

Research Article

Museum specimens answer question of historic occurrence of Nile tilapia *Oreochromis niloticus* (Linnaeus, 1758) in Florida (USA)

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Abstract

Nile tilapia *Oreochromis niloticus* (Linnaeus, 1758) is difficult to distinguish from the blue tilapia *Oreochromis aureus* (Steindachner, 1864), a species with which it readily hybridizes, and that has a well-documented invasion history from 1961 in Florida (USA). Extracting the differential histories of these two tilapia species is of particular interest for Florida invasive species regulation, but also is relevant for at least 32 countries where both species have been introduced. Museum specimens can provide key data to answer historical questions in invasion biology. Therefore I examined preserved specimens at the Florida Museum of Natural History (UF) (1) for misidentified Nile tilapia or the presence of Nile tilapia traits in blue tilapia specimens, (2) for misidentified Nile tilapia in other tilapia collections, and (3) to morphologically characterize Florida specimens of blue tilapia, Nile tilapia, and putative hybrids. The U.S. Geological Survey's Nonindigenous Aquatic Species (USGS NAS) database was also examined for blue tilapia and Nile tilapia records. Blue tilapia lots dated to 1970, putative hybrids were present in blue tilapia lots since 1972 (10 counties), and Nile tilapia lots dated to 2007 (5 counties) in the UF collection. Hybrids were not detectable using the USGS NAS, but the broader range of source data for the two species resulted in earlier dates and wider occurrence than the UF collection (blue tilapia from 1961; Nile tilapia from 2006 in 18 counties). Meristics of Florida tilapia differed slightly from published accounts of tilapia in their native range. In Florida, blue tilapia and hybrids did not statistically differ whereas most counts from Nile tilapia were higher but overlapping. Dorsal fin spine counts of 17 or 18 were nearly diagnostic for Nile tilapia. The best character to distinguish Nile tilapia was distinct caudal fin barring; hybrids had indistinct or incomplete barring whereas blue tilapia lacked caudal barring. The results show that Nile tilapia traits have been present in blue tilapia stocks for at least 45 years, suggesting that early introductions likely contained hybrid tilapia. This study supports the risk-based decision to harmonize blue tilapia and Nile tilapia regulations in Florida.

Key words: Blue tilapia, *Oreochromis aureus*, hybrid, identification, meristics

Introduction

Species invasions are inherently historical events and thus a variety of historical questions are of particular relevance (Williamson 1996). Natural history collections in museums are ideal venues for such investigations. Many questions involve confirmation or differentiation of species identity, including cryptogenic, sibling, or morphologically similar species (Hewitt et al. 2004), evolutionary changes in invasive species (Marisco et al. 2010), and, increasingly, genetic studies (Wandeler et al. 2007). Investigations

disentangling complex invasion history can help resolve issues ranging from eco-evolutionary processes to applied management. Museum collections provide some of the highest quality historic data because researchers can examine the actual specimens. Such specimens therefore represent a treasure trove of data for answering a wide range of historical questions. In particular, museum specimens have been used to provide data on historic ranges of organisms as diverse as insects (DeWalt et al. 2009; Cameron et al. 2011), fishes (Fagan et al. 2005), and mammals (Zielinski et al. 2005).

The history of invasion and establishment of Nile tilapia, *Oreochromis niloticus* (Linnaeus, 1758), in peninsular Florida (USA) is poorly known, especially when compared to the highly similar congener blue tilapia, *Oreochromis aureus* (Steindachner, 1864). Extracting the differential histories of these two tilapia species is of particular interest for Florida invasive species management and regulation. Moreover, distinguishing these species, documenting their invasion history, understanding hybrid dynamics, and determining potentially differential ecological impacts are important questions for many world regions. These species are among the most widely introduced fishes worldwide and have been introduced together into at least 32 countries (Froese and Pauly 2017).

The history of introduction, establishment, and spread of blue tilapia is among the best documented for any non-native fish in Florida (Hale et al. 1995). The Florida Game and Fresh Water Fish Commission (later Florida Fish and Wildlife Conservation Commission, FWC) brought tilapia stock from Auburn University in 1961 to the Pleasant Grove Research Center in Hillsborough County for research on their utility for stocking as food, game, or forage fish and for aquatic weed control (Crittenden 1965; Hale et al. 1995). Although it was quickly determined that blue tilapia was not desirable for these functions, a number of fish had been taken by or distributed to the public (Buntz and Manooch 1968). These fish were released into central Florida waters, particularly into the Peace River basin. By 1968 this non-native species was found in at least 12 central Florida counties (USGS 2017). It is the most widespread and successful of Florida's introduced tilapia species (Shafland et al. 2008), with current populations in nearly all peninsular Florida counties (USGS 2017).

State regulations on possession, culture, and sale of tilapia in Florida differ considerably and are based on morphological identification (Hardin 2011a; Hill 2013). Because of its long history of establishment and spread throughout the peninsula, blue tilapia in most of the state does not require a permit and live sale to the public is legal. This fish supports aquaculture for food and fingerlings, haul-seine fisheries in central Florida and Lake Okeechobee, and cast net fisheries around the peninsula (Hale et al. 1995; personal observations). Conversely, the Nile tilapia, presumably a recent introduction, requires a conditional species authorization with concomitant increased regulatory conditions for containment and live sale to the public is prohibited (Hill 2013). Nevertheless, Nile tilapia is an important food aquaculture species in Florida. The morphological similarity of blue tilapia and Nile tilapia, plus the common

occurrence of hybrids of these and other species in aquaculture stocks (Hill 2011, 2014), has made enforcement and other management by agencies and compliance by industry and the public difficult. In fact, some researchers consider all captive and wild stocks in the United States to be hybrids (Costa-Pierce 2003; B. Costa-Pierce, Rhode Island Sea Grant, personal communication), rendering identification-based management futile.

A joint FWC-Florida Department of Agriculture and Consumer Services risk analysis was funded by the U.S. Fish and Wildlife Service in 2011 to consider relaxing Florida regulations for blue tilapia (Hardin 2011a, b; Hill 2011). It was determined that the difficulty in identifying tilapia stocks and the presence of small numbers of Nile tilapia in fish surveys from the state meant that more information was needed on the distribution, history of introduction, ecological performance, and potential risks of the closely related Nile tilapia and their hybrids. This led to an additional literature review of Nile tilapia (Hill 2014) and a variety of risk management discussions among agencies, academia, and industry. Recommendations included a survey of the state to ascertain current distribution of Nile tilapia and putative hybrids, and an attempt to determine how long this taxon had existed outside of captivity in Florida (Hardin 2011a, b; personal observations). If the Nile tilapia invasion was as recent and discrete as suggested by database records then regulations would likely maintain the *status quo* to slow the spread of this species in the state. Conversely, if Nile tilapia were more widespread, especially if they had been in the region for a relatively long time, then harmonizing blue tilapia and Nile tilapia regulations would improve and streamline management for the agencies and industry at little increase to invasiveness risk.

Confirmed records of Nile tilapia in peninsular Florida dated back only to 2006 (USGS 2017), suggesting that this is a recently introduced species. However, anecdotal reports suggest that Nile tilapia or hybrids have been present since at least the 1970s. Morphological and genetic sampling of limited scope have revealed a greater spatial extent of Nile tilapia individuals than anticipated, raising questions as to the actual time of introduction. The present study assesses whether Nile tilapia has been present but overlooked in Florida, potentially for decades. The overall goal of the study was to determine if evidence of the presence of Nile tilapia or characteristic traits of Nile tilapia existed in historic tilapia collections in the Florida Museum of Natural History (UF). Specific objectives were to (1) examine all blue tilapia specimens for misidentified Nile tilapia or the presence of Nile tilapia traits, (2) determine if

Table 1. Characters known to distinguish blue tilapia and Nile tilapia (Trewavas 1983).

Characteristics	Blue Tilapia	Nile Tilapia
Caudal fin	Vague, variable, or non-existent vertical barring	Distinct, vertical barring
Dorsal fin spines	15–16, mode 16 (rare 14 or 17)	16–18, mode 17
Total dorsal fin spines + rays	27–30, mode 29	29–31, mode 30
Lateral line scales (upper series)	30	31–32
Vertebrae ¹	28–31, mode 30	30–32, mode 31
Breeding color (males) ^{1,2}	Metallic blue on head and flanks; vermilion on dorsal; pink on caudal edge	Red or pink flush

¹Not evaluated in the present study.

²Corresponds well with field observations of spawning males in Florida (personal observations). Spawning male Nile Tilapia locally known as “pinkies” in Florida.

misidentified Nile tilapia existed in other tilapia collections, and (3) morphologically characterize Florida specimens of blue tilapia, Nile tilapia, and putative hybrids.

Methods

Preserved tilapia specimens from UF were examined and identified using morphological characters following Trewavas (1983). Holdings examined in detail included 150 lots labeled as blue tilapia totaling 1,954 individuals, plus 9 lots labeled Nile tilapia totaling 37 individuals (Appendix 1). Additional lots labeled *Oreochromis*, *Sarotherodon*, or *Tilapia* were evaluated for the potential inclusion of misidentified Nile tilapia. Supplemental information was obtained from the U.S. Geological Survey’s Nonindigenous Aquatic Species database (USGS NAS), which obtains data from scientific literature, field biologists, and museums, including UF (USGS 2017).

Distinguishing traits used in the study included presence or absence of caudal fin barring, number of dorsal fin spines, overall number of dorsal fin spines plus rays, and number of scales in the upper (first) lateral line series (Table 1). Blue tilapia has lower but overlapping ranges of most meristic traits (Trewavas 1983). Some pigmentation differences occur, but most, such as male coloration during breeding season, are only useful for live specimens. In practice, distinct caudal barring is the best character (Trewavas 1983) and has been used as the predominant distinguishing character for morphological identification of wild and captive tilapia stocks by Florida state agencies (K. Gestring, FWC, personal communication; personal observations). Distinct barring indicates Nile tilapia but this character is highly variable in bar width, number, distinctiveness, and proportion of caudal fin covered (Figure 1). Two previously recognized subspecies, *O. n. cancellatus* and *O. n. sugutae*, lack caudal barring or have incomplete barring (Trewavas 1983). Interpretations by agency and academic

scientists, and agency compliance staff in Florida, have been that fish (1) with distinct barring have been categorized as Nile tilapia, (2) without barring or with indistinct, fuzzy barring on a portion of the fin as blue tilapia, and (3) with fuzzy barring throughout or distinct barring on only a portion of the caudal fin as potential hybrids (K. Gestring, FWC, personal communication; personal observations). This character is not useful for small juveniles, generally < 50–60 mm standard length, because blue tilapia of this size may have strongly barred caudal fins (Trewavas 1983; personal observations).

One-way analysis of variance was used to test for mean differences ($P < 0.05$) among blue tilapia, hybrid tilapia, and Nile tilapia in dorsal fin spine counts and total dorsal fin and ray counts. Significant tests were followed by *t*-tests to determine which means were different. All analyses were done in Microsoft Excel 2010.

Results

Blue tilapia is the most widely distributed tilapia in the state with records from nearly all peninsular Florida counties (Figure 2). Museum holdings date back to 1970 from Lake Parker in Polk County (UF#146230) whereas USGS NAS records, which are often derived from literature sources, go back to the original introduction in eastern Hillsborough County in 1961 (Figure 2).

At least 32 individual fish in 19 lots labeled as blue tilapia had a level of caudal barring that indicated that they were putative hybrids with Nile tilapia (Table 2). The earliest collection with Nile tilapia characters was in 1972 from Lake Parker in Polk County (UF#91868). Holdings included putative hybrids from 10 counties of peninsular Florida, widely distributed from Duval in the north to Miami-Dade in the south (Figure 2). No evidence was found of Nile tilapia mixed with other species of tilapia.

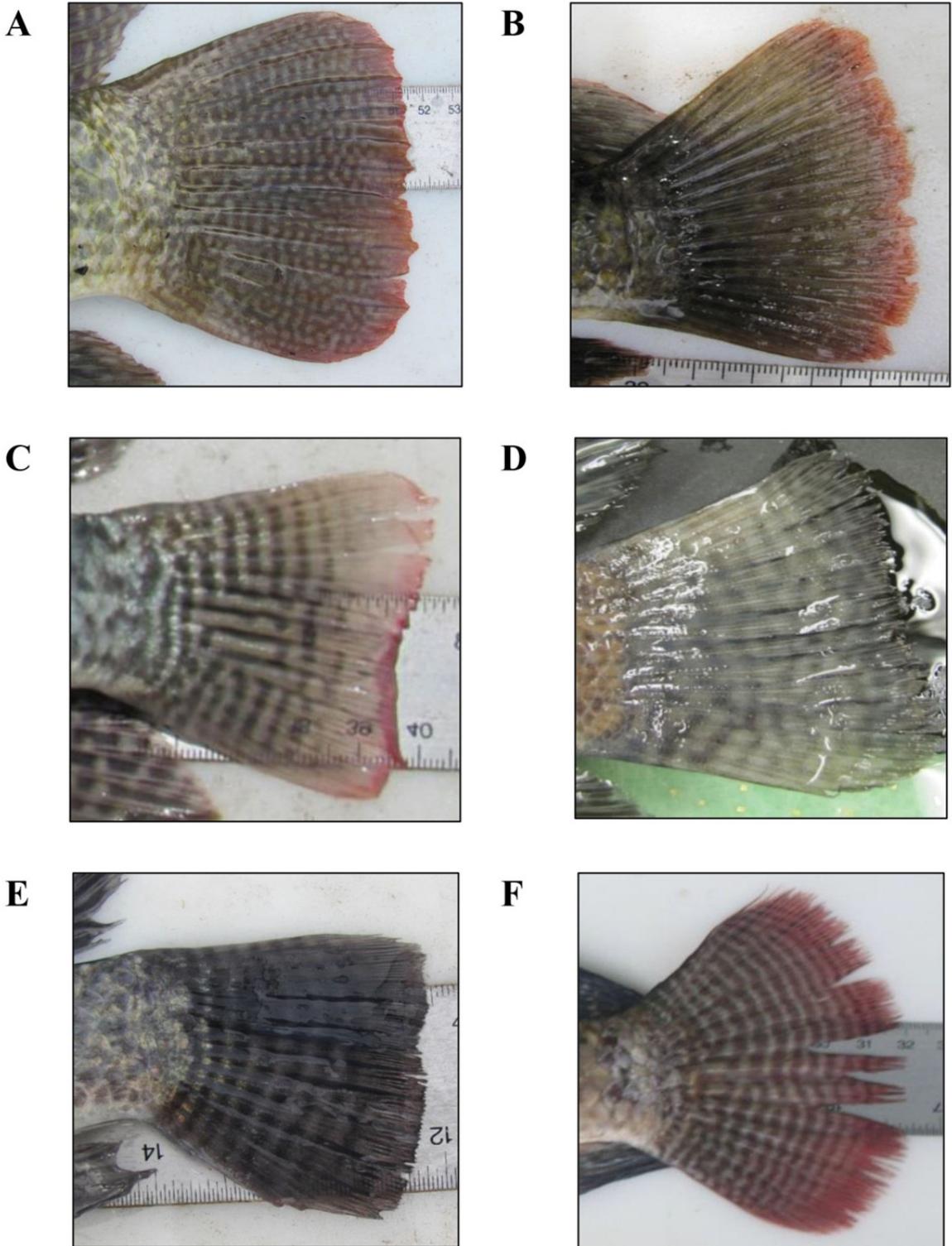


Figure 1. Representative caudal fin patterns of (A) and (B) blue tilapia, (C) hybrid resembling blue tilapia, (D) hybrid resembling Nile tilapia, and (E) and (F) Nile tilapia. Photos A-E by Jeffrey E. Hill; photo F by Florida Fish and Wildlife Conservation Commission.

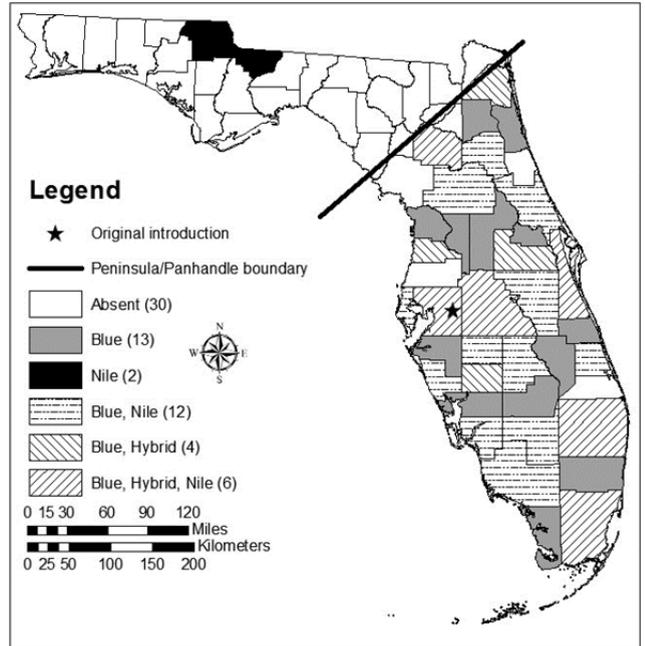


Figure 2. Distribution of tilapia in Florida by county. The numbers in parentheses indicate the number of Florida counties in the category. The solid line separates the peninsula from north Florida/panhandle. Gadsden and Jackson County in the panhandle indicate the presence of Nile tilapia in Lake Seminole on the Florida-Georgia line since the early 1990s (USGS 2017). Source data Florida Museum of Natural History and U.S. Geological Survey Nonindigenous Aquatic Species database.

Table 2. UF catalog numbers, drainage basin, county, and year of collection for Florida blue tilapia specimens with Nile tilapia traits, especially barring on the caudal fin (i.e., putative hybrids).

UF Catalog Number	Drainage	County	Year
91868	Peace River	Polk	1972
146277	Everglades	Palm Beach	1974
146235	Peace River	Polk	1977
146840	Withlacoochee River	Hernando	1977
146294	Everglades	Miami-Dade	1978
146848	Lower St. Johns-Oklawaha River	Orange	1980
146225	Everglades	Palm Beach	1982
146265	Everglades	Palm Beach	1984
146844	Lower St. Johns-Oklawaha River	Alachua	1988
90785	Biscayne Bay	Miami-Dade	1992
90885	Alafia River	Hillsborough	1992
92094	Peace River	Polk	1992
92175	Everglades	Miami-Dade	1992
98921	Tampa Bay	Hillsborough	1993
99000	Lower St. Johns-Oklawaha River	Alachua	1993
126691	Upper St. Johns River	Brevard	2000
182440	Everglades	Palm Beach	2005
187525	Lower St. Johns River	Duval	2013
190583	Peace River	DeSoto	2013

Table 3. Characters of blue tilapia, putative hybrids, and Nile tilapia from Florida specimens.

Characters	Blue Tilapia	Hybrid Tilapia	Nile Tilapia
Caudal fin	Barring vague, broken, or nonexistent	Barring variable; some distinct, vertical barring covering part of fin (proximal, distal, dorsal, or ventral)	Distinct, vertical barring either perpendicular to horizontal plane or curved in relative parallel to distal curve of fin
Dorsal fin spines	14–16, mode 15	14–18, mode 15	15–18, mode 16–17
Total dorsal fin spines + rays	25–30, mode 27	26–30, mode 27	27–30, mode 29
Lateral line scales (upper series)	29–32	29–32	30–32

Table 4. One-way analysis of variance (ANOVA) testing for mean differences among blue tilapia, hybrids, and Nile tilapia for mean dorsal fin spines and mean total dorsal fin spines and rays. Significant ANOVAs were followed by t-tests as a multiple comparison procedure to distinguish different means. An asterisk “*” indicates significant results ($P < 0.05$).

ANOVA (Dorsal fin spines)						
Source of Variation	SS	df	MS	F	P-value	F crit
Between Groups	31.57553	2	15.78776	38.01976	1.11E-14*	3.04199
Within Groups	81.3893	196	0.415252			
Total	112.9648	198				

Blue Tilapia and hybrid: $t_{0.05, 171} = -0.693$, $P = 0.489$

Nile Tilapia and hybrid: $t_{0.05, 55} = 0.574$, $P < 0.0001^*$

ANOVA (Total dorsal fin spines and rays)						
Source of Variation	SS	df	MS	F	P-value	F crit
Between Groups	16.54534	2	8.272672	4.756404	0.013368*	3.204317
Within Groups	78.26716	45	1.73927			
Total	94.8125	47				

Blue Tilapia and hybrid: $t_{0.05, 9} = -1.518$, $P = 0.163$

Nile Tilapia and hybrid: $t_{0.05, 12} = -0.943$, $P = 0.364$

Blue Tilapia and Nile Tilapia: $t_{0.05, 7} = -3.013$, $P = 0.0196^*$

Meristics of blue tilapia and hybrids hardly differed (Tables 3 and 4). Dorsal spine counts of blue tilapia averaged 15.3 (SD = 0.60) and hybrids averaged 15.4 (SD = 0.80). The dorsal spine count of blue tilapia ranged from 14 to 16 (mode = 15, 58% of individuals) and of hybrids ranged from 14 to 18 (mode = 15, 61% of individuals), but only 2 of 31 hybrids had a count > 16. Both had a modal count for total dorsal spines and rays of 27 (38% frequency for both). Lateral line scales in the first series ranged from 29 to 32 in both groups.

Morphologically “good” Nile tilapia (i.e., those that possessed characters of Nile tilapia and lacked evidence of potential hybridization with blue tilapia) were not represented in the collection until 2007 (UF# 176314) from Alachua County. Museum holdings of Nile tilapia were relatively few, with specimens from Alachua, Brevard, Lee, Miami-Dade, and Palm Beach County. U.S. Geological Survey records showed a distribution of Nile tilapia across peninsular Florida in at least 18 counties (Figure 2) since 2006 (first collected in Brevard County).

Meristic counts for Nile tilapia were generally higher, though overlapping to an extent with blue tilapia and putative hybrids (Tables 3 and 4). Nile tilapia had a significantly higher dorsal fin spine count (16.5, SD = 0.71) than blue tilapia or hybrids. The modal count was 17 (46% of individuals), but 16 was nearly as common (42%). The mean total count of Nile tilapia dorsal spines and rays was higher than for blue tilapia, though neither was different from the mean count for hybrids. Lateral line scale counts in the first series were 30 to 32.

Discussion

The analysis of museum specimens showed that tilapia bearing traits characteristic of Nile tilapia have been present in Florida since at least the early 1970s and suggests that early stocks imported to the state were mixed. This supports anecdotal observations by fisheries biologists and commercial fishermen that tilapia resembling Nile tilapia have been widespread in the state for decades but were not recognized as such until relatively recently. Nevertheless, until the present study there were no data testing this hypothesis. Without actual specimens preserved over time, it is unlikely that this question could have been answered by other means.

It seems likely that some blue tilapia individuals originally obtained from Auburn University were actually Nile tilapia or hybrids (Hardin 2011b; present study). The original stocks were called Nile tilapia (i.e., *Tilapia nilotica*), though the identification was later changed to blue tilapia (*Tilapia aurea*) in 1966 (Hale et al. 1995). This inconsistency in taxonomy is not surprising given that blue tilapia was only just becoming recognized as a separate species from Nile tilapia (Trewavas 1966; see also Trewavas 1983), the two species are difficult to distinguish (Trewavas 1983; present study) and hybridize (Hill 2011, 2014), and the small numbers of founders precluded detailed morphological analysis of a large series of specimens. Nile tilapia genes were likely spread with blue tilapia throughout much of the peninsula as this species moved through Florida’s often-connected basins, sometimes with assistance from humans who

stocked tilapia for food, forage for sport fish, and for aquatic weed control (Hale et al. 1995). That some established populations show little evidence of Nile tilapia traits is not surprising given the presumably small numbers of Nile tilapia in the original stocks that may have reduced the probability of humans moving individuals with Nile tilapia traits.

Limited genetic evidence suggests that blue tilapia populations in Florida are hybrids with Nile tilapia or Mozambique tilapia *Oreochromis mossambicus* (Peters, 1852). Of 17 assumed blue tilapia individuals collected in 2011 from north-central, west-central, and south Florida and submitted for analysis, only 9 were identified as blue tilapia using genetic barcoding with mitochondrial DNA (Hardin 2011b). The remaining specimens were classified as Nile tilapia or the subfamily Pseudocrenilabrinae. Subsequent genetic analysis of the 9 “blue tilapia” showed the presence of Nile tilapia or Mozambique tilapia genes (Hardin 2011b). Further genetic surveys of increased spatial range and sample size are needed to better understand the extent of hybridization in Florida’s tilapia stocks (e.g., Costa-Pierce 2003).

Despite the presence of Nile tilapia traits in wild Florida tilapia stocks, specimens of morphologically “good” Nile tilapia were not found in UF collections until 2007. Anecdotal reports from fisheries biologists and commercial fishermen state that Nile tilapia has been present at least in central Florida (e.g., Polk County, near the site of the original introduction of blue tilapia; Hale et al. 1995) since the 1970s or 1980s as indicated by male tilapia bearing a bright pink or light red flush during breeding season (F. Langford, Florida Game and Fresh Water Fish Commission, retired, personal communication). These individuals, locally called “pinkies” (personal observations), exhibit a reliable characteristic of Nile tilapia (Trewavas 1983). The first confirmed records in peninsular Florida came from Cane Creek in Brevard County along the east coast in 2006 (Shafland et al. 2008; USGS 2017). Since then, the USGS NAS list records from nine additional peninsular Florida counties from the Oklawaha River basin (St. Johns) in northern Florida to canals south of Lake Okeechobee. Nile tilapia and putative hybrids have been collected from numerous systems in peninsular Florida in recent years (Hardin 2011b; K. Gestring, FWC, personal communication; unpublished data). Increased spatial scale of surveys are needed to determine the geographic range of Nile tilapia in Florida.

The present study cannot answer the question of why Nile tilapia is seemingly more prevalent in collections since 2006. Some have suggested that this is a case of “look and you will find it—what is

unsought will go undetected,” a quote from Sophocles. Fisheries biologists, invasion ecologists, and ichthyologists in the state were not aware of the potential presence of a highly similar species hidden within populations of the widespread and common blue tilapia. Blue tilapia is highly variable in coloration and pattern, including caudal patterns (Figure 1), obscuring the potential presence of Nile tilapia traits. For example, an early collection (2008) of a Nile tilapia from Lake Lochloosa in Alachua County was not recognized as such and was incorrectly identified as a blue tilapia. Later collections from the region were correctly identified. Perhaps now that the presence of Nile tilapia is well known the species is recognized from a variety of locations. I speculate that this is a partial answer but the lack of unquestionable Nile tilapia in earlier collections suggests that other factors are important. A potential explanation is an increase in propagule pressure from an existing or new introduction pathway, but there are no data to test this hypothesis. The limited spatial extent of tilapia aquaculture in Florida and the general lack of proximity of collected Nile tilapia and aquaculture facilities suggest an alternative source (Hardin 2011b). Some movement of tilapia occurs related to commercial fishing which may explain some locations but not others (Hardin 2011b). Both species are salt-tolerant (Avella et al. 1993) and capable of using brackish water habitats of river mouths and estuaries for dispersal and overwinter survival (Idelberger et al. 2011; Schofield et al. 2011; Lowe et al. 2012), potentially increasing their geographic range (Brown et al. 2007).

The most common trait indicative of Nile tilapia or its genes was caudal fin barring, consistent with previous use by agency staff and academic scientists identifying wild and cultured tilapia stocks. However, the trait is variable and specimens of putative blue tilapia frequently had distinct barring on the proximate half of the caudal fin or indistinct barring throughout the caudal fin. Caudal barring was generally distinct in specimens identified as Nile tilapia, though some specimens had wider or narrower bars or bars that were perpendicular to the horizontal plane versus bars that were parallel to the fin margin (Figure 1). A single Nile tilapia in a series of specimens from the C-51 Canal in Palm Beach County had a near lack of distinct barring with the caudal fin resembling a darker version of the ovals in a wavy pattern commonly seen on blue tilapia (UF #237949).

Fin and lateral line counts from Trewavas (1983) were slightly different in Florida specimens (Tables 1 and 3). Modal dorsal fin spine counts and total spine and ray counts were lower for Florida specimens

than for the African specimens examined by Trewavas (1983). A dorsal fin spine count of 17 or 18 was nearly diagnostic for Florida Nile tilapia but was also rarely seen in putative hybrids. A dorsal spine count of 16 was a common value in Nile tilapia and two individuals had a count of 15. Total dorsal fin spine and ray counts less than 27 were only observed in blue tilapia or hybrids in Florida. Lateral line scale counts overlapped extensively.

The main motivator for the present study was a series of risk assessments and related activities investigating the potential consequences of relaxing state regulations on blue tilapia (Hardin 2011a, b; Hill 2011, 2014). A panel of experts considered most potential environmental effects of blue tilapia in Florida as low or low-medium. This result was based on the relatively sparse literature on blue tilapia effects in Florida (reviewed in Hill 2011; see also Schofield and Loftus 2015) with considerable additional information from the panel member's own data and experiences (Hardin 2011a). More concern (i.e., medium risk) was expressed over the potential spread and effects of Nile tilapia or hybrids, in particular for locations that currently have few or no blue tilapia (Hardin 2011a). Subsequent risk screens using the Fish Invasiveness Screening Kit (FISK; Copp et al. 2009; Lawson et al. 2013) rated both species in the lower end of medium risk (Lawson et al. 2015). Although the morphological and ecological similarity of blue tilapia and Nile tilapia, along with risk screening scores, suggest that their effects might be similar, performance of Nile tilapia and hybrids relative to the blue tilapia in Florida is not known nor is it known if tilapia effects might be exacerbated by the interaction of the two species. Like blue tilapia, Nile tilapia is an aggressive species (Martin et al. 2010) with a variety of potential effects on aquatic ecosystems ranging from alteration of phytoplankton and macrophyte communities to competition for food and habitat with native fishes (Canonico et al. 2005). Conversely, assessments of actual impacts are few and documentation of negative effects is largely anecdotal or correlative (Pullin et al. 1997; De Silva et al. 2004, 2006; Arthur et al. 2010). Overall, risk managers decided that potential impacts would not increase unacceptably considering the long-term presence of Nile tilapia in Florida and the current widespread geographic range of the species.

The results of this study suggest that the integration of Nile tilapia traits (and presumably genes) into Florida's tilapia populations is not a recent phenomenon but occurred nearly 50 years ago (evidence of hybrids since 1972) and perhaps nearly 60 years ago (original blue tilapia introduction in 1961). Nile tilapia has been increasingly recognized

as widespread in Florida's established tilapia stocks since the mid-2000s. These facts documented in the present study, along with the difficulty in tilapia identification, obvious mixing of species gene pools, and the difficulty that industry and the public have in obtaining legal tilapia stocks, even from wild collection, plus a variety of risk assessment and management activities, provide natural resource managers with vital information for regulatory decision making in a risk-based context. All of this information has led to a decision to harmonize blue tilapia and Nile tilapia regulations in Florida beginning 14 March 2017.

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Supplementary material

The following supplementary material is available for this article:

Appendix 1. Museum Material Examined.

This material is available as part of online article from:

http://www.reabic.net/journals/bir/2017/Supplements/BIR_2017_Hill_Appendix_1.xlsx