Aquaculture 350–353 (2012) 117–129

Contents lists available at SciVerse ScienceDirect

Aquaculture

journal homepage: www.elsevier.com/locate/aqua-online

Review

The importance of selective breeding in aquaculture to meet future demands for animal protein: A review

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ARTICLE INFO

Article history:
Received 21 July 2011
Received in revised form 3 April 2012
Accepted 9 April 2012
Available online 16 April 2012

Keywords:
Aquaculture
Potential
Selective breeding
Animal protein

ABSTRACT

Aquaculture is the fastest growing food production industry, and the vast majority of aquaculture products are derived from Asia. The quantity of aquaculture products directly consumed is now greater than that resulting from conventional fisheries. The nutritional value of aquatic products compares favourably with meat from farm animals because they are rich in micronutrients and contain high levels of healthy omega-3 fatty acids. Compared with farm animals, fish are more efficient converters of energy and protein. If the aquaculture sector continues to expand at its current rate, production will reach 132 million tonnes of fish and shellfish and 43 million tonnes of seaweed in 2020. Future potential for marine aquaculture production can be estimated based on the length of coastline, and for freshwater aquaculture from available land area in different countries. The average marine production in 2005 was 103 tonnes per km coastline, varying from 0 to 1721 (China). Freshwater aquaculture production in 2005 averaged 0.17 tonnes/ha, varying from 0 to close to 6 tonnes per ha (Bangladesh), also indicating potential to dramatically increase freshwater aquaculture output. Simple estimations indicate potential for a 20-fold increase in world aquaculture production. Limits imposed by the availability of feed resources would be lessened by growing more herbivorous species and by using more of genetically improved stocks.

Aquaculture generally trails far behind plant and farm animal industries in utilizing selective breeding as a tool to improve the biological efficiency of production. It is estimated that at present less than 10% of aquaculture production is based on genetically improved stocks, despite the fact that annual genetic gains reported for aquatic species are substantially higher than that of farm animals. With an average genetic gain in growth rate of 12.5% per generation, production may be dramatically increased if genetically improved animals are used. Importantly, animals selected for faster growth have also been shown to have improved feed conversion and higher survival, implying that increased use of selectively bred stocks leads to better utilization of limited resources such as feed, labour, water, and available land and sea areas.

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0044-8486/$ – see front matter
doi:10.1016/j.aquaculture.2012.04.008

1. Introduction

Humanity's greatest problem has been to secure food suitable to meet nutritional needs. It has been said that, 'Without food, nothing else matters' (Warwick and Legates, 1979). Many areas of the world currently lack adequate food supplies. Of the 2009 population of 6.7 billion people, 960 million were undernourished (Johnson, 2009), and the human population is predicted to increase to 9.1 billion by 2050 (Diouf, 2009). This population growth, combined with increased average income and increased urbanization with associated shifts in diet towards more nutritious and higher quality foods, is expected to result in almost a doubling of the demand for food (Diouf, 2009). This illustrates that a serious food crisis already exists, and is expected to increase in coming years. It is an enormous task to increase food production to meet the future demand.

When discussing the food crisis Kutty (2010) points out that our long-term perspectives about providing adequate food for the world's growing population have to change dramatically. The same author further states that, 'The land-based food production systems, despite further expansion and intensification, are limited. We have to turn to water and not too much to land for additional food production, through available sustainable technologies and evolving new innovations, which would ensure our food and nutritional security'. According to Duarte et al. (2009) neither land-based nor marine-based food production alone will suffice to feed humanity in the future, an intelligent integration of marine- and land-based food production is required to meet this essential goal. Marra (2005) discussed the importance of mariculture in the future and argued that a major change in food production is required by moving the production of animal protein from land to the ocean. However, Waggoner (1994) expresses an optimistic view on future plant production: 'If average fields in the world sixty or seventy years hence, when we are likely to number ten billion, yield as much food as today's potato fields in Ireland, wheat fields in France, or corn fields in Iowa, large portions of the land currently in crops can revert to Nature'. This view is supported by Gjølberg (2010), who argues that many countries can increase agriculture production considerably. He points out that much of the potentially rich agricultural land is actually underutilised, and argues that the solution is to pass on knowledge about fertiliser use and modern agronomy techniques.

With this in mind it is of interest to discuss the role of aquaculture in meeting the future demand for animal protein. Today 53% of fish and shellfish production takes place in freshwater (FAO, 2009) which constitutes only 1% of the globe's surface, while the very large areas covered by sea- and brackish water are currently only marginally utilised. An important part of increasing the future aquaculture production is to improve the biological productivity of farmed species of fish, shellfish (crustacean and molluscs) and seaweeds. The role of selective breeding will therefore be discussed. Investments in well planned and managed breeding programs are unique, because genetic gains obtained in such programs are eternal and cumulative. They are never 'used up', and never 'wear out' (Weller, 2006).

Quantitative genetics and selective breeding represent a young field of science, and the technology uptake in the aquaculture sector has been slow compared with plant and farm animal industries. Reasons for this are likely to be many and not easily explained. In this review we demonstrate the potential for large genetic improvement in aquatic species and we make some estimations and predictions about the scope for future increased aquaculture production through greater utilisation of genetically improved stocks.

2. Status of aquaculture production

Asia dominated the world's production of fish and shellfish in 2008 (producing 88% by volume), followed by the Americas, Europe, Africa and Oceania (4.6%, 4.5%, 1.8% and 0.3% respectively, Table 1). Likewise, nearly all seaweed production also takes place in Asia, with China alone producing 2/3 of the world's production (FAO, 2009).

As shown in Table 2, aquaculture production has nearly doubled, and the value of aquaculture products has more than doubled, over the last ten years.

A high proportion of the total aquaculture production (>41%) takes place in freshwater (Table 3), despite the fact that freshwater and oceans cover 1% and 71% of the earth's surface, respectively. Considering fish only, 84% is produced in freshwater and 5.9% in the sea, and during the last ten years production of marine fish has only increased by a mere 2.6%. The main factors limiting marine aquaculture include the relatively high costs (e.g. investments in infrastructure,

Table 1
Aquaculture production and value by continents 2008 (FAO, 2010a).

Continent	Production, million tonnes		Value of production, billion US$
	Fish and shellfish	Aquatic plants	
Asia	46.7	15.7	84.9
America	2.4	–	9.4
Europe	2.3	–	8.6
Africa	0.9	–	2.0
Oceania	0.2	–	1.0
Total	52.5	15.7	105.9

Table 2
World production of fish and shellfish by principal producers and total plant production (FAO, 2009).

Country	1998		2007	
	Quantity, tonnes'000	Value, US $'million	Quantity, tonnes'000	Value, US $'million
China	18,722	19,412	31,420	39,685
India	1908	2254	3355	4384
Vietnam	339	717	2157	4526
Indonesia	630	1810	1393	2462
Thailand	595	1657	1390	2433
Bangladesh	575	1061	946	1523
Chile	293	971	830	5277
Norway	411	1144	830	2978
Japan	767	3062	766	3173
Philippines	313	595	710	1234
Egypt	139	327	636	1193
Total fish and shellfish	28,413	42,145	50,329	87,013
Total plant	8007	5042	14,859	7539

Table 3
Production of aquatic animals and plants, amount and value in 2007 (FAO, 2009).

Species	Production		Value of production	
	Million tonnes	%	Billion US$	%
Fresh water fish	26.8	41.0	32.5	34.4
Diadromous fish	3.3	5.0	13.4	14.2
Marine fish	1.9	2.9	6.5	6.9
Crustaceans, brackish	4.9	7.5	20.2	21.4
Molluscs, marine	13.1	20.1	12.8	13.5
Other animals	0.4	0.6	1.6	1.7
Aquatic plants, marine	14.9	22.9	7.5	7.9
Total	65.2	100.0	94.6	100.0

maintenance, transport of feed), limited areas sheltered from ocean swells, and the high developmental costs and risks associated with off-shore aquaculture technologies. Despite these factors we will show that the largest potential for future expansion of aquaculture lies in the marine environment.

As stated by Diouf (2009) an increase in income will result in a higher demand of quality food. Today the continents with highest incomes, namely North America, Europe and Oceania, have much higher consumption of animal and fish protein compared with other continents (Table 4).

Variation in the per capita protein consumption between continents is remarkably high, and the average consumption is nearly twice as high in North America as compared with Africa. On a world basis plant protein represents 55% of human consumption, farm animals 38%, and fish 6% (FAO, 2009). High consumption of fish is seen in Japan with an average of 21 g of protein per day, followed by Norway and Portugal each with 16 g. People in central Asian countries consume less than 1 g of fish protein per day on average. Some smaller countries have an extremely high daily consumption of fish protein per capita, i.e. the Maldives (45 g), Greenland (31 g), and Iceland (27 g) (FAO, 2008). The percentage of fish of the total animal protein consumed varies from 7.1% in South America to 22.3% in Asia. The variation among individual countries is even larger, for example the ratio of fish to terrestrial animal protein consumed in Japan is 41, whereas the corresponding figure in the USA is 0.08. These statistics are likely to reflect differences in culture (habits, tastes and exposure), ability to access sea and freshwater resources, development of sustainable and efficient production, and education about the health value of fish consumption (FAO, 2008)

3. Fish and shellfish for human consumption: comparison with meat from farm animals

Although their nutritional value may vary, fish and shellfish are in general good sources of nutrients. Fish is easily digestible and contains a well balanced amino acid composition. Fish are regarded as healthy, not only because of the content of the omega-3 fatty acids but also because of their content of micronutrients (Centre of Excellence Seafood and Health (CESSH), 2011; Luten, 2008) and amino acids.

Table 5
Main components (%) in muscle from fish as compared to beef (Ruyter, 2010).

Component	Fish normal	Beef
Protein	16–21	20
Fat	0.2–25	3
Carbohydrate	0.5	1
Ash	1.2–1.5	1
Water	66–81	75

The muscle composition of fish and beef is similar, with the exception of the fat content of some fish species (Table 5).

In terms of amino acid composition, fish compare very favourably with red meat (Table 6). Particular vitamins and minerals which are present in relatively high concentrations in seafood are of special interest for their role in preventing life style disorders (Ruyter, 2010).

Fish is a healthy source of nutrients that compares favourably to other sources of animal protein. As fish is a good source of the long-chained $n-3$ fatty acids it is believed that a diet rich in fish will reduce the risk of developing coronary heart diseases and some cancer types and may be helpful in alleviating some cases of depression and anxiety (Abeywardena and Patten, 2011; Dyck et al., 2011; Karr et al., 2011). Because it consists of healthy fats and many essential amino acids and nutrients, many countries would benefit from increasing their consumption of fish.

4. Efficiency of fish production

Fish are generally more efficient converters of feed into meat than warm blooded animals, due to higher maintenance and respiratory costs for the latter. On average only 2% of the consumed energy is used for biomass production in homeotherms compared with 17% in poikilotherms (Smith, 1992). In Table 7 the retention of energy and protein for Atlantic salmon is compared with pigs and poultry, which are the most efficient meat producing land-based farm animals. The genetically improved salmon had 2.3 and 1.6 times higher rates of energy retention than poultry and pigs, respectively. Retention of protein was also higher in salmon compared with poultry (1.5 times) and pigs (1.75 times) (Bjørkli, 2002 cited by Ytrestøyl et al., 2011). Thodesen et al. (1999) found that the retention rate of Atlantic salmon had been improved by 20% during five generations of selection primarily for growth rate. Neely et al. (2008) concluded that selection over 16 generations for growth rate in coho salmon also resulted in improved feed efficiency and energy allocations.

5. Potential of aquaculture production

5.1. Growth in aquaculture production

For several years the catch of fish and shellfish has been stable at around 90 million tonnes per year, and the harvest of seaweeds at approx. one million tonnes (FAO, 2009). FAO (2008) stated that 'The maximum wild capture fisheries potential from the world's oceans has probably been reached'. For aquaculture the situation is different. Aquaculture production of fish and shellfish has grown by an average

Table 4
Food balance sheets in 2007 (FAO, 2008).

Continent	Total food supply (1000 tonnes)	Population (×1000)	Per capita Supply (kg)	Total Protein	Farm animal protein	Fish protein	Fish/animal protein	Fish/total protein
				Grams per capita per day				
Africa	8153	964,669	8.5	63.5	13.9	2.5	17.9	3.9
America N	8217	341,747	24.0	113.5	72.1	5.7	7.9	5.0
America S	5437	569,689	9.5	79.8	39.1	2.8	7.1	3.5
Asia	75,207	4,029,340	18.7	72.5	23.1	5.1	22.3	7.1
Europe	16,145	730,868	22.1	102.5	58.0	6.7	11.5	6.5
Oceania	868	34,486	25.2	97.8	61.9	6.5	10.4	6.6
World	114,027	6,670,799	17.1	77.3	29.6	4.8	16.1	6.2

Table 6
Content of essential amino acids (Ruyter, 2010).

Amino acids	Fish	Milk	Eggs	Beef
Lysine	8.8	8.1	6.8	9.3
Tryptophan	1.0	1.6	1.9	1.1
Histidine	2.0	2.6	2.2	3.8
Phenylalanine	3.9	5.3	5.4	4.5
Leucine	8.4	10.2	8.4	8.2
Isoleucine	6.0	7.2	7.1	5.2
Threonine	4.6	4.4	5.5	4.2
Methionine–cystine	4.0	4.3	3.3	2.9
Valine	6.0	7.6	8.1	5.0

Table 7
Percent retention of energy and protein in pigs, poultry and Atlantic salmon (Bjørkli, 2002 cited by Ytrestøyl et al., 2011).

	Pigs, edible parts	Poultry, edible parts excl. skin	Atlantic salmon, fillet
Energy	14.1	10.2	23.0
Protein	17.9	20.7	31.4

of 7.7% per year over the last decade (FAO, 2009). No other food production sector shows a similar growth rate. In 2007 around 63 million tonnes of the catch from fisheries were used for direct human consumption while the rest was mainly used for the manufacture of fish meal and fish oil (FAO, 2009). Therefore, the 50 million tonnes produced in aquaculture in 2007 represents 44% of total fish and shellfish that were consumed directly by humans.

The production of seaweeds reached 14.8 million tonnes in 2007 and has increased by 8.5% annually over the last ten years (FAO, 2009). The majority of kelp (*Laminaria japonica*), wakame (*Undaria pinnatifida*), laver (*Porphyra tenera*) and green laver (*Monostroma nitidum*) that are produced are used for direct human consumption, representing 9.0 million tonnes or 61% of total seaweed production (FAO, 2006). Today most seaweed production takes place in temperate waters. Possibilities for future expansion are considerable, particularly in the tropics.

Attempts to predict future production in aquaculture are not easy, but Fig. 1 shows a projection based on the average yearly increase over the last ten years of 7.7% for fish and shellfish and 8.5% for seaweed. If this trend continues, the production is estimated to reach 132 million tonnes of fish and shellfish and 43 million tonnes of seaweed, totalling 175 million tonnes per year in 2020.

5.2. Marine production

Few attempts have been made to quantify the future potential for aquaculture growth. Until now 84% of fish production has been taking place in freshwater, 10% in brackish water and 6% in marine waters. Freshwater fish represented 41% of total aquaculture production in 2007 (Table 3). From a resource point of view, future expansion will most likely take place in the marine environment. According to FAO (2010b) most of the future aquaculture expansion will occur in the seas and oceans, certainly further offshore, perhaps even as far as the high seas.

Today cage culture fish farming is well developed in sheltered coastal areas. Marine production is also possible in earthern ponds or concrete tanks. For shellfish and seaweed, production technology is well developed for farming in sheltered areas as well as in less exposed open sea. Integrated Multi-Trophic Aquaculture (IMTA) is a concept for combining fish, shellfish and seaweed production that could have large potential (Chopin, 2012). In addition there is a large potential for recirculation systems based on fresh- and seawater. The possibilities for expansion are many and it is difficult to see the limitations from a technical point of view, given the vast areas available for farming.

The length of coastline is an important indicator of natural resources, and data on this parameter are readily available (World Resources Institute, 1992). The length of coastline in major aquaculture countries (The World Factbook, 2010) and marine production numbers (FAO, 2007) are shown in Table 8. As expected, the variation in production level per km coastline among the listed countries is large, ranging from as much as 1721 tonnes/km in China to 9 tonnes/km in the USA. Seaweed is included in these production figures; excluding seaweed the corresponding production range is from 973 to 9 tonnes/km. China has the highest relative production per km coastline, mainly because of the intensity and size of its shellfish production. Looking at diadromous and marine fish the production varies from 93 tonnes/km in Chile to 1 tonne/km in India.

In coastal areas aquaculture production competes with other activities such as fishing, transport and in particular tourism and recreational use. Regulation of the use of the coastal areas is a duty of governments. However, it is of vital importance that aquaculture production is allowed to expand in order to meet future demands for food.

The Directorate General of Fisheries in Indonesia has estimated the country's potential for annual marine aquaculture production to be 47 million tonnes of fish, shellfish and seaweeds, as reviewed by Gjøen et al. (1996). These figures indicate that Indonesia alone has the potential for producing the present total world aquaculture production. With a coastline of 54,714 km and a production potential of 47 million tonnes per year it could yield 859 tonnes/km of coastline (24 tonnes/km were produced in 2005).

A realistic estimate of future potential for marine aquaculture production is difficult to generate, and it will vary considerably

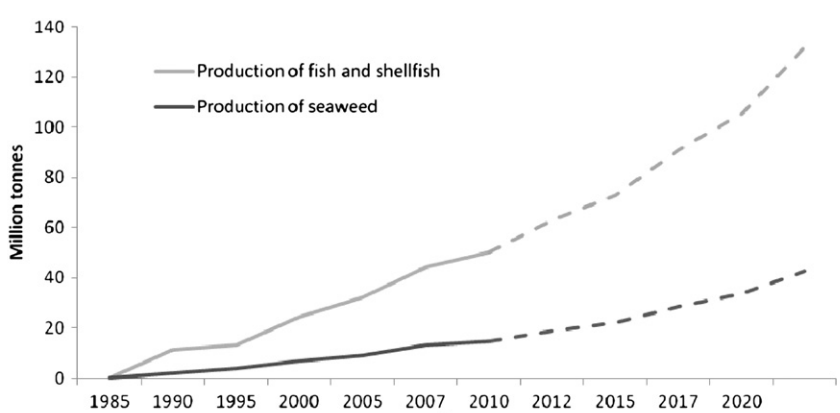

Fig. 1. Historic and projected (dashed) development of aquaculture production. Figures from 1985 to 2007 are from FAO (1995) and FAO (2009). The prognosis until 2020 is based on a yearly increase of 7.7% for fish and shellfish and 8.5% for seaweeds.

Table 8
Marine production of fish, shellfish and seaweed, 2005 in 1000 tonnes (FAO, 2007). Length of coastline in km (The World Factbook, 2010), and production per km coastline.

Country	Molluscs and crustacean	Diadromous and marine fish	Seaweed	Total marine production	Coastline (km)	Tonnes per km coastline		
						Total marine	Total marine−seaweed	Total diadromous and marine fish
China	13,050	1053	10,855	24,958	14,500	1721	973	72
India	190	8	5	203	7000	29	28	1
Viet Nam	476	–	30	506	3444	147	138	5
Indonesia	285	279	911	1475	54,714	24	10	5
Thailand	753	16	4	773	3219	240	239	5
Bangladesh	83	–	–	83	580	143	143	10
Japan	427	307	508	1242	29,751	42	25	8
Philippines	84	290	1339	1713	36,289	47	10	8
Korea Rep.	323	90	621	1034	2413	429	171	37
Egypt	3	165	–	168	2450	68	68	67
Chile	99	599	15	713	6435	110	108	93
Norway	4	652	–	656	25,148	26	26	26
France	208	42	–	212	3427	62	62	12
USA	142	42	–	184	19,924	9	9	2
World total	17,409	4523	14,790	36,722	356,000	103	62	13

among countries and temperature zones. As a simple estimation, if the average production per km coastline increases from the present level of 103 tonnes/km to the current Chinese production level of 1721 tonnes/km, the impact on world marine production would be as shown in Table 9.

These figures show that the potential for marine aquaculture expansion is large when considering the vast areas available. The highest figure of 613 million tonnes would be achieved if the world's average marine production per km of coastline grew to levels similar to that achieved by China in 2005. Canada and Russia have very long coastlines (202,080 and 37,653 km, respectively), of which large parts face towards the Arctic region with limited possibility for aquaculture production due to low temperatures. By including only a half of these countries' coastline the remaining length was 236,000 km. Given this adjustment, world production would reach 406 million tonnes if on average 1721 tonnes/km could be produced (Table 9). A more realistic prognosis would be to look at a marine production of 240 tonnes/km coastline which has been exceeded by three countries (China, Republic of Korea and Thailand), in which case the total world production would be 85 million tonnes.

In marine aquaculture some effluents from the production facilities in the form of organic matter and minerals, particularly phosphorus, will be produced. This could to some extent be reduced by polyculture of fish with shellfish or algae. Lindal et al. (2005) found that blue mussel culture at the mouth of a fjord reduced pollutants, particularly phosphorus. However, Csavas (1995) points out that although culturing filter-feeder molluscs are usually considered environmentally beneficial, nitrogen and phosphorus removed in their meat is not significant compared to their total weight. Furthermore the metabolites from molluscs could contribute significantly to the organic load in the culture environment. Possible environmental problems could also be reduced by keeping areas free from farming for a period after each harvest.

Table 9
Estimates of aquaculture production based on length of coastline and with reduced coastline for Canada and Russia, million tonnes per year.

Aquaculture production tonnes/km	Estimated production potential [a]	Estimated production potential with reduced coastline[b]
103	37	24
250	89	59
500	178	118
750	267	177
1000	356	236
1250	445	295
1500	534	354
1721	613	406

[a] Total world's coastline is approximately 356,000 km.
[b] Reduced coastline assumes that half of Canada's coastline (202,080 km) and of Russia's (37,653 km), is useful for aquaculture production, giving a total coastline of 236,000 km.

5.3. Freshwater production

Estimates of freshwater aquaculture potential in different countries are difficult to find. Levels of production per unit of land area vary greatly among countries (Table 10). Bangladesh and Vietnam in particular have high production per km^2. Only a small part of the total land area of the top 15 major aquaculture countries is utilised for aquaculture production. The potential for increased production in fresh water is greatest in temperate and tropical areas. Large land masses sometimes contain areas with limited or unstable access to freshwater. The use of recirculation systems opens large potential for development, particularly since such systems require minimal space and water. For some species recirculation is now extensively used for fry and fingerling production.

Table 10 demonstrates the large production potential for freshwater aquaculture. Excluding desert regions (the worlds deserts greater than 50,000 km^2 size total 31 million km^2 in area (http://en.wikipedia.org/wiki/List of deserts by area)) and including half of the remaining land area, 59 million km^2 could be considered the maximum world land area having suitable conditions for expansion of freshwater production. By using this number and assuming that the average production level could be increased from the present level of 0.17 to 1.0 tonnes of fish

Table 10
Production of freshwater fish in major aquaculture countries in 2005 (FAO, 2007), land area (The World Factbook, 2010) and production per km^2.

Country	Fresh water fish, 1000 tonnes	Land area, 1000 km^2	Tonnes per km^2 land area
China	17,905	9326	1.92
India	2640	2973	0.89
Indonesia	633	1826	0.35
Thailand	371	512	0.72
Bangladesh	799	134	5.96
Japan	4	375	0.01
Philippines	184	298	0.62
Korea Rep.	6	98	0.06
Egypt	371	995	0.37
Chile	0	749	0
Norway	0	307	0
Spain	0	500	0
France	8	546	0.01
USA	287	9162	0.03
World total	25,778	148,940	0.17

per km^2, the total annual freshwater production of fish would be 59 million tonnes. Likewise, if the average production could reach the present levels obtained in China and Bangladesh, the world's total freshwater fish production could potentially reach 113 and 352 million tonnes, respectively.

The main limitation to growth of freshwater culture is the removal of soluble nutrients from the farms, primarily organic matter from faeces and excess feed. Although organic matter can be removed using alternative methods of purification, it is not possible to achieve complete extraction of organic matter in practice.

An exciting possibility for aquaculture production is that of combining fish and rice cultivation. Such production systems are well established in most rice producing countries, but there is large variation among countries as well as between different production systems. According to Halwart and Gupta (2004) production of fish per crop of rice, without additional feeding, ranges from 100 to 750 kg per ha. With feeding, up to 1800 kg per ha is achievable. Furthermore, it has been shown that the combination of rice and fish usually increases rice production by around 12% (Halwart and Gupta, 2004). Kangmin (1988) reported an increase in rice production of 8 to 47.3% when fish and rice were combined in China.

Combined rice-fish production is very low on a world basis. Exceptions are Egypt and Madagascar where 37.4% and 11.8% of total rice fields are used for rice-fish farming, respectively. China use close to 4% of their rice fields for combined production. In most Asian countries only 1% is used for combined production (Halwart and Gupta, 2004). Total rice production covers close to 70 million ha but not all rice farms are suitable for rice–fish production. Kangmin (1988) estimated that 77% of the rice fields in China could be used for rice–fish culture. Considering an annual production of 500 kg fish per ha of rice fields, the production potential of fish from rice paddies in China alone is of the order of 25 million tonnes.

5.4. Sea ranching

An option for increasing aquaculture production is by sea ranching. McNeil (1980) reported that sea ranching of Pacific salmon dates back to 1872 in the McCloud River in California. In the early 1880s many hatcheries were established in Europe and North America for releasing fry and fingerlings in order to strengthen natural populations of salmon (Donaldson, 1968) and cod species (Dannevig, 1910). A major breakthrough came in 1950s with improved feed technology and the work of L. Donaldson and his co-workers at The College of Fisheries, Seattle (Isaksson, 1988). In 1949 Donaldson's team released 23,000 Chinook salmon fry (*Oncorhynchus tshawyscha*) from a pond in Seattle and 23 returned four years later (Hines, 1976). During several generations of selection the return rate increased, while the age of the returning fish was reduced (Donaldson and Menasveta, 1961). Carlin (1969) reports significant difference in recapture frequency between full-sib groups, and Jonasson (1994) reported a response to selection of 27% during one generation. To this day sea ranching is practiced for a number of species in several countries (FAO, 2004).

Sea ranching implies that animals are released into the marine environment and no artificial feeding is needed as the animals feed on plankton and plants produced in the sea. Harvesting is possible because the target species either do not move far from where they are released (e.g. molluscs and types of algae), or eventually return to the site of release (e.g. salmon).

Release of fry and smolts have mainly benefited the fisheries of Pacific salmon in the Pacific Ocean, Atlantic salmon in North America and North Europe, and numerous recreational fishermen in rivers and shores around the world. Private sea ranching companies have been established in USA (e.g. Oregon Aqua-Foods, Newport, Oregon) and in Iceland (Isaksson, 1988), with variable economic success.

5.5. Limitation of feed resources

Sourcing enough feed to supply the future increase in aquaculture production is a large challenge. However, there are several possible solutions. Alternative sources of raw materials for feed need to be considered. One potential way of increasing the supply would be to make more efficient use of all by-products from the fishing industry that are processed into fish meal or directly fed as a moist pellet. This could represent a large quantity because filet yields typically vary between 35 and 60% and some fish species are not used as human food and currently treated as waste. In order to reduce the quantity of waste by-products going into the sea, economic incentives, capacity for storage, treatment of the “waste material” on board, and facilities on shore for the production of fish meal are needed. Bacterial protein meal, produced using natural gas (methane) as a carbon source, has been shown to be an excellent substitute for fish meal in fish feed (Aas et al., 2006). Other potential sources of feed are the by-products from terrestrial farm animals like blood, intestine and feathers from poultry. Feed for carnivorous fish species can to a large extent be substituted with grain protein and oils instead of animal protein and fat (Gatlin et al., 2007). Use of algae and aquatic macrophytes are good sources for farmed fish but should not exceed 15–20% of dietary protein requirements (Hasan and Chakrabarti, 2009). Another possibility is to develop improved seaweeds which can be transformed to protein rich feed for fish through digestion by yeast (Kjærvik, 1994).

Alternatively, we could change the species cultured, and the methods used for culture, so that abundant natural feed resources can be better exploited. Extensive harvest of the primary algae production in the sea by filter-feeding molluscs, and sea ranching of fish, are potential ways of better exploiting natural feed resources existing in the ocean. Consideration should be given to increasing the relative production of herbivorous marine species which need less animal protein. Improved farming and feed technology could reduce waste and thus reduce pollution from the farms. It is well documented that selective breeding improving growth rate also improves feed retention and feed conversion rates (Neely et al., 2008; Thodesen et al., 1999).

In summary, the demand for significantly increased amounts of feed is expected to drive the development of new feed sources and products, some of which may not yet be known to date, and is also expected to lead to a change in the species we culture and methods we use for production.

5.6. Sustainable and ethical development

To achieve sustainable development of aquaculture production, ensuring that future generations are not adversely affected and that the supply of high quality products can be maintained, authorities need to objectively specify the conditions under which expansion can occur. It is essential that detailed regulations for operations of aquatic farms are established in order to avoid negative environmental impacts. Regulations must specify where farming may take place, the density of farms and maximum biomass allowances. Likewise, regulations are needed regarding transportation and handling of waste products, the prevention, monitoring, reporting and treatment of diseases, and handling of acute disease outbreaks. To reduce stress, handling should be minimised, water quality must be met for each species, high quality feed should be given *ad libitum*, and density of animals should not be too high. The sustainability of aquaculture production is clearly relevant for obtaining a more equitable sharing of resources and improvement of environmental health and quality of life (Olesen et al., 2010). Olesen et al. (2000) suggested splitting trait values into non-market and pure market categories so that ethical and sustainable production values can be factored into selective breeding programs.

6. Current status of breeding programs

Modern breeding programs were initiated for plants around 1900 based on the findings from the pioneering hybridization experiments by Mendel (1866), and the same theoretical principles were for the first time applied to terrestrial farm animals some 15 years later (Hagedoorn, 1950). Well-designed breeding programs have since revolutionised the biological efficiency of plant and livestock production through the development of genetically improved, high yielding seed stocks. Aquaculture generally lags far behind plant and terrestrial farm animals with respect to uptake of this technology, many fish and shellfish producers still use wild stocks or production stocks only a few generations removed from the wild (Tave, 1986). However, one of the first documented selection experiments for fish started as early as in 1919 (Embody and Hyford, 1925), selecting for increased survival to furunculosis in brook trout. Since then a series of selection experiments to improve growth rate and disease resistance have been reported (see e.g. Argue et al., 2002; Bondary, 1983; Dunham, 2006; Gitterle et al., 2006; Hetzel et al., 2000; Hussain et al., 2002; Ilyassov, 1987; Kincaid et al., 1977; Kirpichnikov, 1987; Kuzema, 1971; Langdon et al., 2003; Moav and Wohlfarth, 1963, 1973, 1976; Nell and Hand, 2003; Newkirk and Haley, 1983; Schaperclaus, 1962). Large scale family based breeding programs, now established as the industry standard for genetic improvement of aquaculture species, were first introduced for salmonids in the 1970s (Gjedrem, 1985), for Nile tilapia in 1988 (Eknath et al., 1991) and for marine shrimp *P. vannamei* in 1993 (Fjalestad et al., 1997). Since then selection programs utilizing sib information have been implemented for a number of aquaculture species worldwide.

The relatively high heritabilities for economically important traits in fish and shellfish combined with high fecundity and short generation intervals (1–4 years) in most species explain the high genetic gains obtained in many aquaculture breeding programs. Gjedrem and Thodesen (2005) listed 21 estimates of selection response for growth rate in 10 aquatic species, averaging 14% per generation. Additional studies of genetic gain in growth rate report on similar responses (Neira et al., 2006; Rezk et al., 2003; Vandeputte et al., 2009), and Quillet et al. (2005) documented a 3%-unit (29.6% vs. 26.6%) difference in dry matter content between lines of pan-sized rainbow trout selected for high and low muscle fat content. Such responses to selection are four to five-fold greater than what is usually obtained in breeding programs for livestock species. An example of the selection response after five generations in Atlantic salmon shown in Table 11 demonstrates the high genetic gain in growth rate and favourable correlated responses in feed conversion ratio (FCR) and protein- and energy retention. Favourable correlations between growth rate and FCR in finfish are also reported by Ogata et al. (2002), Silverstein et al. (2005) and Neely et al. (2008). In brown trout, however, observed differences in growth were attributed to differences in feed intake alone and not to feed efficiency (Sanchez et al., 2001).

Although the potential for high genetic gains are well documented for aquatic species the development of breeding programs has progressed slowly. A survey based on figures from 2003 referred to by Gjedrem and Baranski (2009) found that there were 60 family based breeding programs covering less that 5% of world aquaculture production. Based on more recent surveys summarised in Table 12, Neira (2010) and Rye et al. (2010) report that the present number of family based selection programs in aquaculture now exceeds 100, and point out that other programs may still have been overlooked. The highest number of breeding programs is reported for tilapia (27), followed by Atlantic salmon (13) and rainbow trout (13), while among the important most reared group of species (cyprinids) only common carp (8) and rohu carp (1) are represented in the list. This is the group of species where genetic improvement would benefit the most people as production is extensive (consisting of many small farms). From these figures it was calculated that approximately 8.2% of the aquaculture production in 2010 is based on genetically improved stocks (Table 12). It is believed that this is an optimistic estimate for most farmed species, except for the case of Atlantic salmon for which solid data demonstrates that around 97% of the world production is based on improved stock (Gjedrem and Baranski, 2009). Taking into account that some breeding programs may be missing in Table 12, and that some large integrated aquaculture companies may be applying in-house individual selection programs, it is reasonable to conclude that less than 10% of aquaculture production in 2010 was based on genetically improved stocks. For recent comprehensive surveys on applied breeding programs in European aquaculture, see the 2009 report from the EU funded “Aqua Breeding” project (Anonymous, 2009), and Neira (2010) and Rye et al. (2010) for a broader perspective on the status in developing and developed countries, respectively.

Table 11
Genetic gain in Atlantic salmon over five generations of selection (Thodesen et al., 1999).

Trait	Improvement selected over wild (%)
Growth rate	+113*
Food consumption	+40*
Protein retention	+9
Energy retention	+14*
FCR[a]	−20*

[a] Feed conversion ratio or kg feed per kg body weight produced. (*, $P<0.05$)

Table 12
Impact of selective breeding programs on the production of different aquaculture species (modified from Neira, 2010 and Rye et al., 2010).

Species	No. of programs[a]	No. of families per program	Average no. of traits selected	World prod. in 2005, (1000 tonnes)
Common carp	8	76	2.0	3044
Rohu carp	1	60–70	2	1196
Silver barb	1	–	1	97
Tilapia Nile	20	229	3.6	1703
Tilapia blue	2	90	2.0	2
Tilapia red	4	125	4.0	–
Tilapia *O. shiranus*	1	51	1.0	–
Channel catfish	1	200	4	380
African catfish	1	70	1	29
Striped catfish	1	182	3	436
Atlantic salmon	13	280	5.4	1236
Chinook salmon	2	100	1.5	24
Coho salmon	4	133	2.7	117
Rainbow trout	13	206	5.2	487
European whitefish	1	70	2.0	1
Turbot	2	60	1.0	7
Atlantic cod	3	110	4.0	8
European seabass	3	100	5	58
Sea bream	4	100	6	111
Freshwater prawn	2	82	1	205
Shrimp, *P. monodon*	3	212	–	723
Shrimp, *P. vannamei*	4	197	2.0	1599
Abalone	3	210	1.7	334
Oysters	3	48	4.3	4615
Mussel	1	60	3.0	1410
Total listed species	101	–	–	17,822
Total all species	–	–	–	48,150[b]

[a] Number of programs using sib information in the selection decisions.
[b] Estimates of production based on improved stock was done as follows: Species not listed in the table represent a production of 30.3 million tonnes, adding 90% of production for common carp and rohu, adding production for oysters and mussel reduced with production in New Zealand and Australia because of their breeding programs, this gives 39.7 million tonnes not based on improved stocks or 8.2% of total production.

7. Interaction between farmed and wild stocks

As domestication and selective breeding of a species progresses, key characteristics of farmed animals will differ more and more from wild stock. Some animals are likely to escape from farms and could interact with the wild stock. The ability of selectively bred escapees to survive, outcompete wild fish and reproduce will no doubt depend on the wild populations, the local environment and ecology, the timing and extent of release(s) and the extent of genetic divergence of the selected stock from the wild stock. It is difficult to test the extent of the introgression of selected stock over time, but one possibility is that because the selectively bred fish are not under the same pressures of natural selection as their wild counterparts, they will gradually become less well adapted to the natural situation: 1. by means of random genetic drift in the absence of selection pressures and 2. by means of artificial selection focusing on improvement of economically valuable traits in the farm environment. It therefore follows that if they are less well adapted, and because of the continuing pressures of natural selection in the wild, that they will be less likely to pass on their genes to subsequent generations, and less likely to influence the long-term genetic makeup of the local population. Alternatively, if selected stocks are under the same pressures of natural selection as their wild counterparts, then the extent of introgression of selected stock will be greater. This issue is complex. For more in-depth discussion on the subject, see e.g. Bentsen and Thodesen (2005), Clifford et al. (1998a, 1998b), Crozier (1993), Skaala and Hindar (1998).

Demand for aquaculture products has also led to the introduction of non-native species to many countries in which production takes place. Escapees of these introduced species could establish viable populations in the new environment and potentially displace local species. As it is not possible to generalise and predict what effect the introduced species will have on local wild populations, a precautionary approach is advisable.

Under any circumstances, the farming sector must reduce the number of escapees as much as possible in order to minimise the effect domesticated stocks may have on the wild fish populations. To further reduce the risk for adverse effects, farming may be based on the use of sterile animals produced by chromosome manipulation (Purdom, 1993) or other means of sterilisation. However, no sterilization technique is 100% effective, and possible side effects of sterilization on other traits also need to be evaluated. The growth rate of triploid fish is generally lower than for diploids (Galbreath and Thorgaard, 1995; Hussain et al., 1995; Jonasson, 1984), although for oysters triploid animals have been found to grow much faster compared with diploids (Guo et al., 1996; Nell et al., 1994).

8. Benefits from worldwide breeding programs

8.1. Increased production

From a production point of view there is much to be gained by producing stock which is genetically improved. Basically all applied breeding programs have improvement of growth rate as a major goal, and most results on selection response for growth cited in this paper were obtained when selection targeted growth rate as the only trait. It is expected that gain for the individual traits in selective breeding programs will be reduced as the number of traits under selection is increased.

In order to give a broad indication of the potential for increased production with increased use of genetically improved stocks in aquaculture farming, below we assume that selective breeding produces 12.5% genetic gain per generation on average. This is the approximate rate of genetic gain measured in most fish and shellfish selective breeding programs (Gjedrem and Thodesen, 2005). Furthermore, we use an average generation interval weighted according to importance in terms of world food production for the farmed species which is calculated as follows:

$$\text{Average generation interval} = \Sigma(x_i \cdot y_i)/\Sigma\ y_i = 2.3\ \text{years}$$

where x_i and y_i are the generation interval and the reported 2005 production level (FAO, 2007), respectively, for species *i*.

Hence the yearly genetic gain for growth rate was calculated to be 5.4% (12.5%/2.3). Fig. 2 shows how aquaculture production would increase under alternative scenarios for use of genetically improved material. Using the average generation interval derived above (2.3 years), 13 years would allow between 5 and 6 generations of selection. The lower line shows that production will increase to 53.2 million tonnes in 2020 if the proportion of genetically improved material is kept at the present level (8.2%, Table 12). The figure also shows the potential for increased production if the use of improved material is increased. If the total aquaculture production were based on genetically improved stock, the production would be doubled in 2020 as compared with 2007. This means that less than six generations of selective breeding can potentially double the production of fish and shellfish.

How the use of selective breeding will develop in the future depends on many local and international factors, and hence is difficult to predict. One challenge is the high number of aquaculture species farmed; in 2005 there were 241 species included in the statistics (FAO, 2007) out of which 124 were reported with production of more than 1000 tonnes. Under the most optimistic scenario at least one breeding program would be developed for each species. In economic terms, highest returns would be gained by focusing the efforts on establishing breeding programs for the species with the highest production and value. In 2005, seven species were reported with production numbers exceeding two million tonnes (FAO, 2007); five carp species (common carp, grass carp, silver carp, bighead carp and crusian carp) combined accounting for 77% of total carp production and 51% of total fish production; Pacific cupped oyster representing 97% of oysters production; and Japanese carpet shell representing 71% of clam production. For these species China's production accounted for between 68 and 85% of the total world production.

During the last few decades, the expansion of aquaculture production has been astonishing; fish and shellfish production were 7.6 times higher and seaweed 2.5 times higher in 2008 compared to 1984 (FAO, 1995, 2010a). There are no reasons to believe that this growth rate (corresponding to 7.7% per year) shall not be maintained or increased in the years ahead. If we optimistically assume that the demonstrated benefits of genetically improved stocks lead to a significant increased uptake of selective breeding technology in major farmed species, a scenario in which 50% or more of the world production in 2020 originates from improved stocks may be realistic. Since improved stocks grow faster, and are more efficient converters of feed, the overall aquaculture production will increase faster as the use of genetically improved stock increases.

Under this scenario, the availability of fish and shellfish for human consumption will increase dramatically. Assuming that the current growth in production of the aquaculture sector is maintained, the production per capita will be more than doubled in 2020 (Table 13), even if the use of genetically improved seed is kept stable at the current level. However, with increased use of genetically improved stocks, production will increase markedly, up to a theoretical maximum of 25.1 kg per capita in 2020, which would represent a more than three-fold increase compared with the consumption in 2007 (Table 13).

8.2. Improved economic value

A substantial benefit of breeding programs stems from reduced production cost per unit (Dickerson, 1970; Smith et al., 1986). Miller

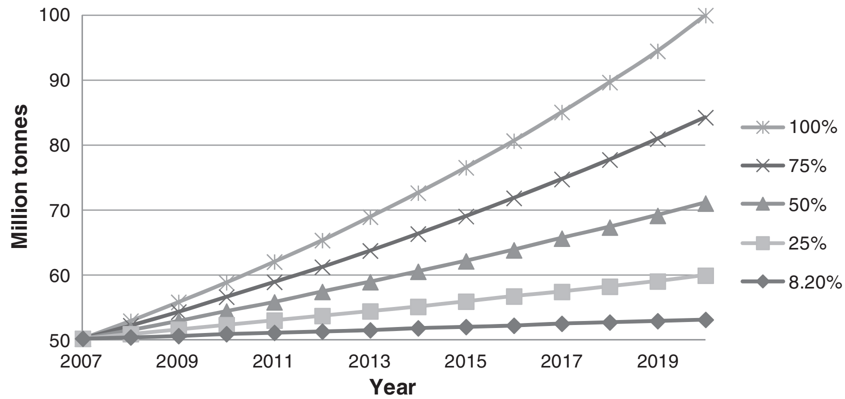

Fig. 2. Aquaculture production (fish and shellfish) based on varying frequencies of genetically improved stocks with a genetic gain of 5.4% per year (12.5% genetic gain per generation/ 2.3 years generation interval).

and Pearson (1979) add that a portion of this saving is retained by the producer, while a portion is also passed on to the consuming public.

The general cost of running breeding programs varies among individual programs, among countries as well as among target species. Two studies about the economic value of breeding programs have been conducted for Atlantic salmon in Norway. Gjerde and Olsen (1990) estimated the genetic gain to be 10% per generation for growth rate and 3% for age at sexual maturation. The corresponding profit was estimated to US $0.13 and $0.08 per kg fish produced, respectively, totalling $0.21 per kg fish. At present close to 100% of Atlantic salmon production in Norway is based on improved stocks (Gjerde et al., 2007). The breeding goal includes growth rate, disease resistance and product quality (Gjedrem, 2010). Estimates of genetic gain are only available for growth rate, and to some extent for feed conversion efficiency and age at sexual maturity. The total added value over seven generations of selection for Atlantic salmon (measured as the profit derived from having fixed costs of production per unit area spread over more kilogram of product or derived from savings in feed costs per kilogram of production) was estimated to be $2.50 per fish produced or around $0.30 per generation per fish or $0.08 per year per kg of salmon produced. In 2010 the Norwegian production reached 1 million tonnes and the economic value of selective breeding was of the order of $80 million.

Little is known about the genetic improvement of disease resistance and product quality traits in breeding programs for Atlantic salmon. The exception is for IPN where Atlantic salmon bred for high resistance showed higher survival compared with salmon bred for low resistance (Storset et al., 2007). However, several diseases with relatively high heritabilities are included in the breeding goal (Gjedrem, 2010) and the expectation is that genetic improvement is obtained (Henryon et al., 2002; Kjøglum et al., 2008). Robinson and Hayes (2008) have estimated that a family based selective breeding program for resistance to a typical disease in Atlantic salmon (assuming a low heritability of 0.1 and selection based on breeding values from disease challenge test data) would result in a benefit cost ratio of around 18:1 and total added value per kilo of fish to the Norwegian industry of $0.31 per year after 10 generations of selective breeding. In addition to the direct benefits from selection for disease resistance, four studies report a positive genetic correlation (averaging 0.29) between growth rate and disease resistance (Gjedrem et al., 1991; Jonasson, 1993; Rye et al., 1990; Standal and Gjerde, 1987) which means that as growth rate increases disease resistance also increases. In shrimp the relationship between growth rate and disease resistance seems to be different than fish because negative genetic correlations have been estimated (Fjalestad et al., 1997; Gitterle et al., 2005). Further, as the growth rate of fish and crustaceans increases, and time to market size becomes shorter, mortality will be reduced simply because the animals live a shorter time. Based on this background information there is high probability that mortality will be reduced by selective breeding programs, in particular when diseases are included in the breeding goal, and that this will have large economic benefits for aquaculture industries.

Investment in effective breeding programs will give high economic returns in future generations because genetic improvement is cumulative over generations and is permanent and sustainable. However, few studies have attempted to calculate the realised economic value of genetic improvement, which implies that it is difficult to find relevant data. For Atlantic salmon Gjerde et al. (2007) estimated the running cost of the breeding programs in Norway $0.01 per kg of fish based on data from Kontali Analyse (2005). The economic value of genetic improvement during 7–8 generations of selection was estimated to be $0.08 and the estimated benefit–cost ratio 8–1 (Gjerde et al., 2007). This is a lower estimate compared with an earlier estimate of benefit–cost ratio of 15/1 by Gjedrem (1997).

In a study of Nile tilapia based on simulations, Ponzoni et al. (2007) estimated benefit/cost ratios by varying different factors in family based breeding programs. Their estimates of benefit/cost ratio varied from 8.5/1 to 60/1. They found that benefit/cost ratios were most sensitive to reproduction efficiency in the nucleus and in hatcheries. For common carp Ponzoni et al. (2008) estimated the benefit/cost ratio to vary from 0 to 42/1. Price of fish and feed cost had a substantial effect on the benefit/cost ratio. In a simulation study of selective breeding for abalone Robinson et al. (2010) estimated a benefit/cost ratio of 48/1. Hence the estimates of benefit/cost ratio in aquatic species do not differ much from those published for farm animals like pigs, sheep and cattle which range from 5/1 to 50/1 (Barlow, 1983; Mitchell et al., 1982).

Under intensive farming conditions it is important to know which factors potentially contribute the most to improved performance. Havenstein et al. (2003) compared the relative contribution of feed improvement and selective breeding to the increase in productivity of broilers. They reported an overall reduction of 68% in number of

Table 13
Prognoses for aquaculture production in kg per capita per year under various scenarios for use of genetically improved stocks.

Year	World human population[a]	Present increase in production (7.6%)	Proportion of aquaculture production based on genetically improved stocks			
			25%	50%	75%	100%
2007	6.6	7.6	7.6	7.6	7.6	7.6
2010	6.8	9.2	9.4	9.4	9.5	9.6
2015	7.2	12.6	13.3	13.8	14.3	14.8
2020	7.6	17.4	19.4	21.1	23.2	25.1

[a] http://www.census.gov/population/international/data/idb/informationGateway.php.

days to harvest during the investigated period of 45 years, and concluded that genetic selection was responsible for 85–90% of the growth rate improvements while improved nutrition accounted for the remaining for 10–15%. During this same period the feed conversion rate was improved from 3.84 to 2.72 kg feed/kg growth, and for this trait selective breeding and feed improvement contributed equally. Likewise in pigs, Fix et al. (2010) estimated a reduction of 15% days to harvest over 21 years and found that genetic improvement was responsible for 50% of the progress. Backfat depth was reduced by 15–20% and 100% of this change was due to genetics.

8.3. Improved utilization of resources

In intensive aquaculture production, feed usually represents more than 50% of the total costs. We therefore need to reduce the amount of feed per kg of production. According to Thodesen et al. (1999), the feed conversion ratio (FCR) of Atlantic salmon was improved by 20% during five generations of selection (Table 11). During this period selection was mainly for growth rate which was improved by 113%, or 22.6% per generation, which is a very high genetic gain. In Section 8.1 an estimate for genetic gain of 12.5% growth rate per generation was used to estimate the potential of selective breeding to improve aquaculture production. FCR would be reduced by around 13.8% per generation for every 12.5% increase in genetic gain for growth rate assuming the same magnitude of correlation as reported by Thodesen et al. (1999).

If we project development over the period from 2007 to 2020 (5.65 generations of selection), the expected reduction in FCR by 2020 would be around 15.6% (13.8%/5 ∗ 5.65). Alternatively we could estimate how much fish could be produced using the amount of feed saved because of the genetic improvement in FER (kg fish/kg feed) as 1/(1–15.6) = 1.18, which means that it is possible to produce 18% more fish on the amount of feed saved.

8.4. Scope for international breeding companies

For terrestrial farm animals the trade of seed stock tends to be dominated by large and internationally oriented breeding companies, particularly in poultry, dairy cattle and pigs. This development has given an advantage in that large companies have had the economic capacity to develop efficient programs for production of high yielding animals. One of the problems they face is the variation in environmental conditions between countries and climatic zones. Therefore a premise for this development is that there is relatively low genotype by environmental interaction (G × E). If G × E is substantial, the alternative is to develop strains which can tolerate specific environmental conditions.

Pirchner (1985) concludes that G × E is important when environment cannot be controlled under farming conditions, and less important when environmental factors can either be partly controlled or standardised. For fish and shellfish there are several estimates of low G × E effects [Gunnes and Gjedrem (1978) for Atlantic salmon; Gunnes and Gjedrem (1981) for rainbow trout; McKay and Gjerde (1986) for Atlantic salmon; Sylven et al. (1991) for rainbow trout in five out of six environments investigated; Myers et al. (2001) for coho salmon; Reddy et al. (2002) for rohu carp; Eknath et al. (1993) for Nile tilapia; Swan et al. (2007) for Pacific oysters]. However, considerable G × E interaction has also been found by some authors [(Moav et al. (1975) for common carp; Sylvén et al. (1991) in one out of six environments for rainbow trout; Langdon et al. (2000) for Pacific oyster; Maluwa et al. (2006) for *Oreochromis shiranus*; Dupont-Nivet et al., 2010 for European seabass (*Dicentrarchus labrax*)], and Ponzoni et al. (2008) showed that economic benefit of breeding programs is reduced with increased G × E. Since results are not consistent it is not possible to draw a general conclusion about the importance of G × E for aquatic species. It is therefore important to investigate possible G × E effects under relevant farming conditions.

Efficient and sustainable breeding programs for aquatic species must have a broad breeding goal aiming at improving traits of economic importance, including non-market value traits. The number of test families must be large and this therefore requires considerable investments. Hence for a genetic improvement program to be economically viable, it must serve a larger production sector. Although most breeding companies still supply only a national industry, a clear trend towards breeding companies serving international markets is now seen for species such as Atlantic salmon, rainbow trout, tilapia and shrimp (Rye et al., 2010).

9. Concluding discussion

Early in 2011 FAO declared that '1 billion people live in chronic hunger', which means that there is an ongoing food crisis in the world. Moreover, the world population is expected to increase rapidly in coming years, and Diouf (2009) points out that strong growth in income and urbanization will occur, with associated shifts in diet structure towards more nutritious and higher quality foods. This implies that the demand for animal protein will increase at a high rate. The prospect of future food shortages is a tragic situation which should raise an immediate engagement from all of us. The important question is how this large problem can be solved or reduced and what role can aquaculture play in this situation?

Most Asian countries have a long history in aquaculture production, while on the other continents the aquaculture sector is relatively young although the potential and natural conditions for aquaculture are very good in most countries. However, basic knowledge about aquaculture production is generally low. Education in aquaculture farming and greater availability of relevant literature is therefore critical for a successful and sustainable expansion particularly in countries with an emerging aquaculture sector.

The potential for increased aquaculture production is large considering space and waters. A large expansion in aquaculture is, however, dependent on competition for space and water with other activities and on increased production of fish feed. Genetic improvement of growth rate, survival and feed conversion efficiency has been shown to reduce space, water and feed requirements, and could have a large effect on world aquaculture production if widely adopted. Genetic improvement also reduces production costs as more animals can be grown using the same resources. Therefore, selective breeding in aquaculture should play an important role in meeting the increasing world demand for animal protein.

To enhance the sustainable development of future aquaculture production we need to increase the number and efficiency of selective breeding programs. The largest benefits will come from focusing on stocks and countries with the highest production. China lacks breeding programs for the world's most important farmed species, except for one family based breeding program for common carp and one for tilapia. Hence, given China's dominant position in aquaculture production, the future global impact of selective breeding will depend to a large degree on the extent of adoption of breeding technologies by China.

There could be several reasons why use of selective breeding in aquaculture is far behind plants and terrestrial farm animals. We deal with small animals where each individual has a low economic value and the production units are relatively small. For many species fry and fingerlings of wild stock are easily obtained and inexpensive. For some species, particularly marine species, there is little knowledge about controlling reproduction. Further there is a lack of knowledge about the economic benefit of breeding programs, as well as a lack of knowledge about quantitative genetics and how to start and run breeding programs. Many aquaculture farmers do not participate in cooperatives or other organisations which have the ability to initiate breeding programs. The investment required to establish effective family based breeding programs are substantial, and farmers are often not willing to pay more for the improved stocks. However, simpler programs facilitating individual selection for growth rate may be efficient and can be run with less investment and low operational costs. Researchers working in the field have not effectively been able to promote the benefits of selective breeding to industry and those extending knowledge to aquaculture lack information and knowledge about the potential of selective breeding. International organizations dealing with aquaculture do not effectively advocate and stimulate the development of selective breeding programs. However, there are some local government and international organisations that have funded the initiation of selective breeding programs. ICLARM together with AKVAFORSK initiated the GIFT project and the World Fish Center continues to support and develop some breeding programs.

In summary, the most pronounced effects farmers would experience in 2020 if they were to use stocks genetically improved through six generations of selective breeding would be: Fish and shellfish could reach market size in half the time, costs of production could be reduced, feed conversion efficiency could be improved, rates of survival could be improved and the same facilities could be used to produce many more kilograms of aquatic species. The main assumptions for these statements are that the market size of fish and shellfish is close to constant over this period, the density, or number of fish and shellfish per production unit remains constant and the time for pond cleaning and for rejuvenation of the sea bed under cages between each generation is short.

We agree with the statement of Colin Nash (2011): 'The future of global aquaculture will depend not on future technological development, but rather on public demand, markets, and commitment to its future success'.

Acknowledgements

We are indebted to Nofima for their financial contribution and to our colleagues for continued and stimulating support. In particular we would like to thank Dr. Bjarne Gjerde, who took the initiative to recommend this review, and Dr. Jørgen Ødegård for their valuable contributions.

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