

# Subspecies Composition of Angled and Electrofished Largemouth Bass in Texas Reservoirs

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**Abstract:** Studies assessing whether there are differences in angling susceptibility between northern largemouth bass *Micropterus salmoides salmoides* (NLMB) and Florida largemouth bass *M. s. floridanus*, (FLMB) have typically been conducted at small study sites and have produced inconsistent results. Thus it is unclear how these results translate to natural populations, particularly those in large bodies of water. We evaluated the genetic composition (seven microsatellite loci) of angled and electrofished collections of LMB from five Texas reservoirs and related these results to angling susceptibility between these subspecies. In the angled collections, a single reservoir exhibited lower FLMB influence (proportion of FLMB alleles) than was found in the electrofished collection (Pinkston,  $P < 0.001$ ). Two populations had fewer non-introgressed FLMB in the angled sample than in the electrofished sample (Pinkston and O. H. Ivie;  $P = 0.010$  and  $0.030$ , respectively). The results were highly dependent on the number of non-introgressed FLMB in the population and, when interpreted in the context of introgression within each reservoir, suggested that non-introgressed FLMB may be more difficult to angle than non-introgressed NLMB and their hybrids. However, the phenotype of reduced angler susceptibility was mitigated by introgression.

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**Key words:** largemouth bass, bass hybrids, angler success

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Numerous studies have attempted to address whether differential angling susceptibility exists between the two subspecies of largemouth bass (LMB), northern largemouth bass *Micropterus salmoides salmoides* (NLMB) and Florida largemouth bass *M. s. floridanus* (FLMB). While most authors found evidence that NLMB were more vulnerable to angling than FLMB (Johnson 1975, Zolczynski and Davies 1976, Bottroff and Lembeck 1978, Rieger et al. 1978, Kleinsasser et al. 1990, Farquhar 2007), a few found no difference (Inman et al. 1977, Wright and Wigtil 1981). Variation in these findings may be due to the source populations or study sites used in each comparison (Philipp et al. 2009) and the differential effect of environmental variables on angling susceptibility for these fish (Maceina et al. 1992). Also, genetic markers were rarely used in these studies, and study populations may have been introgressed, given that collection locations were commonly within the hybrid zone between the two subspecies (Philipp et al. 1983, Barthel et al. 2010, Texas Parks and Wildlife Department unpublished data). Additionally, if few genetic markers are used to differentiate the subspecies, low levels of introgression within individuals may be missed (Williamson and Carmichael 1986, Kleinsasser et al. 1990). While the presence of introgression is not necessarily a flaw in a study evaluating differences in angling susceptibility, the results may be misinterpreted if this possibility is not taken into account, and larger marker panels are now available allowing introgression to be evaluated within individuals (Lutz-Carrillo et al. 2006, Barthel et al. 2010) as well as populations (Philipp et al. 1983).

Small experimental ponds (<0.5 ha) have been the site of most evaluations of angling susceptibility. The densities of fish within these study sites is typically greater than what would be observed in a lake or reservoir (Philipp 1991), temperatures fluctuate over a greater range (Maceina et al. 1992), and the FLMB has been noted to be more skittish in these environments than NLMB or their crosses (Kleinsasser et al. 1990). In addition, most of the studies in small impoundments have examined the relative angling susceptibility of non-introgressed NLMB and FLMB in the same environment. In Texas, this scenario is rarely observed in large water bodies where most angling effort occurs. Genetic surveys of Texas reservoirs (TPWD, unpublished data) indicate that non-introgressed NLMB and FLMB comprise a relatively small portion of the general LMB population. Most individuals are hybrids, and when one subspecies does exist in a non-introgressed state, at any appreciable frequency, it usually does so at the expense of the other. The general observation that these subspecies tend to behave differently in small ponds (reviewed by Maceina et al. 1992), as well as the differences in genetic composition between populations in the wild and at study sites, makes it unclear how the results from small study sites translate to larger water bodies.

Largemouth bass have been stocked in Texas water bodies for more than a century. In the late 1800s, Texas waters were stocked with non-introgressed NLMB from Virginia, Illinois, and Missouri, and locally procured brood stock have been used to produce fingerlings since 1940 (Forshage and Fries 1995). The Texas Parks

and Wildlife Department (TPWD) has also introduced non-introgressed FLMB to Texas waters since 1972, and non-introgressed FLMB has been the primary production fish in hatcheries since 1975. Through 1993, 66 million were stocked into 454 different Texas reservoirs (Forshage and Fries 1995). These stockings have increased as hatchery production has become more efficient and, in the last decade, over 70 million non-introgressed FLMB were stocked into Texas reservoirs (TPWD unpublished data). Thus, contemporary populations in Texas reservoirs consist of NLMB, FLMB, and multiple generations of their hybrids.

The objective of this study was to determine the subspecies composition of angled and electrofished largemouth bass in Texas reservoirs and to relate these findings to the angling susceptibility of these subspecies and their hybrids. Maceina et al. (1992) noted that inconsistent results comparing the two largemouth bass subspecies have been due not only to problems of identification but also to the size of water bodies used to conduct the experiments. With the criticisms of earlier studies in mind, individual fish were taxonomically assigned using multilocus genotypes, and all collections were performed in reservoir environments. The reservoirs sampled were chosen as representative of the range of levels of introgression observed in Texas reservoirs as well as reservoirs frequented by anglers.

**Methods**

Five reservoirs, Kurth, Leon, Canyon, O.H. Ivie, and Pinkston, were selected for this study using data from statewide genetic monitoring surveys that suggested a wide range of introgression levels (TPWD, unpublished data). The reservoirs ranged in size from 181 ha (Pinkston) to 7,749 ha (O.H. Ivie) (Table 1) and represented a variety of stocking strategies, with some receiving multiple stockings and others being stocked only once (Table 2).

Largemouth bass were collected by electrofishings and angling. Angling took place during the day from February through May 2007 in Leon Reservoir and Kurth Reservoir and from February through May 2008 in Canyon, O.H. Ivie, and Pinkston reservoirs (Table 1). Angling occurred from February to May, corresponding to the season with the highest angling effort for bass typically observed in Texas reservoirs (De Jesus and Magnelia 2009). Angling was conducted over multiple days by volunteer anglers and TPWD personnel fishing a variety of artificial lures. Target sample size for angling in each reservoir was 50 small adult bass (254 mm to 355 mm) and 50 large adult bass (>355 mm) to ensure that a wide size range was collected. Length distributions from angling and electrofishing samples in each reservoir were compared with a Kolmogorov-Smirnov test. Specific angling locations were determined by individual angler preference, but angling effort was distributed over a broad area of each reservoir.

**Table 1.** Reservoir size, FLMB influence (proportion of FLMB alleles; TPWD unpublished data), and approximate sampling times for data collection in the study.

Reservoir	Size (ha)	FLMB influence (proportion)	Sampling time frame	
			Electrofishing	Angling
Canyon	3,362	0.72	October–November	February–May
Leon	644	0.28	October–November	February–May
Kurth	294	0.37	March	February–May
O. H. Ivie	7,749	0.76	October–November	February–May
Pinkston	181	0.85	October–November	February–May

**Table 2.** Number of stocked (x1000) northern largemouth bass (NLMB) and Florida largemouth bass (FLMB) for each reservoir over time.

Reservoir	Subspecies	1965–1974	1975–1984	1985–1989	1990–1994	1995–1999	2000–2007
Canyon	NLMB	0	0	30	0	0	0
	FLMB	0	0	34	0	0	0
Leon	NLMB	196	0	0	0	0	0
	FLMB	0	161	76	80	0	0
Kurth	NLMB	0	0	0	0	0	0
	FLMB	0	32	0	42	40	71
O. H. Ivie	NLMB	0	0	0	0	0	0
	FLMB	0	0	4	2,416	31	0
Pinkston	NLMB	0	0	0	0	0	0
	FLMB	0	85	0	0	0	11

Electrofishing was conducted using Smith Root 5.0 or 7.5 GPP units on a boat, boom-mounted with two umbrella, four-anode arrays. Electrofishing occurred at night when surface water temperatures were 18–24 C, according to TPWD standard protocols. Reservoirs were sampled during the fall except for Kurth Reservoir, which was sampled in spring due to extensive hydrilla (*Hydrilla verticillata*) coverage during fall that prevented efficient sampling (Table 1). Each reservoir was sampled at 12–24 sites randomly selected with ArcView’s Random Point Generator extension (Version 1.3) or Minnesota’s Department of Natural Resources Random Sampling Tools extension (MDNR 2005). Electrofishing at each site was continuous for 5 min along the shoreline at night. Every adult bass (>254 mm) collected with electrofishing or angling gear was measured to the nearest mm and a pectoral fin clip was preserved in 70% non-denatured ethanol for subsequent genetic analyses.

Following a modified version of the methods of Crouse and Amorese (1987) and Miller et al. (1988), genomic DNA was isolated from a portion of each fin clip. Recovered DNA was quantified by spectrophotometry (NanoDrop 2000, Thermo Scientific) and adjusted to 50 ng/μL with a low Tris-EDTA buffer (10 mM Tris, 1 mM EDTA, pH 8.0). Alleles at seven microsatellite loci, previously used for the discrimination of largemouth bass subspecies (*Lma12*,

*Msal21*, *Mdo3*, *Mdo6*, *Mdo7*, *Msal13*, and *Msa29*; Lutz-Carrillo et al. 2006, Littrell et al. 2007, Barthel et al. 2010), were then amplified from each sample. Amplicons were imaged by fluorescence, alongside LI-COR 50–350 size standards, on a NEN 4300 DNA sequencer (LI-COR, Lincoln, Nebraska) with sizes resolved using BioNumerics version 6.0 (Applied Maths, Belgium).

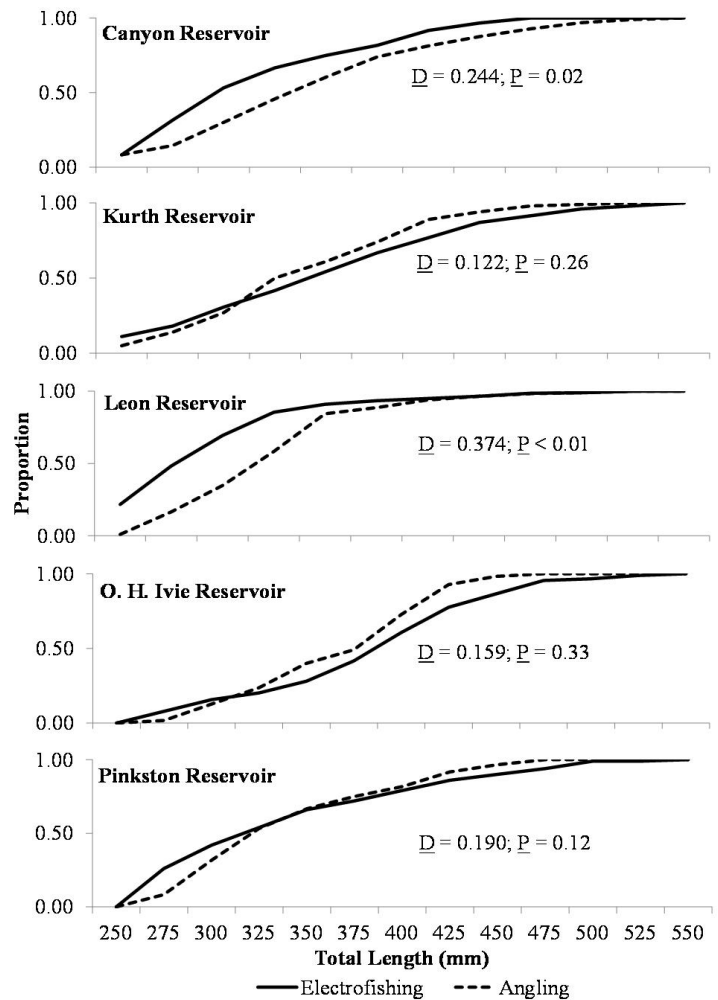
The software STRUCTURE (version 2.3.3, Pritchard et al. 2000) was used to estimate the FLMB influence (proportion of FLMB alleles) of individuals from each collection. STRUCTURE implements a Bayesian clustering algorithm to partition multilocus genotypes into (*K*) groups while minimizing within group departures from Hardy-Weinberg and linkage equilibrium. Using reference samples of NLMB from Kickapoo Reservoir, Texas ( $n=90$ ), and FLMB from Lakes Okeechobee ( $n=30$ ), Down ( $n=30$ ), and Washington ( $n=30$ ), Florida, each fish collected for this study was assigned to a group, or more than one group, based upon its multilocus genotype (admixture model,  $10^4$  burn-in steps,  $10^5$  Markov-chain Monte Carlo iterations, 10 replicate runs,  $K=2$ ). Lake Kickapoo was chosen as an appropriate reference population based on annual genetic monitoring over the last decade (using allozymes and then microsatellites), exhibiting no signs of introgression (TPWD, unpublished data). It was also assumed that NLMB within Lake Kickapoo would be more similar to NLMB in Texas Reservoirs than NLMB collected at distant geographic locales. Coefficients of group membership ( $q$ ; averaged over all replicates) were then used as approximations of the FLMB influence (proportion of FLMB alleles) in each individual. No *a priori* information about sampling locales was included, allowing all assignments to be made based solely on the genetic data. Individuals with  $q$ -values  $>0.05$  to more than one group were considered introgressed. Individuals with  $q$ -values of  $\leq 0.05$  and  $\geq 0.95$  were considered non-introgressed NLMB and FLMB, respectively. STRUCTURE runs including simulated multilocus genotypes ( $n=100$  each of an  $F_1$  generation between the two subspecies and a backcross to each parental subspecies; HYBRIDLAB, version 1.0; Nielsen et al. 2006) indicated that a threshold  $q$ -value of 0.05 resulted in 4.7% of reference samples misclassified as introgressed and 5.0% of simulated backcrosses misclassified as non-introgressed.

Data were classified two ways for analysis: 1) by FLMB influence ( $q$ ; the proportion of alleles derived from FLMB), by individual and group, and 2) by the proportion of fish within a group that exhibited a specified level of FLMB influence. Within reservoirs, estimates of mean FLMB influence in angled and electrofished collections were compared using a Mann-Whitney rank sum test (SYSTAT 11, Systat Software Inc., Point Richmond, California). Assuming that FLMB influence was negatively correlated with angling susceptibility, each test was one-tailed. Additionally,

within reservoirs, the proportion of non-introgressed NLMB and FLMB and the proportion of fish with low and high FLMB influence ( $q \leq 0.20$  and  $q \geq 0.80$ , respectively) were compared between angled and electrofished collections using one-tailed evaluations of the equality of two proportions (SYSTAT 11). A Fisher's exact test was used when cell counts were less than five. Equivalent analyses were performed after removing non-introgressed NLMB and FLMB, comparing only introgressed samples. Significance was determined at  $\alpha=0.05$  in all cases.

## Results

Length frequency distributions of fish angled and electrofished were similar in three reservoirs (Kurth, O. H. Ivie, and Pinkston) and significantly different in Leon and Canyon (275–325 mm fish were caught in higher proportion with electrofishing gear) (Figure 1).



**Figure 1.** Cumulative length frequency of largemouth bass caught by electrofishing and angling in five Texas reservoirs. The K-S test statistic ( $D$ ) and its corresponding  $P$  value are provided.

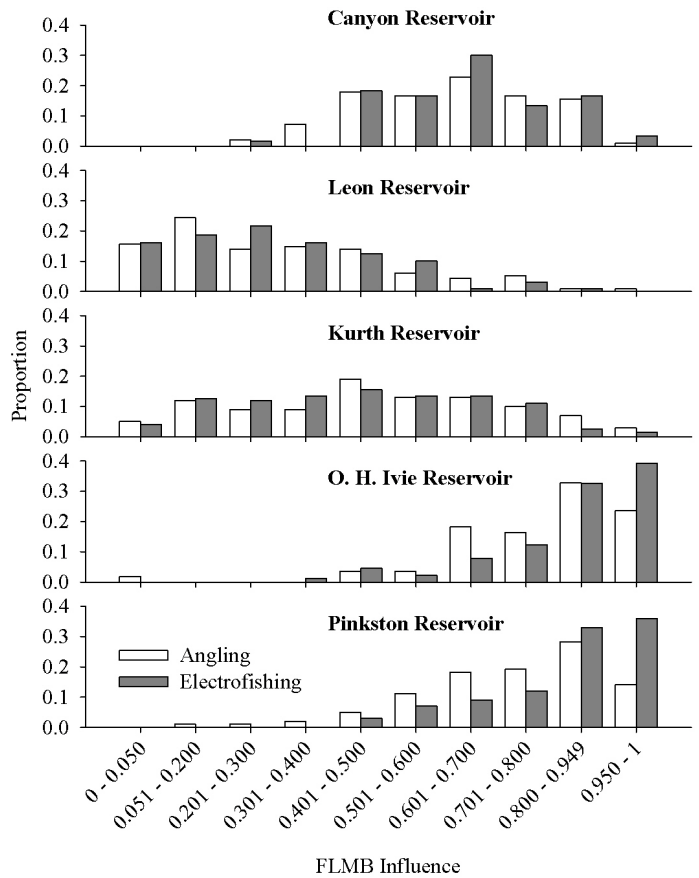
**Table 3.** Site, collection method, sample size, and number of non-introgressed NLMB, non-introgressed FLMB, and hybrids, mean FLMB influence (proportion of FLMB alleles), and the proportion of samples with specified levels of FLMB influence for each collection method and each reservoir. Asterisk (\*) denotes a significant difference between electrofished and angled samples within a reservoir ( $P < 0.05$ ).

Reservoir	Method	Sample size	NLMB	FLMB	Hybrids	FLMB influence (SE)	Proportion of sample at level of FLMB influence					
							$\geq 0.95$	$\geq 0.80$	$\geq 0.80^a$	$\leq 0.20$	$< 0.20^b$	$\leq 0.05$
Canyon	A	96	0	1	95	0.63(0.02)	0.01	0.18	0.16	0.00	0.00	0.00
	E	60	0	2	58	0.65(0.02)	0.03	0.20	0.17	0.00	0.00	0.00
Leon	A	115	18	1	96	0.29(0.02)	0.01	0.02	0.01	0.40	0.29	0.16
	E	199	32	0	167	0.29(0.01)	0.00	0.01	0.01	0.35	0.22	0.16
Kurth	A	100	5	3	92	0.48(0.02)	0.03	0.10*	0.07	0.17	0.13	0.05
	E	199	8	4	187	0.45(0.02)	0.02	0.04*	0.03	0.17	0.13	0.04
O.H. Ivie	A	55	0	13	42	0.81(0.02)	0.24*	0.56*	0.33	0.02	0.02	0.00
	E	89	0	35	54	0.85(0.02)	0.39*	0.73*	0.33	0.00	0.00	0.00
Pinkston	A	99	0	14	85	0.75 (0.02)*	0.14*	0.42*	0.28	0.01	0.01	0.00
	E	100	0	36	64	0.85 (0.02)*	0.36*	0.70*	0.33	0.00	0.00	0.00

a. Proportion of sample with FLMB influence  $\geq 0.80$  excluding FLMB ( $\geq 0.95$ ).  
 b. Proportion of sample with FLMB influence  $\leq 0.20$  excluding NLMB ( $\leq 0.05$ ).

Among samples, mean FLMB influence ranged from 0.29 (SD 0.22) (Leon-angled) to 0.85 (SD 0.15 and 0.16) (Pinkston and O. H. Ivie-electrofished, respectively) (Table 3). Individual and specific FLMB influence ranged from as wide as 0.00 to 0.98 (Kurth—angled), to as narrow as 0.40 to 0.99 (O. H. Ivie—electrofished) (Figure 2). The proportion of non-introgressed NLMB ( $q \leq 0.05$ ) from specific samples ranged from 0 (Canyon, O. H. Ivie, Pinkston—angled and electrofished) to 0.16 (Leon—angled and electrofished). The proportion of non-introgressed FLMB ( $q \geq 0.95$ ) from specific samples ranged from 0 (Leon—electrofished) to 0.39 (O. H. Ivie—electrofished). The proportion of individuals with low FLMB influence ( $q \leq 0.20$ ) ranged from 0 (Canyon—angled and electrofished; O. H. Ivie—electrofished; Pinkston—electrofished) to 0.29 (Leon—angled). The proportion of individuals with high FLMB influence ( $q \geq 0.80$ ) ranged from 0.01 (Leon—electrofished) to 0.73 (O. H. Ivie—electrofished). Between gear types mean FLMB influence was similar in four of five reservoirs (Canyon:  $U = 4608$ ,  $P = 0.50$ ; Kurth:  $U = 9212$ ,  $P = 0.15$ ; Leon:  $U = 11396$ ,  $P = 0.48$ ; O. H. Ivie:  $U = 2215$ ,  $P = 0.17$ ) (Table 3). In Pinkston Reservoir mean FLMB influence was greater for electrofished than angled samples ( $U = 3429$ ;  $P < 0.01$ ) (Table 3).

In two of five reservoirs the proportion of non-introgressed FLMB was greater in electrofished than angled samples (Pinkston Reservoir:  $\chi^2 = 12.64$ ;  $P < 0.01$ ; O. H. Ivie Reservoir:  $\chi^2 = 3.76$ ;  $P = 0.03$ ) (Table 3). Both of these reservoirs also had significantly greater proportions of individuals with high FLMB influence ( $q \geq 0.80$ ) in electrofished than angled samples (Pinkston:  $\chi^2 = 15.37$ ;  $P < 0.01$ ) (O. H. Ivie:  $\chi^2 = 4.25$ ;  $P = 0.02$ ). When non-introgressed FLMB were removed from the analyses, the significant difference in proportion of fish with high FLMB influence between gear types was amelio-



**Figure 2.** Proportion of individuals with specified levels of FLMB influence (proportion of FLMB alleles) in angled and electrofished collections from five Texas reservoirs.



rated in both reservoirs (O. H. Ivie:  $\chi^2=0.00$ ;  $P=0.49$ ; Pinkston:  $\chi^2=0.52$ ;  $P=0.24$ ). In contrast, Kurth Reservoir had a significantly greater proportion of individuals with high FLMB influence in angled than electrofished samples ( $\chi^2=4.21$ ;  $P=0.02$ ) (Table 3). However, this difference dissipated when non-introgressed FLMB were removed from the comparison ( $\chi^2=2.54$ ;  $P=0.06$ ) (Table 3). The proportion of non-introgressed NLMB and fish with low FLMB influence ( $q \leq 0.20$ ) in Leon ( $\chi^2=0.01$  and  $0.73$ ;  $P=0.46$  and  $0.20$ , respectively) and Kurth ( $\chi^2=0.15$  and  $0.00$ ;  $P=0.35$  and  $0.49$ , respectively) were nearly identical in angled and electrofished samples (Table 3). Canyon Reservoir had no non-introgressed NLMB or fish with low FLMB in either gear type, and one fish with low FLMB influence was collected with angling in O. H. Ivie and Pinkston reservoirs, but the difference between gear types was insignificant (Fisher's exact test;  $P=0.38$  and  $0.50$ , respectively) (Table 3).

## Discussion

Overall, most of the fish collected were resolved as hybrids between the two subspecies. Non-introgressed LMB were only recovered in substantial numbers ( $\geq 10\%$  of the angled or electrofished collection) in three populations (NLMB in Leon and FLMB in Pinkston and O. H. Ivie). In Pinkston and O. H. Ivie, FLMB were electrofished at significantly greater rates than they were angled. In Leon, there was no significant difference in proportion of non-introgressed NLMB collected by gear type. Assuming electrofished collections are a reflection of the true composition of the population these results suggest that FLMB were more difficult to angle than expected based on their frequency in the population and that NLMB were angled at expected rates. Thus, in a scenario where both subspecies exist in equal proportions, we would expect FLMB to be more difficult to angle relative to NLMB. The failure to find significant differences between gear types in the proportions of FLMB collected in every reservoir appeared to simply be due to the low proportions of FLMB in some populations.

In two reservoirs (O. H. Ivie and Pinkston) individuals with high levels of FLMB influence (hybrids and non-introgressed FLMB) were collected at significantly greater rates by electrofishing than angling. However, when FLMB were removed from the dataset (leaving only hybrids with high levels of FLMB influence) these differences between gear types disappeared. This suggests that the initial differences between gear types using the entire dataset was skewed by the disproportionate number of FLMB collected by electrofishing and that hybrids, even with high levels of FLMB influence, were collected at expected rates. Therefore, if FLMB and hybrids with high FLMB influence were present in equal proportions, we would expect FLMB to be more difficult to angle. In a scenario where all groups (FLMB, NLMB, hybrids with high and

low levels of FLMB influence) are equally represented in a Texas reservoir, we would expect FLMB to be relatively more difficult to angle, and for all other groups to be angled at equivalent rates.

These results underscore the importance of identifying introgression in studies of angling susceptibility in LMB. While the level of introgression within hybrids did not appear to affect angling susceptibility, the incidence of introgression did, but only when it occurred in the genetic background of the FLMB. Thus, in a study of angling susceptibility, if undetected introgression exists in the FLMB stock (even at low levels) the conclusion may be that they are angled at rates equivalent to NLMB. As Philipp et al. (2009) noted, studies that failed to resolve differences in angling susceptibility between non-introgressed NLMB, non-introgressed FLMB, or their hybrids may have failed due to low levels of undetected introgression in the study populations.

Trophy fish ( $\geq 5.9$  kg) from introgressed populations are represented disproportionately as non-introgressed FLMB relative to the frequency of FLMB in the general population (Lutz-Carrillo et al 2006, TPWD, unpublished data). Thus, in an appropriate environment, genetic composition appears to be a critical component of maximum size in largemouth bass. While most of the differences in growth and maximum size between these subspecies are likely due to intrinsic physiological differences, behavioral differences, such as reduced angling susceptibility, may also play a role. Non-introgressed FLMB that are potentially less susceptible to angling would be removed from populations at reduced rates relative to non-introgressed NLMB or hybrids, allowing a greater proportion of FLMB to reach an older age and greater size. In addition, given the prevalence of catch and release practices, FLMB would be less likely to experience the stress of catch and release events relative to cohabitant non-introgressed NLMB or hybrids, stress events that could reduce growth rates and their potential maximum size (Williamson and Carmichael 1986, Peterson and Brown-Peterson 1992, Waters et al. 2005, O'Conner et al. 2011).

Evaluating differences among non-introgressed NLMB, non-introgressed FLMB, and their hybrids has been a part of fisheries management since their taxonomic differentiation (Bailey and Hubbs 1949). Numerous papers have been published on the differences between these subspecies in meristics, growth, physiology, and mortality (summarized in Kleinsasser et al. 1990). However, consistent evidence of clear differences in angling susceptibility was lacking. In addition, literature concerning angling susceptibility in large reservoirs and the effect of introgression is sparse. While many factors may function concurrently to determine angling susceptibility, including fishing pressure (Mankin et al. 1984, Askey et al. 2006), naivety of individual fish, learned lure avoidance, and stress from catch and release (summarized in Philipp

et al. 2009), our results support the findings of Garrett (2002) and Philipp et al. (2009) that angler susceptibility is also a genetic and heritable trait.

The results presented herein are predicated on the assumption that LMB subspecies and their hybrids, of the sizes collected, were equally available to fall electrofishing at night and spring anglers during the day (with the exception of Kurth, where electrofishing and angling both occurred during the day in spring). The distribution of LMB subspecies and their hybrids are not identical (Maciena et al. 1988); however, habitat preferences and distributional patterns appear to be more similar between the subspecies in southern impoundments than elsewhere (Neiman and Clady 1980, Betsill et al. 1987, Lyons 1995). Electrofishing has been the preferred method for collecting non-biased samples of LMB for genetics studies over the last three decades (Maceina et al. 1988, Johnson and Fulton 1999, Barthel et al 2010) and while capture rates may differ among seasons and throughout the day, no bias in the collection of either subspecies has been observed (Bettross and Willis 1988, McInerny and Cross 2000, Schoenebeck and Hansen 2005). Additionally, Johnson and Fulton (2004) reported that largemouth bass collected using rotenone and electrofishing from impoundments exhibited no differences in genotype frequencies. Thus, a number of variables could have affected the results of this study and should not be discounted. Additionally, some conclusions were drawn from the results of a single population. For instance, Leon Reservoir was the only population that yielded substantial numbers of non-introgressed NLMB from which to draw a conclusion about relative angling susceptibility. Subsequent work comparing angled and electrofished LMB collected from reservoirs over a smaller time frame, and repeating the collections in the spring and fall, could address whether any of these variables affected results presented herein and provide further evidence to support or refute our exploratory findings. In spite of the sampling design limitations, the results presented herein provide biologists with a provocative concept that, in Texas reservoirs, FLMB may be more difficult to angle than NLMB, but the phenotype of reduced angler susceptibility is mitigated by introgression, even at low levels.

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