

## Nile tilapia *Oreochromis niloticus* (Linnaeus, 1758) establishment in temperate Mississippi, USA: multi-year survival confirmed by otolith ages

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### Abstract

Tolerance and adaptability to changing environmental parameters have made Nile tilapia *Oreochromis niloticus* (Linnaeus, 1758) a hardy and desirable aquaculture species. These traits have also enabled this fish to become a highly successful invasive species into temperate and subtropical aquatic environments. Otolith-based ages of Nile tilapia (41.3 – 400.0 mm TL, 1.34 – 1,293 g WW, n = 259) collected from a power plant cooling reservoir and the Pascagoula River proper indicated that feral populations overwintered reaching ages up to 4+ years old in coastal Mississippi, USA; these data confirm their establishment. A survey of mean daily winter (December – February) water temperatures from 2004 – 2010 in this region showed minimum lethal temperatures of < 10°C to occur nearly 11% of the time attesting to the adaptability of the Nile tilapia as an invasive species. One annulus (opaque zone) per year was being deposited from April to August based on marginal increment analysis along with sulcal groove length-age estimation of the young-of-the-year Nile tilapia. Additionally, life history metrics measured for this temperate population of Nile tilapia were nearly identical to those reported from African environments, indicating they are flourishing in this non-native habitat.

**Key words:** Cichlidae, aquaculture, non-native, validation, tilapia

### Introduction

Nile tilapia *Oreochromis niloticus* (Linnaeus, 1758) is native to Africa, ranging from the upper Nile River south to the equator and west to the Atlantic coast (Trewavas 1983). The species is favored among aquaculturists due to its ability to tolerate a wide range of environmental conditions, fast growth, successful reproductive strategies, and ability to feed at different trophic levels. These same traits allow them to be an extremely successful invasive species in subtropical and temperate environments (Peterson et al. 2005).

One of the fallacies that fostered the successful introduction of Nile tilapia and other tilapiine cichlids into temperate environments of the United States (Fuller et al. 1999; Nico and Schofield 2011; Schofield et al. 2011) was the

belief the fish could not survive cold winter temperatures; therefore, concern over escape from aquaculture facilities was minimal. Hargreaves (2000) reports the minimum lethal water temperature for tilapia to range from 7 to 10°C. Peterson et al. (2005) found populations of Nile tilapia thriving along thermal gradients associated with aquaculture facility effluents in coastal Mississippi, USA and suggested thermal refugia coupled with the characteristic oligo-mesohaline habitats of many estuarine areas would increase the likelihood of survival and establishment of non-native Nile tilapia. Mean monthly water temperatures in the winter (December – February) on the Mississippi Gulf Coast typically range from 10 to 17°C with mean daily temperatures ranging from 3 to 19°C (GBNERRSWMP 2010). In fact, non-native Nile tilapia has recently been reported from Nevsehir,

Turkey, the northern most locality of introduction in the Mediterranean region (Mert and Cicek 2010). In this region, monthly winter surface water temperatures were similar to, if not slightly lower than, those observed on the Mississippi Gulf Coast, indicating water temperatures in these areas may not reach fatal minimums for feral Nile tilapia as once perceived. Finally, Nile tilapia and their hybrids also appear to have the ability to adapt to colder temperatures (down to 13.6°C) and possibly inherit cold tolerance (Charo-Karisa et al. 2005). Rising global temperatures (increase of 0.5°C over the past century; McCarty 2001) have already led to natural poleward range extensions of many species (McCarty 2001; Perry et al. 2005; Hickling et al. 2006; Foldrie et al. 2010), as well as enabling invasive species to flourish in new environments (Stachowicz et al. 2002; Rahel and Olden 2008). Moreover, increased temperature tends to reduce native diversity of ecosystems which are then more prone to biological invasion (Stachowicz et al. 1999). This concept is illustrated by the plasticity of Nile tilapia (Duponchelle and Panfili 1998; Duponchelle et al. 1998; Charo-Karisa et al. 2005; Zambrano et al. 2006), allowing easy adaptation to new environments. Recent experimental research has pointed out that Nile tilapia can have important detrimental effects on the structure of the northern Gulf of Mexico food webs through agonistic behavior (Martin et al. 2010), with many invasive cichlids reducing growth and reproduction of native species as well (Lorenz and O'Connell 2008; Doupé et al. 2009; Lorenz et al. 2011).

Previous research has made a strong case for Nile tilapia establishment in coastal Mississippi (Peterson et al. 2004; 2005; 2006). We endeavored to further confirm multi-year survival in this area by examining otolith based ages of individuals from these feral populations. Therefore, our objectives were to 1) validate annuli formation, 2) determine the age of Nile tilapia collected in Mississippi, and 3) examine life-history metrics in relation to age and metrics of Nile tilapia native populations.

## Materials and methods

### *Collection of fish*

Nile tilapia were obtained from two coastal Mississippi, USA watersheds from 2002 – 2006 over the course of several independent projects

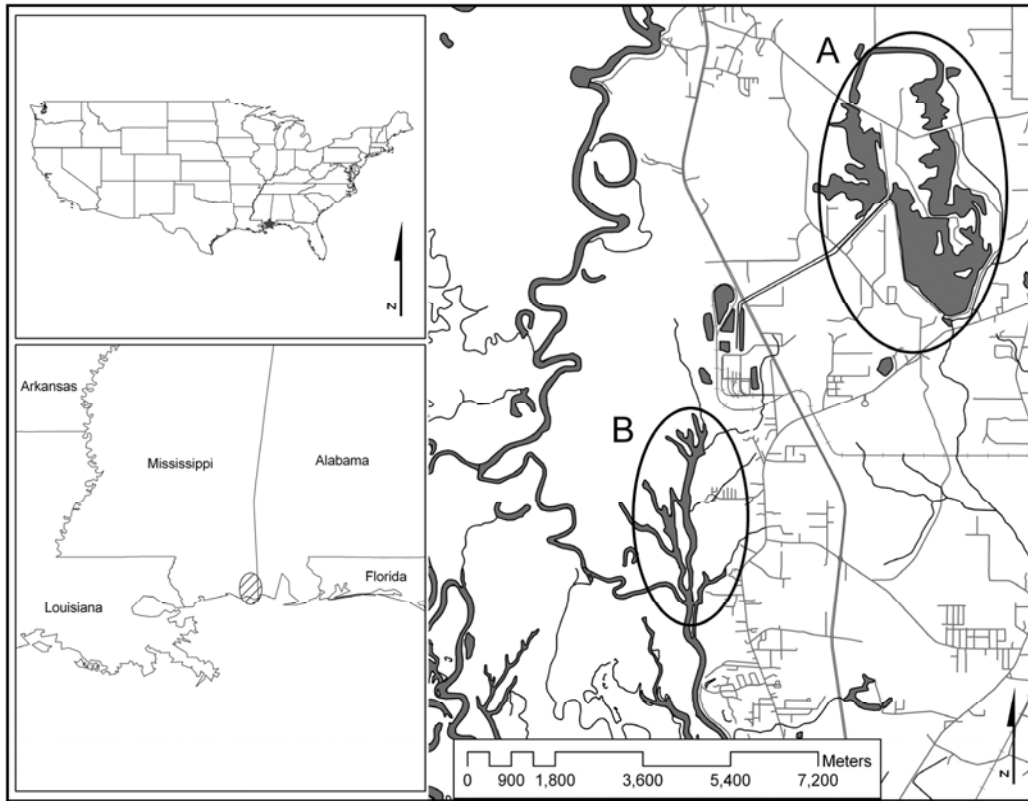
(Peterson et al. 2004; 2005; 2006; Slack et al. 2006). During 2002 and 2004, specimens ('pond' fish) were captured at the Plant Daniel Cooling Reservoir (Jackson Co., Mississippi; Figure 1) located 24 km due north of the Pascagoula River estuary in the Escatawpa River drainage and about 486 water hectares in size (J. Reynolds, Jackson County Port Authority, Pascagoula, Mississippi, personal communication, 2004). The reservoir has a large, established population of Nile tilapia (Peterson et al. 2005; McDonald et al. 2007).

Additional sampling of 'wild' fish was conducted during 2005 and 2006 at numerous stations throughout Clark and Robinson bayous (Jackson Co., MS; Pascagoula River drainage; Figure 1). This area represents individuals introduced into the Pascagoula drainage following accidental releases from nearby aquaculture facilities (Peterson et al. 2005). The outflow from the nearby facilities provided some thermal refugia as geothermal wells were used to heat the ponds (Peterson et al. 2005).

Nile tilapia were collected using a variety of techniques. Trammel nets were the main approach in 2002 – 2004 and were 31 – 61 m long with 0.36 m bar mesh outer panels and a 0.06 m bar mesh inner panel. Nets were fished as either overnight sets (2002) or day sets (2004) and were deployed parallel to the shoreline about 2 – 5 m from the bank. During the later portion of 2004, Nile tilapia were actively targeted with a 2 m cast net fished off the bow of a johnboat in backwater areas of the cooling reservoir. Sampling stations in 2005 – 2006 were fished using hoop nets (1 m hoop diameter; 0.04 m bar mesh) and fyke nets (7.62 m L × 0.91 m H × 5.08 cm bar mesh) set overnight at fixed stations. Sampling in the adjacent bayous consisted of four trammel nets (dimensions as described above) deployed parallel to the shoreline at fixed stations and fished overnight for each sampling event (Slack et al. 2006).

### *Site characterization by water temperature*

Twelve water temperature probes (Hobo® Water Temp Pro, Onset, Inc.) were deployed November 2003 – April 2005 throughout the Plant Daniel Cooling Reservoir to identify thermal gradients within the system. Each probe was attached to a weighted float line approximately one meter above the bottom and programmed to provide an averaged hourly value over the course of their deployment (Slack et al. 2006). Six additional



**Figure 1.** Map of the United State and Mississippi region (insets) with the general study sites in the Escatawpa (A) and Pascagoula River (B) drainages identified by dark circles.

water temperature probes were deployed 28 April 2005 – 15 May 2006 in both Robinson and Clark bayous following the same configurations utilized for the reservoir probes. One probe (Little River Marina) was present at the same location as described by Peterson et al. (2005).

Winter (December – February) water temperature data, recorded as part of the System-wide Monitoring Program of the Grand Bay National Estuarine Research Reserve (Grand Bay NERR), were surveyed from 2004 – 2010 to examine daily mean water temperatures to determine the amount of days at which the temperature fell below the lethal minimum temperature of 10°C. The Grand Bay NERR is located east of the mouth of the Pascagoula River on the Mississippi Gulf Coast, USA and is representative of the sampling region. These data were collected using YSI 6600 data loggers at four permanent stations recording parameters every 15 minutes.

#### *Specimen processing*

Specimens used for otolith aging were fixed in the field in a 95% solution of ethanol (2002) or placed on ice in the field and maintained frozen until data on length and weight could be compiled and sagittal otoliths extracted (2004 – 2006); specimens were processed in the laboratory within two days of collection. Additional voucher specimens were euthanized in the field with MS-222 or clove oil, fixed in 10% formalin solution for 7 – 14 days, washed overnight in fresh water and preserved in 70% ethanol. All voucher specimens were archived in the Mississippi Museum of Natural Science (MMNS) Ichthyology Collection.

Total length (TL, mm) was measured for all fish using digital calipers or a meter tape. Fish < 160 g blotted wet weight (WW, g; 0.001 g) were weighed on an O’HAUS Explorer Pro digital balance (model EP213C; Pine Brook, NJ, USA),

whereas larger fish were weighed on a spring balance (1/8 pound accuracy;  $\pm 57$  g) and the weight converted to grams.

#### *Otolith processing and age estimation*

Sagittal otoliths were removed for annual and daily age estimation, rinsed in water, and stored dry in envelopes; otolith analysis followed Pannella (1971) and Campana and Neilson (1985). The otoliths were mounted in epoxy resin and cut with a Buehler® Isomet® low speed saw (Lake Bluff, IL, USA) in the transverse plane near the primordium. These sections were mounted onto microscope slides with thermoplastic cement and ground using 240 – 1500 grit sandpaper until the sulcus formed a sharp point with the primordium. The otolith sections were given a final polish using Buehler® 0.3  $\mu\text{m}$  Micropolish® Alumina No. 2A Alpha powder (Lake Bluff, IL, USA), and otolith annuli (opaque zones, narrow regions) were counted using an Olympus SZX-ILLK100 dissecting microscope (Olympus America, Center Valley, PA, USA) with transmitted light.

Marginal increment analysis (MIA) was used to confirm annuli formation in adult fish ( $n = 85$ ). Due to the small sample size, all fish with one or more presumed annuli were pooled for the analysis. The distance from the outer edge of the last presumed annulus (opaque zone) to the edge of the otolith was measured using an ocular micrometer (0.01 mm) on an Olympus SZX-ILLK100 dissecting microscope (Olympus America, Center Valley, PA, USA) at 2.5 $\times$  with transmitted light. These measurements were plotted by month ( $\pm 1$  S.E.) to determine the time of annulus formation. Smaller marginal increments denote a period of time near annulus deposition, while larger values indicate an extended time from deposition (Campana and Neilson 1985; Beckman and Wilson 1995).

Each otolith was aged with two blind reads performed at least 3 weeks apart by a single reader counting the otolith annuli. The two different reads were then compared, and the otoliths on which the counts disagreed were reread and compared again. If there was still a deviation, a second reader counted and compared the annuli. If 100% agreement between the different annulus counts did not exist, then the otolith was removed from further analysis.

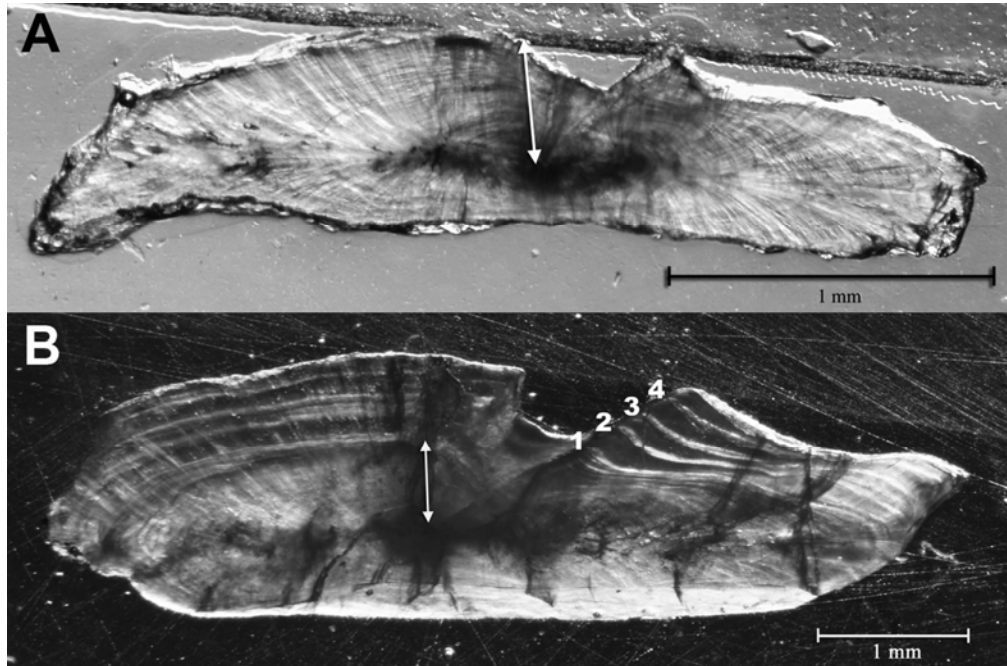
The sulcal groove length (SGL) age estimation technique was used to estimate the age of fish with no annuli ( $< 1$  yr; young-of-the-year

(YOY)) and it relies upon a linear relationship between otolith growth and the growth of the fish in the first year of life (Francis 1995). These body length – otolith radius data are described as the population growth trajectory, which is critical in establishing proportionality between the fish and otolith growth in order to estimate the ages of YOY fish based on otolith measurements from adults (Francis 1995). Gaudie (1996) successfully used a similar technique to estimate ages of blue grenadier (*Macruronus novaezelandiae*), which he found to be strongly correlated to length modes observed in wild fish.

To obtain the SGL, otoliths of YOY fish were measured (mm) along the left side of the sulcal groove in the transverse plane from the primordium to the distal edge of the otolith (Figure 2). The process was also repeated on all fish with at least one annulus ( $n = 85$ ); the measurement on older fish was taken from the primordium to the first annulus instead of the otolith edge. The mean SGL resulting from older individuals was used to calculate SGL ranges that corresponded to three month age increments and this approach allowed the ages of the younger individuals to be estimated based on their respective SGL. The age of fish was used in conjunction with TL and WW to examine weight-age-length characteristics and gain insight into age at sexual maturity.

#### *Statistical Analysis*

We compared male and female Nile tilapia in terms of wet weight (WW, g) and total length (TL, mm) relationships with Analysis of Covariance (ANCOVA), where the covariate was TL. If there was a non-significant relationship between genders, all data were pooled; this included immature fish and adult fish with no gender information (TL and WW data only). Linear regression of TL and SGL was used to verify linear growth rates in YOY fish (Francis 1995) to allow the application of the SGL age estimation technique. A Power Curve function ( $Y = aX^b$ ) was used to describe the TL-WW relationship on the total number of Nile tilapia collected. The von Bertalanffy growth function (VBGF) was fitted to the TL and age data (Ricker 1975; Chen et al. 1992), and is expressed as:  $L_t = L_\infty (1 - e^{-K(t-t_0)})$  where,  $L_t$  is the total length at age  $t$ ,  $L_\infty$  is the asymptotic length,  $K$  is the growth coefficient, and  $t_0$  is the age of the fish at zero length (Ricker 1975). All data were



**Figure 2.** A. Arrow depicts the sulcal groove length (SGL; mm) of a young-of-the-year (YOY) Nile tilapia (100.54 mm TL; 18.23 g WW specimen); SGL = 0.375 mm equating to 6 – 9 months age range. B. Arrow depicts the SGL of an adult Nile tilapia (371 mm TL; 1021 g WW; SGL = 0.575 mm, 4 + yrs by annuli count). This measurement was used to calculate SGL ranges for YOY Nile tilapia (Photographs by G.L. Grammer).

**Table 1.** Sulcal groove length classes used to estimate age in young-of-the-year Nile tilapia. Mean length of primordium to first annulus measured in the transverse plane along the left edge of sulcus in adult Nile tilapia = 0.589 mm.

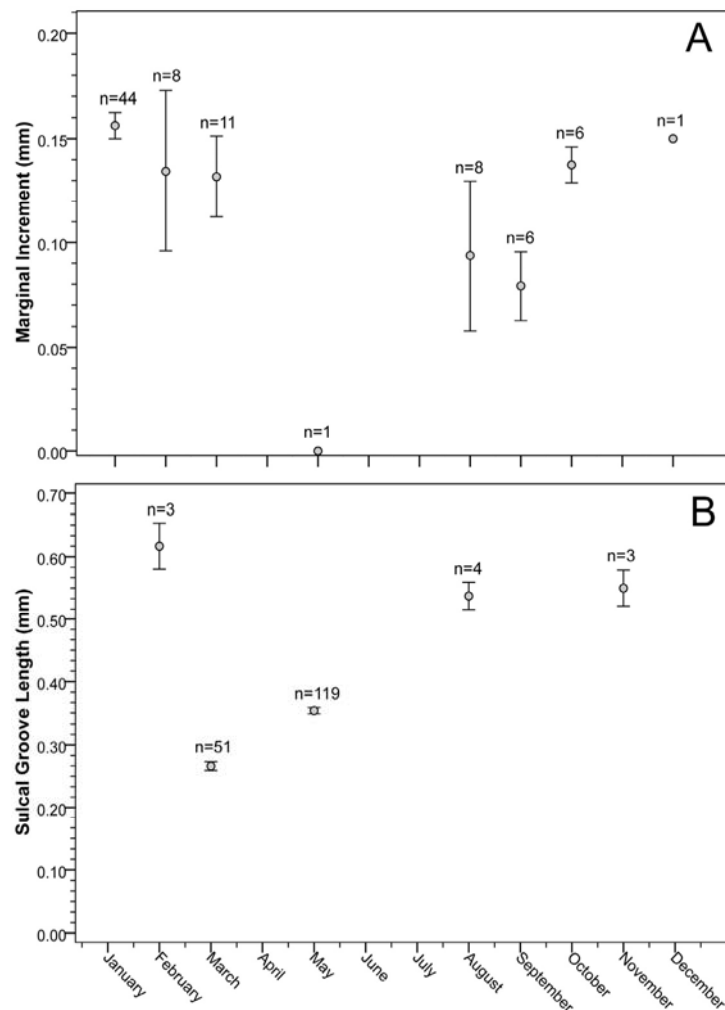
% of 0.589 (n = 85)	Length of increment (mm)	Age (months)	Range (mm)
25	0.147	0 - 3	0.001 - 0.147
50	0.295	3 - 6	0.147 - 0.295
75	0.442	6 - 9	0.295 - 0.442
100	0.589	9 - 12	0.442 - 0.589

checked for homogeneity of variance (Levene’s test) and normality (Kolmogorov-Smirnov one-sample test) prior to analysis and if these assumptions were not met, the data were transformed ( $\log_{10}$ ) prior to analysis (Sokal and Rohlf 1995). All analyses were completed with SPSS 16.0 (SPSS Inc., Chicago, IL, USA) and significant differences were designated if  $p < 0.05$ .

## Results

A total of 259 Nile tilapia (juveniles and adults) were collected from 2002 to 2006 and ranged in size from 41.3 to 400.0 mm TL (1.34 to 1,293 g). All data are presented (mean  $\pm$  1 SE) and analyzed in a non-transformed manner as all data sets met both the normality and homogeneity of variance assumptions. An examination of the temperature probe data illustrated a thermal gradient existing within the Plant Daniel Cooling Reservoir as the data depict a linear correlation ( $r^2 = 0.894$ ;  $p < 0.001$ ) of mean water temperature decreasing along the gradient from the uppermost station (plant effluent) to the lowermost station (return canal). However, the pooled monthly means (across all probes) for the 18 month deployment period illustrated a thermal cycle within the pond that corresponded to normal seasonal temperature fluctuations. Similarly, mean water temperature among the six probes deployed throughout Clark and Robinson bayous differed significantly during the project period (ANOVA:  $F_{(5,55164)} = 106.074$ ;  $p < 0.001$ )

**Figure 3.** A. Marginal increment analysis ( $\pm 1$  S.E.;  $n = 85$ ) of Nile tilapia indicating one increment per year is being deposited in the spring/summer between April and July. B. Sulcal groove length (mm;  $SGL \pm 1$  S.E.;  $n = 180$ ) of Nile tilapia  $\leq 1$  yr increasing from early spring through the fall further supporting the premise that one annulus is deposited per year.



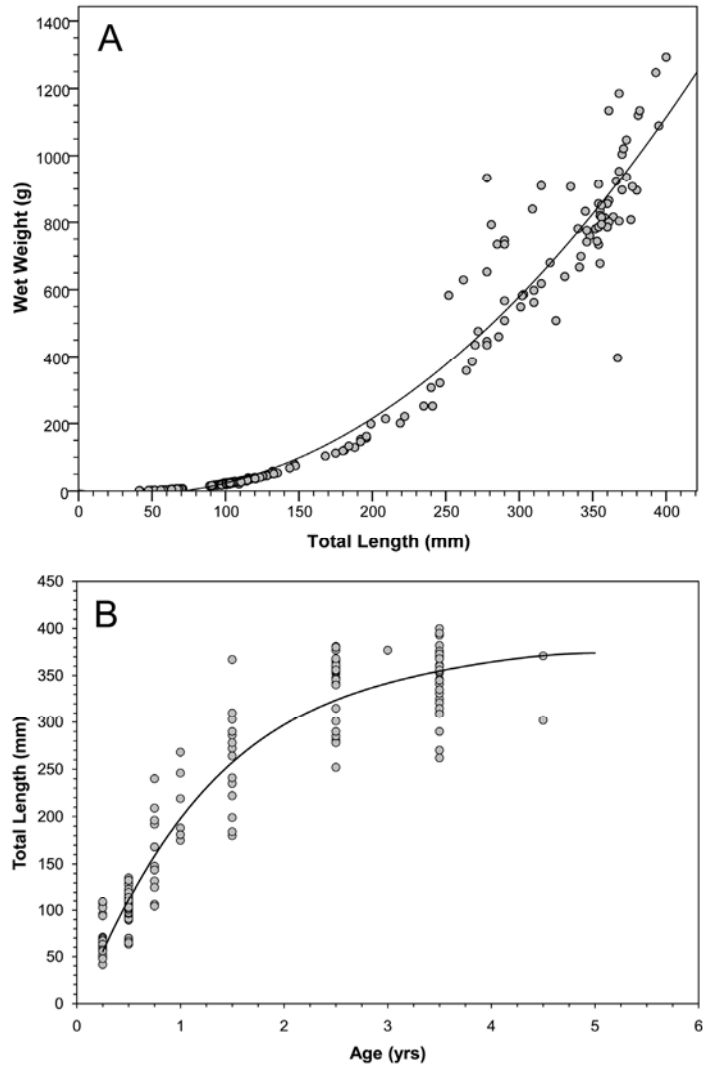
with the water temperatures within the project area again exhibiting a cyclic pattern typical of seasonal changes in temperature. Due to the seasonal signal in water temperature within the cooling pond emulating patterns depicted in the nearby natural system, wild and pond caught fish were pooled for all analyses (wild  $n = 26$ ; pond  $n = 233$ ). Daily mean winter (December – February) water temperatures recorded from 2004 – 2010 at the Grand Bay NERR indicated water temperatures of  $< 10^{\circ}\text{C}$  occurred 10.6% of this time.

#### Otolith analysis

Otolith growth (SGL) was linearly related to TL in Nile tilapia  $\leq 1$  yr ( $r^2 = 0.799$ ;  $p < 0.001$ ;  $n = 180$ ). The SGL ranges corresponding to three

month age increments calculated from the mean SGL (0.589 mm) resulting from older individuals (Table 1). Marginal increment analysis indicated one opaque increment was being deposited yearly between April and July (Figure 3A). The mean SGL is at a minimum in March (0.266 mm) and progressively increased through February (0.617 mm; Figure 3B) supporting the MIA. At this point a young Nile tilapia is almost a year old and would begin to form its opaque increment in the following months as indicated by the MIA (Figure 3A). There does not appear to be an indication of a check (opaque zone) in the fall (mean SGL = 0.550 mm), which supports the premise that one annulus is deposited per year in the spring/summer. Ages for Nile tilapia ranged from 3 – 6 months to 4+ yrs and were distributed among YOY and year classes 1 – 4.

**Figure 4.** A. Plot of total length (mm) versus wet weight (g) of Nile tilapia (n = 259, gender pooled) collected in coastal Mississippi during our study. B. Von Bertalanffy growth function (VBGF) plot of age (yrs) versus total length (mm) of Nile tilapia (n = 259, gender pooled) collected in coastal Mississippi during our study. Equation is  $TL = 165.718 (Age)^{0.671}$  ( $F_{1,257} = 2,847.78, r^2 = 0.917$ ).



### Life history metrics

There was no gender difference in the slope of the TL-WW relationship (ANCOVA homogeneity of slopes,  $p = 0.102$ ); however, WW adjusted for TL differed between males ( $724.42 \text{ g} \pm 17.16$ ) and females ( $692.92 \text{ g} \pm 41.83$ ), but were not statistically significant ( $F_{1,58} = 2.390, p = 0.128$ ). The Power Curve analysis of TL and WW pooled for all fish was  $WW = 0.0000215 (TL)^{2.992}$  ( $F_{1,257} = 41,154.34, r^2 = 0.994$ ; Figure 4A). The VBGF indicated slowing of growth around 3 years of age whereas the analysis for TL and age was  $TL = 165.718 (Age)^{0.671}$  ( $F_{1,257} = 2,847.78, r^2 = 0.917$ ; Figure 4B).

### Discussion

In temperate regions of the northern hemisphere, most species form opaque otolith zones (annuli) during the spring and early summer (April–June), whereas a peak formation period for tropical areas is not as clearly defined (Beckman and Wilson 1995). Opaque zone formation has been attributed to a variety of factors such as food resources, spawning, and climate (Beckman and Wilson 1995), particularly for species in tropical areas (Fowler 1995). However, Pannella (1980) indicated structural differences in otoliths may be related to physiological effects induced by seasonal environmental variation with

temperature being the most important factor. In contrast, Admassu and Casselman (2000) reported biannuli (i.e., two opaque zones per year) to occur in Nile tilapia from Ethiopia and attributed the formation of opaque zones to seasonal decreases in water temperature. Bwankia et al. (2007) also found the deposition of biannuli by Nile tilapia to be closely correlated with decreases in water temperature associated with the two rainy seasons occurring over the course of a year in two lakes in Uganda. We present direct evidence of Nile tilapia producing a single annulus in temperate climates where it has successfully established wild, breeding populations as well as exhibiting nearly identical life history metrics to native, tropical, African populations when compared to appropriate literature from these habitats (e.g., Admassu and Casselman 2000; Bwankia et al. 2007). Weight-length relationships of the temperate Mississippi population ( $b = 2.992$  in the relationship  $Y = aX^b$ ) are almost identical to those presented by Britton and Harper (2006) from Kenya ( $b = 2.908$  in the relationship  $Y = aX^b$ ). Furthermore, our growth trajectory was similar to results from Lowe-McConnell (1958) in East Africa (e.g., current data: 300 mm TL fish = 600 g; Lowe-McConnell: 300 mm TL fish = 600 g), and the Mississippi population's age-length relationships (e.g., 350 mm TL Nile tilapia = 3.5 yrs) reflected those from native habitats (e.g., 350 mm TL Nile tilapia = 3.5 yrs; Bwanika et al. 2007).

In coastal Mississippi, Nile tilapia spawned from March to May and again from August to September (Peterson et al. 2004). Native African Nile tilapia also display the same bimodal spawning pattern (Admassu 1996) indicating two cohorts should be evident; one in the spring and one occurring in the fall (Yosef and Casselman 1995; Admassu and Casselman 2000). We did not, however, observe two cohorts of YOY fish as expected (Peterson et al. 2004), which was most likely a bias of multiple sampling gears used over the course of several independent projects or possibly resulting from a lower first winter survival of the fall cohort. Within the current dataset, the large TL range seen in older age classes as well as the long period over which an annulus is being formed (April – July) is likely the result of the presence of these two different, albeit unverified, cohorts in the coastal Mississippi population.

Nile tilapia are readily able to adapt and thrive in a variety of conditions. An example of this

remarkable adaptability is presented by Duponchelle and Panfili (1998) who found Nile tilapia in reservoirs (from 6 to 8000 ha) of Côte d'Ivoire to become mature between 91 – 132 mm SL (5.6 – 10 months of age). The results confirmed a positive correlation between size/age-at-maturity and the size of the water body in which Nile tilapia were found. Fish living in larger lakes exhibited a higher size/age-at-maturity than did those found in small agropastoral reservoirs. In comparing the Mississippi non-native Nile tilapia population, fifty percent maturity in females has been reported by Peterson et al. (2004) to be 113 mm TL, with the smallest mature female being 79.9 mm TL. Results from the current research would indicate that these fish were between 6 to 9 months old. The Mississippi population was collected in a 486 water hectares reservoir and in smaller streams. These results, again, fit closely with what is seen in native habitats and demonstrates the phenotypic plasticity of the species.

Considering the consistency of both length-weight and length-age relationships between Mississippi populations and native African populations coupled with previous research on this population (Peterson et al. 2004, 2005, 2006; McDonald et al. 2007; Schofield et al. 2011), it can be concluded that the tropical Nile tilapia has successfully invaded a temperate climate with multi-year survivorship. These data are useful for state and federal permitting and management agencies when making critical decisions on approving specific species to culture and citing new aquaculture facility locations (Schofield et al. 2007). These results should especially be taken into account in climatic transition regions where the environmental conditions could potentially allow for the establishment of Nile tilapia upon introduction, particularly as the global temperature is increasing.

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## References

- Admassu D (1996) The breeding season of tilapia, *Oreochromis niloticus* L. in Lake Awassa (Ethiopian Rift Valley). *Hydrobiologia* 337: 77–83, [http://dx.doi.org/10.1007/BF0002\\_8508](http://dx.doi.org/10.1007/BF0002_8508)
- Admassu D, Casselman JM (2000) Otolith age determination for adult tilapia, *Oreochromis niloticus* L. from Lake Awassa (Ethiopian Rift Valley) by interpreting biannuli and differentiating biannual recruitment. *Hydrobiologia* 418: 15–24, <http://dx.doi.org/10.1023/A:1003883419105>
- Beckman DW, Wilson CA (1995) Seasonal timing of opaque zone formation in fish otoliths. In: Secor DH, Dean JM, Campana SE (eds), Recent Developments in Fish Otolith Research. University of South Carolina Press, Columbia, USA, pp 27–44
- Britton JR, and Harper DM (2006) Length-weight relationships of fish species in the freshwater rift valley lakes of Kenya. *Journal of Applied Ichthyology* 22: 334–336, <http://dx.doi.org/10.1111/j.1439-0426.2006.00769.x>
- Bwanika GN, Murie DJ, Chapman LJ (2007) Comparative age and growth of Nile tilapia (*Oreochromis niloticus* L.) in lakes Nabugabo and Wamala, Uganda. *Hydrobiologia* 589: 287–301, <http://dx.doi.org/10.1007/s10750-007-0746-y>
- Campana SE, Neilson JD (1985) Microstructure of fish otoliths. *Canadian Journal of Fisheries and Aquatic Sciences* 42: 1014–1032, <http://dx.doi.org/10.1139/f85-127>
- Charo-Karisa H, Rezk MA, Bovenhuis H, Komen H (2005) Heritability of cold tolerance in Nile tilapia, *Oreochromis niloticus*, juveniles. *Aquaculture* 249: 115–123, <http://dx.doi.org/10.1016/j.aquaculture.2005.04.029>
- Chen Y, Jackson DA, Harvey HH (1992) A comparison of von Bertalanffy and polynomial functions in modeling fish growth data. *Canadian Journal of Fisheries and Aquatic Sciences* 49: 1228–1235, <http://dx.doi.org/10.1139/f92-138>
- Duponchelle F, Panfili J (1998) Variations in age and size at maturity of female Nile tilapia, *Oreochromis niloticus*, populations from man-made lakes of Cote d'Ivoire. *Environmental Biology of Fishes* 52: 453–465, <http://dx.doi.org/10.1023/A:1007453731509>
- Duponchelle F, Pouyaud L, Legendre M (1998) Evidence of environmental effects on reproductive characteristics of Nile tilapia (*Oreochromis niloticus*) populations from man-made lakes of Cote d'Ivoire. *Aquatic Living Resources* 11: 137–144, [http://dx.doi.org/10.1016/S0990-7440\(98\)80110-1](http://dx.doi.org/10.1016/S0990-7440(98)80110-1)
- Doupé, RG, Schaffer J, Knott MJ, Burrows DW (2009) How might an exotic fish disrupt spawning success in a sympatric native species? *Marine and Freshwater Research* 60: 379–383, <http://dx.doi.org/10.1071/MF08184>
- Foldrie FJ, Heck KL, Powers SP, Graham WM, Robinson KL (2010) Climate-related, decadal-scale assemblages changes of seagrass-associated fishes in the northern Gulf of Mexico. *Global Change Biology* 16: 48–59, <http://dx.doi.org/10.1111/j.1365-2486.2009.01889.x>
- Fowler AJ (1995) Annulus formation in otoliths of coral reef fish – a review. In: Secor DH, Dean JM, Campana SE (eds), Recent Developments in Fish Otolith Research. University of South Carolina Press, Columbia, USA, pp 45–63
- Francis RICC (1995) The analysis of otolith data – a mathematician's perspective (what, precisely, is your model?). In: Secor DH, Dean JM, Campana SE (eds), Recent Developments in Fish Otolith Research. University of South Carolina Press, Columbia, USA, pp 81–95
- Fuller PL, Nico LG, Williams JD (1999) Nonindigenous Fishes: Introduced Into Inland Waters of the United States. American Fisheries Society Special Publication 27, Bethesda, Maryland, USA, 613 pp
- Gauldie RW (1996) Ages estimated from average microincrement width in otoliths of *Macrurus novaezelandiae* are verified by length mode progressions. *Bulletin of Marine Science* 59: 498–507
- GBNERRSWMP (2010) Grand Bay National Estuarine Research Reserve System Wide Monitoring Program (GBNERRS WMP) Water Quality Data: 2004 – 2010. <http://cdmo.baruch.sc.edu/get/export.cfm> (Accessed 23 August 2010)
- Hargreaves JA (2000) Tilapia culture in the southeastern United States. In: Costa-Pierce BA, Rakocy JE (eds), Tilapia Aquaculture in the Americas, Volume 2. The World Aquaculture Society, Baton Rouge, Louisiana, USA, pp 60–81
- Hickling R, Roy DB, Hill JK, Fox R, Thomas CD (2006) The distributions of a wide range of taxonomic groups are expanding polewards. *Global Change Biology* 12: 450–455, <http://dx.doi.org/10.1111/j.1365-2486.2006.01116.x>
- Lorenz OT, O'Connell MT (2008) Growth of non-native Rio Grande cichlids (*Herichthys cyanoguttatus*) at different salinities and in the presence of native bluegill *Lepomis macrochirus*. *Journal of Freshwater Ecology* 23: 537–544, <http://dx.doi.org/10.1080/02705060.2008.9664241>
- Lorenz OT, O'Connell MT, Schofield PJ (2011) Aggressive interactions between the invasive Rio Grande cichlid (*Herichthys cyanoguttatus*) and native bluegill (*Lepomis macrochirus*), with notes on redspotted sunfish (*Lepomis miniatus*). *Journal of Ethology* 29: 39–46, <http://dx.doi.org/10.1007/s10164-010-0219-z>
- Lowe-McConnell RH (1958) Observations on the biology of *Tilapia nilotica* Linné in East African waters. *Revue Zoologie Botanique Africaines* 57: 129–170
- Martin CW, Valentine MM, Valentine JF (2010) Competitive interactions between invasive Nile tilapia and native fish: the potential for altered trophic exchange and modification of food webs. *PLoS One* 5(12): e14395, [http://dx.doi.org/10.1371/journal.pone.001\\_4395](http://dx.doi.org/10.1371/journal.pone.001_4395)
- McCarty JP (2001) Ecological consequences of recent climate change. *Conservation Biology* 15: 320–331, <http://dx.doi.org/10.1046/j.1523-1739.2001.015002320.x>
- McDonald JL, Peterson MS, Slack WT (2007) Morphology, density and spatial patterning of reproductive bowers in an established alien population of Nile tilapia, *Oreochromis niloticus* Linnaeus. *Journal of Freshwater Ecology* 22: 461–468, <http://dx.doi.org/10.1080/02705060.2007.9664176>
- Mert R, Cicek E (2010) Range expansion of introduced tilapia species (*Oreochromis niloticus*, L. 1758) in Turkey. *Journal of Animal and Veterinary Advances* 9: 1753–1756, <http://dx.doi.org/10.3923/javaa.2010.1753.1756>
- Nico LG, Schofield PJ (2011) *Oreochromis niloticus*. United States Geological Survey Nonindigenous Aquatic Species Database – USGS NAS. <http://nas.er.usgs.gov/queries/factsheet.aspx?SpeciesID=468> (Accessed 11 March 2011)
- Pannella G (1971) Fish otoliths: daily growth layers and periodical patterns. *Science* 173:1124–1127, <http://dx.doi.org/10.1126/science.173.4002.1124>
- Pannella G (1980) Growth patterns in fish sagittae. In: Rhodes DC, Lutz RA (eds), Skeletal Growth of Aquatic Organisms. Plenum Press, New York, USA, pp 519–560
- Perry AL, Low PJ, Ellis JR, Reynolds JD (2005) Climate change and distribution shifts in marine fishes. *Science* 308: 1912–1915, <http://dx.doi.org/10.1126/science.1111322>
- Peterson MS, Slack WT, Brown-Peterson NJ, McDonald JL (2004) Reproduction in non-native environments: establishment of Nile tilapia, *Oreochromis niloticus* (Linnaeus) in coastal Mississippi watersheds. *Copeia* 2004: 842–849, <http://dx.doi.org/10.1643/CE-04-134R1>
- Peterson MS, Slack WT, Woodley CM (2005) The occurrence of nonindigenous Nile Tilapia, *Oreochromis niloticus* (Linnaeus) in coastal Mississippi: ties to aquaculture and thermal effluent. *Wetlands* 25: 112–121, [http://dx.doi.org/10.1672/0277-5212\(2005\)025\[0112:TOONNT\]2.0.CO;2](http://dx.doi.org/10.1672/0277-5212(2005)025[0112:TOONNT]2.0.CO;2)

- Peterson MS, Slack WT, Waggy GL, Finley J, Woodley CM, Partyka ML (2006) Foraging in non-native environments: comparison of Nile Tilapia and three co-occurring native centrarchids in invaded coastal Mississippi watersheds. *Environmental Biology of Fishes* 76: 283–301, <http://dx.doi.org/10.1007/s10641-006-9033-4>
- Rahel FJ, Olden JD (2008) Assessing the effects of climate change on aquatic invasive species. *Conservation Biology* 22: 521–533, <http://dx.doi.org/10.1111/j.1523-1739.2008.00950.x>
- Ricker WE (1975) Computation and Interpretation of Biological Statistics of Fish Populations. Fisheries Research Board of Canada. Bulletin 191, 382 pp
- Schofield PJ, Slack WT, Peterson MS, Gregoire DR (2007) Assessment and control of an invasive aquaculture species: an update on Nile tilapia (*Oreochromis niloticus*) in coastal Mississippi after Hurricane Katrina. *Southeastern Fishes Council Proceedings* 49: 9–15
- Schofield PJ, Peterson MS, Lowe MR, Brown-Peterson N, Slack WT (2011) Survival, growth and reproduction of nonindigenous Nile tilapia (*Oreochromis niloticus* (Linnaeus, 1758)). I. Physiological capabilities to various temperatures and salinities. *Marine and Freshwater Research* 62:439–449, <http://dx.doi.org/10.1071/MF10207>
- Slack WT, Dugo MA, Peterson MS (2006) Habitat association and dispersion of non-indigenous Nile tilapia (Cichlidae: *Oreochromis niloticus*) in southern Mississippi waterbodies through the use of telemetry. Mississippi Museum of Natural Science. Museum Technical Report 125, 96 pp
- Sokal RR, Rohlf FJ (1995) Biometry: The Principles and Practice of Statistics in Biological Research, 3rd edn. W.H. Freeman, New York, USA, 887 pp
- Stachowicz JJ, Whitlatch RB, Osman RW (1999) Species diversity and invasion resistance in a marine ecosystem. *Science* 286: 1577–1579, <http://dx.doi.org/10.1126/science.286.5444.1577>
- Stachowicz JJ, Terwin JR, Whitlatch RB, Osman RW (2002) Linking climate change and biological invasions: ocean warming facilitates nonindigenous species invasions. *Proceedings of the National Academy of Sciences* 99: 15497–15500, <http://dx.doi.org/10.1073/pnas.242437499>
- Trewavas E (1983) Tilapiine Fishes of the Genera *Sarotherodon*, *Oreochromis* and *Danakilia*. British Museum (Natural History), London, UK, 583 pp
- Yosef T, Casselman JM (1995) A procedure for increasing the precision of otolith age determination of tropical fish by differentiating biannual recruitment. In: Secor DH, Dean JM, Campana SE (eds), Recent Developments in Fish Otolith Research. University of South Carolina Press, Columbia, USA, pp 247–269
- Zambrano L, Martinez-Meyer E, Menezes N, Peterson AT (2006) Invasive potential of common carp (*Cyprinus carpio*) and Nile tilapia (*Oreochromis niloticus*) in American freshwater systems. *Canadian Journal of Fisheries and Aquatic Science* 63: 1903–1910, <http://dx.doi.org/10.1139/f06-088>