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Nguyen Van Sang

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ABSTRACT/SUMMARY

Sang, N.V. (2010). Genetic studies on improvement of striped catfish (*Pangasianodon hypophthalmus*) for economically important traits. Philosophiae Doctor Thesis 2010: 43, Norwegian University of Life Sciences.

The aim of this study was to find non-invasive methods for measuring fillet weight, fillet yield and fillet fat on striped catfish (*Pangasianodon hypophthalmus*), to examine the magnitudes of genetic variance and covariance and potential genotype by environment interaction of economically important traits and finally direct selection response for body weight and correlated response for other traits. As part of the overall aim, modeling of fillet weight and fillet yield on body measurements and fillet fat with Distell Fish Fatmeter measurements were conducted. The final prediction equations achieved high correlations between predicted and observed fillet weight (0.93), fillet yield (0.86) and fillet fat (0.85), with the corresponding low biases of 1.4, 1.1 and 3.9%, respectively.

Body weight, fillet weight, fillet yield, fillet fat and fillet colour were recorded in F2 of both populations 1, tested in the research station pond, and population 2, tested in three production systems; river-net fence, open-river pond and research station pond. Only body weight was recorded in F3 of population 1, and only in research station pond. Moderate to high heritability was obtained for body weight (0.21-0.52) and fillet weight (0.19-0.53), while low to medium heritability was found for fillet yield (0.02-0.09), predicted fillet fat (0.03-0.05) and fillet colour (0.04-0.20). Genetic correlation was positive and high between body weight and fillet weight (0.95-0.96), positive and moderate to rather high between these traits and predicted fillet fat (0.41 and 0.68-0.76, respectively), and low between these traits and fillet colour. The current proposed breeding goal traits are thus likely to be body weight/fillet weight and fillet fat, with fillet colour added later.

Genotype by environment interaction, measured as the genetic correlation of the same trait in different environments, was estimated. GxE interaction existed for all analysed traits in at least one pair of test environments (r = 0.57-0.83). With the average size of the genetic correlations for analysed traits being 0.69 between open-river pond and research station pond, the production being predominantly in the open-river ponds (80%) and the fact that the largest heritabilities found in this environment, it is concluded that testing and selection should be initially carried out in open-river ponds, or eventually that this environment is mimicked in research station pond. Alternatively the breeding program should test all full-sib families in the two largest environments, open-river pond and

research station pond, for subsequent selection of the most stable genotypes across these environments. The last alternative breeding strategies are to test genotypes in all relevant environments or to have one breeding program for each environment.

Selection response, estimated as the difference between least-squares mean of the selected group and the control group, for the trait increased body weight based on individual phenotypes. This was done over the first two generations in two populations. Substantial direct realised selection responses for body weight (4.6-12.4%) were found in both populations and they were significantly different from zero in two out of four instances. Realised heritabilities of 0.28-0.38 for body weight correspond well with the previously found heritability estimates. Correlated realised selection responses for fillet weight (4.5-12.0%) were also substantial and significantly different from zero, and with the same trend as for that with body weight, reflect the considerable heritability and high genetic correlation to body weight.

It is recommended that future works should include the application of optimum contribution selection to maximise the genetic gain, establishing genetic links among populations to uniform improved broodstock and large scale dissemination through multiplier network, testing of new economically important traits, such as salinity tolerance and disease resistance, and eventually also application of genomic selection.

Keywords: Striped catfish, *Pangasianodon hypophthalmus*, prediction equation, heritability, genetic correlation, genotype by environment interaction, selection response, body weight, fillet weight, fillet fat, fillet colour.

SAMMENDRAG

Pangasius (*Pangasianodon hypophthalmus*) er en malle, som på engelsk kalles *sutchi*, *river* eller *striped catfish*. Målet med denne studien har vært å finne metoder for måling av filetvekt, filetutbytte og filetfett på levende fisk, dvs. å finne ikke-destruktive målemetoder. Dette innbefatter modellering av prediksjonsligninger for filetvekt og filetutbytte vha kroppsmål, og prediksjon av filetfett ved bruk av et *Distell Fish Fatmeter.* Videre var målsetningen å estimere genetisk variasjon, kovarians og eventuelt genotype-miljø-samspill for økonomisk viktige egenskaper i denne arten. Også seleksjonsrespons for egenskapen slaktevekt samt korrelert respons i andre egenskaper er undersøkt. De beste prediksjonsligningene oppnådde en høy korrelasjon mellom predikerte og observerte filetvekt (0,93), filetutbytte (0,86) og filet fett (0,85), med tilhørende lave avvik fra de korrekte verdiene på henholdsvis 1,4 %, 1,1 % og 3,9 %.

I F2 generasjonen av populasjon 1 og 2 ble slaktevekt, filetvekt, filetutbytte, filetfett og filetfarge registrert og testet i vanlig produksjonsdam på forskningsstasjonen. I populasjon 2 ble det i tillegg også brukt to andre testmiljøer: *inngjerdet elv* og *åpen elvedam*. Bare slaktevekt har så langt blitt registrert i F3 generasjon, og da bare på forskningsstasjonen og i populasjon 1. Moderat til høy arvbarhet ble funnet for slaktevekt (0,21 - 0,52) og filetvekt (0,19 - 0,53), mens lav til middels arvbarhet ble funnet for filetutbytte (0,02 – 0,09), predikert filetfett (0,03 – 0,05) og filet (0,04 - 0,20). Genetisk korrelasjon var positiv og høy mellom slaktevekt og filetvekt (0,95 - 0,96), moderat til ganske høy mellom disse egenskapene og predikert filetfett (henholdsvis 0,41 og 0,68 – 0,76), og videre lave mellom disse egenskapene og filetfarge. Det foreslåtte avlsmålet blir derfor trolig slaktevekt/filetvekt og filetfett, trolig med filetfarge tilføyd senere.

Genotype-miljø-samspill (GXE) ble målt som den genetiske korrelasjonen mellom målinger på den samme egenskap i ulike miljøer. GXE eksisterte for alle de undersøkte egenskapene, i det minste i en av kombinasjonene av testmiljøene (r = 0,57 til 0,83). Siden de gjennomsnittlige genetiske korrelasjonene for de undersøkte egenskapene var forholdsvis høy (0,69) for testmiljøene *åpen elvedam* og vanlig dam, og produksjonen hovedsakelig foregår i *åpne elvedammer* (80%), samt at største arvbarhet ble funnet i dette miljøet, kan det konkluderes med at testing og seleksjon bør gjennomføres i *åpne elvedammer*, eller eventuelt i et tilsvarende etterlignet miljø, noe en kan få til i noen av forskningsstasjons dammer. Alternativt kan det i avlsprogrammet kjøres tester av alle fullsøskenfamilier i de to viktigste produksjonsmiljøene, åpen elvedam og vanlig dam, for

så å gjøre utvalg av de mest stabile genotypene, disse miljøene sett under ett. De to siste alternativene vil være å teste alle genotyper i alle relevante miljøer, eller å ha et avlsprogram for hvert miljø.

Seleksjonsrespons etter utvalg basert på individuelle fenotyper ble beregnet for egenskapen slaktevekt. Det ble benyttet kontrollgrupper i de to første generasjonene i to av populasjonene. Den direkte seleksjonsrespons for slaktevekt var 4,6 - 12,4 %, og de var signifikant forskjellige fra null i to av fire tester. Realisert arvbarhet var 0,28-0,38 for slaktevekt, noe som samsvarer godt med de arvbarhetene som ble estimater tidligere, da estimert kun innen en generasjon. Korrelert respons for filetvekt var 4,5-12,0 %, også disse var alle signifikant forskjellige fra null. Dette gjenspeiler at det er en betydelig arvbarhet og høy genetisk korrelasjon til egenskapen slaktevekt.

Det er anbefalt videre at det gjøres forskning på og utvikling av: 1) *optimal contribution* teori for å maksimere genetisk fremgang for pangasius, 2) etablering av genetiske koblinger mellom populasjoner og generasjoner slik at en kan få en mer uniform stamfisk, 3) bedre distribusjonen av selektert materiale gjennom oppformeringsstasjoner, 4) andre økonomisk viktige egenskaper, for eksempel salttoleranse og sykdomsresistens og 5) etter hvert også anvendelse av genom-seleksjon.

1. INTRODUCTION

1.1. Life cycle and aquaculture of striped catfish in Vietnam

In Vietnam, the annual aquaculture production has increased dramatically from more than 425,000 tonnes in 1998 to nearly 2.1 million tonnes in 2007, which represent an increase from 24% to 50% of the annual fish production (National General Statistics Office, 2008). Striped catfish (*Pangasianodon hypophthalmus*) is currently the most important freshwater aquaculture species in Vietnam, and the annual production increased from 90,000 tonnes in 2000 (Tung et al, 2001) to 1.2 million tonnes in 2007 (Dung, 2008a), corresponding to 58% of the total national annual aquaculture production. More than 90% of this is marketed as fillet (Tung, 2009), out of which most is exported to over 127 countries worldwide (Dung, 2008b). The export sums to an approximate processed production of 633,000 tonnes with a value of 1.4 million US$ in 2008 (Globefish, 2009). There are a relative few countries (Vietnam, Thailand, Cambodia, Laos, Indonesia, Malaysia, India, Bangladesh and China) where this species can be produced. This advantage helps Vietnam to avoid strong competition and further enlarge the market. In a workshop on the establishment of national striped catfish brand for export, held in November 2004, the Vietnamese Ministry of Fisheries emphasized that the genetic improvement of this species for some specific quality traits called for immediate actions in order to create a national brand. Also recently, striped catfish is considered to be one of the strategic products of Vietnam (Office of Vietnamese Government, 2010).

There are two main rivers in Vietnam, the Red River in North and the Mekong River in south. The indigenous striped catfish is migratory, and is farmed mainly in the Mekong delta. It is known as ‘ca tra’ in Vietnamese, and common name is striped catfish, sutchi catfish or river catfish (Trong et al., 2002; Phan et al., 2009). Recently it is traded as ‘pangasius’; known as a white flesh fish. During the monsoon season between May and August, adult fish migrate upstream to spawn at grounds, all the way from Kratie town in Cambodia, up to the Khone falls on the Cambodia/Laos border. Larvae and fry drift down to the floodplains of central Cambodia and enter newly inundated areas, where they start feeding before they tend to move to deeper areas downstream, such as the Tonle Sap Great Lake and the Mekong delta (Van Zalinge et al., 2002). Based on knowledge of fish migration and spawning, two populations, are normally defined, the Northern and Southern strain, above and below the Khone falls. The former is considered to be a much smaller number (Van Zalinge et al., 2002). From analysis of seven microsatellite loci on adult fish (So et al., 2006a), the level of genetic diversity of the Southern stock was found to be much higher than that of other freshwater fish and even

comparable to marine species. Using the same microsatellite markers, So et al. (2006b) found evidence for several heterogeneous groups within and among the temporally discrete larval peak samples analysed downstream. This was possibly due to population admixture from larvae originating from a several number of families or groups of spawning individuals.

Induced spawning was first time tried in 1978, but good spawning and nursing procedures were not completed before 1996 (Khanh, 1996). Artificially spawned seed has been the only available source for farming since catch of fry from the river was banned in 2000 (Trong et al., 2002). Fecundity of farmed fish ranges from 80,000-190,000 egg/kg (Bui & Nguyen, 2008). Three 7-kg females can thus be sufficient for a one-hectare grow-out pond. Often broodstock has been collected from only one or two grow-out farms, which implies the likely or possible risk of inbreeding depression. According to Sang (2010), approximately 57% of the hatcheries regularly base their brood fish on commercial grow-out ponds, 31% on wild fish and 11% from the national breeding program or from provincial hatcheries (Sang, 2010), but for sustainable development, new international standards require the use of domesticated broodstock.

The most important production systems are *river-net fence* (5%), *internal-field pond* (15%) and *open-river pond* (80%) cultures. The pond size ranges from 0.08 to 2.2 ha, and the pond depth from 2 to 6 m. Stocking density varies from 18 to 125 fish/m^2 (or 5 to 31 fish/m3) whereas the yield is ranging from 70 to 850 tonne/ha/crop (mean of ca 400) (Phan et al., 2009). Striped catfish is omnivorous and has air breather; features which makes it very flexible also in culture. Approximately 97% of the farms use commercial pelleted feed, with protein content from 20-30% (Phan et al., 2009). Phumee et al. (2010) reported that 45% of fishmeal protein can be replaced by soybean meal protein without any adverse effects on growth, feed utilisation and body composition of juvenile fish. Disease outbreaks have in some years influenced the production as well as the product quality. Bacillary Necrosis of *Pangasius* (BNP) caused by *Edwardsiella ictaluri* (Crumlish et al., 2002; Ferguson et al., 2001) is considered to be the most common disease, causing mortality up to 50-90% (Dung et al., 2004), both in the nursing and the grow-out periods (Phan et al., 2009; Sang, 2010). The processors of striped catfish want fish with high fillet yield, but industry figure shows that the fillet yield of this species is only 33% of the total body weight. The present consumer's preference is white coloured fillets (Mai, 2004), that is not-too-fat for fish in general (Gjedrem, 1997).

In fish species such as carp, salmon, tilapia, shrimp and catfish, less than 10% of aquaculture production comes from improved seed (Gjedrem *pers com*). At the global level,

the production from improved fish stocks are very heterogeneous; being fairly small in developing countries (Ponzoni et al., 2007) while practically all production of salmon in Norway, is based on improved stocks (Fjalestad et al., 2003; Gjøen *pers com*). With the captured production now having reached its maximum, the expectation for aquaculture to increase its contribution to the world's sea food production through increased yield is very high (Ottolenghi et al., 2004). Although it is costly to run an advanced breeding program, the return of investment is considered high, the whole production chain considered. For example, the benefit:cost ratio of breeding program for Atlantic salmon in Norway was 15 (Gjedrem, 2000), while that of breeding programs for Nile tilapia ranged from 8.5 to 60 (Ponzoni et al., 2007).

1.2. The initiative for a breeding program for striped catfish

Before we can start a successful breeding program, some basic knowledge and prerequisites are needed: 1) reproduction must be under control, 2) breeding goal should be defined, 3) one must be able to record traits of economical importance, and 4) the magnitude of genetic (co)variation for the important traits should be known (Gjedrem, *pers com*). As mentioned, the reproduction is now managed well in captivity in striped catfish, while the three last aspects are being focused in the present thesis. With these fundamentals established, one can suggest a long-term breeding program for this species in Vietnam.

The base population of this breeding program was made up from stocks collected at three to four different hatcheries in the Mekong Delta, Vietnam. Each stock was collected over the period 1999-2002 from grow-out farms that reared wild fingerlings caught over several seasons and at various locations in the Mekong River. In 2001-2003, fish in the base populations (for easy reference labelled populations 1, 2 and 3 for year-classes 2001, 2002 and 2003, respectively) were mated to produce offspring, hereafter denoted F1. The program is located at the Research Institute for Aquaculture No.2 (RIA2) under the Support for Fresh Aquaculture (SUFA) program by DANIDA (2001-2005); with the specific project name 'Genetic improvement of striped catfish broodstock on growth by individual selection'. In generation F1, populations 1 and 2 were selected for body weight based on individual phenotype, while population 3 was selected for body weight and fillet yield, based on individual and family information. In the consecutive three-year project entitled 'Selective breeding for improving fillet by family selection on striped catfish', funded by the Ministry of Fisheries (2006-2008), fillet weight, fillet yield, fillet fat and fillet colour were recorded. Through this project, a F2 generation of populations 1, 2 and 3 were produced. Moreover, the

level of genetic variation was also evaluated by four microsatellite loci. Recently, the breeding program was continued through a third project named 'Estimating genetic gain for growth and fillet yield in selection program of striped catfish', funded by the Ministry of Agriculture and Rural Development (2010-2012). This project also includes testing families for resistance to bacillary necrosis of *Pangasius* caused by *Edwardsiella ictaluri*. This thesis is based only on data from F2 and F3, in populations 1, and from the F2 generation in population 2.

2. AIMS OF THE STUDY

Traits to be included in a breeding program must be possible to measure with high accuracy, often measured as repeatability, and by using preferably inexpensive and non-invasive methods (Gjedrem, 1997). One aim was thus to find non-invasive methods for measuring fillet weight, fillet yield and fillet fat for these traits to be measured on live fish, which will facilitate the utilisation of both the between and within family variation in selection. The overall result will be a higher selection response. This is covered in paper I.

The nested mating design, one male mated to two females, commonly used in fish facilitate to some extent the estimation or separation of common environmental effects (Gjerde, 2005) while partial factorial design, one male mated to two females and vice versa, will enable even more accurate estimation of additive genetic variance (Berg & Henryon, 1998). To generate F2, a partial factorial mating design was used and the aim was twofold: Firstly, to examine the magnitude of genetic variance and covariance for body weight, fillet weight, fillet yield, fillet fat and fillet colour, tested in the test station environment of an internal-field pond (Paper II). Secondly, the aim was to estimate potential genotype by environment interaction, as a genetic correlation between the same traits tested in different environments; river-net fence, open-river pond and internal-field pond (Paper III).

The magnitude of the selection response is the most important criteria to evaluate the success of a breeding program, and there are four basic approaches that can be used to estimate response from directional selection: 1) deviation from an unselected control when selection is done in one direction; 2) divergent selection, using the deviation between two lines selected in opposite directions; 3) contemporary comparisons through the use of repeated mating; and 4) the statistical approach using the extra contrast facilitated through the animal models, which is based on the linear mixed model theory (Gall et al., 1993). The aim here was to estimate the realised selection response by calculating difference between the selective group and a control population, estimated by the use of least-squares. The interest was in both the direct response in populations 1 and 2, where selection were based on individual

phenotypes for body weight, and the correlated response in other economically important traits (Paper IV).

3. GENERAL DISCUSSION

3.1.Base population

When the breeding program for striped catfish started in 2001, only the population in lower Mekong (Vietnam and Cambodia) was considered (Van Zalinge et al., 2002) and thus contributed to the genetic constitution of the three populations. In the initial phase, we had neither the tool to evaluate the genetic variation, via DNA-markers, nor the capacity to cross the sub-populations. Thus, the base populations became depended on the genetic material that was available in the four involved hatcheries. These were supposed to have a high genetic variation since they collected broodstock from grow-out farms that was known to be rearing wild fingerlings caught at several seasons and locations in the Mekong River. Later research results using molecular genetics have contributed new knowledge showing high level of genetic diversity of the lower Mekong stock, with several heterogeneous groups within and among larvae samples (So et al., 2006 a & b). The diversity of our base population has later been confirmed since no significant differences in level of genetic variation, measured as gene diversity and number of alleles per locus, was found among the base and the first generation (F1) of population 1 of the breeding program and in two wild samples by using four microsatellite loci (Ha, 2010). Additionally, the high genetic variation and substantial selection responses found in this study supports the existence of sufficient genetic variation in the three breeding populations.

3.2.Trait measuring methods

If measurements of traits are possible on live animals by the use of non-invasive methods, both the between and within family variation can be utilised in selection. We thus used body measurements to predict fillet weight and fillet yield and Distell Fish Fatmeter measures to predict fillet fat. Paper II & III show that the predicted traits were heritable, even though quite low. Furthermore, predicted traits showed a high genetic correlation with the corresponding observed fillet weight (0.88) and fillet yield (0.95). With fillet fat considered as an important trait in the breeding goal, it will be crucial to improve the prediction equation further.

3.3.Heritability and genetic correlation

Moderate heritability estimates were obtained for growth traits; i.e. body weight, standard length, fillet weight with skin and fillet weight without skin, whereas low heritability estimates were obtained for fillet yield, fillet fat and fillet colour (Paper II & III). All estimates were quite similar in size over test environments; i.e. in the river-net fence, the open-river pond and the internal-field pond (Paper III). With a low heritability (0.02-0.09) and low to medium genetic correlations to body weight and fillet weight (0.17-0.43), improvement from direct selection on fillet yield is hard to achieve. Considering fillet yield as a breeding goal trait has been criticised and questioned in other species (Powell et al., 2008; Nguyen et al., 2010). It is more likely that the most important breeding goal trait for river catfish is fillet weight, being the product of body weight and fillet yield, which is highly heritable (0.19-0.53) and with a high genetic correlation to body weight (0.95-0.96). Furthermore, a low heritability estimate was obtained for the intestinal fat index and the non-fillet weight (i.e. body weight subtracted the fillet weight without skin, 0.05) and additionally they have high genetic correlations to fillet weight (0.62-0.91) and body weight (0.75-0.83), indicating that it will be difficult to select against the less valuable part of the body and to increase the fillet weight at the same time. Another economical important trait is fillet fat, with a medium to rather high genetic correlation to body weight and fillet weight, while the other quality trait, fillet colour, was not. Thus, initially the most important breeding goal traits will be body weight/fillet weight and fillet fat. Fillet colour should be considered in the long run, but the recording method needs to be improved for this trait. There is an obvious need to use selection index to decide appropriate traits and weights for each trait.

Paper II also discussed the need for improving the experimental design as well as the need for defining optimal traits, e.g. number of days to reach a certain fillet weight instead of just selecting for growth in general. For fillet fat and fillet colour, there is a need to re-estimate these traits at the desired slaughter weight. An alternative is to record these traits at a similar body weight, in order to eliminate the biological size effect on fillet weight, fillet yield and fillet fat, as discussed in salmon (Rye & Gjerde, 1996; Sang, 2004). Such data has been collected for striped catfish, but not yet been analysed.

Bacillary necrosis of *Pangasius* is the most common disease, causing high mortality, 50-90% (Dung et al., 2004; Phan et al., 2009; Sang, 2010). Moreover, Vietnam is considered to be one of the world's five most vulnerable countries when it comes to the effect of sea level rise (Dasgupta et al. (2007). Thus, it may become very important to adapt striped catfish to salinity intrusion by selecting for salt tolerance, as addressed in a stakeholder analysis of the

AQUACLIMATE project (Nagothu et al., 2009). Consequently, genetic parameters of both disease resistance and salinity tolerance traits need to be investigated for the potential inclusion of these traits in the future breeding goal.

3.4.Genotype by environment interaction

Since desirable means and unlarged phenotypic variances for the analysed traits were obtained in the open-river pond, this environment can be considered as the best production system of the three systems; river-net fence, open-river pond and internal-field pond (Paper III). It is thus advised to carry out testing and selection in an open-river pond, or alternatively to mimic that environment in research station pond. An alternative breeding strategy is to test the families in all relevant environments, and then to select families showing the most stable genotypes across these environments. However, before definite conclusions can be drawn, it is advised to test all full-sib families in the two largest environments, open-river pond and internal-field pond. The last alternative considered would be to have one breeding program in each environment, since the cost for this will be the highest.

Before deciding a final breeding strategy, better estimates and further evaluations are required, e.g. a better assessment of the relative importance of various production systems; the effect of improving the grow-out procedures for the internal-field pond at the research station, specifically the feeding and water management; a more comprehensive dataset, e.g. an increased family size to 20-25 in the case of low heritable traits (Sae-Lim et al., 2010); and an economical cost-benefit analysis of running one, two or even three separate breeding programs. Moreover, the global concern for sustainable development, for both terrestrial animal and fish production, is to increasingly use soybean meal instead of fish meal, which is based on wild fisheries. As striped catfish is omnivorous, and recent result shows good possibilities of replacing fish meal with soybean substitutes (Phumee et al., 2010), further testing of fish in different production systems with ‘soybean protein’ feed is anticipated.

3.5.Response to selection

Substantial direct realised selection response was obtained for body weight (4.6-12.4 %) in both populations 1 and 2, and found to be significantly different from zero in two out of four instances, i.e. combinations of populations and environments (Paper IV). The realised heritabilities of 0.28-0.38 presently reported for body weight corresponds well with the first heritabilities estimated based on the analysis of variance by the use of restricted maximum likelihood methods (0.21-0.52) (Paper II & III). Generally, the direct realised selection

response for BW was comparable to or slightly higher than those found in various species by different estimation methods, 5.7-21.2% (Paper IV).

The correlated realised selection responses for fillet weight (4.5-12.0%) were also substantial, and significantly different from zero, in two out of four instances, with the same trend as for that of body weight. This is likely due to the fact that the trait is highly heritable and it has a high genetic correlation with body weight, 0.95 (Paper II). The correlated selection responses for fillet yield without skin, predicted fillet fat and fillet colour were not significant different from zero, which reflects the low heritabilities and the low to medium genetic correlations these traits have with body weight (Paper II).

A weakness of this study was the small number of offspring in the control group in population 2, which may cause an inflated random sampling error variance of the estimated generation means and consequently also the estimated selection response (Gall et al., 1993). Moreover, the shorter grow-out period in F2, compared to that in F1, may influence the realised heritability estimates. The use of a control line was chosen for estimating selection response in this study due to non-tagged individuals in F1, but in the future, we will be able to rely on estimates obtained through the BLUP procedures. This requires improved genetic ties across generations, which will be strengthen with every new generation generated.

To further increase selection response in future generations, it is advised to apply optimum contribution selection (Meuwissen, 1997), which will maximise the genetic gain at a predefined rate of inbreeding. Since the breeding program for this species composes three populations, another opportunity is to create genetic links among populations not only to increase the genetic variation, but also to enhance the uniform improved broodstock. Furthermore, genomic selection (Meuwissen et al., 2001) should be considered in a long time perspective. In fact, the Vietnamese Ministry of Agriculture and Rural Development has initiated a research proposal the discovery of ESTs by microarray development, for growth and disease resistance to bacillary necrosis of *Pangasius*.

Hatchery and grow-out farmers, who use disseminated improved fish from the present breeding program, report higher survival of fingerlings and higher growth rate and fillet yield compared to non-selected fish. With the encouraging selection responses for body weight and fillet weight and the positive reports from users, an even larger dissemination scheme of the improved broodstock can be initiated, which will enable the access of improved fish fingerlings to more farmers.

4. CONCLUSION

i. Substantial genetic variation is documented for body weight and fillet weight, allowing efficient selection for these traits, while fillet yield, fillet fat and fillet colour show low genetic variation.

ii. Initial breeding goal traits should be fillet weight/body weight and fillet fat due to their positive genetic correlation and target of improving fillet output without any increase of fillet fat. Later, fillet colour should also be considered together with disease resistance. There is an obvious need to use selection index to decide appropriate weights for each trait.

iii. The evidence of genotype by environment interaction is found for all analysed traits. It is thus suggested that the breeding program should test and select fish in an open-river pond system, or alternatively in a research station pond to set up to mimic the environment of a open-river pond. Otherwise full-sib groups could be tested in both the two most commonly used production environments, and then selected for the overall performance across environments. Eventually one should also evaluate the need of more than one breeding program.

iv. Substantial and significant direct realised selection response for body weight and corresponding correlated realised selection response for fillet weight have been achieved. It is concluded that in the future, it will be sufficient to monitor the genetic change via BLUP, without the need for control lines.

v. Body measurements on live fish can be used to predict fillet weight and fillet yield, and likewise Distell Fish Fatmeter measurements can be used for fillet fat. To be more efficiently used in a breeding program, the prediction equations for these traits need to be improved, which can be achieved by increasing the number of records, searching for more variables and reducing the measurement error. Also, other related traits need to be examined, e.g. number of days to reach a certain fillet weight instead of just selecting for growth in general.

vi. The experimental design and related techniques should be further improved, e.g. by better feeding procedures, sampling methods at recording, and shortened spawning and nursing periods as well as tagging and harvesting periods.

vii. For future work, it is further advised that the optimum contribution selection should be applied to maximise the genetic gain for a predefined rate of inbreeding. Genetic links among populations should be established to increase genetic variation and to acquire

more uniform improved broodstock and it is also needed to establish a well designed multiplier network, to disseminate improved broodstock. Moreover, other economic important traits need to be examined, e.g. salinity tolerance and disease resistance to bacillary necrosis of *Pangasius* as well as the knowledge base for doing genomic selection should be established.

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List of papers

Paper I: Prediction of fillet weight, fillet yield, and fillet fat for live river catfish (*Pangasianodon hypophthalmus*).

Paper II: Heritability and genetic correlation of economically important traits recorded at a given age in striped catfish (*Pangasianodon hypophthalmus*).

Paper III: Genotype by environment interaction for economically important traits in Striped Catfish (*Pangasianodon hypophthalmus*) in three production systems in Vietnam.

Paper IV: Realised and correlated selection response for increased body weight in Striped Catfish (*Pangasianodon hypophthalmus*).

Paper I

Prediction of fillet weight, fillet yield, and fillet fat for live River Catfish (*Pangasianodon hypophthalmus*)

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Errata for paper I:

1. Correct figure 2 is

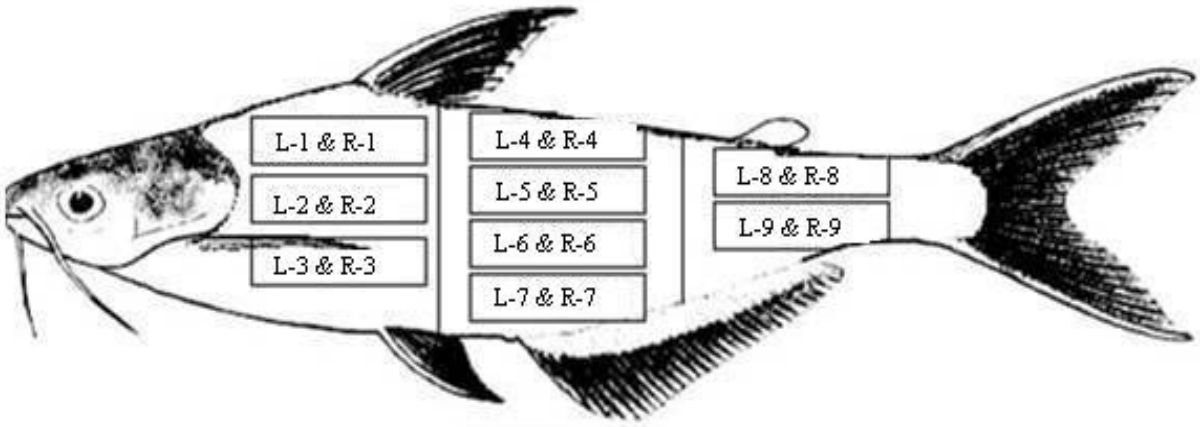

Fig. 2. The nine positions (1–9) of fat measurement done by Distell Fish Fatmeter on the left (L) and right (R) side of the body.

2. The more popular common name of this species is ‘striped catfish’ instead of ‘river catfish’.

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Prediction of fillet weight, fillet yield, and fillet fat for live river catfish (*Pangasianodon hypophthalmus*)

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ABSTRACT

The objective of this study on river catfish (*Pangasianodon hypophthalmus*) was to predict fillet weight and fillet yield from body measurements on live fish, and likewise for fillet fat, from Distell Fish Fatmeter recordings. Fish at marketable size, from the breeding program at the Research Institute for Aquaculture No.2, Vietnam, were randomly sampled and recorded for fillet weight and fillet yield (n=2767) and fillet fat (n=50). For fillet weight and fillet yield, the following body measurements were used; body weight, standard length, and volume, together with length, height, width and circumference at four positions along the body. The fish were also filleted, and the fillet weight (g) and fillet yield (%) were recorded. For modelling of fillet fat, the average of three readings with the Distell Fish Fatmeter was done at nine positions on each side of the fish. These fish were then filleted, and fillets were chemically analyzed for fat content (%). For fillet weight and fillet yield, a random sample of 200 fish were used for estimation, while the remaining (2567) were used for testing the prediction power. For fillet fat, all relevant records were used for estimation while in cross validation one record was left out for prediction and the remaining were used for estimation. Multiple regression procedures with forward selection of variables were used throughout. The final prediction equations were those resulting in the least root mean squared error of prediction, with the correlation between predicted and observed values for fillet weight, fillet yield and fillet fat being 0.93 (5 variables), 0.86 (4 variables) and 0.85 (4 variables), respectively. However, due to the limited sample sizes used in the estimation, all prediction equations were biased. For fillet weight and fillet yield, the prediction equation is likely to be further improved by reducing measurement error in filleting. Additional explanatory variables should also be sought. For fillet fat, there is a need of evaluating numbers of recordings of the chemically analyzed fat and that of the Distell Fish Fatmeter. Increasing the number of records in the data used for estimation is expected to pick up additional marginal effects.

1. Introduction

The Vietnamese river catfish production was 1.2 million tonnes in 2007. Of the total production, 95% was exported as fillets to 75 countries world-wide, with a value of about one billion USD. The industry is constantly seeking means to make the production more efficient, and besides growth rate, fillet traits are of major concern since industry figures indicate that the average fillet yield is only 33%. The processing companies presently pay the farmer a price that is based both on body weight and fillet yield. The two other fillet traits evaluated by the market are fillet fat and fillet colour. Although the influence of these characters on price is not well documented, the industry would like to improve these traits as well.

Worldwide, several aquaculture breeding organizations have evaluated and eventually included fillet traits, such as fillet yield and fillet fat, in their breeding goals (Rye and Gjerde, 1996; Gjedrem, 1997, 2000; Kause et al., 2002; Rutten et al., 2004; Neira et al., 2004; Quillet et al., 2005). Typically, measurements on a large number of families and a large number of animals within each family have to be made for these traits. This involves slaughtering and filleting of full-sibs of the breeding candidates. Also, one or more of the following must take place: calculating of fillet yield, chemical fillet fat analysis and measurement of fillet fat or fillet colour by instrumental methods. This is of course time consuming and costly, especially if fillet fat is to be determined chemically. Moreover, for a breeding program, it is a big drawback that the recordings cannot be done on the breeding candidate itself. However, if measurements of these traits are possible on live animals by the use of non-invasive methods, like Distell Fish Fatmeter for fillet fat or by body measurements for fillet weight and fillet yield, both the between and within family variation can be utilised in selection. Such non-invasive methods will thus be very useful for the Vietnamese breeding program on river catfish, which was started in 2001 with the

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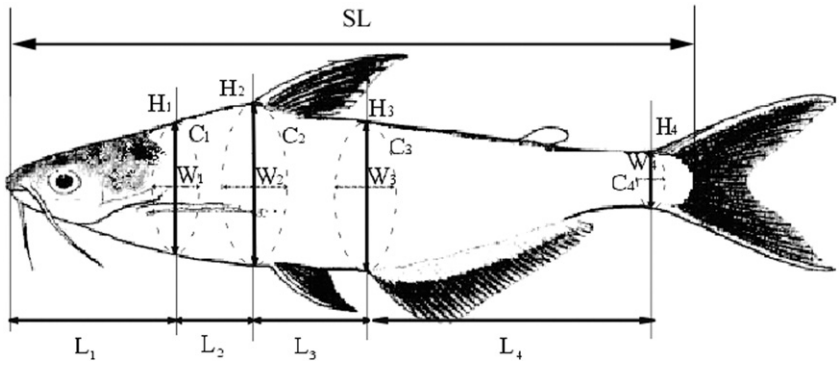

Fig. 1. Recorded characteristics of the body.

aim to improve growth and fillet yield and to monitor fillet fat. For the river catfish industry, prediction of fillet yield and fillet fat by non-invasive methods, before and after processing the fish, will also have additional value for a correct price determination.

The prediction of fillet weight and fillet yield from body measurements (body weight, height, length, width and other dimension of the fish) have previously been done on bass (Bosworth et al., 1998), common carp (Cibert et al., 1999), farmed-raised catfish (Bosworth et al., 2001) and tilapia (Rutten et al., 2004). In these studies the variation of the body measurements explained at maximum 56% of the variation in fillet yield, as given by the coefficient of determination, R^2. Higher prediction power was generally found for fillet weight.

For fillet fat, high correlations between values from Distell Fish Fatmeter and chemical analysed fat have been obtained (in salmon, $R^2=0.80$, Sigurgisladottir et al., 1997; in herring, $R^2=0.71$, Vogt et al., 2002; in Pacific salmon, $R^2=0.93$, Crossin and Hinch, 2005). Built-in equations for these species are included with the Distell Fish Fatmeter while it has not yet been developed for river catfish. Also other non-invasive methods such as Near Infrared, NIR (Atlantic salmon, Solberg et al., 2003 and Folkestad et al., 2008; herring, Vogt et al., 2002) and Computerised tomography, CT (Atlantic salmon, Rye, 1991; rainbow trout, Sigurgisladottir et al., 1997; and halibut, Kolstad et al., 2004) have shown accurate results ($R^2=0.81$–0.92), but these instruments are rather costly and usually more difficult to use on live fish.

The objective of this study was to obtain the first cross-validated prediction equations on live river catfish for both fillet weight and fillet yield, based on body measurements, and likewise for fillet fat, using the Distell Fish Fatmeter.

2. Materials and methods

2.1. Fish material

The fish recorded were from the selective breeding population held at Research Institute for Aquaculture No.2 (RIA2), in the South of Vietnam. The parents used, were from year-class 2001, i.e. the F_1-generation. Partial factorial design was used (Berg and Henryon, 1998), with 95 sires mated with 97 dams, forming 162 families in four batches, during a 30-days period in May–June 2005 a total of 30 families had low fertilization rate and no fingerling. Fry from each family were reared separately until tagging in hapas mounted within an earthen pond. In December 2005, 75 fingerlings in each family were tagged by Passive Integrated Transponders (PIT-tags, Sokymat, Switzerland) and communally stocked in one pond.

Before recording of the traits, fish were starved for two days and anaesthetised by 0.25 ppm ethylene glycol phenyl ether. At the time of recording, the sex could not be determined.

2.2. Fillet weight and fillet yield

After nine months in the grow-out pond (at an age of 15 months), a random sample of 2767 live fish were recorded for body weight (BW, to the nearest 0.1 g), standard length (SL, to the nearest 1 mm), volume (V, to the nearest 0.1 ml), together with length, height, width and circumference at four positions; labelled L_1–L_4, H_1–H_4, W_1–W_4 and C_1–C_4, respectively (Fig. 1). All recordings were completed during a two week period. Length and circumference were measured by using a tape measure (to the nearest 1 mm), and height and width by using callipers (to the nearest 0.1 mm). Volume was recorded as the amount of water flowing out of a full-water bucket after entering a fish (to the nearest 0.1 ml). All fish were recorded by the same person.

The fish were killed by bleeding and filleted by four skilful workers hired from a standard processing company, and each worker was responsible for one of the four stages of the filleting for each fish; bleeding fish and dissecting fillets, removing skin, trimming off red muscle and trimming off fat edges. The skinless fillet after trimming off the fat edge and the red muscle was weighed (FW, to the nearest 0.1 g) and the fillet yield (%) was calculated as FY=(FW/BW)*100.

2.3. Fillet fat

Another sample of 50, nine months old and live fish at marketable size, from the same pond as the 2767 fish above, was measured for fat by Distell Model 692 Fish Fatmeter (Distell Inc., West Lothian, Scotland) using the equipment's research option (IP). In one day, one person did measurements at nine positions on each side of the fish (Fig. 2), and in each position the average of 3 repeated readings from the meter was taken as a record. Unfortunately, the repeated reading at each position was not stored, that could have been used to calculate the repeatability.

The fish were killed by bleeding and filleted as described above, and the trimmed fillets of both sides were jointly analysed chemically for fat content using the Bligh and Dyer (1959) method. All fillets were ground and mixed thoroughly. Ten grams of this mixture was homogenized with a mixture of 10 ml chloroform and 20 ml methanol for 2 min, blended with 10 ml chloroform in 30 s and then blended with 10 ml distilled water in 30 s. The chloroform layer was separated and air-dried. The remainder after drying was weighed (w in gram) and fillet fat (%) was calculated as (w/10)*100.

2.4. Data analysis

2.4.1. Fillet weight and fillet yield

A random sample of 200 of the 2767 recorded individuals were used for estimating the model parameters, with the following independent

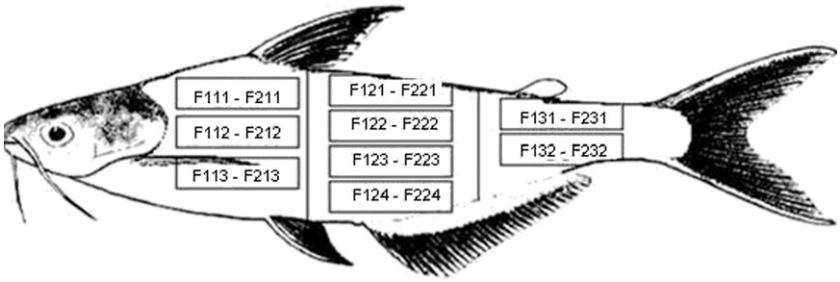

Fig. 2. The nine positions (1–9) of fat measurement done by Distell Fish Fatmeter on the left (L) and right (R) side of the body.

candidate variables considered for fillet weight: BW, SL, V, L_1–L_4, H_1–H_4, W_1–W_4 and C_1–C_4 (see Fig. 1). In order to adjust the independent variables for the effect of the fish size, the following variables were derived by dividing the records of each fish with their body weight: 1/BW, 1 (=BW/BW, becoming the intercept of the model), V_{BW} (=V/BW), SL_{BW}, L_{BW1}–L_{BW4}, H_{BW1}–H_{BW4}, W_{BW1}–W_{BW4} and C_{BW1}–C_{BW4}.

Initially, the *Regression procedure* with forward selection of variables (SAS Institute Inc., 2004) was used with a level of significance, $P<0.10$ for entering the model. Detection of outliers was carried out by calculating standardised residuals and eliminating the observations that had larger values than ±3 standard deviations ($n=12$ of 200). The final round of estimation was again done with forward selection of variables ($P<0.10$).

Finally, the estimated prediction equation was used to predict the observations of the remaining individuals ($n=2567$) and used for cross-validation. The number of observations for prediction was kept as large as possible since genetic parameters of the predicted observations were to be estimated in a successive analysis (Sang et al., unpublished data).

To indicate the quality of estimation, the R^2 and adj-R^2 statistics were used to assess the explanatory power of the models, whilst quality of prediction was evaluated by the root mean square error of prediction (RMSEP), the standard error of prediction (SEP), the bias (tested for difference from zero with $P<0.01$) and the correlation coefficient between predicted and observed values (r). Bias was calculated as: $\text{BIAS} = \left(\sum_{i=1}^{n}(y_i - \hat{y}_i)\right)/n$, where y^i and $\hat{y}^i$ are the observed and predicted values of the trait, respectively. RMSEP was defined as:

$$\text{RMSEP} = \left(\frac{\sum_{i=1}^{n}(y_i - \hat{y}_i)^2}{n}\right)^{1/2}$$

while SEP was calculated as:

$$\text{SEP} = \left(\frac{\sum_{i=1}^{n}(y_i - \hat{y}_i - bias)^2}{n-1}\right)^{1/2}$$

2.4.2. Fillet fat

All 50 individuals were used in estimation of the prediction equations with the 18 Distell records as independent candidate variables. Estimation was in essence carried out as described above for fillet weight and fillet yield. The forward selection option was again used, but now by the GLMSELECT procedure of SAS (SAS Institute Inc., 2004), followed by the same outlier detection ($n=2$ of 50) and a final round of estimation (again using forward selection).

Cross validation was carried out by the use of the predicted residual sum of squares (PRESS) criterion in the GLMSELECT procedure in SAS with CVoption=RAMDOM, by in sequence leaving out one observation at a time and estimating the prediction equation from the remaining records.

As for the fillet weight and fillet yield, the quality of estimation was indicated by the R^2 and adj-R^2 statistics, and the prediction was evaluated by using PRESS, RMSEP, SEP, bias and the correlation coefficient between predicted and observed values.

Finally, the repeatability of Distell Fish Fatmeter records taken in the same position on both sides of the fish (rep) was estimated in a one-way analysis of variance, using the ANOVA procedure of SAS (SAS Institute Inc., 2004). The model was:

$$y_{ij} = \text{fish}_i + e_{ij}$$

where i is the ith fish recorded ($i=1, 2, \ldots, 48$) and j is the jth measurement on each side in the same position ($j=1, 2$). The repeatability was estimated as:

$$\text{rep} = \sigma^2_{\text{fish}}/(\sigma^2_{\text{fish}}+\sigma^2_e)$$

where σ^2_e and σ^2_{fish} refer to the within and between fish variance components, respectively.

3. Results

The number of records, the mean and the standard deviation (SD) of fillet weight, fillet yield or fillet fat as well as body weight of the two datasets used in the analysis are presented in Table 1. Notice the larger mean body weight was found in the dataset used to predict fillet fat than that used for predicting fillet weight and fillet yield. This is likely due to the sampling procedure, which was done by catching fish by the tail from a seining-net with a large number of fish. Fish at this size will be mature at an age of 3.5–4.0 years.

3.1. Fillet weight and fillet yield

The results from the analysis of fillet weight and fillet yield are shown in Tables 2 and 3, respectively. Among the variables, volume had the largest effect in terms of increasing R^2, alone explaining as

Table 1
Number of records (n) in two datasets used to predict either fillet weight and fillet yield (dataset I) or fillet fat (dataset II), with mean and standard deviation (SD) of traits to be predicted, and also that of body weight

	n	Mean	SD
Dataset I	2767		
Fillet weight (g)		322.3	114.6
Fillet yield (%)		35.6	7.0
Body weight (g)		925.8	370.5
Dataset II	50		
Fat %		5.7	2.3
Body weight (g)		1306.1	383.2

Table 2
The regression variables[a] entering the prediction equation for fillet weight at the first six steps in forward selection

Step	Variable(s) entering	R^2	Adjusted-R^2	β	P	RMSEP	SEP	Bias	r
I	Intercept			0.81					
	V	0.84	0.84	0.33	<0.0001	42.71			
II	Intercept			−83.23					
	V	0.85	0.85	0.29	<0.0001	42.05			
	L_4			6.46	0.05				
III	Intercept			−38.93					
	V			0.31	<0.0001				
	L_4	0.85	0.85	6.97	0.03	41.93			
	H_4			−19.93	0.05				
IV	Intercept			−59.39					
	V			0.29	<0.0001				
	L_4			8.33	0.01	42.50			
	H_4	0.86	0.86	−56.30	<0.001				
	W_4			62.35	0.005				
V	Intercept			−86.13					
	V			0.29	<0.001				
	L_4	0.86	0.86	8.24	0.01	41.83	41.82	4.63[e]	0.93
	H_4			−60.05	0.001				
	W_4			47.99	0.06				
	H_1			13.35	0.26				
VI	Intercept			−73.18					
	V			0.29	<0.001				
	L_4	0.86	0.86	8.35	0.01	42.50			
	H_4			−54.87	0.001				
	W_4			53.10	0.04				
	H_1			−8.76	0.22				
	W_1			16.72	0.17				

At each step, the statistics relevant for model fit[b] (coefficient of determination (R^2) and adjusted[c] R^2) and for the quality of prediction[d] (root mean square error of prediction (RMSEP)) are given. For the preferred equation (least RMSEP), results are also given for the standard error of prediction (SEP), the prediction bias and the correlation coefficient between the predicted and observed values (r).
[a]Variables being those indicated in Fig. 1 and in addition; body weight (BW), standard length (SL) and volume (V).
[b]$n=188$.
[c]Adjusted $R^2=1-\frac{n-1}{n-p}(1-R^2)$, with n being number of observations and p number of variables entering the model.
[d]$n=2567$.
[e]Significant different from zero at $P<0.01$.

Table 3
The regression variables[a] entering the prediction equation for fillet yield at the first five steps in forward selection

Step	Variable(s) entering	R^2	Adjusted-R^2	β	P	RMSEP	SEP	Bias	r
I	Intercept	0.74	0.74	5.44		4.10			
	V_{BW}			27.11	<0.001				
II	Intercept			5.03					
	V_{BW}	0.75	0.75	30.24	<0.001	3.42			
	W_{BW1}			−452.70	0.005				
III	Intercept			4.97					
	V_{BW}			29.71	< 0.0001				
	W_{BW1}	0.76	0.76	−1708.38	< 0.001	3.38			
	W_{BW2}			1723.07	0.007				
IV	Intercept			5.39					
	V_{BW}			28.64	<0.001				
	W_{BW1}	0.77	0.76	−2391.81	<0.001	3.31	3.29	0.39[e]	0.86
	W_{BW2}			1752.94	0.006				
	L_{BW4}			254.00	0.08				
V	Intercept			5.72					
	V_{BW}			27.76	<0.001				
	W_{BW1}	0.77	0.77	−3093.26	<0.001	3.38			
	W_{BW2}			1414.39	0.03				
	L_{BW4}			312.76	0.04				
	W_{BW4}			2303.50	0.12				

At each step, the statistics relevant for model fit[b] (coefficient of determination (R^2) and adjusted[c] R^2) and for the quality of prediction[d] (root mean square error of prediction (RMSEP)) are given. For the preferred equation (least RMSEP), results are also given for the standard error of prediction (SEP), the prediction bias and the correlation coefficient between the predicted and observed values (r).
[a]Variables being the ratios between variables indicated in Fig. 1 and body weight (L_{BW1}–L_{BW4}, H_{BW1}–H_{BW4}, W_{BW1}–W_{BW4} and C_{BW1}–C_{BW4}) and in addition; the ratios between standard length and body weight (SL_{BW}), and volume and body weight (V_{BW}).
[b]$n=188$.
[c]Adjusted $R^2=1-\frac{n-1}{n-p}(1-R^2)$, with n being number of observations and p number of variables entering the model.
[d]$n=2567$.
[e]Significant different from zero at $P<0.01$.

much as 84% and 74% of variation in fillet weight and fillet yield, respectively. The preferred model for fillet weight, with the lowest RMSEP, had 5 variables (V, L_4, H_4, W_4 and H_1) and that of fillet yield, 4 variables (V_{BW}, W_{BW1}, W_{BW2} and L_{BW4}). Note that for fillet weight, the last variable entered was not significant at $P<0.10$.

For fillet weight, the correlation between predicted and observed values was 0.93 in correspondence with the R^2 value of 0.86, RMSEP was 41.83 g, and SEP was 41.82 g, as expected somewhat smaller than RMSEP. The prediction bias was 4.63 g, significantly different from zero with $P<0.01$, but only 1.4% of the mean value. For fillet yield, the correlation between predicted and observed values was 0.86 ($R^2=0.77$), RMSEP was 3.31%, and SEP was 3.29%. The prediction bias was 0.39%-points, significantly different from zero at $P<0.01$, but only 1.1% of the mean value (Table 3).

3.2. Fillet fat

Table 4 shows that the estimates of repeatability between the Distell Fish Fatmeter records in the same position at both sides of the body were low to medium (0.29–0.61) except for position number 4 (0.74). These results indicate that recording on both sides of the fish may be potentially valuable in establishing explanatory variables.

The results from analysis of fillet fat are shown in Table 5. The preferred model (least PRESS) included the four variables: R-1, L-3, L-1 and L-9. The measurements at the first position on the right side and the third position on the left side, R-1 and L-3, explained most of the variation in chemical analyzed fat, while a smaller additional variation was explained by L-1 and L-9.

For fillet fat, the correlation between predicted and observed values was 0.85 ($R^2=0.73$), RMSEP was 0.87% and SEP was 0.86%. The prediction bias was 0.22%-points, significantly different from zero at $P<0.01$, which is 3.9% of the mean value.

4. Discussion

4.1. Fillet weight and fillet yield

For fillet weight, the standard error of prediction (RMSEP) became less by inclusion of a non-significant variable in the prediction equation. The final model had 5 variables and explained 86% of the variation in fillet weight. This was less than that obtained by Rutten et al. (2004) in tilapia ($R^2=0.95$, with 5 variables in the equation; BW, SL, height (H), width (W) and corrected length (CL=standard length−head length)), whereas in bass, Bosworth et al. (1998) found a lower R^2-value ($R^2=0.52$, with 3 variables; total visceral weight, distance from posterior dorsal fin to anterior anal fin, and width at posterior dorsal fin).

In our study, volume alone explained 84% of the variation in fillet weight, with higher weight for larger volume. However, in the study of Rutten et al. (2004) in tilapia only body weight was measured (not

Table 4
Estimates of repeatability (r) between Distell fat measurements in the same position[a] at both sides of the body

Position	1	2	3	4	5	6	7	8	9
Rep	0.26	0.55	0.54	0.74	0.61	0.41	0.51	0.49	0.39

[a] Position indicated in Fig. 2.

Table 5
The regression variables[a] entering the prediction equation for fillet fat at the first five steps in forward selection

Step	Variable(s) entering	R^2	Adjusted-R^2	B	P	PRESS	RMSEP	SEP	Bias	r
I	Intercept			11.41						
	R-1	0.25	0.23	−0.21	0.007	73.23	1.24			
II	Intercept			10.01						
	R-1	0.61	0.59	−0.28	<0.001	44.46	0.96			
	L-3			0.14	<0.001					
III	Intercept			11.52						
	R-1			−0.25	<0.001					
	L-3	0.68	0.65	0.14	<0.001	39.12	0.90			
	L-1			−0.09	0.04					
IV	Intercept			9.04						
	R-1			−0.25	<0.001					
	L-3			0.14	<0.001					
	L-1	0.73	0.70	−0.08	0.03	36.32	0.87	0.86	0.22[e]	0.85
	L-9			0.06	0.05					
V	Intercept			9.25						
	R-1			−0.25	0.007					
	L-3			0.15	<0.001					
	L-1	0.74	0.71	−0.09	0.04	36.87	0.88			
	L-9			0.07	0.05					
	R-9			−0.02	0.52					

At each step, the statistics relevant for model fit[b] (coefficient of determination (R^2) and adjusted[c] R^2) and for the quality of prediction[d] (predicted residual sum of squares (PRESS)) are given. For the preferred equation (least PRESS), results are also given for the root mean square error of prediction (RMSEP), the standard error of prediction (SEP), the prediction bias and the correlation coefficient between predicted and observed values (r).
[a]Variables being those indicated in Fig. 2.
[b]$n=48$.
[c]Adjusted $R^2 = 1-\frac{n-1}{n-p}(1-R^2)$, with n being number of observations and p number of variables entering the model.
[d]PRESS, from in sequence leaving one record out and estimating the prediction equation from the remaining records.
[e]Significant different from zero at $P<0.01$.

volume) and it was included in the prediction equation. In our material, volume was highly correlated to both standard length ($r=0.86$) and body weight ($r=0.77$), meaning that when using a statistical method that is less likely to include highly colinear variables (forward selection) as here, all variables will not enter the same prediction model. If the farming and processing industry prefers to use body weight instead of volume, in order to save measuring time, they can use an alternative prediction equation of the following 5 independent variables (SL(β=17.76), BW(8.24), C3(47.99), W4(13.35), L4(−60.05) and intercept (−613.3)) with the R^2 of 0.82, SEP of 43.65 g, and r of 0.89. In practice, an even simpler alternative is a model with only SL and BW (SL (β=22.93), BW(0.03) and intercept (−611.5)) with R^2 of 0.76, SEP of 61.01 g, and r of 0.86.

Beyond volume, some additional variation in fillet weight was explained by 4 body measurement variables (L_4, H_4, W_4 and H_1). Three of these variables are in the caudal part of the fish. It is logical that a fish with longer tail length (L_4) increases fillet weight as this caudal portion contributes almost half of the whole fillet. Additionally, fillet weight seems to be influenced by the conformation in the tail, through the variables H_4 and W_4. It is also logical that enhanced height in front (H_1) is associated with an enlarged amount of meat in forefront part of the fish.

For fillet yield, RMSEP was least with 4 variables, and the final model explained 77% of the variation, which is lower than that for fillet weight. However, this is higher than that obtained by others; e.g. Bosworth et al. (2001) found a R^2 of 0.56 in farm-raised catfish using three ultrasound image variables (muscle area at the anterior insertion of the dorsal fin, at the insertion of the pelvic fin, and at the anterior insertion of the anal fin) while Rutten et al. (2004) obtained R^2 of 0.15 in tilapia, with 4 variables in the best model (SL, H, W and CL). In our study, volume corrected for body weight had the largest positive effect on R^2, and only minor additional variation was explained by other body measurement variables (W_{BW1}, W_{BW2} and L_{BW4}). A somewhat larger yield is resulting from smaller width towards the head, a larger width at the dorsal fin and a longer tail.

In cross validation of the models, both for fillet weight and fillet yield, the values for SEP were, as expected, somewhat lower than the values for RMSEP, as SEP was corrected for a significant bias. This bias may be a consequence of the limited sample size used in estimation, meaning that the estimates did not perfectly represent the true values. Another consequence of the limited sample size used for estimation was a reduced power to find regressors with only marginal effects, explaining the tendency towards preferring a larger number of variables when evaluating the model on RMSEP rather than R^2. In fact, R^2 only increased marginally (results not shown) from going beyond 200 observations in the sample used for estimation, and this number was chosen in order to have a largest possible number of predicted observations. These will be used to calculate the heritability of observed and predicted (indirect) traits and the genetic correlations to the observed and predicted traits (Sang et al., unpublished data), a prerequisite for evaluating the quality of the prediction equation in a breeding program.

A higher correlation between predicted and observed values was obtained for fillet weight than for fillet yield. For both variables, this correlation may be increased further by training of filleters and recorders, reducing the measurement error. Additionally, and especially for fillet yield, there is still scope for searching other explanatory variables, e.g. variables related to the shape of trimmed fillet, as shown by Bosworth et al. (1998). Another improvement could be to analyze fillet yield with a logistic regression model, since variable is restricted outcome; 0–100%.

4.2. Fillet fat

The correlation between predicted and observed fillet fat values in the present study ($r=0.85$) was lower than or comparable to that by Crossin and Hinch (2005) in Pacific salmon using the same instrument ($r=0.98$, with four positions above and along the lateral line on each side, $n=117$) and Vogt et al. (2002) in herring ($r=0.84$, with one position between the head and the dorsal fin on each side, $n=60$). Both these investigators used the manufacturer's built-in equations for prediction. It is probably very difficult to obtain very high r, because internal organs, fat edge and red muscle influenced Distell's values, but not the chemical analysis of fat in the trimmed fillets.

Contrary to fillet weight and fillet yield, it is considered too costly to chemically analyze a large number of fish for genetic analysis, so that a selection program with fillet fat included has to rely on the prediction of the trait.

For fillet fat, the correlation between predicted and observed values was lower than that found for fillet weight or fillet yield. The explanatory variables used were the average of three readings at each of the nine positions on each fillet, which to some extent reduced the measurement error in the independent variables. However, the low repeatability of the Distell Fish Fatmeter measures in the same position on the two sides of the body indicates that the repeatability between repeated readings in the same position may also be low. Thus, to increase the predictive value, a separate analysis should be conducted to determine how many readings that are needed at the same position for this species. Finally, more marginal effects may be picked up as significant in the estimation phase when using a larger data set, the overall prediction power is then expected to increase, and this can also reduce the bias. Also, more data should be collected to get the prediction equation confirmed on other samples of fish, e.g. at different ages and sizes. Note also that the estimation may also become inaccurate from the fact that the chemically analyzed fat is determined with error. If one had analyzed fat in both sides separately, the repeatability of the chemically analyzed fat could have been calculated, and used to make inference on the number of records of chemically analysis of fat per fish.

5. Conclusion

The results of this study indicate that body measurements on live river catfish can be used to predict actual fillet weight and fillet yield, and that fillet fat measured by the Distell Fish Fatmeter and by chemical analysis on live market sized fish are well correlated. The prediction equations for fillet weight and fillet yield can be improved by reducing measurement error (filleting), searching for additional variables, and collecting more data. For fillet fat there is primarily a need for evaluating number of readings with the Distell Fish Fatmeter in each position, and to increase number of records in the data used for estimation in order to pick up more marginal effects and to reduce the bias. The repeatability of chemically analyzed fat should also be estimated.

Overall, outcomes from the present study open up for the possibility to use non-invasive methods to measure fillet weight, fillet yield and fillet fat for the farming and processing industry as well as in breeding programs for river catfish. However, before being applied in breeding, genetic parameters for the traits studied need to be estimated.

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Paper II

Heritability and genetic correlation of economically important traits recorded at a given age in striped catfish (*Pangasianodon hypophthalmus*)

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Abstract

The objective of this study was to estimate heritability and genetic and phenotypic correlations between body weight, specific growth rate, standard length, fillet weight, fillet yield, intestinal fat, fillet fat and fillet colour in striped catfish (*Pangasianodon hypophthalmus*). Predicted data was also available for fillet weight, fillet yield and fillet fat. A data set consisting of 2767 records (all traits) and 2567 records (predicted fillet weight and predicted fillet yield) from the F2 generation and 6540 records (body weight, specific growth rate and standard length) from the F3 generation were collected in 2006 and 2009, respectively. Partial factorial and nested mating designs were used, respectively, to generate the F2 and F3 generations, with 162 and 156 full-sib families from 95 sires and 97 dams, and 93 sires and 156 dams. Model validation by model fitting (for random effects) and predictive ability (breeding values in F2 on phenotypes in F3, for fixed effects) concluded the statistical model used to analyse the data; containing random effects of additive genetics and common environment and covariates of number of days from spawning till tagging and number of days from tagging till first harvest, respectively. A univariate animal model was used to estimate variance components while a bivariate setup was used to estimate genetic correlations. Moderate heritability was obtained for body weight (0.21-0.34) and fillet weight (0.19-0.22), while low heritability was found for fillet yield (0.03-0.05), intestinal fat (0.04), predicted fillet fat (0.04) and fillet colour (0.04). Of predicted traits, only that for fillet weight showed a heritability with the potential of utilising the information on the selection candidate itself (h^2=0.10). As most of the variation of fillet weight is explained by the variation in body weight and the two traits are highly genetically correlated (0.95-0.96), most of the selection response for fillet weight will be due to a generally larger fish. Thus, there will be little scope for improvement of fillet weight from an increased fillet yield. It is therefore proposed to select for either increased fillet weight, being the product of body weight and fillet yield, or increased body weight as well as fat traits, showing an undesirable positive genetic correlation with both body weight and fillet weight.

Keywords: Pangasianodon hypophthalmus, body weight, fillet traits, fat traits, fillet colour, partial factorial design, heritability, genetic correlation.

1. Introduction

Striped catfish is the most important freshwater aquaculture species in Vietnam. Production was about 90,000 tonnes in 2000, and has been increasing dramatically in recent years, to approximately 1.2 million tonnes in 2007 (Dung, 2008a). A total of 90% of the production is fillets (Tung, 2009), which are exported to over 127 countries worldwide (Dung, 2008b). The export sums to an approximate processed production of 633,000 tonnes with a value of 1.4 million US$ in 2008 (Globefish, 2009). The producers, processors and exporters are therefore becoming increasingly aware of the importance of quality traits such as fillet yield, fillet fat and fillet colour besides growth rate, to meet the requirement in the market.

The selective breeding program for improving economically important traits in striped catfish started in the Southern National Breeding Centre for Freshwater Aquaculture (NBCEFAS), under the Research Institute for Aquaculture No.2 (RIA2) in 2001. Three base populations (populations 1, 2 and 3; pertaining to year-classes 2001, 2002 and 2003, were established from wild stocks. In F1, populations 1 and 2 were selected for body weight on phenotype, while population 3 was selected for body weight and fillet yield, using combined selection. Inclusion of fillet yield as a second trait was motivated by the assumed high economic importance of this characteristic. Fillet yield is regarded as an important trait for improvement of fish production efficiency (Flick et al., 1990; Bosworth et al., 1998; Cibert et al., 1999; Bosworth et al., 2001; Kause et al., 2002). Industry figures show that fillet yield of this species is only 33% of the total body weight, which is much lower than for instance in salmon, with about 69% (Powell et al., 2008). Later, the consumer's preferences for white colour fillet (Mai, 2004) and tendentious preference for leaner fish lead to monitor these traits (fillet fat and fillet colour) in the breeding program.

In fish, studies on the genetic improvement of body weight when recorded at a given age are relatively abundant, while studies on fillet weight, fillet yield or quality traits like fillet fat and colour are fewer. Generally, the published estimates of heritability of body weight over species are moderate in size (reviewed by Gjedrem, 1997, 2000; Vandeputte, 2003; Nguyen et al., 2007; Navarro et al., 2009b). For fillet weight, moderate heritability was also reported in several species, in tilapia (Rutten et al., 2004; Nguyen et al., 2010); in gilthead sea bream (Navarro et al., 2009a), in rainbow trout (Kause et al., 2002 & 2007); in Atlantic salmon (Powell et al., 2008) and in Coho salmon (Neira et al., 2004). For fillet yield, heritability estimates found are low to moderate in common carp (Kocour et al., 2007), tilapia (Rutten et al., 2005), gilthead sea bream (Navarro et al., 2009a), rainbow trout (Gjerde & Gjedrem, 1984; Elvingson, 1992; Kause et al., 2002; Quillet et al., 2005; Kause et al., 2007), Atlantic salmon

(Gjerde & Gjedrem, 1984; Powell et al., 2008) and Coho salmon (Neira et al., 2004). For fat percentage and fillet fat, heritability estimates found are quite high for rainbow trout (Gjerde & Shaeffer, 1989; Kause et al., 2002; Sang, 2004) and Atlantic salmon (Rye & Gjerde, 1996; Quinton et al., 2005; Powell et al., 2008), but not for common carp (Vandeputte, 2003), Coho salmon (Iwamoto et al., 1990; Neira et al., 2004) or Arctic char (Elvingson & Nilsson, 1992). For meat and fillet colour (assessed by human eye or by use of various devices), low to high heritability estimates have been obtained (Gjerde & Gjedrem, 1984; Gjerde & Schaeffer, 1989; Iwamoto et al., 1990; Elvingson & Nilsson, 1992; Rye & Gjerde, 1996; Kause et al., 2002; Sang, 2004; Quinton et al., 2005; Powell et al., 2008).

The traits selected for in a breeding program are often genetically correlated. Thus, if the selection program focuses on body weight alone, ignoring the potential for change in other traits, e.g. carcass quality traits, it may result in unwanted side effects. Experience from selection programs in aquaculture is that product quality should not be ignored (Alderson, 2001); since traits that may be at acceptable levels at the outset of the program, e.g. fecundity, fillet fat and fillet colour, should be monitored to see whether they change unintentionally. High positive genetic correlation between fillet weight and body weight have been reported in various species, in tilapia (r = 0.99, Rutten et al., 2004; r = 0.96, Nguyen et al., 2010), in gilthead sea bream (r = 0.96, Navarro et al., 2009a), in rainbow trout (r = 0.93-0.94, Kause et al., 2002 & 2007), in Atlantic salmon (r = 0.99, Powell et al., 2008) and in Coho salmon (r = 0.98, Neira et al., 2004). Moderate to high positive genetic correlations between fillet/fat percentage and body weight have been reported, e.g. in rainbow trout (r = 0.38, Kause et al., 2002; r = 0.90, Sang, 2004), Atlantic salmon (r = 0.42, Rye & Gjerde, 1996), and Coho salmon (r = 0.36, Iwamoto et al., 1990; r = 0.73, Neira et al., 2004). Also high positive correlation between fat percentage and fillet weight in Atlantic salmon was found (0.82, Powell et al., 2008). Low negative to moderate positive genetic correlations (r = -0.23-0.61) between fillet/flesh colour and fillet/flesh fat have been reported in salmon (reviewed by Gjedrem, 1997; Kause et al., 2002; Sang, 2004; Quinton et al., 2005). The same authors have also reported low to moderate positive genetic correlations (r = 0.10-0.64) between fillet/flesh colour and body weight in salmon.

Growth data is known to be affected by common environmental effects pertaining to full-sibs, due to the separate rearing from hatching to tagging (Rye & Mao, 1998; Winkelman & Peterson, 1994; Pante et al., 2002; Rutten et al., 2005) and possibly a maternal effect (Henryon et al., 2002). Thus, the use of appropriate mating designs, like the partial factorial design, and

statistical models are needed to adequately separate these effects (Berg & Henryon, 1998; Henryon et al., 2002; Blanc, 2003; Gjerde, 2005).

The overall goal of the present study was to estimate heritability and genetic and phenotypic correlations of body weight, specific growth rate, fillet weight, fillet yield, predicted fillet fat, intestinal fat and fillet colour in striped catfish when slaughtered at a given age by use of an appropriate statistical genetic model, evaluated by use of both model fit and model predictive ability. In addition, predicted fillet weight and predicted fillet yield were analysed as it would allow information on the selection candidate to be utilised in prediction of breeding values. These genetic parameters will be applied in the breeding program of striped catfish at RIA2.

2. Materials and methods

2.1. Parental fish, mating, hatching, nursing and individual tagging

2.1.1. Base population and the F1 generation

The base population was made up from stocks from three different hatcheries in the Mekong delta, Vietnam. Each stock was collected over the period 1999-2001 from grow-out farms that reared wild fingerlings caught at several seasons and locations from the Mekong River. In 2001, fish in the base population (population 1, year-class 2001) were mated in single pairs to produce offspring, denoted F1. These fish were not individually tagged, so selection for body weight was done only on individual phenotype (Table 1). These selected F1 broodstock and their offspring (F2) were individually tagged and recorded (Table 1).

2.1.2. The F2 generation

In 2005, F2 families were produced in May-June, which is the main spawning season for this species. A partial factorial mating design, i.e. one male mated to two females and vice versa, was used to facilitate estimation of common environmental effects pertaining to full-sibs (Berg & Henryon, 1998). Full-sib families were produced in four batches over a total period of 34 days (Table 1). By stripping 43, 13, 31 and 16 males, respectively and mating them to the same number of females, 206 families of fertilized eggs were produced in the four batches. Fertilized eggs were washed to remove sticky layers, otherwise causing fungus problems, and then incubated in separate net-jars in one cement tank. Fertilized eggs usually hatch 22-24 hours after fertilization. A total of 14 families were considered to have too little fry and were thus discarded.

Around 20-25 hours post hatching; approximately three thousands start-fed fry were randomly sampled from each family and reared separately in one m^3 fibreglass tanks. At this stage, fry was fed with newly-hatched artemia, moina and blood-worm. The water source and water exchange were the same for all rearing tanks. To reduce the tank effect on full-sib family performance, on average 300 fry from each full-sib family were randomly sampled at 20-days from first feeding and reared separately in net hapas in one earthen pond. Fry were then fed by blood-worm and standard commercial pellet feed. The net hapas were cleaned frequently to maintain good water circulation and thus even out environmental effect among the families. At this stage, a total of 30 families were discarded due to no, or only a few, fingerlings produced.

At the average size of 45.9 grams and average age of 171 days, 75 individuals from each full-sib family were randomly sampled and marked by Passive Integrated Transponder tags (PIT-tags, Sokymat, Switzerlands) (Table 1). Tagging was done over 47 days in December 2005 and January 2006. Tagged fish were kept for one week in family hapas to monitor mortality before they were communally stocked in a 2000 m^2 pond at the NBCEFAS - RIA2. In total, 12,190 fish were tagged, representing 162 families, from 95 sires and 97 dams (Table 1). The fish were fed *ad libitum* with commercial pelleted feed, containing 22-28% protein.

2.1.3. The F3 generation

In 2008, F3 families were produced in June and July. This time, a nested mating design was used for practical reasons, i.e. one male was mated to two females. Full-sib families were produced in five batches over a total of 28 days. In total, 156 full-sib families were produced from 93 sires and 156 dams. Otherwise stripping, fertilization, incubation and nursing were done as already described for F2.

In November and December 2008, over 31 days, an average of 51 individuals from each full-sib family were randomly sampled and marked by Passive Integrated Transponder tags (PIT-tags, Sokymat, Switzerlands) at an average weight of 34 grams and age of 147 days. Tagged fish were kept one week in family hapas to monitor mortality, before they were communally stocked in a 2000 m^2 pond at the NBCEFAS - RIA2. In total, 7,975 fish were tagged (Table 1). Commercial pelleted feed containing 22-28% protein was used.

2.2. Fish testing and data recording

2.2.1. F2 data

Fish were individually weighed at tagging (TW, ±0.1g). In August-September 2006, after an average of 270 days of culture (measured to the first harvest date, representing an approximate age of 15 months), 2767 fish (i.e. on average 17.5 individuals per family, representing 158 families, from 93 sires and 94 dams; Table 1) were randomly sampled and recorded within 16 days. Body weight (BW, ±0.1g); specific growth rate (SGR = 100*(Ln BW – Ln TW)/*t*, where *t* is the number of days from tagging till first harvest); standard length (SL, ±0.1cm); fillet weight, with and without skin (FWWS and FWWOS, ±0.1g); fillet yield, with and without skin (FYWS and FYWOS, ±0.1%); intestinal fat index (IFI, %) and fillet colour (FC, 1-3) were recorded and calculated. The skinless fillet is the fillet after removing skin and trimming off the fat edge and red muscle. Fillets on both sides of the fish were weighted, and fillet yield was calculated (FY=100*FW/BW). IFI equals the weight of dissected fat surrounding internal organs, as a percentage of the body weight. FC was classified by the filleter into 3 categories for white, pink and yellow colour of the meat, respectively. Furthermore, predicted fillet weight without skin (PFWWOS, ±0.1g); predicted fillet yield without skin (PFYWOS, ±0.1%) and predicted fillet fat (PFF, ±0.1%) were individually determined by the prediction equations of Sang et al. (2009), to allow these measures to be recorded on the selection candidate. For each fish, the relevant variables needed for using these prediction equations were measured. The number of observations used for predicting fillet fat were 2767, while for fillet weight and fillet yield, 200 of the observations were used to develop the prediction equations; so number of observations was only 2567.

Each trait was recorded by the same person for all fish. The fish were killed by bleeding, and then filleted by four skilful workers hired from a standard processing company. Each worker was responsible for one of the four stages; bleeding fish, dissecting fillets, removing skin and trimming off red muscle and fat edges. The latter worker also recorded fillet colour.

2.2.2. F3 data

Also for these fish, tagging weight was individually recorded (TW, ±0.1g). In September and October 2009 (after an average of 317 days of culture) 5640 fish from 142 families, 88 sires and 142 dams, were randomly sampled and recorded within 56 days. Body weight and standard length were recorded. As before, each trait was recorded by the same person for all fish.

2.3. Data analysis

2.3.1. Model comparison and fit

As an initial analsyis, body weight was plotted against harvest date (Fig. 1), which illustrated that bigger fish were sampled first (since they may be easier to catch). Thus, it was concluded that the defined grow-out period should be limited upwards by the first harvest date.

To find the best model, number of days in hapa from spawning till tagging (*nursetime*), number of days in grow-out from tagging till first harvest (*growtime*) and number of days from spawning till first harvest (*harvestage*) were analysed through a regression analysis, with both linear and quadratic terms, using the F2 data for all traits.

For one trait, body weight, which was recorded both in F2 and F3, and by using the representative significant effects (*nursetime* and *growtime*) from the described regression analysis and nested within each generation (since *nursetime* and *growtime* were different for the F2 and the F3 generation, Table 1), a model including an additive genetic effect was compared to a model that in addition contained a random effect of hapa affecting each full-sib family. Model fits were compared and random effects were included based on a likelihood-ratio test of the two models (e.g. Lynch and Walsh, 1998).

In the next step, models with different fixed effect structures for body weight (with the preferred random structure concluded from the analysis described above) were compared based on their ability to predict family performance in F3 based on data from F2 only. Predictive ability was estimated through the correlation between mid-parent EBVs (based on data from F2 only) and raw family means in F3. This correlation is expected to be proportional to the realized accuracy of selection (Ødegård et al., 2007). As the models differed only with respect to fixed effects, a high accuracy of selection indicates more accurate correction for fixed effects in F2 generation, and thus better prediction of offspring performance in the F3 generation. The model that had the best predictive ability for body weight was then chosen for estimation of genetic parameters for all traits.

2.3.2. Estimation of genetic parameters

For variance component estimation in the F2 data, each trait was analysed univariately with the following linear model:

$$Y_{ijkl} = \mu + b_1 X_i + b_2 X_j + f_k + a_l + e_{ijkl} \qquad (1)$$

where Y_{ijkl} = one observation for one trait for fish *1*, in full-sib family *k*, at nursetime *i* and growtime *j*; μ = overall mean for the trait; b_1 = the regression coefficient of the phenotypic value of the trait on *nursetime* (X_i), b_2 = the regression coefficient of the phenotypic value of the trait on *growtime* (X_j), f_k = the random environmental effect common to full-sib family *k* ~ $N(0, \mathrm{I}\sigma_f^2)$; a_l is a random additive genetic effect of fish *l* with $\mathbf{a} = \begin{bmatrix} a_1 & .... & a_p \end{bmatrix}' \sim N(\mathbf{0}, \mathbf{A}\sigma_a^2)$, p is the number of animals in pedigree (p = 2754 for predicted fillet weight and predicted fillet yield; 2954 for other traits in F2; and 8824 for F3), A is the additive relationship matrix and e_{ijkl} is a random residual for fish *l*, $\mathbf{e} = \begin{bmatrix} e_1 & .... & e_N \end{bmatrix}' \sim N(\mathbf{0}, \mathbf{I}\sigma_e^2)$, where *N* is number of records for the relevant trait, and **I** is an identity matrix of dimension *N*, while σ_f^2, σ_a^2 and σ_e^2 are corresponding variance components.

When joint analysis of F2 and F3 data was possible, relevant for BW, SL and SGR, a main effect of generation was included in the model and the regression coefficients in (1) were nested within generation, otherwise the same model was used.

Phenotypic and genetic correlations were estimated using a bivariate setup of (1). The models were solved using restricted maximum likelihood, as implemented in the ASReml software release 2.0 (Gilmour et al., 2006), assuming that the parents of F2 full-sib families (F1 fish) were unrelated.

3. Results

3.1. Phenotypic mean and variation

Mean and standard deviation (SD) of the recorded traits in the two generations are given in Table 2. Note that the fish were slaughtered at approximately the same size, close to one kg, in both generations, that the fillet weight in percentage of body weight, i.e. the fillet yield is low (35.6% for fillet weight without skin) and that the fillets have an average fat percentage close to four, with a predominantly white colour. The SD was high, 227.6-370.5 g for body weight and 114.6 g for fillet weight without skin, while it was low (7.0) for fillet yield without skin.

3.2. Model comparison and fit

Estimates of linear and quadratic regression coefficients of *nursetime*, *growtime* and *harvestage* on traits, using F2 data are presented in Table 3. Generally, most traits were significantly ($P < 0.05$) affected by both linear and quadratic effects of *nursetime*. Furthermore, no traits was affected by a quadratic effect of *growtime*. Thus, logically,

harvestage being the sum of *nursetime* and *growtime*, were affected by both linear and quadratic terms, for most of the traits. Notably, the coefficient of determination (R^2) was quite moderate for all these models, for BW, SL and fillet weight (0.12-0.38), but small for other traits (< 0.001 to 0.07) (results not shown).

For body weight, and for the preferred modelling of *nursetime* and *growtime* from the presented regression analysis (Table 3), models with only an additive genetic effect were compared to a model that also contained a random contemporary effect of hapa, i.e. common environmental effect pertaining to full-sibs. The latter model fitted the data for body weight, measured in both F2 and F3, clearly better than the model with only an additive genetic effect, as tested with a likelihood-ratio test (Table 4).

Finally, the preferred model, for body weight, with two random effects was tested for the fixed structure in the model. Seven models were compared (Table 5) by calculating the correlation between the mid-parent EBV, based on data from F2, and the phenotypic average of offspring in F3. Table 5 shows that correction for fixed effects clearly enhances the correlation, being the largest for model 6, which includes linear regression on *nursetime* and *growtime*. The regression coefficients in this model were 4.01 and 12.02, respectively.

3.3. Heritability

The estimated additive genetic and common environmental variances, heritabilities and common environmental effect are presented in Table 6. Heritabilities larger than 0.15 were estimated for BW, SGR, SL, FWWS and FWWOS. However, heritability estimates for FYWS, FYWOS, IFI and FC were all low. For predicted traits, PFWWOS was estimated with the highest heritability, however only half the size (0.10) relative to that obtained for FWWOS. For PFYWOS and PFF, heritability estimates were even lower.

The common environmental effect was especially large for SGR (0.30-0.47).

3.4. Genetic and phenotypic correlations

Estimated phenotypic and genetic correlations for all traits based on the data from F2 are presented in Table 7. Generally, genetic correlations were larger than phenotypic correlations. Very high genetic correlations were estimated between BW and SL and fillet weight traits (FWWS, FWWOS and PFWWOS; ≥0.95). Internally, fillet weight traits were highly correlated (≥0.88) as were fillet yield traits (FYWS, FYWOS and PFYWOS; ≥0.78) and the two fat traits (IFI and PFF; 0.83).

BW, SL and fillet weight traits were found with low to moderate positive genetic correlations with fillet yield traits (0.07-0.43). Similarly, genetic correlations with the two fat traits were positive, ranging from 0.34-0.89; largest between PFWWOS and PFF, while the traits were seemingly genetically uncorrelated with fillet colour.

Generally, fillet yield traits were negatively genetically correlated with either IFI or PFF (0.06 ÷ - 0.41), but positively correlated with fillet colour (0.35-0.47).

Both IFI and PFF were found to be genetically uncorrelated with fillet colour.

Finally, the genetic correlation between SGR and body weight was positive, whereas SGR somewhat strangely showed negative genetic correlations with fillet weight traits.

4. Discussion

The model validation carried out clearly demonstrated the importance of a proper adjustment for fixed effects in these data, with considerable effect on the predictive ability of the estimated breeding values. With a partial factorial design, as used in the present breeding scheme, the final model should, as expected, contain the effects of additive genetics and common environment of full-sib family, while for the fixed effects; linear regressions of number of days from spawning till tagging and number of days from tagging till first harvest were advised. An additional quadratic effect of the former might have been included to account for possible compensatory growth (e.g. Jiwyam, 2010), but the validation did not support this.

Further improvement of the predictive ability of estimated breeding values could potentially be obtained by some adjustments of the experimental design and related techniques. Firstly, one should aim at shortening the spawning and nursing periods of full-sib families in tanks and hapas, by upgrading hatchery capacity and improving nursing techniques. Secondly, tagging and harvesting periods should be reduced by strengthening manpower. This will minimize the variation in the length of nursing and grow-out among full-sib families. Furthermore, alternative seining methods, e.g. separation in advance and netting of fish in separate parts of the pond for daily harvest and recording, need to be considered to avoid sampling of the bigger fish early, which made correction for number of days from tagging till harvest difficult with our data.

If compared across species, the achieved fillet yield of 35.6% was similar to that found in tilapia (35.7-37.3%, Rutten et al., 2004 & 2005), but much lower than in rainbow trout (63.2%, Kause et al., 2002) and Coho salmon (56.5-59.3%, Neira et al., 2004). As expected,

the average for fillet fat (4.3-5.7%) was lower than that of many other popular aquaculture species, e.g. rainbow trout (12.5-17.1%, Kause et al., 2002 & Sang, 2004), Atlantic salmon (14.5-16.7%, Rye & Gjerde, 1996) and gilthead sea bream (7.4-10.9%, Navarro et al., 2009a).

The CV was high for most traits, especially for body weight and fillet weight (24.1-40.0%), indicating a considerable selection potential for these traits. The lower CV for body weight in F3 compared to F2 (24.1% vs. 40.0%) may be explained by the tagging of smaller sized fingerlings in F3, which reduces the variation among families prior to grow-out, which may again reduce dominance and competition.

The main results of this study were estimates of heritabilities and genetic correlations between the recorded traits not reported before for striped catfish. Moderate heritability estimates were obtained for growth traits (BW, SL, FWWS and FWWOS), whereas low heritability estimates were obtained for fillet yield, fat traits and fillet colour. Likely, the most important breeding goal trait for river catfish is fillet weight, being the product of body weight and fillet yield. In fact, processors pay for fillet yield in a sample of fish and additionally for the total biomass (body weight) in the pond, which is equivalent to fillet weight. As fish are normally slaughtered at a fixed average weight, it would be profitable to increase fillet weight per fish without simultaneously increasing other and less valuable body parts. Thus, one alternative would be to select indirectly, for both body weight and fillet yield, or directly for fillet weight. In the first alternative, selection for increased body weight would be effective in improving fillet weight as it has a moderate heritability and high genetic correlation with fillet weight (0.95-0.96). However, there is a risk that selection would be inefficient if a too large relative weight is given to fillet yield, due to its low heritability and quite low genetic correlation with fillet weight. Furthermore, the use of fillet yield in selection programs of fish has recently been criticized by Nguyen et al. (2010). The trait is a ratio and is then expected to have a low genetic variance (Powell et al., 2008), exactly what we found (low heritability). This is not strange as low realized heritability for a ratio trait is often found (e.g. food conversion ratio in pig, Webb and King, 1983).

The alternative is to select directly for increased fillet weight, with the risk that one also selects for increased appetite, and thus for more fat. Actually, this is what should expect from the generally positive genetic correlations between fillet weight and fat traits, and which also has been found in salmon (0.82, Powell et al., 2008). On the other hand, fillet colour has a low genetic correlation with both fillet weight and fat traits in this study. Similarly, low genetic correlation between fillet/flesh colour and body weight (0-0.26; Rye & Gjerde, 1996; Kause et al., 2002; Sang, 2004) and fillet/flesh fat (-0.23÷0.33; Gjedrem, 1997; Kause et al., 2002;

Sang, 2004) have been reported in salmon. Thus, a genetic change of fillet weight or fat trait is not expected to induce any genetic change of colour. Thus, with this second alternative only fillet weight and fat traits deserve to be considered initially. Equivalent to this alternative, selection for increased body weight is also increased fillet weight, while it is easier to record and on candidate itself and similar patterns of genetic correlations to fillet fat and fillet colour as that of fillet weight are found. There is an obvious need to use selection index to decide appropriate traits (body weight/fillet weight and fillet fat) and their weights for selection.

The third alternative could be to select for increased fillet weight and to reduce the weight of the remaining parts of the body, e.g. IFI or non-fillet weight (NFW=BW-FW). Analysis was carried out to examine the heritability of NFW and its genetic correlation with the other traits. The heritability was only 0.05, and the trait was highly correlated with fillet weight (0.91), body weight (0.83) and predicted fillet fat (0.89), meaning that it will be difficult to select against the less valuable part of the body and at the same time increasing fillet weight.

A further improvement of this study could have been obtained by considering the breeding goal for growth as the number of days to reach a certain fillet weight. When slaughtering at a certain average age, some fish will have a larger fillet weight than intended, and so need to have number of days to reach a certain fillet weight corrected according to the intensity of growth in the relevant period. Likewise, for predicted fillet weight, fillet fat and colour, there will be a need to correct also these phenotypes. The genetic material in F2 was either the offspring of fish selected for increased body weight in F1 or the offspring of parents belonging to a control group. This has potential of enhancing the genetic variance, but the effect should not be too large as only 43 parents and 508 offspring contributed with information in the control group.

Approaches that are also needed may have the potential of increasing heritability of fillet weight and especially fillet yield as alternative recording methods of fillet weight/fillet yield, e.g. ultrasound imaging or other scanning technologies, recording fillet weight/fillet yield at a similar (or a certain) body weight, and improving the prediction equation for the two traits. Improvement of how we measure the fat traits is also needed to increase heritability, especially for PFF. For fillet colour, a finer colour scale or other methods need to be developed and tried, e.g. a colour fan or automatic visual colour evaluation by camera (Folkestad et al., 2008), as used in salmon. However, development of a proper colour fan for striped catfish is not straightforward since fillet colour may depend on different pigments, and distribution of colour is not continuous, from white to pink and yellow (Mai, per. communication).

Among the predicted traits, only predicted fillet weight was estimated with a heritability that would notably utilise information on measured on the selection candidate itself. Predicted fillet weight was genetically highly correlated to fillet weight and had a similar pattern for genetic correlations with fat and colour as fillet weight itself.

In this study, a common environmental effect was evident for most of the important breeding goal traits, except PFF. There are several possible reasons for this. First of all, fish were reared separately for a long period (150-170 days) in hapa before tagging, which is equal to approximate two thirds of the grow-out period, (270-285 days), and to a large tagging weight (33-45g). Consequently, compensatory growth (Rodul Amin, 2005; Jiwyam, 2010) for groups with a long period in hapa is likely to occur, together with potential competitive benefits for larger fish. Substantial common environmental effect were also found in other studies for both BW (0.23, Luan, 2010; 0.19, Maluwa et al., 2006; 0.23, Maluwa & Gjerde, 2007), and body traits in tilapia (0.15-0.26, Ponzoni et al., 2005 & Nguyen et al., 2007) and likewise for BW in rainbow trout (0.17, Su et al., 1996).

The factorial design used in this study allows estimating common environmental effects (Berg & Henryon, 1998), which potentially also takes into account maternal and dominance genetic effects on each family. Some effects may not be possible to account for, e.g. the effect of early sexual maturity of males. However, frequency of early sexually mature males at recording is generally low for this species, and negative effects of early maturing males on growth of fish have not been reported so far.

5. Conclusion

This study on striped catfish has shown that proper modelling of the fixed effects influencing the various traits is essential. Fillet weight was found to be moderately heritable (0.19-0.22) with a high genetic correlation with body weight (0.95-0.96), the latter trait with heritability at least as big as for fillet weight, allowing for efficient indirect selection. Fillet weight had a moderate positive genetic correlation with fillet fat and was almost uncorrelated with fillet colour, while the two latter traits were genetically uncorrelated and had low heritabilities (0.04). Thus, selection on fillet weight/body weight is expected to increase fat percentage indirectly. Both traits need to be considered simultaneously in breeding program, either, body weight and fillet fat or fillet weight and fillet fat. It is proposed to strengthen the experimental design and related techniques, as well as to improve the recording of the breeding goal traits.

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Table 1. Description of the selective breeding program of striped catfish in Vietnam, population 1.

Parameters	Generation		
	F1	F2	F3
Production year	2001	2005	2008
Mating method[a]	Single pair	Partial factorial	Nested
Spawning date[a]	4 batches in 56 days in May-July	4 batches over 34 days in May-June	5 batches over 28 days in June-July
No. of sires[a]	75	95	93
No. of dams[a]	75	97	156
No. of families produced	75	162	156
No. of days from spawning till tagging			
- Average	97	171.3	147.4
- Min	-	146.0	139.0
- Max	-	196.0	154.0
No. of tagged fish in total	6,900[b]	12,190	7,975
No. of days from tagging till first harvest:			
- Average	300.0[c]	269.4	285.4
- Min	-	261.0	275.0
- Max	-	283.0	306.0
No. of families recorded with data:	-	158	142
-From no. of sires	-	93	88
-From no. of dams	-	94	142
Traits recorded	Body weight and standard length	Body weight, standard length, fillet weight, fillet yield, intestinal fat, fillet fat and fillet colour	Body weight and standard length
Traits selected for	Body weight	Body weight & fillet yield	Body weight
Selection method	Phenotypic selection	Combined selection	BLUP

[a]In previous generation; [b]Non-tagged fish; [c]No. of days from communal stocking till first harvest.

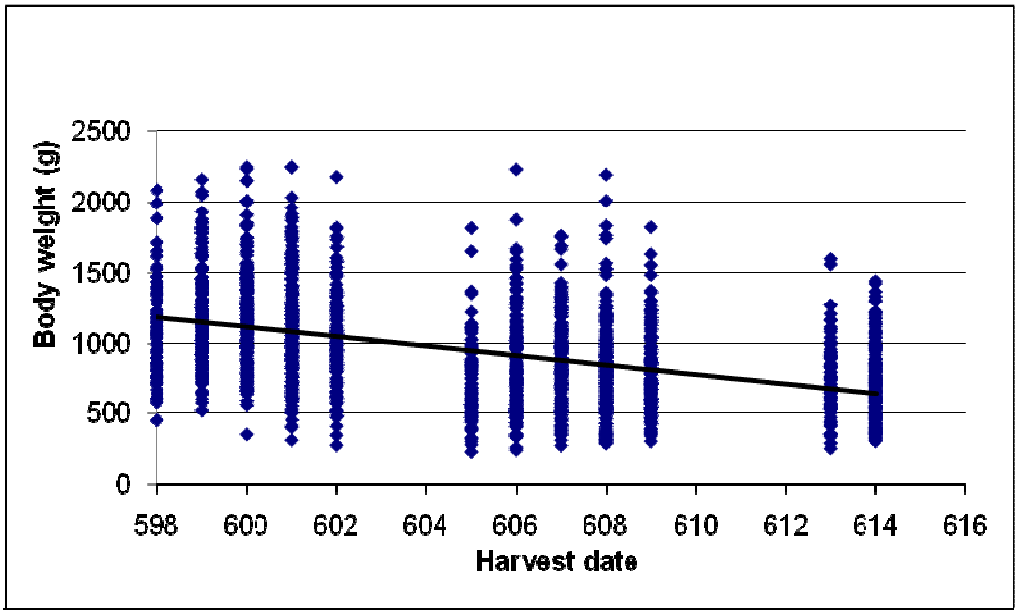

Fig. 1. Plot of body weight by harvest date for F2 data recorded in 2006. The trend is indicated by the solid line.

Table 2. Mean and standard deviation (SD) of recorded traits in F2 and F3.

Trait	F2[a]		F3[b]	
	Mean	**SD**	**Mean**	**SD**
Tagging weight, TW (g)	45.9	22.3	33.6	20.8
Body weight, BW (g)	925.8	370.5	944.2	227.6
Specific growth rate, SGR [c)]	1.20	0.2	1.10	0.2
Standard length, SL (cm)	39.8	4.2	38.8	2.7
Fillet weight with skin, FWWS (g)	455.9	163.7		
Fillet weight without skin, FWWOS (g)	322.3	114.6		
Predicted fillet weight without skin, PFWWOS (g) [d)]	317.5	111.1		
Fillet yield with skin, FYWS (%) [e)]	47.6	9.0		
Fillet yield without skin, FYWOS (%) [f)]	35.6	7.0		
Predicted fillet yield without skin, PFYWOS (%)[d)]	35.2	6.0		
Intestinal fat index, IFI (%)[g)]	2.6	1.2		
Predicted fillet fat, PFF (%)	4.3	0.7		
Fillet colour, FC (1-3) [h)]	1.4	0.5		

[a] $n = 2767$.

[b] $n = 5640$.

[c] SGR = specific growth rate = $100(\ln(BW) - \ln(TW))/t$, where t is the total number of days from tagging till first harvest.

[d] $n = 2567$.

[e] FYWS = fillet yield with skin = 100(FWWS/BW).

[f] FYWOS = fillet yield without skin = 100(FWWOS/BW).

[g] IFI = intestinal fat index = weight of fat surrounding internal organs to the body weight in percentage.

[h] FC = fillet colour, 1 = white, 2 = pink and 3 = yellow.

Table 3. Estimated linear and quadratic regression coefficients (β) for *nursetime* (number of days in hapa from spawning till tagging), growtime (number of days in grow-out from tagging till first harvest) and *harvestage* (number of days from spawning till first harvest) on the different traits investigated (using F2 data) and their level of significance (*P*).

Traits[a]	Nursetime				Growtime				Harvestage			
	Linear		Quadratic		Linear		Quadratic		Linear		Quadratic	
	β	*P* [b]	β	*P*	β	*P*	β	*P*	β	*P*	β	*P*
TW	7.04	***	-0.02	ns	na	na	na	na	na	na	na	na
BW	116.36	***	-0.35	ns	-56.85	***	0.14	ns	167.78	***	-0.18	***
SGR	-0.12	***	<0.001	***	na	na	na	na	-0.04	***	<0.001	ns
SL	0.92	***	-0.003	***	-0.11	***	0.001	ns	1.05	**	-0.001	*
FWWS	35.98	**	-0.12	**	-18.19	***	0.05	ns	37.14	***	-0.04	ns
FWWOS	32.97	*	-0.11	*	-11.75	***	0.03	ns	22.26	***	-0.02	ns
PFWWOS	10.39	***	-0.05	***	-10.54	***	0.03	ns	30.48	**	-0.03	*
FYWS	-13.41	*	0.04	*	2.95	ns	-0.006	ns	11.47	*	-0.01	*
FYWOS	-10.56	ns	0.03	ns	-2.37	**	0.005	ns	11.50	*	-0.01	*
PFYWOS	-2.08	*	0.005	**	0.95	***	-0.002	ns	0.63	***	-0.001	ns
IFI	3.98	ns	-0.01	ns	1.30	*	-0.003	ns	0.93	*	-0.001	ns
PFF	0.56	ns	-0.001	ns	0.67	ns	-0.001	ns	3.37	ns	-0.004	ns
FC	-2.31	ns	0.007	ns	-2.30	***	0.004	ns	-0.81	***	0.001	ns

[a] TW = tagging weight; BW = body weight; SGR = specific growth rate; SL = standard length; FWWS = fillet weight with skin; FWWOS = fillet weight without skin; PFWWOS = predicted fillet weight without skin; FYWS = fillet yield with skin; FYWOS = fillet yield without skin; PFYWOS = predicted fillet yield without skin; IFI = intestinal fat index; PFF = predicted fillet fat; FC = fillet colour.

[b] * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$, ns: $P > 0.05$, na: not analysed.

Table 4. Likelihood-ratio test (LR), and its level of significance (*P*), for best fit of the two models; one containing an additive genetic effect and a random contemporary effect of hapa, Full model, and the other with only an additive genetic effect, Null model; A fixed structure with linear regression of *nursetime* and *growtime*, nested within generation (F2 and F3 data) was used in both models.

Model	logL	LR[a]	*P*
Null model	-7326.93		
Full model	-7288.82	76.22	< 0.001

[a] LR = -2[log(null model) - log(full model)].

Table 5. Predictive ability of seven models (effect included is denoted by an x) used for genetic analysis of body weight, measured as Pearson correlation coefficient (r) between mid-parent EBV, based on sib testing (F2), and phenotypes of their full-sib progeny (F3). 142 families in the data set.

Model	Fixed effects					Random effects		r	*P*
	Nursetime[a]								
	Discrete classes[b]	Linear regression	Quadratic regression	Grow-time[c]	Harvest-age[d]	Additive genetic	Common environment		
1						x	x	0.08	0.34
2	x					x	x	0.13	0.13
3				x		x	x	0.11	0.19
4					x	x	x	0.19	0.03
5	x			x		x	x	0.18	0.04
6		x		x		x	x	0.23	0.01
7		x	x	x		x	x	0.21	0.02

[a]Nursetime = number of days in hapa from spawning till tagging, either as a regression or as a class variable.

[b] 9 classes.

[c]Growtime = number of days in grow-out from tagging till first harvest as a regression.

[d]Harvestage = number of days from spawning till first harvest as a regression.

Table 6. Estimated additive genetic (σ^2_a), common environmental variances (σ^2_f), heritability (h^2) and common environmental effect (c^2) with their standard error (±se) for recorded traits in F2 and F2+F3 data.

Trait[a]	σ^2_a	σ^2_f	h^2 [b] ± se	c^2 [b] ± se
F2+F3				
BW	21081.5	8759.05	0.34±0.13	0.14±0.06
SGR	0.005	0.017	0.15±0.12	0.47±0.06
SL	1.60	2.05	0.24±0.09	0.19±0.04
F2				
BW	15079.60	9532.98	0.21 ±0.08	0.13±0.04
SGR	0.01	0.02	0.21±0.14	0.30±0.07
SL	1.25	2.25	0.13±0.13	0.23±0.07
FWWS	3725.78	2339.98	0.22±0.08	0.14±0.04
FWWOS	1789.66	1157.11	0.19±0.08	0.13±0.04
PFWWOS	740.96	1585.95	0.10±0.11	0.22±0.06
FYWS	2.65	1.58	0.03±0.04	0.02±0.02
FYWOS	2.29	1.14	0.05±0.04	0.02±0.02
PFYWOS	1.96	1.05	0.04±0.04	0.02±0.02
IFI	7.44	18.60	0.04±0.06	0.11±0.04
PFF	0.02	0.01	0.04±0.03	0.01±0.02
FC	0.01	0.02	0.04±0.06	0.08±0.03

[a]TW = tagging weight; BW = body weight; SGR = specific growth rate; SL = standard length; FWWS = fillet weight with skin; FWWOS = fillet weight without skin; PFWWOS = predicted fillet weight without skin; FYWS = fillet yield with skin; FYWOS = fillet yield without skin; PFYWOS = predicted fillet yield without skin; IFI = intestinal fat index; PFF = predicted fillet fat; FC = fillet colour.

[b] $h^2 = \sigma^2_a / \sigma^2_p = \sigma^2_a / (\sigma^2_a + \sigma^2_f + \sigma^2_e)$ and $c^2 = \sigma^2_f / (\sigma^2_a + \sigma^2_f + \sigma^2_e)$, where σ^2_a, σ^2_f, σ^2_e and σ^2_p are the additive genetic, common environment of full-sibs, environmental and phenotypic variance components, respectively.

Table 7. Estimated phenotypic (above diagonal) and genetic (below diagonal) correlations, with their standard errors (± se), between the different traits recorded in F2.

Trait[a]	BW	SGR	SL	FWWS	FWWOS	PFWWOS	FYWS	FYWOS	PFYWOS	IFI	PFF	FC
BW	-	0.16±0.04	0.86±0.01	0.84± 0.01	0.80± 0.01	0.67±0.02	-0.22± 0.03	-0.22± 0.02	-0.21±0.02	0.57± 0.02	0.20± 0.03	-0.05± 0.03
SGR	0.31±0.38	-	0.73±0.02	-0.08±0.05	-0.13±0.04	-0.04±0.04	-0.47±0.2	-0.45±0.02	-0.41±0.02	0.16±0.04	0.03±0.03	-0.19±0.03
SL	0.99±0.01	0.98±0.03	-	0.87±0.01	0.85±0.01	0.96±0.01	0.12±0.03	0.08±0.03	0.13±0.02	0.53±0.02	0.14±0.03	-0.05± 0.03
FWWS	0.96± 0.07	-0.30±0.10	0.98±0.02	-	0.96± 0.01	0.92±0.01	0.24± 0.02	0.17± 0.02	0.07±0.01	0.57± 0.02	0.32± 0.02	-0.06± 0.03
FWWOS	0.95± 0.10	-0.32±0.10	0.98±0.02	0.99± 0.01	-	0.85±0.01	0.23± 0.01	0.29± 0.02	-0.06±0.02	0.45± 0.02	0.31± 0.02	-0.04± 0.03
PFWWOS	0.96±0.11	-0.26±0.11	0.99±0.01	0.99±0.01	0.88±0.15	-	0.22±0.03	0.17±0.02	0.19±0.02	0.54±0.02	0.25±0.02	-0.08±0.03
FYWS	0.38± 0.08	-0.46±0.15	0.16±0.28	0.43± 0.16	0.43± 0.16	0.31±0.18	-	0.92± 0.01	0.96±0.01	-0.05± 0.03	0.04± 0.03	0.04± 0.03
FYWOS	0.23± 0.11	-0.57±0.12	0.11±0.28	0.41± 0.21	0.41± 0.21	0.32±0.18	0.78± 0.15	-	0.77±0.01	-0.10± 0.02	0.08± 0.02	0.01± 0.02
PFYWOS	0.15±0.17	-0.46±0.15	0.07±0.28	017±0.16	0.24±0.14	0.22±0.16	0.97±0.05	0.95±0.16	-	-0.08±0.02	0.11±0.02	-0.02±0.02
IFI	0.62± 0.17	0.04±0.12	0.75±0.10	0.44± 0.32	0.75± 0.05	0.81±0.07	-0.34± 0.20	-0.26± 0.19	-0.41±0.14	-	0.25± 0.02	-0.08± 0.03
PFF	0.41± 0.11	0.26±0.14	0.34±0.08	0.76± 0.10	0.68± 0.10	0.89±0.11	-0.33± 0.21	0.06± 0.22	-0.26±0.24	0.83± 0.25	-	-0.07± 0.02
FC	-0.21± 0.13	-0.45±0.11	0.06± 0.12	-0.07± 0.29	-0.08± 0.29	0.09±0.16	0.47± 0.19	0.35± 0.23	0.46±0.21	-0.06± 0.17	-0.01± 0.15	-

[a] TW = tagging weight; BW = body weight; SGR = specific growth rate; SL = standard length; FWWS = fillet weight with skin; FWWOS = fillet weight without skin; PFWWOS = predicted fillet weight without skin; FYWS = fillet yield with skin; FYWOS = fillet yield without skin; PFYWOS = predicted fillet yield without skin; IFI = intestinal fat index; PFF = predicted fillet fat; FC = fillet colour.

Paper III

Genotype by environment interaction for economically important traits in Striped Catfish (*Pangasianodon hypophthalmus*) in three production systems in Vietnam

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Abstract

Body weight, fillet weight, fillet yield, predicted fillet fat and fillet colour were recorded for 132 families in river-net fence, 115 families in open-river pond and 206 families in internal-field pond environments, with respectively 10, 11 and 13 individuals on average per family. The genotype by environment interaction was estimated as a genetic correlation between the same trait in different environments, and several statistically significant interactions were found by a likelihood-ratio test. The primary practical implication is that testing and selection in the future is proposed to be carried out in an open-river pond environment rather than as now in an internal-field pond, since the largest part of production takes place in this type of environment and also the highest heritabilities of traits were found in this environment. However, it is proposed to continue testing of full-sib groups in both these environments, open-river pond and internal-field pond, to establish precise genetic parameters and to evaluate how genotype by environment interaction should be taken into account in the future. This will involve the possibility to select for stable genotypes across environments, and also the alternatively with multiple breeding programs should be considered.

Keywords: Pangasianodon hypophthalmus, body weight, fillet weight, fillet fat, fillet colour, partial factorial design, heritability, genotype by environment interaction.

1. Introduction

Since the start of intensive farming of striped catfish (*Pangasianodon hypophthalmus*) in Vietnam, several production systems have been developed. The most important ones are river-net fence, internal-field pond and open-river pond cultures, with the last system being the predominating one. Also cage culture was practised when this species was first farmed, but the popularity of the system ceased due to its high production cost. The three remaining rearing systems are different in terms of fish density, water depth, water temperature, water flow, feeding level and length of the grow-out period.

The optimal strategy for improving performance of economical important traits in farmed species depends on the relative magnitudes of genetic and environmental effects and the interaction of these two effects, i.e. the genotype-environment interaction (GxE) for the traits. Currently for striped catfish, the important traits are growth and fillet yield, with fillet fat and

fillet colour being two other potentially important traits. Furthermore, as this species is farmed in fresh water in the three mentioned environments, it is crucial to ensure that genetic improvement is realized in all environments for the traits of interest.

GxE exists when a specific change of environment have a greater effect on some genotypes than on others, but for practical considerations the effect is only crucial when genotype A is superior to genotype B in environment X, while it is inferior in environment Y. One way to measure GxE is to consider a trait, which has been recorded on full-sibs that have been reared in two different environments, as effectual two distinct traits, and then use the estimated genetic correlations between these two traits as an expression for the GxE. If the genetic correlation between performances in different environments is close to unity, it implies that GxE is negligible (Falconer & Mackay, 1996). However, if GxE does exist, a separate breeding program for each production system may be considered, depending on the cost-benefit ratio. According to Robertson (1959), a genetic correlation of 0.8 has been considered as a threshold for determining the biological importance of GxE as a larger correlation would lead to only minor re-ranking.

Genotype-environment interaction can be classified into; strain by environment, individual by environment and gene by environment interaction. The first two can be accounted for by the magnitude of re-ranking of strains or individuals (i.e. progeny group) respectively over different test environments. The second is still the most common used measure of GxE interaction so far (Lin & Tagashi, 2002).

In rainbow trout tested in five fish-farms along the coast of Norway, a significant individual GxE for body weight was found, but it accounted for only a small amount of the total variation (Gunnes & Gjedrem, 1981). The same was true for body weight in rainbow trout tested in fresh and brackish water in Sweden (r = 0.58, Sýlven et al., 1991), in Pacific oyster in five Australian farms (r = 0.11-0.46, Swan et al., 2007), and for fillet fat in rainbow trout tested in two Northern and Southern farms in Norway (r = 0.36, Sang, 2004). Furthermore, the existence of individual GxE at some extent was found, for body weight of Chinook salmon tested in three sites in Canada (r = 0.59-0.69, Winkelman & Peterson, 1994), in tilapia (*Oreochromis shiranus*) tested in farms at different altitudes in Malawi (r = 0.63-0.74, Maluwa et al., 2006), in Atlantic cod tested at different locations in Norway (r = 0.58, Kolstad et al., 2006) and in rainbow trout tested in fresh and brackish water in Finland (r = 0.61, Kause et al., 2003). In Atlantic salmon tested at six cage farms in Norway, Wild et al. (1994) concluded that GxE was important for early sexual maturity. Also, Sang (2004) found

GxE interaction at some extent for body size, yield, carcass quality and external traits in rainbow trout tested in two farms in Norway.

Thus, preferably before establishing a breeding program, GxE of economically important traits in striped catfish should be investigated in the most commonly used environments in Vietnam, since GxE of economic important traits for this species has not yet been investigated. Actually, there are few studies that have estimated genetic variation and GxE in warm water fish species; but studies have been conducted in the tilapias; *Oreochromis shiranus* (Maluwa & Gjerde, 2006; Maluwa et al. 2006) and *Oreochromis niloticus* (Eknath at al., 1993 & 2007; Bentsen et al, 1998; Luan, 2010).

The aim of the present study was to examine the magnitudes of genotype by environment interaction for some economically important traits in the initiated breeding program for striped catfish in Vietnam. The traits examined were body weight, fillet weight and fillet yield, predicted fillet fat and fillet colour, measured on full-sib groups of one population tested in the three different environments; river-net fence, open-river pond and internal-field pond, which are the production systems most commonly used in the Mekong delta of Vietnam.

2. Materials and methods

2.1. Parental fish, mating, hatching, nursing and individual tagging

2.1.1. Base population and the F1 generation

The base population consisted of stocks from four different hatcheries in the Mekong delta, Vietnam. Each stock was sampled over the period 1999-2002 from grow-out farms that reared wild fingerlings caught at several seasons and locations in the Mekong River. In 2002, fish in the base population (year-class 2002, population 2) were mated in single pairs to produce offspring (denoted F1) at the Southern National Breeding Center for Freshwater Aquaculture (NBCEFAS), under Research Institute for Aquaculture No.2 (RIA2). However, these fish were not individually tagged, so selection in F1 was on phenotype for body weight. Offspring in F2 were individually tagged and recorded (Table 1).

2.1.2. The F2 generation

In 2006, F2 families were produced in April and May, corresponding to the main spawning season for this species. A partial factorial mating design, i.e. one male mated with two females and vice versa, was used (Berg & Henryon, 1998). Full-sib families were produced in six batches over a total of 34 days (Table 1). By stripping 16, 24, 25, 31, 9 and 15 males, respectively, mated to the same number of females, 240 groups of fertilized eggs were

produced in the six batches. Incubation and nursing were done as described in Sang et al. (submitted). There were 208 families that had enough fingerlings to be used for testing.

For each of the three test environments, an average of respectively 14, 14 and 65 individuals from each full-sib family were randomly sampled and marked individually by Passive Integrated Transponder tags (PIT-tags, Sokymat, Switzerlands). Tagging was done over 29 days, 43 days and 44 days, respectively, in January-February 2007, at average ages of 267 days, 276 days and 234 days, respectively (for river-net fence, open-river pond and internal-field pond). The average tagging size was 26.8, 26.5 and 28.1 grams, respectively, for the three test environments. Tagged fish were kept for one week in family hapas to monitor mortality before they were communally stocked in the three test environments (Table 1); a river-net fence of 30 m^2 with four meter depth, a fence of 48 m^2 with three meter depth, at one side of an open-river pond of 9.000 m^2, and an internal-field pond of 2000 m^2, with one and half meter depth at the NBCEFAS - RIA2. In total, 1937, 1621 and 13409 fish (Table 1) were tagged, representing 139 families (from 92 sires and 86 dams), 119 families (from 78 sires and 74 dams) and 208 families (from 121 sires and 118 dams), respectively. The average stocking density was 16.1, 11.3 and 4.5 individuals per m^2 for the three test environments, respectively. Fish were fed *ad libitum* in the river-net fence (on average 1.50% of fish body weight per day), and according to their appetite and water quality both in the open-river pond (average, 1.29% of fish body weight per day) and in the internal-field pond (average, 0.97% of fish body weight per day). Commercial pelleted feed containing 22-28% protein was used.

2.2. Data recording

Individually weighing of fish was carried out at tagging (TW, ±0.1g). Furthermore, in July 2007, after the average of 160 days of culture, all survived fish from the river-net fence (n=1338, i.e. on average ten individuals per family, representing 132 families, from 89 sires and 83 dams) were harvested and recorded within four days. Similarly, in August 2007, after an average of 191 days of culture, all survived fish from the open-river pond (n=1272, i.e. on average 11 individuals per family, representing 115 families, from 76 sires and 72 dams) were also harvested and recorded within three days. And last, in September 2007, after an average of 262 days of culture, from the internal-field pond, the fish were sampled and recorded within 14 days (n=2635, i.e. on average 13 individuals per family, representing 206 families, from 120 sires and 117 dams). Body weight (BW, ±0.1g); fillet weight without skin (FWWOS, ±0.1g); fillet yield without skin (FYWOS, ±0.1%); and fillet colour (FC, 1-3) were recorded and calculated. Furthermore, predicted fillet fat (PFF, ±0.1%) was individually determined by

the prediction equation of Sang et al. (2009). For each fish, the relevant variables included in the prediction equation were measured. The skinless fillet is what remains after removing skin and trimming off the fat edge and red muscle. Fillet yield was calculated from fillets on both sides of the fish (FYWOS=100*FWWOS/BW). FC was classified either as white, pink or yellow.

For all fish, each trait was recorded by one and the same person. Four skilful workers hired from a standard processing company killed and filleted the fish. Each worker was responsible for one of the following; bleeding fish, dissecting fillets, removing skin and trimming off red muscle and fat edges. Additionally, the latter worker recorded fillet colour.

2.3. Data analysis

As in Sang et al. (submitted), body weight was plotted against harvest date, illustrating that bigger fish were sampled first (since they may be easier to catch). Thus, it was concluded that the defined *growtime* (number of days in grow-out from tagging till first harvest) should be limited upwards by the first harvest date. Actually, the linear model used to estimate variance components in univariate analysis utilising F2 data was the same as validated and utilised by Sang et al. (submitted):

$$Y_{ijkl} = \mu + b_1 X_i + b_2 X_j + f_k + a_l + e_{ijkl} \qquad (1)$$

where Y_{ijkl} = one observation for one trait for fish l, in full-sib family k, at nursetime (number of days in hapa from spawning till tagging) i and growtime j; μ = overall mean; b_1 = the regression coefficient of the phenotypic value of the trait on *nursetime* (X_i), b_2 = the regression coefficient of the phenotypic value of the trait on *growtime* (X_j), f_k = the random environmental effect common to full-sib family $k \sim N(0, \mathbf{I}\sigma_f^2)$; a_l is a random additive genetic effect of fish l with $\mathbf{a} = \begin{bmatrix} a_1 & .... & a_p \end{bmatrix}' \sim N(\mathbf{0}, \mathbf{A}\sigma_a^2)$, p is the number of animals in pedigree (p equals 1510, 1420 and 2872, respectively for river-net fence, open-river pond and internal-field pond), A is the additive relationship matrix and e_{ijkl} is a random residual for fish l, $\mathbf{e} = \begin{bmatrix} e_1 & .... & e_N \end{bmatrix}' \sim N(\mathbf{0}, \mathbf{I}\sigma_e^2)$, where N is number of records for the relevant trait, $\mathbf{I}$ is an identity matrix of dimension N, while σ_f^2, σ_a^2 and σ_e^2 are corresponding variance components. All records were utilised in the univariate analysis.

In estimation of genetic correlation between the same traits recorded in different environments, a bi-variate set-up of model (1) above was used with covariates of *nursetime* and *growtime* nested within environments. The error covariance between the traits in two test

environments was set to zero since individual fish did not have simultaneous records in more than one test environment. As in univariate analysis, the models were solved using restricted maximum likelihood, as implemented in the ASReml software release 2.0 (Gilmour et al., 2006), assuming that the parents of F2 full-sib families (F1 fish) were unrelated. Due to convergence problem, the co-variance of random common full-sib effect of the same trait between two environments was fixed to zero. A likelihood ratio (Lynch and Walsh, 1998) was used to test whether the genetic correlation between the same traits in two environments was significantly different from unity. It is given by LR = -2[log(r|z) - log(|z)], where log(|z) is the maximum of the likelihood function for the full model; i.e. the model allowing to estimate the genetic correlation, and log(r|z) is the maximum of the likelihood function for the null model; i.e. one in which the genetic correlation is fixed to nearly unity, 0.99. The LR test statistic is asymptotically distributed as χ_r^2, with *r* degrees of freedom (in our case, *r* = 1). All records were also used in the bivariate analysis. However, only 110, 131 and 114 full-sib families had data in both of the following environments, river-net fence and open-river pond, river-net fence and internal-field pond, and open-river pond and internal-field pond, respectively.

3. Results

3.1. Phenotypic mean and variation

The phenotypic mean and standard deviation (SD) of the recorded traits are presented in Table 2. In the open-river pond, fish were observed with smallest SD for body weight, fillet weight and fillet yield. SD of BW was largest in the internal-field pond and largest, similar in size, for FWWOS and FYWOS in the river-net fence and in the internal-field pond. For PFF, the lowest mean and SD was obtained in the open-river pond and the internal-field pond, while the fish had a tendency to become fat in the river-net fence. FC was desirable (towards white) in the river-net fence and the open-river pond.

3.2. Heritability

Heritabilities and common environmental effects of full-sibs for the examined traits in the three test environments are presented in Table 3. In all three environments, moderate to high heritabilities (0.33-0.53) were estimated for growth traits (BW and FWWOS), while low to moderate heritabilities (0.02-0.20) were estimated for FYWOS, PFF and FC, most expressed for FC. The common environmental effect was largest for FWWOS in the river-net fence, 0.16.

The estimated variance components of the recorded traits are presented in Table 4. For the growth trait and fillet yield, the phenotypic variance (V_p) was the least in the open-river pond, while intermediate values were found for PFF and FC in that environment (as in Table 2). Again, the largest phenotypic variance for PFF and FC were in the river-net fence and in the internal-field pond, respectively.

3.3. Genotype by environment interaction

For each trait in pairs of test environments, the genetic correlations as well as the likelihood-ratio test (LR) of whether the genetic correlation was significantly different from unity are presented in Table 5. Generally, genetic correlations of traits recorded in the river-net fence and in the open-river pond were the highest ones, except for fillet yield (0.57), being significantly ($P < 0.05$) different from unity between these environments. Significant was also the genetic correlation for FC (0.76). For the genetic correlation between the internal-field pond and the two other environments, a significant lower than unity correlation was found for both BW (0.81 and 0.71, respectively) and FWWOS (0.78 and 0.73, respectively) both in the river-net fence and in the open-river pond. For FC, a significant estimate of 0.60 was obtained between the internal-field pond and the river-net fence.

4. Discussion

The estimated heritabilities in the present study confirm the results of Sang et al. (submitted), with high heritability for body weight and fillet weight, and lower estimates for fillet yield, predicted fillet fat and fillet colour; also all estimates being similar in size over environments. However, estimates for body weight and fillet weight as well as fillet colour were higher in this population than in the population studied by Sang et al. (submitted). Also, in this population, base animals of the relationship matrix (A) were in F1 and either belonged to a selected group (parents selected on phenotypes) or a control group. This should have only a minor effect on the genetic variance, as discussed by Sang et al. (submitted).

In the present study, the best production results, a desirable mean for a lower phenotypic variation was obtained in the open-river pond, corresponding to the better environment of the three. This is probably caused by the feed being more evenly distributed at a rather optimal rate; as also indicated by the lowest value for predicted fillet fat, Table 2. In the river-net fence, the phenotypic variances were unlarged, relative to that of the open-river pond, except for fillet colour, especially for predicted fillet fat for which the mean was also high. This is likely due to higher daily feed rate (1.5%) and also competition among the densely stocked

fish with the use of a narrow feed frame applied in the 30-m^2 net pen. However, the largest phenotypic variance for growth traits with the low mean and the lowest phenotypic variance for predicted fillet fat (Table 2 & 5, respectively) were found in the internal-field pond, which in case probably can be explained by the lower feeding rate (0.97%) and also by the feeding procedure, which implied spreading out the feed at fairly limited parts of the pond, both matters causing increased competition. Fillet colour in this environment was towards yellow, which is due to the low level of water exchange.

Today the predominant production system in Vietnam is the open-river pond, estimated to make up about 80% of the farms and thus production (Phan et al., 2009). According to Phuong and Oanh (2009), 5% of the total production was done in river-net fences, meaning that about 15% of the current production is made in internal-field ponds. However, uncertainty exists in these figures, so better assessment of the relative importance of various production systems is thus needed.

With the majority of the production being done in open-river ponds and the breeding program carried out in the internal-field pond, the program is left with several challenges. First, there is a need for confirmation of the size of the genetic correlations between productions in these two environments, achievable with a more comprehensive dataset that may improve the precision of the estimates. Estimates were likely unbiased as 110 families were included, with 10 individuals each. Thus, with more data, the average genetic correlation should not be much different from the average obtained now, 0.69. This is confirmed by Sae-Lim et al. (2010), except an increased family size to 20-25 in the case of low heritable traits. However, altogether we have assumed that the genetic correlations are unaffected by restricting the covariance between the common environment effects to zero. With this size of the genetic correlation found in this present study and with the production being predominantly in open-river ponds, which also gave the largest heritabilities, it is likely that testing and selection should rather be carried out in this environment than in an internal-field environment, as done now. This can alternatively be done by mimicking the open-river pond environment at the research station. This should imply a deeper internal-field pond, increased water exchange, and feed should be distributed at a higher daily rate and also be spread out more evenly in the pond. An alternative breeding strategy that may perform better across environments is to test genotypes in both or all relevant environments and then select families showing the most stable genotypes across these environments (Lin & Togashi, 2002). In the initial phase of the breeding program this should likely imply testing of all full-sib families in the two largest environments, in order to also improve estimation of the genetic correlation

across environments. A last alternative will be to consider more than one breeding program, one for each environment. Since the breeding program for this species is still in its initial phase, more data on size of environments as well as importance of GxE are needed for several traits, before a final decision is made. Finally, an economical cost-benefit analysis will have to be carried out to decide if for instance two (or alternatively three) separate breeding programs may be worthwhile.

5. Conclusion

In the three environments considered, river-net fence, open-river pond and internal-field pond, significant ($P < 0.05$) GxE interactions between several traits were estimated, as a genetic correlation. With one breeding program and the majority of production in the open-river pond (80%), in which the traits also expressed the largest heritability, an open-river pond should likely be used for testing and selection. This implies a revision of the present scheme, which at current is done in the internal-field pond. It is advised to test full-sib groups both in the open-river pond and the internal-field pond, to establish a basic for precise genetic parameter estimates and a proper evaluation of future breeding practises, where also selection for stable genotypes across environments and multiple breeding programs should be considered.

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Table 1. Description of the selective breeding program of river catfish in Vietnam, population 2.

Parameters	Generation			
	F1	F2		
	Internal-field pond	River-net fence[a]	Open-river pond[b]	Internal-field pond[c]
Production year	2002	2006		
Mating method[d]	Single pair	Partial factorial		
Spawning date[d]	4 batches in 14 days in June	6 batches over 34 days in April-May		
No. of sires[d]	79	122		
No. of dams[d]	79	118		
No. of families produced	79	208		
No. of days from spawning till tagging				
- Average	122	267.1	275.7	234.2
- Min	-	252.0	254.0	212.0
- Max	-	281.0	297.0	256.0
No. of fish for tagging in total	7,900[e]	1,937	1,621	13,409
No. of days from tagging till first harvest:				
- Average	285.0[f]	159.5	190.7	262.2
- Min	-	147.0	178.0	249.0
- Max	-	176.0	207.0	278.0
Area (m^2)	3.500	30	48	2000
Water depth (m)	1.5	4	3	1.5
Stocking density (fish/m^3)	2.3	16.1	11.3	4.5
No. of families recorded with data:	-	132	115	206
-From no. of sires		89	76	120
-From no. of dams		83	72	117
Traits recorded	Body weight and standard length	Body weight, fillet weight, fillet yield, fillet fat and fillet colour		
Traits selected for	Body weight	-	-	Body weight & fillet yield
Selection method	Phenotypic selection	-	-	Combined selection

[a]River-net fence: fed an average of 1.50% of fish body weight daily, commercial feed with 22-28% protein; strong water flow and constant high temperature in river.
[b]Open-river pond: fed an average of 1.29% of fish body weight daily, commercial feed with 22-28% protein; water exchange of about 30% daily with high and fluctuating water temperature.
[c]Internal-field pond: fed an average of 0.97% of fish body weight daily, commercial feed with 22-28% protein; exchange water within three days of about 30% with low and fluctuating water temperature.
[d]In previous generation.
[e]Non-tagged fish.
[f]No. of days from communal stocking till first harvest.

Table 2. Mean and standard deviation (SD) of analysed traits in the three test environments.

Trait	River-net fence[a]		Open-river pond[b]		Internal-field pond[c]	
	Mean	SD	Mean	SD	Mean	SD
Tagging weight, TW (g)	26.8	8.7	26.5	8.6	28.1	9.3
Body weight, BW (g)	926.2	177.9	964.8	161.0	883.1	264.0
Fillet weight without skin, FWWOS (g)	328.6	94.5	336.3	63.9	300.4	96.6
Fillet yield without skin, FYWOS (%) [d)]	34.8	4.8	35.5	2.1	33.7	4.3
Predicted fillet fat, PFF (%)	9.7	5.0	5.1	3.1	6.4	2.6
Fillet colour, FC (1-3) [e)]	1.4	0.5	1.4	0.6	2.3	0.8

[a] n = 1338.
[b] n = 1272.
[c] n=2635.
[d] FYWOS = fillet yield without skin = 100(FWWOS/BW).
[e] FC = fillet colour, 1 = white, 2 = pink and 3 = yellow.

Table 3. Estimates of heritability (h^2) and common environmental effect of full-sibs (c^2), with their standard error (*se*), as well as the level of significance for the regression of the analysed traits on *nursetime* and *growtime*, in each of the three test environments.

Trait[a]	River-net fence				Open-river pond				Internal-field pond			
	$h^2 \pm$ se	$c^2 \pm$ se	Nurse-time[b]	Grow-time[b]	$h^2 \pm$ se	$c^2 \pm$ se	Nurse-time	Grow-time	$h^2 \pm$ se	$c^2 \pm$ se	Nurse-time	Grow-time
BW	0.41±0.09	0.06±0.04	*	*	0.52±0.12	0.06±0.04	ns	ns	0.48±0.09	0.10±0.03	*	*
FWWOS	0.33±0.07	0.16±0.09	*	*	0.53±0.11	0.03±0.04	ns	ns	0.43±0.08	0.07±0.03	*	*
FYWOS	0.09±0.06	0.10±0.07	*	*	0.03±0.07	0.05±0.04	ns	ns	0.02±0.02	0.00±0.00	ns	ns
PFF	0.03±0.03	0.01±0.01	ns	ns	0.05±0.10	0.11±0.05	ns	*	0.05±0.04	0.02±0.02	ns	ns
FC	0.16±0.08	0.04±0.03	ns	ns	0.10±0.08	0.02±0.04	*	ns	0.20±0.06	0.03±0.02	ns	ns

[a] BW = body weight; FWWOS = fillet weight without skin; FYWOS = fillet yield without skin; PFF = predicted fillet fat; FC = fillet colour.
[b] * = $P < 0.05$, ns: $P > 0.05$.

Table 4. Estimated additive genetic (V_a), common environmental (V_c), residual (V_e) and total phenotypic (V_p) variances for each trait analysed, in each of the three test environments.

Trait[a]	River-net fence				Open-river pond				Internal-field pond			
	V_a	V_c	V_e	V_p	V_a	V_c	V_e	V_p	V_a	V_c	V_e	V_p
BW	14582.7	2106.0	18561.0	35249.7	13851.6	1590.4	11397.6	26840.0	34217.7	6924.2	30661.4	71803.0
FWWOS	2628.0	1311.1	4011.5	7950.6	2237.3	117.5	1874.7	4229.5	4587.1	780.4	5366.7	10734.0
FYWOS	1.01	1.13	8.96	11.1	0.11	0.21	4.02	4.34	0.43	0.00	18.83	19.25
PFF	0.6	0.2	17.0	17.8	0.02	1.00	8.20	9.23	0.27	0.12	4.93	5.32
FC	0.04	0.01	0.20	0.25	0.04	0.01	0.33	0.38	0.13	0.02	0.49	0.63

[a]BW = body weight; FWWOS = fillet weight without skin; FYWOS = fillet yield without skin; PFF = predicted fillet fat; FC = fillet colour.

Table 5. Estimates of genotype by environment interaction as a genetic correlations (*r*) between the same trait in pairs of test environments, with standard error (*se*) of the estimates as well as likelihood-ratio test (LR) of whether the genetic correlation is significantly different from unity.

Trait[a]	River-net fence & Open-river pond		River-net fence & internal-field pond		Open-river & internal-field pond[g]	
	r ± se	LR[b]	r ± se	LR[b]	r ± se	LR[b]
BW	0.83±0.11	ns[c]	0.81±0.09	*	0.71±0.14	*
FWWOS	0.80±0.17	ns	0.78±0.14	*	0.73±0.13	*
FYWOS	0.57±0.19	*	0.80±0.14	ns	0.78±0.18	ns
PFF	0.73±0.16	ns	0.63±0.17	ns	0.60±0.20	ns
FC	0.76±0.11	*	0.60±0.15	*	0.70±0.18	ns

[a]BW = body weight; FWWOS = fillet weight without skin; FYWOS = fillet yield without skin; PFF = predicted fillet fat; FC = fillet colour.

[b]LR = -2[log(null model) - log(full model)].

[c]* = $P < 0.05$, ns = $P > 0.05$.

Paper IV

Realised and correlated selection response for increased body weight in Striped Catfish (*Pangasianodon hypophthalmus*)

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Abstract

In the breeding program for striped catfish in Vietnam, selected fish as well as a control group were kept over the first two generations in two populations to monitor genetic change, from phenotypic selection for increased body weight. This practise was established as individuals in the first generation that was exposed to selection were not individually tagged. Selection produced substantial selection response for body weight (4.7-12.4 %). A corresponding correlated selection response was obtained for fillet weight (4.5-12.0 %), known to be highly correlated to body weight, but no significant response was obtained for fillet yield, fillet fat and fillet colour, as these traits are less heritable, with low or only medium genetic correlation to body weight.

Keywords: Pangasianodon hypophthalmus, body weight, fillet weight, realised selection response, correlated selection response, realised heritability.

1. Introduction

Monitoring genetic change can be done by calculating the phenotypic difference of selected fish to that of an unselected control (Rye and Gjedrem, 2005), assuming that the control and selected individuals have been exposed to the same environment. The phenotypic mean of the selected individuals to that in the control is either a direct or correlated response depending on whether it is calculated for the selected trait or other traits, respectively.

The expectation for the realised responses are the product of the heritability and the selection differential among parents, meaning that the realised heritability can be calculated as the ratio of the direct response to the selection differential for parents.

In the breeding program for striped catfish initiated in Vietnam, selected fish as well as a control group were kept for the first generations of selection, carried out for increased body weight. Thus, the aim was to calculate the direct selection response for body weight and from this the realised heritability of this trait, but also the correlated response in other analysed traits; fillet weight, fillet yield, fillet fat and fillet colour.

2. Materials and methods

2.1. Base population and the F1 generation

The base populations, for population 1 and 2 (year-classes 2001 and 2002), respectively, were made up from stocks from three and four different hatcheries in the Mekong delta, Vietnam. Each stock was collected over the period 1999-2002 from grow-out farms that reared wild fingerlings caught over several seasons and locations in the Mekong River.

2.1.1. Population 1

Within 65 days in May-July 2001, 75 families were produced by mating one male to one female, in the base of population 1, to establish F1. Fry from each family were reared separately until tagging and communal stocking and grow-out in October 2001, in the research station pond, representing a typical production environment of an internal-field pond. On average 92 individuals from each family, in total 6900 individuals, with an average start weight of 19.8 grams were tested. After 11 months of grow-out, 900 fish were randomly sampled to know the phenotypic distribution of body weight. These fish were left back to the pond, before a random sample of 120 fish with an average body weight close to the population mean was picked out as the control group. Finally, as much as 887 fish, the best 18.1 %, out of the remaining 4890 surviving fish, on body weight were chosen to make up the selected group. Fish in both groups were marked on their head by carving number 1 for selected and 2 for control, and stocked in the same pond for continued growing and conditioning.

Then in May-June 2005, for selected and control groups respectively, 131 and 31 full-sib families of F2 were produced by the partial factorial mating design, i.e. one male mated to two females and vice versa. This was formed by 78 sires x 79 dams and 17 sires x 18 dams, from the selected and control groups, respectively. A total of 10020 and 2170 fingerlings were tagged from the selected and control groups respectively, and tested in one research station pond. Finally, within 16 days in August-September 2006, after an average of 270 days of culture, 2259 individuals from the selected group (approx. 17 per family) and 508 individuals from the control group (approx. 16 per family) were sampled and recorded. Body weight (BW, g), fillet weight without skin (FWWOS, g), fillet yield without skin (FYWOS, %), predicted fillet fat (PFF, %) and fillet colour (FC, 1-3, 1 = white, 2 = pink, 3 = yellow) were considered further analyses. Details are given in Sang et al. (submitted *a*).

2.1.2. Population 2

A total of 79 families in F1 were produced by mating one male to one female, over 14 days in June 2002. Fry from each family were reared separately until tagging and communal stocking and grow-out in October 2002, in one research station pond. A total of 7900 individuals, 100 individuals in each family, with an average start weight of 25.8 grams were tested. After 10 months of grow-out, phenotypes for body weight were recorded in a random sample of 900 fish. These were reused, before sampling 120 fish with an average body weight close to the population mean as the control group. The selected group, 1809 fish, with the highest phenotype for body weight made up 25.4 % of the remaining 7117 fish that survived. These fish were marked as done with population 1.

A total of 175 and 33 full-sib families (F2) were produced for the selected and control groups, respectively, in April-May 2006, by partial factorial mating. Actually, 122 sires x 118 dams and 23 sires x 20 dams were used for the selected and control groups, respectively. A number of tagged fish from the two groups were tested in either of three environments, river-net fence, open-river pond and internal-field pond (respectively, 1737 and 200, 1471 and 150, 10896 and 2513). Finally, within 4, 3 and 14 days, after 160, 191 and 262 days of culture, 1197 and 141, 1114 and 118 and 2227 and 428 individuals from the selected and control groups, and from the three test environments, respectively, were sampled and recorded. The number of full-sib families in the control group that was recorded in each of the three test environments was 16 (13 sires x 13 dams), 13 (10 sires x 9 dams) and 33 (23 sires x 20 dams), respectively. The same traits were analysed as in population 1. Further details can be found in Sang et al. (submitted *b*).

2.2. Statistical analysis

Estimates of least-squares mean, used for calculation of direct realised selection response for body weight as well as for correlated realised selection responses for the remaining traits in population 1 and 2, in each environment, were obtained from the following linear mixed model:

$$Y_{ijkl} = \mu + G_i + b_1X_j + b_2X_k + e_{ijkl}$$

where Y_{ijkl} is one observation for one trait of individual l belonging to group (selected or control) i, at *nursetime* (number of days in hapa from spawning till tagging) j and *growtime* (number of days from tagging till first harvest) k, μ is the overall mean, G_i is the fixed effect of

the *i*th group (i = 1 for the selected group and 2 for the control group), b_1 = the regression coefficient pertaining to *nursetime* (X_j), b_2 = the regression coefficient pertaining to *growtime* (X_k) and e_{ijkl} is a random error of the *l*th individual. The covariates, *nursetime* and *growtime* were the same as included in previous analyses (Sang et al., submitted *a* & *b*), and the analysis was carried out by the MIXED Procedure in SAS (SAS Institute Inc., 2004).

Direct realised selection response for body weight (R), and correlated selection response (CR) for the remaining traits, were estimated as the difference between the least-squares mean of the selected (LSM_S) and the control groups (LSM_C) in F2; i.e. $R/CR = LSM_S - LSM_C$ (in percentage: $R\%/CR\% = 100*(LSM_S - LSM_C)/LSM_C$).

For body weight, the realised heritability (h^2) was calculated as $h^2 = (LSM_S - LSM_C)/S$, where S is the difference between the mean body weight of the selected parents and those of the control.

3. Results and discussion

Number of recorded fish, mean and standard deviation of analysed traits for the various populations, generations, environments and fish groups are presented in Table 1. The small number of offspring in the control group in population 2 in two of the environments, river-net fence (n = 141) and open-river pond (n = 118) will result in inflated random sampling error variance of generation means, and thus lead to uncertainty in selection response estimates (Gall et al., 1993).

Direct realised selection response for body weight in different populations and environments are presented in Table 2. In both population 1, tested in the internal-field pond, and population 2, tested in the open-river pond, realised responses for body weight were substantial, significantly different from zero (12.4 % and 6.1 %, respectively). As expected, the response was positive also for population 2 when tested in the river-net fence (4.7 %) and in the internal-field pond (5.4 %). The generally lower response in population 2 might be explained by the somewhat lower selection intensity (higher selection proportion, p = 25.4 %) relative to that in population 1 (p = 18.1 %). The direct realised selection response for BW in population 1 was comparable to that found in other species, while those found for population 2 were in the lower range. Actually, estimates of 10-15 % have been calculated for growth in cold water species, by use of various methods (Gjedrem, 2000), 6.7-17.0 % have been found for body weight in carps based on control/selected populations and BLUPs (Mahapatra et al., 2007; Vandeputte et al., 2008), similarly 5.7-11.4 % have been obtained for body weight in tilapia (Gall & Bakar, 2002; Ponzoni et al., 2005; Maluwa & Gjerde, 2007; Khaw et al.,

2008), results of 9.3-21.2 % have been reported for body weight in shrimp based on control/selected populations (Argue et al., 2002; Preston et al., 2004), and similarly 9.6-21.1 % for shell height in pearl oyster (He et al., 2008).

The high estimates of realised heritability of body weight (0.28-0.38, Table 2) corresponds well with those heritability estimates currently reported, from analysis of variance with restricted maximum likelihood (0.21-0.52) (Sang et al., submitted *a* & *b*). The longer grow-out period in the F1, 330 days, compared to 270 days in F2 for population 1 and correspondingly in population 2, in F1, 300 days relative to 147, 180 and 246 days in F2, respectively, for three test environments may especially influence the selection differential and thus the estimates of realised heritability.

Correlated realised selection responses for other traits than body weight are also presented in Table 2, in the two populations, tested in various environments. In two of the four situations (populations and environments), FWWOS was significantly increased for selected fish (12.0 - 6.1 %). This is due to a considerable heritability of fillet weight and the high genetic correlation to body weight, 0.95 (Sang et al., submitted *a* & *b*). For FYWOS, PFF and FC, the correlated selection responses were not significant, but these traits also have been estimated with a low heritability and with low or only medium genetic correlation to body weight (Sang et al., submitted *a*). Realised correlated responses have also been reported in other species; for body weight when selecting on shell height in pearl oyster *Pinctada fucata* (He et al., 2008), and for improved feed conversion ratio when selecting on growth in Atlantic salmon (Gjedrem, 2000).

As fish in F1 were not individually tagged and phenotypes were not individually recorded, the use of a control line was chosen to monitor genetic change over the first two generations of selection. An alternative would have been to use BLUP, but the predicted breeding values of parents would in case only have relied on the data of offspring, as the parents were not recorded themselves; considered to be less reliable than use of a control line, initially. In future, however, with all individuals tagged and recorded with phenotype in every generation, one should rather rely on BLUP, but one should aim at using some parents across generations, to improve the data structure. This would eliminate the need for a control line.

4. Conclusion

In river catfish, phenotypic selection of parents on body weight produced substantial realised selection response among the offspring. The corresponding realised heritability estimates for body weight (0.28-0.38) was in accordance with corresponding estimates

obtained in the offspring generation, with an analysis of variance (0.21-0.52). As expect, a substantial correlated realised selection response was obtained for fillet weight, as the trait is highly genetically correlated with body weight, 0.95 (however, not for fillet yield, predicted fillet fat and fillet colour). These results imply that selection on body weight is expected to produce a positive selection response in the most important breeding goal trait, fillet weight. With individual tagging and recording of phenotypes for all fish established, it is advised to base future selection on BLUPs, also to monitor genetic change without the need for a control population.

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Table 1. Number of recorded fish, mean and standard deviation (SD) of analysed traits[a] for different populations, generations and fish groups, tested in different environments.

					BW		FWWOS		FYWOS		PFF		FC	
Population	Generation	Fish group	Environment	N	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
1	F1	Selected	Internal-field pond	887	1143.7	240.1	-	-	-	-	-	-	-	-
		Control		120	769.9	334.0	-	-	-	-	-	-	-	-
	F2	Selected		2259	954.2	370.3	328.3	114.4	35.5	7.0	4.30	0.70	1.39	0.50
		Control		508	839.5	352.1	295.6	109.0	35.8	6.6	4.26	0.75	1.34	0.47
2	F1	Selected	Internal-field pond	1809	927.2	204.0	-	-	-	-	-	-	-	-
		Control		120	771.6	249.1	-	-	-	-	-	-	-	-
	F2	Selected	River-net fence	1197	932.5	176.2	329.7	93.6	34.8	4.8	9.72	4.99	1.37	0.50
		Control		141	906.2	186.2	308.8	87.3	34.6	4.7	9.01	4.44	1.38	0.53
		Selected	Open-river pond	1114	973.3	160.6	345.7	63.6	35.4	2.1	5.04	3.12	1.41	0.61
		Control		118	917.4	162.6	326.7	60.9	35.5	1.7	5.10	2.54	1.40	0.60
		Selected	Internal-field pond	2227	887.2	246.2	303.2	92.9	33.7	4.3	6.39	2.56	2.31	0.81
		Control		428	830.1	267.5	283.3	104.2	33.9	4.5	6.42	2.12	2.30	0.80

[a]BW = body weight; FWWOS = fillet weight without skin; FYWOS = fillet yield without skin = 100(FWWOS/BW); PFF = predicted fillet fat; FC = fillet colour.

Table 2. Estimates of direct realised/correlated responses (R/CR), and as percentage of that of the least-squares means (LSM) of the control (R%/CR%), as well as the selection differential (S) and the realised heritability (h^2) in two populations; one tested in three environments.

Population	Generation	Environment	Fish group	Direct realised response					Correlated response							
				BW[a]					FWWOS[a]		FYWOS[a]		PFF[a]		FC[a]	
				LSM	R	R%[b]	S	h^2	LSM	CR%[b]	LSM	CR%[b]	LSM	CR%[b]	LSM	CR%[b]
1	F1	Internal-field pond	Selected - control	-	-	-	273.8	-	-	-	-	-	-	-	-	-
	F2		Selected	949.4	104.5	12.4**	-	0.38	319.3	12.0**	35.6	0.4 ns	4.07	2.10 ns	1.40	3.70 ns
			Control	844.9			-		285.2		35.5		3.98		1.35	
2	F1	Internal-field pond	Selected - control	-	-	-	155.6	-	-	-	-	-	-	-	-	-
	F2	River-net fence	Selected	956.2	43.3	4.7 ns	-	0.28	351.8	5.9 ns	35.9	0.6 ns	10.00	5.26 ns	1.53	-0.39 ns
			Control	912.9			-		332.3		35.7		9.50		1.53	
		Open-river pond	Selected	981.6	56.7	6.1*	-	0.36	349.9	6.1*	35.5	-0.6 ns	5.18	-3.18 ns	1.43	0.70 ns
			Control	924.9			-		329.8		35.7		5.35		1.42	
		Internal-field pond	Selected	893.6	45.9	5.4 ns	-	0.29	303.0	4.5 ns	33.7	-0.6 ns	6.21	0.32 ns	2.32	0.76 ns
			Control	847.7			-		290.0		33.9		6.19		2.31	

[a]BW = body weight; FWWOS = fillet weight without skin; FYWOS = fillet yield without skin; PFF = predicted fillet fat; FC = fillet colour.

[b]** = $P < 0.01$, * = $P < 0.05$, ns = $P > 0$.