REPRODUCTION OF DOMESTICATED STRIPED BASS: COMMERCIAL MASS PRODUCTION OF FINGERLINGS

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ABSTRACT

Most commercial hybrid striped bass (HSB) farms rear sunshine bass produced by mating wild-caught female white bass *Morone chrysops* with male striped bass *Morone saxatilis*. The opposite hybrid (palmetto bass; *M. saxatilis* X *M. chrysops*) has been used less often because wild or domestic female striped bass are viewed as too difficult to reproduce when needed. Beginning in the early 1990s, our investigations at North Carolina State University, focused on developing detailed understanding and control of the reproductive biology of female striped bass while domesticating the species in captivity. These studies established the basic methodology required to reliably reproduce the domestic females to generate striped bass and palmetto HSB. Results of recent fingerling production trials using palmetto and sunshine HSB fry from domesticated (F_2-generation) parents demonstrated unequivocally the value of female striped bass as broodstock in the HSB farming industry. We repeatedly used domesticated striped bass females to generate palmetto HSB fingerlings using extensive (pond) culture methods on private farms with egg fertility and hatching rates, larval survival, and fingerling yields comparable to those obtained using fully mature, wild female striped bass captured on or near their spawning grounds. Reproductive performance of the female striped bass and survival of their progeny through the fingerling production cycle were also equal to or better than corresponding values for domesticated female white bass and their sunshine HSB progeny. This is the first report, of which we are aware, on the use of domesticated striped bass for commercial mass production of fingerlings.

INTRODUCTION

Farming of hybrid striped bass (HSB; genus *Morone*) is one of the fastest growing segments of United States aquaculture, with production of foodfish approaching five million kg/yr. Although efforts at domesticating *Morone* species are underway (Harrell and Webster 1997), most commercial HSB hatcheries still generate sunshine bass produced from wild-caught female white bass *Morone chrysops* and male striped bass *Morone saxatilis*. The opposite hybrid (palmetto bass; *M. saxatilis* X *M. chrysops*) has been used less often because wild or domestic striped bass females are viewed as too difficult to reproduce when needed. Beginning in the early 1990s, our investigations at North Carolina State University (NCSU) focused on developing detailed understanding and control of the reproductive biology of female striped bass (Sullivan et al. 1997). Parallel investigations were simultaneously conducted on white bass and white perch *M. americana*. We exploit the latter species as a laboratory model for *Morone* reproductive biology (Jackson et al. 1995).

Captive broodstocks were established and a detailed picture of their gametogenic cycle was acquired with respect to circulating levels and actions of important sex steroids (estradiol 17β; [E_2], testosterone [T] and 11-ketotestosterone) relative to specific stages of gonad maturation (Woods et al. 1992; Woods and Sullivan 1993; Tao et al. 1993; Blythe et al. 1994ab; Berlinsky et al. 1995; Jackson and Sullivan 1995; Sullivan et al. 1997). Considerable knowledge of the

physiology of oocyte growth was developed with regard to the main yolk precursor protein, vitellogenin (Vg), including development and use of immunoassays for circulating Vg as a marker of female maturity (Tao et al. 1993, 1996; Blythe et al. 1994; Berlinsky et al. 1995; Folmar et al. 1995; Sullivan et al. 1997; Heppell et al. 1999).

We also made many discoveries about the process of final oocyte maturation (FOM), including calibration of blood levels of maturation-inducing steroid (MIS) hormones (17α,20β-dihydroxy-4-pregnen-3-one, DHP; 17α,20β-trihydroxy-4-pregnen-3-one, 20β-S) to specific stages of FOM, detailed characterization of their actions and mechanism(s) of action, functional description of the ovarian MIS receptor, and identification of 20β-S as the main *Morone* MIS (King et al. 1994ab, 1995ab, 1997). We recently found that insulin-like growth factor I (IgF-I) can induce *in vitro* FOM of striped bass oocytes at stages much earlier than either gonadotropin (hCG) or MIS. Other new findings suggest that acquisition of follicular responsiveness to IgF-I may be a critical early step enabling FOM in *Morone* species (Weber et al., 2000; Weber and Sullivan, In Press).

The new knowledge of *Morone* reproductive physiology was exploited to develop improved techniques for tracking the onset and course of maturation while maturing broodstock out-of-season via photothermal conditioning (Blythe et al. 1994ab; Sullivan et al. 1997). Our most recent experiments, involving exposing striped bass to various combinations of static or annually-cycling day length and water temperature, revealed a striking dependency of vitellogenesis and oocyte growth on low temperature (Clark 1998). Based on these findings, we utilize mixed well and surface water sources to expose broodfish held in outdoor tanks to a thermal cycle appropriate for normal maturation (Hodson and Sullivan 1993; C.V. Sullivan, unpublished).

Our fish are induced to mature and spawn using implanted pellets that chronically release a potent, synthetic analog of gonadotropin-releasing hormone (GnRHa), a technique we pioneered for *Morone* species (Woods and Sullivan 1993; Hodson and Sullivan 1993; Sullivan et al. 1997). However, problems remained with identifying when females become responsive to GnRHa. We recently discovered that female striped bass whose (biopsied) follicles are capable of undergoing FOM in response to IgF-I *in vitro* respond to GnRHa implants *in vivo* to complete FOM and fully ovulate. This finding forms the basis for a new bioassay to select females competent to respond to the GnRHa implants (Weber et al., 2000).

The basic and applied research on striped bass maturation was accompanied by empirical development of improved methods for broodstock husbandry and efforts to fully domesticate the species. Aside from proper photothermal conditioning, improved husbandry involves minimizing handling and associated stress and feeding the fish an adequate ration of an appropriately formulated broodstock diet (Hodson 1995; Sullivan et al. 1997). We have now taken several different stocks of striped bass through a number of filial generations of domestication. For the purposes of this paper, "domesticated" refers to fish reared for two or more generations in captivity.

The present study was undertaken to test the value of our domesticated striped bass, broodstock husbandry methods, and spawning techniques for mass production of HSB fingerlings at commercial scale. In collaborative research with North Carolina HSB growers, we repeatedly spawned domesticated females to generate palmetto HSB fry which were used to produce fingerlings through application of extensive (pond) culture methods on private farms. For these females, egg fertility and hatching rates, larval survival, and fingerling yields were comparable to those obtained using fully mature wild fish captured on or near their spawning grounds. Our results also showed that reproductive performance of the female striped bass and survival of their progeny through the fingerling production cycle were equal to or better than corresponding values for domesticated female white bass and their sunshine HSB progeny.

MATERIALS AND METHODS

Striped Bass Broodstock

The 4-yr-old domestic (F_2-generation) female striped bass broodstock (avg. BW 4.32 kg) used in this study were produced at the NCSU Pamlico Aquaculture Field Laboratory (PAFL) in Spring of 1994. They were generated as a cross between domestic (F_1-generation) female striped bass from PAFL with domestic (F_1- and F_2-generation) male striped bass of Chesapeake Bay origin that were obtained from the Crane Aquaculture Facility (CAF; University of Maryland) in Baltimore. The F_1-generation domestic females were obtained in 1990 from the South Carolina Department of Natural Resources striped bass hatchery in Bonneau, where they were produced from wild parents captured from the Santee-Cooper drainage. The F_2-generation broodfish were reared to maturity out of doors in 0.1-ha ponds and then 6-m-diameter circular pools at PAFL as described previously (Hodson and Sullivan 1993) with the exception that they were fed at a rate of 1.5% BW, three times/wk with a special diet (CAF-Striped Bass Broodstock Diet 'B': Ziegler Brothers; Gardners, Pennsylvania, USA). Male striped bass used to produce sunshine HSB were from the same stock as the domesticated striped bass females.

The wild striped bass used in this study to produce sunshine HSB were obtained from commercial pound nets near the mouth of the Roanoke River in North Carolina and transported to a local fish farm (North State Fisheries[NSF]; Pinetown, North Carolina, USA) for spawning.

White Bass Broodstock

The domestic (F_2-generation) white bass broodfish used in this study (BW range 0.45-0.52 kg) were 2 yr of age and generated as a cross between 2-yr-old, F_1-generation domestic parents performed at PAFL in 1996 (Hopper 1999). The parents originated as a cross of wild adults obtained from tributaries of the Ohio River with adults captured from the Lake Erie basin that was performed in an attempt to enhance genetic variability. Various (sibling) groups of fry arising from this cross were pooled and used to generate fingerlings under extensive culture conditions at PAFL, which were then reared to maturity in 0.1-ha ponds using standard HSB culture practices (Harrell and Webster, 1997). Separate sibling groups were pooled, transported to a local fish farm (Carolina Fisheries [CF]; Aurora, North Carolina, USA), and stocked into ponds there for fingerling production and growout to maturity. To avoid inbreeding, mature CF males were crossed with the mature PAFL females to generate the F_2-generation domesticated white bass, which were then reared to maturity in ponds at PAFL (Hopper 1999). The white bass were fed a standard HSB growout diet (Southern States, Inc.; Farmville, North Carolina, USA) according to the feed manufacturer's recommendations based on the average weight of fish subsampled from the ponds at irregular intervals.

Wild white bass used at one commercial hatchery (CF) to produce palmetto HSB were obtained from commercial pound nets in Lake Erie and those used for this purpose at the other hatchery (NSF) were captured by hook and line from impoundments of various tributaries to the Catawba River in North Carolina.

Spawning of Female Striped Bass

The female striped bass were seined from their home pools in mid-April (1998) and subjected to ovarian biopsy under anesthesia to obtain oocytes for staging maturity as described by King et al. (1994ab). All of the fish used in spawning trials had naturally initiated at least the early stages of final oocyte maturation (oocyte stage $\leq$ 14 h; Rees and Harrell 1990) as made evident by coalescence of the lipid droplets in the ooplasm or migration of the oocyte germinal vesicle.

The females were treated with a synthetic analogue of human gonadotropin-releasing hormone (GnRHa) at doses of 50 to 150 µg administered in implanted (i.m.) cholesterol/cellulose pellets (Hodson and Sullivan 1993; Sullivan et al., 1997), tagged for rapid identification with strips of colored yarn tied to their dorsal fins through small punctures, and held individually or in small groups (2-3 fish) in 2-m-diameter circular tanks until ovulation and spawning. Eight of the 27 females required a subsequent injection of human chorionic

gonadotropin (hCG; 330 IU/kg BW) to hasten ovulation (Hodson and Sullivan 1993). All of the females ovulated and were spawned within 48 h after GnRHa implantation.

At spawning, females were stripped of their eggs for *in vitro* fertilization with semen from the F_2-generation domestic male white bass. Aside from the use of GnRHa implants, spawning operations and incubation of fertilized eggs and fry were conducted using standard HSB hatchery procedures (Rees and Harrell 1990).

Spawning of the wild female striped bass was conducted similarly at a private farm (NSF) where the resulting palmetto bass fry were stocked into a fertilized pond for growout.

Spawning of Female White Bass

Approximately 50 of the domesticated (F_2-generation) female white bass were seined from their home ponds in early April and taken into the hatchery where they were held for approximately 1 wk in 2-m-diameter circular tanks supplied with excess fresh well water at 18 C. To induce final maturation and ovulation the fish were injected with hCG at a dosage of 150 IU/kg BW. Approximately 32 h later, the females were stripped of their eggs for *in vitro* fertilization with semen from the F_2-generation striped bass males. The fecundity (range), egg fertility (average) and yield of fry per female (range) were approximately 100-150,000, 50%, and 50-60,000, respectively. Spawning operations and incubation of fertilized eggs and fry were conducted using standard sunshine HSB hatchery procedures (Kohler 1997).

Fingerling Production Trials

Once they had fully developed mouth parts and could commence feeding (4-6 d after hatching), the palmetto HSB fry were transported to the local fish farms (CF, NSF) for stocking into fertilized, outdoor, fingerling production ponds. In general, the ponds were fertilized and zooplankton blooms therein were managed according to the standard procedures (Geiger and Turner 1990). Production of HSB fingerlings in North Carolina is a highly competitive business and the exact details of pond management on the private farms are proprietary and cannot be reported here.

When they were old enough to begin feeding (3-4 d after hatching), the sunshine HSB fry were transported to the local fish farms (CF, NSF) for stocking into fingerling production ponds as described above for palmetto HSB.

Approximately 30-40 d after stocking, the fingerling production ponds were harvested by repeated seining, the fingerlings were transported to rectangular vats for subsampling and enumeration, and the number and percentage return of palmetto or sunshine HSB were recorded (Brewer and Rees 1990; Hodson 1995).

RESULTS

Representative results of spawning trials utilizing the domesticated (F_2-generation) female striped bass and male white bass to produce palmetto HSB fry are shown in Table 1. In several successive spawning trials involving implantation of 27 female striped bass with GnRHa, 96% of the females spawned successfully with an average

Table 1. Production of original-cross hybrid striped bass fry at the NCSU Pamlico Aquaculture Field Laboratory (see Table 1) using domestic (F_2-generation) female striped bass and male white bass parents. GnRH-a was administered in cholesterol/cellulose implants (Hodson and Sullivan 1993).

Trial	Fish (N)	GnRH-a Dose	Oocyte Diameter Mean (SEM)	Number Spawned	Fry Produced Mean (SEM; N[1])
1	4	100 µg	1,082 (38.6) µm	4	163,547 (31,774; 3)
2	8	100 µg	1,036 (14.1) µm	7	96,199 (43,600; 5)
3	6	100 µg	1,050 (22.3) µm	6	243,898 (37,667; 6)
4	9	50 - 150 µg	1,101 (29.3) µm	9	247,699 (40,215; 8)
[1]Fry production not quantified for all females spawned					Average 187,836

Table 2. Pond production of original-cross hybrid striped bass (palmetto HSB) fingerlings (Phase-I; 30-40-d-old) on commercial farms using fry produced at the NCSU Pamlico Aquaculture Field Laboratory (see Table 1) from domestic (F_2-generation) female striped bass and male white bass parents. Results for fry produced from wild broodstock at a private farm (NSF) are shown for comparison. CF=Carolina Fisheries. NSF=North State Fisheries.

Farm Pond	Size (ha)	Stocked (N)	Rate (N/ha)	Harvested (N)	Harvested (%)
Domestic Broodstock					
CF-3	1.21	500,000	413,233	350,000	70
CF-B3	1.62	1,000,000	617,284	500,000	50
CF-B4	1.62	900,000	555,555	400,000	44
NSF-1	1.72	900,000	523,256	600,000	67
					Average 58%
Wild Broodstock					
NSF-3	1.72	1,200,000	697,674	400,000	33

yield of 187,836 4-6-d-old fry/female or 43,480 fry/kg female BW, based on results recorded for 22 of the fish of 4.32 kg average BW.

Table 2 shows results of fingerling production trials utilizing these F_3-generation domesticated palmetto HSB fry on commercial farms to generate Phase I (30-40-d-old) fingerlings with conventional pond culture techniques. Various farm ponds ranging from 1.21 to 1.72 ha in size were stocked with the fry at rates from 413,223 to 617,284 fry/ha, yielding survival rates to fingerling harvest ranging from 44 to 70% with average survival of 58%. The overall yield of Phase I fingerlings was 1,850,000 from the four ponds or 299,838 fingerlings/ha. Comparable results for a commercial 1.72 ha pond stocked with fry produced from a wild female striped bass at a rate of 697,674 fr/ha were 33% survival and 232,558 fingerlings/ha, respectively.

Results of the fingerling production trials utilizing palmetto HSB fry produced from domesticated female striped bass can be compared to those of trials conducted simultaneously on the same farms that utilized sunshine HSB produced from domesticated female white bass and male striped bass (Table 3). Various ponds (0.81-1.72 ha) were stocked with domesticated (F_3-generation), sunshine HSB at rates ranging from 174,419 to 962,963 fry/ha. Those stocked with fry produced from domestic parents yielded

Table 3. Pond production of reciprocal-cross hybrid striped bass (sunshine HSB) fingerlings (Phase-I; 30-40-d-old) on commercial farms using fry produced at the NCSU Pamlico Aquaculture Field from domestic (F_2-generation) female white bass and male striped bass parents. Results for fry produced from wild broodstock at private farms (NSF, CF) are shown for comparison. CF=Carolina Fisheries. NSF=North State Fisheries.

Farm Pond	**Size (ha)**	**Stocked (N)**	**Rate (N/ha)**	**Harvested (N)**	**Harvested (%)**
Domestic Broodstock					
CF-N	1.21	700,000	578,512	150,000	21
CF-N1	1.01	600,000	594,059	220,000	37
CF-M	1.21	700,000	578,512	250,000	36
NSF-2	1.72	1,200,000	697,674	450,000	37
					Average 33%
Wild Broodstock					
CF-M1	0.81	780,000	962,963	200,000	25
CF-N2	0.81	400,000	493,827	200,000	50
NSF-4	1.72	300,000	174,419	100,000	33
NSF-5	1.72	600,000	348,837	330,000	55
					Average 41%

207,767 fingerlings/ha or an average survival rate of 33%. Corresponding values for ponds stocked with fry produced from wild parents were 164,032 fingerlings/ha and 41% survival, respectively. In either case, fingerling yields were less than achieved using palmetto HSB produced from domesticated female striped bass.

DISCUSSION

The results of this study are remarkable in several respects. They represent the first report, of which we are aware, of repeated mass production of palmetto HSB fingerlings from domesticated striped bass on commercial farms. It is clear that yields of fry from the domesticated female striped bass are equivalent to those from fully mature, wild female striped bass captured on or near their spawning grounds (Table 2, bottom). The average yield of 43,480 4-6-d-old fry/kg female BW from the domesticated female striped bass can be compared with average values of 43,260 (range 20,000-60 143) 1-d-old fry/kg (Experiment 4, Hodson and Sullivan 1993) or 67,402 (range 30,000-121 927) 5-d-old fry/kg (Experiment 5, Hodson and Sullivan 1993) obtained for wild fish spawned by the same investigators using similar methods as in the present study.

The equivalency between domesticated and wild striped bass in reproductive performance appears to hold as well in comparisons with wild fish volitionally spawning together to produce striped bass fry, especially if we take into account the expected decrease in fertility due to hybridization and the difficulty in predicting ovulation time of striped bass as required to strip eggs for *in vitro* fertilization to produce HSB (Rees and Harrell 1990). As an example, the average yield of striped bass fry from several wild Roanoke River (North Carolina, USA) females that we induced with GnRHa implants to spawn in tanks in an experiment at Edenton National Fish Hatchery was 57,485 fry/kg female BW (Table 2.6; Sullivan et al. 1997).

Rates of recovery of Phase-I fingerlings from commercial farm ponds stocked with the F_3-generation domesticated HSB fry were outstanding, among the best ever recorded on the two farms (L. Brothers - Carolina Fisheries and H. Griffin III – North State Fisheries, personal communication). Average production of domesticated palmetto HSB for the trials shown in Table 2 was 29,8412 fingerlings/ha. The corresponding value for domesticated sunshine HSB produced in the trials summarized in Table 3 is 202,507 fish/ha. For comparison, a 1986 survey of 12 successful striped bass hatcheries located in the southeastern United States revealed that, during 1984-85, average production of Phase-I fingerlings at these hatcheries was 135,905 fish/ha (Brewer and Rees 1990), although yields of up to 197,680 Phase-I fingerlings/ha have been reported (Fitzmayer et al. 1986).

Review of the data for ponds stocked with progeny produced from wild fish in this study (Tables 2 and 3, bottom) suggest that the extraordinary yield of fingerlings from ponds stocked with domesticated HSB were likely due, in part, to the skill of the farmers involved at creating and maintaining suitable zooplankton blooms as well as the prevalence of favorable weather patterns during Spring of 1998. Nonetheless, results of the fingerling production trials demonstrate unequivocally that domesticated striped bass can be used to produce palmetto HSB fry with survival rates in outdoor ponds equivalent to progeny of wild striped bass and domesticated or wild white bass. Although data could not be obtained from the farmers on growth rates or size-frequency distributions for the Phase-I fingerlings at harvest, they did not report any unusual incidence of stunting and described the fingerlings as 'normal' by comparison to those produced from wild broodfish in prior years.

We attribute the excellent reproductive performance of our domesticated striped bass to several factors. First, the fish have been in captivity for two generations and we have likely benefited from passive domestication (Hallerman 1994). Second, our fish are fed a special diet (CAF-Striped Bass Broodstock Diet "B"; Ziegler Brothers) based on the U.S. Fish & Wildlife Service open formula salmon diet, with the exceptions that squid meal is substituted for fish (herring/menhaden) meal and squid oil replaces up to 25% of the fish oil in order to increase levels

of ω-3 and ω-6 fatty acids that promote larval development and survival (Watanabe 1982). Third, we use multiple well- and surface-water sources to provide the fish with proper thermal conditioning during gonadal maturation (Sullivan et al. 1997). Specifically, we alter flow rates of CastleHayne aquifer well water (~18 C) versus brackish surface (South Creek) water to provide seasonally cycling temperature similar to what the fish would experience in nature (Blythe et al. 1994ab; Clark 1998). Large or abrupt fluctuations in water temperature just prior to and during the spawning season are strictly avoided, as they impair final maturation and ovulation (Sullivan 1997). Fourth, the fish are held at low density in large (6- m diameter) circular pools and, other than activities associated with hatchery spawning, handling is kept to an absolute minimum, being limited to semi-annual census as needed to update inventory records and calculate growth and feeding rates. Handling stress is especially damaging to the health of adult striped bass (Harms et al. 1996) and it is known to disrupt the reproductive neuroendocrine system at multiple levels (Sumpter et al. 1994). Before introduction of these advances in broodstock husbandry the reproductive performance of our striped bass was highly unreliable.

In contrast, our domesticated white bass broodstock were produced and reared in outdoor ponds using the very same methods used for production of HSB foodfish without any special diet, photothermal conditioning, or handling practices (Hopper 1999). The fish were reproduced shortly after being harvested from the ponds. After being held for only 1 wk in hatchery tanks at 18 C, they were injected with hCG and then spawned to produce sunshine HSB for use in the fingerling production trials. Other investigators have made considerable progress on domesticating white bass and reproducing the domestic fish both in- and out-of-season using rearing tanks supplied by recirculating water systems and intensive culture methods (Kohler et al. 1994; Smith et al. 1996; Kohler 1997). However, this is the first report we know of that indicates white bass can be domesticated and reproduced using simple pond rearing techniques, established HSB hatchery procedures, and extensive fingerling production methods. The North Carolina HSB producers have been quick to adopt this approach and at least two commercial hatcheries now maintain domestic white bass and lesser numbers of male striped bass as broodstock in outdoor ponds.

Rearing white bass broodstock outdoors precludes reproducing the fish year-round after maturing them when needed under artificial photothermal cycles (reviewed by Sullivan et al. 1997). However, we have extended the natural spawning season of our domestic white bass by moving selected fish indoors in early spring for coldbanking and delayed spawning up to 3 mo after the normal season, allowing us to triple crop some outdoor, commercial fingerling production ponds (Hopper 1999). Coldbanking refers to the practice of holding spermiating males or females with nearly fully grown oocytes at low temperature (10-12 C) for extended periods before they are warmed to normal spawning temperature for reproduction after the natural season. Because HSB fry stocked into fertilized outdoor ponds, where they feed on natural zooplankton, can be harvested as (Phase-I) fingerlings after only 30 d, those produced from coldbanked parents can be used to restock the ponds two or more times over a single extended spawning season.

Full development of HSB farming to a level comparable to the 'broiler' chicken industry in the United States will require complete control of the reproductive biology of both striped bass and white bass, year-round reproduction of the fish to produce HSB for growout, and selective breeding of both parental lines to improve production efficiency (Harrell et al. 1990; Harrell and Webster 1997). The results of the present study clearly demonstrate that captive breeding and domestication of striped bass are achievable goals and that the domesticated fish can exhibit reproductive performance equal to or better than their wild counterparts. Future research on striped bass reproduction should involve out-of-season spawning of the fish to produce commercially significant quantities of fingerlings, and eventually deliver proven methods for year-round mass production of palmetto HSB.

Our results also show that white bass can be domesticated and utilized as broodstock for

sunshine HSB production using simple pond culture methods. This finding should be especially significant to producers growing HSB in outdoor ponds, a farming practice which presently encompasses about half of the total production of HSB in the United States. Coupled with the coldbanking methods described above, pond production of white bass broodstock will lessen the dependence of growers on wild fish for spawning, decrease fingerling costs, and increase yields of HSB for growout.

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