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Family–tank interactions on early growth performance of yellow perch reared in single-family tanks versus mixed-family tanks as inferred using microsatellite pedigrees

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Abstract

From 17 families, 400 fingerlings were evenly stocked into four replicates of each of five groups: single family from an Ohio strain, single family from a North Carolina strain, three families from the cross of five strains, 12 families from the cross of five strains and a combination of all 17 families. After rearing for 27 weeks, the progeny from the 17 families could be confidently assigned to their family of origin at the rate of 97.9%. The cross-bred multi-families (12-family and 3-family groups) from different strains gained significantly more weight than both single-family groups in separate tanks throughout most of the experiment ($P < 0.05$), but no significant differences were detected in body weight among the four groups in the all-family communal tanks ($P > 0.05$). Both single families grew significantly faster in the all-family communal tanks than in single-family tanks by the end of the experiment ($P < 0.05$). In addition, no correlation was detected between family mean weight obtained from the multi-family tanks (12-family and 3-family groups) and the family mean weight in the all-family tanks. These results indicated that there were strong effects of genotype by environment interactions on early growth performance of yellow perch.

Keywords: yellow perch, early growth, DNA parentage analysis, genotype by environment, breeding programme

Introduction

Yellow perch *Perca flavescens* is an ecologically and culturally important species in the Great Lakes region (GLR) and the Midwest United States. The demand for yellow perch has remained very high in the GLR as they are the traditional fish species used in local restaurants, social organizations and the Friday night fish fry dinners that are a staple in many Great Lakes states. Historically, the supply of yellow perch largely relied on capture fisheries in the Great Lakes, but during the 1980s and 1990s, wild harvests began to decline from 58 million kg year^{-1} to the current limit of < 3 million kg year^{-1}. Because of a mild taste and firm flesh with low fat and phospholipid content (Malison 2000), yellow perch are recognized as one of the finest-flavoured species among all panfish and have been widely introduced throughout the southern and western regions of the United States, southern British Columbia and other countries. Yellow perch aquaculture has received tremendous interest in the Midwest and elsewhere in the United States during the past 20 years, due to their high market demands, the decline in wild populations and concern over microcontaminant levels in Great Lakes fish. Some major techniques for artificial reproduction (Kayes 1977), commercial production of feed-trained fingerlings (Held, Malison & Kuczynski 1998) and grading and production method (Malison & Held 1992; Wallat, Tiu, Wang, Rapp & Leighfield 2005) have been developed successfully, greatly

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facilitating the yellow perch industry. However, these propagation activities and aquaculture operations have been carried out with little or no genetic control in different hatcheries and farms. To improve broodstock and the growth rate of yellow perch, Ohio State University has undertaken an integrated selective breeding programme for this species.

Genetic improvement of aquaculture species offers a substantial opportunity for increasing production efficiency, health, production quality and, ultimately, profitability in aquaculture industries. The potential of these gains has long been recognized as a significant impetus for aquaculture. Increased profits resulting from genetic improvement have been realized in terrestrial domesticated livestock species, agricultural, horticultural and ornamental plant, forest trees and aquaculture species, such as salmonids, tilapia and catfish. A combination of traditional selection (quantitative genetic) and marker-assisted breeding (molecular genetic) offers substantial potential for improvement of yellow perch. Molecular fingerprinting or 'tagging' allows us to reconstruct the pedigrees of communally reared individuals without performing physical tagging, so that crossing between related fish is minimized for each generation and common environmental effects can be reduced (Doyle & Herbinger 1994). This technique has been demonstrated to be successful in providing for high selection intensities, low inbreeding and extreme economy and efficiency (Naish & Skibinsh 1998; Herbinger, Reith & Jackson 2003).

An understanding of the effects of genotype by environment interaction ($G \times E$) is essential to ensure that maximum genetic gains are achieved for a molecular marker-assisted breeding programme. One particular issue of concerns is that the performances of individuals when families are reared separately are not necessarily representative of those in mixed family tanks with different strains (Herbinger, O'Reilly, Doyle, Wright & O'Flynn 1999). Thus, estimates of G × E for juveniles reared in mixed tanks with different families and strains versus single-family tanks are needed. Significant genotype by environment interaction is well documented for some aquaculture species such as salmonids (McKay, Friars & Ihssen 1984; Hanke, Friars, Saunders & Terhune 1989; Sylvén, Rye & Simianer 1991; Winkelman & Peterson 1994).

This study evaluated the effects of family by tank interactions on the phenotypic growth expression of yellow perch by comparing family growth performances raised in single-family tanks with the growth performances of the same and different families from different strains raised in multi-family tanks using microsatellite markers.

Materials and methods

Mating and fry production

Thirty-six broodfish (12 ♀: 21.0–27.6 cm; 24 ♂: 15.5–24.5 cm) with passive integrated transponder tags were selected from 2004 year-class broodstock (progeny from diallele cross of Maine (ME), Pennsylvania (PA), North Carolina (NC), Ohio (OH) and Michigan (MI) strains) from the Ohio Genetic Improvement of Farmed-fish Traits Program, and 12 mating sets were made in spring of 2006. The genetic variation and distance of the five populations have been documented previously (Brown, Wang, Li, Givens & Wallat 2007). For each mating set, one female and two males were placed in a 55 L round tank for spawning. The fish in 10 sets spawned naturally during the night, resulting in fertilization by either one or two males. Two sets were strip-spawned and eggs of the female from each set were combined with the milt of both males. Fertilized eggs were incubated in 25 L round tanks with flow-through well water for 11–12 days at the temperature of 11–12 °C. Twelve mating sets were successfully hatched and hypothetically resulted in a minimum of 14 and a maximum of 36 full- and half-sib families for the experiment. At the same time, two single families from OH broodstock (F_x originally from Lake Erie) and NC strain (Perquimans River, NC) were produced, respectively, using the same procedure. Similar numbers of fry from 10 out of the 12 mating sets were stocked into one 0.1 ha pond for nursery. Two of these 12 sets were stocked to another pond, and two single families into two additional ponds. The fish were nursed in the four ponds with the same total density using the pond-fertilization method for 6 weeks; then fish were harvested and feed trained in 400 L round tanks for 3 weeks (Malison 2000).

Tank experiment

The tank experiment for growth was conducted in 0.5-diameter tanks (55 L) for 21 weeks at the Ohio State University South Centers Wet Lab. The experiment consisted of five treatments, each having four replicated tanks (Fig. 1). The five treatments were a single family from the OH strain (1FOH), a single

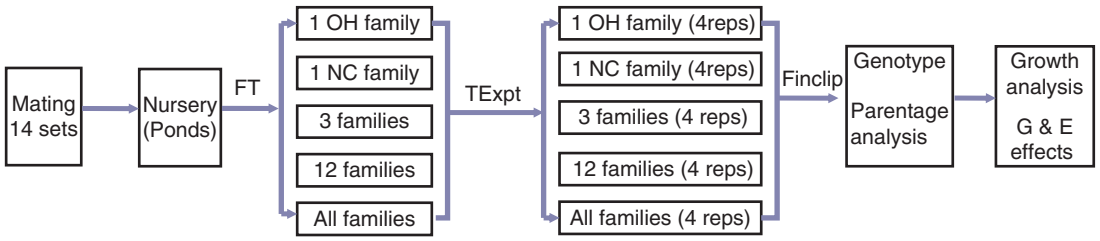

Figure 1 Summary of experimental protocols for the experiment where 17 families of yellow perch were raised in single-family tanks versus in multi-family tanks. FT, feed training; TExpt, tank experiment.

family from the NC strain (1FNC), three families from crosses (3FCR, from two mating sets), 12 families from cross (12FCR, from 10 mating sets) and all 17-family group (17ALL). A total of 400 fish from each of the first four treatments groups were evenly stocked into four replicated tanks, resulting in 16 tanks in total. For the all-family treatment, 100 fish from each of the four groups were distributed to each of the four replicated tanks, resulting in 4×25 fish per tank. Stocked fish were acclimated for 2 weeks before the experiment. The first four treatments versus the all-family treatments were used to examine the growth differences between two single-family groups and two types of mixed-family groups (3FCR and 12FCR) in a separate environment compared with a communal environment. The two single-family 1FOH and 1FNC treatments compared against the all-family treatment (17ALL) were designed to test the growth differences of the single families in single-family tanks versus multi-family/strain tanks. Comparing two types of mixed-family tanks with all-family tanks allowed for the evaluation of potential family–tank interactions.

Throughout the experiment, fish were fed manually three times daily at 8:00, 12:00 and 4:00 hours with commercial 1.0–1.5 mm floating feed (Silver Cup, 45% protein, 16% fat; Nelson and Sons, Murray, UT, USA). Each feeding time lasted at least 15 min. The feeding rates were 6% of body weight (BW) at the beginning, and then reduced 1% BW every month until reaching 3% BW. Feeding amount and mortality were recorded for each tank. Feeding ration was adjusted biweekly based on new weights and survivals. Daily temperature and dissolved oxygen (DO) were recorded for representing tanks using a YSI 51B DO metre (Yellow Spring Instruments, Yellow Spring, OH, USA). All tank temperatures were maintained at 22 ± 1 °C, and water exchange rates were 0.5 L min^{-1}. The DO levels over the experiment in tanks were 5.50–9.00 mg L^{-1}, with a mean of 7.56 ± 1.92 (SD) mg L^{-1}. All tanks were siphoned daily.

Samplings and measurements

A non-lethal biopsy (fin clip) was taken from each sampled fish and preserved immediately in 95% ethanol for DNA analyses and subsequent parentage analysis. In total, 36 potential parents (12 females and 24 males) and 480 offspring (96 from each group) were sampled in February 2006 and January 2007 respectively. For the growth performance experiment, 30 fish from each tank (120 fish per group) were individually weighed every 2 weeks during the experiment. Before sampling, fish were deprived of food for at least 16 h. They were then blotted dry with paper towels and weighted to nearest 0.1 g. In each case, the fish were returned to their respective tanks.

Microsatellite and parentage analyses

The 36 parents and 480 offspring (96 from each group) were genotyped. Genomic DNA was extracted from fin tissues of the yellow perch using the method described by Li, Wang, Givens, Czesny and Brown (2007), and parents and progeny were genotyped with four highly polymorphic microsatellite loci (YP17, YP49, YP60 and YP109; Li *et al.* 2007). Amplification of microsatellite loci was performed with the three-primer system, where a universal primer having the same sequence as the universal tail had a 5′-label of FAM, TET or HEX (Li *et al.* 2007). Polymerase chain reactions were conducted in 6 μL mixes containing 3 μL of JumpStart RedMix (Sigma, St Louis, MO, USA), 1.5 pmol of both non-tailed and labelled primers and 0.1 pmol of the tailed primer, 25 ng of DNA, in the presence of 100 μM spermidine. Amplification was performed in PTC-200 thermal cyclers (MJ Research, Waltham, MA, USA) using an initial denaturation at 94 °C for 2 min, followed by 35 cycles of 30-s denaturation at 94 °C, 30-s annealing at a locus-specific temperature (Li *et al.* 2007), 30-s extension at 72 °C and a final 5-min extension at 72 °C. Amplification products were separated using

an ABI 3130 Prism DNA genetic analyzer and the results were analysed using GENEMAP® 4.0 software.

Family assignment was carried out, and heterozygosity, polymorphism information content (PIC) and the presence of null alleles were estimated using the program CERVUS Version 2 (Marshall, Slate & Kruuk 1998). The genotyping error rate for CERVUS was set at 1%. For any fish that were assigned with $<95\%$ confidence, the genotypes were manually compared with their putative parent and any mismatches were evaluated. The progeny not being confidently assigned were excluded from all further analyses. Genotyping data from two single-family groups were analysed to compare the true pedigrees of them.

Calculation and statistical analyses

The absolute growth rate (AGR) was calculated as follows: $\text{AGR} = (W_t - W_0)\, t^{-1}$, where t is the number of rearing days, W_t is the mean BW (g) at day t and W_0 is the mean initial BW (g). Differences in the mean BW and AGR were analysed using two-way analysis of variance (ANOVA) ($P<0.05$) in SAS. Duncan's test was followed for mean separation when significant differences were indicated by ANOVA. Similarity in family mean weights of fish between mixed-family groups and all-family groups was analysed by correlating the mean family weight using Pearson's linear correlation coefficient in SAS.

Results

Allele frequencies and family assignment

Allele sizes exhibited by the yellow perch progeny ranged between 223 and 335 base pairs (bp) at YP17, 111 and 156 bp at YP49, 192 and 248 bp at YP60 and 129 and 198 bp at YP109. The average total number of alleles observed per locus was 15 (ranging from 10 to 20) and the mean observed heterozygosity was 0.75 ± 0.02 SE (Table 1); however, there were marked variations in heterozygosity levels among the loci, with YP17 and YP109 having the lowest (0.62) and the highest (0.89) variability respectively (Table 1). Alleles of yellow perch genotyped from tanks were consistent with those found in the 36 parents, which exhibited a relatively high level of allelic diversity. Allelic diversity in the broodstock provided good resolving power (mean PIC = 0.75, Table 1) for assigning parentage to progeny. Use of four microsatellites allowed for all yellow perch progeny from the single and the 3-family groups to be assigned to a putative family of origin. All the assignments for 1FNC and 96.9% for 1FOH matched their true parents. The progeny from 12-family and all 17-family treatments could be confidently assigned to their family of origin at the rate of 97.9%. The levels of null alleles segregating at all loci were negative and the observed homozygote frequencies were relatively low.

Two single-family groups versus two multi-family groups

In the separate environment (tank), the 12-family and 3-family treatments gained significantly more weight than both single-family treatments from week 9 and week 18 to the end of the experiment ($P<0.05$) respectively (Fig. 2); the mean weight of fish in the 12-family tanks was also significantly heavier than that of fish in 3-family tanks during week 9 to the end of experiment ($P<0.05$), and no significant differences were detected in BW between the two single-family treatments throughout most of the experiment ($P>0.05$). Fish in the 12-family tanks also gained significantly more weight than that in all-family tanks from week 9 to the end of the experiment ($P<0.05$). Similarly, AGRs of the 12-family and 3-family treatments were significantly higher than those of two single-family treatments (Fig. 3) throughout most of the experimental periods in separate tanks ($P<0.05$). However, no significant differences were detected in BW among the four groups in the all-family communal tanks ($P>0.05$; Fig. 4).

Two single families in single-family tanks versus in all-family tanks

Both single NC and OH families gained significantly more weight in the all-family communal tanks than in single-family tanks by the end of the experiment ($P<0.05$; Table 2). Fish in the all-family tanks had a lower coefficient of variation (CV) than the fish in the single-family tanks (Table 2). These results indicated that there were strong effects of family by environment (tank) interactions.

Two multi-family groups in multi-family tanks versus in all-family tanks

There was no significant difference in the mean weight of fish in group 3FCR between multi-family

Table 1 Number of alleles (*k*), polymorphism information content (PIC), expected heterozygosity (He) and estimates of null alleles (Null) of yellow perch progeny from 17 families

	1FNC				1FOH				3FCR				12FCR				17ALL			
Locus	*k*	PIC	He	Null	*k*	PIC	He	Null	*k*	PIC	He	Null	*k*	PIC	He	Null	*k*	PIC	He	Null
YP17	3	0.54	0.61	−0.26	4	0.52	0.58	−0.16	5	0.62	0.69	−0.19	8	0.62	0.69	−0.17	7	0.60	0.67	−0.18
YP49	4	0.69	0.74	−0.15	4	0.58	0.65	−0.14	8	0.60	0.67	−0.11	10	0.71	0.76	−0.08	11	0.68	0.73	−0.06
YP60	12	0.76	0.80	−0.10	10	0.74	0.78	−0.12	6	0.57	0.63	−0.09	9	0.67	0.71	−0.07	9	0.77	0.80	−0.07
YP109	6	0.70	0.75	−0.15	9	0.75	0.79	−0.13	9	0.73	0.78	−0.13	11	0.68	0.72	−0.12	16	0.83	0.85	−0.07
Mean	6	0.67	0.73	–	7	0.65	0.7	–	7	0.63	0.69	–	10	0.67	0.72	–	11	0.72	0.76	–

1FNC, single family of NC fish; 1FOH, single family of OH fish; 3FCR, 3 families from crosses; 12FCR, 12 families from crosses; 17ALL, all the four groups including 17 families.

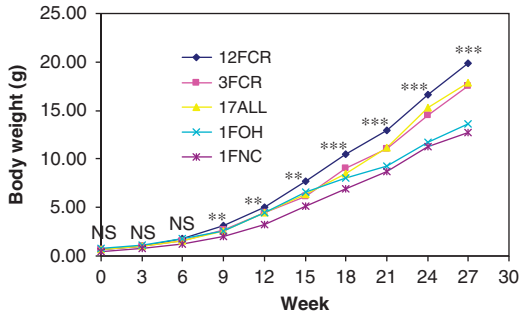

Figure. 2 Mean weights of yellow perch in single OH family tanks (1FOH), single NC family tanks (1FNC), 3-familiy tanks (3FCR), 12 family tanks (12FCR) and all-family tanks over the experimental period. NS, no significant difference ($P > 0.05$) among the five groups; **Significant difference ($P < 0.05$) between 12FCR and (1FOH+1FNC+3FCR+17ALL); ***Significant difference ($P < 0.05$) between 12FCR and (1FOH+1FNC+3FCR+17ALL), and significant difference ($P < 0.05$) between 3FCR and (1FOH+1FNC).

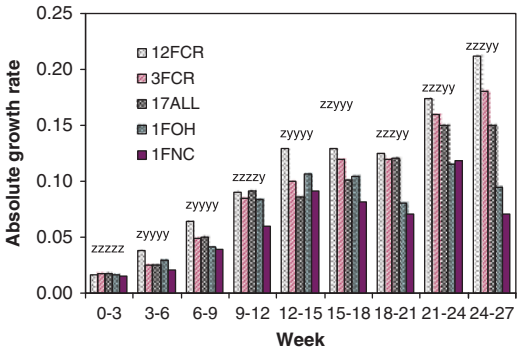

Figure 3 The absolute growth rate of yellow perch in single OH family tanks (1FOH), single NC family tanks (1FNC), 3-familiy tanks (3FCR), 12 family tanks (12FCR) and all-family tanks (17ALL) over the experimental period. The groups with the same letter were not significantly different ($P > 0.05$).

tanks (3FCR+12FCR) and the all-family tanks ($P > 0.05$), while a significantly heavier weight was detected for group 12FCR in multi-family tanks than in the all-family tanks ($P < 0.05$; Table 2). However, the observed correlation between family mean weight obtained from the multi-family tanks (3FCR+12FCR) and the family mean weight in the all-family tanks was not significant ($r = 0.32$, $P > 0.05$; Fig. 5). The absence of a correlation indicates that most of the families in multi-family tanks did not exhibit the same growth performance in all-family tanks, which reflects mostly environmental/tank effects rather than genetic differences among the families, suggesting strong effects of genotype by environment interactions on early growth of yellow perch.

Discussion

The use of four microsatellite markers with DNA parentage analyses allowed us to reliably assign 97.9% of progeny back to one of 17 families. The performance of microsatellites to allocate offspring to their parents is affected by the number of markers, allelic diversities of markers and/or genotype variations among parents (Marshall *et al.* 1998; Bernatchez & Duchesne 2000). Another recent study in our laboratory showed that 98.4% of offspring could be correctly allocated to one of 30 families with the addition of three more markers (seven markers in total) in a simulated assignment (Wang *et al.* 2009). Nevertheless, more molecular markers that promote higher resolution will be useful and needed to further improve the efficiency and accuracy of parentage analysis for the commercial-scale yellow perch breeding programme that requires at least 50 families per generation.

Studies of genotype by environment interactions on phenotype have been reported widely in the past decades in various aquatic animals (Gjerde & Schaeffer, 1989; Bagley, Bentley & Gall, 1994; Herbinger *et al.* 1999; Fishback, Danzmann, Ferguson & Gibson 2002; Jerry, Preston, Crocos, Keys, Meadows & Li 2006; Saillant, Dupont-Nivet, Haffray & Chatain 2006; Wang & Li 2007). Studies in yellow perch have demonstrated that environmental factors like temperature and density can have a profound influence on growth (Power & Van den Heuvel 1999; Tidwell, Coyle, Evans, Weibel, McKinney, Dodson & Jones 1999; Headley & Lauer 2008). However, no study has evaluated the influence of family by tank on early growth performance of yellow perch reared in single-family tanks versus in mixed-family tanks using DNA markers. In this study, the cross-bred families (12-family and 3-family groups) from different strains gained significantly more weight than both single-family groups in separate tanks throughout most of the experiment, but no significant differences were detected in BW among the four groups in the all-family communal tanks. In addition, both single families grew significantly faster in the all-family communal tanks than in single-family tanks by the end of experiment. These results indicated that there were strong effects of genotype by environment interactions on early growth performance. The cross-bred families theoretically had a larger gene pool and it was not surprising that they grew faster in separate treatments. On the other hand, it appeared that the communal rearing or polyculture of different strains/crosses improved the growth of those two single families in the all-family communal tanks. Although no report has been found on this issue, there are several similar reports of growth improvement by polyculture of different species, such as common carp *Cyprinus carpio* with silver carp *Hypophthalmichthys molitrix* (Yashouv 1971), Atlantic salmon *Salmo salar* with Arctic charr *Salvelinus alpinus* (Holm 1989) and *Tilapia rendalli* with *Oreochromis shiranus* (Chikafumbwa, Costa-Pierce, Jamu,

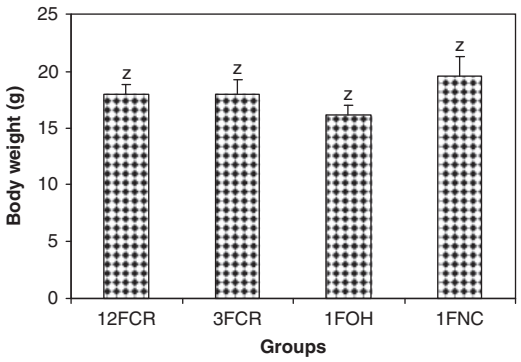

Figure 4 Mean weight of single OH family (1FOH), single NC family (1FNC), 3 families crosses (3FCR) and 12 families of crosses (12FCR) in the communal tanks. The groups with the same letter were not significantly different ($P > 0.05$).

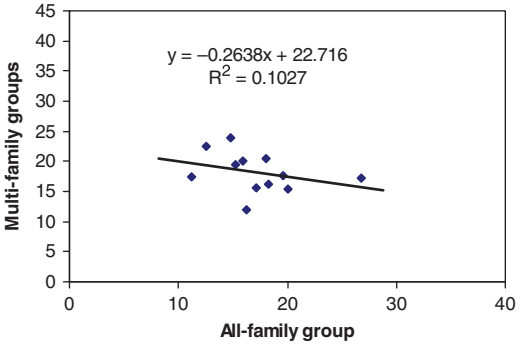

Figure 5 Correlation between the mean family weight in mixed-family tanks (12FCR + 3FCR) and the mean family weight in all-group tanks.

Table 2 Mean ± SE of body weight of experimental fish in single family (1FNC and 1FOH) and mixed-family groups (3FCR and 12FCR), along with coefficients of variation (CV), and differences in CV in the single family tanks, mixed-family tanks and all-family tanks

	Single-family tank		Mixed-family tank		All-group tank		
	$W_t \pm$ SE (g)	CV	$W_t \pm$ SE (g)	CV	$W_t \pm$ SE (g)	CV	CV difference
1FNC	12.72 ± 0.47^z	28.81	–	–	19.60 ± 1.68^y	19.13	9.68
1FOH	13.56 ± 0.42^z	23.44	–	–	16.15 ± 0.87^y	18.56	5.18
3FCR	–	–	17.48 ± 0.80^z	35.19	17.95 ± 0.87^z	32.65	2.54
12FCR	–	–	19.90 ± 0.97^y	35.19	17.91 ± 1.29^z	32.92	2.27

Means within a row followed by different superscript letters were significantly different ($P < 0.05$).

Kadongola & Balarin 1993) and common carp *C. carpio* with blue tilapia *Oreochromis aureus* (Papoutsoglou, Petropoulos & Barbieri 1992; Papoutsoglou, Miliou, Karakatsouli, Tzitzinakis & Chadio 2001), which all led to improved growth of one or both species versus monoculture. As Holm (1989) indicated, the mixing of species in polyculture could result in decreased intraspecific aggression. Similar effects might be present in the communal rearing of different geographical strains. The higher CV in the two single-family groups in our current study indicated that there could be stronger social interaction costs in those tanks. Some other fish species such as bluegill are also reported to show more aggressiveness and a higher size variance in a monoculture system (Wang, Hayward & Noltie 2000). Similarly, a strong variation among family tank mean weights was observed in Atlantic salmon in the single-family tanks verse in mixed tanks (Herbinger *et al.* 1999). These results indicate that single-family rearing could enlarge genetic variation, resulting in undesirable environmental artefacts for a breeding programme.

Overall, the experimental fish did not reach optimal growth in all tanks due to the relatively high density in the small tanks and low temperature. Reported optimum temperature for growth of yellow perch ranged from 23 to 25 °C (Hokanson 1977). However, this should not have influenced comparative analysis across the treatments, because the effect should have been similar for all tanks.

There was no correlation between the family mean weight obtained from the multi-family tanks (12FCR and 3FCR) and the family mean weight in the all-family tanks detected in this study. The absence of a correlation indicates that there was a strong variation among family mean weight within and among multi-family tank groups, which reflects mostly environmental effects rather than genetic differences among the families.

Evaluation of the molecular pedigrees and the effective number of broodfish generated important information regarding the breeding strategy. In this study, only 17 families were identified with DNA markers, which was only one more than the known number of half-sib families we produced; thus, we suspected that most of the $n = 3$ spawning sets resulted in only pair matings in most cases, although they were believed to increase the success of mating. This reduction in the number of breeders would have gone undetected without the molecular pedigrees. The ramification of these results for the yellow perch breeding is that a matrix of paired matings would be a more successful strategy for the identification of future superior broodfish and that attention to shared alleles and relatedness among broodfish (Doyle & Herbinger 1995) is an essential strategy.

Feeding level, fish density, water temperature and DO are the most important environmental factors relative to fish growth in aquaculture settings. During the period of the experiment, we attempted to maintain these environmental factors in all tanks as similar as possible, and are confident that the observed differences in BW and growth rates among groups of different families were not attributable to differences in environment factors. Recommended stocking density is about 100–200 fish m^{-3} for tank grow out of fingerlings (Pillay & Kutty 2005). We do believe that the high stocking density of 100 fingerlings for each 55 L tank had some effect on the growth performance of experimental fish, especially during the late part of the experiment, but this effect should have been similar for all tanks and should not have influenced comparative analysis across the groups. Reported temperature for the growth of yellow perch ranges from 11 to 26 °C, with optimum temperatures ranging from 23 to 25 °C (Hokanson 1977). All recording days of water temperatures (21–23 °C) were close to the optimum temperature ranges during the experimental period.

In summary, the present study demonstrated that microsatellite pedigrees are useful and essential for tracking individual family performance and evaluating interactions of genotype by environment on phenotypic trait expression for yellow perch. Our results indicate that there were strong effects of genotype by environment interactions on early growth of yellow perch families reared in single-family tanks versus in mixed-family tanks.

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