

Reproduction in Nonnative Environments: Establishment of Nile Tilapia, *Oreochromis niloticus*, in Coastal Mississippi Watersheds

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Tilapia, in general, are known for their plasticity in growth, reproduction, and age- and size-at-maturity that not only make them an excellent aquaculture taxa but also allow them the ability to invade and become established in nonnative environments. We investigated aspects of reproductive biology and recruitment of the nonindigenous Nile Tilapia, *Oreochromis niloticus*, collected in the Pascagoula River watershed and from Simmons Bayou, a small tidal system of Biloxi Bay, Mississippi, over a 16-month period. Males ranged from 32.6–430.0 mm total length (TL) and females from 31.7–349.0 mm TL. The Gonadosomatic Index (GSI) for males or females indicated year-round reproduction with increased spawning intensity in spring (March to May) and in late summer (August to September). Small juveniles (≤ 25 mm TL) were collected every month of the year except March, and multiple size classes were collected suggesting successful recruitment of young. The smallest female with mature oocytes was 79.9 mm TL, and the size class where 50% of the females were mature was 113 mm TL. Batch fecundity (BF) ranged from 30–2603 oocytes for females, and there was a significant relationship between \log_{10} -BF and \log_{10} -TL and \log_{10} -BF and \log_{10} EBW. Relative fecundity ranged from 0.89–11.75 oocytes/g EBW. Although Nile Tilapia have low fecundity, parental care ensures that the majority of their eggs will survive to the juvenile stage. Low fecundity is further offset by the ability to spawn multiple broods throughout their year-round reproductive season. These reproductive characteristics may give the species a competitive advantage over native fishes. We expect Nile Tilapia to further invade and spread in these coastal watersheds.

IN aquatic ecosystems, species introductions are a problem worldwide, and the threats of nonindigenous species have been fully recognized for decades (C. S. Elton, 1958, reviewed in Goldburg et al., 2001). Introduced species are considered the second greatest cause of biological diversity loss after habitat destruction (Vitousek et al., 1997). Members of the Cichlidae are recognized as having the potential to alter aquatic communities into which they are introduced (Courtenay, 1997). This is, in part, because of their tolerance of variable environmental conditions (Trewavas, 1983). They are also trophic generalists (Dempster et al., 1993; Traxler and Murphy, 1995), and their reproductive biology is characterized by short generation time, multiple clutches and extended breeding seasons (Naylor et al., 2000, 2001; Coward and Little, 2001; Stickney, 2002). In fact, populations of tilapia species in nonnative environments have become numerically dominant in a variety of habitats (Crutchfield, 1995; Faunce and Paperno, 1999), in part, because of these adaptations.

Brackish marshes along the northern Gulf of Mexico (GOM) provide a quality environment for various life stages of freshwater and the early

life-stages of estuarine-dependent species (Peterson and Meador, 1994). Unfortunately, the GOM is one of the least studied regions of the United States in terms of introduction of aquatic species (Ruiz et al., 2000; Carlton, 2001). Occurrence of the maternal mouthbrooding Nile Tilapia, *Oreochromis niloticus*, has been observed in coastal waters of Mississippi (M. S. Peterson, W. T. Slack, and C. M. Woodley, unpubl.) as early as 1989. This species is a widely used aquaculture species worldwide (Costa-Pierce, 2003) and has been termed the “aquatic chicken” for its extraordinary production capabilities (Coward and Little, 2001). Nile Tilapia life history in native environments is characterized by low fecundity, extended spawning seasons, maturity at a small size, and a fast growth rate (Coward and Bromage, 2000; Turner and Robinson, 2000). However, reproduction of this species in nonnative environments and the role it plays in their establishment has not been well investigated. The general objective of this work is to quantitatively establish that nonindigenous Nile Tilapia have breeding populations and are established in coastal watersheds in Mississippi. Specifically, we quantified (1) gender-based, length-weight relationships, (2) size at 50% ma-

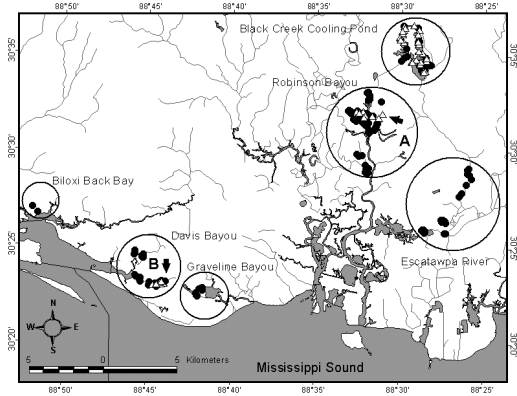


Fig. 1. General map of stations and areas where 280 collections were made over the course of this study in coastal Mississippi. Solid circles represent sampled areas where Nile tilapia was not present; triangles represent areas where Nile tilapia was present. The arrows in circles A and B refer to the location of the aquaculture facilities.

turity, (3) reproductive season, (4) batch and relative fecundity, and (5) size-fecundity relationships.

MATERIALS AND METHODS

We sampled monthly at two fixed stations in Robinson Bayou in the Pascagoula River system and four fixed stations at Simmons Bayou, Mississippi, between 16 November 2000 and 18 June 2002 (Fig. 1). Both of these areas have aquaculture facilities that are or have been permitted for Nile Tilapia. Additional stations within these areas and within other Coastal River systems were also sampled periodically to determine extent of the Nile Tilapia invasion. During each collection, six water quality metrics were recorded. Summary statistics for each of these metrics are presented in M. S. Peterson, W. T. Slack, and C. M. Woodley (unpubl.) and only water temperature (C) is reported here. Fixed stations were sampled with seines and dipnets, whereas general area stations were sampled with trammel nets, hook and line, minnow traps, and plastic coated wire crab traps. Vouchered specimens were euthanized in the field with MS-222 (ASIH, AFS, AIFRB, 1988), fixed in 10% formalin for 7–14 days, washed overnight in fresh water, and preserved in 70% ethanol. Cichlid scientific names follow Trewavas (1983) and Shafland (1996), and all specimens are archived in the Mississippi Museum of Natural Science (MMNS) Ichthyology Collection.

The Gonadosomatic Index (GSI) was calculated for males and females each month follow-

ing the formula $GSI = GW/EBW \times 100$, with GW = gonad weight (g) and EBW = eviscerated body weight (g). Batch fecundity (BF) was determined for sexually mature females with oocytes ≥ 1.0 mm diameter. Preliminary oocyte size-frequency analysis ascertained that oocytes ≥ 1.0 mm form a distinct batch and that there is only one batch of large oocytes at a time in the ovaries. A portion of the ovary was weighed (PGW), and all oocytes ≥ 1.0 mm were counted (N) under a dissecting microscope. Batch fecundity was calculated following the formula $BF = N \times (GW/PGW)$. Relative batch fecundity (RF), expressed as number of oocytes/g EBW, was calculated for each fish as $RF = BF/EBW$. Sexual maturity was determined by GSI and inspection of oocyte sizes; all females with oocytes ≥ 1.0 mm were considered sexually mature regardless of GSI value. Analysis of covariance (ANCOVA) with TL as the covariate was used to compare \log_{10} -EBW between genders, first checking for parallelism of slopes between genders and then checking the Y-intercepts (EBW) for differences, if the slopes were parallel. Additionally, linear regression was calculated between TL and EBW. Analysis of variance (ANOVA) was used to examine female RF by month. If a significant *F*-value was noted, monthly values were separated with Sidak pairwise comparisons. To estimate the size at 50% maturity for female Nile Tilapia, we fit the percent of fish with mature oocytes per 10 mm TL size class to a series of logistic (S-shaped) functions. The best fit model was $Y = e^{[b_0 + (b_1/t)]}$, where t = size class and b_0 and b_1 are estimated parameters. This nonlinear regression was estimated through successive iterations of the Lavenberg-Marquardt algorithm until minimization of residuals. A regression of EBW versus GSI was performed for all sexually mature males and females to ascertain if GSI was independent of fish weight. Regressions with BF or RF as the dependent variable and female size (TL or EBW) as the independent variable were calculated to describe these relationships. Batch fecundity, RF, TL, and EBW were \log_{10} -transformed and GSI data were arcsine square-root transformed prior to analysis (Sokal and Rohlf, 1995). All values were considered significant when $P < 0.05$, and all statistics were conducted with SPSS (Vers. 11.5, Chicago, IL).

RESULTS

Males used in the TL versus EBW analyses ranged from 32.6–430.0 mm TL (169.5 ± 9.18 SE, $n = 153$), whereas females ranged from 31.7–349.0 (107.95 ± 4.63 SE, $n = 188$). The

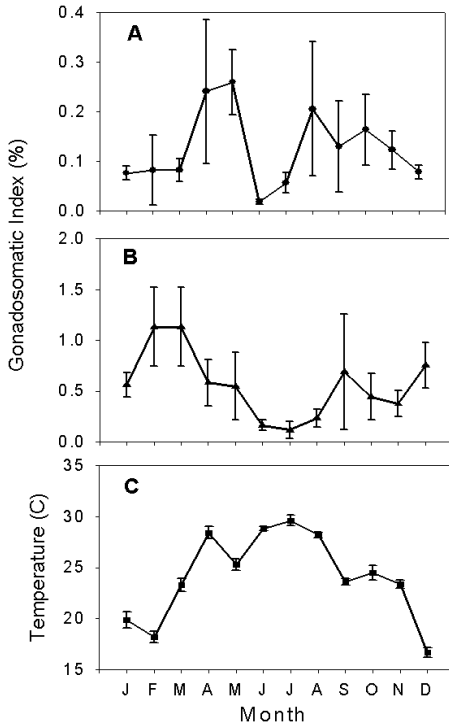


Fig. 2. Reproductive seasonality of male (A) and female (B) *Oreochromis niloticus* determined by monthly gonadosomatic index (GSI; mean \pm SE). Sample sizes for males are ≥ 5 for any month except February, June, July, and October ($n = 124$), and February and July for females ($n = 178$). (C) Monthly water temperature (C, mean \pm SE) for all stations where *O. niloticus* were collected.

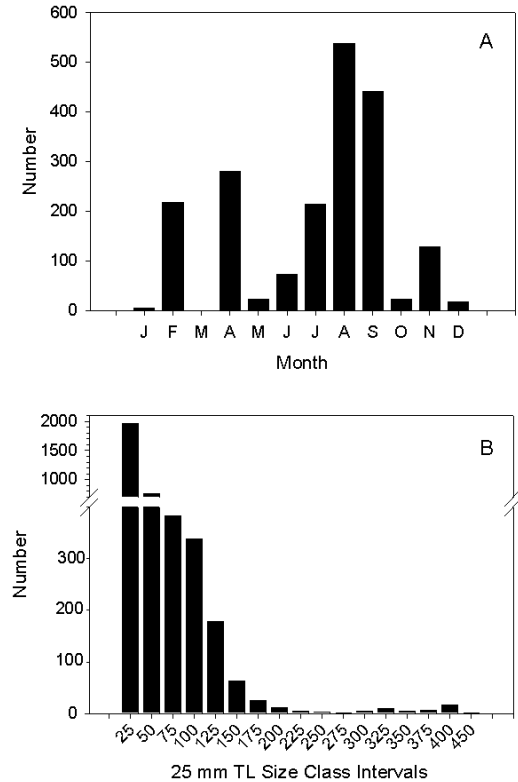


Fig. 3. (A) Recruitment of Nile Tilapia into coastal Mississippi watersheds, as demonstrated by the number of Nile tilapia (≤ 25 mm TL) captured at all stations by month and (B) the number of Nile Tilapia in 25 mm TL size classes for all collections.

ANCOVA indicated the gender-based TL versus EBW relationships were parallel (ANCOVA, $F_{1,336} = 0.444$, $P = 0.505$), but there was no \log_{10} -EBW difference between genders ($F_{1,336} = 0.203$, $P = 0.652$). Thus, genders were pooled, and there was a significant relationship between \log_{10} -TL and \log_{10} -EBW ($F_{1,339} = 88995.20$, $P < 0.0001$, $r^2 = 0.996$), with the equation being \log_{10} -EWT = $3.098(\log_{10}$ -TL) - 5.049 .

Arcsine male GSI versus EBW ($r^2 = 0.037$, $n = 124$, $P = 0.032$) and arcsine female GSI versus EBW ($r^2 = 0.024$, $n = 178$, $P = 0.040$), although significantly related, explained very little ($< 3.7\%$ of the variation) and were not deemed biologically meaningful relationships. Thus, GSI was a useful metric for estimating spawning preparedness for this species. There was an increase in spawning intensity in spring (March to May) and a lower intensity level in late summer (August to September) in both male and female GSI, suggesting these are times of more intense reproduction (Fig. 2A–B). These peaks appear to correspond with the spring increase and late

summer decrease in water temperature (Fig. 2C). However, some reproduction occurred year round, as evidenced by the presence of small juveniles (≤ 25 mm TL) every month of the year except March in the sampling areas (Fig. 3A) and successful recruitment of young into larger size classes in the systems examined (Fig. 3B).

The smallest individual found with mature oocytes was 79.9 mm TL. Estimated TL at 50% female maturity was 113 mm TL (110 mm TL size class), based on data presented in Figure 4. Batch fecundity ranged from 30–2603 oocytes for females ranging from 79.9–349.0 mm TL (6.3–703.7 g EBW). Fecundity counts were completed in females in all months except July and August, when no mature oocytes were found. There was a significant relationship between \log_{10} -BF and \log_{10} -TL ($r = 0.889$, $n = 31$, $P < 0.0001$) as well as between \log_{10} -BF and \log_{10} -EBW ($r = 0.891$, $n = 31$, $P < 0.0001$). Thus, BF-values are expressed as relative fecundity to eliminate the confounding effects of fish weight

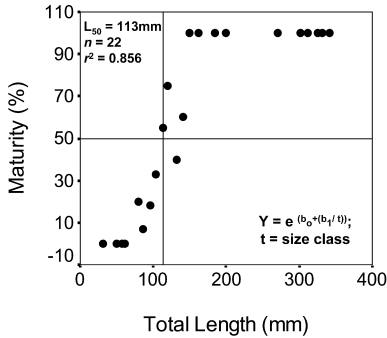


Fig. 4. Plot of percentages of mature female *Oreochromis niloticus* (those with oocytes ≥ 1 mm diameter) by 10 mm TL size class. The TL where 50% of the individuals are mature (L_{50}) equals 113 mm TL.

on fecundity comparisons. Relative fecundity ranged from 0.89–11.75 oocytes/g EBW with a mean of 4.57 (± 0.48 SE, $n = 31$). However, \log_{10} -RF and \log_{10} -EBW were correlated ($r = 0.496$, $n = 31$, $P < 0.01$).

DISCUSSION

Coastal wetland environments in the northern GOM are characterized by warm temperate/subtropical waters and salinity that ranges from about 25 psu (practical salinity units) in near-shore environments to tidally influenced fresh water farther up in the watershed. These environmental conditions support a large ichthyofaunal diversity (Rakocinski et al., 1997; Ross, 2001) but are also quality environments for nonindigenous species. Tilapia species are known for their tremendous plasticity in a number of vital life-history metrics (growth, reproduction, age- and size-at-maturity, etc.; Turner and Robinson, 2000) that not only make them excellent aquaculture taxa but also allow them the ability to invade and become established in nonnative environments. Escape of nonindigenous Nile Tilapia into Mississippi wetlands has resulted in an established population in coastal Mississippi (M. S. Peterson, W. T. Slack, and C. M. Woodley, unpubl.; present study).

Individuals greater than 349 mm TL in our collections were always male. However, there was no difference in transformed EBW between genders when adjusted for TL. Male Nile Tilapia typically grow larger than females (Boulenger, 1908; Lowe-McConnell, 1958), and de Graaf et al. (1999) found that mean growth rates (g/d) for males (0.78 ± 0.03 SE) were greater than for females (0.22 ± 0.02 SE). Occurrence of larger males may be associated with a system that is dominated by males (Fryer and

Iles, 1972) or may be related to high water temperature exposure of young within 15-day post-fertilization, as progressively higher temperatures (> 34 – 36 C) induce sex-reversal and higher proportions of males (Baroiller et al., 1995).

Female Nile Tilapia in coastal Mississippi reach sexual maturity as small as 79.9 mm TL, with 50% maturity being achieved by 113 mm TL. This maturity schedule is typical of Nile Tilapia in native and nonnative environments (Appendix 1). Size at maturity for nonindigenous and cultured populations of Nile Tilapia, however, is much smaller than those noted for native East African lake populations which range from 200–390 mm TL (Trewavas, 1983; Stewart, 1988). Moreover, unfavorable environmental conditions such as changes in lake water level and associated resource availability (Kolding, 1993) or overfishing (Lowe-McConnell, 1982) leads to a dramatic decrease in size at 50% maturity (Appendix 1). These data support early claims that Nile Tilapia can spawn within the first year of life in their native environments (Lowe-McConnell, 1958). Introduced tilapia apparently also spawn during their first year of life. In Alabama, McBay (1961) noted Nile Tilapia between 96 and 118 mm TL (50-day-old) had eggs and suggested that, if spawned early in the spring after temperature reached 21 C, these fish could reproduce within their first summer of life. Duponchelle and Panfili (1998) noted that Nile Tilapia in French reservoirs matured as early as 5.6–10 months of age and that size-at-maturity correlated with reservoir area. Both size- and age-at-maturity were very plastic among the eight populations they studied (up to 20–30 mm between consecutive years), supporting plasticity of this species in native and nonnative environments.

The overall low GSI values and the modest seasonal peaks observed for both male and female Nile Tilapia are no doubt related to the large variation in GSI each month, suggesting some fish each month were reproductively active, whereas others were not in spawning condition. The low GSI values we observed are consistent with year-round spawning and are similar to GSI values reported by Al Hafedh et al. (1999) for males (0.56–0.61) and females (0.63–0.71). Our GSI data coupled with the year-round presence of females with mature oocytes, small juveniles (≤ 25 mm TL) occurring in all months except March, and recruitment of young fish into larger size classes strongly suggest Nile Tilapia is spawning year round and is established in coastal Mississippi. In the tropics, Nile Tilapia also appears to breed year round,

although there is a peak in the rainy season (Trewavas, 1983).

An increase in water temperature appears to be closely associated with the initiation of spawning (Turner and Robinson, 2000). Indeed, the spring increase in spawning intensity based on GSI of Nile Tilapia in Mississippi corresponds with water temperature increasing to above 22 C. This general pattern appears in both native and nonnative environments worldwide. In fact, reproduction occurs in most months of the year in nonnative populations in France but at a lower level that appeared to be driven by day length when water temperatures were above 22 C (Duponchelle et al., 1999). They hypothesized that breeding seasonality in tilapias is controlled at a high level by photoperiod that determines the annual breeding cycle, and a lower level, which is controlled by the conjunction of environmental variables (temperature, rainfall, resource availability, etc.) that modulates the interannual variation in breeding intensity and duration. They based this hypothesis on findings that maximum fecundity occurred about one month after the highest water temperature, and that fecundity variation was closely related to photoperiod and chlorophyll *a* concentration.

Nonindigenous Nile Tilapia exhibit the advanced reproductive strategy of maternal mouthbrooding, which translates into low fecundity. Babiker and Ibrahim (1979) provided evidence that females have multiple batches of eggs, breed more than once in a season, and that fecundity was more strongly correlated with TL ($r = 0.860$) and weight ($r = 0.806$) than with age ($r = 0.694$). The number of eggs is dependent on the size of the female in both native and nonnative environments (Appendix 1). Batch fecundity also increased significantly with both TL and EBW in Nile Tilapia in our watersheds; thus, our RF estimates of 0.89–11.75 oocytes/g EBW should be used to compare fecundity values for Nile Tilapia of different sizes. However, RF values recorded for coastal Mississippi Nile Tilapia (4.57 ± 0.48 oocytes/g EBW) are smaller than those reported in the literature (Appendix 1).

Female Nile Tilapia brood eggs, embryos, and young in their mouths, and we noted in a number of instances (typically around peak GSI periods) that Nile Tilapia in our system had one of the three developmental stages in their mouths. Males aggressively guard the nests, and females aggressively guard their free-swimming young after first release; this parental care may continue for up to three weeks (Trewavas, 1983; Baroiller et al., 1995; Coward and Bromage,

2000). Although we did not attempt to count eggs in the mouth of Nile Tilapia, they probably do not brood or care for young longer than 14 mm long (Boulenger, 1908; Trewavas, 1983). Estimates of the number of eggs held in female mouths range from 705 eggs (from a 305 mm TL female; Lowe-McConnell, 1955) to 2000 eggs (size not specified; E. B. Worthington, 1929, cited in Lowe-McConnell, 1955), similar to BF estimates in the literature and in Mississippi.

Although Nile Tilapia has low fecundity, parental care assures that the majority of their eggs will survive to the juvenile stage. Furthermore, low fecundity is offset by the ability to spawn multiple broods throughout their year-round reproductive season. These reproductive characteristics may give the species a competitive advantage over native fishes because the intrinsic rate of population increase plays a significant role in determining which introduced species survive and proliferate in nonnative environments (Ruiz et al., 2000). Presence of nonindigenous tilapia species can have severe consequences on native fish fauna, as introduced *Oreochromis* spp. can literally occupy all available habitat with their spawning sites (McKaye et al., 1995), thus interfering with spawning by native nest-building species. Research on reproductive behavior, spawning frequency, and definitive histological descriptions would further elucidate some of the indirect impacts of Nile Tilapia on native fauna. Based on evidence of healthy reproductive populations in coastal Mississippi, we expect Nile Tilapia to continue to invade these watersheds.

ACKNOWLEDGMENTS

C. M. Woodley, C. Vervaeke, B. Lezina, G. Waggy, J. Finley, M. Partyka, J. Brookins, and M. Dugo provided field and laboratory assistance. R. and G. Scott allowed access to their property for sampling. J. D. Williams of the Florida Caribbean Science Center verified our tilapia. Sampling was completed under blanket permit to the Gulf Coast Research Laboratory and was conducted under USM IACUC 169-099. Voucher specimens are archived in the MMNS (24735–29431) in Jackson. The Mississippi Department of Wildlife, Fisheries and Parks funded this project to MSP and WTS through grant F-129.

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APPENDIX 1. SUMMARY OF REPRODUCTION METRICS IN NILE TILAPIA IN NATIVE AND NONNATIVE ENVIRONMENTS. SL = Standard Length, TL = Total Length. * = based on diet protein; # = based on photoperiod.

Season	Size at 50% maturity	Smallest mature female	Batch fecundity (mean ± SE) [size or size range]	Relative fecundity (mean ± SD or SE)	Native or nonnative	Reference
		90 mm TL	300–500 oocytes/fish [110–129 mm TL]		Native	Babiker and Ibrahim, 1979
	390 mm TL (1953)		2800/oocytes/fish [290–320 mm TL]		Native	Kolding, 1993
	260 mm TL (1992)					
Year round; peak in rainy season (Apr–Aug)	275 mm TL (earlier)	120 mm TL (dwarf population)	340 [170 mm TL]		Native	Lowe-McConnell, 1955
	245 mm TL (1960)		3706 [570 mm TL]			Lowe-McConnell, 1982
	200 mm TL (1972)					Trewavas, 1983
Mar–Jul	270 mm TL (1985)	200 mm TL (1985)			Native	Stewart, 1988
	296 mm TL (1975)	24.5 mm TL (1975)				
Jan–Sep; peak in Apr–May, Aug	91–132 mm SL (1995)		149–2797 [36–975 g; 1995]		Nonnative	Duponechelle and Panfili, 1998
	112–147 mm SL (1996)		178–1898 [78–501g; 1996]			Duponchelle et al., 1999
						Duponchelle et al., 2000
	30 g	87 mm TL (12.7g)	50–220 oocytes/fish [90–135 mm TL]	6 (90 mm) – 2 (160 mm) eggs/g	Nonnative (culture)	de Graaf et al., 1999
	97–104 mm TL			5.9 ± 2.1 – 8.6 ± 2.6 eggs/g (SD)	Nonnative (culture)	Al Hafedh et al., 1999*
			2020 ± 80 – 2408 ± 70 eggs/spawn (SE)	6.0 ± 0.2 – 7.2 ± 0.2 eggs/g (SE)	Nonnative (culture)	Campos-Mendoza et al., 2004#
				7.33 ± 0.62 oocytes/g (SE)	Nonnative (culture)	Bhujel et al., 2001
Year round; more intense in Mar–May and in Aug–Sep	113 mm TL (110–115 mm TL size class)	79.9 mm TL	30–2603 oocytes	4.57 ± 0.48 (0.89–11.75) oocytes/g (SE)	Nonnative	Present study