (2, N = 448) = 66.74, $P < 0.0001$) and males (χ^2 (2, N = 534) = 52.63, $P < 0.0001$). Within the saline zone, mature fish (80%) were much more abundant than immature fish, whereas in fresh water, immature fish (77%) were much more abundant. This pattern was similar across both sexes (see Fig. 8). Although some immature hilsa were found within each zone, this provides further evidence of the importance of fresh water as a favourable habitat for spawning and as nursery grounds for immature hilsa before they migrate downstream to complete their life cycle. It also highlights the potential importance of the saline zone as habitat for mega-spawners (large, old females) (Froese, 2004). Although female fish caught in brackish and saline waters were, on average, similar in length and weight, the mature proportion of saline specimens was much higher (78%) than the mature proportion of brackish water specimens (64%), indicating that the most fecund females are most likely to be found in the saline zone.

Baran et al. (2015) also found Myanmar's saline zone to be dominated by mature fish, whereas fish were more mixed between mature and immature in inland freshwater areas. Studies elsewhere have similarly found freshwater areas to be dominated by immature hilsa (eg Almukhtar et al., 2016).

Monthly variation in maturity was also observed, although the sample sizes of mature and/or immature fish were too small for statistical testing in some months and zones (see Fig. 9). The year-round presence of immature individuals indicates that some level of spawning activity takes place all year round, but it is difficult to establish clear patterns in this activity. Across all the ecological zones together, the percentage abundance of immature hilsa was highest in December (59%) and November 2018 (55%) and lowest in June

Figure 8. Percentage abundance of immature (n = 310) and mature hilsa (n = 547) by ecological zone.

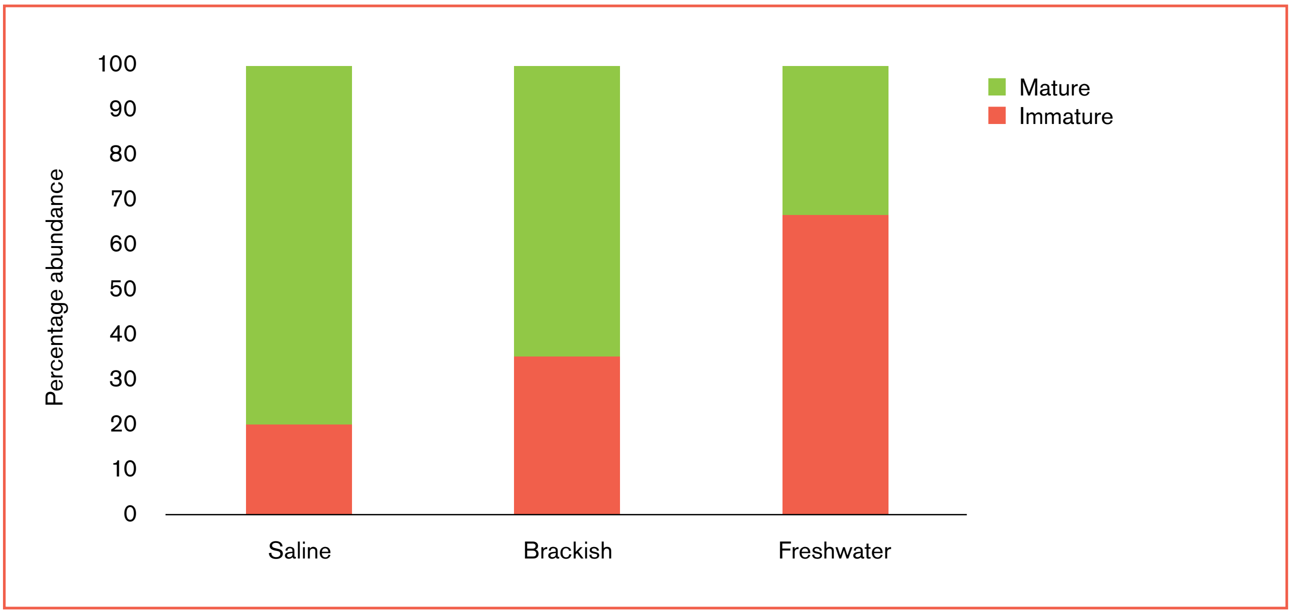
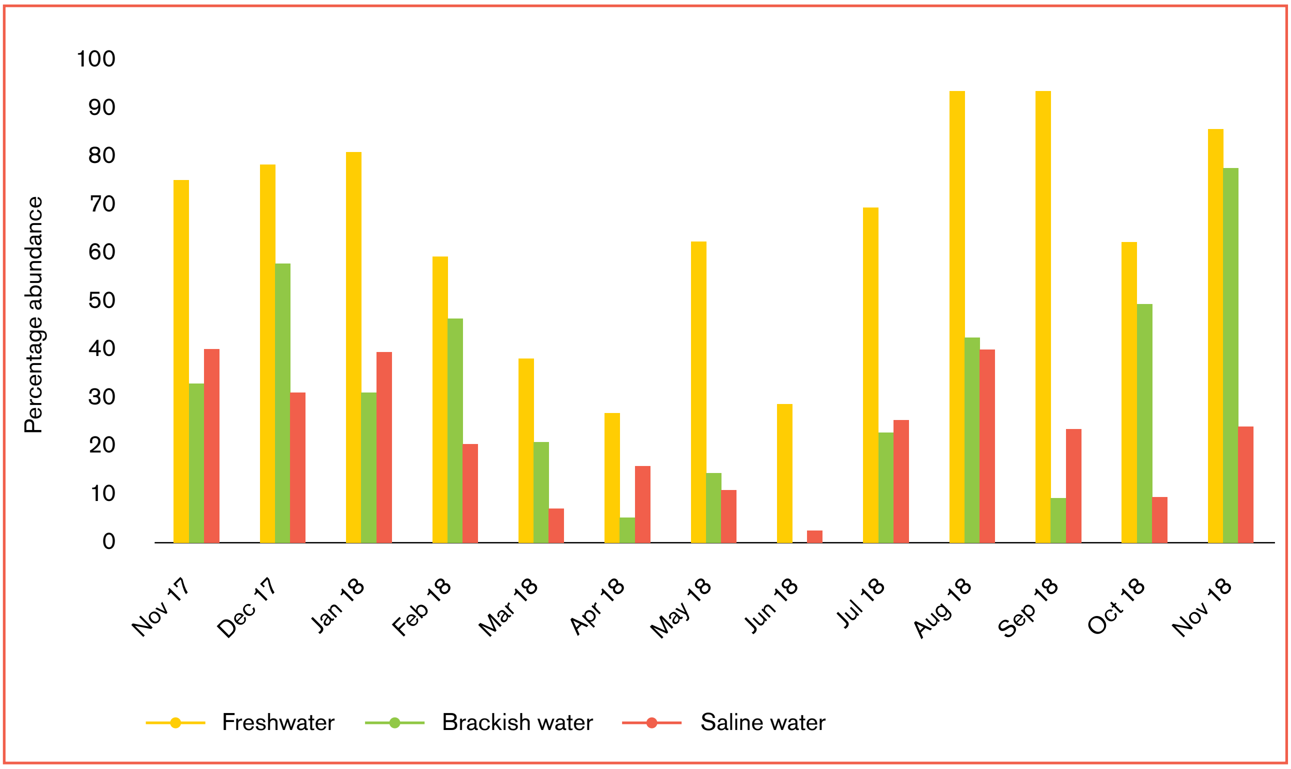


Figure 9. Percentage abundance of immature hilsa by month and ecological zone (immature n = 310 and mature n = 547).



(6%). Since hilsa are thought to reach maturity within six to 12 months (Milton, 2009), this is consistent with a main spawning season from July to September, but also supports the possibility of an additional spawning season in April–May.

In the freshwater zone, where most spawning activity occurs, immature hilsa were most abundant in August (93%) and September (94%), declining to a low of 27% in April. Since hilsa fry are thought to become juveniles after around six to ten weeks (Ahsan et al., 2014), it is possible that some of these immature hilsa caught between August and September are from a main July–September spawning season. But given that hilsa may not reach maturity for six to 12 months, some of them could also be from a winter spawning period, while the low in April could be explained by a lull in spawning prior to an additional April–May spawning season (see Section 3.2). The percentage abundance of immature hilsa peaks later in brackish water (November 2018), probably reflecting the migration path of immature hilsa towards the sea, following the main spawning season from July–September. The abundance of immature hilsa in saline water is more difficult to interpret, but the low of 2.7% in June coincides with a complete absence of immature hilsa in brackish water. Again, this is consistent with major spawning activity occurring in fresh water from July to September, since by June the next year those offspring are likely to have migrated back to saline water and reached maturity.

Key findings from assessing the maturity of hilsa samples include the following:

- Within the saline zone, mature fish (80%) were much more abundant than immature fish, whereas in fresh water, immature fish predominated (77%), highlighting the importance of fresh water as a favourable habitat for spawning and as nursery grounds for immature hilsa before they migrate downstream through brackish waters to reach maturity in coastal waters.
- Across all ecological zones, the percentage abundance of immature hilsa peaked in December (59%) and November 2018 (55%), and was lowest in June (6%), which is consistent with a main spawning season of July–September.
- In the freshwater zone, where most spawning activity occurs, immature hilsa were most abundant in August (93%) and September (94%), declining to a low of 27% in April. This could be evidence of additional spawning seasons in January–February and April–May.
- The percentage abundance of immature hilsa peaked in November 2018 in brackish water, probably reflecting the migration path of immature hilsa towards the sea, following a main spawning season in July–September.

3.4 Sex ratio

Sex ratio divergence can be driven by a range of factors, including genetics, differences in habitat occupation, growth rates, and different natural or fishing mortality rates. Sex change might be part of the hilsa's reproductive cycle, and it could also provide an indication of where and when male and female hilsa congregate for spawning.

Sex data were available for 982 specimens. Of these, 534 (54%) were female and 448 (46%) were male. Overall, the ratio of males to females (0.84:1) significantly diverged from the commonly expected 1:1 ratio (see Table 3), indicating that female hilsa are significantly more common than males in Myanmar. This divergence was driven largely by specimens collected from the freshwater zone. The ratio of males to females in these samples was 0.48:1, which is even more significantly different from 1:1 than the overall sample. Conversely, the sex ratios of fish collected from brackish and saline zones were not significantly different from 1:1 (0.95:1 and 1.04:1, respectively).

When samples were pooled by ecological zone but separated by maturity, the sex ratio of immature fish (0.68:1) was much lower than that of mature fish (0.94:1). The sex ratio of the immature group significantly diverged from 1:1 (see Table 3), indicating that females are more common than males at this stage, whereas the sex ratio of the mature group alone did not significantly differ from 1:1. Given the high percentage abundance of immature fish found in fresh water (Section 3.3), the difference in sex ratios between mature and immature fish may also explain the divergence among freshwater specimens.

Previous research on hilsa has also reported monthly fluctuations in sex ratio with an overall predominance of females, as well as changes in sex ratio according to body length (Amin et al., 2005; Ahsan et al., 2014; Roomiani et al., 2014; Flura et al., 2015). Differences in sex ratio between different ecological zones could be because males and females migrate in separate shoals, and differences corresponding to body length could be related to different rates of growth, natural mortality or fishing mortality. The difference between immature and mature hilsa sex ratios in this study could also be evidence of sequential hermaphroditism, where fish begin life as one sex and change sometime later to the other. In many fish species, sex change is part of the reproductive cycle and is typically triggered by changes in social structure or attainment of a critical age or size (Todd et al., 2016). Evidence of protandrous (male-to-female) hermaphroditism has been found in other species of *Tenualosa* (Blaber et al., 1996), but the results from this study indicate female-to-male hermaphroditism. Further research is required to confirm the existence and explore the nature of sex change in hilsa.

Over time, females were more abundant from December to February and from August to October, while males were more abundant in November (2017 and 2018) and the period from March to June (see Fig. 10). The only month when the sex ratio did not diverge at all from the expected 1:1 was July, but divergence was not significant in March, April or September. Equal or near-equal sex ratios can be an indication of spawning activity, which requires that male and female fish congregate in order to ensure that eggs and spermatozoa are released into water in close proximity to support successful external fertilisation (Bhaumik and Sharma, 2012).

Table 3. Distribution of male and female hilsa sampled from the Ayeyarwady Delta (November 2017 to November 2018) and results of chi-squared analyses, by sample group. χ^2, chi-squared; P, p-value; N, total sample size.

	Males	Females	Sex ratio	Chi-squared results for significant divergence from 1:1
All specimens	448	534	0.84:1	χ^2 (1, N = 982) = 7.53, P < 0.01
Freshwater zone	165	79	0.48:1	χ^2 (1, N = 244) = 30.31, P < 0.0001
Brackish zone	166	174	0.95:1	-
Saline zone	203	195	1.04:1	-
Immature	126	184	0.68:1	χ^2 (2, N = 325) = 10.85, P < 0.001
Mature	265	282	0.94:1	-

Figure 10. Monthly sex ratio (number of males/number of females) observed for hilsa (n = 982) and expected sex ratio (1:1). The scale of the y axis represents the number of males for every one female. Ratios significantly diverged from 1:1 ($P < 0.05$) in all months apart from March, April, July and September.

More equal sex ratios in September, March–April and, particularly, July, could therefore support the evidence from Section 3.2 that major spawning activity occurs during the periods from July to September and from April to May. However, given the overall sex ratio divergence of freshwater specimens, this observation would require further exploration by comparing larger samples of mature fish collected in different months and zones.

Key findings from the analysis of sex ratios across space and time include the following:

- Overall, and in fresh water, females predominate over males, while in brackish and saline waters, sex ratios are more equal.
- Among immature hilsa, females predominate over males, whereas the ratio is closer to 1:1 for mature hilsa. This could reflect a difference in growth rates between males and females, or some form of hermaphroditism.
- The sex ratio divergence observed in fresh water probably reflects the divergence seen amongst immature specimens, supporting other evidence from this study that the freshwater zone is an important spawning area and nursery area for immature hilsa.
- Fluctuations in sex ratio by month indicate that males and females congregate for spawning in July, September, and from March to April, but larger sample sizes would be required to draw robust conclusions.

4

Conclusions and recommendations

The reproductive and growth characteristics analysed in this study together provide a more detailed picture of hilsa reproduction across the Ayeyarwady Delta. Our findings demonstrate when and where spawning hilsa most require protection, and highlight the need for different management strategies in different ecological zones, which are utilised by the different life stages of hilsa.

4.1 Current fishing restrictions do not coincide with hilsa spawning season

Monthly patterns in the gonadosomatic index (GSI – the relationship between gonad weight and overall body weight) and the length–weight relationship (LWR) clearly show that major spawning activities occur in fresh water during the period July–September, with September being the most important month. Myanmar's current fishing restrictions apply at various times between May and August, depending on location. The timing of these restrictions may coincide with the spawning migration of hilsa as they move upstream through the brackish zone, but is unlikely to provide sufficient protection for brood and spawning hilsa in freshwater areas.

We can therefore conclude from our findings that the current fishing restrictions do not adequately protect hilsa during its main spawning period. Ideally, access to fishing in freshwater areas would be restricted from the end of July to the end of September. But given the short-term costs that these restrictions place on local fishing communities (Khaing et al., 2019), we recommend that access to fishing in freshwater areas be restricted during the main spawning month of September.

4.2 Freshwater nursery grounds require year-round protection

The spatial distribution of fish size and maturity across the ecological zones clearly shows that the freshwater zone holds not only spawning grounds but also nursery grounds. It will therefore be important to implement measures here for the protection of juvenile hilsa, such as mesh-size regulations and sanctuaries where fishing is restricted throughout the year, or at least for long enough after the main spawning season to allow time for recruitment.

4.3 Marine protected areas could support spawning stock

It is clear from this study and others that most hilsa, once they have reached maturity, spend a portion of their life cycle feeding in saline waters. We recommend the creation of no-take marine protected areas in the saline zone. This would provide protection for mature hilsa, particularly the large, older females (mega-spawners), which we have shown spend time predominantly in the saline zone. Protection of these mega-spawners within their feeding grounds should help to maintain a healthy spawning stock biomass, ie a sufficient stock of fish capable of reproduction.

4.4 Migratory routes must be maintained

Since hilsa migrate between the sea and fresh water to breed, feed and grow, effective management of their migratory routes is required. The success of any management measures to protect spawning, nursery, or feeding grounds will depend on upstream and downstream migration routes remaining open and fishing pressure being controlled. As previously stated, current fishing restrictions may help to protect hilsa on their upstream migration through the brackish zone, with effective enforcement. Our analysis of GSI indicates that June may be the most critical month for protection of hilsa on their upstream migration, but further research on migratory routes and timings would allow for more precisely targeted fishing access restrictions within critical brackish-water corridors.

4.5 Management should be adaptive

It is important that the spatial and temporal aspects of each of these management measures are flexible and adaptable enough to keep pace with environmental change. For instance, any combination of factors, such as fluctuations in rainfall, temperature, upstream runoff and sediment input, could help to explain the large difference in mean GSI values seen in this study between November 2017 and November 2018. Building on this study, interannual variation in the length and timing of spawning seasons, and the environmental factors which underpin it, must be monitored over the long term if fishing restrictions are to be effective into the future.

4.6 Research gaps

Additional peaks and troughs in freshwater GSI values and seasonal patterns in the abundance of juveniles indicate that spawning probably happens more than once a year in Myanmar, but we cannot establish with certainty when or where additional spawning periods occur without further investigation through analysis of gonad histology or otolith microchemistry. Variations in the trace element compositions of otoliths can be used as retrospective spawning indicators and would also allow the identification of any potential landlocked populations and associated fisheries management needs (Sturrock et al., 2015). Research of this nature has begun, but until results are available, we recommend focusing management measures to protect spawning hilsa on the period in which we can say with certainty that large numbers of hilsa spawn, namely the July–September period, with a particular focus on the critical month of September.

Appendices

Table A1. Analysis of variance (ANOVA) results testing equality of a) mean total lengths (cm) (F(5, 976) = 49.1, P < 0.0001) and b) mean body weights (g) (F(5, 975) = 59.42, P < 0.0001) between male and female hilsa sampled during different months, from November 2017 to November 2018, from the three ecological zones of the Ayeyarwady Delta. Weight (g) and length (cm) were log transformed to meet the assumptions of ANOVA. Log, natural logarithm; df, degrees of freedom; SS, sum of squares; MS, mean square; F, F-value; P, p-value; * indicates an interaction term.

Log total length					
	df	SS	MS	F	P
Zone	2	11.50	5.75	109.19	< 0.0001
Sex	1	0.94	0.94	17.85	< 0.0001
Sex * Zone	2	0.49	0.24	4.64	< 0.01
Log body weight					
	df	SS	MS	F	P
Zone	2	141.1	70.57	127.03	< 0.0001
Sex	1	16.1	16.09	28.97	< 0.0001
Sex * Zone	2	7.8	3.92	7.05	< 0.001

Table A2. Analysis of covariance (ANCOVA) results testing for equality of log-transformed weight (g) against log-transformed total length (cm) regression slopes and y-intercepts between male and female hilsa collected from the brackish zone, freshwater zone, and saline zone of the Ayeyarwady Delta from November 2017 to November 2018 (F(8, 967) = 4,680, P < 0.001). Log, natural logarithm; TL, total length (cm); df, degrees of freedom; SS, sum of squares; MS, mean square; F, F-value; P, p-value; * indicates an interaction term.

	df	SS	MS	F	P
Log TL	1	646.1	646.1	37303.9	< 0.001
Zone	2	1.01	0.5	29.1	< 0.001
Sex	1	0.76	0.76	50.0	< 0.001
Log TL * Zone	2	0.29	0.14	8.3	< 0.001
Zone * Sex	2	0.28	0.14	8.0	< 0.001

Table A3. Analysis of covariance (ANCOVA) results testing for equality of log-transformed weight (g) against log-transformed total length (cm) regression slopes and y-intercepts between months when hilsa were collected from the brackish zone ($F(25, 2791) = 4680$, $P < 0.001$), freshwater zone ($F(25, 1499) = 1613$, $P < 0.001$), and saline zone ($F(25, 3724) = 1592$, $P < 0.001$) of the Ayeyarwady Delta from November 2017 to November 2018. Log, natural logarithm; TL, total length (cm); df, degrees of freedom; SS, sum of squares; MS, mean square; F, F-value; P, p-value; * indicates an interaction term.

Brackish zone					
	df	SS	MS	F	P
Log TL	1	2778.28	2778.28	114934.91	< 0.001
Month	12	25.08	2.09	86.46	< 0.001
Log TL * Month	12	24.59	2.05	84.78	< 0.001
Freshwater zone					
	df	SS	MS	F	P
Log TL	1	2765.60	2765.60	39660.66	< 0.001
Month	12	36.77	3.06	43.95	< 0.001
Log TL * Month	12	10.29	0.86	12.30	< 0.001
Saline zone					
	df	SS	MS	F	P
Log TL	1	1148.87	1148.87	39431.12	< 0.001
Month	12	3.67	0.31	10.48	< 0.001
Log TL * Month	12	7.11	0.59	20.34	< 0.001

Table A4. Mean monthly values of b parameter from length–weight relationship of hilsa sampled from the three ecological zones of the Ayeyarwady Delta (November 2017 to November 2018). Shared superscript letters indicate no significant difference detected between sample months within the ecological zone, according to Tukey's HSD test ($P < 0.05$). n, sample size; SE, standard error.

	Freshwater zone		Saline zone		Brackish zone	
Month	Mean ± SE	df	Mean ± SE	df	Mean ± SE	df
Nov 2017	3.14 ± 0.09^{c}	1499	3.22 ± 0.06^{cd}	3724	3.30 ± 0.04^{fg}	2791
Dec 2017	3.21 ± 0.08^{c}	1499	3.15 ± 0.05^{bc}	3724	3.16 ± 0.04^{def}	2791
Jan 2018	3.22 ± 0.06^{c}	1499	3.17 ± 0.05^{bcd}	3724	3.01 ± 0.06^{bcd}	2791
Feb 2018	3.16 ± 0.04^{c}	1499	3.12 ± 0.04^{bc}	3724	2.89 ± 0.06^{bc}	2791
Mar 2018	3.13 ± 0.05^{c}	1499	2.97 ± 0.05^{b}	3724	3.10 ± 0.04^{cde}	2791
Apr 2018	3.08 ± 0.05^{c}	1499	3.20 ± 0.06^{bcd}	3724	3.10 ± 0.02^{d}	2791
May 2018	3.08 ± 3.08^{c}	1499	3.19 ± 0.09^{bcd}	3724	3.33 ± 0.06^{efgh}	2791
Jun 2018	2.45 ± 0.28^{bc}	1499	3.48 ± 0.08^{d}	3724	3.53 ± 0.07^{gh}	2791
Jul 2018	3.09 ± 0.20^{c}	1499	3.25 ± 0.11^{bcd}	3724	2.66 ± 0.10^{b}	2791
Aug 2018	2.01 ± 0.20^{b}	1499	2.40 ± 0.11^{a}	3724	2.61 ± 0.14^{b}	2791
Sep 2018	0.94 ± 0.22^{a}	1499	2.13 ± 0.08^{a}	3724	0.43 ± 0.11^{a}	2791
Oct 2018	3.10 ± 0.06^{c}	1499	3.08 ± 0.05^{bc}	3724	3.51 ± 0.02^{h}	2791
Nov 2018	2.93 ± 0.09^{c}	1499	2.95 ± 0.06^{bc}	3724	3.16 ± 0.04^{def}	2791

Table A5. Monthly gonadosomatic index (GSI) values with standard error (SE) for female hilsa collected from the Ayeyarwady Delta. Gonadosomatic index (GSI) values were log-transformed to meet the assumptions of ANOVA. Shared superscript letters indicate no significant difference detected between sample months, according to Tukey's HSD test ($P < 0.05$). Log, natural logarithm; n, sample size; Min, minimum; Max, maximum; SE, standard error.

Month	n	Min	Max	Mean ± SE
Nov 2017	36	0.50	23.05	8.61 ± 0.86^{ab}
Dec 2017	50	0.02	24.05	6.41 ± 0.67^{abc}
Jan 2018	58	0.19	13.77	4.20 ± 0.48^{bcd}
Feb 2018	57	0.42	13.77	5.03 ± 0.43^{ab}
Mar 2018	25	0.15	15.62	4.30 ± 0.81^{bcd}
Apr 2018	29	0.24	14.69	6.69 ± 0.71^{ab}
May 2018	26	0.09	8.91	3.40 ± 0.56^{bcd}
Jun 2018	31	0.24	11.52	6.09 ± 0.64^{ab}
Jul 2018	36	0.40	22.27	5.29 ± 0.49^{abcd}
Aug 2018	62	0.35	19.25	4.43 ± 0.45^{bcd}
Sep 2018	45	0.29	12.16	2.75 ± 0.50^{d}
Oct 2018	48	0.18	11.13	3.42 ± 0.59^{cd}
Nov 2018	31	0.50	23.05	8.61 ± 0.71^{a}

Table A6. Analysis of variance (ANOVA) results testing equality of mean gonadosomatic index (GSI) values between female hilsa sampled during different months from November 2017 to November 2018 from the Ayeyarwady Delta. GSI values were log transformed to meet the assumptions of ANOVA ($F(12, 512) = 5.795, P < 0.0001$). Log, natural logarithm; df, degrees of freedom; SS, sum of squares; MS, mean square; F, F-value; p, p-value.

	df	SS	MS	F	P
Month	12	111.1	9.3	5.8	< 0.0001

Table A7. Analysis of variance (ANOVA) results testing equality of mean gonadosomatic index (GSI) values between male and female hilsa sampled from November 2017 to November 2018 from the Ayeyarwady Delta. GSI values were log transformed to meet the assumptions of ANOVA ($F(1, 939) = 727.1, P < 0.0001$). Log, natural logarithm; df, degrees of freedom; SS, sum of squares; MS, mean square; F, F-value; p, p-value.

	df	SS	MS	F	P
Sex	1	983.6	983.6	727.1	< 0.0001

Table A8. Analysis of variance (ANOVA) results testing equality of mean gonadosomatic index (GSI) values between female hilsa collected from three ecological zones of the Ayeyarwady Delta from November 2017 through November 2018. Gonadosomatic index (GSI) values were log transformed to meet the assumptions of ANOVA. Similar superscript letters indicate no significant difference detected between sample groups, according to Tukey's HSD test ($P < 0.05$). Log, natural logarithm; n, sample size; Min, minimum; Max, maximum; SE, standard error.

Nov-17	n	Min	Max	Mean ± SE
Brackish	12	0.78	16.40	6.75 ± 1.60^{abcde}
Freshwater	15	0.48	14.59	8.20 ± 1.26^{abc}
Saline	9	0.06	12.70	3.94 ± 1.54^{abcde}
Dec-17	**n**	**Min**	**Max**	**Mean ± SE**
Brackish	18	0.18	11.27	7.08 ± 0.96^{abcde}
Freshwater	24	0.02	24.05	7.02 ± 1.13^{abcde}
Saline	8	0.21	6.21	3.37 ± 0.07^{abcde}
Jan-18	**n**	**Min**	**Max**	**Mean ± SE**
Brackish	13	0.19	11.73	4.20 ± 1.03^{abcde}
Freshwater	27	0.38	13.76	4.14 ± 0.72^{abcde}
Saline	18	0.37	13.77	4.28 ± 0.84^{abcde}
Feb-18	**n**	**Min**	**Max**	**Mean ± SE**
Brackish	21	0.57	7.95	4.86 ± 0.61^{abcde}
Freshwater	16	0.42	11.16	3.72 ± 0.92^{abcd}
Saline	20	0.63	13.77	6.26 ± 0.69^{abcd}
Mar-18	**n**	**Min**	**Max**	**Mean ± SE**
Brackish	12	0.15	8.46	2.04 ± 0.77^{cde}
Freshwater	8	6.31	15.61	9.77 ± 0.73^{ab}
Saline	5	0.46	1.78	5.14 ± 0.22^{abcde}
Apr-18	**n**	**Min**	**Max**	**Mean ± SE**
Brackish	11	0.24	10.80	5.08 ± 0.13^{abcde}
Freshwater	9	5.99	14.69	10.54 ± 0.45^{a}
Saline	9	0.90	12.10	4.82 ± 1.30^{abcde}
May-18	**n**	**Min**	**Max**	**Mean ± SE**
Brackish	8	0.09	4.02	1.89 ± 0.57^{bcde}
Freshwater	10	0.18	8.90	3.22 ± 1.08^{abcd}
Saline	8	0.49	8.11	5.14 ± 0.82^{abcde}
Jun-18	**n**	**Min**	**Max**	**Mean ± SE**
Brackish	9	1.11	10.70	7.89 ± 0.94^{abcd}
Freshwater	5	0.75	11.52	5.97 ± 2.20^{abcde}
Saline	17	0.24	10.91	5.16 ± 0.83^{abcde}

Jul-18	n	Min	Max	Mean ± SE
Brackish	10	0.40	12.99	3.05 ± 0.84^{abcde}
Freshwater	7	3.18	22.27	10.82 ± 1.60^{abcd}
Saline	19	1.20	19.69	4.44 ± 0.31^{abcde}
Aug-18	**n**	**Min**	**Max**	**Mean ± SE**
Brackish	23	0.36	19.25	5.14 ± 0.79^{abcde}
Freshwater	15	0.47	18.33	10.54 ± 0.82^{bcde}
Saline	24	0.21	17.85	4.62 ± 0.73^{abcde}
Sep-18	**n**	**Min**	**Max**	**Mean ± SE**
Brackish	14	0.35	10.63	2.28 ± 0.93^{de}
Freshwater	12	0.29	12.16	2.00 ± 1.05^{e}
Saline	19	0.29	10.78	3.58 ± 0.70^{abcde}
Oct-18	**n**	**Min**	**Max**	**Mean ± SE**
Brackish	15	0.18	10.10	3.23 ± 1.03^{bcde}
Freshwater	9	0.40	10.66	3.68 ± 1.52^{abcde}
Saline	24	0.20	11.13	3.44 ± 0.84^{cde}
Nov-18	**n**	**Min**	**Max**	**Mean ± SE**
Brackish	8	3.72	14.24	9.05 ± 1.03^{abc}
Freshwater	8	1.29	23.05	10.64 ± 2.30^{abcd}
Saline	15	0.50	11.23	7.29 ± 0.96^{abcd}

Table A9. Analysis of variance (ANOVA) results testing equality of mean gonadosomatic index (GSI) values among female hilsa sampled from November 2017 to November 2018 in three ecological zones of the Ayeyarwady Delta. Gonadosomatic index values were log transformed to meet the assumptions of ANOVA. Log, natural logarithm; df, degrees of freedom; SS, sum of squares; MS, mean square; F, F-value; P, p-value. $F(38, 846) = 3.82$, $P < 0.001$.

	df	SS	MS	F	P
Date	12	117.1	9.3	6.3	< 0.001
Zone	2	1.8	0.9	0.6	> 0.05
Date * Zone	24	101.13	4.2	2.9	< 0.001

Acronyms and abbreviations

ANOVA	(see glossary)
ANCOVA	(see glossary)
BW	Body weight
DoF	Department of Fisheries
GSI	Gonadosomatic index
GW	Gonad weight
Log	Logarithm
LWR	Length–weight relationship
MoALI	Ministry of Agriculture Livestock and Irrigation
SE	Standard error
SL	Standard length
TL	Total length

Glossary

Allometric growth (positive or negative): the change in shape or density of a fish as it grows, as indicated by a length–weight relationship exponent parameter (b) of more or less than 3. Negative allometric growth implies the fish becomes more slender as it becomes longer and is indicated by a $b < 3.0$. Positive allometric growth implies the fish becomes relatively stouter or deeper-bodied as it increases in length and is indicated by a $b > 3.0$.

Allozyme: a variant form of an enzyme which differs structurally but not functionally from other allozymes coded for by different alleles at the same locus. Allozymes are used as molecular markers to gauge evolutionary histories and relationships between different species.

Analysis of variance (ANOVA): a collection of statistical models and their associated estimation procedures (such as the 'variation' among and between groups) used to analyse the differences among group means in a sample.

Analysis of covariance (ANCOVA): a general linear model that blends ANOVA and regression. It is used to test the effects of categorical variables on a continuous dependent variable, controlling for the effects of selected other continuous variables, which covary with the dependent.

Anadromy, anadromous: fish that migrate from the sea to fresh water to spawn.

Amphidromy, amphidromous: fish that migrate between fresh and salt water at some stage of the life cycle other than the breeding period.

Chi-squared test: also written as χ^2 test, is commonly used to determine whether there is a significant difference between the expected frequencies and the observed frequencies in one or more categories.

Clupeid, Clupeidae: a family of ray-finned fishes, comprising, for instance, the herrings, shads, sardines, hilsa, and menhaden.

Coefficient of determination (R^2): in regression analysis, it describes the goodness of fit, ie the proportion of variance in a dependent variable that is predictable from the independent variable(s).

Euclidian distance: distance metric used in hierarchical cluster analysis, which is the straight-line distance between two points.

Euryhaline: an aquatic organism able to tolerate a wide range of salinities.

Exponent parameter (b):

Fit (or goodness-of-fit): in statistical modelling, it describes how well-observed outcomes are predicted by a model, based on the proportion of total variance explained by the model.

Gonad: a reproductive gland or sex organ in animals. In males these are testes and in females they are ovaries.

Gonadosomatic index (GSI): the calculation of gonad weight as a proportion of total body weight, as a measure of reproductive capacity.

Isometric growth: growth which is not accompanied by a change in shape or density, ie weight increases as the third power of length (length–weight exponent parameter b is equal to 3).

Linear regression: a linear approach to analysing the relationship between a dependent and one or more independent variable(s).

Log transformation: when a logarithm is applied to raw data. When modelling the length–weight relationships of fish, log transformations linearise models and stabilise variation, increasing ease of outlier detection and making data more appropriate for analysis by linear regression.

Macroscopic analysis: visual inspection (without the use of magnifying tools).

Macroscopic staging: determining the stage of gonad maturation through visual inspection (without the use of magnifying tools).

Hierarchical agglomerative clustering: in data mining and analysis, this is a method of cluster analysis which seeks to group data into clusters based on their similarity.

Histological analysis: examination of tissues using a microscope.

Histological staging: determining the stage of gonad maturation through microscopic examination.

Oocyte: an immature egg cell produced in the ovary.

Otolith microchemistry: a technique used in fisheries management and fisheries biology to delineate stocks and characterise movements and origin of fish. Otoliths are ear bones which contain different concentrations of trace elements and isotopes according to the water they have been in.

Protandrous hermaphroditism: The condition in which an organism begins life as a male and then changes into a female.

P-value: Probability value to determine statistical significance. $P < 0.05$ (5%) is the normal threshold for significance.

Recruitment: the number of juvenile fish surviving to join a population, usually by reaching a life stage at which they can be detected by an observer.

Regression: a set of statistical processes for analysing the relationship between a dependent and one or more independent variable(s).

Spearman's rank test: A technique used to assess the strength and direction (negative or positive) of a correlation between two variables. The Spearman's rank correlation coefficient is denoted by $r_{s.}$

T test: a statistical test used to compare two means.

Tukey's honest significant difference (HSD) test: a statistical test that is used to compare multiple means. It is often used as a post-hoc test following ANOVA, to identify which specific means were significantly different.

Ward's criterion: a criterion applied in agglomerative hierarchical cluster analysis, for choosing the pair of clusters to merge at each step.

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The hilsa is a critically important species for small-scale fishing communities in Myanmar's Ayeyarwady Delta and Rakhine State. Yet current fishing regulations are inadequate and exploitation rates are well beyond sustainable levels. This study analyses key parameters underlying hilsa biology, comparing them across different ecological zones of the hilsa's range in Myanmar and across time. It provides evidence of major spawning activity between July and September in the freshwater zone, particularly in September. We recommend that policymakers restrict access to fishing in freshwater areas at least during the month of September; promote and enforce measures to protect juvenile hilsa; establish marine protected areas to conserve spawning stock biomass; and ensure effective, adaptive fisheries management throughout migratory routes.

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