Introduction
Flesh quality has gained importance among consumers and in the aquaculture industry because it is directly related to human health and nutrition. Flesh quality comprises several different (freshness, appearance, smell, flavor, texture, taste, firmness, juiciness, and processing and hygienic) characteristics. Due to the large number of traits involved and the ensuing complexity, genetic improvement for flesh quality has been almost neglected in breeding programs for aquaculture species. We studied four groups of traits in the Genetically Improved Farmed Tilapia (GIFT) strain: i) carcass (fillet) traits, ii) flesh composition (protein, fat, moisture and ash content), iii) flesh quality attributes (pH, color), and iv) fatty acid composition. In this paper we review the effects of non-genetic factors, and we report genetic parameters and correlated responses in flesh quality traits to selection for high growth in GIFT. The discussion includes other farmed aquaculture species.

Non-genetic factors

Nutrition. The effects of diets (protein, fat and carbohydrate content) and feeding regimes (ad libitum vs. restricted) on flesh quality of aquatic animals are well documented in the literature (e.g. Rasmussen, 2001). Supplementing fish diet with dry Spirulina powder reduces fatness, which improves the taste, texture, flavor, firmness and overall flesh quality of farmed fish. For salmonids, the farmed fish acquire their flesh color through supplementation with the carotenoid astaxanthine in the feed. Fatty acid composition can be changed through use of diets containing different oil-seeds such as linseed or fat lipids, or through manipulation of n-3 to n-6 ratio. In brief, some desirable characters of fish fillet can be improved effectively through optimization of diets.

Season. The effect of season includes fluctuation in temperature, humidity, rainfall and other environmental factors as well as changes in culture and management practices. Among these factors, the effect of temperature on flesh quality is predominant. Season is also related to availability of feedstuff and feed quality, thus affecting both performance and flesh quality of fish species (e.g. Roth et al., 2004).

Sex. Sex difference for body traits is well documented in tilapia and other aquatic species. Weight difference leads to variation in fat content which in turn affects chemical composition and flesh quality and fatty acid composition (Nguyen et al., submitted).
Age. Age is related to maturity status of an animal. Mature animals tend to convert food into fat rather than protein deposition. The difference in levels of fatness among animals causes variation in chemical composition, flesh quality and fatty acid composition (Nguyen et al., submitted). This effect is also demonstrated in other fishes (e.g. Johnston, 1999).

Others. Several other factors (particularly pre- and post-slaughter conditions) such as transportation, handling, conditioning, fasting, killing method, chilling and storage are also reported to have impact on flesh quality in fish (Rasmussen, 2001; Poli et al., 2005). It is, however, difficult to quantify and include these factors in statistical models for genetic analysis of these traits.

Between strain (or line) variation

Several studies compared flesh quality of wild and farmed fish, e.g. in salmon (Johnston et al., 2006), in sea bass and sea bream (Grigorakis, 2007). Overall, the wild fish have a better taste and flavor than the cultured counterpart. We evaluated flesh quality of the GIFT strain vs. red tilapia, and found that there was no noticeable difference in the majority of flesh quality parameters between the two strains (Ponzoni et al., 2006; Khaw et al., 2006). Karapanagiotidis et al. (2006) reported no difference in fatty acid composition between Nile and red tilapia.

Within strain (line) variation

Heritability. Figure 1 presents heritabilities for proximate composition and flesh quality attributes. Across species, the estimate for protein content was low, while the heritabilities for fat and moisture contents were generally moderate. The wide range of heritabilities for flesh quality attributes were observed, with the mean of 0.05 for pH and 0.31 for color. The estimate for instrumental color was somewhat higher than scale or panel color. In GIFT tilapia, the heritabilities for fatty acids varied from low to high (Nguyen et al., submitted). These results indicate possibilities for genetic improvement of flesh quality traits through conventional selective breeding.

Figure 1: Heritabilities for chemical composition and important flesh quality attributes in Rainbow trout\(^a\), Atlantic and Cohor salmon\(^b\) and Nile tilapia\(^c\)

\(^a\)Average from Gjerde and Gjedrem (1984), Gjerde and Schaeffer (1989), Kause et al. (2002) and Tobin et al. (2006); \(^b\)Average from Gjerde and Gjedrem (1984), Iwamoto et al. (1990), Rye and Gjerde (1996), Niera et al (2004), Quinton et al (2005), Norris and Cunningham (2004), Powel et al (2008) and Viera et al (2009); and \(^c\)Hanzah et al. (in preparation)
Correlations. Table 1 shows genetic correlations between flesh quality and body weight (the sole selection criterion of many breeding programs). The genetic correlation between protein content and body weight reported was very weak. The genetic correlations of fat with body weight were moderate to high and mostly positive, with one exception reported to be negative in rainbow trout by Kause et al. (2002). The estimate between moisture and body weight was positive in salmon and tilapia, but negative in rainbow trout. Color exhibited a moderate to high positive correlation with body weight.

**Table 1: Genetic correlations of flesh quality traits with body weight**

<table>
<thead>
<tr>
<th>Traits</th>
<th>Protein</th>
<th>Fat</th>
<th>Moisture</th>
<th>pH</th>
<th>Color</th>
</tr>
</thead>
<tbody>
<tr>
<td>R Trout</td>
<td>0.12</td>
<td>-0.12</td>
<td>0.10</td>
<td>-</td>
<td>0.36</td>
</tr>
<tr>
<td>Salmon</td>
<td>-</td>
<td>0.51</td>
<td>-0.32</td>
<td>-</td>
<td>0.33</td>
</tr>
<tr>
<td>Tilapia</td>
<td>-0.16</td>
<td>0.32</td>
<td>0.11</td>
<td>0.11</td>
<td>0.77</td>
</tr>
</tbody>
</table>


Consequence of selection on flesh quality

The effects of selection for increased performance on flesh quality were examined in a series of experiments in GIFT tilapia. To the best of our knowledge, there has been no comparable study in other aquaculture species.

Carcass traits. The selection program for high growth in GIFT has resulted in significant increase in fillet weight. The accumulated response in fillet weight up to the latest generation of selection in the spawning season 2008 was 23% (Nguyen et al., in press). In contrast to fillet weight, change in fillet yield was non-significant. Our results in tilapia were consistent with those reported in livestock species.

Flesh composition and flesh quality attributes. We examined fillet composition (protein, fat, moisture content) and two important flesh quality parameters (pH and color) in the GIFT strain. Mixed model analyses showed that flesh composition traits in the selection line did not differ from the control.

Fatty acid composition. A sub-set of GIFT fillet samples was randomly chosen for fatty acid (FA) analysis. Our results show that there were no major changes in FA composition as a consequence of the long term selection for high growth in the GIFT strain. This is partially explained by the non-significant difference in fillet fat content between the selection and control line. The negligible changes in FA composition of GIFT indicate that selection for high growth had very limited impact on FA composition.

Discussion and future direction

Genetic improvement of certain flesh quality traits would be well received by consumers. However, the inclusion of these traits, especially fatty acids, in breeding objectives may be fraught with difficulties: i) high cost of chemical analysis, ii) lack of efficient methods of data recording, iii) complex biological and physiological control, and iv) lack of pricing
systems that reward the producer. The benefit of including quality traits in breeding programs depends greatly on their economic values. Unless pricing systems place high emphasis on meat quality and the cost of routine data collection (i.e., after slaughter on relatives of selection candidates) is reduced, conventional selection may not be justified. Marker-assisted selection could be a promising strategy once functional genes, candidate genes or QTL regions in tight population-wide linkage disequilibrium are closely mapped. To date, no causative mutations or genes with major effects have been reported for flesh quality in aquaculture species. In addition to technical constraints, the cost to benefit relation for the application of marker assisted selection in aquaculture breeding programs should also be justified. With the recent development of genome sequencing, genomic selection opens a new opportunity for the improvement of flesh quality traits. To the best of our knowledge, the high-throughput SNP genotyping is still under development for Atlantic salmon in Norway and for tilapia in the Netherlands. Hence, the potential of genomic selection in fish is still to be ascertained.

**Conclusion**

Our results in GIFT tilapia indicated that there was genetic variation in flesh quality traits which provides scope for genetic improvement. There was very limited impact of selection for increased growth rate on flesh quality traits. However, a close monitor of their correlated changes as a result of selection for high productivity is recommended in breeding programs. Strategies for genetic improvement of flesh quality traits should be further studied.

**References**