Localized Spatial and Temporal Variation in Reproductive Effort of Florida Bass

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Localized Spatial and Temporal Variation in Reproductive Effort of Florida Bass

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Abstract

Few studies have explored annual reproductive effort of fish populations, yet factors such as skipped spawning could influence recruitment processes. We estimated the number of broods produced annually as an index of reproductive effort for Florida Bass *Micropterus floridanus* across four lakes in north-central Florida. Snorkel surveys were used to estimate reproductive effort in the lakes from 2010 to 2012. Mark–recapture methods were used to estimate the abundance of Florida Bass in each lake during each year. All four lakes contained high-density Florida Bass populations that showed evidence of relatively slow growth. Average relative weight in all populations was low, ranging from 65.4 to 68.8 for adults (≥25.0 cm TL). Annual reproductive effort (estimated number of broods) varied among lakes and across years. We found evidence for multiple spawning events per adult and for skipped spawning. Devils Hole Lake produced the highest number of broods in all 3 years, ranging from 1.62 broods/spawner in 2012 to 3.72 broods/spawner in 2011 (median = 3.24 broods/spawner in 2010). All other populations exhibited skipped spawning, with the proportion of nonreproductive adults varying across years. Picnic Lake fish had the lowest number of broods overall (only 0.02 broods/spawner in 2011 and 0.01 broods/spawner in 2012). The other two lakes showed variable levels of spawning effort. Spawner abundance in these populations was not related to the estimated annual number of broods, contrary to the general assumption made for many population models. Variability in annual reproductive effort may be more common than anticipated, potentially clouding the relationship between spawner abundance and recruitment. Estimation of annual reproductive effort may provide insight into density-dependent population regulation and recruitment processes.

Fish species that are characterized as iteroparous annual spawners are assumed to follow an annual reproductive cycle that culminates in spawning each year after a fish reaches maturity (Rideout et al. 2005). Departure from this cycle, in which a fish does not spawn annually, is commonly referred to as “skipped spawning” and has been noted for many iteroparous annual spawners in both marine and freshwater systems (Jørgensen et al. 2006; Rideout and Tomkiewicz 2011). Skipped spawning can result from an interruption of gonad maturation prior to spawning or from retention of ripe gonads through the spawning season. The cycle of normal gonad development in fishes can be interrupted at multiple points in relation to different environmental or behavioral factors. In females, interruption of the reproductive cycle can be caused by environmental factors (e.g., low temperature, pollution, or low dissolved oxygen) or nutritional factors (e.g., low food availability, infestations with parasites, or viral infection) that occur before vitellogenesis or during the vitellogenic stage (Rideout et al. 2005). Behavioral or population-level interactions (i.e., fish density, mate availability, or habitat availability) can result in retention of ripe gonads throughout the spawning season by both sexes (Rideout et al. 2005).

The majority of skipped spawning reported in the literature has been described for iteroparous marine species (Rideout et al. 2005; Rideout and Tomkiewicz 2011). Skipped spawning has been observed in the freshwater black basses *Micropterus* spp., including Smallmouth Bass *M. dolomieu* and Florida Bass *M. floridanus* (Swingle 1944; Chew 1973; Barwick and Holcomb...
Black basses are generally described as iteroparous, annually spawning species, with the male providing parental care to the brood until the school of fry disperses (Warren 2009). Research in Nebish Lake, Wisconsin, suggested that only female Smallmouth Bass were iteroparous, while the majority of males sampled during the study only reproduced once in their lifetime (i.e., were semelparous; Baylis et al. 1993). In the same lake, a large proportion of males and females failed to spawn in each year (Raffetto et al. 1990). A male bass may initiate spawning behavior, but if that individual does not produce a brood in a given season (i.e., because he abandons spawning behavior prior to gamete deposition or because he fails to court a female), he would be described as having exhibited skipped spawning. A male may also abandon his brood prior to juvenile independence (i.e., fry dispersal). These cases could also be considered a form of skipped spawning by males, and such behavior has been observed during multiple studies (Philipp et al. 1997; Suski and Ridgway 2007; Parkos et al. 2011). A long-term study of Smallmouth Bass on Lake Opeongo, Ontario, observed that 50.5% of 1,187 nesting males did not rear their broods to independence (Suski and Ridgway 2007).

Skipped spawning by a large proportion of a population would result in fewer total broods produced during a season than could be possible if all mature adults spawned. High levels of skipped spawning in Florida Bass populations have resulted in reproductive failure (i.e., year-class failure) in some cases (Chew 1973; Smith 1976). However, skipped spawning could be a mechanism for recruitment compensation, such that lower numbers of successful broods could increase the juvenile survival rates. This could cause the number of recruits per successful brood to vary inversely with the number of broods (i.e., recruitment compensation; Walters and Martell 2004). Chew (1973) found cases in which only a portion of the adult population of Florida Bass spawned, but substantial year-classes were produced. Thus, identifying the conditions under which skipped spawning occurs is important for understanding recruitment processes and mechanisms for density dependence in fish populations.

The Florida Bass is an upper-trophic-level species, and thus the population demographics of Florida Bass are highly influenced by changes in resource limitation (Wilbur et al. 1974). The reproductive physiology and behavior of Florida Bass have been well described (Carr 1942; Clugston 1966; Chew 1974; Isaac et al. 1998; Warren 2009). Generally, Florida Bass are categorized as iteroparous annual spawners, but few studies have explored spatial and temporal differences in adult abundance and the number of broods produced annually. The objective of this study was to quantify Florida Bass reproductive effort (i.e., the estimated number of broods produced annually) in a series of north-central Florida lakes.

### METHODS

**Study area.**—Four neighboring lakes were selected to allow for the comparison of reproductive effort across a localized spatial scale. The lakes were located within a 204-ha area (Figure 1). The four lakes ranged from 2.7 to 26.2 ha in surface area and from 2.3 to 3.7 m in mean depth (Table 1). A previous study by Canfield and Hoyer (1992) measured the limnological characteristics and aquatic macrophyte coverage of all four lakes (Table 1). At the time of that study, three of the lakes (Keys Pond, Devils Hole Lake, and Picnic Lake) were classified as acidic and clear, with generally low productivity; Keys Pond and Devils Hole Lake were considered mesotrophic, and Picnic Lake was considered oligotrophic. Big Fish Lake was classified as eutrophic, having a relatively high pH, total nitrogen concentration, and chlorophyll-α concentration (Table 1). During the summer in 2010 and 2011, water quality (i.e., pH, total nitrogen, total phosphorus, and chlorophyll α) and aquatic vegetation (i.e., percent area covered and percent volume infested) were re-assessed in each lake. The updated measurements were similar to the water quality and aquatic vegetation coverage assessments made in the 1980s by Canfield and Hoyer (1992).

All four lakes are located on private, undeveloped land. Access to the lakes is restricted, and recreational fishing is negligible. Florida Bass and Bluegills *Lepomis macrochirus* are abundant in all four lakes. The Lake Chubsucker *Erimyzon sucetta*.

### TABLE 1. Limnological characteristics of the four study lakes in Putnam County, north-central Florida. Average adult Florida Bass density (adult density; fish/ha) for each lake and average density of adults by trophic state for 56 Florida lakes (Hoyer and Canfield 1996) are presented.

<table>
<thead>
<tr>
<th>Lake</th>
<th>Mean (max) depth (m)</th>
<th>Mean Secchi depth (m)</th>
<th>Mean pH</th>
<th>Mean total P (µg/L)</th>
<th>Mean total N (µg/L)</th>
<th>Mean chlorophyll α (µg/L)</th>
<th>Trophic classification</th>
<th>Mean adult density (fish/ha), 2010–2012</th>
<th>Mean adult density for Florida lakes by trophic state</th>
</tr>
</thead>
<tbody>
<tr>
<td>Big Fish</td>
<td>2.5 (4.8)</td>
<td>2.9</td>
<td>8.7</td>
<td>15.0</td>
<td>1,496.7</td>
<td>8.0</td>
<td>Eutrophic</td>
<td>63</td>
<td>28 (75)</td>
</tr>
<tr>
<td>Devils Hole</td>
<td>3.7 (6.9)</td>
<td>4.2</td>
<td>5.5</td>
<td>10.7</td>
<td>333.3</td>
<td>6.6</td>
<td>Mesotrophic</td>
<td>34</td>
<td>18 (56)</td>
</tr>
<tr>
<td>Keys Pond</td>
<td>2.3 (6.0)</td>
<td>3.0</td>
<td>5.7</td>
<td>5.3</td>
<td>1,850.0</td>
<td>5.6</td>
<td>Mesotrophic</td>
<td>22</td>
<td>18 (56)</td>
</tr>
<tr>
<td>Picnic</td>
<td>2.6 (4.6)</td>
<td>4.1</td>
<td>4.4</td>
<td>5.0</td>
<td>170.0</td>
<td>1.3</td>
<td>Oligotrophic</td>
<td>23</td>
<td>9 (17)</td>
</tr>
</tbody>
</table>
another important forage species for Florida Bass, is present in three of the lakes (Devils Hole Lake, Keys Pond, and Picnic Lake).

Capture–recapture population estimates.—Fish populations in all of the study lakes were closed to immigration or emigration between water bodies. Florida Bass abundance in each lake was estimated by using capture–recapture methods. Florida Bass were captured with both electrofishing and hook-and-line angling. Capture events were conducted via electrofishing surveys of the littoral zone of each lake by using a Smith-Root 9.0 generator-powered pulsator (GPP) electrofishing unit with a boom-mounted electrode. All of the collected Florida Bass were measured for TL (mm) and weight (kg) and were marked with a pelvic fin clip. Individuals smaller than 25.0 cm TL were considered juveniles based on previous length-at-age data collected by Canfield and Hoyer (1992). These fish were marked with a left pelvic fin clip. Adult Florida Bass (≥25.0 cm TL) were marked with a right pelvic fin clip, and each adult was scanned for the presence of a PIT tag (Biomark). If no previous tag was detected, a uniquely numbered PIT tag was implanted by insertion into the body cavity between the pelvic fins (Harvey and Campbell 1989). Hook-and-line angling was accomplished by using a variety of artificial lures, and fish were marked in the same manner as those captured by electrofishing. Recapture events for population estimation included 600-s transects covering the entire perimeter of each lake. The Jolly–Seber population estimator for multiple recapture events was used to estimate the population size of adult Florida Bass in each lake (Jolly 1965; Seber 1982).

Relative weight ($W_r$) was used as a general measure of Florida Bass condition among lakes (Wege and Anderson 1978; Anderson and Neumann 1996). For adult Florida Bass (≥25.0 cm TL) in each lake, $W_r$ was calculated as

$$W_r = \left( \frac{W}{W_s} \right) \times 100,$$

where $W$ is the wet weight (g) of each individual and $W_s$ is the length-specific standard weight (Wege and Anderson 1978; Anderson and Neumann 1996). To avoid biases resulting from increased gonad weight, adults that were collected during the period immediately prior to spawning each year (December–February) were not included in $W_r$ calculations.

Brood counts.—To determine the proportion of adults that spawned in each lake during each spawning season, we quantified the number of broods per spawning adult by assuming a 1:1 (male : female) sex ratio. Surveys estimating the number of broods in each lake were conducted during the spring spawning season in 2010–2012. Water temperatures in the littoral
zone of each lake were monitored throughout the study period with Onset HOBO temperature loggers placed at approximately 1.0–1.5-m depth. Temperature loggers were set to record water temperature (°C) every 4 h. Average daily water temperature was calculated for each lake throughout the year. Boat surveys were conducted once weekly, starting before water temperatures approached the optimum spawning temperatures reported for black basses (15–23°C; Chew 1974; Philipp et al. 1997). Snorkel surveys were initiated when evidence of spawning activity was observed (i.e., nest building and increased presence of adults in the littoral zone).

The littoral zone (depth = 0.0–3.0 m) of each lake was mapped and divided into approximately equal-area transects by using ArcMap version 9.3. The two smaller lakes (<10 ha; Keys Pond and Big Fish Lake) were divided into four transects, whereas the larger lakes (>10 ha; Picnic and Devils Hole lakes) were divided into 10 transects. Annual changes in water level were monitored by using a stationary water level gauge located in the littoral zone of each lake. Total lake area and littoral area were then quantified for each spawning season by adjusting for annual changes in water level.

Snorkel surveys were conducted twice weekly (every 3–4 d) on all four lakes for the duration of the spawning season. Two new transects were randomly chosen for each survey, resulting in a total of four new transects covered in each lake during each week. To cover the littoral zone represented in each transect, snorkelers swam in a tight weaving pattern perpendicular to the shoreline out to approximately 3.0-m depth. A brood was defined as any stage of young that was present (i.e., eggs, larvae, or fry). Reproductive effort was defined as the annual number of broods; thus, a brood had to be present to be counted. For example, an empty nest that did not contain a brood was not counted. Male Florida Bass construct a nest prior to courting a female, and it was common—especially early in each season—to see multiple empty nests or “scrapes” present along the survey transects. Because we were not able to determine whether these scrapes would eventually result in a spawned brood, they were not counted. Each observed nest that contained a brood was marked with an individually numbered tag to avoid counting the same nest twice on future surveys. After yolk sac absorption, bass fry will remain in a school rising out of the nest until they reach approximately 3.0 cm in length, when the school will begin to disperse (Kramer and Smith 1960; Jackson and Noble 1995). Development time from egg to fry is inversely related to water temperature (Chew 1974). As temperatures warmed during the spawning season, it became possible for new broods to reach the swim-up fry stage prior to being recorded. Thus, new schools of fry (“fry balls”) that were observed during a snorkel survey were counted as new broods and were included in the annual brood estimate.

The number of broods observed was summed by date and transect for a total brood count (C) each week. The number of broods for each lake in each week (N̂) was estimated as

\[
N̂ = \left( \frac{C}{\alpha \hat{p}} \right)
\]

where \(\alpha\) is the sampling fraction (i.e., area sampled/total littoral area; m²), and \(\hat{p}\) is the overall detection probability (Williams et al. 2002). Variance of \(N\) for each week was estimated as

\[
\text{var}(N̂) \approx \left[ \frac{\text{var}(C)}{E(C)^2} + \frac{\text{var}(\hat{p})}{\hat{p}^2} \right] N^2,
\]

where the expected count (E(C)) is the product of the area sampled (\(\alpha\)) and \(N\). The variance in count (\(\text{var}(C)\)) was estimated as

\[
\text{var}(C) = m \left[ \hat{p} S^2 (1 - \alpha) + \hat{s}^2 \right],
\]

where \(m\) is the number of counts conducted (e.g., transects sampled) for the week, \(S^2\) is the variance in the weekly count estimate, and \(\hat{s}^2\) is the mean variance for all counts on areal units within \(A\) (Williams et al. 2002). Weekly estimates of the number of broods were summed over the spawning season to yield an estimate of the annual number of broods in each lake. Confidence intervals and SDs for the estimated annual number of broods were generated using parametric bootstrap by conducting 1,000 iterations (with replacement) of a random normal distribution from the weekly \(N\) and \(\text{var}(N)\) estimates.

To measure the probability of brood detection \(\hat{p}\), multiple dependent observer counts were conducted once weekly in each lake (Cook and Jacobson 1979; Nichols et al. 2000). During these counts, one snorkeler (the secondary observer) surveyed both of the randomly chosen transects. The first snorkeler to cover the area (the primary observer) marked each brood observed in a nest and counted all free-swimming fry balls that were observed during the initial swim of the transect. The secondary observer then swam the transect while recording the same information. The two observers’ counts of nested broods and fry balls were compared to determine how many broods were missed. The observers switched their roles as primary and secondary when observations were initiated on a new sample unit. Brood detection probability for each observer (\(\hat{p}_1, \hat{p}_2\)) and the overall \(\hat{p}\) (Cook and Jacobson 1979) were calculated as

\[
\hat{p}_1 = \frac{x_{11}x_{22} - x_{12}x_{21}}{x_{11}x_{22} + x_{22}x_{21}},
\]

\[
\hat{p}_2 = \frac{x_{11}x_{22} - x_{12}x_{21}}{x_{11}x_{22} + x_{11}x_{12}},
\]

\[
\hat{p} = 1 - \frac{x_{12}x_{21}}{x_{22}x_{11}},
\]
where \( x_{ij} \) represents the number of broods (i.e., nested broods and fry balls) counted by observer \( i (i = 1, 2) \) on the sample units when observer \( j (j = 1, 2) \) was the primary observer. Variance of \( \hat{p} \) was calculated as described by Cook and Jacobson (1979). We looked for effects of adult Florida Bass abundance and condition (i.e., \( W_r \)) on the estimated number of broods.

RESULTS

Population Characteristics

All four lakes contained high-density Florida Bass populations showing evidence of relatively slow growth. Adult density in each lake was above the average for corresponding trophic state as reported by Hoyer and Canfield (1996) in a study of 56 Florida lakes (Table 1). Length frequency distributions were similar among the lakes, with the majority (range = 84–95%) of adult Florida Bass falling between 25.0 and 35.0 cm TL and with relatively few individuals growing larger than 40.0 cm TL (Figure 2). Given the lack of fishing mortality in these lakes, the small adult sizes indicate that growth is relatively slow.

Brood Detection Probability

Brood detectability rate varied among observers and based on observer experience level. In 2010 and 2011, overall \( \hat{p} \) was 0.97 (SD = 0.0095), while in 2012 \( \hat{p} \) was estimated at 0.65 (SD = 0.0095). The \( \hat{p} \) for individual observers increased with observer experience level. For example, a relatively inexperienced observer (i.e., first year involved in the study) had an average \( \hat{p} \) of 0.53 in the first half of the spawning season and ended with a whole-season \( \hat{p} \) of 0.74. Observers' brood detectability carried...
over into the next season, with experienced observers (i.e., those with two or more years of experience) having higher seasonal $\hat{p}$ (i.e., $\hat{p}_1 = 0.87$, $\hat{p}_2 = 0.98$) than observers in their first season (i.e., $\hat{p}_3 = 0.62$).

Overall $\hat{p}$ (i.e., all observers combined) did not vary by brood stage. Average $\hat{p}$ of broods in nests was 0.74 (SD = 0.31, n = 26; all observers, lakes, and years combined). Average $\hat{p}$ of free-schooling fry balls was also 0.74 (SD = 0.38, n = 20; all observers, lakes, and years combined). However, when considering observer experience, the level of detectability differed slightly by stage, particularly for inexperienced observers (those with less than 1 year of experience). For inexperienced observers, the detectability of fry balls (mean $\hat{p} = 0.48$, SD = 0.39, n = 10) was lower than the detectability of broods associated with a nest (mean $\hat{p} = 0.63$, SD = 0.37, n = 13). For experienced observers (i.e., those with two or more years of experience), the detectability of fry balls averaged 1.0 (SD = 0.0, n = 10) and the detectability of broods associated with nests averaged 0.86 (SD = 0.20, n = 13).

**Annual Reproductive Effort**

Reproductive effort varied substantially among lakes. Florida Bass in Devils Hole Lake exhibited the highest reproductive effort during all 3 years, ranging from 317 estimated broods (SD = 21.3) in 2012 to 741 broods (SD = 38.0) in 2011 (median was 639 broods [SD = 26.6] in 2010; Table 2). In Big Fish Lake, Florida Bass produced 96 estimated broods (SD = 10.5) in 2010 and 4 broods (SD = 1.0) in 2011 (Table 2). The number of broods observed in Big Fish Lake during 2012 was zero. Florida Bass in Keys Pond demonstrated similar nesting effort in all 3 years: 9 broods (SD = 0.3) in 2010; 12 broods (SD = 2.2) in 2011; and 11 broods (SD = 2.7) in 2012 (Table 2). Picnic Lake was surveyed in 2011 and 2012, and an estimated 9 broods (SD = 1.5) and 3 broods (SD = 1.0), respectively, were produced (Table 2). During each spawning season, the earliest broods were observed in Devils Hole Lake. Spawning was initiated when the water temperature was close to 20°C in 2011 and 2012. Water temperatures were slightly colder in 2010 than in the subsequent 2 years, and the first nests were observed when the temperature

**TABLE 2.** Abundance and density of adult Florida Bass (≥25.0 cm TL) in the four study lakes (north-central Florida) during 2010–2012. Annual reproductive effort in each study lake is summarized as the estimated number of broods produced annually. Also included are the estimated proportion of adults that produced broods during each spawning season and the number of potential spawners (assuming a 1:1 sex ratio). Values in parentheses represent 95% CIs.

<table>
<thead>
<tr>
<th>Lake</th>
<th>Year</th>
<th>Adult abundance (N)</th>
<th>Adult density (fish/ha)</th>
<th>Estimated number of broods</th>
<th>Potential spawners</th>
<th>Broods per potential spawner</th>
</tr>
</thead>
<tbody>
<tr>
<td>Big Fish</td>
<td>2010</td>
<td>165 (125–238)</td>
<td>56</td>
<td>96 (85–125)</td>
<td>83</td>
<td>1.16</td>
</tr>
<tr>
<td></td>
<td>2011</td>
<td>162 (121–231)</td>
<td>59</td>
<td>4 (2–6)</td>
<td>81</td>
<td>0.05</td>
</tr>
<tr>
<td></td>
<td>2012</td>
<td>171 (127–245)</td>
<td>74</td>
<td>0a</td>
<td>86</td>
<td>0.00</td>
</tr>
<tr>
<td>Devils Hole</td>
<td>2010</td>
<td>394 (328–491)</td>
<td>34</td>
<td>639 (584–691)</td>
<td>197</td>
<td>3.24</td>
</tr>
<tr>
<td></td>
<td>2011</td>
<td>397 (343–467)</td>
<td>34</td>
<td>741 (670–817)</td>
<td>199</td>
<td>3.72</td>
</tr>
<tr>
<td></td>
<td>2012</td>
<td>392 (342–444)</td>
<td>35</td>
<td>317 (282–365)</td>
<td>196</td>
<td>1.62</td>
</tr>
<tr>
<td>Keys Pond</td>
<td>2010</td>
<td>71 (56–102)</td>
<td>18</td>
<td>9 (8–9)</td>
<td>36</td>
<td>0.25</td>
</tr>
<tr>
<td></td>
<td>2011</td>
<td>70 (57–97)</td>
<td>21</td>
<td>12 (8–16)</td>
<td>35</td>
<td>0.34</td>
</tr>
<tr>
<td></td>
<td>2012b</td>
<td>–</td>
<td>–</td>
<td>11 (5–16)</td>
<td>35</td>
<td>0.31</td>
</tr>
<tr>
<td>Picnic</td>
<td>2011</td>
<td>731 (435–1,419)</td>
<td>28</td>
<td>9 (6–12)</td>
<td>366</td>
<td>0.02</td>
</tr>
<tr>
<td></td>
<td>2012</td>
<td>452 (314–703)</td>
<td>19</td>
<td>3 (1–5)</td>
<td>226</td>
<td>0.01</td>
</tr>
</tbody>
</table>

*No nests were observed in Big Fish Lake during 2012 due to low visibility throughout the spawning season. Annual reproductive effort was likely low but not zero.

bWater levels were too low in Keys Pond during 2012 to estimate population abundance using mark–recapture electrofishing. The potential spawners and broods per spawner estimates for 2012 were calculated by assuming a relatively stable population (N = 70 adults) as was observed in 2010 and 2011.

**TABLE 3.** Average (SE in parentheses) relative weight ($W_r$) of adult Florida Bass (≥25.0 cm TL) in each of the four study lakes (2011–2012); and average $W_r$ of adults sampled during the summer postspawning period through the fall in 2011, with corresponding reproductive effort (broods/potential spawner) estimated for the 2012 spawning season.

<table>
<thead>
<tr>
<th>Lake</th>
<th>Population mean $W_r$</th>
<th>Postspawn–fall 2011 $W_r$</th>
<th>2012 broods per potential spawner</th>
</tr>
</thead>
<tbody>
<tr>
<td>Big Fish</td>
<td>68.6 (2.56)</td>
<td>68.0 (2.71)</td>
<td>0.00a</td>
</tr>
<tr>
<td>Devils Hole</td>
<td>68.8 (1.14)</td>
<td>69.6 (0.95)</td>
<td>1.62</td>
</tr>
<tr>
<td>Keys Pond</td>
<td>67.5 (4.05)</td>
<td>69.4 (2.78)</td>
<td>0.34</td>
</tr>
<tr>
<td>Picnic</td>
<td>65.4 (1.07)</td>
<td>64.4 (3.81)</td>
<td>0.01</td>
</tr>
</tbody>
</table>

aNo nests were observed in Big Fish Lake during 2012 due to low visibility throughout the spawning season. Annual reproductive effort was likely low but not zero.
reached 15°C. During all 3 years, spawning in all lakes ceased at water temperatures of 27–28°C.

The proportion of mature adult Florida Bass that spawned (i.e., broods per potential spawner) varied among lakes and across years within lakes. The annual proportions ranged from 0.01 broods/potential spawner in Picnic Lake during 2012 to 3.73 broods/potential spawner in Devils Hole Lake during 2011 (Table 2; Figure 3). The proportion of adults that spawned also varied within lakes across all years. Three lakes (Big Fish Lake, Keys Pond, and Picnic Lake) showed some level of skipped spawning by a percentage of the adult population during each year (Table 2; Figure 3). Across years, Keys Pond had moderate adult spawner proportions ranging from 0.25 to 0.34 broods/potential spawner (median = 0.31; Table 2). In Big Fish Lake, the proportion of spawners was relatively high in 2010 at 1.16 broods/potential spawner but then decreased to 0.05 broods/potential spawner in 2011 (Table 2; Figure 3). Picnic Lake showed consistently low spawner proportions for the 2 years of observation (0.01–0.02 broods/potential spawner; Table 2; Figure 3). Devils Hole Lake was the only lake that exhibited no evidence of skipped spawning by adult Florida Bass across all 3 years, with the proportion of spawning adults ranging from 1.62 broods/potential spawner in 2012 to 3.73 broods/potential spawner in 2011 (Table 2; Figure 3).

Average Wr was calculated for adults that were sampled from the summer postspawn period through the fall in 2011 (prior to the 2012 spawning season). Devils Hole Lake, which had the highest observed proportion of spawning adults (broods/potential spawner; in 2012), also had the highest observed Wr (Table 3). Picnic Lake, which had the lowest observed proportion of spawning adults, had the lowest observed Wr (Table 3). However, for this time period, Wr values of Florida Bass from all four study lakes would still be considered poor.

Annual reproductive effort of Florida Bass was not related to the annual abundance of adults (Figure 4). Although Picnic Lake had the highest adult Florida Bass abundance due to its
large size relative to the other lakes, it consistently had the lowest estimated number of broods (Table 2; Figure 4). The three other lakes had relatively consistent abundance across years but exhibited variation in the number of broods produced annually (Table 2; Figure 4). Thus, based on these results, the abundance of adult Florida Bass would not serve as a useful indicator of annual reproductive effort across lakes.

DISCUSSION

Annual reproductive effort of a population is difficult to quantify; thus, there is a lack of data on spatial and temporal changes in the reproductive effort of fish populations (Rideout et al. 2005). As such, the reproductive strategy of adult fish is generally assumed to be similar across populations, and annual reproductive effort is assumed to be related to the abundance of mature adults (Walters and Martell 2004). However, variability in reproductive effort has been reported for many fish species (Rideout et al. 2005; Jørgensen et al. 2006; Rideout and Tomkiewicz 2011). Application of these assumptions to black bass species has been questioned, and the need for further research has been recognized due to the lack of a relationship between adult abundance and reproductive effort (Ridgway and Philipp 2002). The populations of Florida Bass in this study exhibited variation in the estimated number of broods produced across localized spatial and temporal scales. Among neighboring lakes and within a given lake across years, we found evidence for multiple spawning events per adult and for skipped spawning. The proportion of adults that skipped spawning in any given year varied from moderate (~25–50% of the adults did not attempt to spawn) to severe (>90% of adults did not attempt to spawn).

The high proportion of spawning adults (broods/potential spawner) observed in Devils Hole Lake over multiple years indicates that both females and males likely spawned multiple times in a season. In southern latitudes, where the spawning season is prolonged, multiple spawning events by individuals of both sexes have been observed for Largemouth Bass *M. salmoides* (Dadzie and Aloo 1990; Gran 1995; Isaac et al. 1998; Waters and Noble 2004). Similar to other black bass species, female Florida Bass exhibit asynchronous maturation of ova, suggesting that they have the ability to spawn multiple times throughout the spawning season and the potential to spawn in the nests of multiple males (i.e., batch spawning; Chew 1974; Rosenblum et al. 1991; Tyler and Sumpter 1996; DeWoody et al. 2000). Furthermore, male Florida Bass whose nests failed as a result of egg removal in a hatchery initiated additional spawning events (Isaac et al. 1998). High rates of nest failure may result in multiple spawning events by males in order to produce a successful brood.

Skipped spawning has been observed in many fish populations in both marine and freshwater systems. The proportion of the population that forgoes spawning in a season often remains elusive due to the difficulty in defining, and thus quantifying, annual reproductive effort by individual fish over successive years (Rideout et al. 2005). In this study, skipped spawning was the more common reproductive strategy among the neighboring Florida Bass populations. Proportions of each population that did not spawn in a given season varied among lakes and within lakes across years. Populations exhibiting skipped spawning were generally described as having shortened and highly inconsistent spawning effort relative to the populations with high reproductive effort (e.g., Devils Hole Lake in all years and Big Fish Lake in 2010). We defined reproductive effort as the estimated number of broods; however, broods vary in size. Thus, the number of individuals in a brood can provide a more detailed indicator of total reproductive effort. Future studies could increase the detail associated with quantifying reproductive effort by incorporating brood size at the earliest stages (i.e., number of eggs) prior to compounding mortality effects related to the environment and predation.

The selection of the four study lakes from among the many lakes in the area was based on a combination of relatively small size, water clarity, a defined depth profile, and little anthropogenic disturbance (via recreational angling or shoreline development). The closed Florida Bass populations in these study lakes allowed for more confidence in population and brood estimates and likely more homogeneous populations. However, the results reported here are probably not transferable to large systems with greater heterogeneity in environmental and population-level factors (Baylis et al. 1993).

The probability of detection $\hat{p}$ is an important parameter that needs to be addressed when using count-based abundance estimators (Williams et al. 2002). In visually based surveys, detection is typically assumed to differ based on environmental conditions that would affect visibility. In this study, we noted that the variation in $\hat{p}$ was more closely related to observers—particularly observer experience level—than to environmental conditions. This highlights the importance of quantifying $\hat{p}$ to
account for heterogeneity among observers as well as the environment. It also suggests that future studies may benefit from including observers in their levels of stratification of sampling effort so as not to confound potential observer effects with other predictor variables.

Our estimates of annual reproductive effort should be considered underestimates when considering the true annual reproductive effort (i.e., total number of broods spawned). We were unable to account for some environmental effects on observations and behavioral aspects of Florida Bass reproduction that would result in an underestimation of reproductive effort. The study lakes were chosen in part for their relatively high average Secchi depths (Table 1). However, water clarity in Big Fish Lake during the 2012 spawning season was the lowest observed among the 3 years, and no broods were detected by any of the observers. Age-1 recruits that would have been spawned during that season were observed in early 2013 (S.L.S., personal observation); therefore, it is clear that reproduction occurred, although we were unable to quantify it due to low visibility. Water clarity levels for Big Fish Lake in 2010 and 2011 and for all other lakes during all study years were close to the average reported and likely had little effect on estimates of the number of broods. Studies of black bass reproduction have observed that schooling fry balls will combine into larger schools, with one or multiple males guarding them until dispersal (Carr 1942; Allan and Romero 1975; Warren 2009). In our study, a fry ball was counted as a single brood because we were unable to determine whether multiple fry balls were schooling together. Another potential bias arose because we did not count nests in which a brood was not observed. We were unable to determine whether an empty nest (1) had contained a brood that was abandoned and lost or (2) was a newly constructed nest in which a brood would be produced in the future. Thus, these nests were not counted, possibly resulting in the underestimation of annual reproductive effort. However, the effect of this bias would not be expected to vary among lakes or among years, so the relative differences in reproductive effort among lakes were probably indicative of real differences.

We did not determine the sex ratio of the population in each lake; therefore, our estimates of reproductive effort were made under a general assumption of a 1:1 (male : female) sex ratio. This assumption meant that the estimate of reproductive effort was reliant on male nesting behavior, as it was assumed that each brood was produced by only one male and only one female. This may not be the case, particularly in systems where mortality rates and age at maturity vary by sex. In Nebish Lake, Wisconsin, female Smallmouth Bass were found to mature later than males, resulting in a male-biased adult sex ratio (Raffetto et al. 1990; Baylis et al. 1993). Previous studies have also observed that multiple females may contribute to the brood of one male (DeWoody et al. 2000). Our results assumed that each male had a potential female, but we were unable to verify this assumption. Limited availability of mates would likely have a greater impact on annual reproductive effort if female numbers were biased low, resulting in a higher number of males that are unable to produce a brood. A sex ratio that is skewed toward females may be less limiting because multiple females may spawn in the nest of a single male, thus reducing the potential for a high number of females to retain gametes (i.e., due to an inability to find a mate).

Annual reproductive effort varied among lakes and within lakes across years, but the mechanisms influencing effort during a given year were unclear. Previous research on skipped spawning in fish populations indicates that environmental, nutritional, and population-level effects can influence reproductive effort (Rideout et al. 2005). Environmental factors (i.e., pollution, habitat, and water temperature) were unlikely to have impacted the reproductive effort of the four study populations. All of the study lakes are located on private, undeveloped land with highly restricted access and can be described as pristine Florida lakes. A broad littoral zone containing suitable spawning habitat (i.e., structure and vegetation) was available in each lake. Fluctuating water levels affected the amount of littoral area that was available across years in each lake, but due to the prolonged spawning season, spawning habitat availability would not have been restricted. Cold spells can delay or interrupt the spawning behavior of Florida Bass (Chew 1974; Mesing and Wicker 1986), but no large swings in temperature occurred during the spawning seasons over the duration of this study. The lowest water temperatures were observed early in the 2010 spawning season, but no interruption of spawning behavior or reduction of annual reproductive effort was observed for Devils Hole Lake, in which spawning was most common. Considering the prolonged spawning seasons for Florida Bass in their native range (Rogers and Allen 2009), cold spells may interrupt spawning behavior briefly but would be unlikely to affect the annual reproductive effort of a population.

Picnic Lake, which had the lowest estimated number of Florida Bass broods in all seasons, was also the most acidic of the study lakes. Increasing acidity in George Lake, Ontario (e.g., pH was 6.5 during 1961 and ranged from 4.8 to 5.3 in 1971–1972), and in other northern lakes has resulted in fish mortality events and failure to spawn (Beamish et al. 1975; Haines 1981). Unlike the increasing acidification reported in northern lakes, evidence suggests that the pH in Picnic Lake has been consistently low for the past 20 years and that the lake likely undergoes small seasonal changes in water chemistry, similar to other lakes in north-central Florida (Brezonik et al. 1982; Canfield and Hoyer 1992). Naturally acidic, clear, oligotrophic lakes comprise about 10–15% of Florida’s lakes (Canfield et al. 1985). The persistence of Florida Bass populations in these acidic lakes may reflect a difference in acid tolerance compared with northern Largemouth Bass populations (Canfield et al. 1985). However, we cannot rule out the hypothesis that low pH contributed to skipped spawning at Picnic Lake.

Poor condition (i.e., insufficient energy reserves) is the most commonly reported cause of skipped spawning (Rideout et al. 2005; Rideout and Tomkiewicz 2011). Spawning of fish in
captivity can be interrupted when diets are controlled (Hislop et al. 1978; Burton and Idler 1987; Rijnsdorp 1990; Maddock and Burton 1994; Bunnell et al. 2007). Adults in the wild that are classified as being in a nonreproductive state have been observed to exhibit poorer condition than reproductive individuals (Burton and Idler 1987; Rideout et al. 2000). If condition is a cause, females are able to enter a resting stage, and the annual reproductive cycle is interrupted prior to vitellogenesis (Rideout et al. 2005; Rideout and Tomkiewicz 2011). Females may also complete their annual reproductive cycle but retain and ultimately reabsorb their eggs via follicular atresia (Scott 1962; Hislop et al. 1978; Ma et al. 1998; Kennedy et al. 2008). Less is known about the possible effect of poor condition on skipped spawning in males (Rideout and Tomkiewicz 2011). Condition of adult Florida Bass in the four study lakes would be considered “poor” in comparison with other populations of Florida Bass and Largemouth Bass (Bennett 1970; Anderson and Neumann 1996). It is likely that condition alone did not drive the differences in annual reproductive effort among lakes because Florida Bass in all lakes displayed poor condition, but the degree of skipped spawning varied widely. It is not known whether the growth, age structure, and mortality of the populations varied substantially. Length frequency data indicated only minor differences, but future studies should estimate all vital rates and evaluate whether they are related to spawning frequency.

The best methods for determining the mechanisms that affect spawning frequency would likely require monitoring at the level of the individual. Tracking of uniquely tagged adults during the spawning season (as per Waters and Noble 2004) coupled with brood monitoring surveys would provide a robust approach for differentiating physical versus environmental variables that may influence spawning frequency. Gonad sampling before, during, and after the spawning period would provide important information regarding size and age at maturity, changes in gonad maturation through time, and the number of adults that have entered resting or retaining stages without spawning (Swingle 1943; Chew 1973). Gonad sampling methods in most cases would require mortality of sampled individuals, which has the potential to influence population dynamics, particularly in small systems like those in this study. Another potential method of tracking individual reproductive stage involves the quantification of steroid concentrations that influence gonad maturation and spawning behavior (i.e., testosterone, 11-ketotestosterone, estradiol, progesterone, and vitellogenin). Steroid concentrations cycle seasonally and drive gonad maturation processes; thus, they can allow the sex and maturity stage of individuals to be determined. Blood sample collection is generally nonlethal, and individuals can be resampled through time. Quantification of steroid concentrations in black bass species, particularly Largemouth Bass and Florida Bass, has typically been used to examine the influence of environmental contaminants on physiology (Sepúlveda et al. 2001; Gross et al. 2002; Martyniuk et al. 2009). Studies conducted on sturgeons often use steroid concentrations as indicators of the reproductive stage of individuals during the spawning season (Webb et al. 2002; Webb and Doroshov 2011; Shaw et al. 2013).

Skipped spawning could be a mechanism for recruitment compensation in fish populations, but few studies have considered this factor in recruitment processes. Compensation refers to a negative feedback interaction that would stabilize a population by offsetting the losses of individuals via mortality (i.e., natural or fishing mortality; Rose et al. 2001). Recruitment compensation implies that the number of offspring recruiting to a population per mature adult increases at low population sizes because the resources available to individuals would be greater at a low density (DeAngelis et al. 1991). Stable average recruitment has been noted in many fish species across a wide range of spawner abundances (Hilborn et al. 1995; Walters and Martell 2004). Per-capita recruitment rates (i.e., number of recruits per adult) in fish species are often inversely related to population size (Cushing 1995; Myers et al. 1999; Rose et al. 2001; Allen et al. 2011). We found that annual reproductive effort was not positively related to spawner abundance. However, lower annual reproductive effort through skipped spawning could provide a mechanism for compensatory recruitment, possibly increasing juvenile survival during years when the number of broods produced is low. Additionally, recruitment models for many species may be ineffective because they fail to incorporate data on stock demography and individual variability in spawner quality (Trippel 1999; Marshall et al. 2003; Tomkiewicz et al. 2003; Rideout et al. 2005). This is true of the black basses, as there is no clear relationship between spawner abundance and recruitment for any of these species (Parkos and Wahl 2002; Ridgway and Philipp 2002), leading to much debate (Allen et al. 2013; Parkos et al. 2013). In the case of black basses, variability in annual reproductive effort may be more common than anticipated, thereby clouding the relationships between spawner abundance and recruitment. Thus, attempts to understand recruitment processes should consider variable reproductive effort as a mechanism influencing juvenile survival rates, and the lack of a stock–recruit relationship should not be viewed as definitive proof that adult population dynamics are irrelevant.

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