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ORIGINAL ARTICLE

# Spawning season, recruitment, and growth of the freshwater prawn *Macrobrachium lamarrei* (H. Milne-Edwards, 1837) in a perennial wetland, northeastern Bangladesh

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## ABSTRACT

Spawning season, recruitment, and growth of the freshwater prawn *Macrobrachium lamarrei* were studied in a perennial wetland, northeastern Bangladesh during October 2016 to September 2017. Spawning season was estimated based on the monthly variations of percent ovigerous females. Recruitment and growth were estimated using the time series of the length-frequency distributions. We compared the von Bertalanffy growth function (VBGF) and the Pauly and Gaschütz growth function (PGGF) to identify any seasonal oscillation in growth rate. Ovigerous females occurred almost throughout the year, indicating a prolonged spawning season with two peaks between March–April (minor peak) and June–September (major peak). Both males and females with modal size ~ 8.0 mm carapace length first recruited in October, which synchronized with the major peak spawning season. There was seasonality in growth rate; hence, PGGF was adopted as the best-fitting model to describe the growth of both sexes. The estimated equations were $L_t = 17.86\ (1- \exp\ [-2.432\ (t/_{12} - 0.072) - (1.766/2\pi)\ \sin\ \{2\pi\ (t/_{12} - 0.982)\}]$ for males and $L_t = 23.18\ (1- \exp\ [-1.342\ (t/_{12} + 0.106) - (0.388/2\pi)\ \sin\ \{2\pi\ (t/_{12} - 0.209)\}]$ for females. Sexual dimorphism was found with larger size in females than males. Longevity was estimated to be ~ 14 months for both sexes. These findings can be useful to formulate management measures for this prawn.

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## Keywords

Bangladesh, freshwater prawn, growth parameters, *Macrobrachium*, spawning season.

## Introduction

*Macrobrachium* Spence Bate, 1868 is one of the most diverse genera of the family Palaemonidae comprising more than 250 species (Molina *et al.*, 2020) and found in almost all types of freshwater and estuarine habitats in tropical and subtropical regions (Holthuis, 1980). *Macrobrachium* species are important both economically as a valued human food and ecologically in determining the dynamic and structure of aquatic ecosystems (Etim and Sankare, 1998). *Macrobrachium lamarrei* (H. Milne-Edwards, 1837) is distributed in south Asian countries including India (Milne-Edwards, 1837), Pakistan (Kazmi and Kazmi, 1979), Bangladesh (Ali *et al.*, 1980), Myanmar (Cai and Ng, 2002), and Nepal (Sharma and Subba, 2005).

In Bangladesh, 24 species of freshwater prawns — including 10 species of *Macrobrachium* — are recorded (Akand and Hasan, 1992), among which *M. lamarrei* is one of the commercially important species (Rahman, 2002). In the past, freshwater prawns were abundant in the rivers, beels (relatively large surface, static waterbody that accumulates surface run-off water through an internal drainage channel), canals, streams, and ponds of this country (Ahamed *et al.*, 2014). However, their production has been declining due to both natural and man-made catastrophes, degradation of aquatic environments, and reduction of wetlands and water areas (Graaf *et al.*, 2001). Many of these valuable species have been threatened or endangered (on the verge of extinction) (IUCN Bangladesh, 2015). Therefore, it is essential to take proper management measures for their conservation and sustainability.

Management plans are very important for sustainable exploitation of commercially important fisheries (Simon, 2015) and this requires basic population dynamics information (*e.g.*, growth, reproduction, recruitment, and mortality) for the target species (Kutkuhn, 1981; Smith *et al.*, 1990). Information on various aspects of the life history of a population allows (a) modeling of group dynamics, and (b) predicting future stock potential through tracking of age classes or cohorts over time. Such modeling and prediction help to assess the population productivity and sustainability, which is essential to formulate management strategies (Campana, 2001; Hutchinson and Ten Brink, 2011; Higgins *et al.*, 2015). Some studies have been done on *M. lamarrei*. For example, Koshy (1969) reported the sexual dimorphism from India, Sharma and Subba (2005) studied the fecundity from Nepal, Ara *et al.* (2014) studied the length-weight relationship from Bangladesh, while Hussain and Manohar (2016; 2017) reported the reproductive biology from India. However, there is sparse information on the population parameters, namely growth, recruitment, and mortality of the species *M. lamarrei* from Bangladesh or elsewhere. Therefore, in order to provide the knowledge and baseline information required for the management of *M. lamarrei*, our study addresses the spawning season, recruitment, and growth of this species.

## Materials and Methods

### *Sampling*

Monthly samples of *M. lamarrei* were collected from a perennial wetland having a surface area of 2.42 hectares with an average depth of 2 meters near the Fisheries Field Laboratory of the Faculty of Fisheries, Bangladesh Agricultural University, northeastern Bangladesh (23°58'N 89°38'E) during October 2016 to September 2017. Sampling was done during daytime from 10:00 am to 12:00 pm using a fine-meshed (2 mm) push net. After sampling, the specimens were immediately preserved in 10 % neutralized formalin in a plastic container to avoid decomposition, and then transferred to the laboratory for further analysis.

*Measurements*

Specimens were sexed by morphological examination of either the second cheliped or the genital pore (Sharma and Subba, 2005). Mature individuals were sexed easily by large, spiny, and strong second cheliped as males, whereas in females they were small and smooth. In the case of juveniles, sex determination was done under a stereo microscope based on the presence of genital pores. In males, they are in the coxa of the fifth pair of walking legs, but in females, they are in the coxa of the third pair of walking legs. Carapace length (CL) was measured from the posterior edge of the orbit to the mid-dorsal posterior edge of the carapace using a digital slide caliper to the nearest 0.01 mm.

*Spawning season*

To estimate the spawning season, all females collected were classified as ovigerous (carrying fertilized eggs beneath their abdomen) or non-ovigerous. Spawning season was estimated based on the monthly variation of percent ovigerous females. Regional air temperature, rainfall, and photoperiod data were obtained for the study period from https://www.worldweatheronline.com/mymensing-weather-averages/bd.aspx to correlate with the spawning season of *M. lamarrei* using Spearman rank-correlation test.

*Length-frequency analysis*

Carapace length frequency distributions by sex with 1 mm interval were constructed for each sample. A series of component normal distributions were fitted to the frequency distribution of each sample by sex using FAO-ICLARM Stock Assessment Tools (FiSAT) based on Bhattacharya's (1967) method. Each component normal distribution was assumed to represent an age group in the population. This analysis provided the mean CL and proportion of each age group explained by each component normal distribution.

*Determination of birth-date and longevity*

Birth-date was assumed to be an arbitrary day approximately in the middle of the main spawning season (Ohtomi, 1997). Ages (in months) were then calculated from the assigned birth-date for the mean CLs belonging to each of the cohorts, and longevity was estimated from the time series of length-frequency distributions (Ohtomi, 1997).

*Age assignment and fitting growth curves*

Growth patterns of CL for both male and female *M. lamarrei* were modeled by fitting two equations to the mean CL at ages, which were estimated for each component normal distribution at each sampling date. One is the most commonly used von Bertalanffy (1938) growth function (VBGF), which can describe growth appropriately and has been used extensively for decapod crustaceans. The second one is the modified VBGF, *i.e.*, the Pauly and Gaschütz (1979) growth function (PGGF), that incorporates seasonal variations in growth rate, as the molting of individuals within a year class in crustaceans is asynchronous. These two equations are: VBGF, $L_t = L_\infty[1- \exp\{-K(t - t_0)\}]$; and PGGF, $L_t = L_\infty(1- \exp[-K(t/_{12} - t_0) - (CK/2\pi) \sin\{2\pi(t/_{12} - t_s)\}]$, where $L_t$ is CL (mm) at age t (month), $L_\infty$ is the asymptotic CL (mm) corresponding to the CL that the shrimp would attain at infinite age (*i.e.*, the length of the shrimp would attain if it were to grow indefinitely), K is the intrinsic growth rate (per month for VBGF and per year for PGGF) at which $L_\infty$ is approached, $t_0$ is the hypothetical age at which CL would be zero, C is the amplitude of seasonal growth oscillation, and $t_s$ is the age at beginning of growth oscillation. The goodness of fit of these equations was compared on the basis of Akaike (1973) information criterion (AIC) and coefficients of determination ($r^2$). The AIC was calculated as: $AIC = n \ln Y_{min} + 2r$, where n is the number of observations, r is the number of estimated parameters, and $Y_{min}$ is the minimum value of the objective function (residual sum of squares/n). Lower AIC value indicates the best-fitted model, and the closer the $r^2$ value approaches 1, the better the model fit. An F-test was conducted to compare the growth curves between sexes according to Chen *et al.* (1992): $F = [(S_p-S_m-S_f)/r]/ [(S_f+S_m)/ (n_m+n_f-2r)]$, where $S_m$ is residual sum of squares (RSS) for males, $S_f$ is RSS for females, $S_p$ is RSS for pooled data, nm is number of plots for males, $n_f$ is number of plots for females, and r is number of parameters.

## Results

The collection details for *M. lamarrei* used in our study are given in Tab. 1. A total of 1092 individuals were collected during this study, consisting of 524 (48.0 %) males and 568 (52.0 %) females. The carapace length (CL) for both males and females ranged from 4.0–20.0 mm.

*Spawning season and birth-date*

Ovigerous females of *M. lamarrei* occurred throughout the year except in December (Fig. 1). The monthly percentage of ovigerous females was lowest in January (2.08 %) and highest in September (60.87 %). The percentage of ovigerous females rose in February and remained high during March-April. Two spawning peaks were recorded, with an initial peak in March-April (minor peak) and a second peak in June-September (major peak). Monthly average air temperature, rainfall, and photoperiod were correlated with the spawning season of *M. lamarrei* (Fig. 1), which indicated a significant relationship with temperature ($r_s = 0.742$, $P < 0.01$) and rainfall ($r_s = 0.622$, $P < 0.05$), but no relationship was found with photoperiod ($r_s = -0.189$, $P = 0.279$). The birth-date of this species was arbitrarily assigned on 1 August (approximately the middle of the major spawning peak).

**Table 1.** Details of *Macrobrachium lamarrei* samples collected from a wetland, northeastern Bangladesh (CL = carapace length, OF = ovigerous females).

| | | Male | | Female | | |
|---|---|---|---|---|---|---|
| **Sampling date** | **Total individuals** | **Total number** | **CL range (mm)** | **Total number** | **Total OF** | **CL range (mm)** |
| 24 October 2016 | 102 | 51 | 4.0-14.2 | 51 | 7 | 4.0-13.8 |
| 21 November | 86 | 41 | 6.5-16.7 | 45 | 7 | 7.2-16.1 |
| 16 December | 107 | 54 | 6.0-17.4 | 53 | 0 | 7.5-16.9 |
| 14 January 2017 | 80 | 39 | 5.8-16.0 | 41 | 1 | 6.0-15.5 |
| 17 February | 62 | 26 | 9.0-18.0 | 36 | 3 | 6.0-16.1 |
| 19 March | 66 | 37 | 6.2-18.5 | 29 | 15 | 9.2-18.3 |
| 13 April | 72 | 41 | 9.8-19.1 | 31 | 15 | 9.7-17.0 |
| 16 May | 73 | 47 | 10.9-19.0 | 26 | 4 | 9.8-18.0 |
| 17 June | 78 | 33 | 10.9-18.9 | 45 | 22 | 7.6-18.1 |
| 16 July | 104 | 44 | 8.2-19.3 | 60 | 22 | 9.2-19.1 |
| 18 August | 146 | 65 | 7.1-20.1 | 81 | 48 | 6.4-19.0 |
| 26 September | 116 | 46 | 9.0-20.0 | 70 | 43 | 8.3-20.0 |

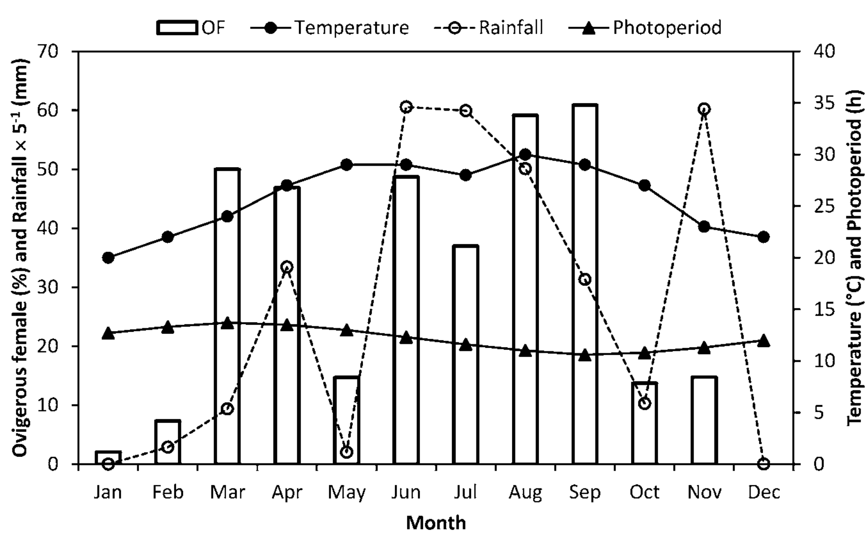


**Figure 1.** Monthly changes in percentage occurrence of ovigerous females of *Macrobrachium lamarrei* collected from a wetland, northeastern Bangladesh and average monthly variations of rainfall, air temperature and photoperiod during October 2016 to September 2017.

*Length-frequency distribution, recruitment, and longevity*

Length-frequency distributions for both sexes throughout the year revealed a polymodal pattern (Figs. 2, 3). Unimodal size distribution was observed during October, December, and March-June in males; and October-December in females. Bimodal size distributions were identified during January–February and July–September in males, whereas in females it was in January-May and July-September. Trimodal size distributions were observed during November for males and June for females. So, the majority of the months showed bimodal distributions indicating two cohorts associated with two recruitment pulses. However, the only cohort showing successive growth was first recruited to the fishing ground in October with a mean CL of ~ 8.0 mm and existed until the following September for both sexes (Figs. 2, 3). The life span was calculated from the time series of the length-frequency distributions using the assigned birth date 1 August, and was estimated to be ~ 14 months for both sexes.

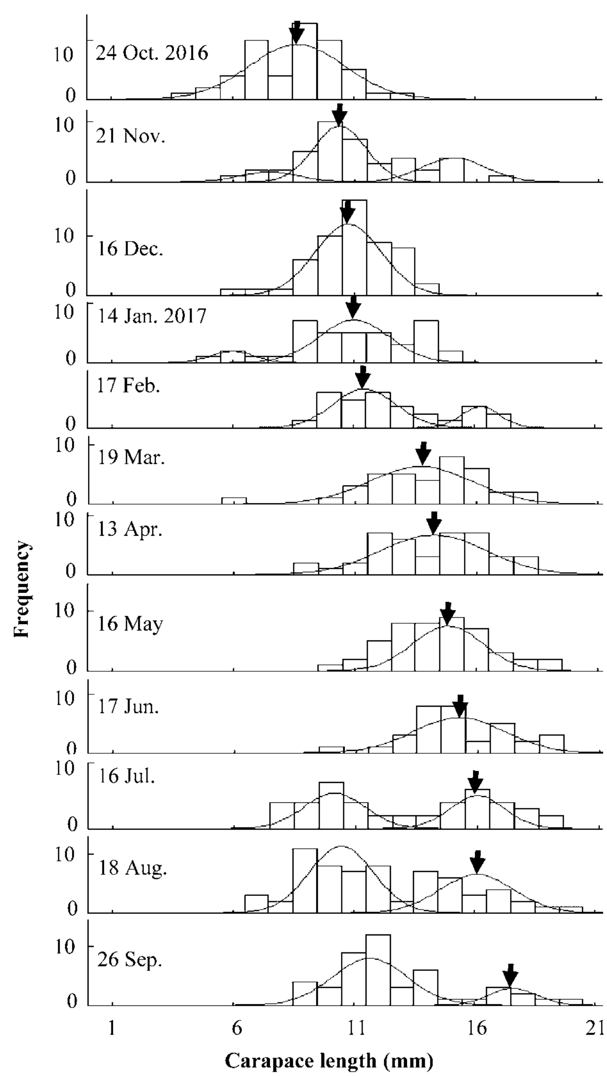


**Figure 2.** Length-frequency distributions of male *Macrobrachium lamarrei* collected from a wetland, northeastern Bangladesh during October 2016 to September 2017. Curves show the normal distributions, and arrows trace the progress of the cohort.

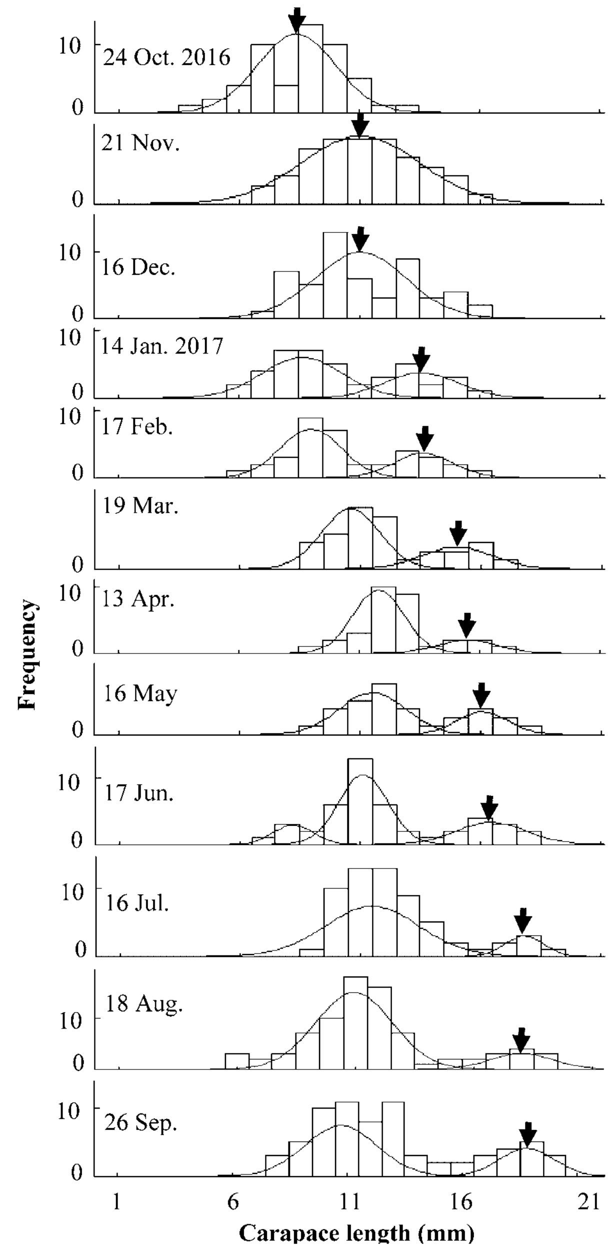


**Figure 3.** Length-frequency distributions of female *Macrobrachium lamarrei* collected from a wetland, northeastern Bangladesh during October 2016 to September 2017. Curves show the normal distributions, and arrows trace the progress of the cohort.

*Growth pattern*

The estimated growth functions obtained from fitting two different growth models to mean CLs at ages of both male and female *M. lamarrei* are shown in Tab. 2. In males, lower AIC but higher $r^2$ values were obtained for PGGF than VBGF. In females, VBGF provided a slightly lower AIC value but higher $r^2$ value than for PGGF. Therefore, PGGF was adopted as the appropriate growth model for our study population of *M. lamarrei* (Fig. 4) given lower AIC and higher $r^2$ values indicating model goodness of fit. Females had higher $L_\infty$ but lower K values than males. The growth curves showed seasonal oscillation (C) of 0.73 in males and 0.29 in females. Hence, an F-test revealed a significant difference in growth curves between sexes ($F = 25.38$, $P < 0.01$).

**Table 2.** Growth parameters obtained from fitting two growth models to mean carapace lengths at ages of *Macrobrachium lamarrei* ($L_\infty$ = asymptotic carapace length (mm), K = growth coefficient, $t_0$ = theoretical age at zero length, C = intensity of seasonal growth oscillation, and $t_s$ = age at the beginning of growth oscillation).

| Model | Sex | Growth parameters | | | | | AIC | $r^2$ |
|---|---|---|---|---|---|---|---|---|
| | | $L_\infty$ | K | $t_0$ | C | $t_s$ | | |
| von Bertalanffy | Male | 42.48 | 0.024 | -6.924 | - | - | -15.21 | 0.974 |
| | Female | 20.94 | 0.143 | -1.043 | - | - | -13.45 | 0.979 |
| Pauly and Gaschütz | Male | 17.86 | 2.432 | 0.072 | 0.726 | 0.982 | -23.33 | 0.990 |
| | Female | 23.18 | 1.342 | -0.106 | 0.289 | 0.209 | -12.27 | 0.983 |

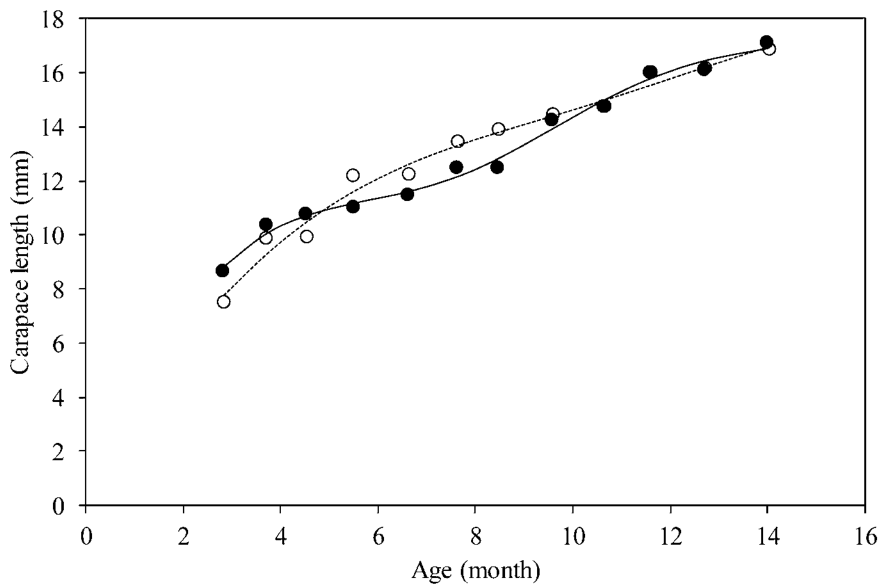


**Figure 4.** Growth curves for male and female *Macrobrachium lamarrei* collected from a wetland, northeastern Bangladesh during October 2016 to September 2017. Solid circles with solid line indicate males and open circles with dashed line indicate females.

## Discussion

Estimation of various aspects of life history is indispensable for sustainable exploitation of commercial fisheries (Vitale *et al.*, 2006). This study provides information on some life history traits of *M. lamarrei*; spawning season, recruitment, and growth, for example. The spawning season of several *Macrobrachium* species have previously been studied indicating that their spawning mostly occurs between April and November, *e.g.*, *M. dux* (Lenz, 1910) (Arimoro and Meye, 2007), *M. gangeticum* Spence Bate, 1868 (Jayachandran, 2001), *M. idella idella* (Hilgendorf, 1898) (Jayachandran, 2001), *M. lanchesteri* (De Man, 1911) (Phone *et al.*, 2005), and *M. malcolmsonii* (H. Milne Edwards, 1844)

(Jayachandran, 2001). *Macrobrachium amazonicum* (Heller, 1862), on the other hand, was found to spawn throughout the year (Sampaio *et al.*, 2007), as our study reported for *M. lamarrei*. We found ovigerous females to be present throughout the year, except in December, indicating a prolonged spawning season with two peaks, a minor peak and a major peak. The minor peak was in spring (March–April) and major peak was in summer-autumn (June–September). This finding was in accordance with the study of Hussain and Manohar (2016, 2017) from Indian waters, who also reported an extended spawning season of this species with two peaks, though the duration of peaks were different (May–June, "major peak"; and November–December, "minor peak") than the present study. Spawning activity varies seasonally showing a bimodal/polymodal pattern in many freshwater prawns (Cole, 1958; Omori and Chida, 1988; Guerao *et al.*, 1994; Oh *et al.*, 2002; Lucena-Fredou, 2010; Hussain and Manohar, 2016; 2017). The most common factors influencing the spawning season of freshwater decapods are temperature, rainfall, and photoperiod (Pinheiro and Hebling, 1998; Huang *et al.*, 2010). In the present study, the first two environmental variables (temperature and rainfall) showed distinct temporal patterns with significant correlation with the spawning season of *M. lamarrei*. The air temperature of our study site ranged from 20 °C to 30 °C implying relatively high temperatures throughout the year, causing the extended spawning season of this species, as reported for many other species (Kikuchi, 1962; Allen, 1966; Wear, 1974; Bauer, 1992; Oh *et al.*, 2002). Spawning during the period of higher temperatures may intensify the rate of embryo and larval development (Dahan and Benayahu, 1998; Bassim *et al.*, 2002) and enhance settlement rates (Martin and Archer, 1986; Wilson and Harrison, 1998; Nozawa and Harrison, 2005). Nevertheless, a prolonged spawning season might also be a life history adaptation for short life-span species (Bauer, 1989). In our study, the spawning season of *M. lamarrei* significantly coincided with rainfall, indicating a growing trend in the occurrence of ovigerous females with heavy rainfall. High rainfall leads to nutrient enrichment of the habitat by providing increased organic matter from direct surface flow and creating favorable conditions for growth and development of early larval stages (Dato-On-Subong and del Norte-Campos, 2015; Paschoal *et al.*, 2016).

Size distribution of *M. lamarrei* showed bimodality in the majority of months forming two distinct cohorts associated with two recruitment pulses. However, the only cohort that showed successive growth was first recruited in October and was sustained until the following September for both sexes. Recruitment of juveniles for this cohort was likely to take place during the major peak spawning season of June–September, with a time-lag of 2–3 months. The estimated longevity of *M. lamarrei* was ~14 months for both sexes, based on the time series of CL frequency distributions. This was close to the results of some studies that reported a maximum age of small-sized *Macrobrachium* species ranging from 1.5–2 years (Walker, 1979; Howard, 1981; Gray, 1991), whereas others indicated that this range could be up to 3 years (Choudhury, 1970; Chávez-Alarcón and Chávez, 1976; Teshima *et al.*, 2006; Alhassan and Armah, 2011; Vogt, 2018). Longevity is a fundamental parameter for understanding species population dynamics, and may vary between populations of the same species in the same region — and even in the same water body — due to a wide range of different factors including habitat complexity, food availability, predation pressure, and mortality (Carey, 2003; Vogt, 2018). However, the factor(s) leading to variations in longevity in our study, compared to other studies, remain undefined.

Growth of *M. lamarrei* was well expressed by the Pauly and Gaschütz growth function (PGGF) for both sexes, indicating seasonal oscillation in growth rate. Several studies (Jones and Johnston, 1977; Garcia, 1985; Bergström, 1992; Ohtomi and Irieda, 1997) have reported that the growth of crustaceans is associated with molting, and this molting is correlated with seasonal variations in water temperature, spawning, and food intake (plankton is predominant throughout the year in the study site) (Islam, 2015). However, no seasonality in these three parameters was observed in our study. Therefore, at present, it is difficult to conclude what extrinsic factors play an important role for seasonal oscillation in growth of *M. lamarrei*, so it deserves greater attention in future studies.

The estimated growth equations showed higher asymptotic length, but lower growth rate, in females than for males, which concorded with an earlier study by Koshy (1969) from Indian waters. However, most species of *Macrobrachium* show larger sizes for males than females (Koshy, 1969). In females, a larger asymptotic length is a common phenomenon to support egg fecundity (Dailey and Ralston, 1986; Ohtomi, 1997; Colloca, 2002; Ahmed *et al.*, 2007; Ahamed *et al.*, 2012; 2017; Ahamed and Ohtomi, 2012). But a lower average growth rate, due to sharply decreasing growth after reaching sexual maturity, implies higher energy requirements for reproduction (Taylor and Gabriel, 1992; Pescinelli *et al.*, 2014). Conversely, males generally show higher growth rates with an earlier onset of sexual maturity, resulting in lower asymptotic lengths than for females (Phipps, 1774; Hartnoll, 1982).

Finally, this study provides the first information on recruitment and growth of *M. lamarrei* from any geographic region where the species is found. This information will be useful to formulate management measures of this commercially important species and provide an important basis for future studies from other habitats.

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