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Spawning frequency of brood dams and sires in a marine fish stock-enhancement hatchery

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Parentage analysis, employing five hypervariable microsatellite markers, was used to follow spawning patterns of red drum *Sciaenops ocellatus* broodfish in two spawning tanks through most of a calendar year in a marine fish hatchery dedicated to stock enhancement. Five of six dams and all four sires spawned at least once during the year. Variation in dam and sire spawning incidence and in number of progeny produced per dam and per sire translated into reduced genetic effective size (N_e) per spawn by 40.6% in one tank and 50.8% in the other.

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A number of recent articles (Bell *et al.*, 2006) have emphasized that production of coastal and marine fish needs to increase substantially to meet global demand, particularly as overfishing and habitat degradation (Pauly *et al.*, 2002) continue to deplete global fisheries landings. Marine stock enhancement, where cultured animals are released to increase yield beyond levels supported by natural recruitment, is one of the options available to fisheries managers working to maintain sustainable fisheries (Kitada & Kishino, 2006). As noted in a compendium of papers (Leber *et al.*, 2004) presented at an international conference on stock enhancement and sea ranching, there yet remains considerable work to be done on stock enhancement, especially as regards the effects of hatchery-released individuals on wild populations. Genetic considerations, in particular, pervade many recent discussions regarding interactions between hatchery-raised fishes and their wild counterparts (Utter & Epifanio, 2002; Bert *et al.*, 2007; Kitada *et al.*, 2009), with potential, negative genetic effects ranging from reduction of gene and allelic diversity to genotypic (and phenotypic) modification of wild populations to reduced effective population size (N_e). The last, a reduction in N_e , is often referred to as the Ryman–Laikre effect (Tringali & Bert, 1998) and occurs when a small number of hatchery broodfish contribute disproportionately to the overall ('wild' plus hatchery releases) pool of fishes spawning in the next

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generation, thereby increasing significantly the variance in family size in the overall population (Ryman & Laikre, 1991).

In a previous study, Gold *et al.* (2008) examined the potential for a Ryman–Laikre effect in the stock-enhancement programme for red drum *Sciaenops ocellatus* (L.), carried out by the Texas Parks and Wildlife Department (TPWD). Briefly, the TPWD initiated stock enhancement of *S. ocellatus* in the 1980s in response to substantial declines in abundance and recruitment (McEachron *et al.*, 1995); today, the programme releases between 20 and 30 million hatchery-raised fingerlings annually into eight different Texas bays and estuaries (Vega *et al.*, 2003). Parentage data based on genetic analysis of progeny produced from 13 spawning events occurring over a 2 week period were used by Gold *et al.* (2008) to determine the contribution of each of 27 dams and 18 sires to each spawning event. Genetic analysis revealed that 16 of 27 dams (59.2%) and 16 of 18 sires (88.9%) spawned at least once. The average N_e observed for a single spawn was *c.* 43% less than the maximum N_e predicted if all possible mating (dam \times sire) combinations had occurred and if family size per mating (dam \times sire) combination had been equivalent. Nearly 80% of the reduction in N_e stemmed from the actual number of mating combinations and appeared to be due primarily to non-spawning dams. In this study, parentage data were used to follow >20 spawning events in two TPWD spawning tanks throughout most of a spawning year. The objectives were to assess productivity of individual dams and sires over a longer period of time and to assess further the potential for a Ryman–Laikre effect in the TPWD stock-enhancement programme.

Two spawning tanks (VB 3-1 and VB 3-4) maintained at the TPWD CCA/AEP Marine Development Center (MDC) in Corpus Christi, TX, U.S.A., were used in the study. Each tank contained three dams and two sires, obtained by TPWD personnel from the ‘wild’ *S. ocellatus* population offshore of the south Texas coast. Details regarding the operation of TPWD hatcheries in terms of selection, maintenance and periodic turnover of brood fish, as well as details of husbandry, spawning and collection of fertilized eggs may be found in Gold *et al.* (2008). In this study, from *c.* 15 000 to *c.* 30 000 fertilized (buoyant) eggs were collected from several spawns during the 2006 spawning season and incubated separately for *c.* 72 h. Random samples of 100–110 larvae representing separate spawns were then placed into separate sample tubes and fixed in 95% ethanol. Caudal fin tissues, obtained from all 10 brood fish, also were fixed in 95% ethanol.

Genotypes at five microsatellite loci (*Soc11*, *Soc83*, *Soc99*, *Soc407* and *Soc424*) were used in parentage analysis. PCR primer sequences, optimal annealing temperature and amplification protocols may be found in Saillant *et al.* (2004). Amplification products were electrophoresed on 6% polyacrylamide gels and visualized using an ABI Prism 377 sequencer (Applied Biosystems; <http://www3.appliedbiosystems.com>). Analysis of chromatograms and scoring was conducted using GENESCAN 3.1.2 (Applied Biosystems) and GENOTYPER 2.5 (Perkin Elmer; <http://www.perkinelmer.com>). Assignment of offspring to an individual dam and sire was implemented using the programme PROBMAX v. 1.2 (Danzmann, 1997) available at <http://www.uoguelph.ca/~rdanzman/software/PROBMAX/>. Parentage assignment was unequivocal in all cases. Genetic effective size of each spawn was estimated using equations outlined in Gold *et al.* (2008).

All 10 brood fish (dams and sires) and 2392 offspring from VB 3-1 (26 spawns, 96 offspring per spawn) and 2112 offspring from VB 3-4 (22 spawns, 96 offspring

per spawn) were genotyped at the five microsatellites; genotypes of individual fish may be found at <http://wfsc.tamu.edu/doc/> under the file names 'VB 3-1 genotypes' and 'VB 3-4 genotypes'. Summary data are presented in Tables I (VB 3-1) and II (VB 3-4); data for each spawning tank include date of each spawn, dams and sires contributing to a spawn, and number of offspring produced from each dam \times sire combination. Graphic representations of the contribution of each dam and each sire to each spawn in both tanks are presented in Figs 1 and 2. Five of the six dams and all four sires spawned at least once during the calendar year; no progeny were recovered from dam 2 in VB 3-4.

The pattern of spawning activity differed markedly between the two tanks. On average, each of the 26 spawns in VB 3-1 involved 1.65 (of three) dams and 1.95 (of two) sires, with 3.23 dam \times sire (mating) combinations, whereas each of the 22 spawns in VB 3-4 involved 1.04 (of three) dams and 1.91 (of two) sires, with 2.0 dam \times sire combinations. The spawning frequency of individual dams also differed between the two tanks: in VB 3-1, dam 1 contributed to five spawns (19.2%), dam two to 24 spawns (92.3%) and dam three to 14 spawns (53.8%), whereas in VB 3-4, dam 1 contributed to 20 spawns (90.9%), dam 2 to no spawns (0%) and dam 3 to three spawns (13.6%). The number of spawning dams per spawning event also differed between the two tanks; in VB 3-1, all three dams spawned three times (11.5%), two of three dams spawned 11 times (42.3%) and only one of three dams spawned 12 times (46.2%); whereas in VB 3-4, two dams spawned two times (9.1%), while only one dam spawned 20 times (90.9%). The contribution of sires was more evenly distributed across spawns in both tanks; in VB 3-1, sire 1 contributed to 25 spawns (96.1%) and sire 2 to 24 spawns (92.3%), while in VB 3-4, sire 1 contributed to 22 spawns (90.9%) and sire 2 to 21 spawns (95.4%). In addition, both sires in VB 3-1 spawned 23 times (88.5%), while both sires in VB 3-4 spawned 19 times (86.4%). There was also considerable variation in the number of progeny produced per dam and, to a lesser extent, per sire over the calendar year. In VB 3-1, dam 1 produced 298 progeny (11.9%), dam 2 produced 1648 progeny (66.0%) and dam 3 produced 550 progeny (22.1%), while in VB 3-4, dam 1 produced 1886 progeny (89.3%) while dam 3 produced only 226 progeny (10.7%).

The variation in both dam and sire spawning incidence and in the number of progeny produced per dam and sire translated, as expected, into reduced N_e per spawn. These data are tabulated by spawn in Table III. The maximum (expected) N_e per spawn, assuming that all dam \times sire combinations occurred and that family size per spawning pair followed a Poisson distribution across all spawning pairs, was 4.80 (estimated using equation 1 in Gold *et al.*, 2008). Considering only the number of dams and sires that actually spawned, but still assuming that family size per spawning pair was distributed randomly, N_e per spawn ranged from 2.00 to 4.80 (mean = 3.57) in VB 3-1 and from 2.00 to 4.00 (mean = 2.65) in VB 3-4 (also estimated using equation 1 in Gold *et al.*, 2008). The average reduction in N_e , when compared to the expected maximum N_e of 4.8 and based only on the actual number of spawning dams and sires, was 25.6% (VB 3-1) and 44.8% (VB 3-4). When considering observed family sizes per spawning pair, N_e per spawn ranged from 2.00 to 3.96 (mean = 2.85) in VB 3-1 and from 2.00 to 4.92 (mean = 2.36) in VB 3-4 (estimated using equations 2, 3a and 3b in Gold *et al.*, 2008), resulting in an average reduction in N_e , relative to the expected maximum, of 40.6% (VB 3-1) and 50.8% (VB 3-4). Overall, the proportion of the reduction in N_e due to the

TABLE I. Summary data from 26 spawns occurring in tank VB 3-1. Dates refer to time when progeny were sampled from pre-fertilized ponds. A total of 96 progeny were genotyped from each spawn

Spawn		Dam 1	Dam 2	Dam 3	Sires
Spawn 1 (16/5/06)	Sire 1	0	4	0	4
	Sire 2	0	92	0	92
	Dams	0	96	0	
Spawn 2 (8/6/06)	Sire 1	0	0	0	0
	Sire 2	0	96	0	96
	Dams	0	96	0	
Spawn 3 (15/6/06)	Sire 1	0	0	87	87
	Sire 2	0	0	9	9
	Dams	0	0	96	
Spawn 4 (16/6/06)	Sire 1	0	67	0	67
	Sire 2	0	29	0	29
	Dams	0	96	0	
Spawn 5 (28/6/06)	Sire 1	45	43	5	93
	Sire 2	0	0	3	3
	Dams	45	43	8	
Spawn 6 (29/6/06)	Sire 1	0	54	8	62
	Sire 2	0	20	14	34
	Dams	0	74	22	
Spawn 7 (15/7/06)	Sire 1	0	21	0	21
	Sire 2	0	75	0	75
	Dams	0	96	0	
Spawn 8 (16/7/06)	Sire 1	40	27	13	80
	Sire 2	0	6	10	16
	Dams	40	33	23	
Spawn 9 (17/7/06)	Sire 1	0	50	13	63
	Sire 2	0	11	22	33
	Dams	0	61	35	
Spawn 10 (19/7/06)	Sire 1	0	2	41	43
	Sire 2	0	41	12	53
	Dams	0	43	53	
Spawn 11 (21/7/06)	Sire 1	0	46	9	55
	Sire 2	0	5	36	41
	Dams	0	51	45	
Spawn 12 (3/8/06)	Sire 1	0	96	0	96
	Sire 2	0	0	0	0
	Dams	0	96	0	
Spawn 13 (7/8/06)	Sire 1	0	27	0	27
	Sire 2	0	69	0	69
	Dams	0	96	0	

TABLE I. Continued

Spawn 14 (8/8/06)		Dam 1	Dam 2	Dam 3	Sires
	Sire 1	0	64	0	64
	Sire 2	0	32	0	32
	Dams	0	96	0	
Spawn 15 (9/8/06)		Dam 1	Dam 2	Dam 3	Sires
	Sire 1	0	48	3	51
	Sire 2	0	13	32	43
	Dams	0	61	35	
Spawn 16 (10/8/06)		Dam 1	Dam 2	Dam 3	Sires
	Sire 1	0	1	88	89
	Sire 2	0	2	5	7
	Dams	0	3	93	
Spawn 17 (12/8/06)		Dam 1	Dam 2	Dam 3	Sires
	Sire 1	0	46	0	46
	Sire 2	0	50	0	50
	Dams	0	96	0	
Spawn 18 (13/8/06)		Dam 1	Dam 2	Dam 3	Sires
	Sire 1	15	1	0	16
	Sire 2	60	20	0	80
	Dams	75	21	0	
Spawn 19 (14/8/06)		Dam 1	Dam 2	Dam 3	Sires
	Sire 1	74	0	5	79
	Sire 2	4	0	13	17
	Dams	78	0	18	
Spawn 20 (15/8/06)		Dam 1	Dam 2	Dam 3	Sires
	Sire 1	49	35	1	85
	Sire 2	11	0	0	11
	Dams	60	35	1	
Spawn 21 (25/8/06)		Dam 1	Dam 2	Dam 3	Sires
	Sire 1	0	40	12	52
	Sire 2	0	3	41	44
	Dams	0	43	53	
Spawn 22 (2/9/06)		Dam 1	Dam 2	Dam 3	Sires
	Sire 1	0	26	47	73
	Sire 2	0	3	20	23
	Dams	0	29	67	
Spawn 23 (3/9/06)		Dam 1	Dam 2	Dam 3	Sires
	Sire 1	0	6	0	6
	Sire 2	0	90	0	90
	Dams	0	96	0	
Spawn 24 (7/9/06)		Dam 1	Dam 2	Dam 3	Sires
	Sire 1	0	95	1	96
	Sire 2	0	0	0	0
	Dams	0	95	1	
Spawn 25 (3/10/06)		Dam 1	Dam 2	Dam 3	Sires
	Sire 1	0	79	0	79
	Sire 2	0	19	0	19
	Dams	0	96	0	
Spawn 26 (6/10/06)		Dam 1	Dam 2	Dam 3	Sires
	Sire 1	0	73	0	73
	Sire 2	0	23	0	23
	Dams	0	96	0	

TABLE II. Summary data from 22 spawns occurring in tank VB 3-4. Dates refer to time when progeny were sampled from pre-fertilized ponds. A total of 96 progeny were genotyped from each spawn

Spawn		Dam 1	Dam 2	Dam 3	Sires
Spawn 1 (25/6/06)	Sire 1	0	0	19	19
	Sire 2	0	0	77	77
	Dams	0	0	96	
Spawn 2 (26/6/06)	Sire 1	96	0	0	96
	Sire 2	0	0	0	0
	Dams	96	0	0	
Spawn 3 (2/7/06)	Sire 1	0	0	43	43
	Sire 2	0	0	53	53
	Dams	0	0	96	
Spawn 4 (14/7/06)	Sire 1	51	0	0	51
	Sire 2	45	0	0	45
	Dams	96	0	0	
Spawn 5 (16/7/06)	Sire 1	2	0	0	2
	Sire 2	94	0	0	94
	Dams	96	0	0	
Spawn 6 (19/7/06)	Sire 1	0	0	0	0
	Sire 2	96	0	0	96
	Dams	96	0	0	
Spawn 7 (23/7/06)	Sire 1	93	0	0	93
	Sire 2	3	0	0	3
	Dams	96	0	0	
Spawn 8 (4/8/06)	Sire 1	18	0	0	18
	Sire 2	78	0	0	78
	Dams	96	0	0	
Spawn 9 (5/8/06)	Sire 1	9	0	0	9
	Sire 2	87	0	0	87
	Dams	96	0	0	
Spawn 10 (7/8/06)	Sire 1	12	0	0	12
	Sire 2	84	0	0	84
	Dams	96	0	0	
Spawn 11 (9/8/06)	Sire 1	14	0	2	16
	Sire 2	57	0	23	80
	Dams	71	0	25	
Spawn 12 (11/8/06)	Sire 1	14	0	0	14
	Sire 2	82	0	0	82
	Dams	96	0	0	

TABLE II. Continued

Spawn		Dam 1	Dam 2	Dam 3	Sires
Spawn 13 (13/8/06)	Sire 1	7	0	0	7
	Sire 2	89	0	0	89
	Dams	96	0	0	
Spawn 14 (15/8/06)	Sire 1	35	0	0	35
	Sire 2	61	0	0	61
	Dams	96	0	0	
Spawn 15 (25/8/06)	Sire 1	23	0	0	23
	Sire 2	73	0	0	73
	Dams	96	0	0	
Spawn 16 (1/9/06)	Sire 1	10	0	0	10
	Sire 2	86	0	0	86
	Dams	96	0	0	
Spawn 17 (2/9/06)	Sire 1	28	0	5	33
	Sire 2	59	0	04	63
	Dams	87	0	9	
Spawn 18 (10/9/06)	Sire 1	3	0	0	3
	Sire 2	93	0	0	93
	Dams	96	0	0	
Spawn 19 (25/9/06)	Sire 1	0	0	0	0
	Sire 2	96	0	0	96
	Dams	96	0	0	
Spawn 20 (8/10/06)	Sire 1	1	0	0	1
	Sire 2	95	0	0	95
	Dams	96	0	0	
Spawn 21 (27/10/06)	Sire 1	4	0	0	4
	Sire 2	92	0	0	92
	Dams	96	0	0	
Spawn 22 (14/11/06)	Sire 1	13	0	0	13
	Sire 2	83	0	0	83
	Dams	96	0	0	

actual number of mating combinations *v.* the family size per mating combination was 63.1% *v.* 36.1% (VB 3-1) and 88.2% *v.* 11.8% (VB 3-4).

The objectives of this study were in part to continue to assess the potential for a Ryman–Laikre effect in the TPWD stock-enhancement programme and in part to assess productivity of individual dams and sires over a spawning season rather than the shorter interval of 2 weeks as in the prior study (Gold *et al.*, 2008). Findings of the two studies are in agreement in several respects. First, not all fish in a given tank

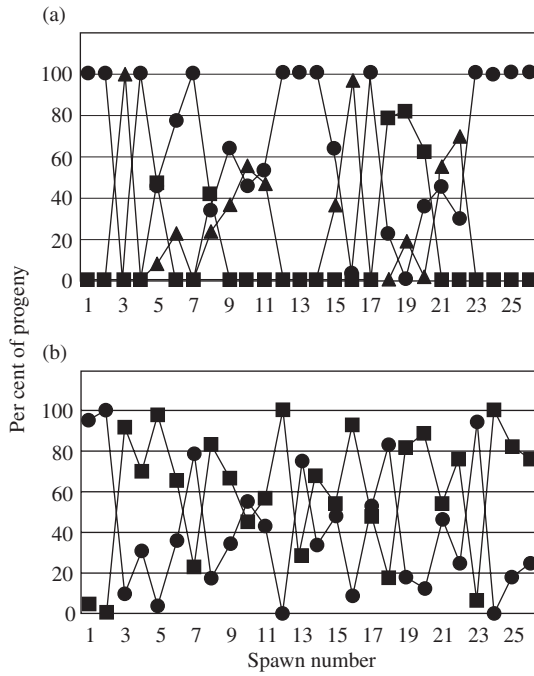


FIG. 1. Contribution to progeny of (a) dams [1 (■), 2 (●) and 3 (▲)] and (b) sires [1 (■) and 2 (●)] by spawn in tank VB 3-1.

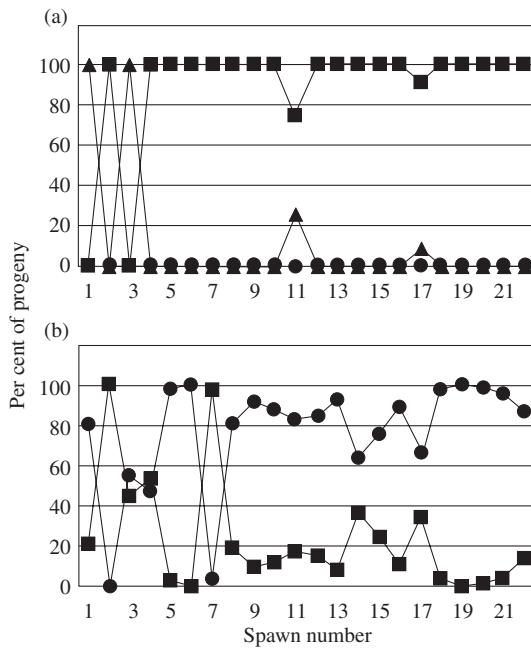


FIG. 2. Contribution to progeny of (a) dams [1 (■), 2 (●) and 3 (▲)] and (b) sires [1 (■) and 2 (●)] by spawn in tank VB 3-4.

TABLE III. Estimates of effective population size (N_e) per spawn based on assuming all possible pair-wise matings occur and that all families contain an equal number of progeny (A), the observed number of pair-wise matings but assuming that all families contain an equal number of progeny (B) and the observed number of pair-wise matings and the observed size of each family (C)

Scenario	Tank VB 3-1			Tank VB 3-4		
	A	B	C	A	B	C
Spawn						
1	4.80	2.70	2.08	4.80	2.70	2.00
2	4.80	2.00	2.00	4.80	2.00	3.92
3	4.80	2.70	2.19	4.80	2.70	2.66
4	4.80	2.70	2.53	4.80	2.70	2.66
5	4.80	4.80	2.93	4.80	2.70	2.04
6	4.80	4.00	3.36	4.80	2.70	2.00
7	4.80	2.70	2.41	4.80	2.70	2.06
8	4.80	4.80	3.67	4.80	2.70	2.36
9	4.80	4.00	3.68	4.80	2.70	2.19
10	4.80	4.00	3.96	4.80	2.70	2.25
11	4.80	4.00	3.95	4.80	4.00	2.99
12	4.80	2.00	2.00	4.80	2.70	2.28
13	4.80	2.70	2.51	4.80	2.70	2.14
14	4.80	2.70	2.57	4.80	2.70	2.60
15	4.80	4.00	3.85	4.80	2.70	2.45
16	4.80	4.00	2.22	4.80	2.70	2.21
17	4.80	2.70	2.66	4.80	2.70	2.90
18	4.80	4.00	2.90	4.80	2.70	2.06
19	4.80	4.00	2.85	4.80	1.00	2.00
20	4.80	4.80	3.03	4.80	2.70	2.02
21	4.80	4.00	3.96	4.80	2.70	2.08
22	4.80	4.00	3.29	4.80	2.70	2.26
23	4.80	2.70	2.12	4.80	—	—
24	4.80	4.00	2.02	—	—	—
25	4.80	2.70	2.34	—	—	—
26	4.80	2.70	2.44	—	—	—
Mean	4.80	3.57	2.85	4.80	2.65	2.36

participate in each spawning event and sires, on average, participate in spawning to a greater extent than dams. In the prior study, each spawn, on average, involved 1.46 (of three) dams and 1.85 (of two) sires, very similar to that observed in VB 3-1 (average of 1.65 of three dams and 1.95 of two sires) when all three dams contributed to at least two spawns. Second, variation in the number of progeny produced per dam was considerable and greater than the variation in the number of progeny produced per sire. Third, the mean N_e per spawn based on both the actual number of dam \times sire combinations and the family size per mating combination was between *c.* 40 and 50% (43.1% in the prior study and 40.6 and 50.8% in VB 3-1 and VB 3-4, respectively, in this study) of that expected if reproductive success was distributed randomly. Finally, the number of actual dam \times sire combinations had a proportionally greater effect on reducing N_e than did variation in family size per spawning pair: *c.* 34 *v.*

c. 9% in the prior study, and 63.1 *v.* 36.1% (VB 3-1) and 88.2 *v.* 11.8% (VB 3-4) in this study. The apparent disparity between the two spawning tanks in the effects of N_e is probably due in large part to the non-spawning dam in VB 3-4.

Results from this study are consistent with results from the prior study, in that effective size per spawn is lower than that expected if reproductive success was distributed randomly among broodfish. The low estimated N_e values (mean 2.85 per spawn in VB 3-1 and 2.36 in VB 3-3) indicate that a Ryman–Laikre effect could occur in Texas bays or estuaries supplemented with hatchery-reared fish, given that recent estimates (Carson *et al.*, 2009) of the long-term effective size of ‘wild’ populations of *S. ocellatus* in four bays and estuaries along the Texas coast ranged from 1302 to 1581. Possible approaches to mitigate this problem in single spawns would be to increase the number of mating combinations per spawn and to equalize the number of progeny generated per mating combination. Of the two, the latter would be difficult to achieve, given the impracticality of genotyping each offspring to determine if multiple mating combinations had occurred and then generating equalized mixes of offspring from each mating combination. The former could be accomplished by increasing the number of brood fish in each spawning tank, although there would be a limit given the size (*c.* 3.66 m in diameter, holding capacity of 12 000 l) of each spawning tank and the average size (1 m in length, 12 kg in mass) of individual *S. ocellatus* dams and sires. Given that the proportion of spawning sires appears greater than the proportion of spawning dams, Gold *et al.* (2008) recommended increasing the number of sires to three in each spawning tank, a practice now employed at TPWD hatcheries.

Gold *et al.* (2008) also raised the question of whether over a spawning season there were dams (or sires) that contributed few or no progeny to a population released for stock enhancement. Results of parentage analysis of spawns from VB 3-4 showed that one dam did not contribute offspring to any of the 22 spawns assayed, and moreover, that another dam contributed only 10.7% of all offspring assayed from VB 3-4 over the calendar year. Whether the low level of dam productivity in VB 3-4 extends to other spawning tanks in TPWD hatcheries is unknown. In the only other published study of this type (as far as is known) Rourke *et al.* (2009) reported even lower levels of broodfish productivity in hatchery spawns of Murray cod *Maccullochella peelii peelii* (Mitchell). In their study, approximately half of the broodfish failed to spawn over a 3 year study period; moreover, the majority of families (38 of 46, 82.6%) resulted from monogamous pairing. The latter was attributed in large part to the suspected monogamous pairing behaviour of *M. p. peelii* in the wild. In the two studies of *S. ocellatus*, the incidence of monogamous pairing is considerably lower, *c.* 15.4% in Gold *et al.* (2008) and 7.7 and 13.6% in VB 3-1 and VB 3-4, respectively (this study). The pairing behaviour of *S. ocellatus* in the wild is not well established and has been assumed to approximate lottery polygyny (Turner *et al.*, 2002), a mating system not inconsistent with the observation that in TPWD hatcheries sires contribute, on average, more to single spawns than do dams. Periodic monitoring and replacing might be a strategy to at least reduce the incidence of non- or low-contributing dams and to marginally increase the number of mating combinations per spawn, thereby potentially increasing the effective size of individual spawns.

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