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Breeding performance and embryogenic development of three strains of *Heterobranchus longifilis* in Nigeria

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Summary

The study sought to investigate the chronology of events and timing of embryogenesis, as well as breeding performances of three strains of *Heterobranchus longifilis* from Nigeria. Fish samples were collected from Benue River in Makurdi, Niger River in Onitsha, and Rima River in Sokoto for this study. Induced spawning of the strains was carried out so that egg development could be tracked from fertilization to hatching using a simple microscope. The microphotographs obtained showed that the embryogenesis of the strains followed a similar pattern to those of other members of the family Clariidae, however with changes occurring in the specific timing of the sequences of events (i.e. interstrain and interspecies differences). When the different strains were compared, the study noted similarities ($P > 0.05$) in the overall breeding performance (except for fertilization rate), survival at different stages of development, timing of embryogenesis, and larvae characteristics. The outcomes of this study, therefore, provide baseline information on what genetic improvement of the species through strain crossing can be attempted in future studies.

Introduction

The members of the family Clariidae are an important part of the freshwater fishes in Africa, Asia minor, and Southeast Asia (Teugels *et al*., 2001; Teugels and Adriaens, 2003). Among the 15 genera of this air-breathing catfish family, *Heterobranchus* and *Clarias* are the two most economically important genera (Teugels and Gourène, 1998; Chandra and Banerjee, 2003; Zayed and Mohamed, 2004; Okomoda, 2018). The four known species of the genus *Heterobranchus* are distinguishable from *Clarias* and other Clariidae by the possession of a large adipose fin that follows the spineless dorsal fin (Teugels, 1996; Agnèse and Teugels, 2001). Although many species of the *Clarias* genus have been extensively studied, research on several members of the genus *Heterobranchus* is still in its infancy as culture is largely localized in Africa (Ataguba *et al*., 2009).

One of the species of interest in this genus is *Heterobranchus longifilis* (Nguenga *et al*., 1996). Its popularity is due to its hardiness, omnivorous feeding habit, large size at adult and survival in brackish water conditions of approximately 10 g L^{-1} (Legendre *et al*., 1992; Suleiman *et al*., 2015; Takoradi *et al*., 2015). Previous studies on *H. longifilis* have included biological, ecological and behavioural evaluations (Nuñez Rodriguez *et al*., 1995; Baras, 1999; Poncin *et al*., 2002), growth under different culture conditions (Legendre *et al*., 1992; Ovie *et al*., 2008), morphological characterization (Legendre *et al*., 1992; Vandewalle *et al*., 1997), hybridization with close relatives (Ataguba *et al*., 2009; Olufeagba *et al*., 2016), and polyculture with other species (Offem *et al*., 2009). In addition, *H. longifilis*, as in other Clariidae (Sule, 2002; Okomoda *et al*., 2017), spawn non-pigmented eggs that are oval and transparent. This makes tracking the embryogenetic development of the fish under the microscope an easy task. Based on this criterion, *H. longifilis* can be an animal model for developmental and embryological studies (Sule and Adikwu, 2004; Hassan *et al*., 2018).

Knowledge of the embryonic development of different species is particularly essential for improving breeding characteristics, aquaculture potentials, and biodiversity of any species (Olufeagba *et al*., 2015). Although some studies have reported chronologically the embryonic development of different catfishes under specific laboratory conditions (Olaniyi and Omitogun, 2014b; Ferosekhan *et al*., 2015; Okomoda *et al*., 2017; Hassan *et al*., 2018), no study has traced the effect of strains on the timing of embryogenesis in fish. This knowledge could help to explain the breeding characteristics of different strains based on their functional trends and their environmental preferences as expressed by the timing of the developmental stages (Koumoundouros *et al*., 2001; Borçato *et al*., 2004). Knowledge of the normal and altered developmental patterns

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that affect survival rate of eggs and hatchlings (Olufeagba, 1999; Morrison *et al.*, 2001) could be used as the basis upon which artificial selection and strain crossing would be initiated for genetic improvement. In this study, therefore, we investigated differences in the breeding characteristics and embryogenetic chronology of *H. longifilis* strains from three ecoregions in Nigeria.

Materials and methods

Sexually matured strains of *H. longifilis* were obtained from three ecoregions in Nigeria, namely: (1) Sahel savanna at the Rima River in Sokoto (Lat. 13.0059°N, Long. 5.2476°E); (2) Guinea savanna at the Benue River in Makurdi (Lat. 7.7322°N, Long. 8.5391°E); and (3) the rainforest region at the Niger River in Onitsha (Lat. 6.1329° N, Long. 6.7924°E). In total, 60 fish samples (comprising of 30 males and 30 females) were obtained from each ecoregion and transported live to the Teaching and Research Farm of the Federal University of Agriculture where the study was conducted. The fish were acclimatized for 1 month and fed with Coppens® (protein = 45% CP; lipid = 12%; ash = 9.5%) with continuous aeration (water quality adequate with temperature (T) = 28.9°C; pH 7.11; conductivity (Cond.) = 663.4 μS cm^{-1}; total dissolved solids (TDS) = 211 mg L^{-1}; dissolved oxygen (DO) = 5.23 mg L^{-1}) in different concrete tanks designated for each ecoregion.

Three pairs each per sex per ecoregion of similar size (2 kg) were then used for the breeding trials following the techniques adopted and reported by Ataguba *et al.* (2009) and Olufeagba *et al.* (2016). In brief, both sexes of the fish were injected with Ovaprim® (Syndel, Canada) at a rate of 0.5 ml/kg and maintained for a latency period of 15 h in separate tanks according to their sex and ecoregion. The eggs from the females of the same ecoregion were then stripped into a bowl by applying light pressure on the abdominal part of the fish. The collected eggs from the same ecoregion were then gently mixed using a chicken feather to make the eggs uniform. The male fish conversely were tranquilized using tricaine methanesulfonate (Wagner *et al.*, 1997) before being euthanized to collect their testes. The milt from the testes of males of the same ecoregion was then used to fertilize the eggs from the same ecoregion as shown below:

Sokoto ♀*H. longifilis* × Sokoto ♂*H. longifilis* (♀SK × ♂SK)
Makurdi ♀*H. longifilis* × Makurdi ♂*H. longifilis* (♀MK × ♂MK)
Onitsha ♀ *H. longifilis* × Onitsha ♂*H. longifilis* (♀ON × ♂ON)

After mixing the milt with the eggs, the sperm cells were then activated by addition of freshwater. Fertilized eggs were quickly spread across the already prepared triplicate hatching troughs ($1 \times 1 \times 0.5\ m^3$) for each ecoregion crosses for the incubation process of the egg. The eggs were maintained in this static system with continuous aeration until they were hatched. Egg diameters were measured ($n = 20$) pre-fertilization and post-fertilization using a Nikon profile projector (model number V-12BD/JA). In addition, 50–100 eggs were taken from each treatment at regular intervals and observed for embryogenetic development under a Nikon dissecting microscope (model number C-DSLS) following the techniques described by Olufeagba *et al.* (2016) and Okomoda *et al.* (2017). After taking data for the early mitotic cell divisions, observations for the subsequent developmental stages were initiated 15 min earlier than reported by Aluko (1995), Olufeagba *et al.* (1999a, 1999b) and Olaniyi and Omitogun (2014b) for the species of the same family. Pictorial evidence of the different developmental stages was then captured and reported as appropriate. During the early mitotic division stages, the percentages of fertilization were determined according to the novel method proposed by Okomoda *et al.* (2018a). The proportion of fertilized eggs was then determined using the relationship given below:

$$\%\ \text{Fertilization} = \frac{\text{Fertilized eggs in the Petri dish}}{\text{Total number of eggs in the Petri dish}} \times 100$$

Hatchability percentages of the eggs from the three ecoregions were also determined using the equation below:

$$\%\ \text{Hatchability} = \frac{\text{No. of hatched larvae}}{\text{Total no. of spawned eggs}} \times 100$$

The total length of the hatched larvae and the yolk major axis length was recorded for the three strains using a Nikon profile projector (model number V-12BD/JA).

Results and Discussion

Although fertilization of eggs is the first initiated steps in the chronology of embryonic development (Haylor, 1993), accurate estimation can only be made during the early mitotic stages due to the synchrony of shape of the animal pole for both fertilized and unfertilized/hydrated eggs (Okomoda *et al.*, 2018a). Fertilized eggs can be discriminated by observing active division seen at the egg animal pole during the 2-eye and the 32-eye stages. This method has been used effectively for African catfish *Clarias gariepinus*, Asian catfish *Pangasianodon hypophthalmus*, and their reciprocal crossbreds (Okomoda *et al.*, 2017, 2018b). Our findings show that fertilization percentage was significantly higher in the Onisha strain (97%) compared with the Sokoto (93%) and Makurdi strains (86%) (Table 1). This is despite having statistical similarity in egg diameters pre-fertilization and post-fertilization. Earlier findings by Nguenga *et al.* (2000) have also reported an 87–95% range for the fertilization rates of some strains of *H. longifilis*. Although Ola-Oladimeji (2015) had stated that better fertilization rates are indices of better gamete quality, the higher fertilization of the Onisha strain did not result in higher hatchability percentages or larvae characteristics. The statistical similarities of the three strains in this regard may be connected to the similar egg characteristics pre-fertilization and post-fertilization. Bromage and Roberts (1995) had linked the breeding quality of broodstocks to the egg size, therefore suggesting that the gametes of the different strains used for the current study could be similar in terms of quality. Many authors have also demonstrated a high positive correlation between egg size and larval traits (Buckley *et al.*, 1991; Rideout *et al.*, 2005; Ataguba *et al.*, 2012, 2013), therefore the similarity of the egg size of the different strains was possibly translated to similar larvae characteristics also as seen in this study.

The egg sizes recorded before and after fertilization in this study are lower compared with the reports of Olufeagba *et al.* (2016) and Olaniyi and Omitogun (2014b) for *H. bidorsalis* (1.2 and 1.0 mm respectively). The values reported by Okomoda *et al.* (2017) for *C. gariepinus* and *P. hypophthalmus*, and their reciprocal crossbreds were also higher compared with our study. Not only has egg size being established to differ with broodstock, but also with species (Thakur, 1980; Bromage and Roberts, 1995; Puvaneswari *et al.*, 2009), therefore this could explain the differences between the sizes reported and those aforementioned. This study also suggested that, regardless of strain, the timing of the different embryonic stages was statistically similar (Table 2). The findings of

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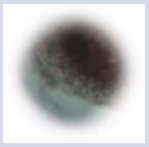
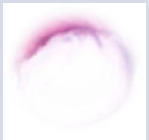
Table 1. Eggs and breeding characteristics of *Heterobranchus longifilis* from different ecoregions in Nigeria

	♀SK × ♂SK*	♀MK × ♂MK*	♀ON × ♂ON*	*P*-value
Egg diameter pre-fertilization (mm)	0.530 ± 0.005	0.595 ± 0.009	0.533 ± 0.003	0.341
Egg diameter post-fertilization (mm)	0.620 ± 0.003	0.664 ± 0.007	0.682 ± 0.008	0.112
% Fertilization	93.31 ± 1.38[b]	86.43 ± 1.14[c]	97.01 ± 2.01[a]	0.004
% Hatchability	85.60 ± 6.97	85.04 ± 1.87	85.12 ± 3.87	0.320
Larvae length (mm)	1.70 ± 0.01	1.75 ± 0.03[a]	1.85 ± 0.07	0.139
Yolk major axis (mm)	0.61 ± 0.02	0.62 ± 0.10	0.64 ± 0.03	0.144

*Numbers are means ± standard errors.[a–c]Means in the same row with different superscripts differ significantly ($P < 0.05$).

Table 2. Embryonic developmental stages of *Heterobranchus longifilis* from different ecoregions in Nigeria (29.2 ± 0.11°C)

SN	Embryonic stages		♀SK × ♂SK*	♀MK × ♂MK*	♀ON × ♂ON*	*P*-value
1	Matured oocytes		0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.244
2	Fertilized eggs		0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.112
3	Animal pole		45 ± 0.10	44 ± 0.09	44 ± 0.04	0.230
4	2-cell stage		53 ± 1.37	52 ± 0.87	58 ± 0.21	0.121
5	4-cell stage		95 ± 1.38	93 ± 0.87	91 ± 0.13	0.199
6	8-cell stage		116 ± 0.13	117 ± 0.80	114 ± 0.30	0.343
7	16-cell stage		123 ± 0.18	133 ± 0.12	131 ± 0.52	0.211

(*Continued*)

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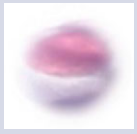
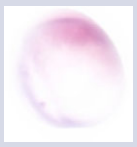
Table 2. (*Continued*)

SN	Embryonic stages		♀SK × ♂SK*	♀MK × ♂MK*	♀ON × ♂ON*	*P*-value
8	32-cell stage		143 ± 0.73	149 ± 0.92	141 ± 0.13	0.645
9	Morula stage		161 ± 0.50	164 ± 0.09	166 ± 0.20	0.090
10	Blastula stage		196 ± 0.13	193 ± 0.80	194 ± 0.30	0.221
11	Gastrulation stage		229 ± 0.58	233 ± 0.92	231 ± 0.28	0.246
12	Hatching		1497 ± 5.30	1496 ± 3.09	1482 ± 2.10	0.115

*Numbers are means ± standard errors. Means in the same row under the same embryonic stage are statistically similar (i.e. non-significantly different) ($P > 0.05$).

Olufeagba *et al.* (2016) had earlier demonstrated that the morula, blastula, gastrulation, and hatching time varied significantly between pure strains of *H. longifilis*, *C. gariepinus*, and their reciprocal crossbreds. The differences in the two species and the interaction between their genetic materials in the hybrids could explain the differences observed compared with our findings for the same species of different strains. It was also noted that the embryonic chronology of *H. longifilis* from the different ecoregions was identical to one another and to other freshwater fish species such as *H. bidorsalis* (Olaniyi and Omitogun, 2014b), *C. gariepinus*, *C. anguillaris* (Kamler *et al.*, 1994; Olufeagba *et al.*, 2009), *P. hypophthalmus* (Okomoda *et al.*, 2018a), *M. montanus* (Arockiaraj *et al.*, 2003) and *Rhinelepis aspera* (da Rocha Perini *et al.*, 2009).

Moments after the eggs are fertilized and the zygote formed, the perivitelline space expands resulting in a clear separation of yolk and the outer protective chorion (Hill and Johnston, 1997; Hassan *et al.*, 2018). This is important for the survival and healthy development of the eggs, as the chorion prevents mechanical damage and infection by microbiota (Korzelecka-Orkisz *et al.*, 2010; Honji *et al.*, 2012). Also, the perivitelline space, which is occupied by protective fluid, ensures the stability of the developing embryo as it cushions the embryo from external injury while permitting the exchange of dissolved gases and essential molecules to and from the yolk (Okomoda *et al.*, 2017, 2018a). Approximately 45 min after fertilization, the bulging of protoplasm occurs as an aggregation to form the animal pole (blastodisc), which is visible on the vegetal pole (i.e. the yolk of the larvae). The timing of aggregation could differ by species, therefore explaining the occurrence at 42 min and 36 min in heteroclarias hybrid (i.e. *Clarias anguillaris* × *H. bidorsalis*) and pure crosses of *H. bidorsalis* as reported by Diyaware *et al.* (2009) and Takoradi *et al.* (2015), respectively. Knowledge of the precise time of the early mitotic cleavage is critical to the production of polyploid organisms (i.e. tetraploids) during chromosome manipulation (Aluko and Aremu, 2001). Within the next 2 h after the formation of the animal pole, cleavage of the blastodisc occurred giving rise to the 2-eye (55 min), 4-eye (92 min), 8-eye (115 min), 16-eye (130 min), and 32-eye stages (145 min). The blastodisc cleavage pattern observed is known as the discoidal meroblastic division of the telolecithal egg (Kimmel and Law 1985; Kimmel *et al.*, 1995; Hall *et al.*, 2004). This means the division is incomplete, therefore partially separating the blastodisc into even daughter cells (i.e. 2, 4, 8, etc.) through

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the formation of cleavage furrows, a process also known as cytokinesis (Buzollo *et al.*, 2011). This cleavage pattern is synchronous, regular and the blastomeres produced are well arranged on the vegetal pole (Olaniyi and Omitogun, 2014b).

As the mitotic division proceeds, it leads to the formation of tinnier irregular cells that are asynchronous and heaped on the animal pole forming a 'mulberry' or 'half-berry' or 'ball-like' shape, which is impossible to count (Honji *et al.*, 2012; Olaniyi and Omitogun, 2012). This period of division extends to cover the morula, blastula and gastrulation stages (Kimmel *et al.*, 1995). Noticeable at this point is the cellular/embryonic movement known as the random quasiperistaltic transitional wave movement (Okomoda *et al.*, 2018a). The pattern of this movement varies and ranges from invagination, involution/ingression, or the spreading out of the enveloping layer towards the vegetal parts of the eggs (Leme dos Santos and Azoubel, 1996; Buzollo *et al.*, 2011). This movement has been erroneously thought to be an exclusive characteristic of fertilized eggs or living embryos (Olaniyi and Omitogun, 2014a) however, in this study, the movement was noticeable in both fertilized and unfertilized eggs. This observation is in line with the earlier reports of Okomoda *et al.* (2017) for African catfish *C. gariepinus* during the morula, blastula, and gastrulation stages. Shortly after this, organogenesis of the embryo begins, therefore putting a stop to the embryonic wave movement. This period is characterized by the formation of somite blocks that differentiate the different parts of the larvae from the head region (i.e. cephalic region with its polster and auditive parts) to the tail region (i.e. the caudal parts with Kupffer's vesicle) (Kimmel *et al.*, 1995; Buzollo *et al.*, 2011; Honji *et al.*, 2012).

At the start of embryogenesis, the *H. longifilis* hatched in a manner different from other members of the family Clariidae. In our study, the embryo emerges/break through the pouch/hollowed membrane using its caudal part. This action is in a similar manner to that reported by Olaniyi and Omitogun (2014a) for *H. bidorsalis*, therefore suggesting that the phenomenon may be a notable characteristic of the genus *Heterobranchus*. For the genus *Clarias*, however, the pattern is different as these fish only break the chorion walls into granules during hatching (Olaniyi and Omitogun, 2014b). Nevertheless, regardless of the process used, hatching of Siluriformes is largely facilitated by myotome blocks of the somite trunk that are tightly packed, therefore generating sufficient muscular contractions that lead to the emergence of the larvae from the chorion (Honji *et al.*, 2012). In this study, the incubation period was approximately 25 h at a water temperature of 29°C. A lesser incubation period (23 h) has been reported by Apochi (2016) for different strains of *C. gariepinus*, despite using a lower water temperature of 26°C. Furthermore, Ramanathan *et al.* (1985) reported that the incubation period in *Mystus punctual* was 24 h at 28°C, while *A. lestiudineus* was reported by Munshi and Hughes (1991) to hatch 10 h 30 min after fertilization. While it is well known that the rate and timing of embryonic development are temperature dependent (de Graaf and Janssen, 1996), it is also important to note that species-specific differences exist, therefore explaining our finding compared with earlier studies.

All the hatched larvae from the different ecoregions had a straight body, partially transparent and with a total length that is approximately double the size of the major axis of the yolk. Unlike the reports of Olufeagba *et al.* (2016) and Okomoda *et al.* (2017) for reciprocal crosses of different catfish, we recorded no abnormal larvae in this study. While postzygotic isolation mechanisms are responsible for the occurrence of abnormality in hybrid crosses (Amini *et al.*, 2007; Koh *et al.*, 2008), abnormality

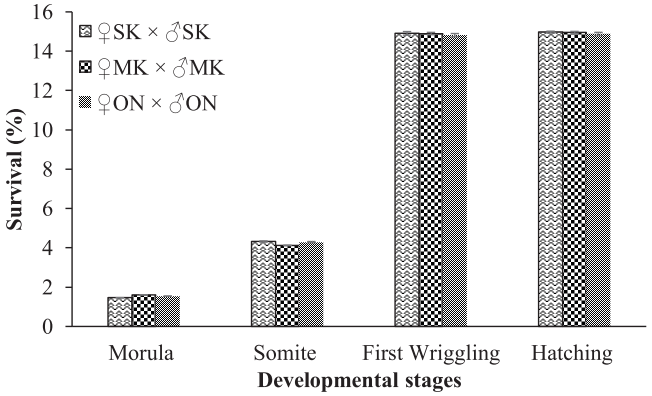

Figure 1. Percentage survival of *Heterobranchus longifilis* from different ecoregions in Nigeria at selected developmental stages. Bars with error bars represent means ± standard errors. Bars for the same developmental stage are not significantly different ($P > 0.05$).

in pure species is a clear index of the consequential effect of low genetic diversity resulting from inbreeding (Okomoda, 2018). Therefore, our finding could be a pointer to lower inbreeding of the stocks from the different ecoregions, however this hypothesis will need to be demonstrated in future studies using genetic characterization. This study also observed similarities in the survival of the developing embryos at different stages of development (Figure 1). Our findings show that the terminal stages of development were the most critical in which the highest mortality was observed in the strains. Similarly, the study by Okomoda *et al.* (2017) also reported somite and hatching stages as the critical moment of development with mortalities of as much as 22%.

Based on the findings of this study, it is therefore concluded that embryogenetic chronology, timing, and breeding parameters of *H. longifilis* were similar regardless of the three strains used.

Ethical standards. Experimental protocols used in the current study was approved by the Federal University of Agriculture Makurdi Committee on Research. As a result, all methods used pertaining to animal care were in tandem with specified international, national and institutional guidelines.

Conflicts of interest. The authors declare that they have no conflicts of interest whatsoever (financial or otherwise).

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