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Heritability of juvenile growth traits in red drum (*Sciaenops ocellatus* L.)

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Abstract

Heritability of juvenile growth rate was estimated for red drum (*Sciaenops ocellatus*), an economically important sciaenid fish in the southern USA. Thirty-eight families were generated via 'natural' spawning of multiple sets of five breeders (three dams × two sires) in individual brood tanks. Offspring were individually tagged with Passive Integrated Transponder (PIT) tags and mixed for grow-out in replicate 'common-garden' tanks. Juvenile growth was followed from 166.4 ± 18.6 to 254.0 ± 27.0 mm (total length). Offspring were assigned *a posteriori* to individual brood fish (dam and sire) based on genotypes at nuclear-encoded microsatellites. Heritability (h^2) of a thermal growth coefficient was estimated using an animal-additive model and a restricted maximum-likelihood algorithm. Estimates of h^2 were 0.33 ± 0.08 and 0.31 ± 0.08 for thermal growth coefficient based on length and weight respectively. These results indicate a significant genetic component in juvenile growth rate in red drum. Estimates of h^2 for condition coefficient (K) at various measurement dates averaged 0.38, suggesting a genetic component to shape in juvenile red drum.

Keywords: heritability, growth rate, red drum, microsatellites

Introduction

The red drum (*Sciaenops ocellatus* L.) is an economically important sciaenid fish in the southern USA. Dramatic declines in population numbers of red drum in the northern Gulf of Mexico during the 1970s and 1980s led to the implementation of harvest restrictions and the prohibition of commercial sale of 'wild' red drum (Matlock 1990). Interest in the aquaculture of red drum began around this time (Gatlin III 2000). Currently, aquaculture production of red drum involves state agencies culturing red drum for stock enhancement (McEachron, McCarty & Vega 1995) and a growing private industry culturing red drum destined to be marketed at a size of 1.0–1.5 kg.

Research on nutrition and husbandry of red drum has been intensive during the past decade (Craig, Neill & Gatlin III 1995; Gatlin III 2002). To date, however, little research has been carried out on the genetic basis of traits (e.g., growth rate, cold tolerance and disease resistance) of potential importance to red drum aquaculture (Lutz 1999). The design of optimal selection strategies for such traits requires knowledge of heritability of individual characters and genetic correlations between characters (Falconer & McKay 1996; Lynch & Walsh 1998). Here, we focused on juvenile growth rate, a trait of major interest to red drum aquaculture as production costs can be lowered significantly by reducing the duration of the rearing cycle.

The potential for selection for increased growth rate has been studied in several fish species of interest to aquaculture (Wohlfarth & Hulata 1989; Knibb 1998; Gjedrem 2000; Saillant, Dupont-Nivet, Haffray & Chatain 2006). Molecular markers such as microsatellites are a useful tool for such studies as the pedigree of individual offspring can be inferred *a posteriori* from multilocus genotypes. Offspring from multiple families can thus be raised in the same tank (i.e., under identical conditions) from very early life stages (e.g., fertilization) when physical tagging is not possible (Herbinger, Doyle, Pitman, Paquet, Mesa, Morris, Wright & Cook 1995; Garcia de Leon,

Canonne, Quillet, Bonhomme & Chatain 1998; Vandeputte, Dupont-Nivet, Chatain & Chevassus 2001). In particular, this approach 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.

Currently, aquaculture of red drum relies on induction of sexual maturation and spontaneous spawning of captive breeders by temperature and photoperiod manipulation (McCarty 1987). Optimal juvenile production, as implemented by the Texas Parks and Wildlife Department (TPWD) in the context of the red drum stock-enhancement programme in Texas waters (R. R. Vega, pers. comm.), 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 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, Cizdziel, O'Malley, Turner, Pruett & Gold 2004) were used in *a posteriori* parentage assignment. Heritability was estimated using animal-mixed models.

Materials and methods

Genetic parameters were estimated in 38 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 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 initial rearing

Brood fish used in the experiment were 'wild' red drum caught off the south Texas coast by TPWD personnel. Brood fish weight and length, respectively, ranged between 5.5–23.0 kg and 848–1102 mm (P. Silva, pers. comm.). Fish were maintained in 13 m^3 brood tanks. A 150-day temperature and photoperiod cycle as described by McCarty (1987) was used to induce sexual maturation and spontaneous spawning of fish starting in the beginning of April 2004. Spawning occurred at night and buoyant eggs were collected at the effluent of each brood tank. Following each spawning event, fertilized eggs were incubated for $\sim$ 72 h under conditions as described in Henderson-Arzapalo (1987). Newly hatched larvae were then transferred to one- or two-acre, pre-fertilized ponds (Colura 1987), where they were grown until they reached an average size of $\sim$30 mm at which time all surviving larvae were harvested and samples were taken for further rearing. Offspring from 35 spawning events involving 20 brood tanks were used in the study. Spawning events occurred during six nights between 3 April and 5 May. Eggs fertilized the same night were pooled in the same incubator and grown in the same pond, except for one spawning night (5 May) where offspring were split into two ponds. Details on spawning dates and larval rearing-pond identifications for offspring of the 20 brood tanks may be found at http://wfsc.tamu.edu/doc (Appendix A).

Larvae from each pond were harvested 33–48 days post-fertilization and a sub-sample ($\sim$2300 to $\sim$6800 pond^{-1}) was placed into a single, 'common-garden' pond for grow-out. All the fish present in the common garden pond were harvested and transported to College Station on 27 July. Fish were allocated at random to three replicate 'common garden' 10 m^3 tanks (1000 fish tank^{-1}) until the beginning of the growth trial. Tanks were connected to a recirculating system equipped with mechanical (sand) filtration and nitrifying biofiltration. Water turnover was $\sim$ 30% h^{-1}, with supplemental aeration provided via air stones. The photoperiod was 12 h light/12 h dark. Water temperature was recorded every day and maintained at 25 °C (range $\pm$ 4 °C) by controlling ambient air temperature. Water quality was monitored weekly and maintained within the optimal ranges for red drum juveniles (Neill 1987) via addition, as needed, of a mixture of well water and concentrated synthetic sea water adjusted to a salinity of 11 g L^{-1}. Fish were fed a commercial diet (EXTRU 400; 40% crude protein, 10% lipid; Rangen, Angelton, TX, USA) to apparent satiation daily.

Juvenile growth trial

On 16 September (134–166 days post-fertilization), the number of fish per replicate 'common garden' group was adjusted to 200 by randomly selecting

fish. Fish were individually tagged with Passive Integrated Transponder (PIT) tags (Biomark, Boise, ID, USA), and the three replicate groups were transferred to (three) 400 L tanks connected to a recirculating system as above. The experimental conditions were the same as described above (initial growth in 10 m^3 tanks). Recurrent degradation of water quality during the course of the experiment led to reduced feeding of all three replicate tanks while restoring activity of the nitrifying biofilters. Food limitations lasted 7 days between 16 September and 21 October and 17 days between 9 December and 10 February (2005).

The weight and length of all fish were recorded at tagging and subsequently on 21 October, 9 December and 10 February (2005). The three measurement dates represented 169–201, 218–250 and 281–313 days post-fertilization respectively. Fin clips ($\sim$ 2–3 mm^{-2}) were taken from all tagged offspring and from all but six possible parents and stored in 95% ETOH.

Genotyping and pedigree analysis

DNA was extracted from tissue samples by using an alkaline-lysis protocol (Saillant, Fostier, Haffray, Menu, Thimonier, Laureau & Chatain 2002). Possible parents (brood fish) and offspring were genotyped at five microsatellites included in Multiplex Panel 4, developed for red drum by Renshaw, Saillant, Bradfield and Gold (2006). Descriptions of the microsatellites, polymerase chain reaction (PCR) reactions, electrophoresis of PCR products and allele scoring may be found in Saillant *et al.* (2004). Offspring that were not matched to a single parental pair based on Panel 4 (202 individuals total) and all possible parents were genotyped using Panels 2 and 3 (Renshaw *et al.* 2006) as needed to achieve unambiguous parental assignment. Genotypes of all possible parents and offspring are available upon request from the authors.

Assignment of offspring to parents based on microsatellite genotypes was implemented using the programme PROBMAX v. 1.2 (Danzmann 1997) available at http://www.uoguelph.ca/ $\sim$ rdanzman/software/PROBMAX/. The percentage of offspring unambiguously assigned to dam and sire was 98.5%. Data from offspring with incomplete pedigrees were excluded from further analysis.

Data analysis

Because breeders present in most brood tanks produced offspring during more than one of the six spawning nights, offspring from a given cross potentially were born on different dates and grown in a different larval rearing pond before entering the 'common-garden' pond. Because both age and environmental effects common to different larval rearing ponds could have impacted fish size during the experiment (and could not be determined and accounted for in the analysis), estimates of heritability of body weight and length reached at the measurement dates could potentially be biased. Estimation of genetic parameters, therefore, was restricted to juvenile growth rate.

Juvenile growth rate was evaluated using the thermal growth coefficient (TGC) of Iwama and Tautz (1981). The TGC model assumes a linear increase in length with time when time is measured on a degree $\times$ day scale (Jobling 2003). Thermal growth coefficient was calculated using weight or length data attained at the four measurement dates according to

$$TGC_{\mathrm{w}} = 1000 \times \frac{\left[\sqrt[3]{W_{\mathrm{f}}} - \sqrt[3]{W_{\mathrm{i}}}\right]}{T \times t}$$

and

$$TGC_{\mathrm{l}} = 1000 \times \frac{[L_{\mathrm{f}} - L_{\mathrm{i}}]}{T \times t}$$

where W_{f} is the final weight, W_{i} is the initial weight, L_{f} is the final length, L_{i} is the initial length, t is the number of days between the initial and final measurement and T is the average temperature during the period considered. Thermal growth coefficients were calculated based on pairs of consecutive measurements and also between the 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 the neperian logarithm of weight and length, and individual fish coordinates along the second principal component were taken as a measure of K. Principal component analysis computations were implemented in PROC FACTOR of SAS® (SAS Institute, Cary, NC, USA).

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

$$y = Xb + Za + e$$

where y is the vector of observations (TGC_{l}, TGC_{w} or K), b is the vector of fixed effects of common replicate

tank, a is the random vector of additive breeding values, X and Z are the design matrices for b and a, respectively, and e is the vector of random errors.

Initial analysis revealed occurrence of a residual correlation between TGC and initial weight or length for each growth period. Initial weight or length were therefore introduced as covariates in the model used to analyse TGC_w and TGC_l respectively.

Owing 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 non-additive genetic effects. The model used 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 multi-trait analyses. The estimates of genetic correlations, generated via bivariate analysis in VCE-5, were unity for several pairs of traits. In these situations, standard errors of the genetic correlations could not be estimated during optimization of bivariate models.

Table 1 Summary statistics, including sample size (n) and mean (± SD) of total length and weight, at four measurement dates during the juvenile growth trial

Measurement dates	Age*	*n*	Length (mm)	Weight (g)
16 September	134–166	600	166.4 ± 18.6	43.3 ± 15.6
21 October	169–201		182.8 ± 20.3	58.8 ± 20.5
12 December	218–250		220.0 ± 23.6	115.3 ± 40.8
10 February†	281–313		254.0 ± 27.0	182.9 ± 62.9

*In days post-fertilization.
†Measurement occurred in 2005.

Results

A total of 38 families (dam × sire combinations) were represented in the sample of 600 offspring. Detailed contributions of individual families to the experimental groups may be found at http://wfsc.tamu.edu/doc (Appendix B). The number of families represented per brood tank (each brood tank contained three dams and two sires) ranged between one and six and averaged 3.2; the number of offspring per family ranged between one (nine families) and 106 (one family).

Heritability of juvenile growth rate

The mean (± SD) length and weight at each of four measurement dates are given in Table 1. The initial and final lengths (mm) were 166.4 ± 18.6 and 254.0 ± 27.0 respectively. The initial and final weights (g) were 43.3 ± 15.6 and 182.9 ± 62.9 respectively. Heritability (h^2) estimates for length and weight TGCs between the initial and final measurements were 0.33 ± 0.08 and 0.31 ± 0.08 respectively (Table 2). Estimates of h^2 for TGC between consecutive measurement periods generally differed significantly ($> 2 \times$ SE) from zero (Table 2).

Phenotypic correlations between TGC_l (thermal growth coefficient based on length) and TGC_w (thermal growth coefficient based on weight) ranged between 0.75 and 0.96 and averaged 0.87. Estimates of genetic correlations between TGC_l and TGC_w, obtained in multi-trait analyses, were close to unity ($0.98 < r_g < 1$). Phenotypic correlations between pairs of TGC_l estimates at various measurement intervals averaged 0.63 (range = 0.31–1.00). Corresponding estimates of genetic correlations averaged 0.91 (range = 0.69–1.00). Similar results were obtained for estimates of TGC_w.

Table 2 Mean ± SD and heritability (h^2) ± SE of weight and length thermal growth coefficient (TGC_w and TGC_l respectively) at four measurement dates during the juvenile growth trial

Measurement date		TGC_l		TGC_w	
		Mean	h^2	Mean	h^2
16 September	21 October	1.58 ± 0.75	0.22 ± 0.06	0.36 ± 0.17	0.28 ± 0.07
21 October	12 December	2.58 ± 0.68	0.32 ± 0.08	0.66 ± 0.17	0.32 ± 0.09
12 December	10 February*	2.12 ± 0.51	0.18 ± 0.07	0.48 ± 0.11	0.13 ± 0.07
16 September	10 February*	2.20 ± 0.48	0.33 ± 0.08	0.53 ± 0.11	0.31 ± 0.08

*Measurement occurred in 2005.

Table 3 Estimates of heritability ± SE (bold, on the diagonal) of condition coefficient (*K*) and of genetic (above diagonal) and phenotypic (below diagonal) correlations between estimates of *K* recorded at four measurement dates during the juvenile growth trial

	16 September	21 October	12 December	10 February*
16 September	0.32 ± 0.07	0.94 ± 0.06	0.67 ± 0.13	0.91 ± 0.08
21 October	0.57	0.28 ± 0.07	0.84 ± 0.07	0.90 ± 0.06
12 December	0.44	0.60	0.47 ± 0.11	0.89 ± 0.09
10 February*	0.30	0.42	0.54	0.44 ± 0.11

*Measurement occurred in 2005.

Heritability of juvenile condition coefficient (*K*)

For each measurement date, condition coefficient *K* was estimated as individual coordinates along the second principal component as obtained during principal component analysis of the bivariate distribution of the neperian logarithm of weight and length. Data were centred and reduced for PCA. The mean and variance of *K* at each measurement were in consequence 0 and 1 respectively. Heritability estimates for *K* (Table 3) ranged between 0.28 ± 0.07 and 0.47 ± 0.11, and averaged 0.38. All estimates of h^2 differed significantly from zero.

Phenotypic correlations between pairs of *K* at various measurement dates were intermediate ($0.30 < r_p < 0.60$); the corresponding genetic correlations, however, were relatively high ($0.67 < r_g < 0.94$) (Table 3). Phenotypic correlations between *K* and length or weight-specific growth rates were low ($-0.06 < r_p < 0.34$; average 0.18). Corresponding genetic correlations were also low ($-0.17 < r_g < 0.21$; average −0.01) and did not differ significantly from zero.

Discussion

Estimates of h^2 for juvenile growth rate were obtained during a growth trial where juveniles were grown from a mean total length (mm) of 166.4 to a mean of 254.0. Heritability of growth rates was 0.33 for length and 0.31 for weight. These estimates constitute the first report to date of heritability of juvenile growth rate in red drum. Heritability values obtained here are in the range of *a priori* estimates of h^2 of growth in other fish species, *viz.*, 0.1–0.3 in several salmonids (Gjedrem 2000), 0.33 in the common carp *Cyprinus carpio* L. (Vandeputte, Kocourb, Mauger, Dupont-Nivet, De Guerry, Rodina, Gela, Vallod, Chevassus & Linhart 2004), 0.20 in Nile tilapia *Oreochromis niloticus* L. (Gall & Bakar 2002) and 0.29 in European sea bass *Dicentrarchus labrax* L. (Saillant *et al.* 2006). The values of heritability estimated in our experiments indicate that selection for increased growth rate in red drum would be successful at the juvenile stage.

The experimental trial in this study was based on the 'common-garden' approach in order to avoid potential bias in estimating heritability induced by individual rearing-unit effects when families are reared separately during a trial. Potential bias, however, could occur if common-environment effects, before entry into the common garden, influenced growth during the assay. In our experiment, offspring that were born on different dates were grown separately during the larval rearing period before being mixed in a 'common-garden' rearing unit. Although restricted to early larval growth, this early separate rearing phase may have been sufficient to generate differences in the initial sizes among larval groups at the time of mixing. Such initial size differences could have influenced growth trajectories during the 'common-garden' rearing phase, including the growth study period 3–4 months later. Potential bias during heritability estimation would be due in part to the effects on growth rate of differences among families in initial fish size. We corrected for this source of bias by introducing initial weight as a covariate during the estimation. The occurrence of an eventual residual bias, however, cannot be ruled out; this bias could be avoided in future experiments by raising families mixed together in 'common-garden' rearing units starting before hatching.

The estimates of heritability may also be biased by occurrence of maternal effects and/or non-additive (genetic) effects such as dominance and epistasis, given that the animal model used assumed that all genetic effects were additive. Reports of maternal effects on growth in other fish indicate that these effects occur primarily during the early life stages and tend to

dissipate 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 not have impacted growth (and heritability estimates) significantly in this study as the experiment was initiated 4–5 months post-hatching (and with eventual effects of initial fish size corrected as noted above). There are only a few reports regarding the magnitude of dominance and epistatic variances in cultured fish in large part because of the complex mating designs required to evaluate these effects (Lynch & Walsh 1998). Significant dominance and/or epistatic effects on juvenile growth in chinook salmon *Oncorhynchus tshawytscha* (Walbaum, 1792) and Atlantic salmon *Salmo salar* L. were reported by Winkelman and Peterson (1994) and Rye and Mao (1998), respectively, whereas no significant non-additive genetic effects on growth traits were found in juvenile common carp (Vandeputte *et al.* 2004) or black bream *Acanthopagrus butcheri* (Munro 1949) (Doupe & Lymbery 2005). Thus, even though assessments of the magnitude and significance of non-additive (genetic) effects on fish growth are inconsistent, it is not possible to rule out such effects on growth in juvenile red drum. The occurrence of significant, non-additive effects can generate upwardly biased estimates of heritability (Gjerde 1986), meaning that heritability (in the narrow sense) for growth in juvenile red drum may be less than estimated here. Another concern in our study lies in the unequal contributions of individual crosses to the mixture of families. Further study that utilizes a more robust experimental design is clearly warranted.

Growth rates at various time intervals during the growth trial displayed relatively high phenotypic correlations (average 0.69) and high genetic correlations (average 0.93) between growth intervals. Significant correlations between growth (body weight) measured at different immature stages have also been reported in other cultured fish species, including rainbow trout *Oncorhynchus mykiss* (Walbaum, 1792) (Su, Liljedahl & Gall 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 and perhaps to market size. However, given that red drum are usually sold at a much larger size than the final size in our experiments (>1 kg versus 182.9 g), further genetic evaluation of growth in red drum to market size fish is needed.

Phenotypic and genetic correlations between length and weight TGCs were close to unity; r_p between length- and weight-thermal growth coefficient ranged between 0.75 and 0.96, while r_g ranged from 0.98 to 1. These high correlations indicate, first, that genetic improvement in both traits could be accomplished merely by selecting on length, and second, that the same or closely linked genes likely are involved in expression of both traits (Falconer & Mackay 1996).

Heritability estimates of condition coefficient *K* generated during the juvenile growth trial generally differed significantly from zero and averaged 0.38. These heritability values are in the range of estimates of h^2 of *K* in other fish, *viz.*, 0.50–0.52 in rainbow trout, (Kause, Ritola, Paananen, Eskelinen & Mäntysaari 2003; Perry, Martyniuk, Ferguson & Danzmann 2005), 0.37 in juvenile common carp (Vandeputte *et al.* 2004) and 0.34–0.52 in Arctic charr *Salvelinus alpinus* L. (Nilsson 1994). Significant heritability of *K* can be interpreted as the occurrence of heritable variation in body shape (Gjerde & Schaeffer 1989) and could be of importance to red drum aquaculture if shape characteristics impact market acceptance (Ankorion, Moav & Wohlfarth 1992; Kause *et al.* 2003). Interestingly, genetic correlations between estimates of *K* at different growth intervals were relatively high (average 0.86), suggesting that genetic differences among red drum at the juvenile stage may translate into shape differences among market-sized fish. A potential concern may be that undesirable shape characteristics could occur as a correlated response to selective breeding for a more rapid growth rate (Kause *et al.* 2003). However, the low and non-significant estimates of genetic correlations between growth rate and *K* obtained in this study suggest that little or no change in *K* would occur as a correlated response to selective breeding for fast growth. Further analysis of body shape on market-sized fish and using a more reliable indicator of body shape may be useful.

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