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Quantitative genetics and heritability of growth-related traits in hybrid striped bass (*Morone chrysops* ♀ × *Morone saxatilis* ♂)

Xiaoxue Wang [a], Kirstin E. Ross [b], Eric Saillant [a], Delbert M. Gatlin III [a], John R. Gold [a,*]

[a] *Center for Biosystematics and Biodiversity, Department of Wildlife and Fisheries Sciences, Texas A&M University, College Station, TX 77843-2258, USA*
[b] *Department of Environmental Health, Flinders University, Adelaide, SA, 5001, Australia*

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Abstract

Commercially farmed, hybrid striped bass – female white bass (*Morone chrysops*) crossed with male striped bass (*Morone saxatilis*) – represent a rapidly growing industry in the United States. Expanded production of hybrid striped bass, however, is limited because of uncontrolled variation in performance of fish derived from undomesticated broodstock. A 10 × 10 factorial mating design was employed to examine genetic effects and heritability of growth-related traits based on dam half-sib and sire half-sib families. A total of 881 offspring were raised in a common environment and body weight and length were recorded at three different times post-fertilization; parentage of each fish was inferred from genotypes at 10 nuclear-encoded microsatellites. Dam and sire effects on juvenile growth (weight and length) and growth rate were significant, whereas dam by sire interaction effect was not. The dam and sire components of variance for weight and length (at age) and growth rate were estimated using a Restricted Maximum Likelihood algorithm. Estimates of broad-sense heritability of weight, using a family-mean basis, ranged from 0.67 ± 0.17 to 0.85 ± 0.07 for dams; estimates for sires ranged from 0.43 ± 0.20 to 0.77 ± 0.10. Estimates of broad-sense heritability of growth rate (based on weight), using a family-mean basis, ranged from 0.69 ± 0.12 to 0.82 ± 0.09 for dams and from 0.69 ± 0.13 to 0.81 ± 0.08 for sires. Similar results were obtained with length data. Both genetic and phenotypic correlations between weight and length were close to unity. High genetic (0.98–0.99) and phenotypic (0.79) correlations between growth rates measured at two time intervals suggested that selection for growth rate at an early life stage could affect growth rate at a later life stage. Estimates of general combining ability (GCA) for growth rates differed significantly among dams and among sires, whereas estimates of specific combining ability (SCA) for each dam × sire combination did not differ significantly from zero. These results suggest that additive-effect genes contributed to the differences in juvenile growth.

Keywords: Quantitative genetics; Heritability; Growth traits; Hybrid striped bass

1. Introduction

Hybrid striped bass (*Morone chrysops* ♀ × *Morone saxatilis* ♂) is one of the fastest growing segments of the finfish aquaculture industry in the United States

* Corresponding author. Tel.: +1 979847 8775; fax: +1 979845 4096.
E-mail address: goldfish@tamu.edu (J.R. Gold).

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(Kohler et al., 2001), ranking fifth in aquaculture production and fourth in value of fish cultured in the year 2000 (Carlberg et al., 2000). The hybrid is similar in appearance to the parental species, but due to heterosis possesses traits such as aggressive feeding behavior and tolerance to a wide range of environmental conditions that make it highly suitable for aquaculture (Bishop, 1968; Myers and Kohler, 2000). A major constraint currently limiting expanded production of hybrid striped bass is suboptimal production efficiency stemming from uncontrolled variation in performance of fish derived from undomesticated broodstock (Woods, 2001). For centuries, selective breeding has played an important role in increasing yield and survival and in improving product quality of farmed animals and plants (Dekkers and Hospital, 2002). In finfish aquaculture, however, commercial interest in selective breeding has been overshadowed by efforts to develop optimal husbandry practices (Gjedrem, 1983). Until recently, only a few fish species have been evaluated in terms of a selective breeding program, the primary species being salmonids and tilapia (Sonesson, 2003). Domestication of striped bass (*M. saxatilis*) was initiated in 1983 by spawning fish collected from the wild. In the 1990s, efforts were initiated to domesticate white bass (Kohler et al., 1994).

Studies of genetic control of production traits in fish are important because of the typically high proportion of genetic variation for such traits and their direct connection to economic value (Gjedrem, 1983; Perry et al., 2004). Phenotypic variation in production traits has been reported in both striped bass and hybrid striped bass (Harrell, 1997; Kohler et al., 2001), as have differences in growth rate within and among different families of striped bass (Woods, 2001). Significant differences in juvenile body weight and in fillet dress-out percentage at market size among hybrid striped bass produced from different geographic strains of white bass also has been documented (Kohler et al., 2001). Improving production efficiency of hybrid striped bass via selective breeding and genetic improvement of broodstock is clearly warranted (Carlberg et al., 2000), and for effective selective-breeding programs to develop, it is essential to have baseline genetic information for commercially important traits such as growth and disease resistance.

The objective of this study was to assess genetic parameters of growth-related traits in hybrid striped bass. Heritability of individual traits and pairwise genetic and phenotypic correlations among traits were estimated, as were general and specific combining abilities for dams, sires, and dam × sire combinations. Information on combining ability is needed to identify potentially superior parents and help define patterns of gene effects in expression of quantitative traits (Comstock et al., 1949; Goyal and Kumar, 1991).

2. Materials and methods

2.1. Production of experimental fish

A classical, factorial design, also known as North Carolina Design II (Roff, 1997), where 10 white bass females were crossed *inter se* with 10 striped bass males, was employed to produce full-sib, half-sib, and unrelated progeny. Matings were carried out during the spring of 2003 at Keo Fish Farms in Lonoke, Arkansas. White bass females were obtained by personnel at Keo Fish Farms via angling in the Arkansas and Mississippi river drainages. Weight of the 10 females ranged from 1.14 to 1.82 kg. The striped bass males had been maintained at Keo Fish Farms for several years. The exact origin of each individual male was unknown; two were obtained originally from 'wild' stocks in Maryland, while the remainder were obtained either in the wild from Lake Ouachita, Arkansas, or were provided by Kent SeaTech Corporation in San Diego, California. Weight of the 10 males ranged from 2.73 to 7.95 kg.

Both females and males were induced to spawn by injection of human chorionic gonadotropin (hCG) according to established procedures (Hodson and Hayes, 1989). Eggs (200,000 to 400,000/female) were collected by stripping, divided into 10 equal aliquots, and placed into 10 separate petri dishes in order to reduce possible bias in family-size due to unequal fertilization and/or unequal hatching success (Fishback et al., 2002). Milt was collected from each male by stripping; 1 ml aliquots of milt were then added to each of the 10 petri dishes. Spawning and fertilization were achieved within a 6–8 h period. Following fertilization, the 100 equally sized batches of fertilized eggs were pooled by sire, resulting in 10 half-sib families, each representing the eggs from 10 dams fertilized by the milt from one sire. Hatching occurred over a 24-h period. All offspring then were pooled and ~300,000 larvae were placed randomly into each of two 1000-l indoor production tanks. The tanks were recycled with well water at 18 °C and a 10 h/14 h of light/dark cycle was maintained. After approximately 4 days, fry were assigned randomly to two outdoor, earthen ponds (4 ha/each). The earthen ponds initially were fertilized with cottonseed meal and inorganic fertilizer to initiate natural production (phytoplankton and zooplankton). After fry begin feeding, they were fed a high-protein meal-type diet. At Phase I (1–4 g), approximately 3500 fingerlings from each of the two

ponds were selected randomly and transported to the Aquacultural Research and Teaching Facility (ARTF) at Texas A&M University in College Station, Texas. The fingerlings were maintained in 1200-l tanks connected to a recirculating system and under the same conditions as the growth trial (see below) until tagging.

2.2. Growth and maintenance of experimental fish

Fish were individually marked with PIT (Passive Integrated Transponder) tags when the majority of fish were >20 g. Based on that size criterion, a first group of fish (Group A, 600 fish) were tagged at 152 days post-fertilization and allocated to six 1200-l tanks (100 fish per tank). A second group of fish (Group B, 400 fish) were grown until they reached adequate size (>20 g) for PIT-tagging (201 days post-fertilization) when they were PIT-tagged and allocated to four 1200-l tanks (100 fish per tank). Initial weight and length of each fish was recorded when they were PIT-tagged and a small clip from the dorsal fin was removed and stored in 70% ethanol for subsequent parentage assignment.

The ten 1200-l tanks were nested within three connected recirculating systems. Water quality was maintained through biological and mechanical filtration; salinity was maintained at 2–3 ppt, using well water and synthetic sea salt (Fritz Industries, Inc., Dallas, TX). Low-pressure electrical blowers provided aeration via air stones; dissolved oxygen levels were maintained at or near saturation. Water temperature was controlled by ambient air and maintained at 25±3 °C throughout the trial. A 12-h light/12-h dark photoperiod was maintained by using fluorescent lights controlled by timers. Fish were fed a commercial striped bass diet (EXTRU 400; 40% crude protein, 10% lipid; Rangen, Inc., Angelton, TX) to apparent satiation twice daily. Weight and length of fish in Groups A and B were measured at 269 and 318 days post-fertilization, respectively (117 days after the first measurement in both cases). After each measurement, fish from the same tank remained as a unit but were assigned randomly to a different tank within the system. The experiment was terminated when total fish biomass reached the maximum carrying capacity of the recirculating systems (389 days post-fertilization). Final weight and length of all fish in both groups were measured at that time.

2.3. Parentage assignment

Parentage of offspring were determined using 10 nuclear-encoded genetic markers (microsatellites) developed and/or adapted specifically for this study (Han et al., 2000; Roy et al., 2000; Ross et al., 2004). Polymerase chain reaction (PCR) primer sequences and reaction conditions for each microsatellite are given in Appendix Table 1. PCR amplification products were screened in 5% denaturing polyacrylamide gels, using an ABI 377 DNA sequencer. Fragment analysis was conducted using GENESCAN® (Applied Biosystem, Foster City, CA, USA) and allele calling was performed with GENOTYPER® (Applied Biosystem, Foster City, CA, USA) software. Multilocus genotypes were used to assign offspring to their parents based on Mendelian principles and using Excel functions incorporated in a macro. The macro is available from the first author (XW).

2.4. Trait assessment

Weight and length were assessed prior and subsequent to initiation of the growth trial in both Groups (A and B). Age at initiation of the growth trial was 152 days post-fertilization (Group A) and 201 days post-fertilization (Group B). Weight and length after initiation of the growth trial were assessed at 269 and 389 days post-fertilization (Group A), and at 318 and 389 days post-fertilization (Group B). Growth rate was estimated as change in weight over time, i.e., $G_r=(W_2-W_1)/(t_2-t_1)$, where t_1 and t_2 are ages at the beginning and end of an interval, respectively, and W_1 and W_2 are the weight of fish at those times (Schreck and Moyle, 1990). Growth rates were measured over two time intervals in both groups: *Interval 1* (152–269 days, Group A; 201–318 days, Group B), and *Interval 2* (152–389 days, Group A; 201–389 days, Group B).

2.5. Statistical analysis

All traits assessed were evaluated according to the following model

$$Y_{ijklm} = \mu + \mathrm{dam}_i + \mathrm{sire}_j + (\mathrm{dam} \times \mathrm{sire})_{ij} + G_k + T(G)_{kl} + \varepsilon_{ijklm} \quad (1)$$

where Y_{ijklm} is an individual observation, μ is the overall mean, dam_i is the random effect of the ith dam, sire_j is the random effect of the jth sire, $(\mathrm{dam}\times\mathrm{sire})_{ij}$ is the random (interaction) effect of the cross between the ith dam and jth sire, G_k is the fixed effect of the kth group, $T(G)_{kl}$ is the fixed effect of the lth tank nested within the kth group, and ε_{ijklm} is the random residual. Tank effect was not included in the analysis of weight and length data at the initial measurement (152 days post-fertilization for Group A; 201 days post-fertilization for Group B). In addition, preliminary analysis revealed

that interactions between group or tank effects and sire and dam effects did not account for a significant part of the phenotypic variance; consequently, these interactions were not included in the model.

Significance of random (genetic) and fixed effects was determined by analysis of variance (ANOVA); Type IV estimable functions were used to calculate the sum of squares for each effect. Variance components and their standard errors were estimated using the REML algorithm implemented in VCE-5 (Kovac and Groeneveld, 2002). Broad-sense estimates of heritability on an individual basis (h_i^2) were computed as four times the ratio of the dam or sire component of variance to the total phenotypic variance. In order to predict response to selection of breeders based on performance of their offspring, estimates of broad-sense heritability also were generated on a half-sib family-mean basis as outlined in Holland et al. (2003). This parameter predicts the fraction of the selection differential expected to be gained when selection is practiced on a half-sib family unit (Holland et al., 2003). Heritability (h_f^2) for dam and sire were calculated as the proportion of the variance of dam half-sibs or sire half-sibs relative to the phenotypic variance of dam or sire half-sib family means for a particular trait according to the following:

$$h^2_{f(\mathrm{dam})} = \frac{\sigma^2_{\mathrm{dam}}}{\frac{\sigma^2_\varepsilon}{se} + \frac{\sigma^2_{\mathrm{dam\times sire}}}{s} + \sigma^2_{\mathrm{dam}}} \quad ;$$

$$h^2_{f(\mathrm{sire})} = \frac{\sigma^2_{\mathrm{sire}}}{\frac{\sigma^2_\varepsilon}{de} + \frac{\sigma^2_{\mathrm{dam\times sire}}}{d} + \sigma^2_{\mathrm{sire}}}$$

The values σ^2_{dam}, σ^2_{sire}, and $\sigma^2_{\mathrm{dam\times sire}}$ represent the variance components of dam, sire, and dam by sire, respectively; σ^2_ε is the residual. The values d, s, and e are the number of dams, sires, and tanks. Because of the unbalanced experimental design, these numbers were derived as harmonic means (Holland et al., 2003). Standard errors for estimates of h_f^2 were approximated using the 'delta' method described in Hohls (1996). REML estimates of variance components and associated variances and covariances used to compute h_f^2 and their standard errors were obtained from PROC MIXED in SAS (2004).

Two-trait REML analysis in VCE-5 (Kovac and Groeneveld, 2002) was used to estimate pairwise genetic correlations (and their standard errors) between weight and length at each measurement age and between growth rates measured at the two time intervals. Genetic correlations were based on sire and dam (co)variance components obtained when employing the analysis model (Eq. (1)). Pairwise phenotypic correlations among traits were estimated via Pearson's product–moment correlation coefficient, as implemented in the SPSS, the Statistical Package for Social Sciences (SPSS Inc., 2001).

The expected performance value of an interspecific hybrid is a function of the general and specific combining abilities of the two parental individuals (Falconer and Mackay, 1996). The general combining ability (GCA) of a sire (or dam) is defined as the average performance value of offspring from this sire (dam) when crossed to all other dams (sires) and expressed as a deviation from the mean of all (dam by sire) crosses. The specific combing ability (SCA) of a cross represents the deviation of the performance of this cross from the expected performance based on the GCA of the dam and the sire involved in the cross; SCA also is a measure of the dam by sire interaction effect(s). Best Linear Unbiased Predictors (BLUP) of individual sires, dams, and cross, and their standard errors, were generated in PEST 4.2.3 (Groeneveld and Kovac, 1990) and used as estimates of GCAs of sires, dams, and SCAs of crosses, respectively. BLUPs were obtained for growth rates and were based on the analysis model (Eq. (1)).

3. Results

3.1. Parentage assignment of offspring

A total of 881 offspring were available for parentage assignment; 879 (99.8%) of these were assigned unambiguously to a specific dam, while 841 (95.5%) were assigned unambiguously to a specific sire (Table 1). Paternity of 40 offspring could not be determined using the available microsatellites; 33 of these offspring, however, could be assigned to one of two sires (Table 1). Of the possible 100 full-sib families, 96 were represented with at least one offspring, and all 20 dams and sires contributed to the final total, ranging from 2.0% (Dam 8) to 17.8% (Dam 9) for dams and 5.2% (Sire 1) to 17.5% (Sire 10) for sires. Contribution of individual dams and sires to groups A and B was relatively even, varying from 2.0% (Dam 8, Group B) to 19.8% (Dam 9, Group A) for dams and 4.3% (Sire 1, Group B) to 20.4% (Sire 10, Group A) for sires. Similarly, families were relatively evenly distributed among the different tanks (data not shown).

3.2. Weight and length

Mean and range of weight and length for offspring in Groups A and B measured before (days 152 {A} and 201 {B}) and after (days 269 {A}, 318 {B}, and 389 {A and B}) initiation of the growth trial are shown in Table 2. Overall survival was approximately 86% during the

Table 1
Number of offspring identified for each of 100 full-sib families generated in the 10×10 factorial cross

Cross	Dam 1	Dam 2	Dam 3	Dam 4	Dam 5	Dam 6	Dam 7	Dam 8	Dam 9	Dam 10	Unknown[b]	Sum
Sire 1	6	4	4	9	3	0	3	2	14	1	0	46
Sire 2	6	12	17	20	6	6	13	1	19	8	1	109
Sire 3	5	6	10	14	9	4	9	4	12	7	0	80
Sire 4	4	2	12	16	9	3	7	1	4	13	0	71
Sire 5	7	13	6	8	7	2	2	3	17	13	0	78
Sire 6	10	8	5	8	9	3	5	1	8	6	0	63
Sire 7	3	6	9	7	6	0	10	0	12	11	1	65
Sire 8	2	7	14	13	6	3	3	0	25	21	0	94
Sire 9	5	13	7	14	13	2	9	1	11	8	0	83
Sire 10	3	18	23	29	22	6	14	3	29	7	0	154
Sire 1/Sire 2[a]	0	5	6	4	5	0	2	2	5	4	0	33
Unknown[b]	0	0	1	0	0	2	0	0	1	1	0	5
Sum	51	94	114	142	95	31	77	18	157	100	2	881

[a]Either Sire 1 or Sire 2.
[b]Dam or sire could not be determined (see text).

8-month growth trial. A total of 6% of tagged fish lost their PIT-tags during the growth trials and were re-tagged when weight and length measurements were taken. When the experiment was terminated (389 days post-fertilization), the average weight over all fish (Groups A and B) was 281.9 (range=96.9–540.0 g), while the average length was 270.6 (range=195.0–387.0 mm).

3.3. Genetic effects on weight and length

Results from tests of significance of genetic (dam, sire, and dam×sire interaction) effects on weight and length prior to initiation of the growth trials are shown in Table 3. Effects of dam and sire on weight and length were significant ($P<0.05$), whereas effect of dam×sire interaction was not ($P>0.05$). Effect of group was significant for both traits. The estimate of the dam component of variance was up to two-fold greater than that of sire for both weight and length data. Corresponding estimates of broad-sense heritability (individual basis, h_i^2) were between 0.14 and 0.17 for dams and 0.07 and 0.08 for sires (Table 3). Estimates of heritability based on family means (h_f^2) for both dam and sire (both traits) differed significantly (>two standard errors) from zero. Estimates of h_f^2 for dams were greater than 0.67 for both traits, while estimates for sires (both traits) were greater than 0.43. Genetic correlations between weight and length based on the sire and dam components of variance were unity; the phenotypic correlation was 0.95.

Results of tests of significance of genetic (dam, sire, and dam×sire interaction) and non-genetic (group and tank) effects on weight and length at the two measurement ages subsequent to initiation of the growth trials are

Table 2
Mean (S.D.) of weight and length at different fish ages (in days post-fertilization) for Groups A and B

Post-fertilization	Day 152{A}	Day 201{B}	Day 269{A}	Day 318 {B}	Day 389 {A and B}
Weight (g)	23.2 (15.4)	32.5 (17.4)	181.9 (46.8)	182.7 (54.9)	281.9 (76.5)
Range (g)	6.0–100.5	8.9–117.6	46.0–360.8	69.8–342.0	96.9–540.0
Length (mm)	120.5 (22.2)	134.0 (20.0)	226.7 (18.1)	233.7 (21.9)	263.5 (22.6)
Range (mm)	84.0–195.0	95.0–204.0	159.0–278.0	145.0–284.0	195.0–387.0
Number of fish	608	401	549	369	783

Table 3
Probability of significance of genetic and group effects (based on ANOVA) and estimates of heritability (h^2±S.E.) for weight and length measured before initiation of the growth trial

	Trait (Groups A and B)[a]	
	Weight	Length
Effect		
Dam	<0.0001	<0.0001
Sire	0.0364	0.0478
Dam×Sire	0.6245	0.6387
Group	<0.0001	<0.0001
Heritability (h_i^2)		
Dam	0.14±0.07	0.17±0.08
Sire	0.08±0.04	0.07±0.04
Heritability (h_f^2)		
Dam	0.67±0.17	0.71±0.15
Sire	0.46±0.20	0.43±0.20
Number of fish	804	

h_i^2 is heritability estimated on an individual basis; h_f^2 is heritability estimated on a family-mean basis.
[a] Group A measured at 152 days post-fertilization. Group B measured at 201 days post-fertilization.

Table 4
Probability of significance of genetic and environmental effects (and interactions), based on ANOVA, and estimates of heritability ($h^2 \pm$S.E.) for weight and length measured during the growth trial

	Measurement 1[a]		Measurement 2[b]	
	Weight	Length	Weight	Length
Effect				
Dam	<0.0001	<0.0001	<0.0001	<0.0001
Sire	0.0223	0.0039	<0.0001	<0.0001
Dam × Sire	0.6465	0.3497	0.6610	0.5747
Group	<0.0001	0.3769	0.0037	0.0068
Tank (Group)	<0.0001	<0.0001	<0.0001	<0.0001
Heritability (h_i^2)				
Dam	0.45±0.16	0.41±0.16	0.30±0.13	0.32±0.13
Sire	0.11±0.05	0.15±0.07	0.28±0.10	0.28±0.10
Heritability (h_f^2)				
Dam	0.85±0.07	0.83±0.08	0.74±0.12	0.76±0.11
Sire	0.58±0.16	0.66±0.14	0.77±0.10	0.77±0.10
Number of fish	733		726	

h_i^2 is heritability estimated on an individual basis; h_f^2 is heritability estimated on a family-mean basis.
[a] Measurement 1: Day 269 (Group A) and Day 318 (Group B) post-fertilization.
[b] Measurement 2: Day 389{A and B} post-fertilization.

shown in Table 4. Effects of dam and sire on weight and length were significant ($P<0.05$) at both measurement ages, whereas effect of dam × sire interaction was not ($P>0.05$). With one exception (effect of group on length at the first measurement), effects of group and tank (nested within group) were significant on both weight and length at both measurements. REML analysis revealed that estimates of the variance components of dam were two- to four-fold greater than those of sire for both weight and length at the first measurement age, whereas the variance components were similar at the second (final) measurement age. Corresponding estimates of h_i^2 at these two measurement ages were between 0.30 and 0.45 for dams and 0.11 and 0.28 for sires (Table 4).

Estimates of h_f^2 for both traits for both dam and sire exceeded 0.58 and differed significantly from zero (Table 4). However, estimates of h_f^2 for dam and sire did not differ significantly from one another. Genetic correlations between weight and length for both dam and sire at the two measurement ages ranged from 0.97 to 0.99; the phenotypic correlation between weight and length ranged from 0.93 to 0.96 at the two measurement ages, respectively.

3.4. Genetic effects on growth rates

Growth rate during the first and second period averaged 1.24±0.32 g/day and 1.18±0.30 g/day, respectively. Tests of significance of genetic (dam, sire, and dam × sire interaction) and non-genetic (group and tank) effects on growth rate at the two time intervals are shown in Table 5. Effects of dam and sire on growth rate at both intervals differed significantly from zero ($P<0.05$), while effect of dam × sire interaction did not ($P>0.05$). Both group and tank (nested within group) effects were significant at both time intervals. The estimate of the variance component of dam was two times greater than that of sire during the first interval, while the variance components were similar during the second interval. Corresponding estimates of h_i^2 were greater than 0.31 for dams and 0.17 for sires (Table 5). Estimates of h_f^2 at both time intervals for both dam and sire were greater than 0.69 and differed significantly from zero (Table 5). Estimates of h_f^2 for dam and sire did not differ significantly from one another at either time interval. Genetic correlations of growth rate at both time intervals were 0.99 based on the dam component of variance and 0.98 based on the sire component of variance; the phenotypic correlation was 0.79.

3.5. General and specific combining abilities

Estimates (and standard errors) of GCA for the 10 dams and 10 sires on growth rate at Intervals 1 and 2 are shown in Figs. 1 and 2, respectively, and revealed considerable differences in general combinability among both dams and sires. Estimated GCA values for individual dams and sires were consistent at both time

Table 5
Probability of significance of genetic and environmental effects (and interactions), based on ANOVA, and estimates of heritability ($h^2 \pm$S.E.) for growth rate measured at two intervals during the growth trial

	Growth rate	
	Interval 1	Interval 2
Effect		
Dam	<0.0001	<0.0001
Sire	0.0015	<0.0001
Dam × Sire	0.8360	0.7256
Group	<0.0001	0.0154
Tank (Group)	<0.0001	<0.0001
Heritability (h_i^2)		
Dam	0.54±0.18	0.31±0.13
Sire	0.17±0.07	0.37±0.13
Heritability (h_f^2)		
Dam	0.69±0.12	0.82±0.09
Sire	0.69±0.13	0.81±0.08
Number of fish	782	701

h_i^2 is heritability estimated on an individual basis; h_f^2 is heritability estimated on a family-mean basis.
Interval 1: Day 152–Day 269 {A} and Day 201–Day 318 {B}.
Interval 2: Day 152–Day 389 {A} and Day 201–Day 389 {B}.

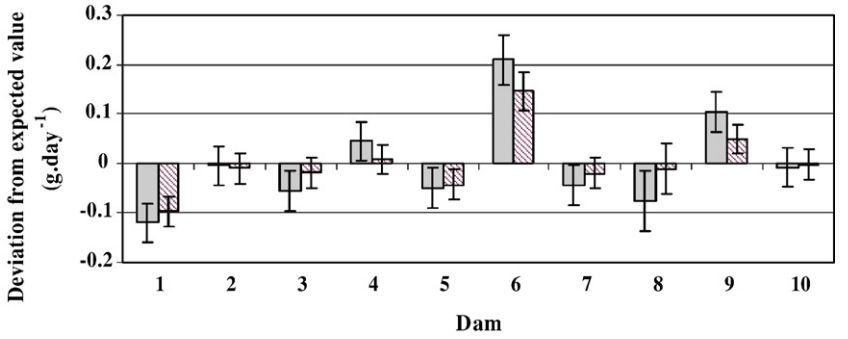

Fig. 1. Estimates of General Combining Ability (GCA) for growth rates for each of 10 dams at Intervals 1 and 2 (cf Table 5). Interval 1 (solid), Interval 2 (cross-hatched); error bars represent one standard error.

intervals; GCA values for dams, however, were generally higher at Interval 1, while GCA values for sires were generally higher at Interval 2. Positive GCA values were obtained for dams 4, 6, and 9, and for sires 2, 8, 9, and 10. GCA values at both intervals differed from zero by more than one standard error for dams 6 and 9 (Fig. 1) and for sires 2, 9, and 10 (Fig. 2). Estimates of SCA for each possible dam × sire combination (96 pairwise combinations total) did not differ significantly from zero (data not shown).

4. Discussion

4.1. Parentage assignment

The 10 polymorphic microsatellites used in this project yielded unequivocal parentage (sire and dam) assignment for >95% of the 881 progeny assayed and eliminated the need for separate rearing of full- or half-sib families that can confound genetic and environmental effects (Vandeputte et al., 2004). Similar results have been obtained in studies of other farmed fish species including rainbow trout, Atlantic salmon, and common carp (Herbinger et al., 1995; Norris et al., 2000; Vandeputte et al., 2004). In addition, progeny were recovered from 96 of the 100 possible dam × sire combinations, with the number of progeny recovered per dam and per sire in this study being relatively uniform. We attribute the success in recovering representative progeny in part to the mating strategy where equal aliquots of eggs from each dam were separated and fertilized separately with equal aliquots of milt from each male. Such a strategy potentially reduces possible bias caused by unequal fertilization and/or hatching success (Fishback et al., 2002).

4.2. Genetic effects on growth and growth rates

Significant dam and sire effects on both weight and length were found prior to initiation of the growth trials when fish had reached an average weight and length of ~23 g and 120 mm (Group A) and ~32 g and 134 mm (Group B), respectively. For both traits, dam effect was approximately two-fold greater than sire effect, with estimates of broad-sense individual basis heritability (h_i^2) ranging from 0.14 to 0.17 for dams and 0.07 to 0.08 for sires; the dam × sire interaction (both traits), however, was non-significant. Significant dam and sire effects for the same growth parameters also were found

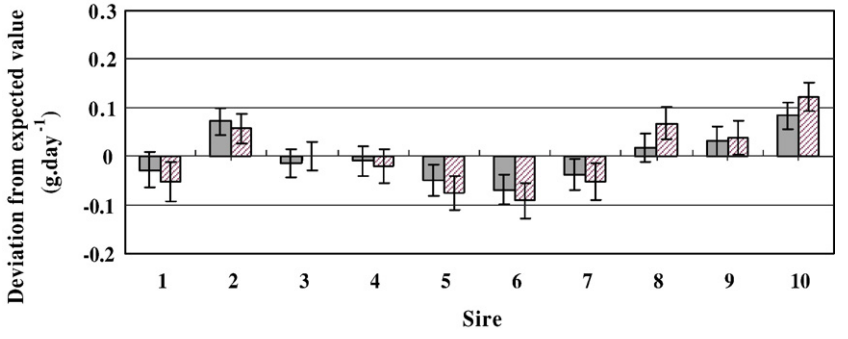

Fig. 2. Estimates of General Combining Ability (GCA) for growth rates for each of 10 sires at Intervals 1 and 2 (cf Table 5). Interval 1 (solid), Interval 2 (cross-hatched); error bars represent one standard error.

at two measurement ages subsequent to initiation of the growth trials. Values of h_i^2 for weight and length, respectively, ranged from 0.41 to 0.45 for dams and 0.11 to 0.15 for sires (measurement age 1), and 0.30 to 0.32 for dams and 0.28 (both traits) for sires (measurement age 2). For both traits, dam effect was considerably greater than sire effect at the first measurement age, but not the second; the dam × sire interaction (both traits) was non-significant at both measurement ages. Nearly identical results were obtained with growth rates estimated at each of two time intervals measured subsequent to initiation of the growth trials; dam and sire effect(s) were significant at both intervals, whereas dam × sire interaction was not.

To our knowledge, this study is the first to report the magnitude of genetic effects on body weight and length and growth rate in hybrid striped bass. Significant dam and sire effects on early growth have been reported for other cultured fish species, including rainbow trout (Gall and Huang, 1988; Herbinger et al., 1995; Wangila and Dick, 1996; Fishback et al., 2002), common carp (Vandeputte et al., 2004), Nile tilapia (Gall and Bakar, 2002) and European sea bass (Garcia de Leon et al., 1998; Saillant et al., 2006). In several of these studies (Herbinger et al., 1995; Wangila and Dick, 1996; Garcia de Leon et al., 1998) dam effects on early growth were more pronounced than sire effects and it was hypothesized that this could be due to a maternal phenotypic effect. In a factorial design, dam effect is expected to include both additive-genetic effects and maternal phenotypic effects (Falconer and Mackay, 1996). It also is commonly observed that maternal effects lessen with age in fish (Refstie, 1980; Herbinger et al., 1995; Garcia de Leon et al., 1998), and this could account for the observation in our study that dam effects were greater than sire effects only during early growth stages. However, methods to estimate maternal effects in factorial designs rely on the assumption that covariances between paternal and maternal half-sibs are equivalent with respect to inherited nuclear genes (Lynch and Walsh, 1998). Such an assumption cannot be made *a priori* in hybrid striped bass, thus precluding estimation of phenotypic maternal effects. Further characterization of maternal phenotypic and genetic effects, using an appropriate experimental design, is clearly warranted.

4.3. Genetic and phenotypic correlations {growth and growth rates}

Genetic and phenotypic correlations between weight and length for both dams and sires over both measurement ages ranged from 93% to 99%. Genetic correlations between growth rates at the two measurement periods also were high for both dams and sires (0.98–0.99). High genetic and phenotypic correlations between body weight and length have been reported in juveniles of other cultured fishes, including common carp (Vandeputte et al., 2004), Atlantic salmon (Gunnes and Gjedrem, 1978), rainbow trout (Refstie, 1980; Fishback et al., 2002; Henryon et al., 2002), and chinook salmon (Winkelman and Peterson, 1994). High correlations between growth (body weight) measured at different stages (before sexual maturation) also have been reported in other cultured fish species, including rainbow trout (Su et al., 1996, 2002) and European sea bass (Saillant et al., 2006), and indicated that growth estimated at early stages could be used as a predictor of growth at later stages. Finally, the magnitude of genetic correlations between traits is thought to generally reflect the extent to which the same genes are involved in expression of the traits (Falconer and Mackay, 1996). Taken together, the high genetic and phenotypic correlations found in our study indicate that a selective breeding program for either (or both) traits in hybrid striped bass would result in increased fish size (weight and length) at juvenile stages and potentially larger fish at harvest.

4.4. Heritability, combining ability, and selection strategy

The significant sire and dam components of phenotypic variance of growth traits in the interspecies F_1 hybrids evaluated in this study indicate that selective breeding could be implemented in either or both parental species. In such a breeding program, however, candidate dams and sires can only be evaluated based on the performance of their crossbred offspring. Combining ability analysis for growth rate revealed significant differences in GCA values among both dams and among sires at both growth intervals measured; SCA values for each possible dam × sire combination, however, did not differ significantly from zero. General Combining Ability (GCA) primarily reflects additive-genetic effects, whereas Specific Combining Ability (SCA) primarily reflects dominance, additive-genetic × dominance, and dominance × dominance interaction effects (Sprague and Tatum, 1942; Falconer, 1981). Results of the present study indicate that additive-effect genes contributed to most of the genetic differences in juvenile growth of hybrid striped bass.

In order to predict response to selection implemented on the basis of progeny testing, we estimated heritability of growth traits on a family-mean basis for both dams and sires. These estimates of heritability, with one

exception, exceeded 0.58 for growth (weight and length) and growth rate for both dams and sires, and differed significantly from zero at developmental times measured both prior and subsequent to initiation of the growth trial. The exception was heritability of sire on weight and length prior to initiation of the growth trial, where estimates of h_f^2 were 0.46 (weight) and 0.43 (length). Estimates of heritability for growth rates at the two time intervals essentially paralleled those for body weight and length, i.e., h_f^2 estimates for both dams and sires exceeded 0.69 and differed significantly from zero. In addition, estimates of h_f^2 for dams were invariably higher than estimates for sires for all traits at earlier developmental stages, i.e., prior to initiation of the growth trial and at the first time interval after initiation of the trial.

The estimates of heritability based on sire or dam family means should be interpreted in the context of a selection program based on half-sib family units. The estimates represent the fraction of the selection differential to be gained if breeders were selected based on the crossbred progeny testing conducted in our study. Accordingly, the high heritability estimates obtained in this study indicate that a substantial fraction of the selection differential would be expected to be gained in offspring of selected parents. Selection response and heritability, however, are dependent on the accuracy of the estimate of the combining ability of breeders. Consequently, h_f^2 for the traits assessed here may differ in a selective breeding program where the number of breeders tested and number of progeny assayed differ from those employed in this study. Further assessment of the expected response to selection as a function of the number of parents tested, number of progeny measured, and magnitude of genetic variance may be warranted in order to design selective breeding programs for hybrid striped bass. Estimating phenotypic variance on a family-mean basis is commonly employed in plant breeding when inbred lines or different species are used to generate F_1 hybrids for production purposes (Betran and Hallauer, 1996; Wolf et al., 2000; Holland et al., 2003). In such situations, estimates of heritability for quantitative traits such as grain yield or plant height generally range from 0.6 to 0.9 (Betran and Hallauer, 1996; Wolf et al., 2000).

Narrow-sense heritability generally is of primary interest in pure-bred selective breeding programs, in part because it measures the extent to which phenotypes of progeny can be predicted based on genes transmitted from parents (Falconer, 1981), and in part because dominance and epistatic effects, while typically present in first generation (F_1) offspring, are partially lost in future generations (Argue et al., 2003). In hybrid striped bass, however, the F_1 offspring are the production unit, meaning that both additive and dominance effects could be exploited in a selective breeding program (Hallerman, 1994). In this sense, a selective breeding program for production of hybrid striped bass could be to select parents (or parental lines) that produce better quality (faster growing) F_1 offspring regardless of whether genetic effects were additive, dominant, or epistatic. In addition, the genetic disequilibrium expected in interspecific hybrids may render estimates of narrow-sense heritability meaningless (Gordon, 1999).

The significant differences in GCA values among both dams and sires and the heritability estimates for growth and growth rates (both dams and sires) suggest that both 'backward selection' and 'reciprocal recurrent selection' would be successful in producing more rapidly growing hybrid striped bass. In backward selection (Gordon, 1999), parents with superior combining ability are identified and then used repeatedly to propagate desired offspring. Reciprocal recurrent selection or RRS (Falconer and Mackay, 1996) requires development and maintenance of 'pure' breeding lines of each parental species, where breeders are selected each generation within each parental line based on their crossbred performance. Backward selection does not require maintaining pure lines in each species but genetic progress in this approach is lost when selected breeders are culled or die. RRS on another hand would allow accumulation of genetic progress from one generation of selection to the next. However, application of significant selection differential in selected lines while maintaining sufficient effective size in order to prevent inbreeding likely would involve high cost and significant infrastructure. Given the low margin and investment capacity of the current hybrid striped bass industry in the United States (J. Carlberg, personal communication), development of a RRS program may not be economically feasible in the short term. Further economic evaluation of both approaches for hybrid striped bass production is clearly warranted.

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Appendix A

Table 1
Primer sequences, annealing temperature (T_a), and reference for microsatellites used in parentage assignment

Microsatellite	Primer sequences (5′–3′)	T_a (°C)	Reference
*Hsb*1B	F: GCAGCAGAAGTTGG GACTGGT R: GGCACCAAACAAGACA TATAGTGA	54	Ross et al. (2004)
*Hsb*1C	F: GTACGGTGTTCCTGCC TCA R: GGAGTGTCCATAGATAC AGTAAGTG	47	Ross et al. (2004)
*Hsb*6C	F: CAGAAACACTCGCTTCG CATCA R: GGAGCGTTCTTCAATGTT CTCTCAA	57	Ross et al. (2004)
Hsb7C	F: GGCTGAGGGCAGTAG TCAGA R: GGTGATACTGGTGGG TTTCAA	52	Ross et al. (2004)
SB6	F: ACAGCAAAGATAAACA TCTG R: TTCATGATGTTTCACC AGG	46	Han et al. (2000)
SB83	F: TGGGCCTGATTGGAAT CAAAA R: GATAGGTTGTATCAATG TTGC	50	Han et al. (2000)
SB13	F: TGCTGAGCCGGTAATTC AAG R: CACACATATGCATGG ATGCA	51	Han et al. (2000)
SB 91	F: AGACACCAGATAAGGA GA R: AAATAGATTCACACAA GG	58	Roy et al. (2000)
SB 113	F: GATCGCGGTTATTACAGT R: GACTATCTCCCCTGAAAT	50	Roy et al. (2000)
SB 117	F: TTAAAGTTTTCCAGTCAT R: CTTTTTAGAGCCAGTGTT	52	Roy et al. (2000)

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