Enhancing fish performance in aquaculture

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Implications

- Aquaculture is the fastest-growing global agricultural industry as a result of advances in fish genetics, nutrition, feeds, culture systems, and management.
- The genetic and phenotypic diversity of fish has been capitalized to yield rapid gains in aquaculture production through a coordination of genetics, nutrition, and management such that aquaculture now produces more than half of the fish consumed by humans globally.

Key words: culture systems, genetics, management, nutrition

Introduction

The Food and Agriculture Organization of the United Nations defines aquaculture as farming of aquatic organisms including fish, mollusks, crustaceans, and aquatic plants where farming implies some form of intervention in the rearing process and individual or corporate ownership of the stock being cultivated (FAO, 1988). In a recent report, the Food and Agriculture Organization emphasized the importance of enhancing aquaculture production to meet the daunting challenge of feeding a global population expected to reach 9.6 billion people by 2050 (FAO, 2014). At present, increases in fish production globally outpace population growth, largely due to important advances in aquaculture production. As a result, aquaculture now produces more than half of the fish consumed by humans and is projected to increase to 62% by 2030 to meet increasing demand (FAO, 2014).

Although various types of technologies have been examined to improve fish growth and performance, productivity largely depends on interactions among genotype, nutrition, and environment. Significant advances in fish genetics, nutrition and feeding, culture systems, and management have cumulatively enhanced fish performance and increased overall global productivity. Technological advancements in these areas that enhance fish performance in aquaculture are discussed in this review.

Fish Genetics

Unlike terrestrial livestock, aquaculture covers a broad range of species with unique genetic makeup and environmental requirements. The genetics and biology of fish provide some distinct advantages over terrestrial livestock production. Fecundity is typically very high in cultured fish species (e.g., 10,000 eggs/kg for salmonids), and the process of fertilization can often be controlled. The external fertilization of fish eggs allows for a high degree of genetic manipulation, from selective crosses, to hybridization, to chromosome set manipulation, and gene transfer.

Domestication

Domestication of fish species lags behind that of terrestrial livestock, which have been kept in captivity for thousands of years. The process of domestication is itself a potent performance enhancer. In aquaculture, both natural selection for overall fitness and directional selection for improved production and behavioral traits occur, creating populations of fish better adapted to the production environment. It can be argued that fish species from the earliest aquaculture enterprises have reached some level of domestication, which has, in turn, led to their success as commercial aquaculture species. These include several species of carp, first cultured more than 3,000 yr ago, and a handful of species whose commercial production began fairly recently (mid- to late 1900s), including Atlantic salmon, rainbow trout, tilapia, and channel catfish. The high fecundity of fish leads to a high level of genetic variation, which provides for relatively rapid domestication under controlled environmental conditions.

Breeding programs

Selective breeding programs for food fish are a relatively recent endeavor for improving fish performance, and the number of breeding programs has increased substantially in the past 20 yr, particularly in Atlantic salmon, rainbow trout, channel catfish, and tilapia. These programs now play a critical role in the enhancement of fish performance, leading to higher overall production and economic gains. Given the high degree of genetic variation observed in wild fish populations, there is extraordinary potential for rapid gains through selective breeding. Even so, it was estimated that less than 5% of global aquaculture production comes from scientifically managed breeding programs (Gjedrem, 2005).

Selective breeding exploits the high level of genetic variation associated with many of the production traits of cultured fish. For most selection programs, growth enhancement is the priority, as it is easily quantified and highly heritable. For new aquaculture species, it is becoming increasingly common to have some type of selection involved early in the domestication process, typically for improved growth and yield. Estimated gains in the Norwegian Atlantic Salmon program are between 8 and 10% per generation (Gjoen and Bentsen, 1997).

While mass selection for growth traits can be effective, sophisticated breeding programs rely on family selection to minimize inbreeding. Of course, this requires that family units be easily identified, either through physical separation or tagging. For programs such as GIFT (Genetic Improvement of Farmed Tilapia), this is accomplished by maintaining genetically distinct breeders in hapas, fixed net enclosures within ponds. These simple structures are ideal for spawning tilapia, as they require little investment and allow for easy fish handling, making them suitable for use.
in family selection programs in developing countries. The GIFT program proved successful in enhancing the performance of Nile tilapia, demonstrating a more than 80% improvement in growth performance after five generations of selection (World Fish Center, 2004). The GIFT program is now on its 20th generation of selectively bred tilapia and has been disseminated to 16 countries on five continents. The program boasts almost 10% improvement per generation and suggests there are no signs of this level of improvement decreasing. Now, new research frontiers are ongoing to enhance other economic traits, such as salinity and temperature tolerance, flesh characteristics, and feed conversion (World Fish Center, 2015).

DNA markers, such as microsatellites and single nucleotide polymorphisms (SNP), have also become an important part of modern breeding programs. This technology allows for parentage determination and pedigree construction. Utilization of family selection and DNA markers has contributed to the dominance of Atlantic salmon in the global aquaculture industry. General claims from the Atlantic salmon industry are that over the past 40 yr, the time from egg to harvest has been cut in half, feed efficiency has been improved, survival is greater, and flesh quality is constantly better.

**Chromosome set manipulation**

Many fish display a high degree of plasticity in phenotypic expression, which enables a range of genetic manipulations, often observed in nature, that are not possible in terrestrial livestock. Since fertilization for fish takes place externally, it is possible to manipulate the number of chromosomes in the progeny or to derive offspring from wholly maternal or paternal origins (reviewed by Dunham, 2004). The key to these processes is altering egg development.

The development of an egg without fertilization leads to the production of offspring derived from a single sex. During gynogenesis, the eggs are activated by inert sperm, produced by ionizing radiation. Diploid gynogens are then created by inhibiting either the second meiotic division or the first mitotic division of the developing egg using temperature or pressure shock (Figure 1). More often, chromosome set manipulation is used to improve performance through polyploidy induction, yielding once-off gains in performance (Figure 1). Here the eggs are fertilized with normal active sperm, and a shock is applied during the second meiotic division to retain the second polar body, yielding offspring with two sets of chromosomes

![Figure 1. Chromosome set manipulation in fish: production of gynogenic and triploid progeny.](https://academic.oup.com/af/article-abstract/6/4/42/4638815)

**Figure 2.** The potential of xenotransplantation for aquaculture: Transplantation of blue catfish germ cells (spermatogonia) into larval triploid (sterile) channel catfish. Production of blue × channel catfish hybrids, two species which do not normally mate and for which milt is not easily collected, has been proposed using this method. Success would lead to pond spawning of xenogenic male catfish producing blue catfish sperm with normal female channel catfish to capture the vigor observed in hybrid blue × channel catfish.
from the female and one set from the male. In species in which the onset of sexual maturity is associated with reduced growth, triploidy provides a means of preventing energy allocation toward gonad development since triploids tend to be effectively sterile. For this reason, triploidy has been used to enhance production in several aquaculture species including common carp (Basavaraju et al., 2002), channel catfish (Wolters et al., 1982), and rainbow trout (Bye and Lincoln, 1986). Triploids may also exhibit higher survival, hybrid vigor, sterility, and greater disease resistance (Parsons et al., 1986; Dorson et al., 1991).

Xenogenesis

The ability to sterilize fish through triploidy may become an important tool for one of the newest technologies to be proposed for aquaculture, that of xenotransplantation. With this technology, sterile fish of one species (usually a congener) serve as a host for the primordial germ cells of the species to be produced. Initially developed as a potential solution to produce threatened and endangered salmonid fry using surrogate hosts, it holds a great deal of potential for food fish species with unique challenges. The first successful use of this technology was to produce rainbow trout offspring from triploid salmon xenotransplanted with rainbow trout primordial germ cells (Okutsu et al., 2007). Examples of where this technology may be implemented in food fish production includes the production of large species with long generation times via surrogate hosts of small body size and shorter generation time. In addition to reducing the generation time, this technology would reduce costs with relation to both facility and feeding requirements. The example often cited is the production of tuna fry using a smaller surrogate species such as a mackerel. Another area where this technology has potential application is the production of desirable hybrids between two species that do not mate or mate at a low rate naturally, such as blue and channel catfish, whose hybrid exhibits desirable vigor (Figure 2).

Hybridization

Hybridization exploits dominance genetic variance and has been described as useful for enhancing fish performance in several ways (Tave, 1993). One is as a “quick and dirty” method; when heritability is low, hybridization is used to improve productivity by capitalizing on dominance genetic variance. Another is to incorporate hybridization into a selective breeding program as a last step to enhance performance of fish for grow-out. A third way is to use hybridization to produce new breeds or strains with superior performance characteristics, as is done in the hybrid striped bass industry. Unfortunately, hybridization is not always effective, and the genetics of the fish dictate the degree of performance enhancement or, possibly, loss.

Gene transfer

As already stated, the high fecundity, general ease of gamete collection, and control over fertilization associated with fish provide exceptional conditions for gene transfer technologies. Research exploded in this area in the late 1980s and into the 1990s, such that several species of growth hormone (GH)-transgenic fish were produced in research facilities around the globe. Initial results suggested poor transgene integration and heritability. Over the years, the technology was improved, new constructs were developed, and significant increases in growth performance were documented, particularly in salmonids. Through this research, an all-piscine GH construct was developed and successfully integrated into Atlantic salmon, cutting the time to market in half and successfully transferring that performance advantage to their offspring (Du et al., 1992). These fish represent the first, and currently only, GMO animal to be approved for human consumption in United States.

Nutrition and Feeding

Over the past 25 yr, aquaculture feeds have undergone major changes that have greatly increased performance of farmed fish and contributed to increased aquaculture production worldwide. Although aquaculture has ancient origins, development of intensive aquaculture production where fish are fed nutritionally complete feeds was hampered by lack of knowledge of specific dietary requirements of fish. Feeds were formulated empirically rather than by rational formulation. This situation changed when a nutritionally complete, semi-purified diet for fish was developed (Halver, 1957). Using this diet, single essential nutrients could be supplemented at various levels and dietary requirements estimated by measuring fish performance (NRC, 1972). To date, dietary requirements of most vitamins, essential amino acids, some minerals, and essential fatty acids have been determined for about 20 species of fish and several species of shrimp (NRC, 2011).

Feed technology

The adoption of cooking-extrusion technology to produce pelleted feeds for farmed fish has been one of the most important performance-enhancing technologies in aquaculture. Early feeds for fish were manufactured using compression pelleting, similar to feeds for livestock and poultry. Some species of fish, e.g., salmon and trout, consume feed rapidly, but others, such as catfish and shrimp, feed more slowly. Feed pellets must remain intact long enough after feeding to be located and consumed by fish. Compressed pellets lack water stability, leading to nutrient leaching prior to being consumed. Further, because of their density, compressed pellets sink rapidly. In contrast, using cooking-extrusion technology, pellet density can be adjusted to produce floating feeds, slow-sinking feeds, or fast-sinking feeds (Hardy and Barrows, 2002). Extruded pellets are also harder than compressed pellets, making them better suited for automatic feeding systems and improving water stability. The cooking-extrusion process greatly increased starch gelatinization, which improves starch digestibility in fish and also results in starch becoming a nutritional pellet binder (Hilton et al. 1981). This has allowed feed formulators to reduce the percentage of starch in feeds, making room for higher protein or lipid levels. The feed mash is under pressure as it moves down the barrel of an extruder, keeping moisture in a liquid form. When the feed moves through the pelleting die into atmospheric pressure, moisture turns to vapor, creating small air pockets in pellets. This allows pellets to soak up and retain added oil, making it possible to produce very high lipid feeds. Using vacuum-infusion systems, salmon feeds can be produced with more than 30% lipid. Because pellets produced by cooking-extrusion are less likely to fracture, they can be delivered to fish using mechanical or pneumatic feed delivery systems. Using underwater cameras or sonar devices to detect uneaten pellets falling to the bottom of large marine salmon pens,
feed delivery systems now automatically adjust feeding levels to match feed consumption, reducing feed waste. These advances, all made possible by the adoption of cooking-extrusion technology, have resulted in an increase in feed consumption by slow-eating fish and shrimp; lower feed conversion ratios in the salmon and trout industries, from an average of 1.5 through 1.6 up to 1.0 through 1.2; and shortening of production cycles, especially in the salmon farming industry (Torrissen et al., 2011).

**Microdiets**

The development of microdiets for fish that undergo a larval stage is another performance-enhancing technology that has transformed the marine aquaculture industry. Although marine aquaculture production has increased greatly over the past two decades, production of fry for stocking marine pens has been a major bottleneck, limiting greater expansion of this industry. At first feeding, marine fish larvae are too small to consume conventional feed particles, and therefore, are fed live prey, such as rotifers and Artemia nauplii, until they reach a size at which they can transition to crumbled feed particles. Percentage survival of marine larvae from hatching to the fingerling stage was in the single digits until development of micro-diets. Feed particles for larval fish must be very small, nutritionally complete, homogeneous and water-stable, yet attractive and digestible to larvae (Hardy and Barrows, 2002). Small feed particles have a large surface area-to-volume ratio that accelerates leaching rates of water-soluble nutrients, so this fact adds a degree of complexity to development of microdiets. The two general categories of microdiets are crumbled and on-size feeds, terms that relate to the processes by which they are produced. Crumbled feeds are made from conventional extruded pellets that are fractured and then passed through screens to separate particles into different size ranges. On-size feeds, in contrast, are small pellet-like particles produced using other technologies, such as microextruded marumerization (MEM), particle-assisted rotational agglomeration (PARA), sprayed beadlets (Villamar and Langdon, 1993), or microencapsulated feeds (Barrows and Hardy, 2000). By combining two processing methods, such as microencapsulation with the PARA process, it is possible to produce complex feed particles in which small, water-stable, microencapsulated particles are embedded inside larger particles.

**Refinement of requirements**

Refinement of estimates of the requirements of fish for essential dietary nutrients and identification of conditionally required nutrients represent another performance-enhancing advancement, albeit an incremental one. As defined by the NRC (2011), nutrient requirements of fish are reported as minimum dietary levels needed to support maximum performance of fish or shrimp under experimental conditions when fed diets typically made using semi-purified ingredients. Requirements do not take into consideration factors that may increase dietary requirement levels of specific nutrients, such as life history stage, environmental conditions, or antagonistic interactions among feed ingredients that reduce nutrient availability or interfere with normal metabolism. For example, the dietary histidine requirement of Atlantic salmon is reported to be 0.8%. This level is relatively easy to achieve in normal salmon feed formulations. However, juvenile Atlantic salmon require nearly twice as much histidine in their diet for a relatively short period after transfer from freshwater to seawater to prevent cataracts (Waagbo et al., 2010). Other nutrient requirement levels for fish can vary with feed formulation. For example, the dietary zinc requirement of juvenile salmonids is reported to be 15 to 30 ppm. However, when feeds contain high-ash fish meal or high amounts of phytic acid, zinc digestibility is reduced and deficiency signs appear (Ketola, 1979; Hardy and Shearer 1985; Richardson et al., 1985) unless dietary zinc is fortified to higher levels. Similarly, dietary phosphorus digestibility is not a fixed value in fish feeds but rather is inversely proportional to dietary bone content (Sugiura and Hardy, 2000). Taurine is an example of a conditionally required nutrient. Most freshwater fish have the capacity to synthesize taurine at a rate sufficient to meet physiological needs. However, when rainbow trout are fed high-soy diets, taurine synthesis cannot keep up with taurine loss, making it necessary to supplement feeds with taurine to prevent a reduction in fish performance. Marine fish lack the capacity to synthesize taurine, but high fishmeal or animal protein feeds contain sufficient taurine to support growth. It’s only when animal protein is replaced with plant protein that taurine must be supplemented.

**Culture Systems and Management**

The goal of culture system management is to provide an environment where the performance potential afforded by genotype and nutrition can be fully realized. Unmanaged waters are unproductive because food is scarce. Food availability can be increased by enhancing natural productivity or by providing manufactured feed. But providing more food does not allow for unlimited production because metabolic activities inside the culture system cause environmental conditions to deteriorate. After the animals’ nutritional needs are met, dissolved oxygen availability is usually the first factor to affect fish performance. Fish also produce carbon dioxide, ammonia, and organic wastes as by-products of metabolism. Waste accumulation affects animal performance after oxygen needs are met. Common fish culture systems include ponds, cages, flow-through systems, and recirculating aquaculture systems. Fish production from ponds varies widely, but the global average is about 2,500 kg/ha. Production in flow-through raceways can be 100 times greater than from ponds, and annual production in recirculating aquaculture systems can exceed 2 million kg/ha. Increasing aquaculture production requires ever-increasing management inputs (and costs) to address the environmental limitations on growth and performance, as shown in Table 1 for tilapia grown in ponds.

**Table 1. Blue tilapia (Oreochromis aureus) production in ponds at increasing levels of management input.**

| Management input                  | Annual production (kg/ha) | Limiting factor    |
|-----------------------------------|---------------------------|--------------------|
| Stocking only                      | 100–500                   | food               |
| Stocking, pond fertilization      | 1,000–3,000               | food               |
| Stocking, feeding                 | 2,000–4,000               | dissolved oxygen   |
| Stocking, feeding, aeration        | 4,000–10,000              | waste removal      |
| Stocking, feeding, aeration,      | 20,000–50,000             | waste removal      |

**Ponds**

Ponds are small bodies of standing water where environmental conditions are the result of natural processes occurring within the water body (Tucker and Hargreaves, 2012). This is an important distinction because environmental conditions are more easily controlled in other systems—by water flow in cages and raceways and by separate engineering processes in recirculating systems. Production costs are lower in ponds than other
culture systems, and ponds account for about 80% of finfish aquaculture and nearly all shrimp production.

Pond water temperature closely follows air temperature, and it is impractical to heat or cool pond water. In temperate climates, pond-grown fish must tolerate wide changes in water temperature, often ranging from near freezing to more than 35°C. Other pond environmental variables—especially dissolved oxygen levels—also change over time because biological activity varies in seasonal and daily cycles. In some ponds, conditions change from optimum to lethal in hours. Most water quality variables in ponds are difficult, impractical, or expensive to control. Dissolved oxygen supply is an exception, and mechanical aerators are often used to provide more oxygen and improve fish performance (Figure 3). Because water quality varies greatly, animals commonly cultured in ponds—such as carps, catfishes, tilapias, and penaeid shrimp—are among the hardier species with respect to environmental tolerance.

Traditional aquaculture ponds simultaneously confine fish and treat wastes. Greater control over production can be achieved by physically separating the animal-confinement and waste-treatment functions. In these partitioned ponds, fish are confined to a small water volume where dissolved oxygen availability is easily managed (Figure 4). Water is cycled through a much larger basin where wastes are removed and oxygen is replenished. Fish production can be several times greater than in traditional ponds (Tucker et al., 2014).

The ponds described above are photoautotrophic systems because plant photosynthesis is the dominant process affecting the environment. Plants—usually phytoplankton—produce oxygen as a by-product of photosynthesis and assimilate wastes produced by fish. Photoautotrophic systems are difficult to manage because environmental conditions vary in response to daily and seasonal cycles of plant metabolism. The waste-treatment capacity of photoautotrophic systems is ultimately limited by the energy available from sunlight.

To provide better control of the culture environment, pond systems have been developed where oxygen is supplied entirely by aerators and wastes are removed by bioflocs—suspended aggregations of algae, bacteria, protozoans, fecal matter, and uneaten feed (Browdy et al., 2012). Bioflocs not only treat wastes, but also are a highly nutritious food. Intensive turbulent mixing is key to successful operation of biofloc systems because flocs must be suspended to function properly. Biofloc systems are expensive to operate, require technical expertise, and work best for growing animals—such as shrimp and tilapia—that can feed directly on the flocs as a supplement to manufactured feed. Annual production can exceed 50,000 kg/ha in intensively managed biofloc systems in tropical regions.

**Cages**

Cages are submerged or floating enclosures located along a shore or pier, or anchored and floating offshore, either in fresh or salt water.
Environmental conditions are determined by the quality of the surrounding water and the rate of water flow through the cage. Water flow depends on tides, surface currents, and other natural water movements to provide a continual supply of oxygenated, high quality water and sweep away wastes produced during culture. The only control the culturist has over these factors is selecting appropriate sites based on long-term records of water quality, climate, current velocities, and sea conditions.

An amazing variety of cage designs and mooring systems have been developed over the last 30 yr to facilitate cage culture in various waters (Langan, 2012). Cages are the most practical (often the only practical) culture system for growing marine fish in commercially significant quantities. At present, the most common cage-cultured marine fish are cool-temperate species such as Atlantic salmon, seabass, sea bream, yellowtail, and even tuna. Many other marine temperate and tropical marine fish have also been grown in cages. Cages are also used in freshwater to grow tilapia, carp, temperate basses, and pangasid catfishes.

**Flow-through systems**

Flow-through systems consist of tanks, troughs, raceways, or small ponds with water passing once through the culture unit (Figure 5). Water entering the culture unit provides dissolved oxygen and water leaving the tank carries away waste products. Water may be reconditioned and reused as it passes through a series of culture units, but water is not reconditioned and passed through the same unit more than once (Fornshell et al., 2012).

Flow-through aquaculture requires large water volumes near the optimum temperature for fish growth because heating or cooling is impractical. Water for raceways may be diverted from streams (Figure 3) or from springs or artesian wells. Regardless of the source, water flows through the facility by gravity.

Flow-through systems are most commonly used to grow coldwater fish, such as trout and the freshwater stages of salmon, because sources of consistently cold water are easier to find than sources of consistently warm water. Other than research facilities (many of which use small flow-through systems, such as aquaria or small tanks), flow-through systems are not used to grow brackish or saltwater species.

Production initially is determined by water flow, which determines the amount of dissolved oxygen available to meet fish metabolic demands. For trout and salmon production, relationships among production and water flow are well known, and facility design and production decisions are easily calculated. Production can be increased by adding oxygen to water in the culture unit or to water flowing from one unit to another. In systems with oxygen supplementation, accumulation of ammonia, carbon dioxide, or fine solids will eventually limit production (Boyd and Tucker, 2014).
Recirculating aquaculture systems

Recirculating aquaculture systems (RAS) confine fish in tanks at very high densities. A large portion of the water flowing out of the culture tank is recycled back to the tank after oxygen is added and wastes are removed. Recirculating systems use little water from outside sources, and wastes are concentrated into a small volume, allowing facilities to be located where water is scarce or where effluent regulations preclude use of other culture systems. Biosecurity is easy because the facility can be securely enclosed—usually indoors—and little water is exchanged with outside sources (Ebeling and Timmons, 2012).

Despite numerous advantages, aquaculture production from recirculating systems is small relative to other culture systems because they are expensive to build and operate. Recirculating systems are currently used to produce high-value products and in situations where there is a dependable market for locally produced fresh fish that cannot be grown year-round in outdoor systems.

Fish must be confined at high densities and grown rapidly to offset high production costs. Rapid growth is obtained by providing high-quality feeds and maintaining optimum environmental conditions for growth and health. Water temperatures are controlled throughout the year and rates of oxygen use and waste production can be estimated with good accuracy and these rates can be used to precisely design systems that provide a near-perfect environment for fish growth.

Overall system design incorporates a series of unit processes, each engineered to perform a certain task. Particulate solids are removed by filters, toxic dissolved nitrogen compounds are removed by bacterial nitrification in biological filters, carbon dioxide is removed by gas strippers, and oxygen is added by aerators or oxygenators (Figure 6). Processes to control pH and alkalinity, remove nitrate and dissolved organic matter, and disinfect the water may also be required depending on production goals and the species cultured. In most facilities, monitoring and control devices oversee important processes so that environmental conditions never deviate from acceptable ranges.

**Conclusions**

Aquaculture is the fastest-growing agricultural industry. This growth hinges on advances in fish genetics, nutrition, culture systems, and management. The number and complexity of cultured fish species makes for a diverse and complex industry in which the requirements for optimal production performance are constantly being defined and redefined. The unique genetic and phenotypic plasticity of fish coupled with rapid innovations in nutrition, systems, and management have led to sustained growth and increased resource use efficiency. As a result, global fish production is on target to meet the demand created by rapid human population growth.

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