Separating genetic and environmental influences on temporal spawning distributions of largemouth bass (*Micropterus salmoides*)

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Abstract: Environmental and genetic factors influence fish spawning periodicity (i.e., the distribution of spawning events during the breeding season), but their relative contributions have rarely been evaluated. We evaluated the relative contribution of genetic and environmental effects on spawning periodicity by rearing Florida largemouth bass (FLMB, *Micropterus salmoides floridanus*) from Lake Okeechobee and intergrade largemouth bass (ILMB, *Micropterus salmoides salmoides × M. s. floridanus*) from Lake Seminole in a similar environment. Fish from each genetic source population were translocated to experimental ponds at an intermediate latitude in Gainesville, Florida, in September 2003. We used estimated ages of offspring as an index of spawning events to compare spawning distributions between brood sources in ponds and related those results to spawning distributions at source populations for 2004. FLMB began spawning earlier than ILMB in all ponds, and FLMB had a longer spawning season than ILMB. Similarly, FLMB at Lake Okeechobee began spawning earlier and had a longer spawning season than ILMB at Lake Seminole. Environmental factors (e.g., temperature effects) influenced spawning periodicity for both FLMB and ILMB, but spawning periodicity was also influenced by genetic composition in ponds because translocated fish reflected characteristics of their source populations. Thus, both environmental factors and genetic composition influenced spawning periodicity.

[Traduit par la Rédaction]

Résumé : Les facteurs environnementaux et génétiques influencent la périodicité de fraye (c’est-à-dire la répartition des événements de fraye au cours de la saison de reproduction), mais leurs contributions relatives ont rarement été évaluées. Nous avons déterminé les contributions relatives des effets génétiques et environnementaux sur la périodicité de fraye en élevant des achigans à grande bouche de Floride (FLMB, *Micropterus salmoides floridanus*) du lac Okeechobee et des formes intergrades de l’achigan à grande bouche (ILMB, *Micropterus salmoides salmoides × M. s. floridanus*) provenant d’un environnement similaire au lac Seminole. Nous avons transféré des poissons de chaque population-source génétique dans des étangs expérimentaux à une latitude intermédiaire à Gainesville, Floride, en septembre 2003. Nous avons utilisé la dates estimées des rejetons comme indice des événements de fraye afin de comparer la répartition de la fraye chez les reproducteurs des deux origines dans les étangs et de réunir ces résultats aux répartitions de la fraye dans les populations sources en 2004. Les achigans à grande bouche de Floride commencent à frayer plus tôt que les ILMB dans tous les étangs et les FLMB ont une saison de fraye plus longue que celle des ILMB. De même, les FLMB au lac Okeechobee commencent à frayer plus tôt et ont une saison de fraye plus longue que les ILMB au lac Seminole. Les facteurs environnementaux (par ex., les effets thermiques) influencent la périodicité de la fraye chez les FLMB et les ILMB, mais la périodicité de la fraye est aussi affectée par la composition génétique dans les étangs parce que les poissons transférés reflètent les caractéristiques de leur population source. Ainsi, tant les facteurs environnementaux que la composition génétique affectent la périodicité de la fraye.

Introduction

Genetic and environmental factors influence fish spawning periodicity (i.e., the distribution of spawning events during the breeding season), but their relative contributions are often difficult to discern. Many studies (e.g., Ludsin and DeVries 1997; Garvey et al. 1998) have illustrated the importance of hatching (i.e., early- versus late-hatched fish in a year class) to growth and survival of age-0 fishes, but few have evaluated the factors influencing spawning periodicity. Spawning initiation (i.e., the onset of the breeding season) is regulated by environmental factors such as temperature and photoperiod (Kramer and Smith 1960; Lam 1983), and thus, spawning seasons occur later in the year at high latitudes.
relative to low latitudes (Conover 1992). Spawning season duration is often inversely related to latitude, in part because adults cease spawning when offspring no longer have a chance for overwinter survival (Johannes 1978; Munro et al. 1990; Conover 1992). Spawning periodicity has been related to multiple environmental factors, such as water temperature (Conover 1992), photoperiod (Heidinger 1975), changes in water levels (Ozen and Noble 2002), and food availability during gonadal development (Koslowski 1992). For example, Atlantic cod (Gadus morhua) in the Baltic Sea delayed spawning during years of cooler spring water temperatures (Wieland et al. 2000). Largemouth bass (Micropterus salmoides) began spawning in a Puerto Rico reservoir, which was thermally stable (24–30 °C) through the year, when photoperiod began to increase during winter (Ozen and Noble 2005). Spawning duration was also related to water level fluctuations in Puerto Rico reservoirs (Ozen and Noble 2002).

Genetic composition of a stock also influences spawning periodicity. Reproductive processes in fish are regulated, in part, by endogenous hormone cues (Patiño 1979; Van Der Kraak et al. 1998), which are regulated by genes (e.g., Densov et al. 2001). Genotypic effects have led to synchronous spawning of predators in relation to prey abundance, thus resulting in high availability of food resources for newly hatched larvae, assuming increased foraging opportunities at hatching leads to increased survival for offspring (Hjort 1914; Cushing 1975). Atlantic herring (Clupea harengus harengus) exhibit genotypic influences to spawning periodicity across their broad latitudinal range because hatching within specific larval retention areas is related to increased local food availability (i.e., plankton blooms) for larvae in that specific locale (Cushing 1975; Sinclair and Tremblay 1984). Similarly, genetics can influence spawning periodicity because evolution of multiple spawning or a prolonged spawning season may prevent loss of an individual’s annual reproductive output because of environmental conditions (Conover 1992; Fox and Crivelli 1998). However, the relative contributions of genetic and environmental influences are poorly understood, and variable spawning initiation and periodicity are often attributed to phenotypic plasticity (Baylis et al. 1993; Conover and Schultz 1997). Contributions of genotypic variability to phenotypic patterns have largely been ignored (Conover and Schultz 1997).

Largemouth bass provide an excellent species for evaluating genetic and environmental influences on spawning periodicity because they have a wide native geographic distribution with a natural genetic gradient, as indicated by latitudinal clines in allele frequencies at several loci (Philipp et al. 1983). Ecologically, juvenile largemouth bass suffer from differing mortality factors across latitudes (Garvey et al. 1998), and spawning periodicity strongly influences juvenile largemouth bass survival and recruitment (Ludsin and DeVries 1997; Pine et al. 2000). Thus, differing selection pressures may exist along the latitudinal distribution of largemouth bass that would facilitate localized adaptations for spawning periodicity. Comparisons among genetically verified fish indicated that northern largemouth bass (NLMB, Micropterus salmoides salmoides) spawned earlier than Florida largemouth bass (FLMB, Micropterus salmoides floridanus) and intergrade largemouth bass (ILMB, M. s. salmoides × M. s. floridanus) when stocked together in Illinois ponds and a Texas reservoir (Isely et al. 1987; Maceina et al. 1988), but those studies occurred outside the native range of FLMB. No studies have separated environmental influences on spawning periodicity from genetic influences by comparing populations with known genetic contrasts while monitoring environmental conditions.

Genetic differences across the distribution of largemouth bass have been recognized for decades. NLMB and FLMB have been recognized as distinct subspecies for more than 50 years (Bailey and Hubbs 1949). NLMB are endemic to the northern United States, FLMB naturally occur in south Florida, and ILMB occur in north Florida, several southeastern states (e.g., Georgia, Alabama, Mississippi, South Carolina, North Carolina, Virginia, and Maryland), and other areas where introductions have occurred. Kassler et al. (2002) recommended elevating the status of FLMB from a subspecies to species status (i.e., Florida bass, Micropterus floridanus) based on discriminant function analysis of meristic characters, allozyme analysis, and mitochondrial DNA (mtDNA) data. Physiological attributes (e.g., temperature tolerances) and relative survival differences have also been reported for translocated fish in several performance evaluations (e.g., Cichra et al. 1982; Philipp and Whitt 1991). However, phenotypic variability in morphometric and life history traits of broadly distributed species is not uncommon (Schultz et al. 1996). At the time of our study, the taxonomic nomenclature accepted by the American Fisheries Society remains at the subspecies level.

We compared temporal hatching distributions between a population of FLMB from Lake Okeechobee in south Florida and an ILMB population from Lake Seminole at the Florida–Georgia border. Lake Okeechobee represents a pure population of FLMB, and Lake Seminole is an intergrade population (Philipp et al. 1983). We used estimated hatch dates from sagittal otoliths as indices of spawning periodicity assuming that hatching occurred 2 days after fertilization. Spawning periodicity was compared between brood sources for fish reared in environmentally similar experimental ponds at an intermediate latitude. We also assessed whether the trends found in experimental ponds corresponded to the spawning periodicity for the two natural populations at their source lakes. Our study design allowed us to maintain similar environmental conditions during brood fish sexual maturation at the intermediate latitude and evaluate influences of genetic factors to spawning periodicity. If genetic composition affected spawning periodicity, we expected spawning of translocated fish to reflect the periodicity of their source populations. In contrast, we surmised that if environmental factors more strongly influenced spawning periodicity, then translocated fish that spawned in ponds would have similar distributions, and pond distributions would differ from both source-lake populations.

Materials and methods

Pond methods

Brood largemouth bass were captured by electrofishing at Lake Okeechobee, Florida (latitude: 27°7′N), and Lake Seminole, Florida (latitude: 30°44′N), during September 2003 (Fig. 1). Using brood fish from Lakes Okeechobee and Seminole allowed us to nearly encompass the maximum latitudinal
distance in Florida and, therefore, nearly the maximum environmental gradient (i.e., temperature and photoperiod) acting as selective pressures on spawning periodicity. Philipp et al. (1983) observed clinal variation in allele frequencies at several loci in largemouth bass that had been collected from Lake Seminole in north Florida down to Lake Okeechobee. Philipp et al. (1983) failed to detect NLMB alleles at Lake Okeechobee and estimated a subspecific NLMB:FLMB genomic presence of 49:51 at Lake Seminole based on electrophoresis of two diagnostic enzyme loci. Recent analyses at the same loci also detected no northern alleles at Lake Okeechobee and indicated that largemouth bass at Lake Seminole were highly introgressed and had likely been introgressed for an extended time period (B.L. Barthel, Illinois Natural History Survey, 1816 South Oak Street, Champaign, IL 61820, unpublished data). Analyses of mtDNA and allozyme data have resulted in Lakes Seminole and Okeechobee being grouped into separate largemouth bass genetic conservation management units within Florida (B.L. Barthel, unpublished data).

Brood stock from source populations were size-selected within 300–430 mm total length (TL) so that fish were of a reproductively mature size (Chew 1974) and to avoid influences of brood fish size on spawning periodicity (Miranda and Muncy 1987; Goodgame and Miranda 1993). Adult fish were transported to Gainesville, Florida (latitude: 29°43′N), using an aerated 2 m x 3 m fish transport tank within 24 h of capture (Fig. 1).

We stocked six experimental ponds in Gainesville, Florida, with brood fish. Ponds approximately measured 25 m x 5 m, with an average maximum depth of 1 m, and were parallel to each other with a 3 m levee separating each pond. One week prior to stocking, the ponds were treated with rotenone (5% liquid rotenone; >3 mg·L⁻¹), drained to ensure no fish remained, and then refilled. Each pond was randomly assigned 10–11 brood stock from a single lake (N = 3 replicates per brood source) assuming a similar sex ratio for each group (Chew 1974). Brood fish were fed 90–110 mm (TL) golden shiners (Notemogonus chrysoleucas) at 3.5% of largemouth bass biomass per day (Miranda and Hubbard 1994) until spawning behavior was observed in spring. Aquatic vegetation in ponds was maintained at a minimum using manual removal, but removals were ceased when largemouth bass spawning bed construction was first

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Table 1. Earliest, median, and latest hatch dates of Florida (Lake Okeechobee fish) and intergrade (Lake Seminole fish) largemouth bass (Micropterus salmoides) translocated to experimental ponds at Gainesville, Florida, in 2004 and corresponding mean water temperatures.

<table>
<thead>
<tr>
<th>Source</th>
<th>Pond</th>
<th>N*</th>
<th>Earliest</th>
<th>Median</th>
<th>Latest</th>
<th>Hatch range (days)</th>
<th>Earliest</th>
<th>Median</th>
<th>Latest</th>
</tr>
</thead>
<tbody>
<tr>
<td>Okeechobee</td>
<td>A</td>
<td>30</td>
<td>26 Jan.</td>
<td>2 Apr.</td>
<td>7 Apr.</td>
<td>67</td>
<td>12.4</td>
<td>18.2</td>
<td>18.6</td>
</tr>
<tr>
<td></td>
<td>B</td>
<td>40</td>
<td>1 Feb.</td>
<td>29 Feb.</td>
<td>9 Mar.</td>
<td>37</td>
<td>12.3</td>
<td>12.3</td>
<td>18.4</td>
</tr>
<tr>
<td></td>
<td>C</td>
<td>41</td>
<td>12 Feb.</td>
<td>21 Feb.</td>
<td>7 Mar.</td>
<td>24</td>
<td>15.1</td>
<td>15.4</td>
<td>22.6</td>
</tr>
<tr>
<td>Seminole</td>
<td>D</td>
<td>40</td>
<td>7 Mar.</td>
<td>12 Mar.</td>
<td>18 Mar. 11</td>
<td>17.7</td>
<td>14.2</td>
<td>17.7</td>
<td></td>
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<tr>
<td></td>
<td>E</td>
<td>40</td>
<td>22 Feb.</td>
<td>27 Feb.</td>
<td>5 Mar.</td>
<td>12</td>
<td>15.7</td>
<td>14.0</td>
<td>19.6</td>
</tr>
<tr>
<td></td>
<td>F</td>
<td>40</td>
<td>6 Mar.</td>
<td>11 Mar.</td>
<td>16 Mar. 10</td>
<td>20.6</td>
<td>16.0</td>
<td>19.4</td>
<td></td>
</tr>
</tbody>
</table>

* N = number aged.

Field methods

Hatching dates at source lakes were estimated using age-0 largemouth bass captured at Lake Okeechobee during February, April, and June 2004 and at Lake Seminole during May and July 2004. The earlier trip at Lake Okeechobee was conducted because of the potential for early hatching at low latitudes (Gran 1995). Age-0 largemouth bass were collected using 10 m x 10 m block nets and applying rotenone at 3 mg·L⁻¹. Twelve block nets were set at each lake during each sampling event, and fish were collected using dip nets by wading investigators.

Laboratory analyses

A subsample of age-0 largemouth bass from experimental ponds and source lakes were size-selected for age estimation so that the age sample mirrored the length–frequency of the fish collected at each water body (Pine et al. 2000). Selected age-0 largemouth bass were measured (TL; mm) and weighed (wet weight; 0.001 g), and their sagittal otoliths were removed. Sagittal otoliths were prepared using the methods of Miller and Storck (1982). Each otolith was read by two independent readers, and ages were averaged when they agreed within 3 days between readers. If agreement was not met, the otolith was reread by both readers and discarded if agreement was not met (N = 0 for pond fish). Some early-hatched age-0 fish from source populations were too old (>150 days) for reliable age estimation in July, but we assumed their hatch dates were represented in samples collected earlier in the year (i.e., February or April–May). Median hatch date in ponds was compared between stocking sources using a nonparametric median test (Zar 1999). Mean hatch date, mean water temperature at first and median hatch date, and mean hatching duration in ponds were compared between broodstock sources using one-way analysis of variance (ANOVA). Quantitative comparisons between pond and source lake spawning distributions were not performed because of differences in parental size distributions. However, source lake spawning patterns were used to evaluate whether spawning periodicity observed in ponds was similar to source populations in their native environment.

Results

Several largemouth bass nests (N ≥ 3-pond⁻¹), with guarding males, were observed in each pond, and age-0 bass were captured in all six experimental ponds. Female largemouth bass may use multiple nests and deposit multiple egg clutches during a spawning season (Heidinger 1975), thus we assumed that bass progeny in our experimental ponds represented offspring from several families. About 20 age-0 bass were selected for age estimation from each pond during each sample. Age estimates were only made for 30 age-0 bass from pond A (Lake Okeechobee brood stock) because of a low sample size (N = 25) and small TL distribution during April. The low sample size in April was likely due to a high mortality event because all fish collected were <25 mm, except one individual was 32 days older and much larger than any other fish in that sample.

In ponds, FLMB had initial hatching dates beginning as early as 26 January and as late as 12 February (Table 1; Fig. 2). In contrast, the range of initial hatch dates was 22 February to 7 March for ILMB (Table 1; Fig. 2). On average, median hatch date in ponds was 11 days earlier for FLMB than for ILMB (χ² = 31.22, df = 1, P < 0.001), and mean hatch date in ponds was 5 days earlier for FLMB (F = 5.10, P = 0.025) (Table 1). FLMB began spawning at cooler water temperatures (12.3–15.1 °C) than ILMB (15.7–20.6 °C) in experimental ponds (F = 7.82, df = 4, P = 0.049), but water temperatures at median hatch date did not differ between brood types (F = 0.010, df = 4, P = 0.771) (Table 1). Hatching duration in experimental ponds ranged 24–72 days for FLMB and 10–12 days for ILMB (Table 1). FLMB hatching duration was marginally different than ILMB hatching duration (F = 5.40, df = 4, P = 0.08), but low statistical power (N = 3-treatment⁻¹) reduced our ability to detect a difference...
Our results indicated both environmental and genetic effects on spawning periodicity of largemouth bass. Translocation illustrated environmental effects on hatching periodicity because rearing FLMB in research ponds at a higher latitude led to later hatching than at Lake Okeechobee. Similarly, rearing ILMB in research ponds at a lower latitude led to earlier hatching in ponds than at Lake Seminole (Fig. 4). Genetic effects on hatching periodicity were also evident because translocated fish reflected characteristics of their brood source populations. For example, FLMB hatched earlier and had longer hatching distributions than ILMB in both the pond experiment and at brood source lakes (Fig. 4).

Relative differences in spawning times between brood sources in ponds were detected despite the low number of families and adult sizes represented by our pond brood fish relative to source lake populations. Although our intent was to compare relative differences between brood sources in ponds, source lake hatching patterns mirrored our pond results, providing further support for a genetic contribution to spawning periodicity. This corroboration occurred even though our brood fish samples were not representative of the entire spawning population from the source lakes (i.e., lower range in brood fish size in ponds compared with lakes).

**Discussion**

Environmental and genetic factors influenced spawning timing and periodicity of translocated largemouth bass. Environmental and genetic effects to breeding periodicity have rarely been investigated, but have been shown in some cases for terrestrial (e.g., Japanese macaques, *Macaca*...
fuscata; Fooden and Aimi 2003) and aquatic species (e.g.,
Atlantic salmon, Salmo salar; Donaghy and Verspoor 1997).
For example, Atlantic salmon exhibited a reversal in hatching
order between two populations when reared in a hatchery
versus their native rivers (Donaghy and Verspoor 1997).
Donaghy and Verspoor (1997) attributed the reversal in
hatching order to a genotype–environmental interaction;
although they could not explain the mechanism leading to
the reversal, they suggested that local genetic adaptations to
water temperatures were responsible. Environmental influ-
ences were evident by a temporal shift in the onset of
spawning for translocated brood fish. In our research ponds,
FLMB began spawning later than their source population did
at Lake Okeechobee, which is located much farther south. In
contrast, ILMB in research ponds began spawning before
their source population at Lake Seminole, which is further
north. Water temperatures were the most plausible explanation
for observed temporal shifts because temperatures at median
hatch date were similar between FLMB and ILMB in experi-
mental ponds and field collections, but similar patterns in
ponds and source lakes suggested a genetic component to
spawning periodicity.

Genetic factors played a role in spawning timing because
FLMB from Lake Okeechobee spawned earlier in the research
ponds than ILMB from Lake Seminole, even though temper-
atures, photoperiod, and water levels were similar in all ponds
during brood fish sexual maturation and spawning. Adapta-
tions for reproductive strategies that maximize individual
fitness via offspring survival and reproductive success should
occur within an environment given a heritable component
and selection pressure on phenotypic variability (Endler 1986).
Einum and Fleming (2000) documented a "critical episode
of selection" following the emergence of Atlantic salmon
fry, which resulted in a phenotypic shift towards earlier
emergence. A heritable component to breeding date has been
established for some salmonids (Siitonen and Gall 1989;
Gharrett and Smoker 1993), thus Einum and Fleming
(2000) concluded that local adaptations for breeding dates
are possible and may explain the variability in breeding
dates within and among Atlantic salmon populations. The
evidence of a genetic component to breeding times in our
study and other studies is not surprising given that local
populations of fishes, with restricted gene flow, have an
underappreciated capacity to adapt to local selection
(Conover and Schultz 1997).

In our study, FLMB exhibited protracted spawning periods
in both ponds and lakes relative to ILMB. Protracted spawn-
distributions increase the likelihood that individuals with
differing hatching dates will experience differing environ-
mental conditions (Narimatsu and Munehara 1999). Mild
winter water temperatures that typically occur in peninsular
Florida likely prevent exposure of early-hatched fish to very
cold temperatures (<12 °C) that would limit survival, as per
Philipp et al. (1985). Atypical winter cold fronts can reduce
growth or survival of early-hatched largemouth bass at Lake
Okeechobee, thus reproductive success may vary among years
for early- versus late-hatched fish. Garvey et al. (2002) found
a similar pattern for bluegill (Lepomis macrochirus) at Lake
Opinicon, Ontario, and hypothesized that protracted spawning
distributions maximized lifetime fitness in variable environ-
ments where temperature regulates juvenile survival.
Conversely, early spawning (e.g., in December) of large-
mouth bass at Lake Seminole would likely result in very
limited offspring survival. Lake Seminole fish began spawn-
ing at suitable temperatures in March and spawned over a
relatively shorter period compared with Lake Okeechobee
fish. A contracted spawning distribution at Lake Seminole
maximizes the growing season for most age-0 bass (e.g.,
Conover 1992) at the more northern latitude. Contracted
spawning seasons for ILMB at Lake Seminole could be the
result of stabilizing selection, where progeny from both
early and late hatching times are at a survival disadvantage,
which ultimately leads to individuals adapted to spawning
within a shorter time period (Schultz 1993). Protracted
spawning distributions of Lake Okeechobee fish and con-
tracted spawning distributions of Lake Seminole fish appear
better suited for the environments found at each source lake
and inherent environmental influences on juvenile survival.
Philipp et al. (1985) found a lower \( \alpha \) threshold temperature (i.e., the theoretical lower limit to embryonic development) for FLMB than for ILMB. Philipp et al. (1985) hypothesized that NLMB evolved strategies that delay spawning to prevent exposure of embryos to lethally cold temperatures, whereas FLMB evolved to allow spawning at lower and higher temperatures relative to NLMB. Our results support this hypothesis, and we conclude that largemouth bass spawning seasons are locally adapted to environmental conditions.

Natural selection may also lead to spawning periodicity that is synchronized with prey species abundance to maximize food availability for progeny (Sinclair and Tremblay 1984). The relationship between reproductive timing and food supply has been described by the “match/mismatch hypothesis”, which asserts that temperate fishes spawn at a fixed time corresponding to peaks in plankton production, and offspring survival depends on how well their production matches with food production (Cushing 1975, 1990). At Lake Okeechobee, prey fish likely spawn earlier than at Lake Seminole because of earlier spring warming. Earlier hatching of fish at Lake Okeechobee, relative to hatching times at more northern latitudes, may lead to increased survival because of a size advantage relative to prey fish, which is a prerequisite for piscivory (Mittelbach and Persson 1998). Potential prey fish at low latitudes commonly have extended spawning seasons (Conover 1992) (e.g., mummichog, *Fundulus heteroclitus*; Conover 1990) relative to spawning seasons at more northern latitudes. Thus, differences in spawning periodicity we observed may have resulted from selection for optimal environmental conditions, food availability, or a combination of these factors.

Previous studies comparing spawning timing of largemouth bass indicated that NLMB and ILMB hatched earlier and at cooler water temperatures than FLMB (Isely et al. 1987; Maceina et al. 1988), which is contrary to our findings. These previous comparisons were conducted in Illinois and Texas, respectively, which are outside the native range of FLMB and have much cooler winter water temperatures than FLMB experience in their native range. Our pond study was conducted in a transition zone where both pure FLMB and ILMB populations naturally occur (Philipp et al. 1983), so brood fish were reared in temperatures that did not vary as widely from local conditions compared with Isely et al. (1987) and Maceina et al. (1988). Isely et al. (1987) and Maceina et al. (1988) also used sympatric populations of NLMB and FLMB, potentially allowing for confounding effects of hormonal cues and (or) reproductive behaviors, which may have influenced spawning times. We used separate ponds for each genetic source to prevent interbreeding and behavioral influences between brood source types. Broodstock lengths may have also contributed to differing results among studies because larger largemouth bass have been shown to spawn earlier than smaller individuals (Goodgame and Miranda 1993), and a large range in length distribution of spawning bass likely leads to extended spawning activities (Miranda and Muncey 1987). In our study, we used similar-sized brood stock from both sources to minimize potential size effects on spawning in ponds. Adult size distributions in ponds did not reflect adult size distributions at source lakes, thus we focused our comparisons of spawning distributions between ponds and used lake spawning periodicities to evaluate the relative differences. Adult size structures did not drastically differ between source lakes (M.W. Rogers, unpublished data), thus fish size effects on spawning periodicity were probably similar for both source populations. We standardized brood fish size in ponds, and spawning periodicity trends were similar to lake populations for each source, providing further evidence of a genetic component to spawning periodicity.

Comparisons of spawning periodicity using otoliths only reveal data for survivors and not the true distribution if age- or size-selective mortality occurs (Miller and Storck 1984; Isely et al. 1987). Our analyses only allowed for comparisons of surviving offspring between brood sources, which is the main concern for management and conservation purposes, but fish that hatched and incurred high short-term mortality had lower detection probability in our study. Sample timing is important to our results because differing mortality among ponds could have biased spawning periodicity results, especially if sensitivities to mortality factors differed by source. For example, FLMB are less tolerant of cold temperatures than ILMB (Williamson and Carmichael 1990; Philipp and Whitt 1991). We found only one individual in one of the Lake Okeechobee broodstock experimental ponds that was hatched in January, suggesting a high mortality event. Our median hatch date results for Lake Okeechobee experimental fish would not have differed without capturing the early-hatched individual, but the spawning duration for that pond would have been shorter. Our age-0 fish from both ponds and lakes were in the range of 13–73 days and 18–136 days, respectively, which provided a valid assessment of relative spawning times between sources. Interpretation of our results should consider potential biases of sample timing on combined spawning distributions. Fish hatched prior to April collections were potentially available for collection during both samples, which would shift median estimates to earlier in the year. In contrast, early-hatched fish also endured mortality factors for a longer time period relative to later-hatched fish, which could potentially shift our estimated spawning distributions towards later in the year. Lastly, termination of our experiment in mid-May could have led to an underrepresentation of fish that would have hatched later; however, we detected no hatching during the 30-day period prior to ending the experiment, suggesting that our data represent the entire spawning distributions. In summary, comparisons of our results with future studies should consider the time of collection for age-0 fish and potential influences on the apparent spawning distributions.

Environmental experiences of brood fish prior to relocation may persist and confound apparent genetic effects in common environment studies (Conover and Schultz 1997). Earlier spawning of FLMB could be partially due to environmental influences prior to relocation if FLMB were further in their annual reproduction cycle and gamete development was more advanced than ILMB when they were translocated. We stocked brood fish into experimental ponds in mid-September when such effects should have been minimized. Gross et al. (2002) reported that plasma sex steroid concentrations were low for male and female FLMB in September for fish reared at Gainesville, Florida, in their study. Increased gonadosomatic index of FLMB reared in Gainesville, Florida, began in November and peaked in February–March, which was strongly correlated with gonadal
maturation (Gross et al. 2002). We translocated brood fish at least 3 months before spawning occurred at either lake. A future study utilizing progeny of translocated fish would further reveal genetic influences on spawning periodicity. Transplanting studies are useful for evaluating the genetic basis of phenotypic variation in spawning periodicity, but the genetic component we identified suggests further need to test and develop hypotheses to determine natural selection processes responsible for observed differences (Conover and Schultz 1997).

An important consideration when interpreting our study results is that our fish were only from two lakes, thus we did not have a random sample of FLMB or ILMB genotypes. Recent genetic studies concluded that our source populations were from differing genetic conservation management units (B.L. Barthel, unpublished data); however, we did not include brood fish from a range of lakes for each genetic conservation unit.

Our study has implications to management decisions regarding fish stocking programs. Outbreeding depression effects (e.g., lower recruitment, adult abundance, and fish size structure) of stocking FLMB with native LMB populations have not been reported throughout a widely distributed range of public water bodies stocked in the United States. However, Gharrett et al. (1999) reported outbreeding depression in the F₂ generation of pink salmon (Oncorhynchus gorbuscha) that were hybrids of stocks with distinctly different breeding seasons and warned that deleterious effects of outbreeding depression may take decades to detect. In a series of common garden experiments, Philipp et al. (2002) concluded that hybridization of largemouth bass from widely separate geographic locations (e.g., Florida, Illinois, Texas, and Wisconsin) with native Illinois fish led to a more than a 50% reduction in reproductive fitness relative to the original, local stock. Our study did not address individual- or population-level effects of mixing ILMB and FLMB, but genetic factors played a role in spawning timing and periodicity of translocated largemouth bass. Observed spawning periodicity appeared to be better suited for, and a local adaptation to, the environments found at each source lake. Genetic variation among local populations is likely prevalent (Conover and Schultz 1997), therefore we recommend that agencies take a conservative approach in stocking programs to avoid potential outbreeding depression. We also recommend that agencies develop long-term studies that evaluate effects of mixing stocks with phenotypic differences in life history strategies.

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