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Lock-ins to the dissemination of genetically improved fish seeds

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ABSTRACT

Well-functioning fish seed systems are crucial for human nutrition and improved livelihoods. Yet fish seed systems have received considerably little attention in the diffusion process for genetically improved strains. This study examined how seed systems of genetically improved fish strains function, assessed constraints faced, and explored entry-points to increased diffusion. To address these objectives, the study combined the seed systems performance assessment framework with innovation systems thinking. Data came from participatory multi-stakeholder workshops and interviews with tilapia hatchery operators and grow-out farmers in Bangladesh. We found that tilapia seed production and dissemination was profitable and cost-effective indicating a business case for supply chain actors. However, there were several binding constraints including low adoption of elite broodstock, vulnerability to weather shocks and diseases, poor quality of complementary inputs, intermittent electricity supply, hidden costs of seed transportation, and limited market access. These constraints and their causes interacted, creating systemic lock-ins through blocking mechanisms related to incomplete enforcement of regulatory frameworks to control hatchery practices and quality of inputs; limited knowledge about broodstock management, quality seed production, and disease management; weak adaptive capacity to weather shocks; and limited access to credit. Projects, programs, and policies targeted at accelerating adoption of good quality fish seed should focus on the following important aspects. First, strengthening institutional capacity to monitor and enforce quality control. Second, increasing advocacy and knowledge transfer about benefits and sources of elite broodstock. Third, promoting adoption of better management practices by hatcheries and farmers including adaptation to weather shocks. Fourth, leveraging partnerships with local service providers as intermediaries. Fifth, using social networks for information diffusion among farmers.

1. Introduction

Increasing farmers' access to good quality seed in developing countries is a top priority for the global human development agenda, and has been shown to substantially increase income, reduce poverty, improve food security and nutrition, and generate employment (Dey, 2000; Yosef, 2009; Kassie et al., 2011; Shikuku et al., 2019a; Nasr-Allah et al., 2020). Yet efforts and investments targeted at increasing adoption of quality seed with demonstrated productivity and profitability gains have only been partially successful, and adoption rates remain strikingly low (Pamuk et al., 2014). One reason could be that seed systems as important mechanisms by which various sources of supply meet farmers' demands for seed and the traits they provide (Lipper et al., 2010; McGuire and Sperling, 2016; Kansiime and Mastenbroek, 2016; Spielman and Kennedy, 2016; Almekinders et al., 2019) face multiple interacting constraints, possibly creating a systemic lock-in through so-called blocking mechanisms (Turner et al., 2016; Wesseling and Van der Vooren, 2016; Joffre et al., 2018). The presence of lock-ins means that efforts to augment resources for initial establishment of seed systems by "injecting" new varieties and strains into existing systems may have limited adoption and development impact if other binding constraints are not addressed at the same time. In other words, the presence of lock-ins necessitates systemic interventions to unlock the potential of fish seed systems to disseminate high quality seed in an inclusive, timely,

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affordable, and sustainable manner.

The concept of socio-technological lock-in was first applied in agriculture to understand obstacles to a transition toward sustainable practices (Cowan and Gunby, 1996; Fares et al., 2012; Magrini et al., 2016). This concept analyzes relationships between different dimensions within socio-technical systems that can generate interdependencies and self-reinforcing blockages leading to a systemic lock-in (Meynard et al., 2018). Lock-ins have been identified as causes for non-adoption of innovations in agriculture, limiting diversification of crops (Magrini et al., 2016; Meynard et al., 2018), adaptation to climate change (Chhetri et al., 2010), and adoption of integrated pest management for crops (Cowan and Gunby, 1996; Wolff and Recke, 2000) or multi-resistant wheat cultivars (Vanloqueren and Baret, 2008). In aquaculture, studies identifying and characterizing lock-ins are limited (Joffre et al., 2017). Joffre et al. (2018) apply this concept to analyze the blockages hindering adoption of sustainable intensification practices in the Vietnamese shrimp sector. As in agriculture, innovations in aquaculture face obstacles that are not only technical or economic related, but also operate in the social, cultural or institutional dimensions and can interact to create systemic lock-ins.

In this study, we assessed constraints operating in multiple dimensions and analyzed how they interact among themselves to create dependencies and lock-in impeding proper functioning of seed systems of genetically improved fish strains. Despite the crucial contribution of aquatic food systems to improved human wellbeing (Thilsted et al., 2016; Filipski and Belton, 2018; Rashid and Zhang, 2019; Headey and Alderman, 2019), studies on seed systems are crop dominated (Hirpa et al., 2010; Kansiime and Mastenbroek, 2016; Almekinders et al., 2019), and analysis of seed systems for improved fish strains is scant. At the same time, contexts are increasingly changing and characterized by global climate change and frequent occurrence of disease outbreaks in the fish industry (Ahmed and Diana, 2016; Ahmed et al., 2019; Barange et al., 2018; Jansen et al., 2018). Achieving sustainable production of fish under increasingly volatile conditions requires efficient and well-functioning seed systems. Suggestions for improvement essentially require knowledge of the status and performance of the existing seed system (Hirpa et al., 2010).

Understanding how fish seed systems function is important for three reasons. First, seed systems can either preserve or diminish the quality of seed disseminated. There are at least three important dimensions of fish seed quality, namely genetic (strain purity and level of improvement), sanitary (absence of diseases), and physiological (survival rate). Degeneration, that is, the loss of quality along these dimensions has yield-reducing effects (Almekinders et al., 2019). Therefore, understanding the quality effects of seed systems is important for moral justification of scaling genetically improved fish seeds. Second, ensuring a sustainable business case for value chain actors is increasingly recognized as an essential ingredient for successful scaling of agricultural innovations (IDIA, 2017; Woltering et al., 2019; Low and Thiele, 2020). This essentially requires an evaluation of the profitability and cost-effectiveness of seed production and distribution operations. Third, seed systems evolve over time, shaped by changes in business incentives, technological, biophysical, socioeconomic, and institutional factors (Maredia et al., 1999). Our understanding of such drivers of change and their interactions within fish seed systems is far from perfect, yet crucial for the design of cost-effective dissemination systems for good quality fish seed.

Using the tilapia seed system in Bangladesh as a case, this study: (i) described and analyzed the status and performance of currently operating tilapia seed dissemination models; and (ii) identified constraints and entry-points to delivering quality fish seed to farmers. The analysis provides policy and investment implications, in Bangladesh and similar contexts, for: (i) improving the capacity of fish seed systems for timely and sustainable delivery of good quality seed of desired traits to farmers; (ii) supporting sustainable aquatic food systems which are strategically important for economic development and food and nutrition security, particularly for the poor in developing countries (Roos et al., 2007; Thilsted et al., 2016; Headey et al., 2018; Headey and Alderman, 2019); and (iii) establishing an "inclusive" approach and making quality seeds available to poor farmers.

The study is organized as follows. The next section explains the context while the following section describes models of tilapia seed dissemination in Bangladesh. The subsequent section explains the methodology while the following section presents the results. The final section discusses the results and concludes.

2. Tilapia in Bangladesh

2.1. The case study

Tilapia is the second most important farmed fish globally, next to carps. More than five million metric tons of farmed tilapia are produced each year globally, with Nile tilapia (*Oreochromis niloticus*) ranking third in terms of total global fish production (FAO, 2020). Global tilapia production was valued at US$9.8 billion in 2015. Bangladesh has a long history of tilapia farming (Table 1). The Mozambique tilapia (*Oreochromis mosambicus*) was first introduced in Bangladesh from Thailand in 1954. The Chitralada strain of Nile tilapia (*Oreochromis niloticus*) was introduced in Bangladesh by UNICEF in 1974 followed by Red tilapia (hybrid of *Oreochromis mossambicus* x *Oreochromis niloticus*) from Thailand in 1987 and 1988. The genetically improved farmed tilapia (GIFT) strain was introduced by Bangladesh Fisheries Research Institute (BFRI) and WorldFish (formally known as ICLARM) in 1994, 2005, and 2012. Of tilapia strains introduced to Bangladesh, contribution of the GIFT strain, establishment of hatcheries, and production of mono-sex (all male) fry has made tilapia one of the most important aquaculture species in Bangladesh (Alam et al., 2019). Mono-sex culture of male tilapia is often preferred to a mixed-sex system because males are substantially larger than females (e.g., Ponzoni et al., 2005; Nguyen et al., 2007). Fig. 1 presents a historical timeline of important events in GIFT tilapia dissemination since 1990s.

With the introduction of genetically improved strains, tilapia has increasingly become popular in Bangladesh. In 2017, Bangladesh was the fourth largest tilapia producer by volume in the world (Bangladesh Department of Fisheries, 2018), after China and Indonesia in the Asia-Pacific region (FAO, 2016) and Egypt in Africa. Tilapia production in

Table 1
Tilapia strains, their sources, and traits: Source: Hussain et al. (2014).

Year	Species/Strain Name	Source	Traits
1954	*O. mossambicus*	Thailand (Hussain, 2004)	Early maturation, prolific breeding habits in ponds, more saline tolerant
1974, 1987, 2002, 2010	*O. niloticus* (Chitralada Strain)	Thailand (Hussain, 2004); R. I. Akhand (pes. Com.)	Fast growing, attractive body color, excellent breeder
1988	*O. mossambicus* X O. niloticus (Red mutant strain)	AIT, Bangkok, Thailand (Hussain, 1994; 2004)	Hybrid but take part in reproduction, red body color, fast growing
1994, 2005, 2012	*O. niloticus* (GIFT strain)	Philippines (Hussain, 2004); Malaysia (Hussain et al., 2011)	Fast growing, high yielding, less fecund, high survival, attractive body color
2003	*O. niloticus* (Genomar strain)	Philippines; R.I. Akhand (Pes. Com)	Fast growing, attractive body color
2008	*O. niloticus* (GIFU Strain)	China (Hasan et al., 2014)	Fast growing, attractive body color; more saline tolerant
2011	*O. niloticus* (FaST strain)	Philippines; R.I. Akhand (Pes. Com)	Fast growing, good survival, late maturing
2004, 2011	*O. niloticus* (Swansea YYmale (GMT, Fishzen) strain)	Philippines; R.I. Akhand (Pes. Com)	Fast growing, good survival

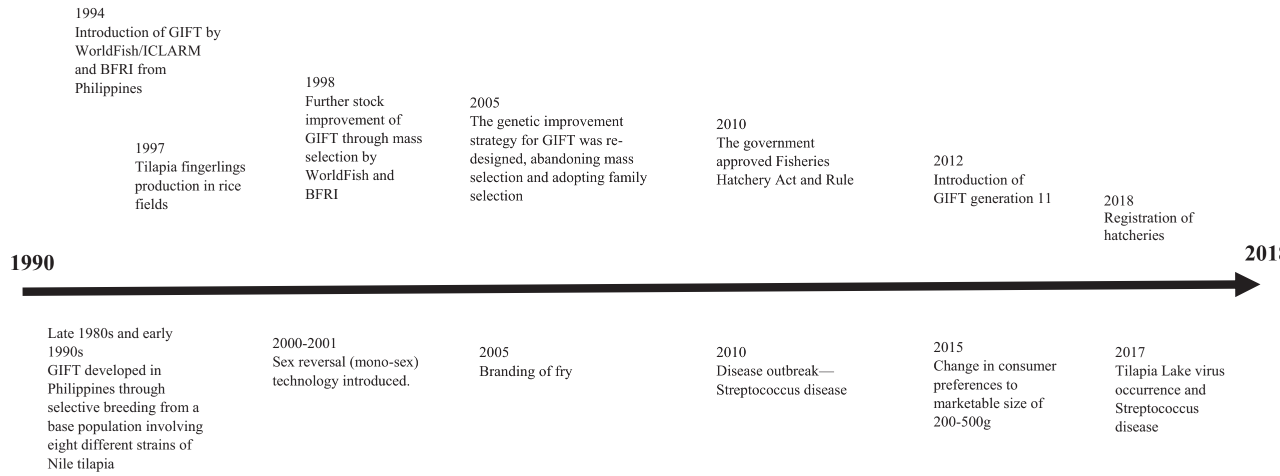

Fig. 1. Historical timelines of important events in Bangladesh's tilapia industry.

the country increased tremendously from 24,662 metric tons in 2009/2010 to 316,286 metric tons in 2017/2018 (Fig. 2). Most of the tilapia produced in Bangladesh is consumed domestically. Tilapia in the country is farmed in both monoculture and polyculture with other fish and is characterized by a range of productions systems including extensive, semi-intensive and intensive. In homestead ponds operated by small scale farmers using homemade, locally available inputs (e.g., rice bran, wheat bran, and mustard oil cake), productivity ranges from 1.5 to 2.0 metric tons/ha per crop cycle (Belton et al., 2011; Alam et al., 2012). In contrast, in intensive production systems practiced by commercial farmers using high quality inputs (e.g., industrially manufactured extruded pelleted feed), productivity ranges from 8 to 10 metric tons/ha per crop cycle (Alam et al., 2012). Tilapia can be stocked in any month in a year in Bangladesh by holding fry in nursery ponds, hapas, or cages. However, the peak stocking season is from April to August. On average, each crop cycle takes four months, so farmers usually have two crops per year (Alam et al., 2012).

Although the tilapia sector has grown fast in the past, it now faces new challenges such as climate change and biosecurity including the emergence of Tilapia Lake Virus (TiLV) (Jansen et al., 2018). Without adequately addressing current and emerging challenges, the ability of tilapia seed systems to sustain delivery of quality seed will be severely compromised. Furthermore, existing models for dissemination of improved tilapia strains in Bangladesh are not well documented and little is known about their performance including constraints faced.

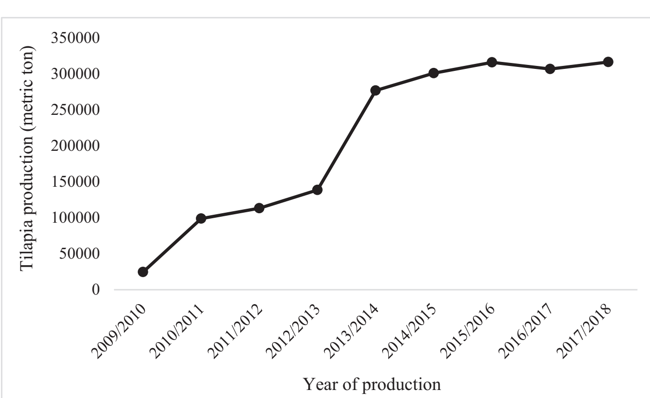

Fig. 2. Trends in tilapia fish production in Bangladesh from 2009/2010 to 2017/2018.

2.2. Models of tilapia seed dissemination in Bangladesh

There are three models of tilapia seed dissemination in Bangladesh (Fig. 3). The first model, which we denote as *model 1*, starts with a few private sector hatcheries performing a specialized function of producing quality broodstock of the genetically improved farmed tilapia (GIFT) using rotational cohort breeding. Rotational cohort mating scheme involves dividing the selected population into groups (cohorts). In each cohort, individuals are selected based on their own performance. In each generation, males from one cohort are systematically mated with females from another cohort (Lind et al., 2012). The rotational pattern changes in each generation. Breeding hatcheries in *model 1* sell breeder seed to multiplier hatcheries which in turn sell mono-sex seed to grow-out producers. The Breeding hatcheries under *model 1* also sell mono-sex seed to grow-out producers. Under proper incentives, *model 1* can be effective in ensuring quality control as multipliers are expected to replace broodstock regularly by sourcing elite germplasm from the breeding hatcheries, thereby ensuring the supply of latest strains to the farmers.

Model 1 was established in Bangladesh in 2011 with the support of WorldFish. A few private sector hatcheries were identified considering the interest of the owners and their willingness to use eight separate ponds as cohort. The eight separate ponds are used to maintain eight cohorts (each cohort comprising fish from 7 to 8 families). Keeping the families separate using a practically applicable rotational breeding technique is useful to avoid inbreeding. A further requirement was the willingness of hatchery owners to follow necessary protocol to conduct rotational cohort breeding to produce GIFT mixed-sex fry. In some cases, instead of using eight separate ponds, a pond was partitioned into eight parts using fencing. The identified hatcheries received quality broodstock of GIFT from Jitra, Malaysia and BFRI. In addition, WorldFish provided technical support to the breeding hatcheries under *model 1*.

The second model, which we denote as *model 2*, involves private sector multipliers obtaining GIFT mixed-sex fry from the public sector tilapia breeding nucleus (TBN) at BFRI. The multiplier hatcheries then produce GIFT mono-sex fry for selling to grow-out farmers. In this model, the TBN uses family selection based on performance of the individual fish and their relatives (Kohinoor et al., 2016). The TBN only sells mixed-sex fry to GIFT multiplier hatcheries—it does not sell mono-sex fry to grow-out farmers.

The third model, denoted *model 3*, involves hatcheries producing and disseminating non-GIFT strains such as Chitralada and FaST. Mass selection, also called "individual selection", is used in this model based on own performance of the individual fish for the trait of interest (Lind et al., 2012). For example, if the trait of interest is harvest body weight, then the heaviest fish (down to a cut-off point) will be selected. In this

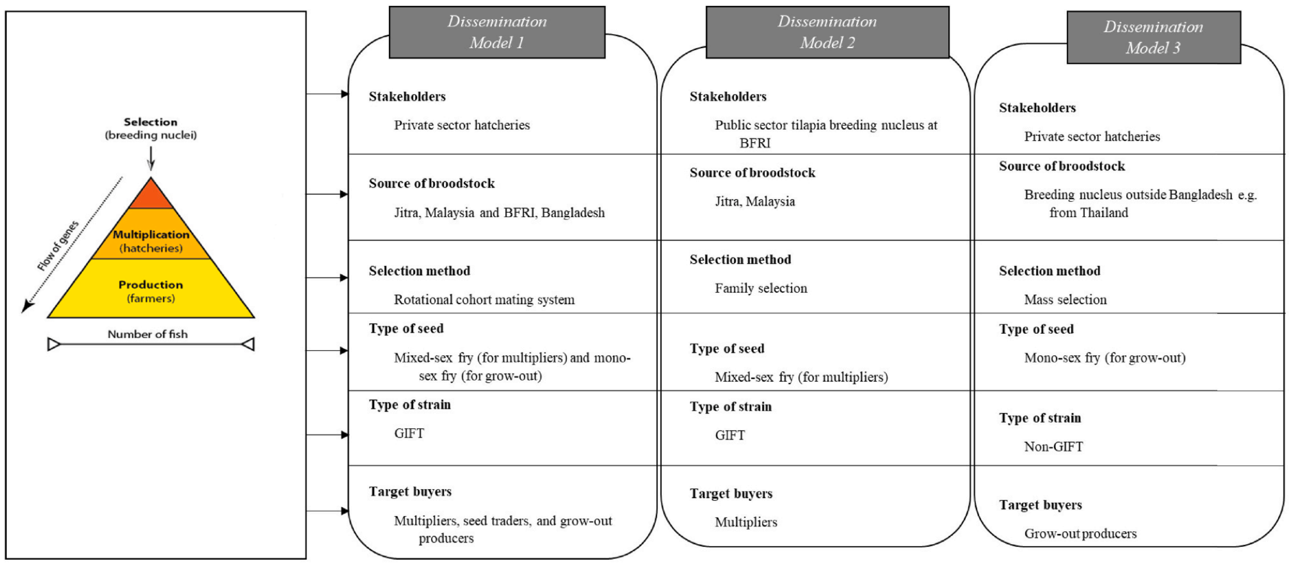

Fig. 3. Tilapia seed dissemination models in Bangladesh.

model, the breeding nucleus are located outside Bangladesh.

3. Methodology

3.1. Analytical framework

The analytical approach combined insights from the framework by Weltzien and Brocke (2001) as developed by Hirpa et al. (2010) to analyze the performance of the tilapia seed system under the three models described above (Section 2.2), and the innovations system thinking (Klein Woolthuis et al., 2005; Van Mierlo and Leeuwis, 2010; Wieczorek and Hekkert, 2012; Joffre et al., 2018) to understand constraints and opportunities from a systemic perspective (Fig. 4).

According to Weltzien and Brocke (2001) and Hirpa et al. (2010),

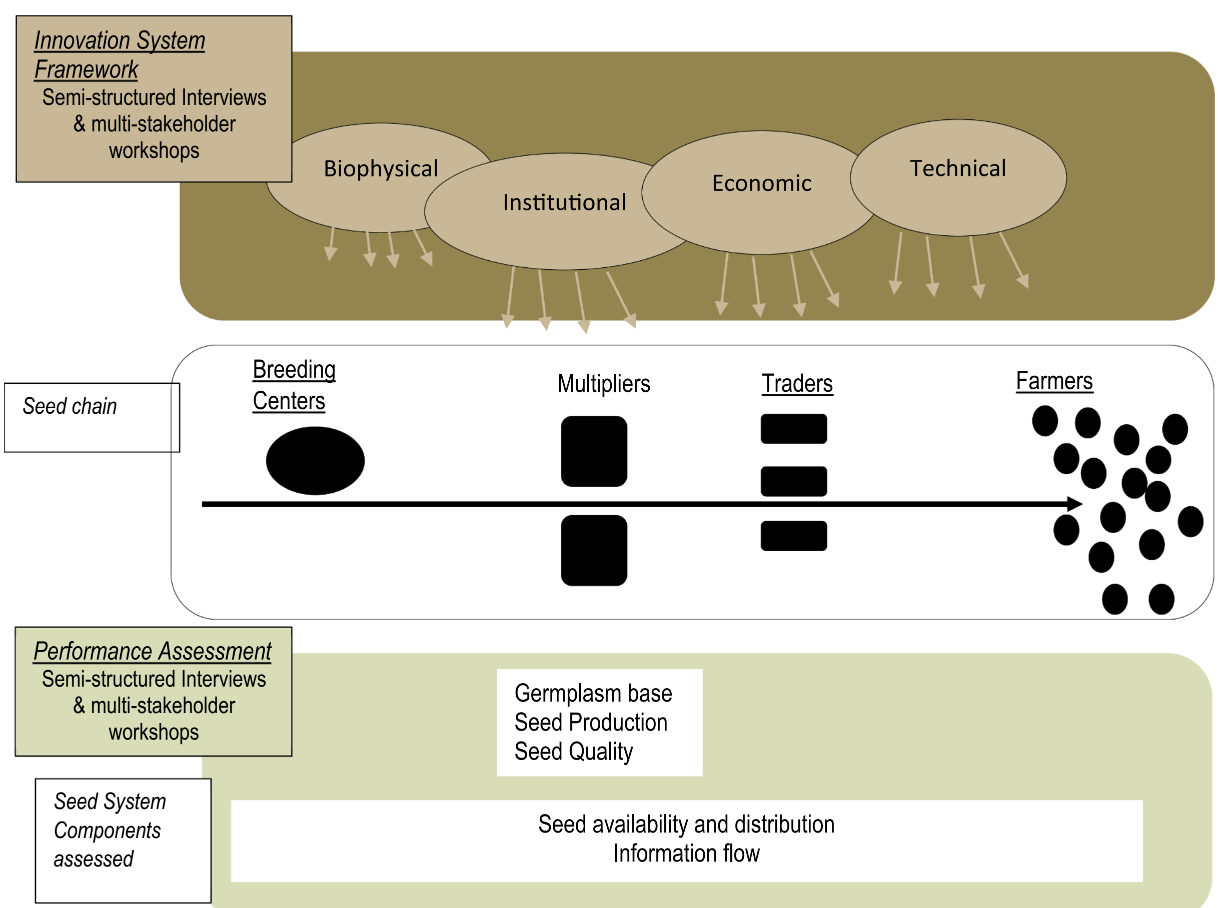

Fig. 4. Analytical framework for assessing fish seed system.

functions of a fish seed system can be analyzed based on four components that overlap and interact including germplasm base, seed production and quality, seed availability and distribution, and information flow. Our modified approach considered seed production and seed quality as two separate components.

The *germplasm base* component includes the strains grown and the associated traits, the extent of usage, and the history and origin of the strains. Analysis of the germplasm component provides an understanding of processes for strains change, such as sources for new strains. In the current context, the analysis of the germplasm component thus includes interactions between farmers and institutions that enhance the germplasm base of fish. Furthermore, tilapia is farmed in diverse culture systems, agro-climatic environments, and management conditions (Ponzoni et al., 2011). Diversity of tilapia production environments may result in genotype by environment (G × E) interaction (Ponzoni et al., 2011; Khaw et al., 2012). Therefore, the germplasm base component also considers the environment for selection.

The *seed production* component refers to all activities leading to the production of fish seed. Specific issues to address relate to quantity of seed produced, the cost of production, and profitability of seed production. The *seed quality* component can be defined as the ability of tilapia seed to grow and survive to mature fish that produces a high yield within the time limits set by the growing cycle. Fish seed quality is affected by seed health, seed purity, and genetic quality. Important issues of focus under the seed quality component include broodstock management, biosecurity measures implemented, management practices adopted for quality, and certification. The component of *seed availability and distribution*, concerns the timely access of farmers to adequate amounts of the required strain. This component also relates to transport and delivery of seed to farmers. Timeliness is crucial for obtaining the expected yield. Relevant questions relating to this component are: What is the actual origin of seed that farmers are growing? Is the market always able to satisfy farmers' demand for seed? Are there any contractual arrangements and how do they influence distribution of seed? The *information flow* component covers issues such as: What information is available to farmers and hatcheries? Where do farmers and hatcheries obtain new information? How is information exchanged among farmers? What type of information are farmers searching? These aspects are especially relevant in the context of change and innovation (Hirpa et al., 2010).

Our analysis was further guided by an analytical framework based on innovation systems thinking to enable a systematic assessment of constraints in tilapia seed systems. Innovation system thinking perceives and analyzes innovations as transformative processes involving changes in both technological and non-technological elements of agricultural systems (Turner et al., 2016). The framework, therefore, integrates technical, biophysical, economic, and institutional dimensions (Lamprinopoulou et al., 2014; Joffre et al., 2018). Consistent with this framework, innovation is the outcome of a process involving multiple stakeholders and their broader regulatory and support environment (Joffre et al., 2017). Our approach followed a two-step analytical process to analyze constraints to dissemination of quality tilapia seed. In the first analytical step, the constraints and the reasons behind them were classified into five dimensions of structural elements that affect the functioning of the seed system toward production and timely delivery of adequate amounts of good quality fish seed. The dimensions include biophysical, technological, physical and knowledge infrastructures, institutional, and economic. In the second analytical step, we analyzed how the identified constraints and their causes interact and generate blocking mechanisms that negatively influence the seed system.

3.2. Data collection

Data to analyze performance of the seed system came from two surveys. We conducted personal interviews with breeding and multiplier hatchery operators in Bangladesh. A pre-existing list of tilapia hatcheries was obtained from WorldFish, Bangladesh office and validated to retain only those that were active in the production and selling of tilapia fish seed. This process retained 96 hatcheries: 56 under *model 1*; 17 under the *model 2*; and 23 under the *model 3*. The survey was implemented by a team of trained enumerators during July-August 2019 using a pre-designed questionnaire programmed in open-data-kit (ODK). The survey modules captured data about broodstock management, biosecurity, seed production and sales, cost of seed production, management practices implemented to maintain quality, certification, and business environment including demand for quality fish seed. In addition to the hatcheries survey, we used farmers survey data from a separate but related study conducted in early 2019 by WorldFish with the aim of assessing on-farm performance of improved tilapia strains (Van Tran et al., 2020). The sample comprised 473 tilapia grow-out producers randomly selected across 14 districts in Bangladesh. A special module asked questions about farmers' access to different types of information including production and marketing.

Data to analyze constraints to tilapia seed dissemination came from three participatory multi-stakeholder workshops held in Dhaka, Mymensingh, and Jashore. Dhaka was selected to capture a national level perspective while the purposive selection of Mymensingh and Jashore targeted geographical areas popular in tilapia farming and with active presence of the three dissemination models described in Section 2.2 above. Workshop participants represented five stakeholder groups comprising research, breeding hatchery operators, multipliers, private companies, and grow-out farmers. Selection of workshop participants was purposive, based on their knowledge and experience of tilapia fish seed dissemination.

3.3. Data analysis

To operationalize the analytical approach, we applied descriptive analysis and conducted profitability analysis to evaluate seed dissemination systems for tilapia seed in Bangladesh. The "orth_out" command in STATA 16 was used to assess differences in performance across the three dissemination models. Specifically, variables were regressed on dummy variables for the dissemination models and an *F*-test that all coefficients of the dissemination models dummies equal zero conducted. Failure to reject the null hypothesis that all dissemination model coefficients equal zero indicates no significant difference across the three models. This approach has mostly been used to perform covariates balancing tests (e.g., Shikuku and Melesse, 2020) and applies for both continuous and dummy variables. We analyzed seed availability and distribution by looking at the sources of seed and what characterizes them; ability of the current sources of supply to meet farmers' demand for seed; and the contractual arrangements that existed to ensure farmers access to seed.

Profitability of tilapia seed production was measured as total revenue less total cost. We computed revenue as total quantity of fry sold (number) multiplied by the price per fry. Total cost measured the sum of variable and fixed costs including cost of broodstock, feed, labor, fertilizer, chemicals (e.g., water treatment chemicals), hormones for sex-reversal, electricity, capital, land and equipment lease, interest, and depreciation. We calculated feed cost separately for brood fish and fry, and summed together. Labour cost was calculated as follows. First, we considered two types of hired labor, part-time and full-time. For each type of labor, male and female person-days were computed. Cost for hired labor was obtained by multiplying the total number of person days by the wage for the specific type of labor. Family labor was not included. Some costs were not incurred specifically for tilapia seed production, especially when hatcheries produced other species of fish as well. This makes it difficult to disentangle the cost of producing tilapia seed from that of producing other species of fish. With the caveat that we cannot completely rule out over-estimation or underestimation of costs of tilapia seed production, our approach weighted each cost category by the multiplier's—only for those producing tilapia plus other species—self-estimated proportion of the cost incurred for tilapia relative to other species. All prices were converted to US$ using the World Bank's 2018 official exchange rate for Bangladesh. In order to assess the cost-effectiveness of tilapia seed production, we divided total revenue by total cost to obtain the benefit–cost ratio (BCR).

Market structure can affect performance of seed systems (Spielman and Kennedy, 2016). In order to understand the degree of competition in the tilapia seed market, we applied the most widely used measure, the four-firm concentration ratio (CR4), defined as the percentage of tilapia fish fry sold by four hatcheries that sell the greatest volumes (Dillon and Dambro, 2018). A CR4 statistic must be interpreted with reference to some scale that connects it to levels of market competition (Dillon and Dambro, 2018). A common rule of thumb is that a CR4 ratio below 20 is consistent with substantial or perfect competition, a range of 20–60 suggests possible non-competitive behavior, and greater than 60 indicates a high likelihood of some degree of market power (Dillon and Dambro, 2018).

To analyze the quality aspect, we asked whether multiplier hatcheries replaced broodstock with elite broodstock or relied on own seed for broodstock production; what strategies they implemented to ensure biosecurity and seed quality; whether hatcheries separated broodstock along multiple dimensions including age and sex; whether they maintained separate batches of seed up to the time of selling; and whether they kept records including about the weight of fry and fingerlings at the time of sale, the batch number, the type of strain sold, and age of the fries and fingerlings. Our analysis of the information aspect probed for hatcheries' and farmers' information needs and sources.

Finally, we applied the Rapid Appraisal of Agricultural Innovation Systems (RAAIS) methodology (Schut et al., 2015) to analyze constraints to seed dissemination. Workshop participants, in their homogeneous groups, identified the constraints faced in relation to production and dissemination of tilapia seed. This was followed by a discussion and transitive ranking of top-five constraints from the most serious to the least severe. Participants then categorized the constraints along five important dimensions of complex aquaculture problems, namely biophysical, technological, economic, institutional, and political. For each constraint, the level at which each constraint operates along the seed value chain was identified. This was followed by a discussion and mapping of the possible interactions between the constraints.

4. Results

4.1. Germplasm base

There are currently five GIFT breeding hatcheries actively operating under *model 1* and distributed across the country as follows: two in the north (Mymensingh); one in northwest (Rangpur); one in southwest (Magura); and one in the south (Barguna). Selection for breeding is done in the respective regions. Breeder seed is then sold to multiplier hatcheries both within and outside the regions of selection. In *model 2*, family selection only happens in Mymensingh although BFRI has research stations in different regions across the country. Selection under *model 3* happens outside Bangladesh.

4.2. Tilapia seed availability and distribution

4.2.1. Sources of improved tilapia seed

Table 2 summarizes the main characteristics describing three main sources of improved tilapia seed in Bangladesh. The two private GIFT breeding hatcheries in Mymensingh (north) under *model 1* produced about 0.8 million mixed-sex fry altogether in 2018. Seven multipliers located in Mymensingh division source seed from these breeding hatcheries. The private GIFT breeding hatchery located in Magura (southwest) and with own multiplier hatcheries across the country produced about 0.3 million mixed-sex fry and 28 million mono-sex fry in 2018. Seventy percent of the mono-sex fry produced was sold directly to grow-out producers and 30% indirectly through seed traders. The 0.3 million mixed-sex fry was used as broodstock by the breeding hatchery's own multiplier hatcheries, altogether supplying 18.2 million mono-sex fry in the southwest region and 103.8 million mono-sex fry to other regions. The remaining two GIFT breeding hatcheries (one in northwest and another one in the south) Produced 9.2 million fry (both mono-sex and mixed-sex) in 2018. Multiplier hatcheries buying mixed-sex fry from these breeding hatcheries supplied 10 million mono-sex fry to grow-out producers in 2018.

There were about 100 multipliers in the country who received the latest GIFT seed from BFRI after 2012 under *model 2*. Workshop participants indicated that 160,000 mixed-sex fry out of the 455,000 mixed-sex fry produced by BFRI in 2018 were sold in Mymensingh. Multipliers in turn supply 19.28 million mono-sex fry to grow-out producers. There were 25 multipliers in Mymensingh operating under this model. In Jashore, about six multipliers obtained mixed-sex fry from BFRI. Multipliers then produced and disseminated about one million mono-sex fry

Table 2
Summary of tilapia seed production and supply system in Bangladesh.

Model characteristics	Model type		
	Private model for GIFT (*model 1*)	Public system for GIFT (*model 2*)	Private model for non-GIFT (*model 3*)
Production method	Cohort breeding hatchery (CBH) system	Family selection	Mass selection
Strain produced	Genetically improved farmed tilapia (GIFT)	GIFT	Non-GIFT
Source of genetic material	Jitra, Malaysia	Jitra, Malaysia	Breeding nucleus are outside Bangladesh in Thailand and Philippines.
Mode of operation	• Breeding hatcheries produce and sell mixed-sex fry to multiplier hatcheries. • Breeding hatcheries also produce mono-sex fry and sell to grow-out producers. • Multiplier hatcheries produce mono-sex fry and fingerlings for selling to grow-out.	• BFRI produces mixed-sex fry and sells to multiplier hatcheries. • Multiplier hatcheries produce mono-sex fry and fingerlings for selling to grow-out producers.	Multiplier hatcheries receive broodstock from abroad and produce fingerlings for selling to grow-out producers.
Distribution of seed	• 85% of fry produced by breeding hatcheries is sold directly to grow-out producers • 10–12% of fry produced by breeding hatcheries are sold indirectly to producers through seed traders. • 3–5% of the fry produced are sold as broodstock to multiplier hatcheries. • Multipliers sell seed directly to farmers (80%) and indirectly through traders (20%)	• BFRI produces about 455,000 mixed-sex fry annually, supplying to multiplier hatcheries. • BFRI does not sell directly to seed traders, nurseries, or grow-out producers.	• There are 60–70 multipliers under this model, producing about 500 million fry in total. • Multipliers sell 95% of fry produced to grow-out producers through commission agents and only 5% directly.

in Jashore. However, there were several hatcheries that obtained GIFT broodstock from BFRI before 2012 and had continued to use their own seed for broodstock development. These multipliers did not collect the fry every year or every alternate year—a suggested good practice to avoid inbreeding. Instead, they produced brood fish using offspring of their own seed, consequently increasing inbreeding and reducing quality. Multipliers in this model produced and disseminated about 750 million mono-sex fry annually.

There were about 60–70 multiplier hatcheries under *model 3* producing about 500 million fry in total. Annually, about 310 million and 22.5 million non-GIFT fry are produced and distributed in Mymensingh and Jashore, respectively. Multipliers provided transport support and technical advice to the farmers through agents. Furthermore, multipliers maintained a database of all farmers, linked farmers to feed suppliers, and provided technical training. In addition, they hired quality control experts at the hatchery, checked sex-reversal percentage after 21 days, and checked parasites before delivery of seed to the customers.

4.2.2. Demand for tilapia seed and contractual arrangements

Most hatcheries had experienced a situation where the supply of tilapia seed could not meet demand (Table 3). The difference in the ability to satisfy demand for seed was not statistically significant across the three dissemination models. Fig. 5 shows the main measures taken to respond to supply deficit. The main measures taken included referring clients to another hatchery nearby, asking clients to come back at a later date, and convincing clients to top up with another strain that was available. The hatcheries survey further showed that more than two-thirds of sample hatcheries were in a contractual relationship with their clients (Table 3). Differences in contractual arrangements was not statistically significant across the three models. Contracts were mostly established with farmers (84%), commission agents (38%), and fish seed traders (34%). Contractual agreements mostly involved the price of seed (92%), size of fingerlings (80%), quantity supplied (73%), and date of delivery (59%). We found that significantly less hatcheries under *model 1* than *model 2* and *model 3* provided bonus fry and sold on discount (Table 3).

4.3. Tilapia seed production

Tables 4 and 5 present results of annual fry production, sales, and profitability analysis. While we found no significant difference in the annual quantity of fry produced across the three models, the quantity of fry sold was considerably lower for GIFT hatcheries than non-GIFT hatcheries. Specifically, the average quantity of fry sold by GIFT hatcheries under *model 1* (10 million) was 65% lower than under *model 3* (16.6 million). The corresponding figure for hatcheries under *model 2* was 9.2 million, representing 81% lower sales than for non-GIFT. Overall, total revenue obtained under the non-GIFT model is higher than for GIFT models. Differences in revenue are not statistically significant across the three models. These results measure total production and sales as opposed to production and sales per unit area and are consistent with non-GIFT model being dominated by large scale hatcheries often owned by multinational companies with greater production capacity than GIFT hatcheries. The cost of production was significantly lower for GIFT models than non-GIFT model. We further found that tilapia seed production and selling was equally profitable for all the three models. However, *model 1* was the most cost-effective model with a benefit-cost ratio of 1.99 compared with 1.65 for *model 2* and 1.83 for *model 3*. Furthermore, we calculated a CR4 ratio equal to 19 indicating substantial competition in tilapia fry selling business.

Table 3
Contractual agreements and additional services provided by hatcheries.

Variable	Private GIFT (*model 1*)	Public GIFT (model 2)	Non-GIFT (*model 3*)	*p*-value
Hatchery was unable to satisfy demand for seed	0.82 (0.34)	0.88 (0.33)	0.96 (0.21)	0.279
Hatchery is in contractual arrangement with clients	0.73 (0.45)	0.65 (0.49)	0.65 (0.49)	0.443
Hatchery provided training or advice	0.88 (0.33)	0.82 (0.39)	0.74 (0.45)	0.343
Hatchery provided bonus fry or fingerlings	0.43 (0.50)	0.71 (0.47)	0.83 (0.39)	0.002
Hatchery offered discount on purchased fry or fingerlings	0.14 (0.35)	0.29 (0.47)	0.35 (0.49)	0.097
Observations	56	17	23	

Notes: Figures indicate the proportion of hatcheries. In parentheses are standard deviations.

4.4. Tilapia seed quality

Results of the hatchery survey showed that most sample multiplier hatcheries produced broodstock from own seed (Table 6). The proportion of hatcheries using their own seed to produce broodstock was higher, although only statistically significant at 10% level, among multiplier hatcheries under *model 2* (76%) and *model 3* (83%) than those under *model 1* (58%). The percentage of hatcheries producing broodstock from own seed was considerably lower in Mymensingh than in other regions. The presence of three breeding hatcheries including the public sector breeding nucleus at BFRI and two private sector breeding hatcheries in Mymensingh compared to two in the south may explain the less reliance by multiplier hatcheries in Mymensingh on own seed for broodstock production. Reliance on own seed for broodstock production has a negative effect on quality of seed because of inbreeding and potential mixing of strains. Hatcheries replaced broodstock after every two years, on average.

Hatcheries mostly maintained separate ponds/facilities for different broodstock by sex (91%). Separation of broodstock by age (46%) and strain (23%) was low. Majority (98%) of the sample hatcheries indicated that they maintained separate batches of seed (e.g., by date of spawning and broodstock used) up to the time of selling. All sample hatcheries reported they kept records of their clients including their contact details. Hatcheries also kept records about the quantity of fry and fingerlings sold (80%), weight of fry and fingerlings at the time of sale (36%), the batch number (32%), the type of strain sold (30%), and age of the fry and fingerlings (20%). The most commonly used practices to maintain quality included use of clean water, regular water exchange, improved feeding, careful selection of fry, applying water purifying chemicals, separating broodstock, and using oxygenated bags during transportation of fry and fingerlings.

Sixteen percent of the hatcheries surveyed had experienced abnormal mortality of fry or broodstock. Differences in experience with abnormal fry and fingerlings mortality was not statistically significant across the three models. The main perceived causes of mortality were related to prolonged exposure to extreme high temperature, sudden changes in temperature, poor water quality, and occurrence of diseases. Biosecurity measures are important to reduce occurrence and adverse impacts of diseases. The most common biosecurity measures implemented by hatcheries included disinfection of tanks and equipment, investment in equipment for measuring water quality, and proper disposal of dead fish.

4.5. Information flow

Farmers can obtain information on name, source, yielding ability, marketability of strains and production practices from various sources, such as relatives, neighboring farmers, extension agents, NGOs, researchers, hatchery operators, feed dealers, and fish seed traders. Results of a survey with grow-out producers showed that 45% had access to information about fish farming. Most farmers (82%) receiving information about fish farming reported that it contained advice about tilapia

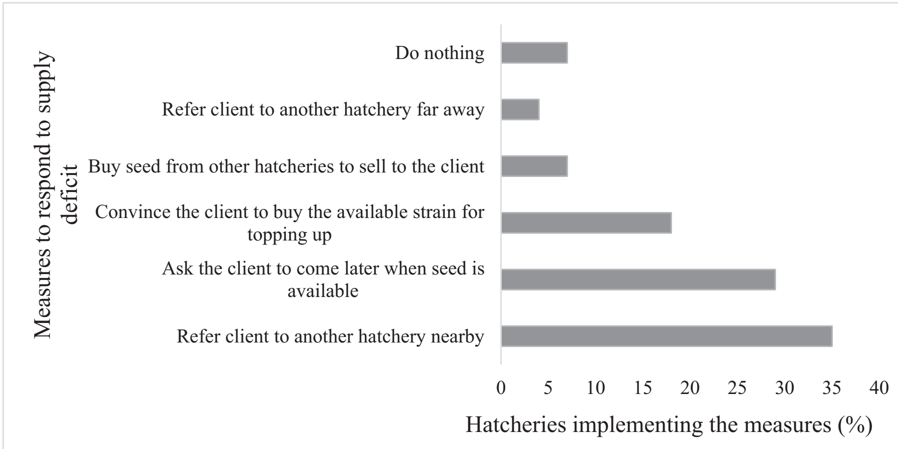

Fig. 5. Hatcheries' responses when they cannot meet demand for seed.

Table 4
Fry production and sales.

Variable	Private GIFT (*model 1*)	Public GIFT (*model 2*)	Non-GIFT (*model 3*)	*p*-value
Quantity of fry produced ('000 per year)	11,854.00 (11,862.00)	13,211.00 (9167.00)	18,176.00 (16,751.00)	0.126
Weight of fry at production (g)	0.04 (0.06)	0.03 (0.05)	0.01 (0.00)	0.039
Length of nursing period (days)	30.05 (4.71)	29.00 (8.54)	29.32 (4.44)	0.727
Quantity of fry sold ('000 per year)	10,041.00 (11,260.00)	9189.00 (7342.00)	16,589.00 (16,094.00)	0.058
Weight of fry at the time of selling (g)	0.30 (0.26)	0.20 (0.06)	0.18 (0.04)	0.015
Price of fry (BDT/piece)	0.61 (0.28)	0.59 (0.23)	0.59 (0.27)	0.900
Observations	56	17	23	

Notes: In parentheses are standard deviations.

Table 5
Profitability of tilapia seed production.

Variable	Private GIFT (*model 1*)	Public GIFT (*model 2*)	Non-GIFT (*model 3*)	*p*-value
Revenue from fry (US$)	71,510.00 (91,536.00)	65,966.00 (48,018.00)	100,234.00 (100,234.00)	0.316
Total cost of production (US $)	35,956.00 (22.818.00)	40,017.00 (21,157.00)	54,667.00 (27,000.00)	0.008
Profit (US$)	35,554.00 (78,824.00)	25,949.00 (45,032.00)	45,567.00 (70,066.00)	0.692
Benefit-Cost ratio (BCR)	1.99	1.65	1.83	
Observations	56	17	23	

Table 6
Broodstock management by hatcheries.

Variable	Private GIFT (*model 1*)	Public GIFT (*model 2*)	Non-GIFT (*model 3*)	*p*-value	Observations
Produce broodstock from own seed	0.58 (0.50)	0.76 (0.44)	0.83 (0.39)	0.072	92
Years before replacing broodstock	2.21 (0.94)	1.71 (0.59)	2.13 (0.87)	0.116	92
Maintain separate batches of seed up to the time of selling	0.98 (0.19)	1.00 (0.00)	1.00 (0.00)	0.704	96
Keep records about the batch number	0.25 (0.43)	0.41 (0.51)	0.48 (0.51)	0.113	96
Keep records about the type of strain sold	0.29 (0.46)	0.41 (0.51)	0.26 (0.45)	0.550	96
Keep records about the age of the fries and fingerlings sold	0.16 (0.37)	0.29 (0.47)	0.22 (0.42)	0.473	96
Experienced abnormal mortality of fry or broodstock	0.14 (0.35)	0.18 (0.39)	0.17 (0.39)	0.915	96

Notes: In parentheses are standard deviations. The difference in sample size (92 in two first lines and 96 in the next ones) is because we omitted two breeding hatcheries that produce mixed sex (early generation seed) and therefore by default use own seed employing rotational cohort breeding system to reduce inbreeding.

farming. The main sources of information about fish farming were neighboring farmers (65%), seed traders (13%), relatives (10%), extension agents (10%), and hatchery operators (9%). However, only 8% of farmers had received training in tilapia fish production. Results of the farmers' survey further indicates that 31% received fish marketing information. The main sources of marketing information included neighboring farmers (75%), seed traders (39%), phone (20%), and relative (10%).

Only 22% of the hatcheries interviewed had received training in broodstock management during two years before the survey. The main sources of training were research organizations, development organizations, and extension agents. The main sources of information about record keeping were other hatcheries (66%), international research organizations (21%), government extension agents (13%), extension agents from non-governmental organizations (NGO) (10%), multinational companies (10%), and DoF (10%).

4.6. Constraints to dissemination of good quality tilapia seed

4.6.1. Poor quality broodstock

The main problem in dissemination of improved tilapia strains was related to poor quality of broodstock and high degree of inbreeding (Table 7). Workshop participants indicated that reliance on own seed to produce broodstock, failure to maintain accurate brood plan, and limited knowledge in proper broodstock management were serious

Table 7
Constraints to quality tilapia seed production in Bangladesh and underlying reasons.

Problematic issue selected by stakeholders	Constraint(s) connected to problematic issue	Underlying reason for constraint	Type of constraint
Poor quality brood fish and high inbreeding	Continued use of own seed for broodstock development	Lack of effective demand. Lack of certification for seed quality. Limited number of registered hatcheries.	Knowledge Institutional
	Weak enforcement of regulatory framework		Market
	Lack of knowledge in brood fish management	Lack of skilled manpower	Knowledge
	Lack of traceability of original broodstock.	Inaccurate record keeping Potential mixing of strains.	Knowledge Market
Abnormal weather conditions	Poor quality of water affecting eggs production and causing fry mortality	Frequent and sudden changes in temperature	Biophysical
Increased disease incidences	Low ability to identify and treat diseases	Lack of knowledge in disease prevention and control Lack of equipment for disease testing	Knowledge Infrastructural
Low quality inputs	Weak enforcement of regulatory framework	Overlapping responsibility in enforcement of regulatory framework.	Institutional
Limited access to market	High competition from unregistered hatcheries and brokers	Weak enforcement of regulatory framework.	Market Institutional
	Lack of coordination between value chain actors to establish quality standards and facilitate market access	Limited platforms for information exchange.	Knowledge Institutional
High transportation cost	Delayed delivery of fry	Poor transport infrastructure Extortions during transportation	Infrastructural Institutional

constraints causing inbreeding. In addition, the absence of certification for fish seed quality combined with imperfect implementation of regulatory frameworks including the Fish Hatchery Act 2010 and Rules 2011 allowed opportunistic behavior of hatcheries. Consistent with our analytical framework, these results support those reported under the quality aspect in Section 4.4.

4.6.2. *Abnormal weather conditions and increased disease incidences*

Workshop participants indicated that extreme high temperature and sudden changes in temperature adversely affected production of quality tilapia seed. Temperature shocks as a constraint was mostly prioritized by breeding and multiplier hatcheries. Abnormal water temperature reduces physiological performance of fish consequently reducing ability to produce eggs and fry. Furthermore, the quality of water is reduced hence increasing fry mortality and the cost of water exchange and treatment. Poor quality of water and unpredictable changes in temperature were identified as the main causes of diseases. We further found that disease outbreaks were increasingly a threat to tilapia seed production. Together, the constraint of abnormal weather conditions and increased disease incidences relates to the seed production aspect of our analytical framework. Workshop participants indicated that during 1990–2018, there has been at least four disease outbreaks affecting tilapia in Bangladesh. At the same time, workshop participants indicated lack of equipment and inadequate knowledge to identify and treat diseases as a major barrier to addressing the problem. These results are also consistent with findings from the hatcheries survey and may explain why water management practices including regular water exchange and investment in equipment for water quality testing were among the main strategies used to reduce abnormal mortality of fry.

4.6.3. *Low quality and high cost of inputs*

Workshop participants indicated that poor quality of inputs especially feed and hormones required for fish sex-reversal affected their ability to produce quality seed. The presence of low quality and adulterated inputs in the market was associated mainly with incomplete implementation of the regulatory frameworks. At the same time, breeding and multiplier hatcheries and the private sector workshop stakeholder groups indicated that the cost of inputs required for fish seed production was too high. High taxes on feed, hormones and other inputs was identified as the main reason for the exorbitant cost. Workshop participants further indicated that improper use of inputs such as hormones substantially raised costs without a commensurate increase in production.

4.6.4. *Limited market access and high transportation cost*

Limited market access and high transportation cost relate to the seed distribution aspect. Multiplier hatcheries perceived lower prices of fish seed relative to the high cost of seed production as a constraint to production of quality tilapia seed. There was also perceived unfair competition from unregistered hatcheries and brokers. Workshop participants indicated lack of full implementation of the Fisheries Hatchery Act 2010 and Rule 2011 and absence of a certification scheme for hatchery and fish seed quality as the main reasons for the perceived unfair competition.[1] Furthermore, there was lack of coordination among value chain actors to establish quality standards and facilitate market access. Small hatcheries found it difficult to compete with large-scale hatcheries providing complementary services in addition to seed.

Most hatcheries in Bangladesh have a wide clientele coverage. For example, hatcheries located in the north have clients in the south and vice versa. Timely delivery of seed requires good roads infrastructure. However, workshop participants indicated that the road network was poor consequently increasing transport and transaction costs associated with delivery of seed to clients. Delayed delivery of fry due to poor roads network reduces survival and growth rates for fish seed consequently negatively affecting yields. Workshops also reported that there were hidden costs incurred during transportation of fish seed including brokerage.

4.7. *Analysis of blocking mechanism*

Based on the constraints identified and the underlying causes, we distinguished four clusters of constraints that formed blocking mechanisms: (a) incomplete enforcement of regulatory frameworks to control hatchery practices and quality of inputs; (b) limited knowledge about

[1] Government issued the Fisheries Hatchery Act 2010 and Fisheries Hatchery Rule 2011 to ensure quality of fish seed supply from public and private hatcheries for sustainable development of fisheries resources in Bangladesh. Under the Act and Rule, every hatchery must have to be registered from the competent authority of the department of fisheries (DOF) and hatchery owners have to declare best health management and pollution control in seed production. The act also proposed to mitigate undesirable practices of inbreeding, inter-specific hybridization, negative selection and improper brood-stock management.

broodstock management, quality seed production, and disease management; (c) weak adaptive capacity to weather shocks; and (d) limited access to credit. These four blocking mechanisms interacted creating a systemic lock-in.

Incomplete implementation of the regulatory framework relates to the quality aspects as explained in the analytical framework and has implications on the general conduct of hatcheries and input suppliers. At the same time, lack of clearly defined standards and absence of a certification scheme for hatcheries and seed quality may hinder successful enforcement of regulation frameworks. Workshop results showed that problems related to weak regulatory frameworks hence low quality of seed and inputs affected mostly breeding and multiplier hatcheries and grow-out farmers.

The second blocking mechanism was poor knowledge in broodstock management, quality seed production, and disease management, consistent with the information flow aspect of our analytical framework. This blocking mechanism affected breeding and multiplier hatcheries and grow-out farmers. If multiplier hatcheries lack knowledge about the benefits and sources of good quality broodstock, demand for such quality elite germplasm will be low. This low demand for quality broodstock may create a vicious cycle whereby multiplier hatcheries sell low quality seed produced from poor quality broodstock, consequently causing farmers to experience depressed yields hence lack of effective demand for improved seed. Lack of skilled labor at hatchery may partly explain the failure to develop good brood plans. Furthermore, the ability of grow-out farmers to select good quality seed was low. In most cases, quality of fish seed is revealed only after stocking through performance outcomes such as growth rate and survival.

The third blocking mechanism related to low adaptive capacity of hatcheries to extreme hot temperature. This problem relates to the seed production aspect as explained in the analytical framework, and mostly affected breeding and multiplier hatcheries and grow-out producers. Reduced ability to produce eggs and fry combined with increased fry mortality associated with rapid changes in temperature require adaptation at hatchery level. In most cases, however, adaptation to weather shocks was only considered at farm level.

The fourth blocking mechanism was related to constrained access to credit and mostly affected farmers, but with spiral impacts to other actors in the seed value chain. Farmers facing liquidity constraints may lack effective demand for quality seed. High interest rates were the main reason for limited access to credit. Optimal on-farm performance of improved seed requires investment in complementary inputs such as feed and water treatment chemicals. Constrained access to credit means that farmers may not undertake such complementary investments. Consequently, improved seed may yield below farmers' expectations.

5. Discussion

5.1. Lock-ins, path dependence, and adoption of improved fish strains

The results suggest that the presence of binding and interacting constraints that create a systemic lock-in may attenuate incentives to disseminate improved fish seeds. Our analysis illustrates the technological lock-in first described by Liebowitz and Margolis (1995), where a dominant technology, impedes the widespread adoption of higher performing technology. The presence of the identified constraints by themselves may not impede adoption of technology, but their combination generates a lock-in.

When compared with agricultural system, similar lock-ins to adoption of improved fish seed are identified. Vanloqueren and Baret (2008) identified 12 factors impeding the adoption of multi-resistant wheat cultivars that operate at all levels from seed producers to farmers and encompass also constraints at the policy level but not solely related to the performance of the seeds. The findings of the current study support insights from the Vietnamese shrimp sector that limited enforcement of regulatory framework combined with mismanagement of ponds and limited access to credit hinder change in practices toward sustainable intensification of aquaculture (Joffre et al., 2018). Hence, tilapia seed system in Bangladesh and more broadly, the tilapia sector from the breeding nucleus to grow-out production will require a systemic intervention to lift those barriers because, like in agriculture, they operate in different dimensions. These results support a recent perspective about the need for systematic analysis of "scaling readiness" of innovations (e.g., Woltering et al., 2019; Sartas et al., 2020). The results further support the need for design thinking approaches (e.g., Toffolini et al., 2020) that recognize complex patterns of relations between scientific knowledge and production of innovation. This approach will help integrate new knowledge generated by research and new representation of processes of interest into the design of fish seed systems. Hence, design thinking will support the integration of various stakeholders' forms of practices and representation of processes of interest to respond to increasingly complex requirements of fish seed systems. Such design thinking approaches hold the promise to unlocking a transformation process of complex multi-locked fish seed systems.

5.2. Inclusive and sustainable dissemination of improved strains

Our results highlight important differences in dissemination models for fish seed with implications for inclusivity and quality. We found that although *model 3* generated greater net returns to multipliers than *model 1* and *model 2*, *model 1* was the most cost-effective dissemination model. Cost-effectiveness has been emphasized by literature as a prerequisite condition for sustainable scaling of agricultural innovations (e.g., BenYishay and Mobarak, 2018; Van Campenhout et al., 2020; Low and Thiele, 2020). In the context of aquaculture, cost-effectiveness in a competitive seed market suggests that *model 1* is beneficial to both large-scale and small-scale multipliers and, therefore, fosters inclusivity. This finding, therefore, has implications for the role of small and medium enterprises in the dissemination and scaling of improved fish strains.

5.3. Key ingredients for improved fish seed systems performance

5.3.1. Increased access to elite germplasm and addressing inbreeding

Generally, the capacity of the seed system to disseminate quality fish seed is currently low with most multipliers relying on their own seed to produce broodstock, potentially increasing inbreeding. Low demand for elite broodstock means that breeding hatcheries may lack a sustainable business model. This partly explains why the role of breeding hatcheries has evolved and now includes supply of mono-sex seed in addition to breeder seed. A possible reason for the low demand is lack of awareness and knowledge exposure about the sources, benefits, and proper management of elite broodstock. Several studies have shown that information externalities can increase adoption of agricultural innovations (BenYishay and Mobarak, 2018; Shikuku et al., 2019b). Advocacy and knowledge exposure among multiplier hatcheries about better management practices including the benefits and sources of good quality broodstock is important to create demand for the elite broodstock. For example, during the workshop, participants indicated that although BFRI offers tests for quality including purity tests, very few multiplier hatcheries were actively seeking such services.

A further issue relates to use of seed exchange networks among hatcheries. As many multiplier hatcheries rely on their own seed for broodstock, encouraging hatcheries to exchange seeds for broodstock (or fry/fingerlings that will be used later as broodstock) would avoid inbreeding, provided the fish are non-related. At the moment only 17% of the multiplier hatcheries exchange broodstock. Health check should be done to ensure no transmission of diseases among hatcheries. Pautasso et al. (2013) provides a comprehensive review about seed exchange networks and shows that such networks enhance genetic diversity in agriculture. Although evidence in aquaculture is missing, reducing inbreeding by stimulating seed exchange networks among hatcheries could be a useful approach to spreading higher genetic diversity within fish seed systems compared to a system where such networks are absent.

5.3.2. Building institutional capacity for quality control

Low quality of agricultural inputs have been shown to explain low take-up of improved seed in developing countries (e.g., Bold et al., 2017). Islam et al. (2007) also indicated existence of inefficient inputs use by hatcheries in Bangladesh. Studies have shown that use of adulterated and low-quality inputs have yield-depressing effects (Bold et al., 2017). The presence of aggregate uncertainty about the quality of inputs may cause farmers to "herd" on inferior technologies (Monzon, 2017). Lack of institutional support was also identified by Ali et al. (2010) as a serious constraint to fish seed production. Certification of hatcheries and fish seed quality is crucial to addressing the problem of poor-quality tilapia seed dissemination. Future studies should evaluate farmers' willingness to pay for quality-certified seed.

5.3.3. Increasing resilience of fish seed systems

Frequent weather shocks and increased disease incidences underscore the urgency for breeding efforts to include resilience traits. Some authors have highlighted the need for high strain turn over to address increasingly challenging climatic shocks and diseases (Atlin et al., 2017; Das et al., 2019). In the intermediate term, promoting wide scale adoption of aquaculture better management practices (BMPs) and enhancing biosecurity would help to improve fish health and reverse trends in abnormal mortality of fry and broodstock. Ultimately, national strategic planning for aquatic animal health and biosecurity is crucial. Exposure and increasing vulnerability to weather shocks also emphasizes the urgent need to promote adaptation at hatchery level. Although most adaptation studies focus at farm level, our results show that impacts of climate-related stress affect multiple actors along value chains. This points to the need to map the risk profiles of various actors within seed systems in order to identify targeted interventions (e.g., Sova et al., 2018).

5.3.4. Awareness and knowledge exposure about improved strains

Our findings showed that farmers' main source of information about tilapia production and marketing were fellow farmers. This finding is consistent with Lee et al. (2019) and emphasizes the important role played by social networks in the diffusion of innovations. This is in line with literature on social learning (e.g., Conley and Udry, 2010). Leveraging social networks for technology diffusion can be an effective approach to achieve wide-scale adoption of improved fish strains. Recently, studies have emphasized the effectiveness of carefully selected and incentivized peer farmers for farmer-to-farmer technology transfer (e.g., BenYishay and Mobarak, 2018; Lee et al., 2019; Shikuku and Melesse, 2020). Some authors have also shown that organizing farmers into clusters can foster interactions and shapes aqua-related risk perceptions subsequently increasing adoption of aquaculture innovations and promoting sustainable intensification (Joffre et al., 2019). A few others have shown that demonstration farms generate positive information externalities by facilitating social learning through induced conversations and information sharing outside of existing social networks (Dar et al., 2019).

Furthermore, we found that hatchery operators, seed traders, and feed dealers were an important source of information to farmers. This means that building the capacity of intermediaries, sometimes referred to as local service providers, within seed systems to provide accurate information in addition to delivering quality seed can help to address informational constraints and fill knowledge gaps currently identified by farmers as a constraint to adoption of improved tilapia strains.

5.3.5. Taking into account the mismatch between genetic and environmental factors

A review of GIFT tilapia by Ponzoni et al. (2011) revealed positive, albeit imperfect, genetic correlations between environments, suggesting that selection for optimal performance in one environment results in favourable, but suboptimal, genetic gains in alternative environments. That is, the review found evidence of genotype by environment interactions (GxE) in GIFT but no evidence that GIFT would perform worse in any of the tested environments than unimproved strains. Where GxE exists (i.e. genetic correlations between environments are less than one), to optimize genetic improvement in every farming environment, it is necessary to maintain nucleus populations for each environment. This is neither financially nor logistically possible in real-world situations. A more plausible approach is to define a breeding goal/objective appropriate to the targeted farming environment/s – whether they be current or future environments – and maintain a single breeding nucleus or, if GxE is extreme, a small number of breeding nuclei. Accordingly, it may be appropriate in the case of aquaculture species to select 'robust' fish that maintain good performance under multiple environments – albeit suboptimal performance in any one environment (Ponzoni et al., 2011). However, such an approach requires the performance of fish to be tested across multiple targeted environments and performance in each to be accounted for in selection decisions, inevitably adding to the cost and complexity of genetic improvement programs.

Our analysis of lock-ins showed that liquidity constraints among farmers is a barrier to investment in complementary inputs necessary for optimal performance of improved fish strains. It is also almost certainly the case that the performance of unimproved strains would improve with investment in 'complementary inputs'. That is, the question of whether poor fish farmers should burden themselves with the cost of complementary inputs is an open question with or without the presence of improved strains.

5.4. The future of fish seed systems

This study has focused on the case of tilapia in Bangladesh, but more broadly concerns seed systems in developing countries' aquaculture. One of the challenges to sustainable aquaculture development is the lack of improved strains of fish (FAO, 2012). To date, aquaculture in developing countries is still largely based on unimproved fish strains which are genetically similar or inferior to wild counterparts (Brummett et al., 2004; Ponzoni et al., 2007). There are only a few examples where aquaculture production has benefited from genetically improved strains (Gjerde et al., 2012). This results in aquaculture with poor growth rate, high mortality, and high production costs. Genetically improved seeds of fish and other aquatic species are essential for increasing productivity and improving socio-economic performance of aquaculture production (Ponzoni et al., 2007; Yosef, 2009).

This study has shown that, similar to agricultural contexts (e.g., Vanloqueren and Baret, 2008) and aquaculture production systems (Joffre et al., 2018), constraints within fish seed systems interact and mutually reinforce each other creating a systemic lock-in. This means that efforts to augment resources for initial establishment of seed systems by injecting new strains into existing systems would enhance performance if accompanied by systemic interventions to unlock the potential of fish seed systems to disseminate high quality seed in an inclusive, timely, affordable, and sustainable manner. Such systemic interventions must extend beyond technological and economic constraints to consider multidimensionality in blocking mechanisms including institutional, sociocultural, and political factors (Berkhout, 2002). A further issue concerns the role of selective breeding in addressing bottlenecks within fish seed systems. An emerging hypothesis concerns the importance of decentralized selective breeding in reducing dependence on costly inputs hence easing liquidity constraints among farmers and increasing resilience to environmental stresses. Similarly, our study found that demand for elite broodstock among multiplier hatcheries was low and suggests options for stimulating increased adoption and encouraging good husbandry and broodstock management practices in order to avoid inbreeding. The role of seed exchange networks in enhancing genetic diversity is well recognized in agriculture (e.g., Pautasso et al., 2013), but less explored in aquaculture. Can a more decentralized selective breeding approach combined with seed exchange networks increase efficiency within fish seed systems? In addition, Little et al. (2007) indicated that decentralized seed systems where aquaculture producers' capacity in seed production is improved can be welfare-enhancing to the rural poor inadequately served by conventional approaches. Can integrated formal and informal, centralized and decentralized seed systems deliver quality seed of farmed fish in aquaculture? We hope future research could address these emerging hypotheses.

6. Conclusion

Effective and well-functioning seed systems are crucial conduits for the dissemination of quality seed to farmers for improved yields and socioeconomic development. We evaluated the fish seed system focusing on tilapia in Bangladesh. The study found that although seed production and dissemination was profitable, there existed interacting constraints within seed systems that caused a systemic lock-in and generated sub-optimal performance. Four blocking mechanisms identified encompass poor enforcement of regulatory framework to hatchery practices and quality of inputs, the limited knowledge in seed productions, a vulnerability to climate variability and constraints to access to financial mechanism.

Our analysis generates important insights for improving the capacity of fish seed systems for timely and sustainable delivery of good quality seed of desired traits to farmers, supporting the growth of aquaculture sector, and establishing an "inclusive" approach and making quality seeds available to poor farmers. Specifically, in order to strengthen fish seed systems within a more sustainable aquatic food system, this study suggests concerted efforts, with five priority actions: increased access to elite germplasm and addressing inbreeding; building institutional capacity for quality control; increasing resilience of fish seed systems; awareness and knowledge exposure about improved strains; and taking into account the mismatch between genetic and environmental factors.

Declaration of Competing Interest

The authors declare that they have no conflict of interest.

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