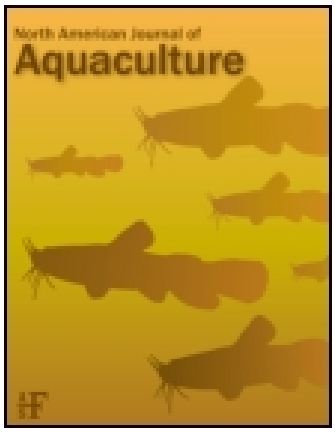

North American Journal of Aquaculture
Publication details, including instructions for authors and subscription information:
http://www.tandfonline.com/loi/unaj20

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Published online: 10 Sep 2014.

To cite this article: J. B. Puritz, M. A. Renshaw, D. Abrego, R. R. Vega & J. R. Gold (2014) Reproductive Variance of Brood Dams and Sires used in Restoration Enhancement of Spotted Seatrout in Texas Bays and Estuaries, North American Journal of Aquaculture, 76:4, 407-414

To link to this article: http://dx.doi.org/10.1080/15222055.2014.920751

North American Journal of Aquaculture 76:407–414, 2014

ISSN: 1522-2055 print / 1548-8454 online
DOI: 10.1080/15222055.2014.920751

ARTICLE

Reproductive Variance of Brood Dams and Sires used in Restoration Enhancement of Spotted Seatrout in Texas Bays and Estuaries

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Abstract

Spawning patterns and reproductive variance of Spotted Seatrout *Cynoscion nebulosus* dams and sires at two restoration enhancement facilities in Texas were assessed across a spawning year by using parentage analysis based on 12 variable microsatellite loci. In total, 72.6% of all dams and sires contributed to at least one spawning event, although in contrasting patterns. Across all spawning events assayed, more sires contributed to each spawn, on average, than did dams; dams had considerably higher variance in reproductive success than sires. Dams alternatively had a higher average contribution to the number of progeny from a single spawn but also a much higher variance in the number of progeny produced per spawn. The variation in the number of progeny produced per dam and per sire and the number of actual mating combinations led to an average reduction of 64.3% in the genetic effective population size (N_e) per spawn relative to the maximum N_e that would be expected if (1) all possible dam × sire mating combinations occurred at random and (2) all families contained an equal number of progeny. Averaged over all spawns, the actual number of mating combinations accounted for approximately 83.6% of the total reduction in N_e, while variation in family size accounted for 16.4% of the total reduction in N_e. Results from this and other studies indicate that reductions in N_e of hatchery- or farm-raised progeny stem primarily from noncontributing dams, suggesting that periodic identification and removal of low-contributing dams from broodfish stocks constitute a critical step toward maximizing the N_e of hatchery offspring used in restoration enhancement.

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Received January 30, 2014; accepted April 18, 2014

The Spotted Seatrout *Cynoscion nebulosus* is one of the most targeted and economically important marine fish species in Gulf of Mexico bays and estuaries and represented the single largest recreational catch during 2011 (NMFS 2012). In Texas, the saltwater recreational fishery comprises about 1.2 million fishers (Vega et al. 2011) and has an annual economic impact of over $\$2 \times 10^9$ (Southwick Associates 2007). Spotted Seatrout and another estuarine-dependent sciaenid, the Red Drum *Sciaenops ocellatus*, account for almost two-thirds of the saltwater "fishing days" in Texas and for over $530 million in total fishing expenditures (USFWS and USCB 2008). Substantial declines in recruitment and abundance of Red Drum led to development of hatchery-based restoration efforts by the Texas Parks and Wildlife Department (TPWD) in the mid-1970s (McEachron et al. 1995, 1998); today, the program releases between 20 and 30 million hatchery-raised Red Drum fingerlings annually into eight different Texas bays and estuaries (Vega et al. 2003, 2011). Evidence for overfishing of Spotted Seatrout, including declines in the mean size of landings and declines in the estimated spawning stock, led TPWD to initiate hatchery-based restoration of Spotted Seatrout in 1993 (Vega et al. 2011).

Production of Spotted Seatrout fingerlings by TPWD takes place at two principal facilities: the Coastal Conservation Association Marine Development Center (MDC) in Corpus Christi and Sea Center Texas (SCT) in Lake Jackson. Details of the two TPWD restoration enhancement hatcheries, including broodfish maintenance, spawning, egg collection, incubation, and larval and juvenile rearing, are provided by Colura et al. (1987) and Vega et al. (1995, 2003). Broodfish are maintained in 13,000-L, circular spawning tanks, with each tank containing 15–20 broodfish. Female Spotted Seatrout typically are larger at age than males (Jensen 2009); therefore, TPWD personnel estimate sex based on fish size and attempt to place approximately 10 dams in each spawning tank. Broodfish are fed shrimp, squid, mackerel, and beef liver and are subjected to a 150-d photoperiod–temperature maturation cycle. Fertilized (buoyant) eggs are collected at the effluent of each spawning tank and are incubated separately for approximately 72 h (under conditions described by Henderson-Arzapalo 1987) before relocation to rearing ponds. Larvae remain in rearing ponds for 30 d or until they reach a target size of 30–35 mm TL. Once the target size is reached, the ponds are drained and the fish are harvested, transferred to mobile distribution tanks, and transported to stocking sites. Adult fish used as broodstock are randomly sampled by angling from the wild; each year, 25% of the broodfish are exchanged with wild fish to maintain genetic diversity.

At present, up to 8 million Spotted Seatrout fingerlings are projected for release annually into five Texas bays or estuaries, and over 52 million fingerlings have been released since Spotted Seatrout restoration efforts began. Restoration enhancement of Spotted Seatrout in U.S. waters also is ongoing in Mississippi and South Carolina (J. Franks, Gulf Coast Research Laboratory, personal communication; T. Darden, South Carolina Department of Natural Resources, personal communication) and is under consideration in Florida (M. Tringali, Florida Fish and Wildlife Research Institute, personal communication).

A continuing challenge to restoration enhancement programs involving hatchery-raised fish is that releases are often produced by a small effective number of breeders—that is, individuals that actually contribute genetically to a release population (Ryman and Laikre 1991). This occurs even when there are several breeders in a spawning tank because not all breeders participate in spawning events and not all mating pairs produce the same number of progeny per mating event. The variance in reproductive success of individual dams and sires and the variance in the number of progeny (family size) produced per mating can lead to a reduction in genetic effective population size (N_e) of released fish, which in turn can lead to a reduction in N_e of the "wild" population (Ryman and Laikre 1991; Tringali and Bert 1998). The latter, termed the Ryman–Laikre effect (Tringali and Bert 1998), can potentially increase the incidence of inbreeding and the accumulation of deleterious genotypes, ultimately leading to a reduction in fitness within the fishery (Frankham 1995; Higgins and Lynch 2001). An additional issue is that in many marine species, including Spotted Seatrout, breeders are not easily sexed, so spawning tanks may contain disproportionate numbers of males and females, thereby also potentially increasing the variance in family size of hatchery releases. The possibility of a Ryman–Laikre effect on supplemented wild populations has been the subject of recent studies (Gold et al. 2008, 2010; Hamasaki et al. 2010; Gruenthal and Drawbridge 2012; Loughnan et al. 2013). Two studies (Gold et al. 2008, 2010) involving Red Drum in TPWD hatcheries demonstrated that (1) not all broodfish participated in spawning events; (2) sires contributed to more spawns, on average, than did dams; and (3) the variance in the number of progeny produced per spawn was greater for dams than for sires. The average N_e for a single spawn of Red Drum was approximately 43% less than the maximum expected N_e, and this decrease in N_e was due to the reduced number of mating combinations and the increased variance in family size (Gold et al. 2008).

We used genotypes at 12 nuclear-encoded microsatellites to assess parentage of progeny from spawning events in eight Spotted Seatrout spawning tanks at the two TPWD restoration enhancement hatcheries. The objectives of the study were to assess the productivity of individual dams and sires over a spawning year and to examine individual broodfish reproductive success and variance in family size, as they might affect the N_e of hatchery-released fish. Because we were able to identify individual mating pairs, the sacrifice or early mortality of only a few of the reproductively active broodfish permitted gender identification for all fish that produced progeny.

METHODS

In total, 164 Spotted Seatrout broodfish maintained in eight 13,000-L spawning tanks (four tanks at the MDC and four tanks at the SCT) were monitored during the study. Each spawning

TABLE 1. Estimates of Spotted Seatrout effective population size (N_e) per spawn based on three scenarios: (A) all possible dam × sire matings occur, and all families contain an equal number of progeny; (B) the observed number of dam × sire matings occurs, and all families contain an equal number of progeny; and (C) the observed number of dam × sire matings occurs, and the size of each family is the same as the observed family size. Tanks were located at the Marine Development Center (MDC) and Sea Center Texas (SCT). All spawns occurred in 2010.

	Scenario				Scenario		
Tank (date)	A	B	C	Tank (date)	A	B	C
MDC 3-1 (May 29)	7.00	6.77	5.83	SCT 3-1 (Aug 31)	14.12	6.00	5.34
MDC 3-1 (Jun 2)	7.00	6.77	5.46	SCT 3-1 (Sep 3)	14.12	6.86	4.69
MDC 3-1 (Jun 6)	7.00	3.67	3.54	SCT 3-1 (Sep 5)	14.12	3.00	2.78
MDC 3-1 (Jun 11)	7.00	3.20	3.05	SCT 3-1 (Sep 8)	14.12	2.67	2.02
MDC 3-1 (Jun 16)	7.00	3.60	3.12	SCT 3-1 (Sep 12)	14.12	6.00	5.58
MDC 3-1 (Jun 17)	7.00	3.67	3.26	SCT 3-1 (Sep 14)	14.12	8.89	5.58
MDC 3-1 (Jun 23)	7.00	6.86	5.29	SCT 3-1 (Sep 18)	14.12	8.00	6.17
MDC 3-1 (Jun 27)	7.00	6.93	5.43	SCT 3-1 (Oct 8)	14.12	4.80	2.89
MDC 3-1 (Jul 2)	7.00	3.50	3.26	SCT 3-1 (Oct 10)	14.12	6.86	6.62
MDC 3-1 (Jul 5)	7.00	3.56	3.43	SCT 3-2 (Jun 19)	21.82	3.33	3.23
MDC 3-2 (May 31)	14.40	3.43	2.92	SCT 3-2 (Jun 23)	21.82	6.00	4.62
MDC 3-2 (Jun 18)	14.40	3.56	3.32	SCT 3-2 (Jun 29)	21.82	3.20	2.81
MDC 3-3 (Jun 25)	14.40	3.56	3.33	SCT 3-2 (Jun 30)	21.82	3.43	3.31
MDC 3-3 (Jun 27)	14.40	3.60	3.37	SCT 3-2 (Jul 8)	21.82	3.33	3.13
MDC 3-3 (Jul 30)	14.40	6.54	5.74	SCT 3-2 (Jul 15)	21.82	3.43	2.45
MDC 3-3 (Jul 31)	14.40	9.00	7.48	SCT 3-2 (Aug 26)	21.82	8.73	7.39
MDC 3-3 (Aug 1)	14.40	6.54	5.64	SCT 3-2 (Aug 29)	21.82	8.00	6.43
MDC 3-3 (Aug 2)	14.40	6.22	3.39	SCT 3-2 (Sep 3)	21.82	10.67	5.59
MDC 3-3 (Aug 7)	14.40	11.08	8.91	SCT 3-2 (Sep 4)	21.82	9.60	6.35
MDC 3-3 (Aug 16)	14.40	6.55	5.27	SCT 3-2 (Sep 11)	21.82	10.91	8.33
MDC 3-3 (Jun 4)	13.75	3.56	3.25	SCT 3-2 (Sep 12)	21.82	3.43	2.94
MDC 3-3 (Jun 25)	13.75	3.50	2.59	SCT 3-2 (Sep 20)	21.82	6.00	2.96
MDC 3-3 (Aug 11)	13.75	6.54	5.93	SCT 3-3 (Aug 31)	8.00	3.00	2.68
MDC 3-3 (Aug 12)	13.75	8.00	4.08	SCT 3-3 (Sep 11)	8.00	2.67	2.03
MDC 3-3 (Aug 14)	13.75	3.56	3.24	SCT 3-3 (Sep 14)	8.00	2.67	2.48
MDC 3-3 (Aug 15)	13.75	6.40	5.32	SCT 3-3 (Sep 27)	8.00	2.00	2.00
MDC 3-3 (Aug 18)	13.75	10.18	7.48	SCT 3-3 (Sep 28)	8.00	2.67	2.66
MDC 3-4 (Jun 23)	15.75	3.43	2.75	SCT 3-3 (Oct 19)	8.00	2.67	2.02
MDC 3-4 (Jul 30)	15.75	8.40	6.88	SCT 3-4 (Jun 12)	8.00	3.00	2.65
MDC 3-4 (Aug 1)	15.75	10.18	7.67	SCT 3-4 (Jun 16)	8.00	3.20	2.90
MDC 3-4 (Aug 4)	15.75	3.33	3.14	SCT 3-4 (Jun 21)	8.00	3.20	2.89
MDC 3-4 (Aug 6)	15.75	3.50	2.99	SCT 3-4 (Jun 23)	8.00	3.20	2.90
MDC 3-4 (Aug 11)	15.75	6.00	5.61	SCT 3-4 (Jun 30)	8.00	6.86	4.94
MDC 3-4 (Aug 12)	15.75	10.67	7.22	SCT 3-4 (Jul 2)	8.00	3.20	2.99
MDC 3-4 (Aug 14)	15.75	10.67	8.87	SCT 3-4 (Sep 4)	8.00	3.20	3.07
MDC 3-4 (Aug 15)	15.75	12.31	7.76	SCT 3-4 (Oct 1)	8.00	3.00	2.60
				SCT 3-4 (Oct 6)	8.00	3.20	3.18
				SCT 3-4 (Oct 29)	8.00	3.20	3.12

tank contained between 10 and 31 broodfish. The average number of broodfish per tank was 20.5 ± 2.19 (mean ± SE). Tissue samples (fin clips) were taken from all broodfish, and each fish was marked with a PIT tag. Approximately 31,000 progeny representing at least 22% of the total year's spawning events for each tank were sampled randomly from each of 6–13 separate spawning events occurring at night between May 29 and October 29, 2010. Spawning dates are described in Table 1 and in Table S.1 (see Supplement in the online version of this paper). Random samples of 96–192 larvae from each spawning event were grown in separate tanks until they reached about 2 mm TL; the larvae were then placed individually into separate

TABLE 2. Total number of Spotted Seatrout broodfish per tank and the numbers of dams and sires that contributed to at least one spawn (i.e., as evidenced from genetic analysis of progeny). Tanks were located at the Marine Development Center (MDC) and Sea Center Texas (SCT).

Tank	Total broodfish	Dams contributing to at least one spawn	Sires contributing to at least one spawn	Noncontributing broodfish (sex unknown)
MDC 3-1	18	2	14	2
MDC 3-2	16	6	9	1
MDC 3-3	23	5	11	7
MDC 3-4	22	7	9	6
SCT 3-1	24	5	12	7
SCT 3-2	31	12	10	9
SCT 3-3	20	3	6	11
SCT 3-4	10	4	4	2

sample tubes and fixed in a 20% DMSO buffer (Seutin et al. 1991) by TPWD personnel. Fin clips obtained from all 164 broodfish also were fixed in the 20% DMSO buffer.

All broodfish and sampled progeny were genotyped at 12 microsatellite loci (*Soc99*, *Soc133*, *Soc407*, *Soc419*, *Soc516*, *Soc532*, *Soc564*, *Soc575*, *Soc566*, *Soc609*, *Soc685*, and *Soc694*). The PCR primers, amplification profiles, and annealing temperatures are described by Renshaw et al. (2012). Amplification products were electrophoresed on 6% polyacrylamide gels and visualized using an Applied Biosystems, Inc. (ABI), Prism 377 sequencer. Analysis of chromatograms and scoring were conducted using GeneScan version 3.1.2 (ABI) and Genotyper version 2.5 (Perkin-Elmer). Assignment of individual progeny from each spawning tank to a specific mating pair (i.e., PIT tag x × PIT tag y) was implemented using the program Probmax version 1.2 (Danzmann 1997). PROBMAX was configured to not allow mismatches at any loci; otherwise, default settings were used. Because spawning occurred in separate tanks and broodfish were not mixed between tanks, the number of possible parental combinations (parental matrices) for each spawning tank was limited; the largest was 12 × 10 for tank SCT 3-2. Once gender was established for all mating pairs (see Results), the N_e of each spawn was estimated using equations detailed by Gold et al. (2008). Statistical analysis was performed using JMP version 10.0 (SAS Institute, Inc., Cary, North Carolina).

RESULTS

Of the 164 broodfish that were monitored at both hatcheries, 119 broodfish contributed to at least one spawning event, as evidenced from genetic analysis of progeny. The percentage of nonspawning fish per tank ranged from 6.25% to 55% and averaged 26.0 ± 5.2% (mean ± SE). The gender of these individuals was not identified. All 164 broodfish and a total of 8,730 progeny were genotyped at the 12 variable microsatellite loci (genotypes are available upon request from J. Puritz). The quality of tissue from fingerlings often prevented full genotyping at all 12 loci; consequently, only progeny that could be assigned unequivocally to a mating pair were used in subsequent analyses (7,087 progeny). We assume that some of the mismatches were due to newly arisen mutations or to scoring errors. Insufficient funds were available to re-genotype these mismatches (~1,600 individuals), particularly given that most could not be scored easily for all 12 microsatellites. A few broodfish that had spawned died during the course of the project, and one or two fish in each tank that had spawned during the year were sacrificed at the end of the project. Identification of gender for these fish allowed unequivocal assignment of gender to all fish that had contributed to a spawn. The number of broodfish in

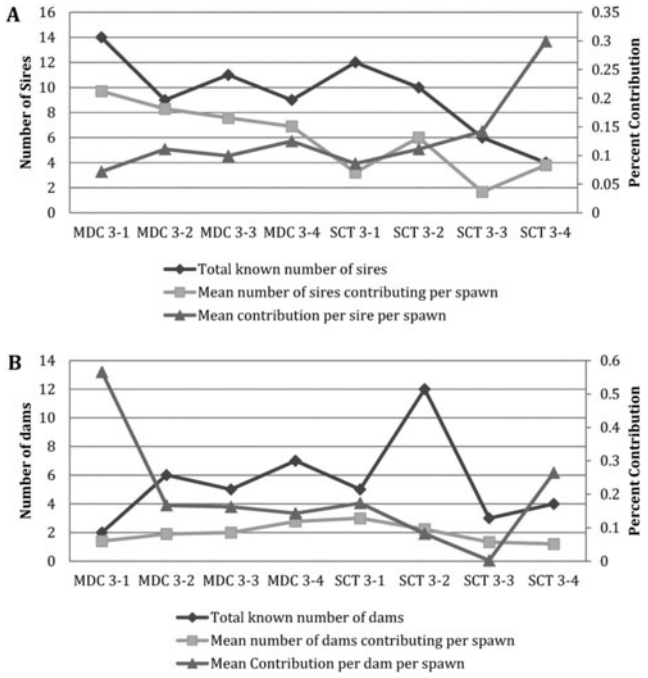

FIGURE 1. Total number of Spotted Seatrout **(A)** dams or **(B)** sires contributing progeny per spawning tank, mean number of dams or sires contributing per spawn, and mean percent contribution (secondary y-axis) per dam or sire per spawn. Tanks were located at the Marine Development Center (MDC) and Sea Center Texas (SCT).

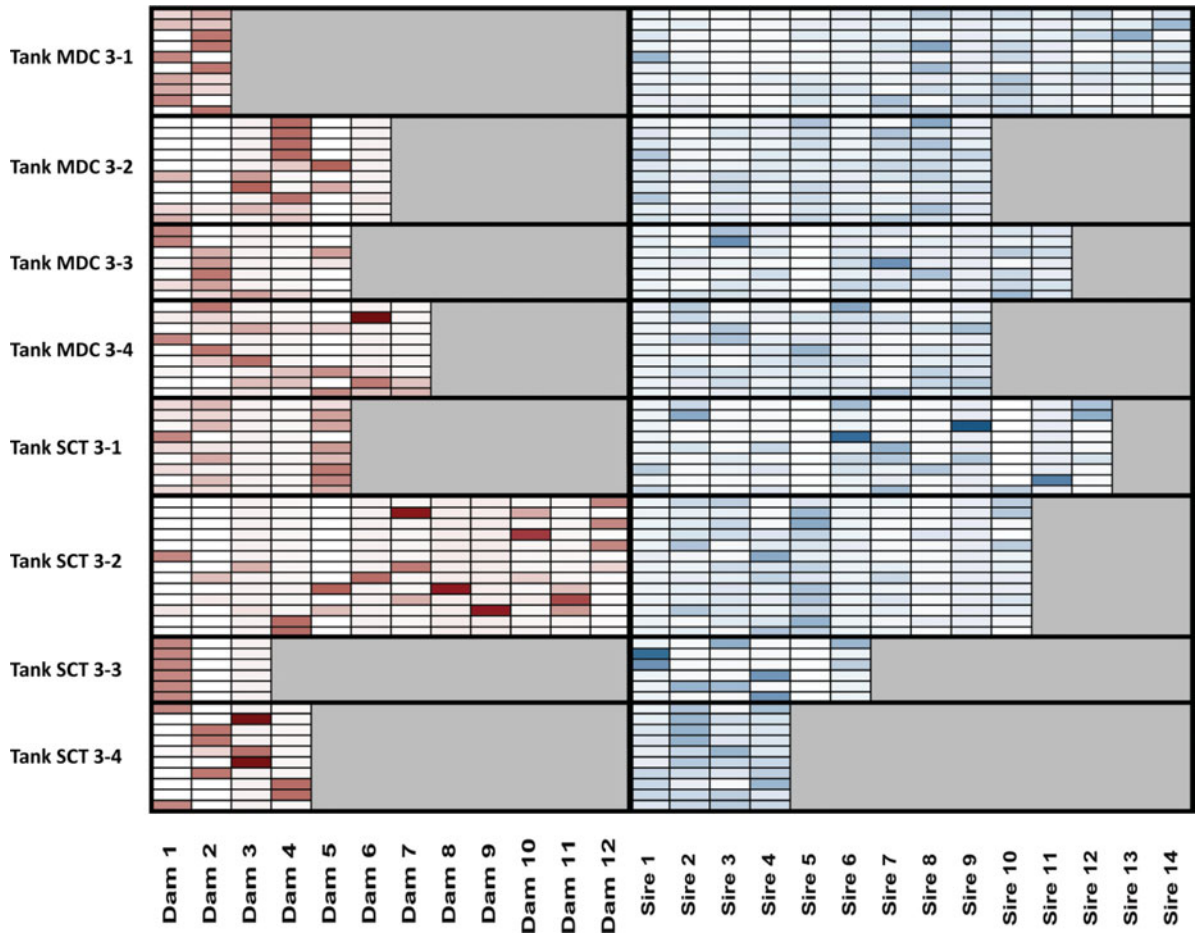

FIGURE 2. Heat map representing the contribution (over the time course of sampling) by each Spotted Seatrout dam and sire to each spawning event in each spawning tank (i.e., as evidenced from genetic analysis of progeny). Each cell represents the percent contribution of the dam (red cells) or sire (blue cells) to each spawning event within each tank. Darker colors in cells represent a greater contribution. Dates of consecutive spawning events in each spawning tank are shown in Table S.1 (online). Tanks were located at the Marine Development Center (MDC) and Sea Center Texas (SCT).

each tank and the number of dams and sires that contributed to at least one spawning event are summarized in Table 2. Summary data for each spawning tank, including the spawning date, the dams and sires contributing to a spawn, and the number of offspring produced from each dam × sire combination, are provided in Table S.1. The total number of dams and sires per spawning tank, the mean number of dams and sires contributing per tank, and the mean contribution per dam or sire per spawn are depicted in Figure 1. The contribution of each dam or sire to each spawning event is shown in Figure 2 (and presented in Table S.1).

Spawning patterns varied between sexes and across tanks. Across both hatcheries, the mean number of contributing dams per tank was 5.5 ± 1.1 (mean ± SE; range = 2–12 dams/tank), and the mean number of contributing sires per tank was 9.4 ± 1.1 (range = 4–14 sires/tank). The mean number of dams contributing to each spawn was 2.0 ± 0.2 and ranged from 1.2 (tank SCT 3-4) to 3.0 (tank SCT 3-1); the number of dams contributing per spawn was correlated with the number of dams in each tank ($r^2 = 0.06$, $P = 0.0343$; linear regression, F-test). The mean number of sires contributing per spawn was 5.9 ± 1.0 and ranged from 1.67 (tank SCT 3-3) to 9.7 (tank MDC 3-1); the number of sires contributing per spawn was highly correlated with the number of sires in each tank ($r^2 = 0.27$, $P < 0.0001$; linear regression, F-test).

The contribution of individual broodfish to all progeny assayed (summed across spawns) from a single tank varied greatly (Figure 3). Overall, 72.5% of the broodfish contributed to at least one spawning event, but spawning patterns varied between sexes and across tanks. Among the broodfish that contributed (i.e., 44 dams and 75 sires), 12 dams (27.3% of 44) and 7 sires (9.3% of 75) contributed to only one spawning event and, on average, contributed only 1% of the total progeny (across all spawning events) surveyed from their respective tanks. Fourteen of the 44 dams contributed less than 5% of the total progeny from their respective tanks, while 3 of the 44 dams contributed over 50% of the progeny; one dam contributed over 99% of the total progeny from tank SCT 3-3. Only two dams (one in tank SCT 3-1 and

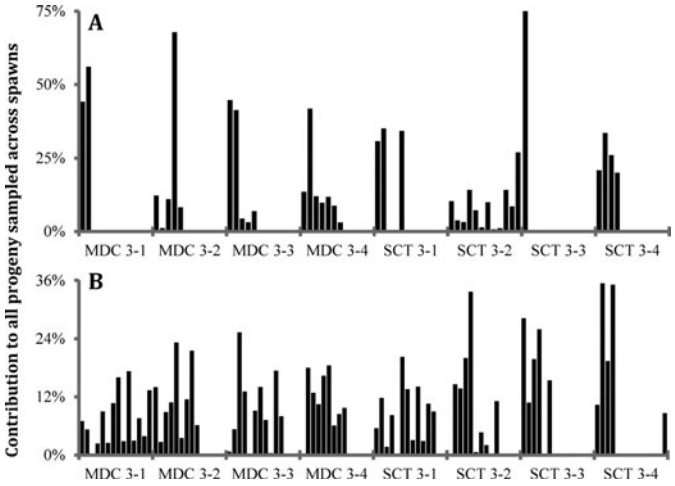

FIGURE 3. Contribution by Spotted Seatrout broodfish to the total number of progeny assayed over the entire spawning season: **(A)** contributions by dams and **(B)** contributions by sires. Each bar represents the percent contribution of an individual broodfish to all progeny sampled from the spawning tank indicated on the *x*-axis. The total number of contributing dams and sires is presented in Table 1. Tanks were located at the Marine Development Center (MDC) and Sea Center Texas (SCT).

one in tank SCT 3-3) contributed to all spawns that occurred in a tank, whereas 12 sires (from different tanks) contributed to all spawns in their respective tanks. The contribution of sires to all progeny (summed across spawns) from a single tank was less variable. Nineteen of the 75 sires contributed less than 5% of the progeny from their respective tanks, 10 sires contributed less than 1% of the progeny in their tanks, and no single sire contributed more than 36% of the progeny in a given tank. Finally, the average contribution (percentage of progeny) of an individual dam to a single spawning event (across all tanks) was 22.6 $\pm$ 1.5%. In contrast, the average contribution of an individual sire to a single spawning event (across all tanks) was lower in both magnitude and variance: 12.2 $\pm$ 0.7%.

Variation in spawning frequency, mating pairs, and progeny contribution of all spawning broodfish led to a decrease in N_e from the expected N_e for each spawning event (Table 1). The maximum expected N_e per spawn across both TPWD facilities, assuming that all possible mating combinations occurred and that the family size per spawning pair was equivalent (scenario A), ranged from 7.0 to 21.8 and averaged 13.39 $\pm$ 0.59 (mean $\pm$ SE). Taking into account the numbers of dams and sires that actually spawned but still assuming an equivalent family size per mating combination (scenario B), the N_e per spawn ranged from 2.00 to 12.31 and averaged 5.44 $\pm$ 0.31. The reduction in N_e per spawn, based on contributing dams and sires (and assuming equivalent family sizes) as compared to the expected maximum (i.e., scenario A versus scenario B), ranged from 1% to 85.3% and averaged 56.4 $\pm$ 2.41% (mean $\pm$ SE). Taking observed family sizes per spawn into account (scenario C) reduced the N_e per spawn even further: N_e per spawn ranged from 2.0 to 8.9 and averaged 4.35 $\pm$ 0.21. The resulting average reduction in N_e per spawn relative to the expected maximum N_e (scenario A versus scenario C) ranged from 16.8% to 88.7%, with a mean of 64.3 $\pm$ 1.87%. Overall, the actual number of mating combinations accounted for approximately 83.6% of the total reduction in N_e per spawn; variation in family size accounted for 16.4% of the total reduction in N_e per spawn.

DISCUSSION

We sought to use microsatellite genotypes to identify the gender of individual broodfish within spawning tanks, to use parentage data to assess productivity of individual dams and sires over a spawning year, and to examine whether broodfish reproductive success potentially reduced the N_e of progeny relative to the theoretical maximum N_e. Our results demonstrated the following: first, across all of the spawning tanks, approximately 27.4% of the fish did not contribute to any of the assayed spawns. Second, sex ratios of broodfish that contributed to at least one spawning event differed from a 1:1 ratio both overall (44 dams and 75 sires contributed to at least one spawn) and within individual spawning tanks (on average, 1.7 more sires than dams contributed to spawns in each tank). Part of this latter difference undoubtedly stems from the greater number of spawning sires per tank. Our results emphasize the difficulty in accurately assigning gender to Spotted Seatrout based on size alone. Whether the observed sex ratio of spawning Spotted Seatrout in TPWD hatcheries is the same as that of spawning fish in the wild is unknown. Sex ratios in wild Spotted Seatrout vary with age, as females grow more rapidly than males (Brown-Peterson et al. 1988; Nieland et al. 2002) and enter the directed fishery earlier than males of the same cohort. However, the sex ratio of fish under the recreational fishery size limit (>15 in or ~380 mm) in Texas bays and estuaries is approximately 1:1 (M. Fisher and J. Tolan, TPWD, personal communication). One suggestion for future work might be to identify the sex of spawning fish by using the approach employed here and then to test spawning productivity of dams and sires under different sex ratios. Third, on average, more sires contributed to single spawns than did dams (6.08 sires versus 2.0 dams). This result is also likely due in part to the greater number of sires than dams in individual spawning tanks. Fourth, dams had considerably higher variance in reproductive success than sires, both in terms of contribution to individual spawns and in terms of contribution over the entire spawning season. Finally, the observed number of mating combinations and the number of progeny produced per combination led to an average reduction of 64.3% in N_e per spawn relative to the maximum N_e that would be expected if all possible dam $\times$ sire mating combinations occurred at random and if all families contained an equal number of progeny. Approximately 83.6% of the total reduction in N_e per spawn was due to fewer mating combinations than expected under random mating, and 16.4% of the reduction was due to variation in family size per combination.

Results from this study are similar to those of prior studies on Red Drum (Gold et al. 2008, 2010): not all broodfish participated in each spawn; sires contributed more, on average, to a spawn than did dams; and dams had considerably higher variance in reproductive success than sires. Perhaps the most critical and comparable result between these prior studies and the present study is the observed reduction in average N_e per spawn. In Red Drum, the average reduction in N_e per spawn over a 2-year period ranged from 43.1% to 45.7%, whereas we found that the average reduction in N_e per spawn was considerably higher for Spotted Seatrout (64.3%). In all three studies, the actual number of mating combinations caused the majority of the observed reduction in N_e (75.6%: Gold et al. 2010; 80%: Gold et al. 2008; 83.6%: present study). Furthermore, in all three studies, a major factor was the higher variance in female reproductive success. Because Red Drum are considerably larger and easier to sex when mature, the typical spawning tank at TPWD hatcheries when the studies by Gold et al. (2008, 2010) were carried out contained three dams and two sires. The typical spawning tank for Spotted Seatrout contains 20.5 fish, on average; of those fish that spawn, the sex ratio per tank is nearly 3 sires : 1 dam. Given the higher variance in productivity for females relative to males of both hatchery Red Drum and Spotted Seatrout, the difference in spawning sex ratio indicates that nonproductive or low-producing dams do have a large effect on reducing the N_e per spawn in Spotted Seatrout. Because the proportion of spawning Red Drum sires was greater than the proportion of spawning dams, Gold et al. (2008) recommended increasing the number of sires to three in each spawning tank as well as monitoring and replacing the noncontributing or low-contributing dams as a strategy to increase the number of mating combinations per spawn. Given the number of low-contributing Spotted Seatrout dams observed in this study, periodic identification (through genetic means) and removal of low-contributing individuals (particularly dams if sex has already been determined) seem to be a reasonable option. The optimal sex ratio for Spotted Seatrout in spawning tanks is a different issue that cannot be addressed with the current data. Increasing the number of sires could potentially increase the N_e per spawn if the proportion of contributing dams remains similar. However, maintaining or even increasing the number of productive dams appears to be a desirable goal given the number of sires that contribute to each spawn.

Almost all of the published studies on the N_e of hatchery- or farm-raised progeny in other broadcast-spawning marine fishes have reported reductions in N_e per spawn, with most such studies documenting a higher variance in dam productivity. These include studies on Murray Cod *Maccullochella peelii* (Rourke et al. 2009), White Seabass *Atractoscion nobilis* (Gruenthal and Drawbridge 2012), and spawned Barramundi Perch *Lates calcarifer* (Loughnan et al. 2013). A large variance in reproductive success also was documented in farmed Gilthead Seabream *Sparus aurata*; however, unlike the other species noted above, the variance in contribution by sires was twice as large as the variance in contribution by dams (Chavanne et al. 2014). The one exception we found was a study of Common Sole *Solea solea* wherein the variance in reproductive success was roughly equivalent between dams and sires (Blonk et al. 2009). Based on our study and most of the above studies, reduction in the N_e of progeny in hatchery- or farm-raised populations appears to be largely due to variance in the reproductive success of broodfish, especially dams.

The average of 2.0 dams and 5.9 sires contributing to a Spotted Seatrout hatchery spawn seems relatively small in comparison with the possible number of spawning adults for this seasonal aggregate-spawning species. Factoring in the number of hatchery offspring that are released each year raises some concern of a Ryman–Laikre effect in wild Spotted Seatrout populations along the coast of Texas. A number of studies have evaluated the population structure of Spotted Seatrout, especially along the Texas coast (King and Pate 1992; Gold and Richardson 1998; Gold et al. 1999, 2003; Ward et al. 2007; Anderson and Karel 2010), but little to nothing is known about the N_e of wild Spotted Seatrout populations. Spawning fish, especially males, aggregate during the spawning season (Baker and Matlock 1993; Helser et al. 1993), and Lowerre-Barbieri et al. (2013) recently reported that the average spawning interval was 2.2 d for male Spotted Seatrout and 9.3 d for females. The mating system in Spotted Seatrout is not well known, but based on the findings of Lowerre-Barbieri et al. (2013), it may approximate lottery polygyny, wherein receptive females randomly encounter males but probably do not have nearly as many opportunities for mating with different partners as do males. If so, this may provide a natural basis for the observed differences in contribution per spawn between dams and sires. In addition, such a mating system also would reduce N_e relative to that expected based on census size and random mating. This emphasizes the need for future studies that directly estimate N_e in wild Spotted Seatrout populations, especially those that might be targeted for restoration enhancement.

ACKNOWLEDGMENTS

We thank S. Bonnot and staff at SCT and R. Chavez and R. Gamez and staff at the MDC for assistance in the spawning and rearing of fish used in the study; A. Hanna for help in the laboratory and with data analysis; and C. Hollenbeck, T. Krabbenhoft, and D. Portnoy for helpful comments on a draft of the manuscript. Work was supported by the Texas Sea Grant Program, the TPWD Coastal Fisheries Division, and Texas AgriLife under Project H-6703. This paper is Number 97 in the series "Genetic Studies in Marine Fishes."

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