Estimates of Heritability of Larval and Early Juvenile Growth Traits in Red Drum (*Sciaenops ocellatus*)

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ABSTRACT. Eighteen to 29 families of red drum were generated via spontaneous spawning of multiple sets of three dams × two sires. In 2002, offspring from spawning events were grown in separate larval ponds to a mean TL of 30.4 mm. In 2003, offspring from spawning events were individually passive integrated transponder (PIT)-tagged and grown in "common-garden" tanks from 121.9 to 166.6 mm. Offspring in both experiments were assigned to parents based on genotypes at four microsatellite loci. Heritability estimates were 0.24 ± 0.06 (larval TL) and 0.48 ± 0.16 (juvenile-specific growth rate in length) and indicate a significant genetic component for both traits.

KEYWORDS. Heritability, growth rate, red drum, microsatellites

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INTRODUCTION

The red drum, *Sciaenops ocellatus*, is an economically important sciaenid fish in southern United States. Interest in red drum aquaculture began in the early 1980s with the development of stock enhancement programs (Lutz 1999). Subsequent implementation of harvest restrictions and the prohibition of commercial sale of "wild" red drum (Matlock 1990) led to further efforts to develop grow-out techniques (Gatlin 2000). Currently, aquaculture production of red drum involves both state agencies culturing red drum for stock enhancement (McEachron et al. 1995) and a growing private industry culturing red drum destined to be marketed at a size of 1.0–1.5 kg (D.M. Gatlin, unpublished data).

To date, little research has been carried out on the genetic basis of traits (e.g., growth rate, cold tolerance, or disease resistance) of potential importance to red drum aquaculture. Design of optimal selection strategies for such traits requires knowledge of heritability of individual characters and of genetic correlations between characters (Falconer and McKay 1989; Lynch and Walsh 1998). Here we focused on larval body size and juvenile growth rate, traits of major interest to red drum aquaculture, as production costs can be lowered significantly by reducing duration of the rearing cycle.

Heritability of growth rate has been estimated in several fish species of interest to aquaculture (Knibb 1998; Wohlfarth and Hulata 1989; Gjedrem 2000; Vandeputte et al. 2004; Saillant et al. 2006). Molecular markers such as microsatellites facilitate these studies as the pedigree of individual offspring can be inferred *a posteriori* from multilocus genotypes. This approach thus allows determination of offspring pedigree and estimation of genetic parameters when families are generated via spontaneous group spawning of multiple males and females maintained in the same brood tank. Offspring from the generated families can thus be raised in the same tank (i.e., under identical conditions) from very early life stages (e.g., fertilization) (Herbinger et al. 1995; Garcia de Leon et al. 1998; Vandeputte et al. 2001).

Currently, red drum hatchery procedures are based on induction of sexual maturation and spontaneous spawning of captive breeders via temperature and photoperiod manipulation (McCarty 1987). Optimal juvenile production, as implemented by Texas Parks and Wildlife Department (TPWD) in the context of the red drum stock enhancement program in Texas waters (R.R. Vega, personal communication), is achieved by conditioning sets of three dams and two sires in the same brood tank for spontaneous spawning. In this study, we estimated heritability (h^2) of larval body size and juvenile growth rate. We used mixtures

of full-sib, half-sib, and unrelated red drum generated at the TPWD Coastal Conservation Association/Central Power and Light (CCA/CPL) Marine Development Center (MDC) in Flour Bluff, Texas. Microsatellites developed for red drum (Saillant et al. 2004) were used in *a posteriori* parentage assignment. Heritability was estimated using animal mixed models.

MATERIALS AND METHODS

Genetic parameters for larval and juvenile growth traits were estimated in 18–29 red drum families generated during spontaneous spawning of multiple sets of breeders (generally three females and two males) conditioned in the same brood tank for spawning at the TPWD CCA/CPL Marine Development Center (MDC) in Flour Bluff, Texas. Depending on the contribution of individual dams and sires present in a brood tank, each spawning event could give rise to up to six dam × sire combinations, with the mixture of offspring generated potentially including full-sib, half-sib, and unrelated fish.

Broodstock Management and Early Larval Rearing

Brood fish used in experiments were wild red drum caught off the south Texas coast. Fish were maintained in 13 m^3 brood tank. Temperature and photoperiod were manipulated following a 150-day maturation cycle (McCarty 1987) in order to achieve spontaneous spawning of fish starting at the beginning of April. Spawning occurred at night. Following each spawning event, fertilized (buoyant) eggs were collected at the effluent of brood tanks and incubated for ~72 h under conditions described in Henderson-Arzapalo (1987). Newly hatched larvae were then transferred to one- or two-acre, prefertilized ponds (Colura 1987) where they were grown until they reached an average size of ~30 mm.

Larval Growth Trial

Offspring from 13 spawning events involving nine brood tanks were used in the larval growth trial. Spawning events occurred between 4 April and 23 April 2002. Offspring from each spawning event were incubated separately and further grown in separate, prefertilized ponds. Harvest of ponds was conducted 41–57 days postfertilization. From 105 to 125 larvae were sampled at random from each pond and total length and

weight (for each larva) recorded. Individual larvae were then placed into cryopreservation tubes, flash-frozen in liquid nitrogen, and stored in an ultracold (–80°C) refrigerator. Fin clips (~4–5 mm^2) were removed from all possible parents (i.e., dams and sires in each brood tank) and stored in 95% ethanol (ETOH).

Juvenile Growth Trial

The juvenile growth trial was conducted in 2003. Offspring from 10 spawning events involving seven brood tanks were used. Spawning events occurred between 8 May and 29 May. Offspring from the 10 spawning events were incubated and grown separately until the beginning of the trial. Two hundred larvae from each spawning event were randomly sampled at harvest of the prefertilized pond (33–46 days postfertilization) and further grown in 10 cages at the CCA/CPL MDC until late July when they were brought to the Aquaculture Research and Teaching Facility (ARTF) in College Station. Fish from each spawning event were maintained in 110-L aquaria connected to a recirculating system (Goff and Gatlin 2004) until the beginning of the growth trial.

On 3 October (127–148 days postfertilization), 45 juveniles from each of the 10 spawning events were selected at random, tagged individually with passive integrated transponder (PIT) tags (Biomark, Boise, Idaho) and allocated randomly to three 400-L replicate tanks. The three tanks were connected to a recirculating system equipped with mechanical (sand) filtration and nitrifying biofiltration. Water turnover was ~30% per hour, with supplemental aeration provided via air stones. The photoperiod was 12-h light/12-h dark, with water temperature maintained at 25°C (range ± 4°C) by controlling ambient air temperature. Water quality was monitored weekly and maintained within the optimal range for red drum juveniles (Neill 1987) via addition, as needed, of a mixture of well water and concentrated synthetic seawater adjusted to a salinity of 11%. Fish were fed a commercial diet (EXTRU 400; 40% crude protein, 10% lipid; Rangen, Inc., Angelton, Texas) to apparent satiation daily.

Total length and weight of individual fish were recorded at tagging and subsequently on 11 November and 2 December (157–178 and 187–208 days postfertilization, respectively). Fin clips (~2–3 mm^2) from each tagged fish were taken at the last measurement (2 December) and stored in 95% ETOH for subsequent pedigree analysis. Fin clips from all possible parents (i.e., dams and sires in each brood tank) had been removed

previously and similarly stored in 95% ETOH. Fish (95 and 17, respectively, at the second and third measurement dates) that had lost their PIT tag were retagged and included in statistical evaluations when pedigree analysis (see below) indicated descent from brood fish that had contributed to only one spawning event. Retagged fish descended from brood fish that had contributed to more than a single spawning event were discarded because the information on early common environment prior to entry in the "common garden" was not known for these fish. Length and weight data ultimately were available for a total of 240 fish.

Genotyping and Pedigree Analysis

DNA was extracted from tissue samples by using an alkaline lysis protocol (Saillant et al. 2002). Possible parents (brood fish) and offspring sampled during the larval and the juvenile growth trial were genotyped at four microsatellites (*Soc* 19, *Soc* 85, *Soc* 402, and *Soc* 428). Descriptions of the microsatellites, PCR reactions, electrophoresis of PCR products, and allele scoring may be found in Saillant et al. (2004). Genotypes of all possible parents and offspring from all experiments are available upon request from the authors.

Assignment of offspring to parents based on microsatellite genotypes was implemented using the program PROBMAX v. 1.2 (Danzmann 1997), available at http://www.uoguelph.ca/~rdanzman/software/PROBMAX/. The percentage of offspring unambiguously assigned to dam and sire for the larval and juvenile growth trials were 97% and 100%, respectively. Data from offspring with incomplete pedigree were discarded from further analysis.

Data Analysis

Larval body size was defined as weight and total length attained at the time of sampling. Juvenile-specific growth rate was determined using weight or length data attained at the three measurement dates. Specific growth rates (SGR) were calculated according to

$$SGR_w = 100 * \frac{[\ln(W_f) - \ln(W_i)]}{T}, \; SGR_L = 100 * \frac{[\ln(L_f) - \ln(L_i)]}{T}$$

where W_f = final weight, W_i = initial weight, L_f = final length, L_i = initial length, and T = number of days between initial and final measurement.

SGRs were calculated based on pairs of consecutive measurements and also between initial and final measurements. Fish condition coefficient (K) was estimated as described in Blanc and Poisson (2006); principal component analysis (PCA) was applied to the bivariate distribution of neperian logarithm of weight and length, and individual fish coordinates along the second principal component were taken as a measure of K. PCA computations were implemented in PROC FACTOR of SAS® (SAS Institute Inc., Cary, North Carolina).

Variance and covariance components and their standard errors were estimated using the restricted maximum likelihood (REML) method as implemented in VCE-5® (Neumaier and Groeneveld 1998). Both univariate and bivariate models were fitted using the animal model

$$Y = Xb + Z_1a + Z_2c + e$$

where Y is the vector of observations (weight or length at sampling for larval growth, SGR for juvenile growth rates, or K); b is the vector of fixed effects of common replicate tank (juvenile growth trials); a is the vector of random additive breeding values; c is the vector of random effects common to offspring from a spawning event; X, and Z_1, and Z_2 are the design matrices for b, a, and c, respectively; and e is the vector of random errors. Initial analysis revealed occurrence of a residual correlation between SGR and initial weight or length for each growth period. Initial weight and length were therefore introduced as covariates in the model used to analyze SGR_w and SGR_l, respectively.

Due to non-contribution to offspring of some of the breeders present in brood tanks during spawning events, all but four mating groups generated incomplete factorial mating designs, precluding estimation of nonadditive genetic effects. The model employed therefore was based on the assumption that all genetic effects are additive. Heritability estimates were derived as the ratio of the estimate of additive variance to the total phenotypic variance. Phenotypic and genetic correlations between traits were calculated as the ratio of the estimated phenotypic or genetic covariance between the two traits to the square root of the product of the phenotypic or genetic variance for each trait as obtained in multitrait analyses. The estimates of genetic correlations, generated via bivariate analysis in VCE-5, for several pairs of traits were unity. In these situations, standard errors of the genetic correlations could not be estimated during optimization of bivariate models.

RESULTS

Heritability of Larval Body Size and Condition

A total of 1,556 offspring from 13 spawning events were used in the study of larval growth. Twenty nine families contributed to the sample, with the number of contributing pairs from individual brood tanks varying between one and six (average 2.9). Family sizes within a spawning event were unequal, with some families contributing only one (four families) or two (one family) offspring. Mean (±SD) length (mm) and weight (g) of offspring at harvest were 30.4 ± 4.2 and 0.25 ± 0.11, respectively (Table 1). Condition coefficient K was estimated as individual coordinates along the second principal component obtained during principal component analysis of the bivariate distribution of neperian logarithm of weight and length data. Data were centered and reduced for PCA. Mean and variance of K were in consequence 0 and 1, respectively.

Estimates of heritability (±SE) for larval length and weight were 0.24 ± 0.06 and 0.22 ± 0.06, respectively. The effects common to offspring from a spawning event accounted for a significant (>2 × SE) fraction of the phenotypic variance in both length (0.11 ± 0.05) and weight (0.09 ± 0.04). Length and weight were highly correlated both phenotypically ($r_p = 0.95$) and genetically ($r_g = 1$). The estimate of heritability for K was 0.004 ± 0.013 and did not differ significantly from zero. The effects common to offspring from a spawning event, however, accounted for a significant fraction of the phenotypic variance of K (0.34 ± 0.07). Phenotypic correlations between K and length or weight were low ($r_p = 0.21$ for length and $r_p = –0.03$ for weight).

TABLE 1. Summary statistics, including sample size (n) for larval and juvenile growth trials and mean (±SD) of weight (W) and total length (TL) at different measurement dates.

Experiment	Measurement dates	Age*	n	TL (mm)	W (g)
Larval growth (2002)	29 May–8 June	41–57	1,556	30.4 ± 4.2	0.25 ± 0.11
Juvenile growth (2003)	3 October	127–148	240	121.9 ± 10.4	19.4 ± 5.2
	11 November	157–178		152.5 ± 14.4	38.3 ± 11.5
	2 December	187–208		166.6 ± 16.9	57.3 ± 18.8

*In days postfertilization.

Heritability of Juvenile Growth Rate and Condition

A total of 240 offspring from 10 spawning events were used in the juvenile growth trial. Eighteen full-sib families were represented in the sample. The number of families per brood tank averaged 2.5, whereas the number of offspring per family ranged between 1 (seven families) and 38 (one family). Estimates of h^2 with and without families represented by only a single offspring differed substantially for all the traits examined. Consequently, the seven families were removed from subsequent analysis.

Mean (±SD) length and weight at each of the three measurement periods are given in Table 1. Initial and final lengths (mm) were 121.9 ± 10.4 and 166.6 ± 16.9, respectively. Heritability estimates for length and weight SGR between the initial and final measurements were 0.48 ± 0.16 and 0.47 ± 0.15, respectively (Table 2). Estimates of h^2 for SGR between the initial and the second measurement differed significantly ($>2 \times$ SE) from zero, whereas estimates of h^2 during the second period did not (Table 2). Estimates of the component of variance due to effects common to offspring from a spawning event accounted on average for 0.4% of the phenotypic variance in growth rate (range 0–10%) and did not differ significantly from zero.

Phenotypic correlations between SGR_L (specific growth rate based on length) and SGR_W (specific growth rate based on weight) ranged between 0.51 and 0.92 (average 0.75). All three estimates of genetic correlations between SGR_L and SGR_W obtained in multitrait analyses were unity. Phenotypic correlations between pairs of SGR_L estimates at various measurement intervals averaged 0.73 (range = 0.42–0.93). Corresponding estimates of genetic correlations were unity. Similar results were obtained for estimates of SGR_W.

TABLE 2. Mean ± SD and heritability (h^2) ± SE of weight and length specific growth rates (SGR_W, and SGR_L, respectively) at different measurement periods during the juvenile growth trial. Age and size data at each measurement are given in Table 1.

Measurement dates		SGR_L		SGR_W	
		Mean	h^2	Mean	h^2
3 October	11 November	0.55 ± 0.12	0.64 ± 0.16	1.64 ± 0.45	0.46 ± 0.17
11 November	2 December	0.30 ± 0.08	0.08 ± 0.08	1.36 ± 0.37	0.11 ± 0.08
3 October	2 December	0.45 ± 0.08	0.48 ± 0.16	1.53 ± 0.31	0.47 ± 0.15

Mean and variance of K were 0 and 1, respectively, as indicated above (larval growth trial). Heritability estimates for K at the three measurement dates were 0.18 ± 0.15, 0.33 ± 0.23, and 0.54 ± 0.15, respectively. Only the estimate of h^2 for K at the last measurement differed significantly from zero. Estimates of the component of variance due to effects common to offspring from a spawning event accounted for 4 to 17% (average 10%) of the phenotypic variance in K but did not differ significantly from zero.

DISCUSSION

Larval body size was measured at harvest (mean length 30.4 mm, mean weight 0.25 g). Estimates of heritability were 0.24 and 0.22 for larval length and weight, respectively. Estimates of h^2 for juvenile growth rate were obtained during a growth trial where larvae were grown from a mean TL (mm) of 121.9 to 166.6. Heritability of juvenile growth rates were 0.48 and 0.47 for length and weight, respectively. These estimates constitute the first report to date of heritability of larval and early juvenile growth in red drum. Heritability values obtained here are in the range of a priori estimates of h^2 of early growth in other fish species, viz. 0.29–0.52 in Atlantic cod (Gjerde et al. 2006), 0.33 in common carp (Vandeputte et al. 2004), 0.20 in Nile tilapia (Gall and Bakar 2002), and 0.29 in European sea bass (Saillant et al. 2006). The estimates of heritability in our experiments indicate that selection for faster growth in red drum would be successful at both larval and juvenile stages.

The experimental trials in this study were based on the common-garden approach in order to avoid potential bias in estimating heritability induced by rearing-unit effects when individual families are reared separately. Potential bias, however, could occur if effects common to offspring from a spawning event influenced growth during the assays. In our experiments, offspring from different spawning events were grown separately during the larval rearing period while separate rearing was prolonged until the initiation of the juvenile growth trial. Separate rearing had a direct effect on offspring growth measured during the larval trial. This effect accounted for a moderate but significant proportion of the phenotypic variance in length and weight (11 and 9%, respectively). The observed variance includes in part common larval-rearing environment effects but also effects of different genetic values among family groups generated during spawning events. The corresponding genetic variance

quantity cannot be estimated and accounted for in the overall estimate of genetic variance, leading to a potential underestimation of heritability.

Juvenile offspring growth rate may also have been influenced indirectly by separate rearing prior to entry in the common-garden, owing to the differences in initial sizes generated among offspring from different spawning events at the time of mixing; such initial size differences could influence growth trajectories in the common garden. Potential bias during heritability estimation was corrected by introducing initial weight or length as a covariate during the estimation. Following this correction, the component of variance due to effects common to offspring from a spawning event was not significant. A residual bias can, however, not be ruled out and could be avoided in future experiments by raising families mixed together in "common-garden" rearing units starting prior to hatching.

The estimates obtained also may be biased by occurrence of nonadditive (genetic) effects such as dominance, epistasis, and/or maternal effects since the animal model employed assumed that all genetic effects were additive. Studies of maternal effects on growth in other fishes indicate that these effects occur primarily during early life stages and tend to disappear within a few months of growth (Herbinger et al. 1995; Garcia de Leon et al. 1998). If this is the case in red drum, maternal effects may have impacted significantly growth (and heritability estimates) during the larval trial but not during the juvenile trial since the experiment was initiated 4–5 months post-hatching, with eventual effects of initial fish size corrected as discussed above. The magnitude of dominance and epistatic variances in cultured fishes is poorly documented likely because of the complex mating designs required to evaluate these effects (Lynch and Walsh 1998). Winkelman and Peterson (1994) and Rye and Mao (1998) reported significant dominance and/or epistatic effects on juvenile growth in Chinook salmon and Atlantic salmon, respectively, whereas no significant nonadditive genetic effects on growth traits were found in juvenile common carp (Vandeputte et al. 2004) or black bream (Doupe and Lymbery 2005). It is thus not possible to rule out occurrence of such effects on growth in juvenile red drum. Occurrence of significant, nonadditive effects would generate upwardly biased estimates of heritability (Gjerde 1986). Heritability (in the narrow sense) for growth in juvenile red drum may therefore be less than estimated here. Finally, the precision of our estimates is limited by the small number of families available in both data sets (29 for larval growth, 11 for juvenile growth). Further study that utilizes a more robust experimental design is clearly warranted.

Because larval and juvenile growth trials were carried out in different years and using different families, correlations between larval body size and juvenile growth rates could not be estimated. Growth rates at various time intervals during the juvenile growth trial, however, showed intermediate phenotypic correlations (average 0.68) and high genetic correlations (average 1.0) between growth intervals. Significant correlations between growth (body weight) measured at different immature stages also have been reported in other cultured fish species, including rainbow trout (Su et al. 1996) and European sea bass (Saillant et al. 2006), and indicate that growth rate estimated at early stages could be used as a predictor of growth rate at later stages.

Phenotypic and genetic correlations between length and weight gains in both larval and juvenile growth trials were close to unity. In the larval trial, r_p between body length and body weight was 0.95 and r_g was 1.0, whereas in the juvenile trials, r_p between length- and weight-specific growth rates ranged between 0.51 and 0.92, and r_g estimates all equaled unity. The high correlations indicate that genetic improvement of both traits could be accomplished merely by selecting on length; they also indicate that the same genes likely are involved in the expression of both traits (Falconer and Mackay 1996).

Heritability of condition coefficient K did not differ significantly from zero in the larval growth trial. In this experiment, a significant component of the phenotypic variance in K (34%) was due to effects common to offspring from a spawning event. This variance component potentially included part of the variance of genetic effects as discussed above. However, the absence of significant genetic variance explained by the animal effect suggests that genetic effects on larval condition were not significant, further suggesting that effects common to offspring from a spawning event reflected essentially early common environment effects. Heritability estimates of K generated during the juvenile growth trial averaged 0.35 (range 0.18–0.54), although only the estimate generated at the final measurement date differed significantly from zero. These heritability values are in the range of estimates of h^2 of K in other fishes, viz. 0.50–0.52 in rainbow trout (Kause et al. 2003; Perry et al. 2005), 0.37 in juvenile common carp (Vandeputte et al. 2004), and 0.34–0.52 in Arctic charr (Nilsson 1994) and suggest occurrence of heritable variation in body shape (Gjerde and Shaeffer 1989). Significant heritability of condition could be of importance to red drum aquaculture if shape characteristics influence market acceptance (Ankorion et al. 1992; Kause et al. 2003). Further analysis of body shape on market-sized fish and employing a more robust experimental design and more reliable indicators of body shape might be useful.

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