Aquaculture 472 (2017) 8–16

Contents lists available at ScienceDirect

Aquaculture

journal homepage: www.elsevier.com/locate/aquaculture

Impact of selective breeding on European aquaculture

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ARTICLE INFO

Article history:
Received 29 September 2015
Received in revised form 29 January 2016
Accepted 7 March 2016
Available online 8 March 2016

Keywords:
Breeding programs
Market share
Aquaculture
Genetic gain
Europe

ABSTRACT

Objectives of this study were to determine the combined market share of breeding companies in aquaculture production in Europe, to describe the main characteristics of breeding companies and their programs, and to provide per species estimates on cumulative genetic gain in growth performance. Surveys were conducted among breeding companies of five major species cultured in Europe: Atlantic salmon, rainbow trout, European seabass, gilthead seabream, and turbot. The market share was estimated as the combined egg or juvenile production of breeding companies relative to the total egg or juvenile production in Europe for each species in 2012. Cumulative genetic gain was estimated from the number of selected generations in current breeding programs, combined with genetic trends, reported selection responses in literature, and phenotypic differences. The combined market share of breeding companies ranged from 43–56% for seabass to 100% for turbot. The total volume of fish production in Europe that originated from selective breeding was 1653–1706 thousand tonnes, corresponding to 80–83% of the total aquaculture production. Over species, there were 37 breeding programs of which the majority performed family selection. Growth performance was universally selected upon.

Cumulative genetic gain in growth performance varied from +65% for turbot to +900% for trout in terms of harvest weight, and from +25% for turbot to +200% for trout in terms of thermal growth coefficient. It is concluded that selective breeding has a major impact on European aquaculture and will contribute to future growth of the sector.

Statement of relevance: This manuscript helps to understand the impact of selective breeding on European aquaculture. It shows that the adoption of selective breeding is much higher in Europe than globally. It demonstrates that selective breeding has led to major improvements. Forecasts of industry trends are made and the importance of selective breeding to future growth of aquaculture production is illustrated.

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1. Introduction

In Europe, the six main cultured finfish species are Atlantic salmon (*Salmo salar*), rainbow trout (*Oncorhynchus mykiss*), gilthead seabream (*Sparus aurata*), European seabass (*Dicentrarchus labrax*), common carp (*Cyprinus carpio*) and turbot (*Scophthalmus maximus*). Together their production accounts for 97% of the total aquaculture production in Europe (Table 1). Aquaculture plays an increasingly important role in global food production and this trend is expected to continue (FAO, 2014). If widely adopted, selective breeding will play an important role in securing the future demand for aquaculture products (Gjedrem et al., 2012).

The start of domestication of most species coincided with early advances in reproductive techniques, which in a few cases, dates back to more than a century ago. Selective breeding generally has a much shorter history and often followed the industrialization of aquaculture as outlined below. The order in the following overview on breeding in aquaculture species is based on the length of the domestication history.

1.1. Carp

Common carp has the longest history of domestication. With the advancement in reproductive techniques during the 19th century, many different strains were developed in Germany and the Czech Republic (Komen, 1990). Since then, genetic improvement has largely relied on crossbreeding of inbred strains and selective breeding plays only a minor role (Janssen et al., 2015; Vandeputte, 2003). Carp will, therefore, not be considered in this study.

1.2. Trout

Rainbow trout was introduced to Europe from the USA in the period 1890–1900, with the primary intent to develop recreational fisheries (Crawford and Muir, 2008). These fish formed the genetic basis for modern trout farming (Gall and Crandell, 1992; Gross et al., 2007).

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http://dx.doi.org/10.1016/j.aquaculture.2016.03.012
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Table 1
Aquaculture production of six major finfish species in Europe in 2012 (FAO, 2015).

Species	Production (1000 t)	Proportion of total production (%)
Atlantic salmon	1487	72
Rainbow trout	253	12
Gilthead seabream	104	5
European seabass	71	3
Common carp	67	3
Turbot	13	1
Other	70	3
Total Europe	2065	100

Hatcheries at the time were part of (re)stocking programs and in selection most emphasis was placed on improvement of fecundity, early sexual maturity and off-season spawning (Donaldson and Olson, 1957; Gall, 1975; Millenbach, 1950). Commercial aquaculture of trout started to develop in the 1950's (Paisley et al., 2010) and in the 1970's multiple hatcheries performed selection schemes with the aim to improve traits relevant for aquaculture, such as bodyweight and precocious maturation, although the scientific basis of these breeding programs was limited (Aulstad et al., 1972; Gjedrem, 1985; Guyomard, 1981; Morkramer et al., 1985).

1.3. Salmon

In the late 1960's, fish from fish farm Mowi AS were used to set up the first breeding program for Atlantic salmon. This program formed the genetic basis for the currently produced Mowi strain (Glover et al., 2009). In the early 1970's, AKVAFORSK collected fish from 40 Norwegian rivers, one Swedish river, and fish farm Mowi to set up the first family selection breeding program, from which the current AquaGen strain originates (Gjedrem, 2012; Gjedrem et al., 1991). Other strains with major contributions to currently farmed salmon in Europe are Bolaks, collected around 1974–1975, and Jakta, collected somewhere in the 1980's (pers. comm. Bakke, 2014).

1.4. Seabream, seabass and turbot

In the south of Europe, aquaculture of European seabass and gilthead seabream started around the 1970's and was initially based on capture of wild larvae and juveniles. Following improvements in reproductive techniques, development of these industries accelerated in the 1990's (Coves et al., 1991; Divanach and Kentouri, 2000; Moretti et al., 1999). At that time, the first breeding programs for seabass were being developed in several countries (Chatain and Chavanne, 2009). The first trials on selective breeding of seabream were carried out in the mid-1990's (Knibb et al., 1997, Knibb et al., 1998) and it was only in the early 2000's that the first commercial breeding programs of seabream were initiated (Brown, 2003; Thorland et al., 2006). Turbot aquaculture started in the 1970's in Scotland and its production expanded rapidly in Southern Europe since 1990. The first breeding programs were initiated in the mid 1990's (Danacher and Garcia-Vazquez, 2007).

In summary, the adoption of selective breeding has spread from the north of Europe towards the south. First attempts for genetic improvement were often based on relatively simple mass selection schemes, but as industries matured more advanced breeding practices such as family selection gained ground.

The impact of selective breeding on European aquaculture can be described by the combined market share of breeding companies in production, traits that are selected upon and cumulative genetic gain. The first description of selective breeding in Europe was published in 2008 and was based on a survey conducted among breeding companies in Europe in 2006 (AquaBreeding, 2008). The study provided information on which traits were selected upon in breeding programs, but not on the combined market share of breeding companies in European production nor on cumulative genetic gain. On a global level, it has been estimated that in 2010 approximately 8.2% of the aquaculture production originated from genetically improved stocks (Gjedrem et al., 2012). In developed countries, this proportion was expected to be higher (Rye et al., 2010), but no specific estimates for the European situation are available. Data on selection response and cumulative genetic gain per species have been reported in literature, but these have not been analyzed in order to estimate cumulative genetic gain in existing breeding programs. In this study, improvements in growth performance, both in terms of harvest weight and thermal growth coefficient, are considered to be most illustrative for cumulative genetic gain, because these are quantitative traits that are universally selected among all five species (AquaBreeding, 2008).

Various methods to estimate cumulative genetic gain have been reported in literature. Genetic trend analysis, the regression of estimated breeding values on generations, provides good estimates of cumulative genetic gain (Blair and Pollak, 1984). Of indicative value is the selection response in early generations extrapolated to a higher current number of selected generations. The best predictors of cumulative genetic gain are common garden experiments, in which wild and selected fish are kept in the same environment to test their performance. In the same environment and in absence of genotype by environment interaction, phenotypic differences equal genetic differences (Blair and Pollak, 1984). Studies involving common garden experiments have, however, not been conducted, except for salmon (e.g. Glover et al. (2009) and Solberg et al. (2013)). Across environments, thermal growth coefficient (TGC) can be used alternatively to compare growth performance of wild and selected fish. TGC corrects for temperature effects on growth performance and is calculated as (Cho, 1992; Iwama and Tautz, 1981):

$$TGC = \frac{\sqrt[3]{W_t} - \sqrt[3]{W_0}}{\sum_{i=1}^{t} T_i} * 1000 \qquad (1)$$

Where W_0 is initial weight; W_t is weight at day t; T_i is daily average water temperature and $\sum_{i=1}^{t} T_i$ is the sum of daily water temperatures over the growing period. A trademark of TGC is that it corrects for heterogeneity in growing period and rearing temperature (Sae-Lim et al., 2013; Trong et al., 2013). Important sources of environmental variation are, thereby, corrected for and differences in TGC of wild and selected fish provide a proxy for genetic differences.

The objective of this study was to assess the impact of selective breeding on European aquaculture by determining:

1. The combined market share of breeding companies.
2. The main characteristics of breeding companies and their programs.
3. Cumulative genetic gain in growth performance.

1 and 2 are addressed based on surveys carried out among breeding companies in Europe. 3 is addressed by combining results from the surveys with a literature review.

In this paper, the term ‘breeding company’ is defined as a company, institute or organization, either private or public, that operates a selective breeding program for a particular species. Some breeding companies operate separate breeding programs for multiple species. Europe is defined as the EU28, Norway, Iceland, Faroe Islands and the Isle of Man. Cumulative genetic gain is defined as genetic gain that has been build up over multiple generations of selection. Two types of selection are distinguished: mass and family selection. In mass selection, breeding values are estimated based on own performance records only, whereas in family selection, records on related individuals are also used.

2. Materials and methods

2.1. Surveys among breeding companies

In a first survey conducted in collaboration with AQUATRACE,[1] questionnaires were distributed among breeding companies in Europe (Chavanne et al., 2016). Breeding companies were identified in the AQUABREEDING[2] research project, complemented by internet search and snowball sampling (Goodman, 1961). This first questionnaire included questions related to the type of selection, the number of selected generations, selected traits, and the quantities of eggs or juveniles produced. Breeding companies were asked not to declare eggs or juveniles that were disposed, and to avoid double counting when both egg and juvenile production data were reported. For all species, egg or juvenile production data of 2012 were collected, except for trout. For trout, 2011 data were collected because 2012 data were not available yet at the start of the survey. As not all companies completed this extensive first questionnaire, a second survey was carried out among the non-respondents of the first survey involving a limited number of questions. The aim of this second survey was to identify whether a breeding company employed mass or family selection and how many eggs or juveniles it produced.

2.2. Total egg and juvenile production in Europe

For the estimation of the market share of breeding companies, an estimate of the total egg or juvenile production in Europe was required. For seabass, seabream, and turbot, juvenile production data were retrieved from FEAP (FEAP, 2014; unpublished results FEAP, 2014). Trout and salmon breeding companies mainly sold eyed eggs, hence egg production data were collected for these species. Contrarily to juvenile production of seabass, seabream, and turbot, egg production data of trout and salmon were not routinely collected on a European level and had to be derived on a per country basis from various sources.

For salmon, per country data were collected, depending on availability, on number of eggs produced, import of eggs, export of eggs and number of eggs used in domestic production. For all countries some data were missing and had to be derived from other data. The data are related as follows:

$$\text{National egg production} = \text{eggs used for domestic production} + \text{export–import} \quad (2)$$

When the number of eggs used for domestic production could neither be obtained nor derived from Eq. (2), this figure was estimated from national fish production data, yield per smolt and egg to smolt survival, according to:

$$\text{Eggs for domestic production} = \text{fish production/yield per smolt/egg to smolt survival} \quad (3)$$

In this equation, means of national fish production statistics of 2012 according to FEAP (2014) and FAO (2015) were used as fish production data. Yield per smolt was 4.39 kg for Norway, 5.49 kg for the Faroe Islands (Marine Harvest, 2014), and it was assumed to be 4.5 kg for Iceland. Egg to smolt survival was assumed to be 80% (pers. comm. Bakke, 2014).

For trout, no complete overview of the trade and use of eggs was required to estimate the egg production for every country. Only national egg production statistics per country were, therefore, collected. When the national egg production was unknown, it was derived with Eq. (2). The quantity of eggs used in production was estimated from fish production, assuming a mean harvest weight and survival, similar to Eq. (3).

[1] AQUATRACE — https://aquatrace.eu/ — 7th Framework Programme for research (FP7)
[2] AQUABREEDING — 6th Framework Programme for research (FP6)

2.3. Market share of breeding companies

Market share is defined as a firm's sales relative to the total sales of all firms in the same industry (Ghosh, 2004). Here, it was used first as the combined egg or juvenile production of breeding companies relative to the total egg or juvenile production in Europe for each particular species. The egg and juvenile production of breeding companies followed from the survey results. Second, to estimate the total aquaculture production in Europe that originated from selective breeding, market shares of breeding companies were multiplied by volumes of fish production per species (Table 1). This volume was divided by the total aquaculture production in Europe to estimate the market share of selective breeding.

For salmon, the combined reported egg production of breeding companies was higher than the total egg production in Europe. The market share of breeding companies could, therefore, not be determined from the combined egg production of breeding companies relative to the total egg production in Europe. Instead, it was estimated as 100% (473 million eggs) minus the part of the egg production that with certainty could not be attributed to breeding companies on a per country basis.

2.4. Cumulative genetic gain

Cumulative genetic gain in trout was estimated both from reported selection responses and by comparison of TGC's of wild and selected fish. Cumulative genetic gain in salmon was estimated from common garden experiments performed in recent generations. Cumulative genetic gains in seabass, seabream, and turbot were estimated both from reported selection responses and from genetic trends. One of the outcomes of the survey was the number of selected generations in current breeding programs. This information was used to extrapolate cumulative genetic gain in a studied generation to current generations in breeding programs. When cumulative genetic gain on either harvest weight or TGC could not be estimated directly, a standard production situation with regard to temperature, initial weight, and harvest weight was assumed to convert cumulative genetic gain in harvest weight to cumulative genetic gain in TGC, and vice versa.

3. Results

Out of 37 existing breeding programs, data of 28 were retrieved in the first survey. An additional nine breeding programs participated in the second survey. All information requested in either survey, was obtained from participating breeding programs. There was only one seabream breeding program from which no data were obtained, but this program was of minor importance and was therefore ignored.

3.1. European egg and juvenile production

An overview of juvenile production data of seabass, seabream, and turbot is presented in Table 2. Greece was the major producer of juveniles for both seabass and seabream and Spain was the major producer of turbot juveniles. For turbot, the reported juvenile production in Spain is probably closer to 17 million (pers. comm. Cabaleiro, 2015).

For trout, the French egg production was based on the assumption that approximately 90% of the egg production originated from breeding companies in the survey (pers. comm. Haffray, 2015) (Table 4). The Polish egg production was calculated from fish production, assuming a mean survival of 35% and a harvest weight of 350 g, corrected for the import of eight million eggs (pers. comm. Anonymous, 2015) while export was assumed zero. The Swedish egg production was calculated from production assuming a mean survival of 45%, a harvest weight of 2 kg and no export nor import of eggs (pers. comm. Funcke, 2015).

Table 2
Juvenile production of European seabass, gilthead seabream, and turbot per country in 2012 (FEAP, 2014; unpublished results FEAP, 2014).

Country	European seabass (million juveniles)	Gilthead seabream (million juveniles)	Turbot (million juveniles)
Croatia	8.1	5.4	0
Cyprus	5.3	8.0	0
France	46.0	30.4	1.3
Greece	184.0	245	0
Italy	40.0	70	0
Spain	36.4	55.0	[a]19.0
Total Europe	319	414	20.2

[a] This figure should rather be 17 million (pers. comm. Cabaleiro, 2015).

The number of eggs used in production in England and Wales was 39 million, calculated from a fish production of 6 824 t (Reese, 2013), an egg to harvest survival of 50%, and a harvest weight of 350 g. This figure was used together with data of Northern Ireland (DARD Fisheries, 2014) and Scotland (Munro and Wallace, 2012) to calculate egg production in the UK.

For salmon, the only unknown variables that could not be calculated directly using Eq. (2) or (3) were the Norwegian egg production and export of eggs (Table 3). The Norwegian export of eggs was calculated by subtracting exports by the other countries from total exports. Total exports by European countries were determined as the sum of imports by European countries and exports to outside Europe, the latter of which were limited to the export of 32.2 million eggs to Chile (Sernapesca, 2014), while imports from non-European countries were negligible (pers. comm. Bakke, 2014). When the Norwegian export was known, the Norwegian egg production could be calculated with Eq. (2) and equalled 360 million. The number of eggs used in production in Norway was calculated at 352 million using Eq. (3), which corresponds well to the 370 million eggs used in production in 2013/2014 (Kontali Analyse cited in Hosteland, 2014). The total egg production in Europe was 473 million.

3.2. Market share of breeding companies

The reported egg and juvenile production per breeding program are presented in Table 5. For seabass, one company did not produce any eggs or juveniles from its breeding program in 2012. Another seabass breeding company indicated to have sold eggs and larvae, which were estimated to have resulted in the production of an additional 40–60 million juveniles in Europe.

The market share of breeding companies per species is presented in Table 6. The only three companies that reproduced turbot operated breeding programs (pers. comm. Cabaleiro, 2015), hence their combined market share was 100%. For salmon, the combined egg production by the seven breeding companies was 513–558 million, which was 40–85 million higher than the total egg production in Europe. The production of 26–31 million eggs in the UK and the Faroe Islands did not originate from the seven breeding companies. This egg production originated from a few small companies that did not have a breeding program (pers. comm. Tinch, 2014) and from a breeding program that was terminated in 2005 (pers. comm. Patursson, 2015). The market share of breeding companies was therefore 93–95% in 2012. Since 2013, the broodstock in the Faroe Islands was replaced by broodstock of one of the seven breeding companies and the market share of breeding companies has increased accordingly to 96–97%.

The total volume of fish production in Europe that originated from selective breeding was 1653–1706 thousand tonnes, corresponding to 80–83% of the total aquaculture production.

Table 3
Production of eyed eggs of rainbow trout in Europe in 2011.

Country	Production (million)	Reference
France	400	Estimate based on pers. comm. Haffray (2015)
Denmark	324	pers. comm. Thomsen (2014)
Italy	265	pers. comm. Grossi (2014)
Spain	259	Ministerio de Agricultura (2014)
Poland	110	Estimated from fish production
Isle of Man	50	pers. comm. Dentler (2015)
United Kingdom	48	Estimate based on pers. comm. DARD Fisheries (2014), Munro and Wallace (2012), Reese (2013)
Norway	40	pers. comm. Korsvoll (2014)
Finland	21	pers. comm. Kause (2014)
Germany	13	Statistisches Bundesamt (2012)
Sweden	13	Estimated from fish production
Total Europe	1543	

Table 4
Production and trade of eyed eggs of Atlantic salmon within Europe in 2012.

Country	Production (million)	Export (million)	Import (million)	Used in domestic production (million)
Norway	360 [C2]	30 [C]	22 [R1]	352 [C3]
Iceland	55 [R2]	54 [R2]	0 [C2]	1 [C3]
UK-Scotland	18.5 [R3]	0 [R3]	44.7 [R3]	63.2 [R3]
Ireland	16.9 [R4]	10.1 [R4]	0.6 [R4]	7.4 [R4]
Faroe Islands	12.5 [R5]	0 [R5]	4.5 [C2]	17 [C3]
UK-rest	10 [R3]	10 [R3]	0 [R6]	0 [R6]
Total Europe	473	104	72	441

R = values from references: [1] Bakke (2014); [2] Jonasson (2014); [3] Munro and Wallace (2012); [4] Robinson (2014); [5] Patursson (2013); [6] Poseidon (2008).
C = calculated: [2] using Eq. (2); [3] using Eq. (3).

3.3. Characteristics of breeding companies and their programs

Two types of breeding companies can be distinguished. The first type controls the entire process from reproduction to harvest and has integrated a breeding program in the production process. The second specialized type of breeding company operates a breeding program as its core activity. These companies operate in an international market for egg/juvenile sales in which they experience a high degree of competition. Most larger scale trout breeding companies, most salmon breeding companies, one medium size seabass breeding company, and one medium size seabream breeding company belonged to this specialized type. Most companies operated a single breeding program. Of the companies that operated a breeding program for seabream, however, four also operated a breeding program for seabass. Only one company operated a breeding program for both trout and salmon.

The combined results of both surveys revealed that for the 37 breeding programs that participated, mass selection was performed in 12 and family selection in 25 breeding programs (Table 5). When family selection was performed, egg or juvenile production tended to be higher than when mass selection was performed. The vast majority of the specialized breeding companies performed family selection. Integrated companies performed mass and family selection about equally often. When mass selection was performed, selected traits were generally limited to growth performance and morphology, whereas in family selection more traits were included (Table 7).

3.4. Cumulative genetic gain

For trout, the highest reported number of selected generations was 20 in mass selection and 14 in family selection. Considering a three year generation interval, the oldest mass selection program started in the mid 1950's and oldest family selection program started in 1972 (AquaGen, 2015). The reported number of selected generations varied strongly among breeding programs and many of the younger programs were established from strains that had previously been selected, often

Table 5
Per species egg or juvenile production from breeding programs and the type of selection performed.

BP	Species	Eggs/juveniles	Million	Selection	BP	Species	Eggs/juveniles	Million	Selection
1	Trout	Eggs	210	f	20			17	f
2			200	f	21			10–15	f
3			188	f	22			10	f
4			120	m	23	Seabass	Juveniles	[a]52–72	m
5			80	m	24			40–60	f
6			30–60	f	25			30	m
7			51	f	26			16	m
8			50	f	27			0	f
9			25	f	28	Seabream	Juveniles	75	f
10			20	m	29			70	f
11			18	f	30			40–60	f
12			2–10	f	31			30–35	f
13			6	m	32			20	m
14			6	m	33			13	f
15			<2	m	34			<2	m
16	Salmon	Eggs	210–230	f	35	Turbot	Juveniles	12	f
17			100–120	f	36			5	f
18			111	f	37			1.3	m
19			55	f					

BP = breeding program.
f = family selection, m = mass selection.
[a] Includes estimated juvenile production from egg sales in Europe.

Table 6
Market shares of breeding companies per species.

	Rainbow trout	Atlantic salmon	European seabass	Gilthead seabream	Turbot
Total reported egg/juvenile production by breeding companies (million)	1006–1048	513–558	[a]138–178	248–275	18.3
Total European egg/juvenile production (million)	1543	473	319	414	18.3
Market share (%)	65–68	[b]93–95	43–56	60–66	100

[a] Includes 40–60 million from egg sales to Europe.
[b] Estimation based on egg production not originating from breeding programs.

in a more rudimentary manner. It was, therefore, assumed that most strains used in breeding programs have been selected for at least eight generations. Selection response on harvest weight varies from 7% (Kause et al., 2005) to 10–13% (Gjerde, 1986) (Table 8). Four studies were used to estimate TGC of wild trout (Appendix A). Martens (2013) reported a TGC of 0.67 for juvenile wild trout (Martens, 2013; Martens et al., 2014). Tymchuk and Devlin (2005) reported a bodyweight of 47 g at 637 days after fertilization at a rearing temperature of 11 °C, corresponding to a TGC around 0.5. Devlin et al. (2013) reported a bodyweight of 39 g at 556 days after fertilization at a rearing temperature of 10 °C, corresponding to a TGC around 0.6. Biro et al. (2006) reported a growth from 0.6 g to 8.5 g in 82 days at a temperature of 10 °C, corresponding to a TGC of 1.5. Much higher TGC's have been reported for strains from breeding programs. Sae-Lim et al. (2013) reported TGC's of 1.43 to 2.07 for a variety of culture systems. Grisdale-Helland et al. (2007) reported TGC's of 2.43 to 2.53 for a strain that was grown from 400 to 850 g in seawater at 11 °C. At the USDA National Center for Cool and Cold Water Aquaculture, strains from three different suppliers to the European market were grown from 6 g to a final weight of 700–1000 g at a temperature around 11 °C. They found TGC's of 2.05, 2.09 and 2.40 for the three different strains (unpublished results Cleveland, 2015). TGC's of 2.4 and 2.7 were also estimated based on ongrowing data, provided by two other breeding companies that participated in the survey. Average TGC of wild trout is around 0.8 and TGC of selected trout is around 2.2, almost 200% higher (Appendix A). Wild trout with a TGC of 0.8, stocked at 10 g, and reared at 12 °C, would reach a harvest weight of 300 g at 473 days. Selected trout with a TGC of 2.2, would after an equal growing period in the same conditions reach a harvest weight over 3 kg instead. The comparison of TGC's of wild and selected trout suggests that cumulative genetic gain in TGC is about +200%, and cumulative genetic gain in harvest weight is roughly +900% (Table 9).

Table 7
Number of breeding programs that reported to select on a given trait in the first survey (n = 28).

Selected traits	Rainbow trout	Atlantic salmon	European seabass	Gilthead seabream	Turbot	Total
Growth performance	9	7	4	5	2	27
Morphology	4	3	3	5	0	15
Disease resistance	4	6	2	2	1	15
Product quality	3	6	1	3	0	13
Processing yield	4	6	2	0	0	12
Reproduction	5	2	0	0	0	7
Feed efficiency	2	2	1	2	0	7

For salmon, the total number of selected generations was generally around 10, of which 4 to 11 generations were based on family selection. Except for the AquaGen program, all programs initially performed mass selection. Around the year 2000, family selection became more widely adopted. Glover et al. (2009) performed a common garden experiment with the Mowi strain selected for 7–8 generations and a wild strain of similar origin. Compared to the wild strain, fish from the Mowi strain were on average 121–131% heavier after equal growing periods and the TGC, calculated from their data, was 42–48% higher. For 7–8 generations, these figures correspond to a selection response of 11–12% on harvest weight or about 5% on TGC. Solberg et al. (2013) performed a common garden experiment with juveniles of the Mowi strain selected for 9–10 generations and a wild strain. Compared to the wild strain, fish from the Mowi strain were 196% heavier after equal growing periods and the TGC, calculated from their data, was 83% higher. For 9–10 generations, these figures correspond to a selection response of 12% on harvest weight or 6.6% on TGC. Assuming similar selection responses across breeding programs, 10 selected generations have resulted in a cumulative genetic gain of about +200% on harvest weight or +80% on TGC. This improvement is further supported by a reduction in

Table 8
Reported heritabilities (h^2) and genetic gain on harvest weight (ΔG) used to predict cumulative genetic gain in growth performance.

Species	h^2	ΔG per generation (%)	ΔG total (%)	# selected generations	Reference
Trout	–	10–13	26–30	2–3	Gjerde (1986)
Trout	0.26–0.27	4.9–7.9	–	3	Kause et al. (2005)
Salmon	–	–	121–131	7–8	Glover et al. (2009)
Salmon	–	–	196	9–10	Solberg et al. (2013)
Seabass	0.4	26.3	–	–	Le Boucher et al. (2013)
Seabass	0.52–0.64	25–30	–	–	Chatain and Chavanne (2009)
Seabass	0.38–0.44	16–25	–	–	Dupont-Nivet et al. (2008)
Seabass	0.44	–	65	2.6	Thorland et al. (2015a)
Seabass	0.34	23	–	–	Vandeputte et al. (2009)
Seabream	0.55	29	–	–	Brown (2003)
Seabream	–	5–10	–	up to 3	Knibb (2000)
Seabream	0.34	–	–	–	Navarro et al. (2009)
Seabream	0.35	13	–	2.6	Thorland et al. (2015b)
Turbot	–	10–15	–	3	Danacher and Garcia-Vazquez (2007)
Turbot	–	–	65	4	pers. comm. Johansen (2015)

growing period to 2–3 years from egg to harvest and an increase in harvest weight to about 5 kg (Marine Harvest, 2014), which rather represents an industry average than the even higher actual growth potential (pers. comm. Bakke, 2015).

For seabass, the reported number of selected generations varied between two and eight. Vandeputte et al. (2009) compared the growth performance of offspring of wild seabass to the offspring of selected sires and wild dams. Harvest weight was 12% higher in offspring of selected sires compared to offspring of unselected parents after equal growing periods. When selecting on both males and females, the predicted selection response on harvest weight was 23%. Similar selection responses on harvest weight were predicted by Chatain and Chavanne (2009); Dupont-Nivet et al. (2008) and Le Boucher et al. (2013) (Table 9). Thorland et al. (2015a) reported a selection response on harvest weight of about 25% in a family selection breeding program, which has resulted in a 65% improvement on growth performance relative to the base population. The performance of the base population relative to the wild was unclear. Selection responses reported in the above studies were all based on the first few selected generations, which may be inflated due to domestication effects (Vandeputte et al., 2009). Based on two to eight selected generations in current breeding programs, cumulative genetic gain in harvest weight is estimated to range from +50% to +150%. Wild seabass with a TGC of 0.55 (based on Vandeputte et al., 2014), stocked at 10 g, and reared at 20 °C, would reach a harvest weight of 350 g at 449 days. A 50% higher harvest weight after an equal growing period would correspond to a TGC of 0.66, and a 150% higher harvest weight would correspond to a TGC of 0.83. Cumulative genetic gain in TGC is, therefore, estimated to range from 20% to 50%.

For seabream, the reported number of selected generations varied between one and five. A few studies have estimated the selection response in seabream breeding programs. Based on a high heritability of 0.55 (Batargias, 1998 in. Brown, 2003), Brown (2003) estimated a selection response of 29% on harvest weight. Assuming a moderate heritability of 0.34 (Navarro et al., 2009), the selection response would be 19% instead. Knibb (2000) reported a 5–10% increase in 'growth rate' per generation of seabream selected for up to three generations. Thorland et al. (2015b) reported an average selection response in harvest weight of 13% over 2.6 selected generations in a family selection breeding program. A selection response in harvest weight of 10% to 15% may thus be expected. Because the highest number of selected generations reported by breeding companies was five, cumulative genetic gain in harvest weight is expected to range up to maximally +100%. Wild seabream with a TGC of 0.39 (based on Knibb, 2000), stocked at 10 g, and reared at 20 °C, would reach a harvest weight of 350 g at 633 days. A 100% higher harvest weight after an equal growing period would correspond to a TGC of 0.53. Cumulative genetic gain in TGC is, therefore, estimated to range up to maximally 40%.

For turbot, the reported number of selected generations varied between three and five. Selection responses on harvest weight were 10–15% for the first generations (Danacher and Garcia-Vazquez, 2007). Based on genetic trend analysis, Johansen (2015, pers. comm.) reported a cumulative genetic gain in harvest weight of +65% at the current generation of one of the breeding programs. Wild turbot stocked at 20 g and reared at 15 °C, reached a weight of 1200 g after 21.5 months (Imsland et al., 2000), corresponding to a TGC of 0.8. A 65% higher harvest weight after the same growing period would correspond to a TGC of 1.0, i.e. a 25% increase. Genetic gain is expected to be similar across breeding programs and is estimated at 65% in harvest weight and 25% in TGC.

A summary of cumulative genetic gains in harvest weight and TGC is presented in Table 9. Most genetic gain has been realized on salmonids, which should largely be attributed to the highest number of selected generations.

4. Discussion

4.1. Market share of selective breeding

This is the first study that estimates the proportion of aquaculture production in Europe that originates from selective breeding. This market share is estimated at 80–83%, which is much higher than the previously reported 8.2% for global aquaculture production (Gjedrem

Table 9
Estimated cumulative genetic gain in harvest weight and TGC[a] by selective breeding in Europe.

	Rainbow trout	Atlantic salmon	European seabass[b]	Gilthead seabream	Turbot
Selected generations	8–20	±10	2–8	1–5	3–5
Selection response on harvest weight (%)	7–13	12	20–25	10–15	10–15
Selection response on TGC (%)	?	6	5–10	7	5
Cumulative genetic gain in harvest weight (%)	+900	+200	+50–150	<100	+65
Cumulative genetic gain in TGC (%)	+200	+80	+20–50	<40	+25

[a] Thermal growth coefficient.
[b] Only based on selection response in first generation and genetic parameters.

et al., 2012). The market share might even be somewhat underestimated, since it was assumed that yield per egg or juvenile was independent of its origin (selective breeding or not). In reality, yield of selected eggs and juveniles is likely to be higher than yield of unselected eggs and juveniles, due to e.g. improved survival or higher harvest weight. Moreover, there might be some bias due to production cycles that exceed one year. Both in the computation of national egg production data for salmon and trout, and in the estimation of the proportion of fish production that originated from selective breeding, fish production data of 2012 were used. Eggs and juveniles produced in 2012 could not have resulted in fish production in the same year, but it was assumed that production growth in successive years could be ignored.

The market share of salmon breeding companies in Europe (93–95%) is very similar to the global market share of 97% (Gjedrem and Baranski, 2009). For trout, the market share of breeding companies in Europe (65–68%) is much higher than the global market share of 27% (Gjedrem and Baranski, 2009). Global estimates for the other species are not available.

Selective breeding is expected to play an increasingly important role in seabass and seabream, because several smaller companies have initiated breeding programs since 2014. On a global level, this positive trend is also observed: the proportion of genetically improved stocks worldwide increased from less than 5% in 2003 (Gjedrem and Baranski, 2009) to 8.2% in 2010 (Gjedrem et al., 2012).

4.2. Characteristics of breeding companies and their programs

Specialized breeding companies play a dominant role in the production of salmonids, while their role in the production of the three Mediterranean species is smaller. This may be partly explained by the way that genetically improved material is distributed. Eggs of salmonids are easily disinfected and shipped over long distances. Juveniles of seabass, seabream, and turbot to the contrary, are less easily transported over long distances and moreover, transportation may increase the risk to spread diseases. This may be an incentive to companies that produce these species to fully control the reproductive cycle and to operate their own breeding program, which would explain the dominance of integrated companies in seabass, seabream, and turbot production.

Concentration of breeding companies in salmon is high compared to the other species, when the volume of fish production and combined market share of breeding companies are taken into account. It is expected that breeding programs integrated with production can relatively easily coexist with other competing breeding programs, because their existence depends rather on the overall performance of the company they are part of than on results obtained by the breeding program itself. This may explain why there is relatively little concentration of breeding companies in the Mediterranean species. The stronger concentration of breeding companies in salmon than in trout can be explained by a rather uniform salmon farming industry, contrasted by a highly diverse trout farming industry. Uniformity within the salmon farming industry allows benchmarking (Soares et al., 2011) and breeding companies often select on similar traits (Table 7). Diversity among the trout farming industry complicates benchmarking and breeding companies often select on different traits. Both benchmarking (Elmuti and Kathawala, 1997) and similarity in selected traits are expected to have led to a higher degree of concentration in salmon than in trout. Looking towards the future, in salmonids further concentration of breeding companies is expected. This trend has already taken place in livestock (Gura, 2007) and is shown by recent mergers in the salmon breeding industry.

4.3. Cumulative genetic gain

Genetic gain in TGC is much lower than genetic gain in harvest weight (Table 9), because TGC describes bodyweight as an exponential function of time and temperature. Advantages of describing genetic gain in terms of harvest weight are its easy interpretation and the common use of bodyweight as a selection criterion. The disadvantage is that harvest weight is strongly dependent of stocking weight, growing period, and rearing temperature. Harvest weight is, thereby, a management parameter largely determined by non-genetic factors. Harvest weight can, therefore, not be compared across conditions. In contrast, TGC is more difficult to interpret, but it does describe genetic growth potential of a strain and can, with caution (Dumas et al., 2007; Jobling, 2003), be compared across conditions.

Comparison of TGC's of wild and selected trout suggest that cumulative genetic gain is around +200% in TGC, or +900% in harvest weight. Although environmental conditions differed in the various studies from which TGC's of wild and selected fish were derived, it may be assumed that rearing conditions were conform modern standards. Bias due to environmental effects is, therefore, expected to be small. Comparison of TGC may suffer from bias due to differences in life stage (Dumas et al., 2007); TGC's of wild trout are based on fish up to 50 g, whereas TGC's of selected trout are based on larger individuals. The comparison, therefore, requires verification by, for example, a common garden experiment. For eight generations of selection, cumulative genetic gain on harvest weight of +900% would correspond to an unrealistically high selection response of 33%. For 20 generations of selection, the selection response on harvest weight would be 12%. The high cumulative genetic gain cannot entirely be explained from the number of selected generations in current breeding programs (up to 20), given that the selection response varies between 7 and 13% (Gjerde, 1986; Kause et al., 2005). This implies that both domestication and early breeding work have contributed substantially to cumulative genetic gain, which is not surprising considering the long history of domestication and breeding of trout.

Results on trout show that phenotypic differences in TGC may be useful indicators of genetic improvement. The genetic component may, however, be obscured by environmental effects, as has been suggested for seabass and seabream (EAS-EATiP, 2014). In farming practice of both seabass and seabream, incidence of diseases has increased (Arechavala-Lopez et al., 2013; Subasinghe, 2009). At the same time, higher inclusion levels of alternative ingredients for fishmeal and fish oil in feed (Rana et al., 2009; Tacon et al., 2011) are likely to have had negative effects on growth performance, because the diet may contain anti-nutritional factors and low levels of essential fatty acids, and have an imbalanced amino acid composition (Gatlin et al., 2007; Turchini et al., 2009). Combined with a high variability in performance among farms stocked with the same genetic material, trends in on farm performance do not support the high theoretical improvements on growth performance (pers. comm. Coli, 2015).

The selection response on harvest weight was generally in the lower end of the often reported 10–20% genetic gain per generation (Gjedrem and Baranski, 2009). The reason may be that in most breeding programs family selection is applied with the objective to improve multiple traits. The more emphasis is put on other traits than growth performance, the less genetic gain in growth performance is realized. Based on results presented in this paper, the overall average selection response on harvest weight is 12%. Assuming an average generation interval of four years, this would correspond to an increase of 3% per year. This is considerable compared to livestock, where annual genetic gain is around 1% in cows (Hill, 2010) up to 2% in poultry (Hill and Bünger, 2004).

4.4. Impact of selective breeding

Gjedrem (2012) showed that selective breeding may play an important role in the future supply of fish, but its impact largely depends on the adoption of selective breeding by the aquaculture sector. Considering that 80–83% of the European aquaculture production already originates from selective breeding, there is not much room for improvement in terms of adoption. Still, in some species adoption could be considerably increased.

Based on an annual genetic gain in harvest weight of 3% and given that 80–83% of the production originates from selective breeding, the sector could grow by 2.4% per year only due to genetic gain in growth performance. Underlying this prediction are the assumptions that growth rate limits production, and genetic improvement in harvest weight leads to a corresponding reduction in the duration of production cycles. In addition, genetic gain in survival related traits also positively affects production, which would facilitate an even faster growth of the sector.

5. Conclusion

Of the total European aquaculture production, 80–83% originates from selective breeding. This is a much higher figure than for global aquaculture production, which is mainly explained by the dominance of salmon farming in European aquaculture and the high combined market share of breeding companies (93–95%) in salmon. There are 37 breeding programs in Europe of which the majority performs family selection. Cumulative genetic gain in growth performance varies from +65% for turbot to +900% for trout in terms of harvest weight, and from +25% for turbot to +200% for trout in terms of thermal growth coefficient. It is concluded that selective breeding has a major impact on European aquaculture and will contribute to future growth of the sector.

Acknowledgments

The research leading to these results has received funding from the European Union's Seventh Framework Programme (KBBE.2013.1.2-10) under grant agreement n° 613611. This work is the result of the collaborative effort of researchers in the FP7 projects 'Aquatrace' and 'Fishboost'. We thank Martin Kocour and Martin Prchal for the information they provided on carp production. We gratefully acknowledge the contributions of companies that participated in the surveys. We also acknowledge the contribution of national institutes in several countries that helped us to collect the relevant data on the trade and production of eggs. We thank two anonymous reviewers for their useful comments.

Appendix A. Reported thermal growth coefficients (TGC) of rainbow trout from various origin.

Origin	TGC	Reference
Wild	0.67	Martens et al. (2014)
Wild	0.5	Tymchuk and Devlin (2005)
Wild	0.6	Devlin et al. (2013)
Wild	1.5	Biro et al. (2006)
Selected	1.43–2.07	Sae-Lim et al. (2013)
Selected	2.43–2.53	Grisdale-Helland et al. (2007)
Selected	2.05–2.4	unpublished results Cleveland (2015)
Selected	2.4–2.7	unpublished results

References

Anonymous, 2015. Personal Communication.

AquaBreeding, 2008. Survey on the Breeding Practices in the European Aquaculture Industry. AquaBreeding final technical report (FP6 EU project N° 044424 cordis.europa.eu/documents/documentlibrary/124722901EN19.doc. Accessed on 4 September 2015).

AquaGen, 2015. http://aquagen.no/en/about-aquagen/history/ (Accessed on 13 February 2015).

Arechavala-Lopez, P., Sanchez-Jerez, P., Bayle-Sempere, J.T., Uglem, I., Mladineo, I., 2013. AS WE SEE IT Reared fish, farmed escapees and wild fish stocks-a triangle of pathogen transmission of concern to Mediterranean aquaculture management. Aquacult. Env. Interac. 3, 153–161.

Aulstad, D., Gjedrem, T., Skjervol, H., 1972. Genetic and environmental sources of variation in length and weight of rainbow-trout (salmo-gairdneri). J. Fish. Res. Board Can. 29, 237–241.

Bakke, H., 2014. Personal Communication.

Bakke, H., 2015. Personal Communication.

Biro, P.A., Abrahams, M.V., Post, J.R., Parkinson, E.A., 2006. Behavioural trade-offs between growth and mortality explain evolution of submaximal growth rates. J. Anim. Ecol. 75, 1165–1171.

Blair, H.T., Pollak, E.J., 1984. Estimation of genetic trend in selected population with and without the use of control population. J. Anim. Sci. 58, 878–886.

Brown, R.C., 2003. Genetic Management and Selective Breeding in Farmed Populations of Gilthead Seabream (*Sparus aurata*) (PhD Thesis) Universtiy of Stirling.

Cabaleiro, S., 2015. Personal Communication.

Chatain, B., Chavanne, H., 2009. Genetics of European seabass (*Dicentrarchus labrax* L.). Cah. Agric. 18, 249–255.

Chavanne, H., Janssen, K., Hofherr, J., Contini, F., Haffray, P., Consortium, Aquatrace, Komen, H., Nielsen, E.E., Bargelloni, L., 2016. A comprehensive survey on selective breeding programs and seed market in the European aquaculture fish industry. Aquacult. Int. 1–21.

Cho, C.Y., 1992. Feeding systems for rainbow trout and other salmonids with reference to current estimates of energy and protein requirements. Aquaculture 100, 107–123.

Cleveland, B., 2015. Personal Communication.

Coli, A., 2015. Personal Communication.

Coves, D., Dewavrin, G., Breuil, G., D., N., 1991. Culture of Sea Bass (*Dicentrarchus labrax* L.). In: McVey, J.P. (Ed.), Handbook of Mariculture. CRC Press, Boca Raton, Florida, pp. 3–20.

Crawford, S.S., Muir, A.M., 2008. Global introductions of salmon and trout in the genus Oncorhynchus: 1870–2007. Rev. Fish Biol. Fish. 18, 313–344.

Danacher, D., Garcia-Vazquez, E., 2007. Turbot - *Scophthalmus maximus*. In: Svåsand, T., Crosetti, D., García-Vázquez, E., Verspoor, E. (Eds.), Genetic Impact of Aquaculture Activities on Native Populations. Genimpact Final Scientific Report. 55–61.

DARD Fisheries, 2014. Personal Communication.

Dentler, J., 2015. Personal Communication.

Devlin, R.H., Sakhrani, D., White, S., Overturf, K., 2013. Effects of domestication and growth hormone transgenesis on mRNA profiles in rainbow trout (*Oncorhynchus mykiss*). J. Anim. Sci. 91, 5247–5258.

Divanach, P., Kentouri, M., 2000. Hatchery Techniques for Specific Diversification in Mediterranean Finfish Larviculture. CIHEAM - Options Mediterraneenes, pp. 75–87.

Donaldson, L.R., Olson, P.R., 1957. Development of rainbow trout brood stock by selective breeding. Trans. Am. Fish. Soc. 85, 93–101.

Dumas, A., France, J., Bureau, D.P., 2007. Evidence of three growth stanzas in rainbow trout (*Oncorhynchus mykiss*) across life stages and adaptation of the thermal-unit growth coefficient. Aquaculture 267, 139–146.

Dupont-Nivet, M., Vandeputte, M., Vergnet, A., Merdy, O., Haffray, P., Chavanne, H., Chatain, B., 2008. Heritabilities and G×E interactions for growth in the European sea bass (*Dicentrarchus labrax* L.) using a marker-based pedigree. Aquaculture 275, 81–87.

EAS-EATiP, 2014. Performance of the Sea Bass and Sea Bream Sector in the Mediterranean. Aquaculture Europe, San Sebastian, Spain.

Elmuti, D., Kathawala, Y., 1997. An overview of benchmarking process: a tool for continuous improvement and competitive advantage. Benchmark Qual. Manag. Technol. 4, 229–243.

FAO, 2014. The State of World Fisheries and Aquaculture. 2014. FAO, Rome.

FAO, 2015. Fisheries and Aquaculture Software. FishStatJ — Software for Fishery Statistical Time Series. FAO Fisheries and Aquaculture Department, Rome.

FEAP, 2014. In: Dehasque, M. (Ed.), European Aquaculture Production Report 2004–2013. Federation of European Aquaculture Producers (53 pp.).

Funcke, O., 2015. Personal Communication.

Gall, G.A.E., 1975. Genetics of reproduction in domesticated rainbow-trout. J. Anim. Sci. 40, 19–28.

Gall, G.A.E., Crandell, P.A., 1992. The rainbow trout. Aquaculture 100, 1–10.

Gatlin, D.M., Barrows, F.T., Brown, P., Dabrowski, K., Gaylord, T.G., Hardy, R.W., Herman, E., Hu, G., Krogdahl, Å., Nelson, R., Overturf, K., Rust, M., Sealey, W., Skonberg, D., Souza, J.E., Stone, D., Wilson, R., Wurtele, E., 2007. Expanding the utilization of sustainable plant products in aquafeeds: a review. Aquac. Res. 38, 551–579.

Ghosh, A., 2004. Increasing market share as a rationale for corporate acquistions. J. Bus. Finan. Acc. 31, 209–247.

Gjedrem, T., 1985. Improvement of productivity through breeding schemes. GeoJournal 10, 233–241.

Gjedrem, T., 2012. Genetic improvement for the development of efficient global aquaculture: a personal opinion review. Aquaculture 344–349, 12–22.

Gjedrem, T., Baranski, M., 2009. Selective Breeding in Aquaculture: an Introduction. Springer.

Gjedrem, T., Gjøen, H.M., Gjerde, B., 1991. Genetic origin of Norwegian farmed Atlantic salmon. Aquaculture 98, 41–50.

Gjedrem, T., Robinson, N., Rye, M., 2012. The importance of selective breeding in aquaculture to meet future demands for animal protein: a review. Aquaculture 350-353, 117–129.

Gjerde, B., 1986. Growth and reproduction in fish and shellfish. Aquaculture 57, 37–55.

Glover, K.A., Otterå, H., Olsen, R.E., Slinde, E., Taranger, G.L., Skaala, Ø., 2009. A comparison of farmed, wild and hybrid Atlantic salmon (*Salmo salar* L.) reared under farming conditions. Aquaculture 286, 203–210.

Goodman, L.A., 1961. Snowball sampling. Ann. Math. Stat. 32, 148–170.

Grisdale-Helland, B., Shearer, K.D., Helland, J., 2007. Energy and nutrient utilization of Atlantic cod, Atlantic salmon and rainbow trout fed diets differing in energy content. Aquac. Nutr. 13, 321–334.

Gross, R., Lulla, P., Paaver, T., 2007. Genetic variability and differentiation of rainbow trout (*Oncorhynchus mykiss*) strains in northern and Eastern Europe. Aquaculture 272, S139–S146.

Gura, S., 2007. Livestock Genetics Companies. Concentration and Proprietary Strategies of an Emerging Power in the Global Food Economy. League for Pastoral Peoples and Endogenous Livestock Development, Ober-Ramstadt, Germany.

Guyomard, R., 1981. Electrophoretic variation in four French populations of domesticated RainbowTrout (*Salmo gairdneri*). Can. J. Genet. Cytol. 23, 33–47.

Haffray, P., 2015. Personal Communication.

Hill, W.G., 2010. Understanding and using quantitative genetic variation. Philos. Trans. R. Soc. B 365, 73–85.

Hill, W.G., Bünger, L., 2004. Inferences on the genetics of quantitative traits from long-term selecition in laboratory and domestic animals. Plant Breed. Rev. 24, 169–210.

Hosteland, L.T., 2014. Flust av rogn til næringen. NF Xpert Økonomi 38–39.

Imsland, A.K., Foss, A., Naevdal, G., Cross, T., Bonga, S.W., Ham, E.V., Stefansson, S.O., 2000. Countergradient variation in growth and food conversion efficiency of juvenile turbot. J. Fish Biol. 57, 1213–1226.

Iwama, G.K., Tautz, A.F., 1981. A simple growth model for salmonids in hatcheries. Can. J. Fish. Aquat. Sci. 38, 649–656.

Janssen, K., Prchal, M., Kocour, M., Berentsen, P.B.M., Komen, H., 2015. Common Carp — Current Status of Selective Breeding in Europe. http://www.fishboost.eu/reports-on-current-status-of-selective-breeding-in-europe.html (Accessed on 14 September 2015).

Jobling, M., 2003. The thermal growth coefficient (TGC) model of fish growth: a cautionary note. Aquac. Res. 34, 581–584.

Johansen, H., 2015. Personal Communication.

Jonasson, J., 2014. Personal Communication.

Kause, A., 2014. Personal Communication.

Kause, A., Ritola, O., Paananen, T., Wahlroos, H., Mantysaari, E., 2005. Genetic trends in growth, sexual maturity and skeletal deformations, and rate of inbreeding in a breeding programme for rainbow trout (*Oncorhynchus mykiss*). Aquaculture 247, 177–187.

Knibb, W., 2000. Genetic improvement of marine fish — which method for industry? Aquac. Res. 31, 11–23.

Knibb, W., Gorshkova, G., Gorshkov, S., 1997. Selection for growth in the gilthead seabream. Sparus aurata L. Isr. J. Aquac. - Bamidgeh. 49, 57–66.

Knibb, W., Gorshkova, G., Gorshkov, S., 1998. Selection and Crossbreeding in Mediterranean Cultured Marine Fish. In: Bartley, D.M., Basurco, B. (Eds.), Genetics and Breeding of Mediterranean Aquaculture Species. CIHEAM, Zaragoza, pp. 47–60.

Komen, H., 1990. Clones of Common Carp, *Cyprinus carpio* (PhD Thesis) Agricultural University Wageningen, Department of Fish Culture and Fisheries & Department of Experimental Animal Morphology and Cell Biology.

Korsvoll, S.A., 2014. Personal Communication.

Le Boucher, R., Vandeputte, M., Dupont-Nivet, M., Quillet, E., Ruelle, F., Vergnet, A., Kaushik, S., Allamellou, J.M., Medale, F., Chatain, B., 2013. Genotype by diet interactions in European sea bass (*Dicentrarchus labrax* L.): nutritional challenge with totally plant-based diets. J. Anim. Sci. 91, 44–56.

Marine Harvest, 2014. Salmon Farming Industry Handbook. p. 2014.

Martens, M.T., 2013. The Comparative Growth and Survival of a Naturalized and Aquaculture Strain of Rainbow Trout (*Oncorhynchus mykiss*) in Laboratory and Whole-Ecosystem Experiments (MSc. Thesis) University of Manitoba, Department of Biological Sciences.

Martens, M.T., Wall, A.J., Pyle, G.G., Wasylenko, B.A., Dew, W.A., Devlin, R.H., Blanchfield, P.J., 2014. Growth and feeding efficiency of wild and aquaculture genotypes of rainbow trout (*Oncorhynchus mykiss*) common to Lake Huron, Canada. J. Great Lakes Res. 40, 377–384.

Millenbach, C., 1950. Rainbow brood-stock selection and observations on its application to fishery management. Prog. Fish Cult. 12, 151–152.

Ministerio de Agricultura, 2014. Estadísticas pesqueras: Producción de acuitcultura. http://www.magrama.gob.es/es/estadistica/temas/estadisticas-pesqueras/acuicultura/encuesta-establecimientos-acuicultura/produccion/default.aspx (Accessed on 28 November 2014).

Moretti, A., Fernandez-Criado, M.P., Cittolin, G., Guidastri, R., 1999. Manual on Hatchery Production of Seabass and Gilthead Seabream. vol. 1. FAO, Rome (195 pp.).

Morkramer, S., Horstgenschwark, G., Langholz, H.J., 1985. Comparison of different European rainbow-trout populations under intensive production conditions. Aquaculture 44, 303–320.

Munro, L.A., Wallace, I.S., 2012. Scottish Fish Farm Production Survey — Report 2012. Marine Scotland Science.

Navarro, A., Zamorano, M.J., Hildebrandt, S., Ginés, R., Aguilera, C., Afonso, J.M., 2009. Estimates of heritabilities and genetic correlations for growth and carcass traits in gilthead seabream (*Sparus auratus* L.), under industrial conditions. Aquaculture 289, 225–230.

Paisley, L.G., Ariel, E., Lyngstad, T., Jónsson, G., Vennerström, P., Hellström, A., Østergaard, P., 2010. An overview of aquaculture in the nordic countries. J. World Aquacult. Soc. 41, 1–17.

Patursson, Ø, 2013. Personal Communication.

Patursson, Ø, 2015. Personal Communication.

Poseidon, 2008. Regulatory Costs and Competitiveness of Scottish Salmon Industry. Poseidon Aquatic Resource Management Ltd. (1 pp.).

Rana, K.J., Siriwardena, S., Hasan, M.R., 2009. Impact of rising feed ingredient prices on aquafeeds and aquaculture production. Food and Agriculture Organization of the United Nations (FAO), Rome, pp. 1–63.

Reese, A., 2013. Survey of aquaculture production of finfish in the UK. Finfish News 15, Cefas 22–28.

Robinson, G., 2014. Personal Communication.

Rye, M., Gjerde, B., Gjedrem, T., 2010. Genetic Improvement Programs For Aquaculture Species In Developed Countries. 9th World Congress on Genetics Applied to Livestock Production. Leipzig, Germany.

Sae-Lim, P., Kause, A., Mulder, H.A., Martin, K.E., Barfoot, A.J., Parsons, J.E., Davidson, J., Rexroad III, C.E., Van Arendonk, J.A.M., Komen, H., 2013. Genotype-by-environment interaction of growth traits in rainbow trout (*Oncorhynchus mykiss*): a continental scale study. J. Anim. Sci. 91, 5572–5581.

Sernapesca, 2014. Estadística de Importación de Ovas por origen 2010-2014. Ministerio de Economia, Fomento y Turismo, Chili. http://www.sernapesca.cl/ (Accessed on 18 December 2014).

Soares, S., Green, D.M., Turnbull, J.F., Crumlish, M., Murray, A.G., 2011. A baseline method for benchmarking mortality losses in Atlantic salmon (*Salmo salar*) production. Aquaculture 314, 7–12.

Solberg, M.F., Skaala, O., Nilsen, F., Glover, K.A., 2013. Does domestication cause changes in growth reaction norms? A study of farmed, wild and hybrid Atlantic salmon families exposed to environmental stress. PLoS ONE 8, 1–11.

Statistisches Bundesamt, 2012. Erzeugung in Aquakulturbetrieben.

Subasinghe, R., 2009. Disease control in aquaculture and the responsible use of veterinary drugs and vaccines: the issues, prospects and challenges. Options Méditerranéennes 86, pp. 5–11.

Tacon, A.G.J., Hasan, M.R., Metian, M., 2011. Demand and supply of feed ingredients for farmed fish and crustaceans: trends and prospects. Food and Agriculture Organization of the United Nations (FAO), Rome, pp. 1–87.

Tinch, A., 2014. Personal Communication.

Thomsen, B., 2014. Personal Communication.

Thorland, I., Papaioannou, N., Kottaras, L., Refstie, T., Papasolomontos, S., Rye, M., 2006. The Kego Breeding Programs for Sea Bream (*Sparus aurata*) and Sea Bass (*Dicentrarchus labrax*) in Greece. 8th Hellenic Symposium on Oceanography and Fisheries, Thessaloniki, Greece.

Thorland, I., Kottaras, L., Refstie, S., Papanna, K., Papaharisis, L., Rye, M., 2015a. Response to Selection for Harvest Weight in European Sea Bass (*Dicentrarchus labrax*) in Greece. ISGA XII, Santiago de Compostella, Spain.

Thorland, I., Kottaras, L., Refstie, S., Dimitroglou, A., Papaharisis, L., Rye, M., 2015b. Response to Selection for Harvest Weight in a Family Based Selection Program of Gilthead Seabream (*Sparus aurata*). ISGA XII, Santiago de Compostella, Spain.

Trong, T.Q., Mulder, H.A., van Arendonk, J.A.M., Komen, H., 2013. Heritability and genotype by environment interaction estimates for harvest weight, growth rate, and shape of Nile tilapia (*Oreochromis niloticus*) grown in river cage and VAC in Vietnam. Aquaculture 384-387, 119–127.

Turchini, G.M., Torstensen, B.E., Ng, W.-K., 2009. Fish oil replacement in finfish nutrition. Rev. Aquac. 1, 10–57.

Tymchuk, W.E., Devlin, R.H., 2005. Growth differences among first and second generation hybrids of domesticated and wild rainbow trout (*Oncorhynchus mykiss*). Aquaculture 245, 295–300.

Vandeputte, M., 2003. Selective breeding of quantitative traits in the common carp (*Cyprinus carpio*): a review. Aquat. Living Resour. 16, 399–407.

Vandeputte, M., Dupont-Nivet, M., Haffray, P., Chavanne, H., Cenadelli, S., Parati, K., Vidal, M.O., Vergnet, A., Chatain, B., 2009. Response to domestication and selection for growth in the European sea bass (*Dicentrarchus labrax*) in separate and mixed tanks. Aquaculture 286, 20–27.

Vandeputte, M., Garouste, R., Dupont-Nivet, M., Haffray, P., Vergnet, A., Chavanne, H., Laureau, S., Ron, T.B., Pagelson, G., Mazorra, C., Ricoux, R., Marques, P., Gameiro, M., Chatain, B., 2014. Multi-site evaluation of the rearing performances of 5 wild populations of European sea bass (*Dicentrarchus labrax*). Aquaculture 424–425, 239–248.