Morphology, Density, and Spatial Patterning of Reproductive Bowers in an Established Alien Population of Nile Tilapia, *Oreochromis niloticus*

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ABSTRACT

In coastal Mississippi aquatic systems, Nile tilapia (*Oreochromis niloticus*) has been introduced via aquaculture practices and appears to have established breeding populations. However, little is known about characteristics of bowers in non-native environments or if reproductive activities vary with water temperature. Therefore, we examined bower morphology, sediment composition, density, spatial pattern, and the distribution of bowers and reproductive leks in relation to thermal gradients within a power plant cooling pond. We found that the Nile tilapia has the appropriate materials for building bowers, can establish active breeding leks, and distributes along thermal gradients. All of these attributes allow for successful invasion and establishment into non-native environments.

INTRODUCTION

Introduced alien species can have profound effects upon native species via competition for resources on many levels. For introduced aquatic species, information on numerous biological levels is required to assess if a species will become established, if it is expanding from the point of introduction, and if it is having an impact on the receiving environment and its native fauna. Nile tilapia (*Oreochromis niloticus*) is one of the most widely cultured aquatic species in the world (Costa-Pierce 2003), in part because its reproductive biology is characterized by short generation time, multiple clutches, and extended breeding seasons (Naylor et al. 2000, Stickney 2002, Peterson et al. 2004). Furthermore, male Nile tilapia build large bowers (reproductive structures where no rearing of young occurs; McKaye et al. 1990) in shallow shorelines, appear to have defined courtship behaviors, aggressively defend the bower from conspecifics and other fishes (Baerends and Baerends-Von Roon 1950, Fryer and Iles 1972, Trewavas 1983), and reproduce on communal display ground called leks (McKaye et al. 1990 and 1991). These advanced reproductive characteristics allow rapid and successful establishment in non-native environments (Peterson et al. 2004) and may impact similar, nest-building species via reproductive activities. For example, the reduced density of native species in power plant cooling ponds with established tilapia species has been attributed to competition during spawning (Noble et al. 1975, Crutchfield 1995). Shafland and Pestrak (1983) noted an 84% reduction in fingerling production by largemouth bass (*Micropterus salmoides*) in Florida ponds with blue tilapia (*Tilapia aurea* = *Oreochromis aureus*) compared to ponds with no blue tilapia. However, they speculated that this reduction was due to direct aggressive interactions rather than competition for spawning sites.

Nile tilapia has been introduced into several Mississippi aquatic systems via aquaculture. Peterson et al. (2004 and 2005) have shown that this species is prevalent in...
coastal Mississippi even though the introduction is relatively new (~1989), that it has established a reproductive population inside and outside aquaculture thermal influences, that the species is capable of over wintering in our warm temperate environment, and that individuals have reached sizes suggesting that they are at least four-six years old. These observations indicate that the Nile tilapia is doing well in coastal Mississippi watersheds near and away from the points of introduction. However, although Nile tilapia is extremely abundant near aquaculture facilities where escapes have been documented and outnumber resident species like largemouth bass, bluegill (*Lepomis macrochirus*), and redear sunfish (*L. microlophus*) (Peterson et al. 2005), the tilapia does do not compete directly with these sport fishes for food resources (Peterson et al. 2006). But, little is known about the interaction between Nile tilapia and co-occurring native sport fishes, in particular those interactions which may reduce the reproductive success of these native species. Understanding the reproductive behavior of Nile tilapia in non-native environments is a crucial step toward developing appropriate management strategies for this species. Since little work has been done to actually characterize the bowers built by male Nile tilapia or to examine bower distribution in non-native environments, the objectives of our study were to examine bower morphology, sediment composition, density, spatial pattern, and the distribution of bowers (within and among leks) in relation to thermal gradients in a power plant cooling pond.

**MATERIALS AND METHODS**

**Study location**

The Pascagoula River is a large river in North America whose course remains relatively unaltered by human activity (Dynesius and Nilsson 1994). The warm-temperate environment coupled with the warm aquaculture discharge into the system provides ideal conditions for Nile tilapia to become established (Peterson et al. 2004 and 2005). We conducted this project within the Plant Daniel Cooling Pond (PDCP), a closed-loop system located in Escatawpa, Mississippi. The PDCP, an impoundment of Black Creek (Pascagoula River drainage), provides cooling water for Mississippi Power and has a large, established population of Nile tilapia. Water temperature data indicate a definite year-round thermal gradient as discharged from Plant Daniel is allowed to cool before it is pumped back into the facility (Slack et al. 2006).

**Bower morphology and sediment composition**

Within the PDCP, active Nile tilapia bowers were characterized by location, density, morphology, and sedimentary composition. We chose 12 locations associated with HOBO Water Temp Pro Loggers along the length of the PDCP (Slack et al. 2006) that were used to document the thermal gradient. At each location, a designated area measuring 45.72 m long by 7.62 m deep was staked out to determine bower characteristics. The PDCP was further divided into three arbitrary thermal zones - “cold” (14.2 - 35.0°C, median = 27.0°C), “middle” (14.9 - 35.4°C, median = 30.5°C), and “hot” (18.5 - 43.9°C, median = 33.3°C). These zones were based on previous water temperature records (Slack et al. 2006), and this thermal stratification allowed us to compare bower activity across the thermal gradient.

To quantify active bower morphology, the bower location was recorded and flagged on the edge of the bower with a stake. The morphology of an active bower was characterized by depth of pit, diameter of pit, height of pit rim above horizontal plane of pond bottom profile, nearest distance to shore, nearest distance to vegetation, and the nearest distance to a drop-off, or point where the bottom profile rapidly changed. The presence or absence of guarding male Nile tilapia at identified active bowers was recorded during subsequent monthly visits. Descriptive statistics for all the morphology
measurements were calculated with SPSS v11.5 software (SPSS, Inc., Chicago, Ill.). To determine if there was any difference in sediment composition, preliminary sediment cores were taken from the center of a bower and from the area immediately outside the rim of the bower. These samples were mud and fine sand with little variation between inside and outside. Thus, subsequent cores (15 cm deep) were taken on one date from both ends of each of the 12 locations with a 4 cm diameter PVC corer. These samples were individually dried and characterized for percent sand/silt/clay (Folk 1980).

Bower spatial pattern and density

The spatial pattern and density of bowers within a location were determined using the Byth and Ripley procedure for distance methods (Krebs 1989). The following distances were measured: (1) point-to-bower distances from randomly selected points to the five nearest bowers (x) and, (2) bower-to-nearest bower distances from a selected bower to the five nearest bowers (r). First, 10 points (2n) were identified within a location by haphazardly choosing a point (site) within a diagram of the location which was marked with a numbered stake. Five of those points were chosen randomly and the distances from each selected point to the five nearest bowers were measured (x). Around each of the remaining five points (n), a 3 m x 3 m plot was marked and the number of bowers within that plot was counted. The distance from each enclosed bower to the five nearest bowers was also measured (r).

To test the spatial distribution of bowers, an Index of Pattern ranging from 0 to 1 was generated using \( I_s = \frac{\sum x_i^2}{\sum x^2 + \sum r^2} \), with 0 representing a maximum uniformity and 1 illustrating a maximum clumping pattern; a random distribution would be indicated by 0.5. The distribution pattern was not random; therefore, a density estimate was made using Diggle’s estimator of population density \( N_i = N_1 N_2 \). Diggle’s estimator of population density has a low bias over a wide range of clumped to uniform patterns and thus allowed for comparisons across locations. The statistical program NEIGHBOR was used to generate the Index of Pattern and the Diggle’s estimate (Krebs 1989).

Bower distribution and water temperature

The number of bowers within each location was counted, each bower was categorized into one of four categories, and their positions were noted on a diagram monthly at all 12 locations from September 2004 through August 2005. Bowers were categorized based on the degree of activity. Category 1 bowers were defined as clean with an actively guarding male. Category 2 bowers were clean with no male. Category 3 bowers appeared to be recently abandoned, with only a thin layer of debris covering the center. Category 4 described bowers covered in debris with no sign of recent activity. Bower counts were made by poling a skiff throughout each location.

Hourly water temperature data obtained from the HOBO Water Temp Pro Loggers were provided by the Mississippi Museum of Natural Science as part of another study (2003-05) being conducted in the area (Slack et al. 2006). Four of the twelve probes were lost before the final water temperatures could be downloaded; thus data from all probes were available only from 1 November 2003 until 12 September 2004. To determine if the previous year (2003-04) water temperatures could, in part, be substituted for the missing data in the sample year (2004-05), a Student’s t-test compared mean water temperature data for the day of sampling plus three days prior to sampling and the corresponding dates from the previous year. No statistical differences between data sets were found (all Student’s t-test ≥ -1.047, p ≥ 0.308) for all locations, and therefore we used water temperature data based on the previous year’s values for those locations and dates that were missing for the sample year. The distribution of bower activity categories along the thermal gradient was plotted using the frequency of categories for each month pooled across locations by thermal zones. A detailed description of bower distribution of each location can be found in McDonald (2006).
RESULTS

Bower morphology and sediment composition

Bower morphology metrics (n = 29 total bowers) were comparable to similar measurements from the literature (Table 1). However, no data were available to describe typical native environment bower distance to shore, vegetation, or drop-off. Sediments showed minimal variation between either end of each location or throughout the PDCP. The sediment composition was mud/fine sand to silt/fine sand (Fig. 1).

Table 1. Bower morphology (m) descriptive statistics at Plant Daniel Cooling Pond and in Nile tilapia native environments (Boulenger 1908, Fryer and Iles 1972, Trewavas 1983). SD = standard deviation, and NA = no available data.

<table>
<thead>
<tr>
<th></th>
<th>N</th>
<th>Minimum</th>
<th>Maximum</th>
<th>Mean</th>
<th>SD</th>
<th>Native</th>
</tr>
</thead>
<tbody>
<tr>
<td>Depth of pit</td>
<td>27</td>
<td>0.350</td>
<td>1.400</td>
<td>0.817</td>
<td>0.198</td>
<td>0.45-2.0</td>
</tr>
<tr>
<td>Diameter of pit</td>
<td>27</td>
<td>0.400</td>
<td>1.900</td>
<td>0.763</td>
<td>0.315</td>
<td>0.5-1.0</td>
</tr>
<tr>
<td>Height of rim</td>
<td>27</td>
<td>0.010</td>
<td>0.500</td>
<td>0.109</td>
<td>0.096</td>
<td>0.1</td>
</tr>
<tr>
<td>Distance to shore</td>
<td>29</td>
<td>1.350</td>
<td>15.200</td>
<td>6.330</td>
<td>4.466</td>
<td>NA</td>
</tr>
<tr>
<td>Distance to vegetation</td>
<td>28</td>
<td>0.000</td>
<td>9.230</td>
<td>1.550</td>
<td>2.211</td>
<td>NA</td>
</tr>
<tr>
<td>Distance to drop-off</td>
<td>29</td>
<td>0.998</td>
<td>14.170</td>
<td>6.851</td>
<td>3.508</td>
<td>NA</td>
</tr>
</tbody>
</table>

Bower spatial pattern and density

The pattern of active lek distribution was considered clumped across the pond as the active bowers only occurred in six locations across the cold to middle zones (1-6). The Index of Pattern for these six locations suggested a random distribution that leaned toward uniform (0.20-0.45; Fig. 2). Diggle’s estimator of population density for all six locations ranged from 0.010 to 0.020 bowers/m², with an overall mean density for active bowers of 0.016 (± 0.004 SE) bowers/m².

Bower distribution and water temperature

Active bowers did not occur in the “hot” temperature zone (locations 9-12) of the pond in the colder months as expected. Instead they were found in the “middle” range of water temperatures (locations 5-8) and moved to the “cold” zone (locations 1-4) as the summer progressed (Fig. 3). Three locations (10-12) in the hot zone showed no active bowers during the sampling period but had many category 3 and 4 bowers. Active bowers appeared in the “middle” temperature zone beginning in November. They appeared in the “cold” zone in January and were exclusively found there after April. The last active bower was observed in the “cold” zone (location 2) in July. These occurrences of active bowers reflected a breeding season of November to July. The occurrence of category 3 and 4 bowers in the “hot” zone may be attributed to the cooler water temperature found throughout the PDCP during the winter of the previous year (Slack et al. 2006).

DISCUSSION

The Nile tilapia appears to access the appropriate habitat components for the creation of its breeding bowers and leks. For example, sediments from leks in coastal Mississippi were mud/fine sand to silt/fine sand and are similar to those described as fine sand (Trewavas 1983) and firm sandy shores (Lowe-McConnell 1958) in the native environments, suggesting that the Nile tilapia is finding building materials analogous to those available to them in Africa. Moreover, depth of pit, diameter of pit, and height of rim were well within the range of literature values (Boulenger 1908, Fryer and Iles 1972, Trewavas 1983), suggesting the construction of bowers is comparable to those created in
the native environment. This is a similar pattern noticed for the Mayan cichlid, *Cichlasoma urophthalmus* Günther, which was introduced to southern Florida. The Mayan cichlid seems to have found a comparable setting to its native environment, facilitating the establishment of a viable population (Faunce and Lorenz 2000), and expansion to other areas (Matamoros et al. 2005).

The spatial arrangement of bowers within leks differed from our predicted clumped distribution. The random (approaching uniform) spatial pattern of the bowers within any breeding lek may be a result of the territoriality of male Nile tilapia (reviewed in Trewavas 1983). The distribution of leks throughout the PDCP did not occur continuously along the shoreline even though the sediment composition did not differ among the twelve locations. The clumped distribution of active leks likely occurred due to the strong temperature gradient in the PCDP. Nile tilapia's reproductive behavior was dynamic and leks that were used appeared related more to the distribution of the appropriate water temperature. It is possible that the category 3 and 4 bowers observed in

![Figure 1. Percent of sand/silt/clay at each location averaged between each end of the location.](image)

![Figure 2. The Index of Pattern for the distribution of bowers within active locations where 0 = uniform distribution, 1 = clumped distribution, and 0.5 = random distribution.](image)
the “hot” zone were constructed during the previous year’s breeding season (or even several years earlier) when the winter was colder and more thermal refuge may have been necessary. Bower construction and activity level thus appears to vary spatially and annually within the PDCP. Clearly, Nile tilapia is very pliable particularly in its behavior and growth (Lowe-McConnell 1958). In fact, water temperature has been shown, in part,

![Graphs of three temperature zones: Cold Zone, Middle Zone, and Hot Zone. Each graph shows frequency of four bower categories by month pooled by temperature zone (cold = locations 1-4, middle = 5-8, and hot = 9-12) from September 2004 through August 2005.]

Figure 3. The mean frequency of the four bower categories by month pooled by temperature zone (cold = locations 1-4, middle = 5-8, and hot = 9-12) from September 2004 through August 2005.
to regulate Nile tilapia reproduction (Duponchelle et al. 1999). Finally, Slack et al. (2006) noted that radio tagged Nile tilapia selected cooler areas of the PDCP in summer and warmer areas during the winter. They noted movement of Nile tilapia within PDCP based on seasonal thermal shifts, with individuals moving to different portions of the PDCP depending on the water temperature. However, movement by radio tagged individuals did not always conform to the longitudinal thermal gradient illustrated within the PDCP. Instead, some Nile tilapia moved laterally into small, shallow, semi-enclosed sections of the PDCP, which were shaded by Spadderdock pads (Nuphar luteum) and had cooler water (reduced by as much as 4.6-6.6°C) than the adjacent main channels in summer.

Based on the bower activity of Nile tilapia within the PDCP, breeding occurred from November through July, with the possibility of reproduction occurring throughout the year in the shallow semi-enclosed lateral ponds. In fact, Peterson et al. (2004) documented year-round reproduction of Nile tilapia in the coastal watershed of Mississippi (including the Pascagoula River and Biloxi River drainages) with one peak in spring and another in late summer, a pattern that is similar to that in equatorial ponds of Africa (Lowe-McConnell 1958). Although the native breeding season of Nile tilapia varies with latitude, this species exhibits an April to August breeding season in Cairo, Egypt with the main breeding peak from April to mid-May (Trewavas 1983). Interestingly, coastal Mississippi and Cairo, Egypt are at similar latitudes. Clearly, coastal Mississippi has the appropriate environmental conditions for Nile tilapia survival and successful reproduction. An increased awareness of Nile tilapia will hopefully lead to more appropriate placement of facilities within the landscape and better management practices of these aquaculture facilities.

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LITERATURE CITED
Costa-Pierce, B.A. 2003. Rapid evolution of an established feral tilapia (Oreochromis spp.): the need to incorporate invasion science into regulatory structures. Biol. Invas. 5:71-84


Trewavas, E. 1983. Tilapine fishes of the genera *Sarotherodon*, *Oreochromis*, and *Danakilia*. British Museum (Natural History), London.