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Can the Global Adoption of Genetically Improved Farmed Fish Increase Beyond 10%, and How?

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Abstract: The annual production from global aquaculture has increased rapidly from 2.6 million tons or 3.9% of the total supply of fish, shellfish and mollusks in 1970, to 66.7 million tons or 42.2% in 2012, while capture fisheries have more or less leveled out at about 90 million tons per year since the turn of the century. Consequently, the future seafood supply is likely to depend on a further increase of aquaculture production. Unlike terrestrial animal farming, less than 10% of the aquaculture production comes from domesticated and selectively bred farm stocks. This situation has substantial consequences in terms of poorer resource efficiency, poorer product quality and poorer animal welfare. The history of biological and technical challenges when establishing selective breeding programs for aquaculture is discussed, and it is concluded that most aquaculture species may now be domesticated and improved by selection. However, the adoption of selective breeding in aquaculture is progressing slowly. This paper reports on a study carried out in 2012 to identify key issues to address in promoting the development of genetically improved aquaculture stocks. The study involved semi structured interviews of 34 respondents from different sectors of the aquaculture society in East and Southeast Asia, where 76% of the global aquaculture production is located. Based on the interviews and literature review, three key factors are identified: (i) long-term public commitment is often needed for financial

support of the breeding nucleus operation (at least during the first five to ten generations of selection); (ii) training at all levels (from government officers and university staff to breeding nucleus and hatchery operators, as well as farmers); and (iii) development of appropriate business models for benefit sharing between the breeding, multiplier and grow-out operators (whether being public, cooperative or private operations). The public support should be invested in efforts of selective breeding on the most important and highest volume species, which may not be a priority for investment by private breeders due to, for instance, long generation intervals and delays in return to investment.

Keywords: aquaculture; breeding programs; selection; business models; technology adoption; Asia

1. Introduction

The annual production from global aquaculture has increased rapidly from 2.6 million tons or 3.9% of the total supply of fish, shellfish and mollusks in 1970, to 66.7 million tons or 42.2% in 2012 [1]. Capture fisheries have more or less leveled out at about 90 million tons per year since the turn of the century, partly because the exploitation has reached or surpassed the carrying capacity of many major fishery stocks [1,2]. Consequently, future increase of (or perhaps even maintaining) the global fish supply depends on the further growth of aquaculture production. For instance, China, the world's largest producer, consumer, processor, and exporter of finfish and shellfish, produces mainly from its highly expanding aquaculture sector, accounting for approximately 72% of its reported domestic fish production. China alone contributes more than 60% of global aquaculture production volume and roughly half of global aquaculture value [1,3,4]. Aquaculture is the country's fastest growing food sector (5% to 6% annual growth in volume from 2000 to 2012), and its output reached 40 million metric tons (including mollusks, excluding algae) in 2012, four times the production volume in 1990 [1,4]. Vietnam is another Southeast Asian country with a tremendous growth of aquaculture production during the past decade (tripled since 2003), exceeding its capture fisheries [1], and with a need and potential for further expansion [5,6].

Terrestrial farm animal production is almost entirely based on populations or breeds that have been genetically domesticated through millennia and are systematically and selectively bred for improved performance often over centuries. This approach has improved the productivity and resource efficiency of the livestock populations many fold beyond the capacity of their wild ancestors. The development of modern animal husbandry would be impossible without domesticated and genetically improved animals.

Aquaculture probably dates back as far as about 2000 B.C. with the development of pond culture in e.g., East Asia, the Mediterranean and Central America, but aquatic animals have not been through a similar process of genetic domestication and selective breeding as terrestrial farm animal species. Less than 10% of the global aquaculture production is based on genetically improved material from modern breeding programs allowing for control of inbreeding as well as genetic selection [7]. As a result, the majority of aquaculture production is still based on wild type animals that are usually poorly adapted to life in captivity. This situation implies poor growth rates and animal welfare, high mortality, inefficient

use of resources such as feeds, water and energy, and higher cost per kg of fish produced. Farming of genetically improved fish has the potential to contribute significantly to increased supply of fish, including in those regions and countries with significant food security and nutrition challenges.

The two major aquaculture species under domestication worldwide are Atlantic salmon and Nile tilapia (3.1% and 4.8% of the global production) [1], which have been subjected to more than 40 years (10 generations) and 20 years (15–20 generations) of selective breeding, respectively [8,9]. However, most of the production of other important aquaculture species such as carps and other cyprinids (38% of the global aquaculture production [1]) is based on stocks that are not expected to differ largely from wild type animals.

Still, the feed conversion efficiency of many farmed fish species is higher than that of domesticated terrestrial farm animals [7], partly because of lower energy requirements for body thermoregulation. Furthermore, an increasing number of studies show considerable genetic variation and significant heritability for a wide range of performance traits in aquaculture species under farming conditions [10], laying the foundation for rapid domestication and performance improvement of specialized aquaculture stocks through modern selection programs [11,12]. Gjedrem and Thodesen [13] listed 21 estimates of selection response for growth rate in 10 aquatic species, averaging 14% per generation, which is more than double the response normally achieved in breeding programs with already highly domesticated terrestrial farm animals. Highly favourable benefit/cost ratios ranging from 8 to 400 are reported for investments in fish selective breeding programs [14–16].

Consequently, the prospects are good for developing high performing and resource efficient domesticated populations and breeds of aquaculture species that may secure the future supply of aquatic animal products and even outperform traditional farm animals in terms of feed conversion efficiency. The question is why a similar domestication process to that in traditional farm animals has not happened during the history of aquaculture, and what can be done to overcome the lack of progress even today in many farmed species. In the following, this will be discussed in terms of biological and technical constraints as well as social and economic conditions, since technology advances alone seem to be insufficient to promote the necessary progress. The discussion is based on literature studies and on results from interviews with stakeholders, including farmers, breeders and experts from the fish farming industry as well as aquaculture scientists and governmental representatives in Eastern and Southeastern Asia, where most of global aquaculture is located today. Following an established interdisciplinary approach applied earlier [17,18], the paper is structured with an initial section reviewing literature and reports on biological and technical constraints followed by a chapter on the perceived needs and interests of actors in Chinese, Malaysian and Vietnamese aquaculture, which is based on the interviews. In Section 4, we discuss the empirical data and semi-structured key-actor interviews to explore the reasons for the slow adoption of selective breeding technology in aquaculture and what can be done to overcome the challenges identified.

2. Biological and Technical Constraints

2.1. Domestication

Genetic domestication is defined as the result of natural and artificial selection of an animal species to adapt to life in a new environment in captivity. Genetic domestication may involve changes of traits like behavior, mortality, disease resistance, feed requirements and others. A prerequisite for genetic changes from domestication of a species is the closing of the life cycle in captivity and genetic separation from wild progenitor stocks. The captive animals must be able to tolerate the new environment, to mature sexually, to reproduce and to give rise to viable progeny in captivity. This will form the base for the accumulation of both natural and artificial selection effects from generation to generation in the new environment. Unlike terrestrial farm animals, most aquatic species reproduce by spawning gametes into the external aquatic environment where the egg is fertilized, followed by external fetal development. Consequently, the environmental conditions (e.g., water temperature and quality) required for successful reproduction are usually more critical than for mammals and birds. Historically, reproduction in captivity of many farmed aquatic species has been quite unpredictable or not occurred at all, and the use of wild-caught seed for stocking in culture has been widespread. This reliance of wild-caught animals excludes, of course, the closing of the life cycle in captivity and accumulation of domestication and selection effects. Even today, culture systems based on wild-caught animals are not uncommon (e.g., *Penaeus monodon* culture, which relies on brood stock collected from the wild, and, occasionally, ponds filled with water containing natural seed). However, in more recent times, techniques have been developed to induce or synchronize sexual maturation (e.g., hormone treatment, temperature and light control), to strip and fertilize eggs and milt, and to incubate and hatch the eggs in a controlled environment of many aquaculture species [19]. This has provided a basis for domestication and selective breeding in many farmed aquatic animals.

2.2. Inbreeding

A second prerequisite for long-term domestication is to prevent the rapid accumulation of inbreeding in farmed stocks. The great fecundity in most aquatic species [19] makes it possible to recruit an entire new generation of production animals from very few parents, which can result in minimal effective population sizes. On-farm reproduction, without careful management and control of selection of brood fish and mating structure is then likely to result in high rates of inbreeding and deterioration of performance because of inbreeding depression [20]. In many cases, inbreeding has created a need for and a tradition of “refreshing” the stocks with wild-caught breeders to reduce inbreeding depression. However, this breaks the life cycle in captivity and disrupts the domestication and selection processes.

Several measures may be used to control and avoid the accumulation of high inbreeding without sacrificing genetic progress. The simplest technique is to exchange breeders between not closely related farm stocks, as has been a historical practice in terrestrial farm animals in many situations. This approach requires some form of organized exchange between farmers or hatcheries as well as tracking of records of the genetic relationship between farmed stocks, practices that have not yet been developed for most aquaculture species. A similar approach may be applied on-farm, provided that sufficient resources are available to maintain several cohorts of physically separated and not closely related samples of brood

stock that may be used in a rotational mating scheme [21,22]. Another procedure to limit the increase of inbreeding is to carry out single pair mating of a sufficiently large number of outbred parents, (e.g., 50) followed by separate hatching and early juvenile rearing of the progeny full-sib families until survival has stabilized. A restricted number of full-sibs from each family (e.g., 30–50) may then be communally stocked without tagging for rearing of a new generation of breeders before repeating the procedure [23]. Finally, techniques for individual identification of breeding candidates (e.g., external branding or tagging, internal electronic tags, DNA fingerprinting) are now available at reasonable costs, making it possible to maintain ancestry records for each breeding candidate. Appropriate mating plans may then be applied to avoid rapid accumulation of inbreeding [24].

2.3. Selective Breeding

In terrestrial farm animals, long-term on-farm natural genetic domestication and genetic separation from their wild progenitor stocks have formed a base for accumulation of response to artificial selection in the farmed stocks. Based on information about individual performance and pedigree, the best performing individuals have been selected as parents of new generations to gradually improve desired traits for farming purposes, and inbreeding could be controlled at a low level. During the latest century, statistical methods have been developed for more accurate ranking of the breeding candidates according to their additive genetic performance. This has significantly improved the prospects of response to selection.

In aquaculture species with incomplete genetic separation between cultured and wild stocks, it is expected that the gene flow from wild breeders will have counteracted the accumulation of possible response to selection in the cultured stocks. Furthermore, the effective population sizes have probably been too low to avoid rapid accumulation of inbreeding and loss of genetic variation in many genetically closed aquaculture populations. Since additive genetic variation is a major prerequisite for response to selection, inbred populations are expected to respond poorly to selection. Several early studies of mass selection (*i.e.*, selection based on individual phenotypes without control of inbreeding) for increased growth performance in closed fish populations showed no significant response [25–28]. As a result, aquaculture breeding has a history of attempts to identify and maintain well performing ‘pure strains’ and to apply crossing between strains to counteract inbreeding and utilize possible heterosis, more similar to the testing of plant varieties and hybrids in plant breeding than to the process of selection within heterogeneous populations practiced in livestock [29].

Consequently, the establishment of a base population for long-term selection in aquaculture should aim at identifying populations with high levels of heterogeneity as well as optimizing the performance in culture. Using genetic material collected from diverse wild stocks has also proven successful in the major selection programs with Atlantic salmon [30] and in the GIFT (Genetic Improvement of Farmed Tilapias) project with Nile tilapia [31]. Several of the tested wild stocks of Nile tilapia even outperformed material collected from cultured stocks [32]. The further process of selection should then be designed to maintain the genetic variation. This may be done for example by combining mass selection with measures to control inbreeding (see above). However, mass selection may only be used for traits that can be measured on the live breeding candidates (e.g., growth performance), and is less efficient for traits with low heritabilities. Mass selection will often require facilities for synchronized mating of a considerable number of breeding pairs to produce progeny of a similar age for testing, and will also

require management involving facilities for separate hatching and early juvenile rearing of full-sib groups [23] or separate stocking of other genetic groups [21,22] that are normally not available at ordinary grow-out farms.

Furthermore, statistical techniques based on pedigree records that have been developed for estimating breeding values to rank and select livestock have also proven to be effective in aquaculture species (e.g., in Atlantic salmon [8], and in tilapias [9]). The techniques depend on keeping parentage records for all breeding candidates, but they provide more accurate estimates of breeding values and consequently increased response to selection, particularly for traits with low heritability. Furthermore, parentage records increase the possibilities to control inbreeding accumulation. Information about the performance of relatives may also be used to select for traits that may not be recorded in the live breeding candidates (e.g., carcass quality traits). Large-scale parentage assignment routines have been complicated or impossible in most aquaculture species until recent decades. However, the introduction of affordable procedures for individual external or electronic tagging or DNA fingerprinting has made parentage assignment an option in most aquaculture species as well. External and electronic tagging require separate hatching and rearing of full-sib progeny groups until the body sizes are sufficiently large for application of tags.

2.4. Breeding Programs

With these technological advances in reproduction, control of inbreeding and pedigree recording, it is now possible to run commercial scale selection programs for most aquaculture species. However, the facilities and skills needed to control reproduction and maintain pedigree records will make it difficult for average fish farmers to establish on-farm selection programs, as has been the case in the history of terrestrial farm animals. Most aquaculture selection programs today are carried out by specialized nucleus operations that focus on brood stock management and repeated testing and selection of new generations of pedigreed breeders. The best non-selected breeders may then be used by farmers or by dedicated hatcheries/fry producers to supply the grow-out farmers with quality seed. If properly organized, a single breeding nucleus may provide seed or brood fish from the recent generation of selection to a number of such multiplier farms. Because of the very high fecundity in most aquaculture species, the multipliers may then offer genetically improved seed in large quantities to grow-out farmers with only one generation delay compared to the genetic progress in the breeding nucleus.

This three-step model (breeding nucleus, multipliers and grow-out farms) has proven successful in salmonids and tilapias [8,9]. Each step may be operated independently, they may be coordinated by collaborative or cooperative organizations, or they may be fully integrated in a closed, vertical business operation. However, the model has proven to require substantial long-term investments without immediate financial returns to the crucial breeding nucleus part of the operation. Still, Ponzoni *et al.* [15,16] estimated benefit cost ratios (BCR) in the range of 8.5–60 for selective breeding programs for Nile tilapia and 22–420 for common carp when assuming initial investment cost of USD 50,000–100,000 and annual recurrent costs of USD 30,000–90,000. Furthermore, the level of initial investment and annual costs showed a relatively small effect on estimated benefit and BCR in these studies, whereas the effect of the price of fish was substantial.

3. Perceived Needs and Interests of Aquaculture Stakeholders in China, Vietnam and Malaysia

One of the objectives of the present study was to gain knowledge and a greater understanding of the specific causes of the limited use of domesticated and genetically improved animals in aquaculture in Southeast and East Asia [7], where 76% of the global fish, shellfish and mollusk aquaculture production takes place [1].

More specific objectives were to improve understanding about the causes of deficiencies in skill development and training in aquaculture breeding and genetics, specific reasons for aquaculture stakeholders' reluctance to invest in selective breeding programs, the reasons for hatcheries and fish farmers' apparent low demand for genetically improved animals, and finally to make recommendations for overcoming challenges of establishing and managing selective breeding programmes for more productive, efficient and animal friendly aquaculture.

3.1. Material and Methods

This interdisciplinary study combined biological and social sciences using the approach described and applied by Olesen *et al.* [17] and Rosendal *et al.* [18]. This implies a methodology of descriptive and explorative case study within the qualitative domain, which allows more in-depth understanding of factors and mechanisms through multiple observations [33]. Interdisciplinary collaboration, involving both biological and social sciences, was needed to address the complex research questions here. For this, the collaboration with scientists at WorldFish allowed for combining competence on genetics and aquaculture with competence on social and economic analysis, including value chain analyses of the aquaculture sector, policy and institutional analysis for the improved governance of aquatic resources as well as methods for breeding improved farm fish for small-scale and household farmers.

The first author worked at WorldFish for six months in January–June 2012, and met with public and private sector stakeholders in Malaysia, Vietnam and China during this period. The stakeholders were granted the right to be anonymous. The three countries were chosen because they all had established tilapia breeding programs with successful adoptions of genetically improved material in the aquaculture industry, whereas there were few or no breeding programs for other important aquaculture species such as carps, African catfish and marine fish species in these countries [7]. Respondents were recruited for interviewing based on existing networks of the authors and using contact persons in research institutions in Malaysia, Vietnam and China. Stakeholders with different background and nationalities (both Western and Asian) were recruited for the interviews. Note that the method used purposely sampled respondents representing the main sectors of the aquaculture industry in the three countries studied, covering breeding, hatcheries, dissemination, middle men and farmers as well as research, development, education and governmental bodies. A total of 34 persons, including seven women, representing the different stakeholder groups in aquaculture were interviewed about fish farming and breeding with focus on tilapias, carps and catfish. The sample included four policy makers from governmental bodies, 20 persons from research institutions and universities, nine from the hatchery sector, 10 involved in selective breeding companies and seven from the farming sector, with the interviews covering various challenges and obstacles to implementing selective breeding programs for farm fish. Breeding and farming enterprises of different scales were represented including both small farmers and hatcheries as

well as relatively large multinational breeding and farming companies, included an integrated company. Based on the limited number of respondents, this material did not qualify for any quantitative analyses and general conclusions. Hence, it was rather used for exploring and gaining understanding of factors and mechanisms that may affect the interests and needs of the actors in aquaculture breeding and farming.

In depth semi-structured interviews using mainly open-ended questions presented in different questionnaires or interview guides were designed for three different categories of actors, *i.e.*, farmers, hatchery operators and academic staff, were applied. Questions were asked about: personal background and organization; farm, hatchery and breeding characteristics; strategies; practices; market; costs; willingness to pay (WTP) for genetically improved seed and perceived limitations, challenges and interests as well as recommendations. Native interpreters with professional background assisted in the interviewing of non-English speaking persons.

3.2. Results

3.2.1. Public Policies

It was clear from the interviews that seed quality is a prioritized area of development in aquaculture by Government in China, Malaysia and Vietnam. In China, long-term funding of breeding programs has been an implemented policy since 2008 [34] through, for instance, approval of annual reports rather than demanding processes with proposals for breeding projects lasting for only three to five years. Governments in China and Vietnam also recognize the need for public funding of fish breeding programs according to the governmental officers and researchers interviewed. As a result, several selective breeding programs have been established in these two countries in recent years, including carps, shrimp, river catfish and tilapia. Respondents in China commented on the resulting significant improvements for research institutions in receiving funding for fish breeding projects in recent years. Still, a higher number of breeding programs were identified in tilapia (>9) than in carps (4) and catfish (1) in these countries. The higher number of breeding programs for tilapia may be due to the successful development and worldwide dissemination of GIFT tilapia [9,21]. However, attempts to mimic the GIFT success by international projects on selective breeding in common carp during the last decade have not yet resulted in the same positive development. Public support of hatcheries for disseminating subsidized improved seed is further carried out in all three countries studied here. This support reflects governmental policies to increase access of farmers to improved seed quality in aquaculture in both Vietnam and Malaysia. In addition, new high-value, often marine species more suitable for export markets are given priority by the governments for development in these countries, whereas lower value species serving domestic markets, such as carps in China and African catfish in Malaysia, get less attention and support according to some respondents. In Malaysia, a tilapia breeding program has been operated through the public support of Malaysia and EU, via WorldFish, since 2001. Apart from that, a public research and development program aims to support private sector initiatives in seed genetic improvement, and optimism about the private actors' possibility to establish and manage aquaculture breeding programs was expressed by a governmental representative. Here, public-private cooperation through support of private industry developments is the main strategy. However, to our knowledge no private operation of selective

breeding program has taken place in Malaysia so far, but some farming relies on imports of seed originating from such family based selective programs abroad, which are run by multinational companies.

3.2.2. Human Resources

In all countries, shortage of human resources, competence and skills in selective breeding was noted as a major challenge to develop breeding programs by the respondents. Insufficient training and competence in selective breeding and its benefits at all levels from farmers' education and training programs to universities was emphasized. This is considered to be a general feature in agriculture in developing countries, and may not be special to aquaculture breeding. However, in both China and Vietnam, funding programs for students to carry out M.Sc. and Ph.D. studies abroad are available. Asian students' lack of skills in the English language, partly due to limited language education in primary school, was, however, mentioned as a relevant challenge, and motivated students often failed to pass English language tests when applying for such fellowships. As we know, Asian students and scientists may be very competitive in other fields such as Information and Communication Technology (ICT), and this result may be a consequence of weaker recruitment to agriculture and aquaculture universities and study programs. It was also pointed out by a respondent that agricultural universities are less popular among students than other universities and study programs.

To our knowledge, textbooks on selective aquaculture breeding are also not available in, for instance, Mandarin and Vietnamese. In Malaysia, English is a lesser constraint at the university level.

In China, collaboration in breeding projects was reported between agriculture university staff and scientists in research institutes serving the aquaculture industry. In both Vietnam and Malaysia, such collaboration was absent and missed by respondents representing both governmental body and research. Competition among actors seemed to reduce the motivation for cooperation and joining efforts to achieve synergies and support aquaculture development. This challenge might explain failures to succeed in establishing breeding and dissemination in more than one example reported by respondents.

3.2.3. Business Strategies and Challenges

The farmers interviewed, including tilapia, carp and catfish farmers, expressed high demand for genetically improved seed and wanted to see the same improvements in carps and catfish as obtained in Nile tilapia. However, it was also noted by farmers, breeders and scientists that there will be a need for more than three years or generations of selection to obtain the significant genetic gain needed to demonstrate and convince more farmers and hence hatcheries to pay a price premium (or royalty) to the nucleus breeding program. The willingness to pay (WTP) a price premium for improved seed with respect to growth and survival among the very limited number of farmers in this study was in the order of 20%. These farmers' stated WTP, which we do not claim to be representative for all farmers in this region, varied substantially between 10% and 100%. It was suggested by respondents that providing farmers free test samples of genetically improved seed, or by other means demonstrate the fish superior performance directly to the farmers, may be necessary to increase farmers' demand and willingness to pay for genetically improved seed.

However, some respondents considered private actors and investments in fish breeding as realistic in future when breeding program, infrastructure and markets are more firmly established, as we can see in the salmon industry today.

It was noted by a respondent that it may be hard for private breeders to reap these economic benefits from carp breeding due to the common and traditional production system and lack of trust and confidence in the improved material and perhaps in new actors of breeding and seed supply.

DNA technology was not considered important for improving the marketing of seed or crucial for establishing breeding programs today by most respondents representing the breeding sector. It was, however, mentioned by some that it may become more important when the breeding sector is more developed as already documented for Atlantic salmon in some European countries.

4. Discussion

4.1. Human Resources

Among fish farmers and aquaculture researchers in the major aquaculture countries, the basic skills needed to induce and synchronize sexual maturation and carry out single pair mating and separate hatching and rearing of progeny full-sib groups now seems to be well established for the most important freshwater aquaculture species and many marine species. Consequently, the life cycle in captivity may be closed, the farmed populations may be genetically isolated from wild stocks, and the process of accumulation of genetic domestication may be started. However, the technical knowledge needed to control the accumulation of inbreeding and to carry out efficient artificial selection for improved performance in culture still seems to be scarce in the aquaculture community. Still, within the three countries studied, there may be well-trained individuals or groups with expertise in breeding programs methodology for traditional farm animals, for example at agricultural universities. Most successful aquaculture breeding programs today are the result of combining skills from fish biology and farming, with farm animal breeding technology, both within and across countries [35].

In order to compensate for the shortage of human skills and competence, cooperation and efficient management of the qualified staff available becomes crucial and creates opportunities for improvements in efficiency. Synergies from cooperation within research, development and teaching at university level could be obtained through for example incentive programs for cooperation projects and by exchange of staff through, for instance, adjunct professor, senior scientist and expert positions (e.g., minor adjunct positions of 10%–20% position) at universities and research institutes, respectively. Further, benefits of the frequently seen assignment of the limited number of highly qualified scientists with doctoral degrees in genetics and breeding to administration positions rather than continued work in research and development can be questioned. This practice, which is not unique to the field of genetics and breeding, may, however, give less or slower progress in science, development, as well as in innovation and implementation of aquaculture breeding. Furthermore, training of farmers and hatchery operators to improve their understanding about selective breeding and the associated benefits should be increased to facilitate more dissemination and farming of genetically improved fish, as aimed at by all the countries studied through, for example, public support of breeding for improved seed quality and dissemination of seed.

4.2. *Initiation of Breeding Programs*

Aquaculture in Asia, and particularly in China, involves a large variety of species compared to terrestrial livestock production, where just a limited number of domesticated species are being farmed. Hence, the need for prioritizing a limited and manageable number of aquaculture species for domestication and selective breeding is crucial. This was considered as a challenge by respondents in China and also stressed by Gjerde and Su Xiaowen [36].

Starting a selective breeding program should then focus on expected benefits of e.g., faster growing fish with higher survival rates and the costs, by improving the aquaculture species in question. Because of the great fecundity of most aquaculture species, a single, well-organized breeding nucleus may supply a huge market with continuously upgraded seed by delivering selected brood stock to a number of multiplier farmers after each generation of selection. Consequently, the running costs of the breeding programs will be more or less constant and independent of the volume of the target industry. The benefit/cost ratio will then often depend more on the volume of the target industry than on the price of the end product, both from the consumers' point of view and from a private business point of view. The total impact of an aquaculture breeding program on food supply and resource efficiency for the society will usually be greater for a large volume species. Furthermore, a small premium on genetically improved seed for a large production volume of a low value species may easily generate more income for a breeding program aiming at seed sales than a higher premium on a limited volume of seed for production of an exclusive and highly priced species. For larger integrated enterprises this may not always be the case. For China and Vietnam, common carp was identified as a prioritized carp species for genetic improvement in 2001 [37]. Common carp constitutes 12.6% of the total volume of cultured freshwater fish in China [1]. Substantial response to selection for improved growth rate has been reported [38]. Selective breeding of common carp accompanied with a well-functioning dissemination program and infrastructure has been shown to be particularly profitable with benefit cost ratios (BCR) between 22 and 420, due to the high reproductive capacity of the species [16].

The start of a selective breeding program will require a heterogeneous base population, because genetic variation is a prerequisite for response to selection. If there is access to a sufficient number of breeding candidates (e.g., 1000 individuals or more) from a well performing and documented heterogeneous genetic source, performance testing and selection (pedigree based selection or mass selection modified to control inbreeding) may be started directly [24]. Otherwise, the genetic variation may be secured by collecting genetic material from a variety of sources. For previously undomesticated species, collecting samples of genetic material from viable and numerous wild stocks of diverse geographic origin has proven successful e.g., for Atlantic salmon [30] and Nile tilapia [31].

Techniques and facilities should then be established for a minimum of 100–150 synchronized single pair matings, followed by separate rearing of full-sib progeny groups until tagging and then individual tagging of all breeding candidates (alternatively parentage determination by DNA fingerprinting). A couple of generations of systematic crossing of breeders of different genetic origin before selection is applied is also recommended to preserve genetic variation within the new, mixed population [31]. Furthermore, a few generations of accumulated response to selection may often be needed to prove the benefits of genetically improved seed to the grow-out farmers and stimulate the willingness to pay a premium.

This entire start phase will evidently require substantial investments without immediate returns. Experiences from salmonids and tilapias suggest a minimum investment period of six to ten years depending on the generation interval of the species. Apart from large integrated companies, it is obvious that most Asian fish farmers do not have the necessary resources to establish private on-farm domestication and selection programs, as has happened during the domestication history of traditional farm animals. Fish farmers' cooperatives or associations may be a tool to initiate breeding programs for key species in the member farms, provided that they are given proper training and professional support. It has been shown that technology improvements with e.g., improved seed quality may contribute to tremendous benefits to a society of small scale farmers [39]. Important success criteria identified from aquaculture development projects involving collective action in Indonesia (Aceh), India and Bangladesh were: common burning issues among farmers (drivers such as poor yields, disease problems, environmental constraints or other constraints that would gain the most from the provision of consistent and relevant improvement); farmer-oriented services, comprising local teams with technical and organizational skills; and collective action through group approaches to reach large numbers of farmers [39]. Economies of scale and knowledge transfer are advantages of collective action, and experience does suggest a good business case for investing through cooperatives and other producer organizations although both group organization and capacity building take time [39].

So far, however, specialized research facilities and substantial national or international public funding has often been necessary during this early phase of domestication programs with a new species. Private investors tend to await the results of the initial efforts and the reaction of the seed market before investing in commercial selection programs. However, recent examples from China of privately funded and successful domestication and selection programs have been reported for new short generation species like red tilapia and blue tilapia [40,41]. Still, as indicated by some interview respondents, it is likely that access to public funding and support will be necessary in the future as well to initiate domestication and selection programs with new species in Asia, in particular for species with longer generation intervals like carps.

4.3. Accumulation and Dissemination of Genetic Progress

Once a selective breeding program is established and operative, plans should be made to obtain long-term sustainable continuation of generation-by-generation accumulation of selection response. Long-term biologically, ecologically and sociologically sound breeding goals are important for sustainable animal production [42]. Such breeding plans should therefore include strategies for generating income to cover the running and development costs of the breeding program and strategies for broadening the breeding goal beyond the common initial short-term goal of improving growth rate.

In the early days of modern selective breeding programs for terrestrial farm animals, it was anticipated that selection limits would be reached quite soon for the traits selected for (e.g., egg production [43]). However, after more than 50 years of intensive selection, substantial response is still maintained in farm animal selection programs, and the average performance of modern farm animals exceeds by far the performance of the most extreme animals in the ancestor populations. This may mainly be explained by the nature of polygenic inheritance [44] and in the longer term also by new mutations [45]. Consequently, aquaculture breeding programs that want to stay in business will have to market genetic material that is

continuously upgraded by new generations of selection. During the early phase of Atlantic salmon farming in Norway, most of the grow-out smolt originated from a single, publicly supported selection program [8]. Today, several large scale, commercial selection programs are competing internationally with their latest generation of selected genetic material. A similar development may be emerging for Nile tilapia selection programs [9].

According to interview respondents, supporting dissemination of genetically improved seed is considered a governmental policy in all of the three countries. Nevertheless, the costs of maintaining and further developing aquaculture selection programs will probably in most cases eventually have to be paid by the grow-out industry, where the benefits of improved production efficiency and product quality are realized in terms of increased profitability on the sales to consumers. Given the very high benefit to cost ratios for investments in selection programs (see above), the premium needed on the price of seed will be marginal, in particular for species with large production volumes. The major problems seem to be to convince grow-out farmers that repeated supply of seed from a well-operated breeding program is worth a premium, and to ensure that the premium flows back through the multiplier farms to cover the costs of the breeding nucleus [17].

A proven method to stimulate the demand for genetically improved seed has often been to offer free test samples to be stocked on-farm in a separate pond or cage along with the genetic material that is commonly used by the farmer. The benefits of using seed from a selection program have then often been obvious without scientific comparisons and have caused a boost in the demand. More scientific approaches have also been used, for instance, when GIFT tilapia was distributed to several Asian countries for testing [46]. It may also be useful to offer training courses to targeted farmers to increase the awareness of the effects on productivity of selective breeding and the importance of always using the latest generation from the selection program.

It was also noted by several interview respondents that western investors in aquaculture selection programs have found it difficult to access Asian seed markets. This was perceived as ‘a lack of sound business culture and practices’ by one European respondent. This perception may however also be due to unfamiliarity with local customs. Guanxi refers to a Chinese system of doing business on the basis of personal relationships and is representative of the business culture throughout much of the non-western world. For example, business partners may be chosen based on personal relationships, and this approach may influence the partnerships available for enterprises in Southeast Asia [47,48] in developing selective breeding in aquaculture. Such challenges were indicated by respondents representing both research, innovation and private breeding. Informal or personal long-term relationships (rather than contractual) are particularly important in Asian countries [47–49]. Such relationships may also be nurtured in aquaculture to provide mutual benefits to both parties in the form of stability, predictability and access to information and technical assistance [50,51]. Such conditions include an information-rich business environment in which fear of losing one’s reputation for trustworthiness is a strong deterrent to unfair business practices. Lovett *et al.* [47] pointed out how eastern and western business practices may already be converging toward systems based on more complete models of trust to deal with the conditions of progress coupled with uncertainty that form our new economic reality. According to Lovett *et al.* [47], dealings among acquaintances rather than relatives (as traditionally in rural China) are becoming more common among urban Asians. As acquaintances can be selected on the basis of ability, there may be a trend towards a more western way of choosing business partners in Asia as it grows [47]. A

corresponding trend has been observed in the Western business practises towards a more complete trust including attachments and considerations of ability. Younger and female Asian respondents in the current study also requested more emphasize of abilities and competence than relationships in research and development in aquaculture, which may reflect a shift in the Asian culture of choosing partners.

A common problem in the early phase of many selection programs, in particular programs based on public funding, is that the funding is insufficient to develop the necessary network of professional and dedicated multiplier farms [8,21,52]. Instead, the programs may have to rely on agreements or contracts with existing hatcheries and seed producers to use selected brood stock from the selection program to produce and market genetically improved seed to the grow-out farmers [17]. The hatcheries may be public, cooperative or private, and often have their own agendas. Because the premium that the grow-out farmers pay for the improved seed has to be claimed by the multiplier farms as a part of the price of the seed, the selection programs may be left dependent on the multipliers' willingness to share their increased profits with the operators of the selection program in terms of royalties, extra price on the brood stock, or other means of reward. As the grow-out farmers gain positive experience with genetically improved seed, resulting in an increased demand and willingness to pay a premium, the multipliers have sometimes seen an opportunity to reap large, short term profits by avoiding paying their dues to the selection program. This situation will however leave the further operation of the selection program short of income. In some cases, this has resulted in lack of continuity of selection and (or) dissemination that has deprived the grow-out farmers of several generations of genetic progress [52]. It has also happened that multipliers that experience a rapidly increasing demand for the improved seed are tempted to use any available, unselected brood stock to scale up their seed production, thus harming the grow-out farmers' confidence and the reputation of the genetic quality of the seed from the selection program [53]. This has increased the awareness of selection program operators about the need for control and monitoring of collaborating multiplier farms. Hussain *et al.* [54] recommended introducing a quality certificate to regulate the relationship between a carp selection program and collaborating hatcheries in Bangladesh. In Ghana, all tilapia material used since 2011 should, according to government recommendations, come from the genetically improved Akosombo strain, to control the quality and health of tilapia seed as far as possible [53]. Here, a number of hatcheries were to be selected and approved by the Government for multiplying and disseminating the Akosombo strain. Anyhow, the early phase of new selection programs should be sufficiently funded to include the operation of dedicated, integrated multiplier farms for direct sales of genetically improved seed to the grow-out industry. For similar reasons, private selection program operators tend to move towards integrated selection and multiplier solutions, where the premium paid on the genetically improved seed will go directly to the integrated operation. In some cases, as also commented by respondents in this study, private breeding companies choose to go for full, vertical integration of selection, multiplying and grow-out farming operations, which implies that only the grow-out farms that are owned or contracted by the operator of breeding nucleus will gain access to the improved genetic material. This will often mean that the production potential of genetically improved seed is not fully exploited, and consequently results in a reduced impact of the selection program on the total grow-out industry. As also noted in these interviews, other selection programs, including public funded actors, have signed contracts with feed companies to increase their funding. By this, the feed companies can offer free or subsidized genetically improved seed as part of their marketing of the feed to farmers. One reason for private breeding companies to

avoid selling their improved seed on the open market is that the seed may easily be reared and used as brood stock by unauthorized hatcheries that may compete with the breeding company on the seed market without having to pay the costs of a selection program. Possible mechanisms for introducing legal intellectual property rights protection of selectively bred aquaculture populations have been discussed and found difficult to implement [55]. However, Atlantic salmon breeding companies seem to be less occupied by the need for legal protection, other than material transfer agreements, than by the competitive advantage of offering the best quality genetic material and the best customer support [17]. Seed produced by unauthorized ‘piracy’ of commercial genetic material from a selection program will often lag behind with as much as two to three generations of selection compared to the material supplied directly from authorized multipliers, and this may easily result in 20%–30% loss in performance [13]. This should normally be a sufficiently large difference to encourage properly informed grow-out farmers to avoid unauthorized genetic material.

Finally, planning for long-term domestication and genetic improvement of performance by selective breeding of aquaculture stocks is not only a question of securing sustainable funding of the operation of the breeding programs. Until now, most breeding programs have focused their breeding goal on increasing the average growth rate or the body weight at harvest, a trait of great economic importance for the grow-out farmers that may easily be recorded in the breeding nucleus and that responds well to selection. However, the evolvement of Atlantic salmon breeding programs has been accompanied by a gradual expansion of the breeding goal to include traits such as those related to sexual maturation, product quality and disease resistance [8]. This has happened as a response to the needs of the grow-out industry and the increased competition between breeding companies on the smolt market. The recent inclusion of resistance to salmon lice in the breeding goal for several salmon breeding programs may be an example of a trait with severe environmental and ethical aspects considered most important by Norwegian public to select for [56]. Most likely, the future seed market for other aquaculture species will request genetic material that is selected for other traits in addition to growth rates. In many Asian countries (e.g., China), aquaculture systems are intensifying as producers seek higher returns on scarce land, water, and coastal zone resources [3]. Such intensification often implies higher stocking densities and growth that may stress the fish and increase the disease problems. Hence, disease problems and other emerging concerns related to feed efficiencies and resilience to environmental fluctuation, become of interest in genetic improvement. Fish disease is a major cause of economic losses and fish welfare problems in aquaculture. This intensification is expected to continue to a large extent. The most significant disease causing losses in tilapia culture is *streptococcosis*. Worldwide losses from the infection have been estimated at \$150 million in 2000 and more than \$250 million in 2008 [57]. Selection to improve the genetic resistance against the disease has the potential for significant economic impact for grow-out farmers. Breeding programs that want to contribute to the future genetic development of aquaculture stocks will consequently need to constantly evaluate the breeding goals of their selection program and to be involved in continuous upgrading of the selection procedures.

5. Conclusions and Recommendations

The biological and technical constraints that have probably prevented fish farmers from developing domesticated and genetically improved aquaculture stocks during the history of fish farming have

gradually been solved during recent decades. It is now possible to run commercial scale selection programs for most aquaculture species, and thus considerably improve the production efficiency (growth rate, survival), the product quality, and the animal welfare in the remaining 90% of the global aquaculture production that is still based on largely wild type genetic material.

However, the implementation of selective breeding in aquaculture is progressing slowly. The technology is too resource demanding for small scale, on-farm initiatives, and requires interaction between specialized operations. Based on interviews and literature review during this study, it was concluded that the adoption of selective breeding programs in commercial aquaculture in Eastern and Southeastern Asia will often depend on long-term public commitment in collaboration with cooperative and private interests to resolve several key issues:

- Financial support of the breeding nucleus operation will usually be needed, at least during the initial five to ten generations of selection, and, in particular, for species with long generation intervals. The early phase support should prioritize established aquaculture species with large production volumes, such as carps, that are not easily subject to investment from private breeders due to long generation interval and delayed profit.

- Training of more people in selective animal breeding technology should be prioritized at all levels, including government officers, university staff, breeding nucleus operators, hatchery operators, and grow-out farmers. Collaboration between different research groups in genetics (institutes and universities) and scholars within the fields of aquaculture and livestock breeding should be encouraged.

- If the private sector is expected to engage in selective breeding and genetic improvement of aquaculture stocks in less prosperous economies, development of appropriate business models are probably more important than legal systems to ensure fair benefit sharing between the breeding, multiplier and grow-out operators. Research is also needed to incorporate private breeders, cooperatives and small-scale farmers into traditional and ‘guanxi’ business management. Experience suggests opportunities for investing through cooperatives and other producer organizations.

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Author Contributions

Conceived and designed the surveys: IO RWP. Conducted field-work: IO. Analysed the data: IO HBB RWP. Wrote the paper: IO HBB MP RWP.

Conflicts of Interests

The authors declare no conflict of interest.

Appendix

A. Questionnaires

A.1. Questionnaire for Fish Farmers

Personal information

1. What is your role/position?
Farm owner, Farm operator/manager
2. If employed by company/institution, is your organization (employer) profit, non-profit, public, private, cooperate, MNC, large national, SME, research
3. Name of organization, employer, location
4. What is your background (education, training and work experience)?

Farm characteristics

5. What fish species is (are) being cultured on your farm?
How important is the production of these species in your country or region (percent of total aquaculture production)? <20%, 20%–50% , 50%–80% or >80%
6. What is the total production on the farm?
Big (tonnes per year), medium (tonnes per year), small scale (tonnes per year), household farmers (kg per year or number of fish with average size)
7. Is the farming full time work?
Or part time work combined with other household income?
Is more than 50% of production on the farm sold?
8. What is the annual turnover (sales from production) on the farm?
(Figures in currencies representing low, medium and large farm with options to check appropriate interval).
9. What are the annual running costs (USD), and what are the main cost factors (e.g., labour, feed, power)? (to reveal whether it is intensive (high input) or extensive (low-input))
10. Did you have disease outbreaks last years?
11. What type of feed is used?

Fish Breeding

12. How was/is the fish or seed of your breeders accessed?
Own breeding (integration), from private hatcheries, from public hatcheries, from middle men.

From hatchery every year, from hatchery every second year, from hatchery more than two years ago, from wild fish population last year, from wild fish population two years ago, from wild fish population more than two years ago

13. If you carry out fish breeding and reproduction on your farm, how is this carried out?
Mass spawning, pair matings, artificial mating
14. Do you select brood fish yourself? If so,
for how long has your current fish population been selected (no. of generations and years of selection)?
How many broodfish do you select?
What trait(s) do you select for and how is the trait measured or recorded?
Body weight, other, please specify
Measured by scale or visually
Why were these chosen?
15. What are the main challenges and problems for breeding the fish today?

Fish seed

16. How is/was the fish seed disseminated to you?
As sexually mature brood fish, fingerlings, fertilized roe
17. What is the price of fish seed?
18. What is the price of harvested fish ex farm (price to farmer)?
What is the harvest weight?
19. What are the costs of the seed in percentage of all costs?
20. What quality or traits do you consider most important? Is price most important?
21. Are you interested in genetically improved fish? Is it easy or hard to provide genetically improved seed of your interest?
22. What characteristics of the seed would you prefer? Please assign which characteristic you prefer the most and least of the following (1–7):
All male, genetic quality (higher growth, survival, carcass yield, disease resistance), standardized size, price, service, education/training, DNA information or technology
23. Are there more than one competing hatchery or middle man, and how competitive are they with respect to price, quality and service? Are these public, private or cooperative programs, owned by non-profit or profit organizations?
24. What price premium are you willing to pay for seed giving 20% faster growth?
<10%, 10%–20%, 20%–30%, >30%
25. What price premium are you willing to pay for seed requiring 20% less feed to reach harvest size?
<10%, 10%–20%, 20%–30%, >30%

26. What price premium are you willing to pay for seed with higher disease resistance such that the survival is increased with 20%?
<10%, 10%–20%, 20%–30%, >30%

Recommendations

- 27 What are your recommendations to governmental bodies, other public organizations and private actors and/or investors to facilitate new breeding programs and to increase dissemination and marketing of genetically improved fish to farmers?
- 28 Other comments?

A.2. Questionnaire for Hatchery Operators

Personal information

1. What is your position?
2. Name of Organization, employer, location
3. Is your organization (employer): Profit, non-profit, public, private, cooperate, MNC, large, national, SME, research, industry
4. What is your background (education, training and work experience)?

Breeding program

5. For what species is (are) the hatchery operating and disseminating in your jurisdiction or country?
How big is the grow out production of these species in your country or region? <20%, 20%–50%, 50%–80%, or >80%.
6. How was/is the fish or seed of for your breeders accessed?
Species?
From external breeding program every year, from external breeding program every second year, from external breeding program more than two years ago, from wild fish population last year, from wild fish population two years ago, from wild fish population more than two years ago
7. What breeding strategy do you apply?
Mass spawning, pair matings, artificial mating, crossing of different strains
8. Do you select brood fish? If so,
For how long has your fish population been selected (no. of generations and years of selection)? How many broodfish do you select? What trait(s) do you select for and how is it recorded/tested? Body weight, other, please specify, why were these chosen?
9. How many families are produced and selected among in your breeding population?

10. Are you applying any DNA technology or chromosome manipulation in your breeding program?
If not, would it be useful, and if so how/why?
11. How big is the genetic gain of your fish per generation and/or year (if available)?
12. How is the breeding program being funded or supported today?
Through income from sales only
Public support only
Through both sales and public support
13. How big are the investments made for the current breeding/selection operation (USD)?
14. What are the annual running costs (USD), and what are the main cost factors (e.g., labour, feed, power)?
15. How much are you willing to pay for seed/breeders giving 20% faster growing fish in the farms while the other traits are not changed?
<10%, 10%–20%, 20%–30%, >30%
16. How much are you willing to pay for seed/breeders requiring 20% less feed to reach harvest size in the farms while the other traits are not changed?
<10%, 10%–20%, 20%–30%, >30%
17. How much are you willing to pay for seed/breeders with higher disease resistance such that the fish survival at harvest on the farm is increased with 20% while the other traits are not changed?
<10%, 10%–20%, 20%–30%, >30%
18. What are the main limitations, challenges and problems for running the hatchery today?

Dissemination program

19. How are the fish disseminated to the farmers, through other hatcheries, middle men or direct to farmers? What infrastructure is needed for this?
20. How is the fish disseminated?
As sexually mature brood fish, Fingerlings, fertilized roe.
21. What are the costs of the dissemination?
22. What is the price of fish seed to grow out farmer?
23. How many fry are disseminated per year?
To how many farms or other hatcheries do you disseminate?
24. What type of grow-out farmers buy your seed?
What is their training/education, intensity (high or low input) and technology level?

	Percentage of customers	Education	Intensity/technology
Big

Medium,
Small scale
Household farmers

25. What quality or traits are the farmers requesting most? Is price more important to farmers?
26. How big is the demand from farmers? Is it easy or hard to market the genetically improved seed? Is all produced seed sold?
27. What would make it easier to market the seed? (e.g., all male, quality, standardization, price, service, education/training of middle men and farmers), DNA information or technology)
28. Are there competing hatcheries, and how competitive are these with respect to price, quality and service? Are these public, private or cooperative programs, owned by non-profit or profit organizations?
29. What price premium would you expect that farmers will pay for seed giving 20% faster growth?
<10%, 10%–20%, 20%–30%, >30%
30. What price premium would you expect that farmers will pay for seed requiring 20% less feed to reach harvest size?
<10%, 10%–20%, 20%–30%, >30%
31. What price premium would you expect that farmers will pay for seed with higher disease resistance such that the survival is increased with 20%?
<10%, 10%–20%, 20%–30%, >30%

Recommendations

32. What are your recommendations to governmental bodies, other public organizations and private actors and/or investors to facilitate new breeding programs and to increase dissemination and marketing of genetically improved fish to farmers?
33. Other comments?

A.3. Questionnaire for Academic Actors

Personal information

1. What is your position?
2. Name of Organization, employer, location
3. Is your organization (employer) profit, non-profit, public, private or cooperate (MNC, large national or SME), research or industry?
4. What is your background (education, training and work experience)?
5. How did you get your education and training?
For example how was it funded?

6. Why did you choose this field of education and training?
7. Do you find your education useful for your current work?

Breeding program

8. For what species is (are) the fish breeding program(s) operating in your jurisdiction or country?
How big is the production of these species in your country?
9. How was the breeding program(s) established? Who took the initiatives and why? How was the upstart funded?
10. Who were the owner(s) and how was the program managed and organized in the first generations of breeding?
11. How big was the investment made to get it up and running?
12. For how long has the program been running (no. of generations and years of selection)?
13. Who are the owner(s) and how is the program managed and organized during the last generations (e.g., private, public, cooperative)?
14. What type of testing and selection strategy is applied and what causes the possible limitations?
15. How was the fish or seed of the base population accessed?
16. How many families are produced and tested in the nucleus breeding population?
17. What traits are recorded and selected for? Why were these chosen?
18. Are you applying any DNA technology or chromosome manipulation in your breeding program?
19. How big is the genetic gain per generation and/or year (if available)?
20. How is the program being funded or supported today?
21. How big are the investments made for the current operation (USD)?
22. What are the annual running costs (USD), and what are the main cost factors (e.g., labour, feed, power)?
23. What are the main challenges and problems for running the program today?

Dissemination program

24. How are the fish disseminated to the farmers, through hatcheries or direct to farmers? What infrastructure is needed for this?
25. What are the costs of the dissemination?
26. What is the price of fish seed to grow-out farmers?
27. How many fry are disseminated?

28. Who are the grow-out farmers buying the seed? Big, medium, small scale or household farmers? What is their training/education, intensity (high or low input) and technology level?
29. What quality or traits are the farmers requesting most? Is price more important to farmers?
30. How big is the demand from farmers? Is it easy or hard to market the genetically improved seed? Is all produced seed sold?
31. What would make it easier to market? (e.g., all male, quality, standardization, price, service, education/training of actors (hatchery operators and farmers), DNA information or technology?)
32. Are there competing breeding programs, and how competitive are these with respect to price, quality and service? Are these public, private or cooperative programs, owned by non-profit or profit organizations?

Recommendations

33. What are your recommendations to governmental bodies, other public organizations and private actors and/or investors to facilitate new breeding programs and to increase dissemination and marketing of genetically improved fish to farmers?
34. Other comments?

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