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Effects of inbreeding on economic traits of channel catfish*

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Summary. Inbred channel catfish (*Ictalurus punctatus*) were produced from two generations of full-sib matings to study the effect of inbreeding on reproduction, growth and survival. A randomly mated control line was propagated from the same base population to be used for the evaluation of the inbred fish. First generation inbred (I1) and control (C1) lines comprised five full-sib families each. Second generation inbred (I2) and control (C2) lines were produced by mating each male catfish from the I1 or C1 line to two females in sequence, one from the I1 and one from the C1 line. The design also produced two reciprocal outcross lines to be compared to their contemporary inbred and control lines. The coefficient of inbreeding for the inbred line increased from 0.25 in generation 1 to 0.375 in generation 2. The inbreeding coefficient was zero for all other lines. The resulting fish were performance tested in two locations, Tifton, Georgia and Auburn, Alabama and no genotype-environment interactions occurred. Results indicated that one generation of inbreeding increased number of days required for eggs to hatch by 21%, but did not significantly influence spawn weight or hatchability score. However, inbred females produced more eggs/kg body weight than control females. Two generations of full-sib mating in Georgia did not depress weight when expressed as a deviation to random controls but was depressed 13–16% when expressed as a deviation to half-sib outcrosses. Second generation inbreds produced in Alabama exhibited a 19% depression for growth rate when compared to either random or half-sib outcross controls. Survival rates at various age intervals was not decreased by inbreeding. The amount of inbreeding depression varied among families and between sexes.

Key words: Channel catfish – Inbreeding – Outcrossing – Full-sib mating – Cage and pond culture

Introduction

Genetic studies of poultry (Blow and Glazener 1953), swine (Dickerson 1942), cattle (Dinkel et al. 1968), and sheep (Terrill 1958) have shown that intensive inbreeding has pronounced effects on production traits of these species. A comprehensive study on the potential usefulness of inbreeding to increase selection response in farm animals has also been reported by Dickerson and Lindhe (1976).

Any pair of individual catfish can produce a large number of offspring annually, making possible the replacement of a whole brood population by one family within one generation. Information concerning the effects of intensive inbreeding on economic traits of fish species is, however, very limited. Ryman (1970) associated lower survival rate in families of Atlantic salmon with inbreeding. Inbreeding studies of rainbow trout (Kincaid 1976a) indicated that one generation of full-sib mating reduced the number of live fish and their body weight at 150 days of age by 16.1 and 24.4% in female families and 22.2 and 31.4% in male families, respectively. Even greater effects of inbreeding depression on body weight at five ages between 77 and 150 days were observed by Kincaid (1976a) after two generations of brother-sister mating. Gjerde et al. (1983) obtained similar results with rainbow trout in Norway. Increased levels of inbreeding resulted in greater growth depression but no additional depression in survival (Kincaid 1976a; Gjerde et al. 1983).

Increased incidence of fry deformities in rainbow trout as a result of inbreeding have also been reported by Aulstad and Kittelsen (1971) and Kincaid (1976b). Moav and Wohlfarth

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(1968) reported that one generation of inbreeding in carp depressed growth rate by 10 to 20%, reduced survival rate, and increased the number of deformed individuals. Bondari (1981) reported that genetic divergence between control and inbred lines of channel catfish, after one generation of full-sib matings, was associated with a differential response to water temperature.

Generally, intensive inbreeding causes a depression on growth and reproductive traits of many livestock and fish species but the extent of depression, if any, on growth, survival and reproduction of channel catfish (*Ictalurus punctatus*) is not known. The information is, however, essential if the potential economic loss to catfish farmers due to inbreeding are to be determined. This study was designed to determine (1) the effect of level of inbreeding from full-sib mating on economic traits of channel catfish and (2) the extent which outcrossing may restore the performance lost during inbreeding.

Materials and methods

The base population, Tifton strain of channel catfish, and facilities used have been previously described (Bondari 1981, 1983). The ancestry and breeding of the Tifton strain has been reported by Dunham and Smitherman (1984). Based on this history Tifton should have a high level of genetic variability, however, Hallerman et al. (1986) detected moderate levels of allozymic variability in this strain.

First generation inbred (F=0.25) channel catfish were produced at the Coastal Plain Experiment Station, Tifton, GA, from five full-sib matings in 1979 (I1 lines). A randomly bred control line (C1) was also propagated from five spawns of the same base population (Fig. 1). Fish were branded and pedigrees were kept to avoid pairing of brothers and sisters in the control line. I1 and C1 lines were grown and evaluated in Georgia. A sample of both lines was retained at Georgia for production of second generation full-sib matings (F=0.375), controls and I×C reciprocal crosses (female × male) when the brood fish were two years old. A sample of both lines was transferred to the Alabama Agricultural Experiment Station, Auburn, AL, for production of second generation inbreds, controls and reciprocal crosses when the brood fish were three years old.

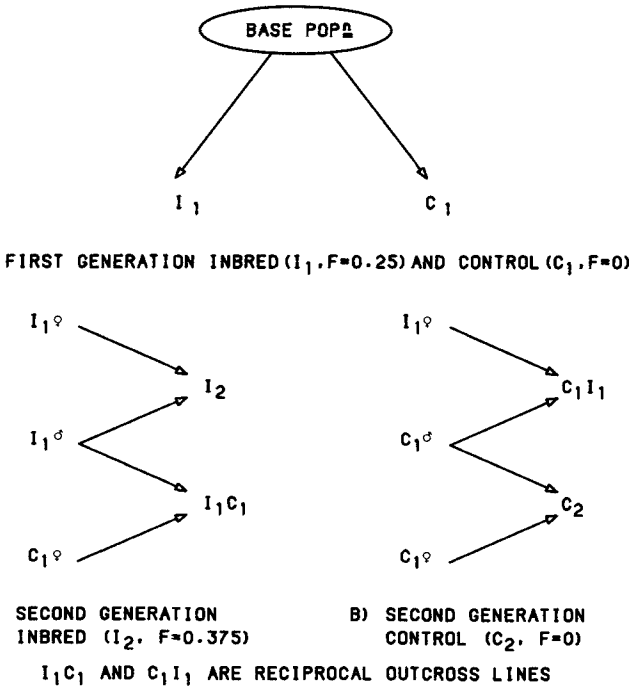

Fig. 1. Experimental design for two generations of inbreeding

The I×C reciprocals were produced to determine if the outcrossing would counteract any effects of inbreeding and to serve as another control to measure the effects of inbreeding (Kincaid 1976a). Individual inbred males were mated to both inbred females (I×I) and control females (C×I) to produce half-sib families. Control males were mated with sisters of the inbred females from the I×I matings to produce I×C since catfish females do not naturally mate with more than one male. C×I alone or the pooled reciprocals give an approximation of the half-sib control used by Kincaid (1976a).

Second generation inbreds (I2) were produced by a second consecutive generation of full-sib matings. Replicate full-sib matings were produced from each of the original five lines. Second generation controls (C2) were produced from random matings among progeny from the original five control spawns. Again, no brother-sister matings were allowed in the control population.

Second generation inbreds, controls and crosses were produced and evaluated at Georgia in 1981 and at Alabama in 1982. Second generation fish produced at Georgia were also transferred to Alabama at 40 weeks of age for performance testing in ponds. Details of the fish culture in Georgia and Alabama follows.

Fish culture in Georgia

Five-year-old parental brood catfish from the base population were pair-mated in 240×150 cm wire-fenced spawning pens located in a 0.1-ha pond to produce the five I1 lines and five C1 families. A 38-liter milk can was placed in each pen for spawn collection. The cans were checked for egg masses 3 times per week. Egg masses were artificially incubated and fry were reared indoors in fiberglass tanks (two tanks per family) for 40 weeks. Larger spawns were split to prevent density differences prior to 4 weeks of age. Each tank contained approximately 5,000 fish from only one full-sib family which were standardized to 500 individuals at 4 weeks of age and to 200 at 12 weeks of age. Body weight was evaluated at 16 and 40 weeks of age. All fish were fed a commercial diet (40% protein) ad libitum five times daily prior to 16 weeks of age and three times daily from 16 to 40 weeks. The hatching day (if hatched over a 2-day period, the earlier day was used) was used as a basis to determine fish age.

Shortly after 40 weeks of age, catfish from both inbred and control lines were heat branded and communally stocked (Dunham et al. 1982) in two floating mesh cages (76 width × 117 length × 122 depth in cm) placed in a two-ha reservoir. Each cage contained 250 fish (25 per family) representing all inbred and control families. A floating feed (38% protein) was fed ad libitum twice daily during the cage culture. Body weight was evaluated at 69 and 95 weeks of age.

The two-year-old first generation fish were pair-mated to produce 15 spawns, five second generation inbred (I2, F=0.375) families (representing all five of the original inbred lines), five control (C2) families and five I1 × C1 reciprocal

families (Fig. 1). Male brood fish from the I1 or C1 line were each paired with 2 females in sequence, one from the I1 and the other from the C1 line. Reciprocal I1×C1 progeny were half-sibs of inbred and control progeny. A second female replaced the first female after a spawn was produced. Second spawns were produced within two to three days. Fish from all full-sib families within C1 or I1 lines contributed offspring to the second generation lines (C2 or I2). Egg masses were transferred to the laboratory and were weighed. Egg weights were then determined from two samples of 10 eggs per egg mass, one sample from the edge and the other from the center. Number of days required for the eggs from each egg mass to hatch and hatchability score, an approximation of percentage hatch (score of 0=no eggs hatched to 10=all eggs hatched), were also determined as described by Bondari (1984). The same individual spawning pens, ponds, tanks, and cages used for the first generation fish were also used to produce and rear the second generation fish.

Stocking densities were the same as the previous generation, but deviated slightly for the cage culture. Two random samples of 20 fish per family (a total of 300 fish/cage) were placed in two cages after the 40-week tank culture. Feeding and management of the fish in tanks and cages were similar to those in generation 1.

Family weight was determined at four weeks and individual weight and length were determined at 12 and 40 weeks of age in tanks and at 52 weeks of age in cages. At the end of the cage test, 20 fish per line (40 females and 40 males) were randomly selected and sacrificed to obtain carcass information. An identical group of 600 fish (45 weeks old) were transferred from the tanks to Auburn, Alabama to be performance tested in ponds, under conditions different from Tifton, Georgia.

Fish culture in Alabama

The 600 fish (second generation inbred, control and outcrosses from two-year-old fish) transferred to Alabama were communally stocked (Dunham et al. 1982) in a 0.4-ha pond supplemented with similarly sized fish to adjust stocking density to 7,410/ha. The fish were fed ad libitum once daily until harvest when they were 65 weeks old. All fish were individually weighed at that time.

In 1982, a sample of adult first generation inbred catfish and their controls were also transferred to Auburn for spawning when three years old. Control and inbred fish were mated in all possible combinations (Fig. 1) in 240×150 cm spawning pens within 0.1-ha ponds. When a spawn was produced, a second female from the opposite line was paired with the same male to produce C1×I1 reciprocals that were half-sibs of the I2 lines and the C2 line. First and second spawns were collected during a three- to four-day period. Nine I2 spawns, 10 C2 spawns, 17 I1×C1 spawns and 10 C1×I1 spawns were produced totalling 46 spawns containing 573,400 eggs. The 9 I2 spawns included at least one spawn from each of the original 5 I1 lines. Spawning rate, percentage of pairs that spawned, was determined. Egg masses were artificially incubated in paddle wheel troughs described by Jensen et al. (1983). Number of eggs and fry were determined volumetrically.

Five replicate families from each type of mating, I2, C2, C1×I1, and I1×C1 were transferred (20 total) to 16 mm mesh wire cages (15×20×10 cm) suspended in a 5,000-l tank. Each of the original I1 lines was equally represented in this test. Stocking rate was 200 fish/cage. Constant aeration was provided and water was completely exchanged twice daily. Fry were fed ad libitum six times daily from 1–4 weeks and twice daily from 4–16 weeks. Stocking rate was reduced to 40 fish/cage from 4–12 weeks and 20 fish/cage from 12–16 weeks. Group weights and numbers were determined at 4-week intervals.

A second sample of fry representing all 46 families was grown in earthen ponds. Fry from all I2 families were pooled, as were fry from all C2 families and fry from all C1×I1 and I1×C1 families. All five of the original I1 lines were represented, but not equally because of differential spawning, fecundity and survival among the five original inbred lines. The three groups were stocked at 500,000/ha in duplicate 0.04-ha earthen ponds. Two-hundred fish/pond were weighed collectively at four, six, and ten weeks of age. The fish were harvested, weighed and restocked in triplicate at 9,880/ha at 16 weeks, sampled at 24 weeks, harvested, weighed and restocked at 7,410/ha at 44 weeks. At 44 weeks of age all fish were heat branded and stocked communally in 12 ponds. The fish were grown until 64 weeks at which time they were harvested. Fish were fed ad libitum once daily during the experiment in ponds.

Relative numbers caught (seinability) was determined at 24 and 44 weeks. Deformities (if any) were enumerated at all samples. At the conclusion of the 64-week growth period, two of the communal ponds were re-stocked, oxygen level was lowered to 1.0 ppm, and mortality enumerated.

Statistical analysis

Data were analyzed by General Linear Model (GLM) procedures of the statistical analysis system (SAS 1982). The model for the unsexed data, collected during the first 40 weeks of age, included effects of replicate, line (genetic group), and family nested within line. The same model was used to analyze the sexed data (collected after 40 weeks of age) for each sex separately. When significant, the family within line mean square was used to determine the significance of line effect, otherwise, the error mean square was used. Families within genetic group were not kept separate when large numbers of replicate families were produced, preventing dam within sire analysis between inbred and outcrossed groups. Arcsine transformation was used to analyze the survival data, but means were reported in original scale (%).

Results

Georgia

All generation 1 females were either inbred or control fish regarding sex limited reproductive traits, such as spawn weight and egg weight. Paternal type (control or inbred) did not affect these traits or those of the embryo, number of days to hatch, hatchability and number of days to swim-up. Inbred and control families did not differ significantly in spawn weight, hatchability score, or the number of days required for fry to swim up (Table 1). Females from the randomly bred control line, however, produced egg masses containing eggs that required one day less to hatch than those produced by the inbred females. Observed body weight of first generation inbreds was 7.4 and 3.9% lower than controls at 16 and 40 weeks of age but was not significantly different than body weight of controls (Table 2).

A significant ($P < 0.05$) body weight depression was observed at 4 weeks of age after two generations of full-sib mating (Table 2). Pooled outcross lines were comparable in 4-week weight to the inbred line but fish from both lines weighed significantly less than those in the control line. Such decline in growth at an early age, however, did not initiate a trend and no further depression was observed for either body weight or total length at 12, 16, 26, or 40 weeks of age, although observed weights of inbreds continued to be 1.3 to 11.1% lower than outcross controls. Survival rates between 4 and 40 weeks of age were not influenced by the mating system applied (Table 2).

Results of the performance evaluation of the first generation fish indicated that even with the weight and length advantages inbred fish had at the initiation of the experiment due to subsampling error, weight gain or length increase of female or male catfish did not differ. When inbred and control lines were compared during the 50-week test in cages, observed length increases were 2.6 to 4.2% lower for inbreds than randomly bred controls (Table 3). No significant decline in performance was detected in the sccond generation fish when randomly bred control and inbred lines were compared in cages. Female catfish from these two lines were comparable in body weight, total length, carcass weight, and dressing percentage but the male inbred fish were superior to the male controls in all these traits. The half-sib outcross fish of both sexes were superior to the randomly bred control fish for all traits. Outcross females were 24.2% larger ($P < 0.05$) than inbred females (Table 3). The 8.0% difference in body weight between half-sib and inbred males was not significant (Table 3).

Table 1. Means for reproductive traits of first generation inbred and control channel catfish

Trait	Control (C)	Inbred (I)	SE[c]
Two-year old fish (Georgia)[d]			
No. of spawns	8	7	
Spawn wt (g)	279.3[a]	287.4[a]	36.1
Egg wt (mg)	24.6[a]	22.1[a]	1.6
No. of days to hatch	4.2[b]	5.1[a]	0.3
Hatchability score	5.6[a]	5.7[a]	0.7
No. of days to swim-up	5.8[a]	6.5[a]	0.5
Three-year old fish (Alabama)[d]			
No. of males paired	56	42	
% Male spawned	48.2[a]	45.2[a]	6.3
No. of females paired	44	54	
% Female spawned	45.5[a]	48.1[a]	6.6
No. of eggs/kg wt	7,711[b]	9,099[a]	295.7
Hatchability (%)	62.5[a]	66.4a	5.2

[a,b] Means within a row with different superscripts differ ($P < 0.05$)
[c] Standard error of least-squares means
[d] No significant sire effects were observed when C×I and I×C reciprocals are partitioned and analyzed

Table 2. Growth and survival (4–40 weeks) of first and second generation inbred (I), control (C), and outcrossed (C×I) channel catfish in Georgia (tank culture)

Trait	Generation 1				Generation 2[e]			
	Age (weeks)	Control (C1)	Inbred (I1)	SE[d]	Control (C2)	Inbred (I2)	C×I[c]	SE[d]
Body wt (g)	4[f]				385[a]	220[b]	273[b]	30.1
	12				4.2	3.9	4.0	0.3
	16	9.4	8.7	1.0	5.9	5.6	6.3	0.5
	26				11.6	14.7	13.9	1.6
	40	65.7	61.8	5.7	41.2	51.4	52.7	5.7
Total length (mm)	12				81	77	79	1.3
	16	106	102	3.2	94	90	92	1.9
	26				114	119	122	3.9
	40	195	195	5.3	171	178	185	6.7
Survival (%)	4–12				84	83	92	4.3
	12–26				98	98	91	4.6
	12–40				79	86	81	4.3

[a,b] Means for generation 1 or generation 2 fish, within a row, with different letters differ ($P < 0.05$). Absence of superscripts indicate no significant line effect detected from the analysis of variance
[c] Pooled reciprocals (I×C and C×I)
[d] Standard error of line means computed as square root of (MSF/NM), where MSF = family within line mean square, N = number of families per line, and M = number of fish per full-sib family
[e] Generation 2 produced from two year-old brood stock
[f] Measured in mg

Table 3. Performance test of channel catfish from control (C), inbred (I), and pooled reciprocal (C×I) lines in Georgia (cage culture) and in Alabama (pond culture)

Trait[c]	Age weeks	Weeks on test	Female				Male			
			C	I	C×I[d]	SE[f]	C	I	C×I[d]	SE[f]
Georgia (generation 1)										
Initial wt	45	0	96	120		4.2**	114	152		7.7**
Weight gain	69	24	480	494		45.3	614	643		52.8
	95	50	642	638		38.9	862	875		58.8
Initial length	45	0	221	236		2.8**	233	251		3.9**
Length increase	69	24	174	167		7.3	188	183		7.3
	95	50	189	177		4.7	210	203		6.0
Georgia (Generation 2)[e]										
No. of fish			93	90	93		106	99	104	
Body wt	52	9	112[b]	125[b]	165[a]	18.1	130[b]	185[a]	201[a]	21.0
Length	52	9	237[b]	245[b]	271[a]	12.6	250[b]	275[a]	288[a]	11.2
Carcass wt	52	9	60[b]	66[b]	101[a]	13.1	71[b]	107[a]	108[a]	11.4
Dressing %	52	9	53.6[b]	54.6[b]	56.9[a]	0.8	52.9[b]	55.8[a]	55.9[a]	0.7
Alabama fish (generation 2 – unsexed)[e]										
No. of fish			186	156	141					
Body wt	79	36	279[b]	272[b]	314[a]	12.3				

[a,b] Female or male means in each row with different superscript letters differ ($P < 0.05$)
[c] Weight (Wt) and total length (TL) measurements in g and mm, respectively
[d] Pooled reciprocals (I×C and C×I)
[e] Generation 2 produced from two-year-old brood stock at Georgia
[f] As described in Table 2
** Control and inbred means differ ($P < 0.01$)

Alabama

Spawning rate and egg hatchability of first generation inbred catfish did not differ from control brood stock (Table 1). Number of eggs/kg body weight was greater ($P < 0.02$) for inbred catfish (9,099) than control catfish (7,711). Females of three inbred lines (23 spawns) had high fecundities (9,412 eggs/kg; 8,840–9,809 eggs/kg) and two lines (3 spawns) had low fecundities (6,162 eggs/kg; 5,546–6,678 eggs/kg). Percentage of brood pairs that spawned was correspondingly high and low in these same lines, 56.5% and 25.0%, respectively. The correlation between fecundity and spawning rate among the five inbred lines was 0.81 ($P < 0.05$). The sire, control or inbred, did not affect spawning rate, fecundity or egg hatchability.

Body weight at 79 weeks of age was not different between the random control and second generation inbred catfish grown in ponds that were produced by the two-year-old brood fish (Table 3). Weight of the pooled half-sib outcrosses was greater ($P < 0.05$) than both control and inbred fish. The same results were obtained with the same fish grown in cages in Georgia. Survival of C2, I2 and C×I reciprocals was 93.0, 78.0 and 70.5%, respectively. Deformities (compressed bodies) were noted in 3 individuals from one inbred line. Survival of the fish from this inbred line was also low.

Inbreeding depression for body weight of I2 inbreds produced from nine spawns of three-year-old brood stock was 30% at 12 and 16 weeks of age when grown in cages when calculated as a deviation from the randomly bred control. Inbreeding depression was 14–22% when calculated as a deviation from the half-sib outcrosses (Table 4). Body weight of each reciprocal outcross was comparable to the control at 16 weeks of age, but differences were observed prior to this age. Survival of the inbred fish was generally comparable to the controls during the four sampling periods in cages (Table 4). Survivals of the I×C reciprocal was greater than the control from 8–12 weeks, but survival of the C×I reciprocal was similar to the control.

Inbreeding depression for body weight of I2 inbreds was 19% at 64 weeks of age when grown in earthen ponds and calculated as a deviation from either the randomly bred control or the half-sib outcross (Table 4). No significant inbreeding depression for body weight was observed prior to 64 weeks of age. Body weight of the pooled C×I reciprocals was always comparable to the control line, but differed from the inbred line at 64 weeks. Rate of growth during winter did not differ among the three groups. Survival rates from 16–64 weeks were significantly greater for inbred and outcross lines than the control line (Table 4). No difference was observed prior to 16 weeks of age. Survival when

Table 4. Body weight, survival and survival during low oxygen of second generation inbred, control and outcrossed channel catfish fry and fingerlings produced by three-year-old brood stock and grown in cages and ponds in Alabama

Trait	Age (weeks)	Control (C2)	Inbred (I2)	C×I[a,e]	I×C	SE[d]
Cage culture						
Body wt (g)	4	0.184	0.158	0.231	0.163	0.02
	8	0.326[b]	0.306[b]	0.300[b]	0.250[c]	0.01
	12	2.13[b]	1.48[c]	1.40[c]	1.86[b]	0.19
	16	4.10[b]	2.87[c]	3.53[b]	3.84[b]	0.25
Survival (%)	0–4	37.0	32.0	32.0	32.0	8.33
	4–8	37.5[bc]	31.8[c]	31.3[c]	50.0[b]	6.50
	8–12	22.7[c]	41.0[bc]	22.5[c]	67.8[b]	9.76
	12–16	90.0[b]	70.3[c]	77.0[bc]	84.7[bc]	6.75
Pond culture						
Body wt (g)	4	1.37	1.19	1.05		0.22
	6	2.62	2.36	2.57		0.24
	10	4.75	4.80	3.80		0.64
	16	12.3	11.0	9.3		2.24
	24	25.0	16.3	17.8		5.31
	44	37.0	25.9	30.4		5.62
	64	350[b]	283[c]	348[b]		14.0
Survival (%)	0–16	15.9	17.8	43.2		7.3
	16–44	52.7[c]	94.3[b]	72.2[b]		5.7
	44–64	68.7[c]	92.3[b]	88.8[b]		2.6
Survival (%) during oxygen depletion*	64	29	46	60		

[a] Female × male
[b,c] Means within a row with different letters differ ($P<0.05$). Absence of superscripts indicate no significant difference among lines
[d] Standard error of least-squares mean
[e] I×C and C×I pooled reciprocals for pond data
* Significant ($P=0.01$) line differences tested by Chi-square

stressed by low dissolved oxygen concentrations was lowest (29%) in C2, intermediate (46%) in I2 and highest (60%) for C×I reciprocals (Table 4). No differences were found among lines for seinability. Deformities were not detected in any group for this year class.

Within the I2 lines, full-sib families responded differently to inbreeding with regard to growth, fecundity and survival. Families that had depressed growth also tended to have depressed survival and reproductive success.

Discussion

The increase in number of days to hatch channel catfish after one generation of inbreeding, and inbreeding depression for body weight after two generations is consistent with the inbreeding depression for growth and reproduction found for other species of fish (Moav and Wohlfarth 1968; Ryman 1970; Kincaid 1976a, b; Aulstad and Kittelsen 1971) and farm animals (Dickerson 1973). However, the slight depression or lack of depression for body weight after one generation, and the lack of depression for other traits indicate that growth, reproduction, and survival in channel catfish may not begin to seriously decline until F reaches or exceeds 0.375. Kincaid (1976a, 1976b) observed depression for growth rate in rainbow trout at F=0.125–0.25.

The minimal depression, compared to other species of fish, observed in the first generation of inbreeding has at least two possible explanations. Inbreeding depression for certain traits could have been underestimated. In the case of reproductive traits, the superior performing lines unequally contribute to the mean, inflating the mean of the inbreds. However, when the observations on the five inbred lines are weighted, we still observe no inbreeding depression. Kincaid (1976a) and Gjerde et al. (1983) both reported similar underestimation of depression for growth rate caused by lower survival of inbreds and subsequent density effects.

The second explanation relates to the genetic background or variability of the experimental strain. The breeding history of Tifton strain should have resulted in a base population with high genetic variability (Dun-

ham and Smitherman 1984). If dominance is important for determination of inbreeding effects, the magnitude of inbreeding depression would be greater for heterozygous populations than for more homozygous populations since a greater number of loci would become homozygous in the variable population with a certain level of inbreeding. However, this is an oversimplification as the number or percentage of loci becoming homozygous for deleterious alleles should be more important than the total number of loci becoming homozygous. A threshold could exist where detrimental effects or depression would occur once a certain level of homozygosity and deleterious gene combinations had been reached. Populations with low levels of genetic variability would be more susceptible or closer to the threshold. This is similar to buffering or canalization proposed by Lerner (1954) and Waddington (1957) for developmental stability but in relation to physiological stability.

The threshold concept can be explained in terms of epistasis. If an enzyme pathway can follow more than one route such as in glycolysis or production of urea (White et al. 1964), the alternative pathway(s) will still function if a locus for one step in one pathway is homozygous for a deleterious recessive. This is an example of duplicate dominant epistasis. As the level of homozygosity increases the probability of two or more critical loci being homozygous for deleterious genes and the total enzymatic process impeded or diminished increases. Inbreeding would then have a lesser effect on populations with high levels of heterozygosity acting as a buffer through epistasis than on more homozygous populations with less buffering ability. Once a certain level of inbreeding and homozygosity is attained the depression would plateau from natural selection against the least viable and most deleterious genotypes.

This hypothesis is supported by the relationship between the loss of genetic variability as measured by isozyme allele frequencies and the assymetry of bilateral meristic traits in rainbow trout (Leary et al. 1985a, b). A 21% reduction in average heterozygosity resulted in a 21% greater average assymetry, and a 44% reduction in average heterozygosity resulted in a minimum of 69% greater average assymetry. The rate of inbreeding depression as measured by assymetry of bilateral meristic traits increased more rapidly as the populations became progressively homozygous. This is also reflected in the correlation, $r = -0.40$ to -0.63, between average heterozygosity and assymetry (Leary et al. 1985b). Unpublished data (Dunham and Smitherman 1986) indicates channel catfish with expected heterozygosities less than Tifton strain, may experience greater inbreeding depression for body weight and survival after one generation of inbreeding ($F = 0.25$) than observed in this experiment.

No genotype-environment interactions were observed when controls, inbreds and outcrosses were grown at two different locations (Georgia and Alabama). Progeny produced by two-year-old brood stock had the same relative performance in cages at Georgia and in ponds in Alabama. Results of the reproductive performance of the three-year-old brood fish in Alabama was also consistent with those of the two-year-old brood fish in Georgia.

The second generation inbred channel catfish produced by three-year-old brood fish grew 19% slower in ponds than the randomly bred control. If the difference in depression from progeny of two-year-old fish and three-year-old fish (subsamples of the same lot of fish) at Georgia and Alabama, respectively, is correct, it may be a result of different lines appearing to develop during the inbreeding as various families and individuals were differently affected by the inbreeding. Kincaid (1976a, b) also observed that the magnitude of inbreeding depression varied among families of inbred rainbow trout. This should be expected since it is likely that different sets of genes would become homozygous in different lines. The higher fecundity (number of eggs/kg female) in some but not all of the inbred lines, and the variable spawning rate, survival and growth rate among inbred lines all illustrate the variable response to inbreeding by individual families and lines.

One alternative explanation of the different depression measured from the progeny of two- and three-year-old brood fish relates to age of sexual maturity. Fast growing salmonids mature earlier than slow growing individuals in the same population (Gall 1986). If this were true in channel catfish, the two-year-old fish that spawned may have been faster growing, more vigorous individuals compared to their full-sibs, inflating the true mean for the inbreds. Only a small percentage of channel catfish mature at two years of age. This relationship between rapid growth and early sexual maturity does not exist among strains of channel catfish (Dunham and Smitherman 1987) but has not been examined within populations.

If the alternative controls for an inbreeding experiment are examined, the results obtained from the two-year-old brood stock in Georgia and the three-year-old brood stock may actually be quite similar. Theoretically, the utilization of outcrossed half-sib families of the inbred lines as controls, as used by Kincaid (1976a), is a stronger control than a randomly bred control. If we compare the second generation inbreds produced from two-year-old brood fish and evaluated at both Alabama and Georgia to the half-sib outcrosses, the inbreeding depression is 13–16%. These values are very near the 19% depression expressed by progeny from three-year-old brood fish when compared to either the half-sib outcrosses or randomly bred control.

The half-sib control may be particularly powerful when the number of families sampled is small. Use of the half-sib control gave expected results for the spawns at two years of age where each inbred line was represented by one replicate family and use of the randomly bred control gave unexpected results, the controls equal or smaller in size than the inbreds. When the number of replicate families per line and number of control spawns was doubled for the spawns at three years of age, the inbreeding depression for body weight measured as deviations from the half-sib control or the random control is the same. Kincaid (1976 a), using the half-sib family control, and Gjerde et al. (1983) using a randomly bred control, report almost identical levels of inbreeding depression for growth rate and survival in rainbow trout. When the number of inbred families and control families are large, the accuracy of the half-sib control and randomly bred control for determination of inbreeding depression appear equal.

Significant depression in body weight which was only significant near the conclusion of cage (12–16 weeks) and pond (64 weeks) tests in Alabama and similarly when the half-sib control is used in Georgia suggests a partial independence of the genetic factors controlling weight gain at different ages. Vanelli et al. (1984) have also reported that after 8 generations of inbreeding, genetic control of the growth pattern in guppy (*Poecilia reticulata*) was manifested in the phenotype at later developmental stages, but was not evident at the earlier ages measured. Gjerde et al. (1983) also report an increase of inbreeding depression for growth rate with age in rainbow trout, but the values reported by Kincaid (1976 a) remain constant or decrease with age.

The performance test also indicated that both female and male catfish from the outcross line were superior in carcass composition to those from the random-bred line (Georgia test). Female catfish from the outcross line were also superior to inbred females but the male catfish from these two lines were comparable in carcass composition.

Two generations of inbreeding resulted in negligible depression for survival in catfish. The absence of inbreeding depression on catfish survival is consistent with the results reported by Lannan (1980) concerning the larval survival of oysters, *Crassostrea gigas,* but not consistent with the inbreeding depression for survival observed in rainbow trout (Kincaid 1976 a).

Inbreeding had detrimental effects on economic traits of channel catfish in this experiment, and inbreeding should be avoided in channel catfish. The growth, survival, tolerance to low oxygen and dressing percentage of C×I reciprocals were equal or better than that of control and inbred lines indicating the detrimental effects of inbreeding can be counteracted by outcrossing.

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