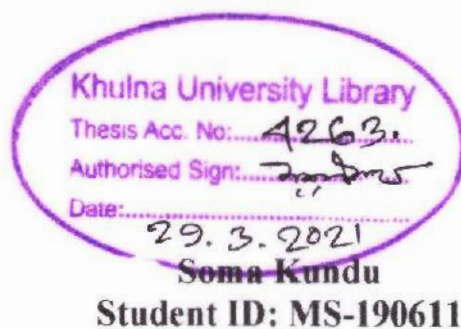


Influence of maternal size, offspring feeding and their interaction on the hatchery outcomes of an Indian major carp, Rohu (*Labeo rohita*)



**Fisheries and Marine Resource Technology Discipline
Khulna University, Khulna
Bangladesh**

December, 2019

Influence of maternal size, offspring feeding and their interaction on the hatchery outcomes of an Indian major carp, Rohu (*Labeo rohita*)

**A Thesis
By
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Student ID: MS 190611
Session: 2019-2020**

A thesis submitted to the Fisheries and Marine Resource Technology Discipline in partial fulfillment of the requirements for the degree of Masters of Science (MSc) in
Fish Genetics & Biotechnology

December, 2019

Influence of maternal size, offspring feeding and their interaction on the hatchery outcomes of an Indian major carp, Rohu (*Labeo rohita*)

Approved as to style and content by



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December, 2019

Declaration

Influence of maternal size, offspring feeding and their interaction on the hatchery outcomes of an Indian major carp, Rohu (*Labeo rohita*)

The results presented in the thesis with the above mentioned title are entirely of the candidate's own investigations and no part of the results has been accepted for any degree nor is it concurrently submitted for any degree.

Soma 16.02.20

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December, 2019

DEDICATED
TO
MY BELOVED PARENTS



Acknowledgement

At first, all my admiration goes to the supreme creator and ruler of the universe, the Almighty Allah for his great mercy to keep me alive and enables me to pursue my education in 'Fisheries and Marine Resource Technology Discipline' as well as to complete my work for the degree of 'Master of Science' in "Fish Genetics & Biotechnology".

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Abstract Broodstocks' size and larval feeding are very crucial in quantitative and qualitative production of gametes and offspring in any fish breeding system. Therefore, this study was carried out to investigate the influence of maternal size, offspring feeding strategy and their interaction on spawning performance and offspring fitness using a highly commercially important aquaculture species, an Indian major carp (*Labeo rohita*). The entire study was comprised of two experiments, such as 1) maternal size effect and 2) maternal size, offspring feeding and their interactive effects. During the study, females were divided into two size groups ('large' and 'small'), while offspring were randomly assigned into two feeding strategies ('everyday' and 'every other day'). The results revealed that larger mothers produced significantly higher amount of eggs with enhanced hatching and reduced deformation rate, and larger sized offspring than the smaller mothers. The offspring feeding strategy disclosed that everyday fed offspring had higher survival and better size than those fed every other day. The study did not find any significant effect of maternal size on egg number and size, and offspring survival, while interaction between maternal size and offspring feeding showed no significant effect on any offspring trait which confirmed that very strong effects of maternal condition and offspring feed deprivation were not compromised with any change. The overall findings of this study suggest that maternal size and regular offspring feeding must be considered to produce high quantity and good quality of gametes and offspring for sustainable production of this valuable species.

Keywords Broodstock size · Gamete quality · Larvae production · Offspring fitness

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Chapter-1

1.0 Introduction

1.1 Background of the study

Body size-dependent reproductive tactics are well known in many fishes which allocate reproductive energy to enhance direct (e.g. eggs, milt, fertilization, hatching, etc.) and indirect (e.g. offspring fitness) spawning benefits (Duarte and Alcaraz 1989; Johnson et al. 2011; Hixon et al. 2014; Barneche et al. 2018). Studies reported that larger females consistently produced more, bigger and good quality eggs (Mehault et al. 2010; Wang et al. 2012; McBride et al. 2015) which had greater success of fertilization and hatching than smaller females (Johnston et al. 2007; Hagmayer et al. 2018). Evidence also demonstrated that larger females not only produced good quality eggs but also allocated their reproductive energy to obtain indirect benefits by producing good quality offspring (Sogard et al. 2008; Rollinson and Rowe 2016; Barneche et al. 2018). Recent studies revealed that females could transfer molecular resources (e.g. nutrients, non-genetic information, etc.) via eggs to increase the fitness of their offspring (Giesing et al. 2011; Morrison et al. 2017). But these direct and indirect outcomes are not so straightforward which depend on many factors such as parental conditions, their nutrition, husbandry, spawning strategy, etc. (Bohe and Labbé 2010; Migaud et al. 2013; Newman et al. 2016; Ljungström et al. 2019) as well as offspring rearing strategies and environment (Rahman et al. 2013; Thompson and Volpedo 2018; Vega-Trejo et al. 2018).

Among many factors, offspring feeding strategy is a crucial one which can affect their survival, behavior, growth and other fitness traits (Devigili et al. 2012; Garrido et al. 2015; Politis et al. 2018). Moreover, studies suggested that larval feeding accounted for the maximum cost in any aquaculture production system (Coyle et al. 2004; Sarker et al. 2013). Therefore, researchers get huge interests about how to minimize feeding cost adopting different strategies such as substituting live feeds (Cahu and Infante 2001), formulating low-cost feeds (Jomori et al. 2005), intermittent feeding (Thongprajukaew and Rodjaroen 2017), etc. Studies found that these feeding strategies could significantly reduce the overall production costs (Lee 2003; Kolkovski 2013).

Although several studies showed that maternal condition and offspring feeding strategy could influence the spawning benefits in different fishes, only a limited number of them explored these

effects on commercially important aquaculture species (e.g. Mehault et al. 2010; Yengkokpam et al. 2013; Falica et al. 2017). Moreover, a very few evidence is available yet about the interactive effect of maternal size and offspring feeding on fish offspring fitness (Vijendravarma et al. 2010; Vega-Trejo et al. 2018). These have attracted scientists to explore the effects of maternal size and offspring feeding strategy on commercial fish hatchery production, and also to know whether offspring of larger females reared with low amount of feed will have better fitness or at least similar performance to the offspring of smaller females providing higher amount of diet. To find out the answers, the present study was conducted by dividing the females into two size groups, while their offspring were further sub-divided into two feeding groups which were fed either everyday or every alternative day. This study was carried out with a highly commercially important aquaculture species, an Indian major carp (*Labeo rohita*).

L. rohita is the most popular freshwater aquaculture species in the Indian sub-continent which produced more than 1,842 and 1,962 million tons during 2016 and 2017, respectively and this production accounted for approximately 3% of total global aquaculture finfish production (FAO 2019). They are largely produced through different culture systems such as polyculture with other carps (Pradhan et al. 2019; Das et al. 2019), mixed culture with other fishes (Wahab et al. 2011, 2019) and prawns (Hossain and Islam 2006; Jana et al. 2019), integrated culture with rice (Dey et al. 2019) and livestock (Kestemont 1995), etc. Since they are highly demanding species, their production requires a huge number of larvae. Unfortunately, the natural sources are unable to provide these vast amount of larvae and therefore, hundreds of carp hatcheries have been established in this region to fulfill the demand (Rahman 2008; Khatun et al. 2017). In these hatcheries, the usage of broodstocks varies based on their availability and market demands. For example, some hatcheries do not have their own broodstock ponds which depend on natural or other sources, while many hatcheries do not have or maintain size and age selective broodstock facilities. Thus, hatcheries use randomly different sized broodstocks to fulfill the market demands which produce various qualities of eggs and offspring. This is a great problem in this big aquaculture industry which is a puzzle to them. On the other hand, many hatcheries try to feed their larvae as less as possible or irregularly to minimize the production cost which is another big issue in this aquaculture system. Therefore, this study was conducted to provide information that broodstocks particularly maternal size is a prerequisite to obtain greater production benefits. Moreover, the study showed that not only the maternal size but also the

offspring feeding strategy and their interactions are very essential to produce good quality larvae for the sustainable production of this species.

1.2 Objectives of the study

The major aims of this study were:

- ❖ To investigate maternal size effect on spawning performance and offspring fitness using a highly commercially important aquaculture species, an Indian major carp (*Labeo rohita*).
- ❖ To explore maternal size, offspring feeding and their interactive effects on Rohu (*L. rohita*)

Chapter-2

2.0 Literature Review

2.1 General Introduction

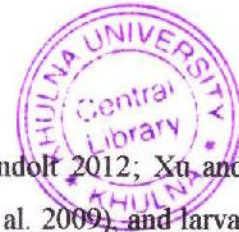
The term 'literature' refers to 'the knowledge (theoretical and practical) of a particular topic' and 'review' means 'the organization of knowledge'. Literature review is an indispensable part of research as it helps researchers to be familiar with the work by building a link between what have been studied on the selected topic and what is going to be studied. It forms the foundation and recapitulates ticklish points upon which all future work will be built.

Some studies have already been driven to pursue how several parental phenotypic traits and feeding regime are correlated with their fertilization success and offspring fitness in different animals. The present study has been planned to explore whether the influence of maternal size, offspring feeding strategy and their interaction on spawning performance and offspring fitness using a highly commercially important aquaculture species, an Indian major carp (*Labeo rohita*). This section of thesis work will give an essence and the approximate review of former research pertinent to the present study.

2.2 Parental influence on offspring

Investigating parental effects on offspring fitness-related traits has been an ongoing interest for evolutionary ecologists (Falica and Higgs 2013), with parental effects driven by both genetic influences (e.g. Johnsen et al. 2000; Klemme et al. 2008), and non-genetic environmental influences (e.g. Freeman-Gallant 1998; Gruebler and Naef-Daenzer 2010). 'Parental effects' comprise both maternal (Dam) effects and paternal (Sire) effects. Parental influences include all trans-generational processes that affect offspring (phenotype & fitness) without alteration of the primary structure of DNA (Youngson and Whitelaw 2008; Bonduriansky and Day 2009; Jablonka and Raz 2009; Kangassalo et al. 2015).

In fishes, the roles of dam and sire influences have been studied in many phenotypic traits in offspring including embryo survival (e.g. Wedekind et al. 2008; Rodriguez-Munoz and Tregenza 2009; Kekalainen et al. 2010), growth (e.g. Bang et al. 2006; Wang 2006; Pitcher and Neff 2007; Evans et al. 2010; Janhunen et al. 2011), disease resistance (e.g. Balfry et al. 1997), embryonic viability (Janhunen et al. 2010), swimming performance (Falica and Higgs 2013), parental body



size impacts on offspring (Iyengar and Eisner 1999, Davis and Landolt 2012; Xu and Wang 2013), anti-predator behaviour (e.g. Evans et al. 2004, Huuskonen et al. 2009), and larval spinal deformity (e.g. Evans and Neff 2009). All of these studies noticed significant parental influences on various aspects of offspring traits regarding different factors that may have different effects at different life stages in the species of interest. However, it is important to recognize 'parental effects' as it provides an important source of variation among offspring, and contribute to the effects of environmental changes on the resulting phenotypes (Janhunen et al. 2010).

2.3 Maternal influence on offspring

Though maternal, paternal, and parental interactions all contribute to the variation in developing larvae (Butts and Litvak 2007), maternal effects are generally considered to be more important than paternal effects, as females usually invest more care and resources in the production of offspring (e.g. Tallamy 1984; Mousseau and Fox 1998; Bonduriansky and Day 2009; Kangassalo et al. 2015). Female effects on offspring traits can be divided into genetic and nongenetic (maternal environment) effects (Huuskonen et al. 2009). The pronounced maternal effects on early life processes, including the viability itself, are unambiguous, since all the essential constituents for sustaining embryonic development are provisioned together with yolk (Heath and Blouw 1998; Heath et al. 1999; Berg et al. 2001; Kamler 2005; Janhunen et al. 2010). In particular, mothers have the ability to modulate egg size and resource content, and this egg size is regarded as a key feature in fish early history (Kangassalo et al. 2015). Egg size may be expressed as egg diameter, egg volume, wet weight, dry weight, energy content per egg or else the content of a key substance (e.g. carbon, nitrogen, protein) per egg. This factors particularly affect the traits expressed in early ontogeny, such as embryonic and larval viability, and development rate (Mousseau and Fox 1998; Fox and Czesak 2000; Bonduriansky and Head 2007). This maternal effect could also serve as a potential adaptive pathway in the course of evolutionary processes (McAdam et al. 2002; Janhunen et al. 2010).

Maternal effects on progeny traits are often documented (Berg et al. 2001; Trippel et al. 2005; McCormick 2006), given the importance of the maternal genetic and female-mediated provisioning of nutrients and other compounds (e.g. hormones) to the eggs (Brooks et al. 1997; Berg et al. 2001; Nadeau 2009) as well as on progeny. Some studies have been conducted to see the maternal effects on offspring traits which revealed that maternal effects on offspring size may

translate into variation in offspring fitness particularly under unfavourable conditions in fish (Reviewed in: Hutchings 1991; Einum and Fleming 1999; Einum 2003, Janhunen et al. 2010). Few other studies have found a positive correlation between female size and egg diameter (Wright and Shoesmit 1988; Murry et al. 2008), and female size and survival of larvae (Arlinghaus et al. 2010). A common feature of many large fish species is that larger and older mother produce higher and bigger offspring with higher viability than small individuals (Chambers and Leggett 1996; Einum and Fleming 1999; Birkeland and Dayton 2005; Johnston et al. 2007). Bigger larvae, having more available food item, less potential predators and better swimming performance, are strongly related to better survival (Perez and Munch 2010; Kotakorpi et al. 2013).

Falica et al. (2017) also found that maternal genetic effects play an important role in larval length and survival, and that these effects decrease with age, possibly due to environmental variation masking genetic effects. Berejikian et al. (2011) reviewed the positive correlation between female body size and offspring size that suggests a potential maternal genetic effect on offspring growth rate. According to Janhunen et al. (2010), maternal effects (e.g. female investment into their offspring via the egg characteristics) are often strong at early life-history stages but generally decline with increasing offspring age (Fox et al. 2003). Nonetheless, the relative influence of maternal identity in affecting offspring fitness can vary by species, populations or by a range of environmental conditions.

2.4 About the model species (Rohu)

2.4.1 General Information

Labeo rohita, known as rohu, is the highly esteemed Indian major carp which belongs to the family Cyprinidae and contributes about 35% in the aquaculture production of India (Mir et al. 2017). It is considered as one of the most important primary fish species for freshwater aquaculture in Asian sub-continent, due to its delicious flesh quality, great economic value, easy culture techniques, rapid growth rate, resistance and better disease (Abidi and Khan 2011; Saha et al. 2015). The higher demand of Rohu requires higher production. So the production capacity of this fish is expected to increase with the increase in the research efforts.



Figure 1: Pictures of Rohu (*L. rohita*) (Source: Wikipidia, 2017)

2.4.2 Classification

Phylum- Chordata

Class- Osteichthyes

Order- Cypriniformes

Family- Cyprinidae

Genus- Labeo

Species – *L. rohita*

2.4.3 Morphology

Rohu has elongated body shape with a short caudal peduncle. Body color is back brownish, silvery on sides and beneath. Dorsal and abdominal profiles are convex. It has fairly depressed snout, projected beyond jaw, thick & fringed lips. Inside of both lips is covered by a cartilaginous part. A pair of short maxillary barbells is present. It exhibit complete lateral line & moderate scale pattern. The description is reviewed from (Talwar and Jhingran 1991; Zakia 2010; Sarma et al. 2017).

2.4.4 Habitat & Ecology

Rohu is the natural inhabitant of freshwater sections of the rivers and thrives well in all fresh (Sarma et al. 2017). They are naturally distributed in the rivers of Bangladesh, India, Pakistan and Myanmar (Talwar and Jhingran 1991; Ullah et al. 2015).

The species is an omnivore and prefer different types of food at different life stages. At their early stage of life, it eats mainly zooplankton, but as it grows, it eats more and more phytoplankton, and as a juvenile or adult, it is an herbivorous column feeder, eating mainly phytoplankton and submerged vegetation.

2.4.5 Breeding

Rohu reaches sexual maturity between two and five years of age. The spawning season of rohu generally coincides with the southwest monsoon extending from April to September. Spawn may be collected from rivers and reared in tanks and lakes (Sarma et al. 2017). The fecundity of Rohu varies from 226,000 to 2,794,000, depending upon the length and weight of the fish and weight of the ovary. The spawn of this fish is collected from rivers during monsoon and reared in tanks and lakes.

Rohu is a eurythermal species and does not thrive at temperatures below 14 °C. It is a fast growing species and attains about 35-45cm total length and 700-800g in one year under normal culture conditions.

2.5 Previous studies on Rohu (*Labeo rohita*)

From the aquaculture perspective, carps are the most important fisheries products. Indian major carps, rohu (*Labeo rohita*), catla (*Catla catla*) and mrigal (*Cirrhinus mrigala*) are the prime carp species cultivated in inland freshwater aquaculture system in Bangladesh and other Asian countries constituting about 87% of the total fresh water production. Among them Rohu is regarded as highly delicious and most popular fish with many other good attributes that make it an outstanding species for aquaculture (Abidi and Khan 2010; Musharraf and Khan 2019b). Although several researches have been conducted by researchers regarding parental influence, genetic variability, diet effects, sperm competition etc. on carp, very few have considered maternal genetic & offspring feeding impacts specifically.

Studies include passive transfer of maternal antibodies and their existence in eggs, larvae and fry of Indian major carp, *Labeo rohita* (Ham.) (Swain et al. 2006), Offspring fitness and fecundity of an Indian major carp, *Labeo rohita* (Ham.) in relation to egg size (Sehgal and Toor 1991), Parentage analysis using molecular marker in Indian major carp (*Labeo rohita*) (Sahoo et al. 2017), Evaluation of intraspecific genetic variation and relatedness among populations of Indian major carp, Rohu (*L. rohita*) through randomly amplified polymorphic DNA analysis (Islam and

Alam 2004), Effect of long term administration of dietary β -glucan on immunity, growth and survival of *L. rohita* fingerlings (Misra et al. 2006), Dietary zinc requirement of fingerling Indian major carp, *L. rohita* (Hamilton) (Musharraf and Khan 2019a), Dietary iron requirement of fingerling Indian major carp, *L. rohita* (Hamilton) on growth and body composition (Musharraf and Khan 2019b) etc.

2.6 Research gap

From the previously reviewed literatures, it is clear that maternal effects, feeding effects & their interaction play vital roles in selective advanced aquaculture system. Offspring survival rate, fitness, growth, quality, culture cost benefits, and overall production success depend on the proper modulation of these two important factors. Many studies have been conducted at different time on different species to observe these effects particularly.

Many studies have been carried out considering the size effects and consequence of parents as well as larvae and reported that larger body size has many benefits, such as increased reproductive success, ability to evade predators and increased competitive ability and social status (Mehault et al. 2010; Vallin and Nissling 2000; McLennan et al. 2016).

Few studies reviewed maternal impacts. For example, Kamler (2005) reviewed 'Parent-egg-progeny' relationships in teleost fishes and found that the key pathway in the 'parent-egg-progeny' relationship are the positive relations between female size, egg size and larval size, the later resulting in variability of larval resistance to starvation and predation. Both, paternal and maternal factors contribute to total viability, operating at different time and in different ways. Kangassalo et al. (2015) studied the intra- and trans-generational effects of larval diet on immune susceptibility in the greater wax moth, (*Galleria mellonella*) and found that maternal nutrition affects immune function in insects while paternal effects are not as important as maternal effects in influencing immune function.

Some other studies consider feeding impacts growth, fitness, immunity and other traits of fish larvae (Shan et al. 2008; Takeuchi 2014; Ali et al. 2016; Musharraf and Khan 2019a; Musharraf and Khan 2019b). Besides the others species many studies chose Rohu (*L. rohita*) to observe various impacts like, evolution of genetic variation (Islam and Alam 2004), diet impacts (Misra et al. 2006; Musharraf and Khan 2019a; Musharraf and Khan 2019b), maternal-egg impacts (Sehgal and Toor 1991). Unfortunately, none of these studies verify maternal impacts and

offspring diet impacts on offspring survival and fitness considering an important carp species, Rohu. Therefore, the present study will be carried out to assess the interactive effects of maternal size and offspring feeding strategy on a popular carp species, Rohu (*L. rohita*).

2.7 Present study

From the previous discussion, it is clear that parental genetic and feeding regime have significant effects on offspring fitness. But specifically in carp species, very little findings have been identified, demonstrating maternal impacts on interaction with dietary modulation. The present study has generated an interest to investigate the 1) maternal size effect and 2) maternal size, offspring feeding and their interactive effects, using Rohu (*L. rohita*), one of the most important Indian major carp.

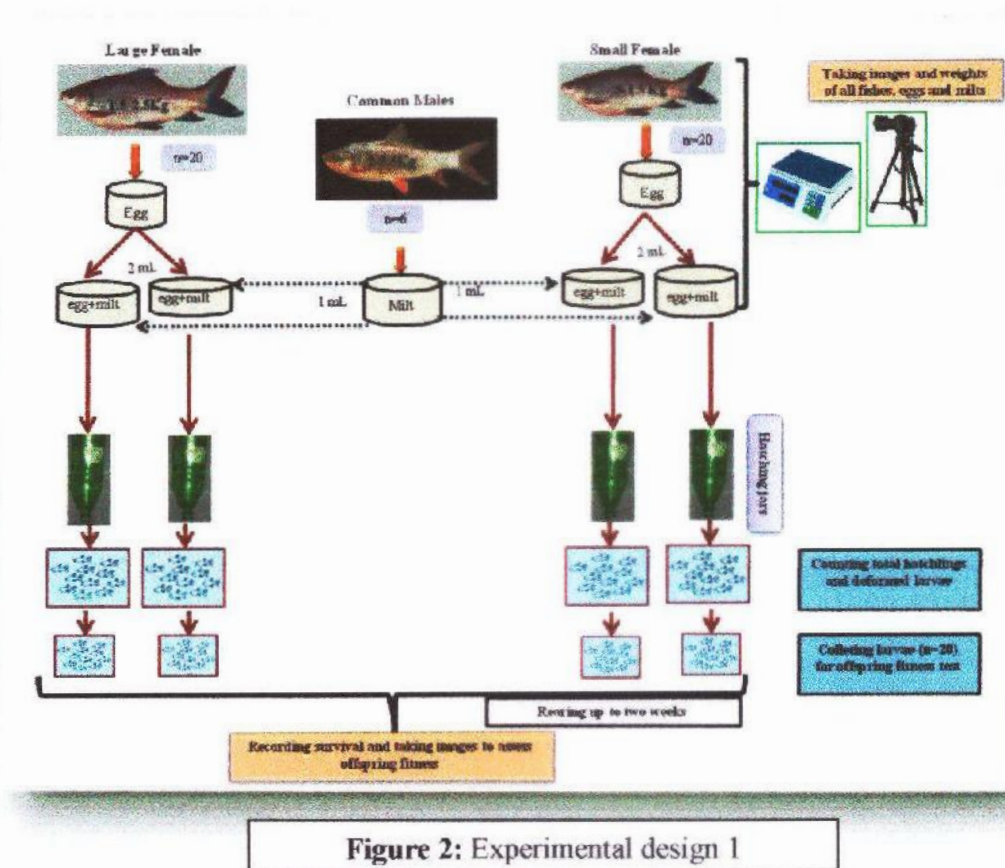
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Chapter-3

3.0 Materials & Methods

3.1 Broodstock selection and rearing

The sexually mature *L. rohita* were reared in broodstock ponds of a commercial carp hatchery (the South Bay Pvt. Ltd. Hatchery, Khulna, Bangladesh) which maintained the breeding protocols to avoid inbreeding problems. The entire study was carried out with two separate experiments- (1) Experiment-1: maternal size effects and (2) Experiment-2: maternal size, offspring feeding and their interactive effects (hereafter called 'maternal size-by-offspring feeding'). In experiment-1, 20 large sized females (weight range: 1.51-2.53kg and mean $\pm$ SE: 1.87 $\pm$ 0.07kg) and 20 small sized females (weight range: 0.53-1.43kg and mean $\pm$ SE: 0.97 $\pm$ 0.07kg) were sorted out, while six males (weight range: 1.80-3.50kg and mean $\pm$ SE: 2.31 $\pm$ 0.11kg) were selected as 'common males' to fertilize the eggs of both female groups (Experimental design 1 in Fig. 2).



In experiment-2, 16 large sized females (weight range: 2.01-2.50kg and mean $\pm$ SE: 2.23 $\pm$ 0.04kg) and 16 small sized females (weight range: 0.80-1.40kg and mean $\pm$ SE: 1.10 $\pm$ 0.05kg) were selected, whereas only four males (weight range: 2.20-2.80kg and mean $\pm$ SE: 2.40 $\pm$ 0.06kg) were selected as 'common males' to fertilize the eggs of both female groups (Experimental design 2 in Fig. 3 and the detailed protocol is given below). The age of all females ranged from 1.5 to 2.5 years, while common males were 2.0-3.0 years old. Finally, these selected males and females were kept experiment-wise separately in large tanks (5000L) up to two days under the same conditions (i.e. feed, water, etc.) before the fertilization process.

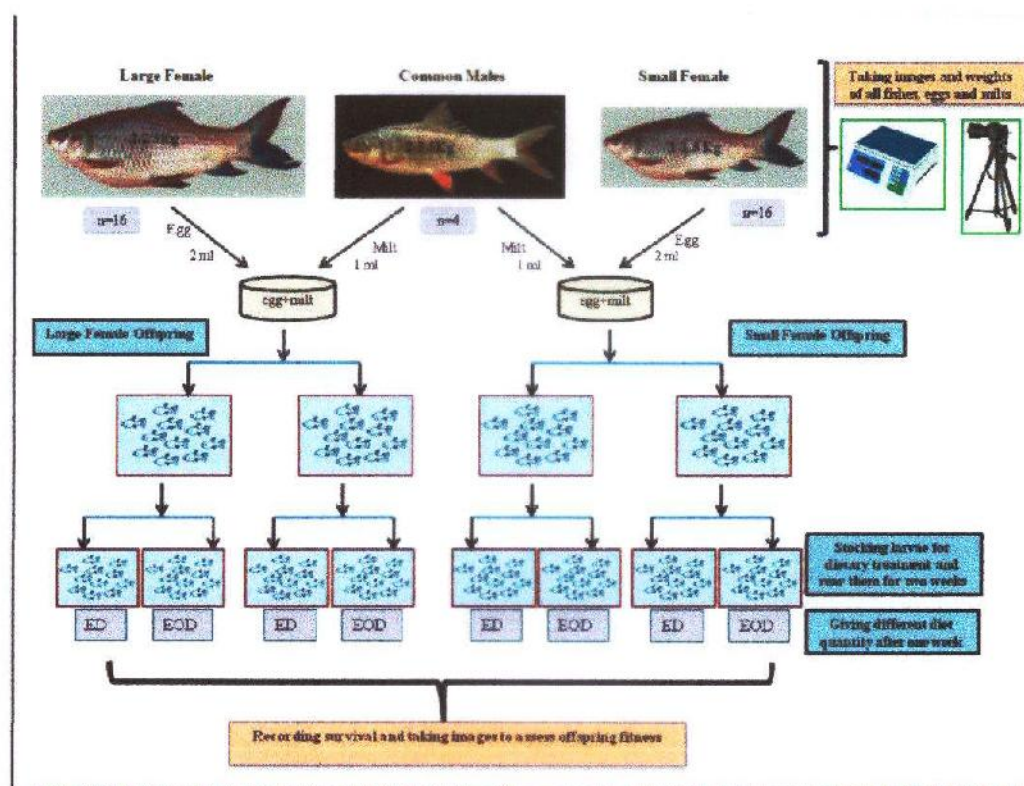


Figure 3: Experimental design 2

3.2 Artificial propagation and fertilization

The artificial propagation technique ('hypophysation') was applied at the base of pectoral fin by using the recommended doses of pituitary glands (PG) (Fig. 4) for induced spawning of Indian major carp (Jhingran and Pullin 1985; Sarder 2007). In brief, females were administered two

times at the rate of 1 mg PG/kg body weight for first time and approximately after 6 hours, the second dose was injected at the rate of 6.0 mg PG/kg body weight. The experimental males were administered only a single dose when the females were injected their second dose at the rate of 1 mg PG/kg body weight. Then they could become ready for artificial spawning after another 6 hours.



Figure 4: Administering the recommended dose of PG

3.3 Measurements of parental phenotypic traits

After collecting sperm and eggs from each male and female, individual's photograph along with their ID was taken with a digital camera (Canon DS126621). Then standard length (distance in cm from tip of the snout to the posterior end of the last vertebra) (Fig. 5) and body area (area covered from tip of the snout to the last mark of caudal peduncle in cm²) (Fig. 6) were measured from the digital photographs taken of each fish, using *ImageJ* software (<http://rsbweb.nih.gov/ij/>). Meanwhile, weight of individual fish was recorded using a digital balance.



Figure 5: Measuring standard length from the digital photograph using *ImageJ*



Figure 6: Measuring body area from the digital photograph using *ImageJ*

3.4 Experimental procedure

The ejected gametes were collected by hand stripping in clean and dry bowls (Fig. 7 & Fig. 8), and immediately weights of total milt and eggs were measured in digital weight machine (Fig. 9 & Fig. 10) and recorded. Then they were stirred well to have random samples from which exactly 1 mL of milt was collected from a common male's pooled milt with individual new syringe and mixed with 2 mL of eggs (collected with a marked new syringe) of individual female (Fig. 11). Thus, eggs from two to four females from each group were mixed with the milt of a common male. The milt was properly mixed with the eggs by adding water and continuous stirring with a clean chicken's feather (Fig. 12). Then the fertilized egg masses were transferred to previously labeled plastic containers (2 L), (Fig. 13) fitted with continuous aerated water flow

and kept for incubation up to 36-40 hours at ambient temperature (28-30°C) until the maximum hatching occurred. Meanwhile, the average total number of eggs per 1 mL were counted, while images of 20 eggs were captured under a microscope (LABOMED, Lx 400) mounted with camera to measure the diameter and area of eggs latter using the *ImageJ* software v-1.46 (<https://imagej.nih.gov/ij/download.html>). During this spawning trail, there were two replications of each female. The whole study was carried out during the first natural spawning cycle to ensure maximum quantity and good quality of gametes (Kucharczyk et al. 2008; Chattopadhyay 2016). Moreover, all collected samples were quickly checked to ensure good quality through visual inspection (Chatakondi 2012; Cogliati et al. 2018).



Figure 7: Egg stripping



Figure 8: Sperm stripping



Figure 9: Egg measurement



Figure 10: Sperm measurement



Figure 11: Addition of sperm and egg



Figure 12: Mixing



Figure 13: Placement in incubation jar

3.5 Offspring rearing and traits measurement

After confirmation of the maximum hatching, the total content of each incubator (i.e. alive and dead hatchlings, unfertilized eggs, etc.) was transported to the 'Wet laboratory' (6 km distance) of the Fisheries and Marine Resource Technology Discipline of Khulna University, Bangladesh. The transportation was done very carefully using the plastic bags filled with the required amount of water and aeration which were carried to the destination by the auto-rickshaws to avoid any travel stress to the offspring. The total number of alive hatchlings in each incubator was counted and reared them maternal family-wise up to three days to start gradually exogenous feeding.

After three days of rearing, the total number of alive and deformed hatchlings was counted and recorded (Fig. 14).



Figure 14: Hatchlings counting

Then 30 good looking offspring (visually had no deformation and active swimmers) were sorted and stocked family-wise in a glass aquarium (50cm×29cm×30cm) (Fig. 15) up to two weeks for the assessment of offspring fitness. In experiment-2, offspring were further randomly assigned to two feeding treatment groups for two weeks, such as 1) everyday feeding (hereafter called 'ED') and 2) every other day feeding (hereafter called 'EOD'). Thus, the design of experiment-2 was able to test not only the effect of offspring feeding level (i.e. 'ED' and 'EOD') but also their interaction with maternal size group (i.e. 'large' and 'small'). During the study, water quality parameters (e.g. dissolved oxygen, temperature and pH) were monitored daily. All offspring were fed *ad libitum* up to the apparent satiation level twice in both feeding groups at 09.00 and 17.00 hours (Khan et al. 2004; Mohapatra et al. 2012). At the end of experiment, offspring number was counted to determine their survival rate and then photograph of each anaesthetized (ice bathed) offspring was taken using a digital camera (Canon DS126621) to measure total length and body area with the *ImageJ* software (Fig. 16 & Fig. 17). The study was conducted up to this larval stage as most of the farmers prefer either three days old hatchling for fingerling business purpose or one/two-week old offspring for production purpose (personal communication).



Figure 15: Stocking in glass aquarium

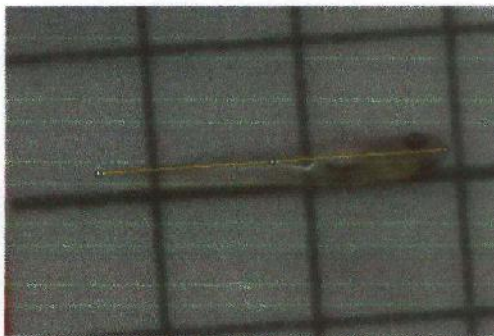


Figure 16: Length measurement

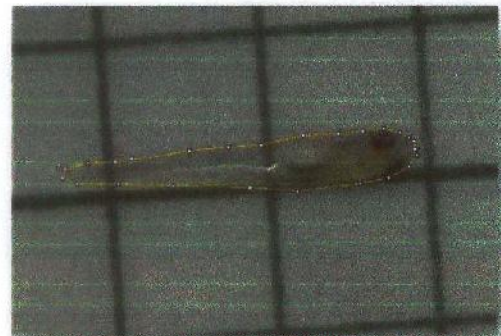


Figure 17: Body area measurement

3.6 Statistical analyses

All analyses were performed using 'R' version 3.5.2 (R Development Core Team 2018). The descriptive statistics (means, SD, SEs, etc.) were calculated using the 'psych' package. The Shapiro-Wilk test of normality and the Levene's tests for homogeneity of variance were done with the 'onewaytests' package.

The univariate analysis of variance (ANOVA) model was performed using the 'car' package to find out any variation in traits, whereas the default Kruskal-Wallis (K-W) test was applied to those traits which were not normally distributed by any transformation but homogenous. The

generalized linear model (GLM) with 'quasi-poisson' family option was applied using 'pscl' package for the 'percentage data' (hatching, deformation and survival rates) which did not comply with the assumptions of any parametric model. The 'quasi-poisson' regression is not only flexible with data assumptions but also allows for over-dispersion in the dependent variable (Mangiafico 2016). To avoid pitfalls of significance testing (the P -value) and also to quantify the magnitude of effects, the effect size was calculated (Cohen 1988) based on the appropriate statistical significance tests. Thus, Cohen's effect size (d) was estimated for ANOVA model (Lakens 2013), Epsilon square (ϵ^2) was calculated for K-W test (Levine and Hullett 2002) and coefficient of determination (r^2) was estimated for GLM (Nakagawa et al. 2017). The correlations among variables were tested and plotted using "Performance Analytics" package to explore any trade-offs. Finally, all graphs were made using 'ggplot2' package.

Chapter-4

4.0 Results

4.1 Experiment-1: maternal size effect

The initial analysis revealed no variation in body weight (K-W: $\chi^2=0$ and $P=1$) and average milt weight (K-W: $\chi^2=0$ and $P=1$) of the common males used in this experiment which also confirmed no effect of common male on any measured trait. On the other hand, females' body weight (ANOVA: $F_{1,38}=86.63$ and $P<0.001$) and standard length (ANOVA: $F_{1,38}=29.58$ and $P<0.001$) were significantly different between two groups. Thus, it was confirmed that the maternal body size might have some effects on reproductive outputs during the hatchery production.

The analyses revealed that the average egg weight, hatching rate, offspring total length and body area were significantly higher, while hatchling deformation rate was significantly lower in larger females than the smaller females (Table 1). The findings also showed no significant variations in number, diameter and area of eggs, and survival rate of offspring (Table 1).

Table 1 Variation among different reproductive traits of *Labeo rohita* due to the difference in maternal body size. Significant values are denoted as *Italic* and bold.

Response traits	Maternal size group (mean±SE)		Stat- value	<i>P</i>	Effect size	Statistical model
	Large	Small				
Average egg weight (g)	222.57±26.25	152.63±14.27	5.48	<i>0.02</i>	$d = 0.74$	ANOVA
Average egg number/g	344.20±16.92	337.25±18.97	0.09	0.75	$d = 0.09$	ANOVA
Average egg diameter (mm)	1.01±0.01	0.99±0.01	0.76	0.38	$d = 0.27$	ANOVA
Average egg area (mm ²)	0.80±0.02	0.80±0.04	0.002	0.96	$d = 0.01$	ANOVA
Hatching rate (%)	76.97±2.73	65.91±4.04	4.98	<i>0.02</i>	$r^2 = 0.12$	GLM
Hatchling deformation rate (%)	4.02±0.78	7.51±1.49	4.81	<i>0.02</i>	$r^2 = 0.11$	GLM
Offspring survival rate (%)	29.33±1.56	26.42±0.9	2.70	0.10	$r^2 = 0.06$	GLM
Offspring total length (mm)	11.25±0.20	10.37±0.11	10.63	<i>0.001</i>	$r^2 = 0.27$	K-W
Offspring body area (mm ²)	16.79±0.38	15.34±0.25	10.07	<i>0.001</i>	$d = 1.00$	ANOVA

4.2 Experiment-2: maternal size-by-offspring feeding effects

Like experiment-1, the initial analysis confirmed no variation in body weight (K-W: $\chi^2=0.49$ and $P=0.92$) and average milt weight (K-W: $\chi^2=0.05$ and $P=0.99$) of the common males used in this experiment and thereby ensured no effect of common male on any measured offspring fitness. Logically, the females selected as the larger group had significantly higher body weight (K-W: $\chi^2=23.55$ and $P<0.001$) than smaller sized group which gave a notion about the possible effect of maternal body size on some offspring traits.

The findings revealed that the offspring survival rate was not significantly influenced by maternal body size (GLM: $\chi^2=0.88$, $P=0.35$ and Fig. 18a) and maternal size-by-offspring feeding (GLM: $\chi^2=0.001$ and $P=0.97$), while the feeding trial showed that ED reared offspring had significantly higher survival rate than those of EOD group (GLM: $\chi^2=8.56$, $P=0.003$, $r^2=0.21$ and Fig. 19a).

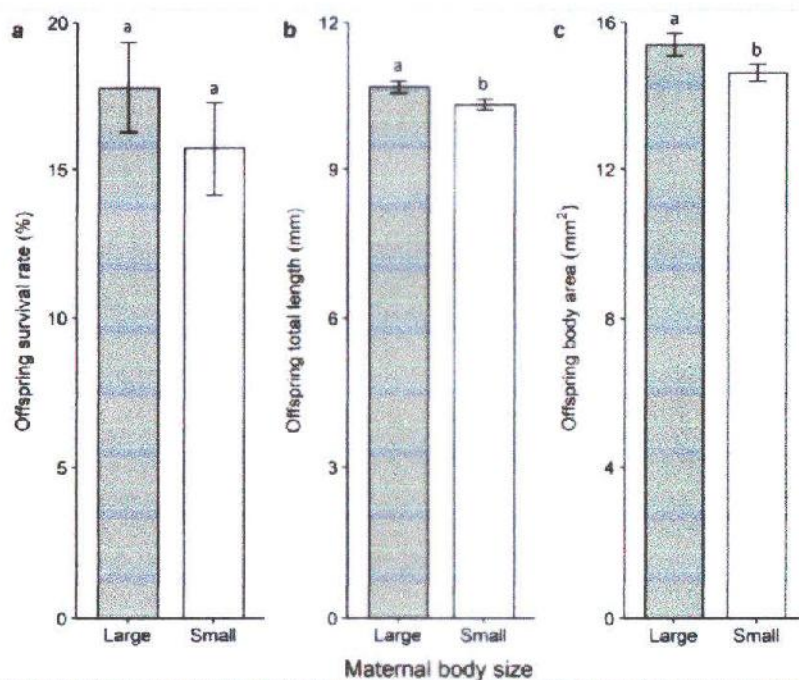


Figure 18: Maternal body size effects on offspring



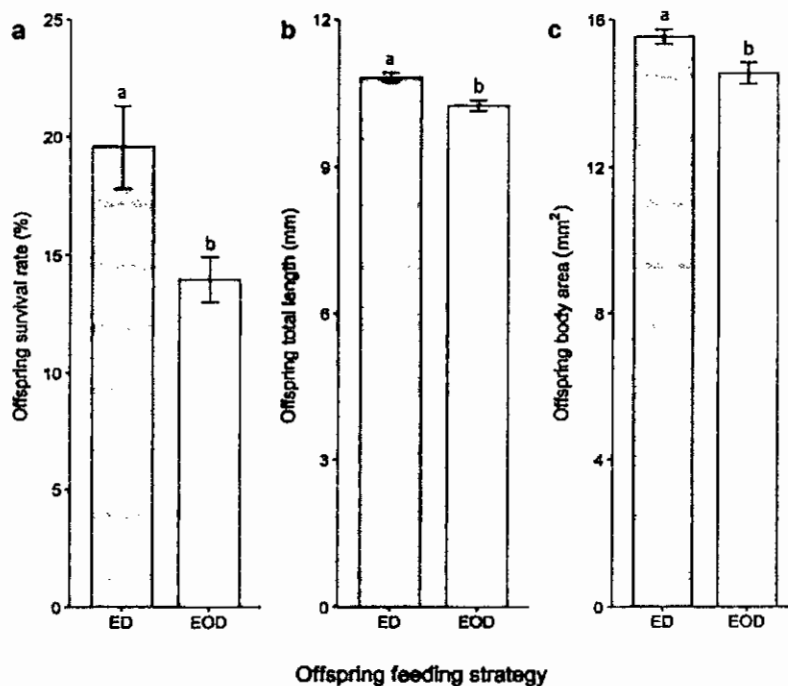


Figure 19: Offspring feeding strategy effects on offspring

The offspring total length was found significantly bigger which was spawned by the larger females than the smaller mother's group (ANOVA: $F_{1,30}=4.78$, $P=0.03$, $d=0.77$ and Fig. 18b). The offspring total length was also found significantly larger when they were assigned to ED feeding group rather than the EOD treatment (ANOVA: $F_{1,30}=14.96$, $P<0.001$, $d=1.36$ and Fig. 19b). The experiment showed no significant effect of the maternal size-by-offspring feeding (ANOVA: $F_{1,30}=0.04$ and $P=0.85$).

The experiment also found that offspring body area was significantly greater in larger female group than the smaller female group (ANOVA: $F_{1,30}=4.13$, $P=0.05$, $d=0.72$ and Fig. 18c), while offspring of ED group had significantly larger body area than EOD group (ANOVA: $F_{1,30}=8.17$, $P=0.007$, $d=1.01$ and Fig. 19c). Consistent with the offspring total length, no interactive effect of maternal size-by-offspring feeding was found on offspring body area (ANOVA: $F_{1,30}=0.06$ and $P=0.80$).

Chapter-5

5.0 Discussion

5.1 Maternal size effect

L. rohita is the topmost freshwater aquaculture species in India, Bangladesh, Myanmar, Nepal and Pakistan which culture and production mostly depend on hatchery produced larvae. Many of the hatcheries do not maintain broodstocks quality especially size selective breeding strategy which has a great impact on gamete quality (Johnston et al. 2007; Hixon et al. 2014; Barneche et al. 2018) and offspring fitness (Johnson et al. 2011; Kindsvater et al. 2013; Falica et al. 2017).

The present study revealed that larger females produced significantly higher amount of eggs and hatchlings which also showed better offspring fitness. In European hake (*Merluccius merluccius*), the fecundity and egg diameter were found positively significantly correlated with the female size (Mehault et al. 2010). Vallin and Nissling (2000) showed that larger females of cod (*Gadus morhua*) produced greater sized and better quality eggs than smaller females. In a meta-analysis with the data of 342 marine fish, Barneche et al. (2018) revealed that fecundity, volume and energy content of eggs were disproportionately higher in larger mothers than smaller mothers. In the present study, average egg weight and hatching rate were significantly positively correlated with the maternal body size (Fig. 20) which corroborates the findings of the above-mentioned studies.

The present study also revealed that offspring survival rate (although not significant through ANOVA analysis) and size were significantly positively correlated, while deformation rate was negatively correlated with maternal size (Fig. 20). However, the correlation outcomes did not show any trade-off between traits. The findings of positive associations between traits are consistent with other studies., such as Kindsvater et al. (2013) found that older and larger females produced significantly larger offspring than the younger and smaller females in swordtail (*Xiphophorus birchmanni*), whereas Falica et al. (2017) disclosed with a quantitative genetic study in Chinook salmon (*Oncorhynchus tshawytscha*) that maternal size and non-additive effects were the most important influencing factors for larval size which could explain a total of 87% of total larval phenotypic variation. In another study, Sogard et al. (2008) explored that older and larger females in five species of rockfish (*Sebastes* spp.) produced

disproportionately more larvae per unit biomass with higher quality (size and condition) than younger and smaller females.

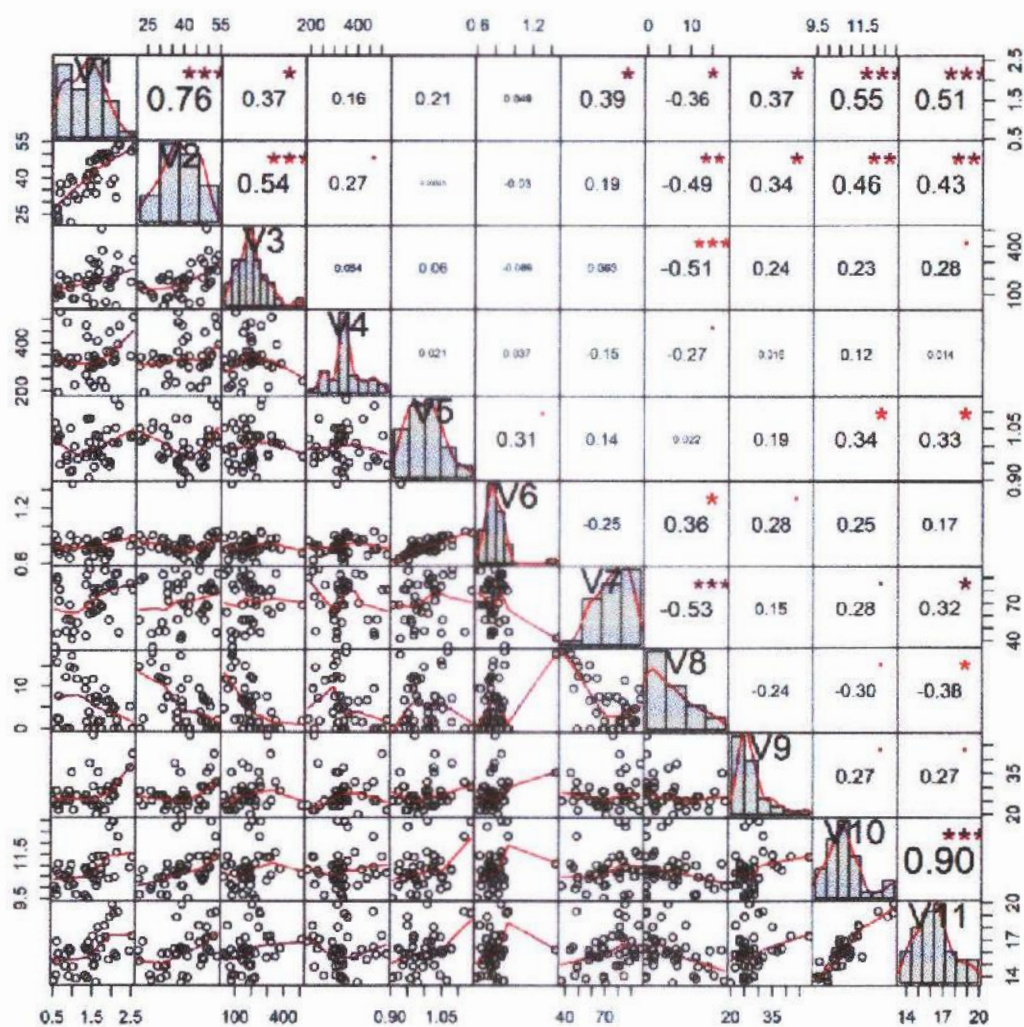


Figure 20: Maternal size effect

The possible reasons of better performances of larger females have been suggested by different studies which could be the variation of females size-dependent reproductive resources (Hagmayer et al. 2018), their energy allocation strategy (Barneche et al. 2018) and trade-offs (Brosset et al. 2016), environmental variability (Jørgensen et al. 2011; Faria et al. 2018), etc. For instance, larger females normally possess greater reproductive resources and therefore, normally produce higher quantity and quality of eggs (Hixon et al. 2014). A recent meta-analysis with 342 marine fish confirmed that larger mothers invested disproportionately more energy to enhance the number and size of eggs (Barneche et al. 2018). Since reproduction is an energetically expensive event in life, small females may obtain benefit by trading off the energy allocation between maintenance (i.e. growth) and reproduction (Brosset et al. 2016). For example, small females of pipefish (*Syngnathus typhle*) allocated more energy for growth rather than fecundity (Berglund 1991), while larger females of eastern mosquito fish (*Gambusia holbrooki*) invested more energy for higher fecundity trading off with offspring size (O'Dea et al. 2015). Further evidence showed that environmental factors such as stressors or stimulators could significantly influence females to manipulate reproductive outcomes in many fishes (Izquierdo et al. 2001; Faria et al. 2018). To avoid any confounding effect of environmental variability during this present study, all females were reared almost under same conditions. However, the higher reproductive performances of larger females of experimental *L. rohita* in the present study might be due to their higher physiological resources, reproductive target-oriented energy investment or hidden energy allocation trade-offs by the smaller females.

5.2 Offspring feeding effect

It has been well documented that quantity and quality of feed can significantly affect growth, behavior, immunity and other traits of fish larvae (Shan et al. 2008; Takeuchi 2014; Navarro-Guillén et al. 2017). Since larval feeding cost is one of the major expenses in hatchery and nursery production systems, farmers try to minimize this cost by adopting different strategies. Feed deprivation is one of the common feeding techniques that was also suggested by some aquaculture scientists to minimize fish feeding cost (Urbinati et al. 2014; Ali et al. 2016). In the present study, offspring of ED feeding group showed significantly better growth performance than those reared in EOD treatment and this finding is in accordance with some other studies. For example, Ali et al. (2016) demonstrated that feeding Nile tilapia (*Oreochromis niloticus*) everyday provided higher final body weight, weight gain and specific growth rate than those of

feed deprivation at weekends during the 26 days experiment. In another study, Okumus and Bascinar (2001) found that daily fed juveniles of rainbow trout (*O. mykiss*) obtained the highest final body weight and better condition factor than those fed five days in a week and every other day.

Some studies of compensatory growth research recommended for a short-term periodic feed deprivation which could help the temporarily starved fish to improve digestive capacity and coping with oxidative stress, but this short-term starvation also inhibited the lipid synthesis which might affect severely to uptake nutrients and energy after subsequent feeding (Yengkokpam et al. 2013; Urbinati et al. 2014). Perhaps the EOD feeding strategy at the very early stage in the present study might cause severe stress to the offspring which could reduce significantly metabolic activities and failed to uptake required nutrients and energy for traits development. To notice this stressful feeding strategy, Yengkokpam et al. (2013) reported that feed deprivation of *L. rohita* fingerlings beyond two days per week could cause severe stress which might reduce metabolic activities and adversely affected growth and health.

5.3 Maternal size-by-offspring feeding effects

The present study revealed no significant interactive effect of maternal size and offspring feeding on any offspring trait. Thus, the findings clearly showed that maternal condition and offspring feeding strategy were the most influential factors. The non-significant interactive effect indicated no genotype-by-environment effect (Falconer and Mackay 1996) which revealed no significantly better fitness of larger mother produced offspring reared in EOD treatment than the offspring of smaller mother kept in ED group or vice versa (Figs. 21a, b and c). However, a recent study revealed the maternal size-by-offspring feeding effect on female age and male size at maturity, and these interactions were apparent even though the offspring were fed with a restricted amount of diet (Vega-Trejo et al. 2018). Whilst a very limited study was conducted with fish regarding this interesting issue, evidence with other aquatic organisms provided the information about interactive effects of parental condition-by-offspring environment (Mitchell and Read 2005; Luquet and Tariel 2016).

The plausible explanation of having no interactive effects in this present study could be because of very strong maternal and environmental impacts which might not compromise with any change in rearing environment (feeding). Therefore, the relative variation in all offspring traits



was occurred only because of highly significant influence of maternal size and offspring feeding strategy separately (Figs. 21a, b and c). These findings suggest that larger females' influence on offspring fitness was deemed because of feed deprivation, while everyday feeding to offspring of smaller females also failed to express their traits normally due to a very strong maternal effect. This non interactive outcome implies an important message to the stakeholders to be very careful about maternal size as well as proper offspring feeding during their breeding and spawning programs.

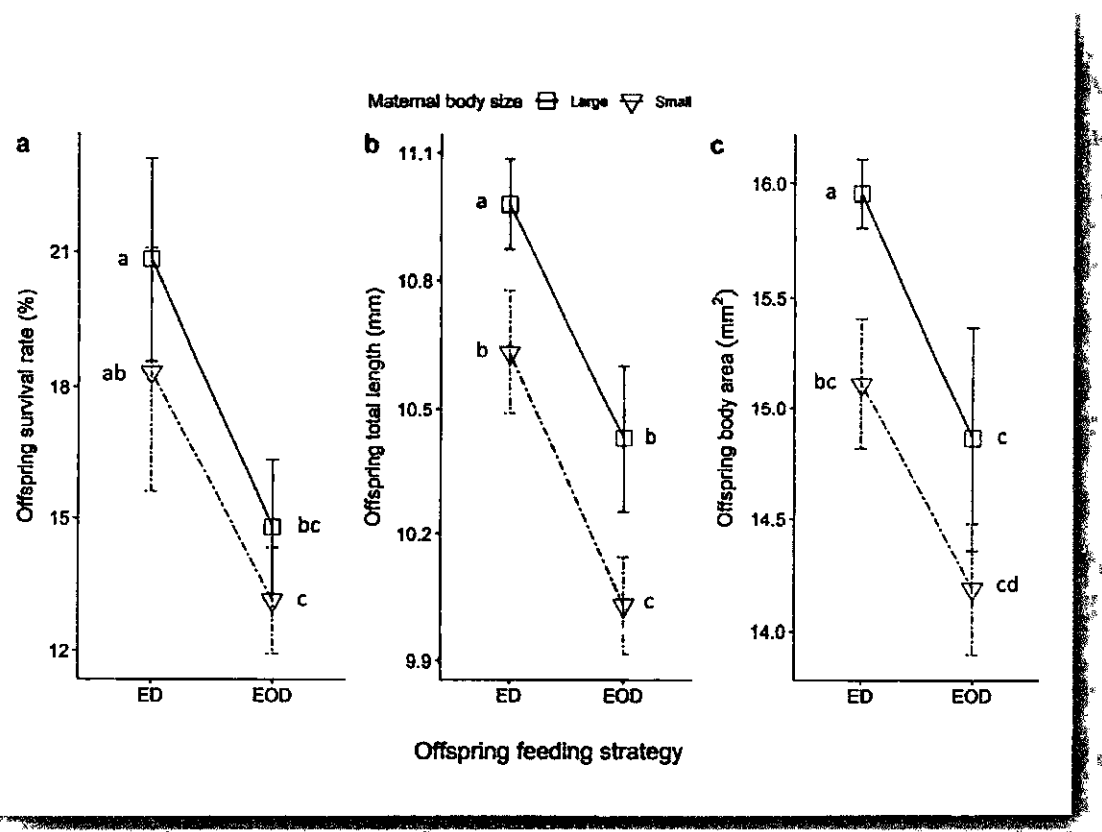


Figure 21: Maternal size-by-offspring feeding effects

Chapter-6

6.0 Conclusion

Parental (maternal and paternal) phenotypic traits (genetic factors) and environmental condition (non-genetic factors) have considerable importance that directly affect the phenotypic traits of offspring and susceptible to produce more viable phenotypic variation. The present study has been conducted to explore the (1)'maternal size' and (2)'maternal size-by-offspring feeding' effects on Rohu (*L. rohita*), an important Indian major carp, considering spawning performance (hatching rate, survival rate) and offspring fitness (total length, body area). The result has revealed (1) significant maternal effects (size) on hatching rate, fitness (total length & body area), egg weight; while large mother have higher positive impacts than small sized mother and (2) significant positive feeding impacts on survival rate and fitness, where ED (everyday feeding) offspring group were more fit than EOD (every alternative day) offspring group. But findings were insignificant in case of some other selected factors such as "maternal size-by-offspring" feeding has no significant interactive effects on offspring fitness and survival rate. Maternal size also revealed no significant effects on survival rate.

However, the overall results provide a manifestation of benefits for 'larger female' and 'everyday feeding' and provide a suggestion to the commercial carp hatchery manager and farmers to ensure mature brood and good feeding opportunity for sustainable production of this species. Finally, to have more confirmation about this issue and to explore more significance variation, still some further research is required to be carried out based on their mating tactics for higher reproductive success and thereby, good offspring production in some other commercially important fish species.

Chapter-7

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Chapter-8

8.0 Appendix

