

ARTICLE

## Assessing the Influence of Tilapia on Sport Fish Species in North Carolina Reservoirs

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### Abstract

Redbelly Tilapia *Tilapia zilli* and Blue Tilapia *Oreochromis aureus* are indigenous to Africa and the Middle East, but now occur throughout the southeastern United States. It is fairly well understood that foraging flexibility and wide salinity, oxygen, and temperature tolerances have led to general invasion success for most tilapia species. Conflicting empirical information about the influence of tilapia on native sport fish species, however, leaves natural resource managers unable to anticipate and prevent further introductions and potential associated risks to native sport fishes. This investigation focused on two North Carolina reservoirs with tilapia populations: Hyco Lake, a large reservoir in northcentral North Carolina and Lake Julian, a small impoundment in western North Carolina. These reservoirs receive heated effluent from power generation, which is assumed to provide winter refuge for tilapia at a time when temperatures would otherwise lead to mortality. We assessed relative abundances of the tilapias and native sport species (Bluegill *Lepomis macrochirus*, black basses *Micropterus* spp., and Black Crappie *Pomoxis nigromaculatus*) in these systems and examined their trophic interactions via diet and stable isotope analyses in both lakes. In Hyco Lake we assessed potential spatial interactions and influences on relative abundance using a priori candidate models and model selection via Akaike's information criterion (AIC). These analyses indicated little evidence of tilapias influencing the relative abundances of the sport species in Hyco Lake. In both lakes, however, we did find substantial diet overlap between the tilapias and Bluegill along with isotopic niche overlap between Blue Tilapia and Bluegill in Lake Julian and Redbelly Tilapia and Bluegill in Hyco Lake. Due to the omnivorous and flexible diet of all three species these interactions were not surprising, but the ultimate influence on Bluegill growth and size structure is unknown. Overall, our results suggest that tilapia are exploiting trophic niches that are not used by the sport fishes of interest in these two very different reservoir systems and that their direct impact on sport species is not substantial.

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Freshwater organisms are strongly affected at a global scale by anthropogenic factors such as invasive species introductions, habitat alteration, exploitation, and pollution (Dextrase and Mandrak 2006). Invasive species in freshwater systems are a leading cause of native species endangerment and extinction, second only to habitat loss (Canonica et al. 2005). Quantification of the impact of invasive species on freshwater native species is essential because freshwater flora and fauna are among the most threatened in the world (Dudgeon et al. 2006). Biologists and managers must understand the potential for range expansions of invasive species and the influence they may

have on native species for the development of effective management and mitigation strategies (Moyle and Light 1996; Vander Zanden et al. 2004).

Most established invasive species are characterized as highly tolerant and exhibit plasticity in life history traits that allow occupancy of a variety of habitats (Russell et al. 2012). Members of a tribe in the family Cichlidae, collectively known as tilapia, flourish globally due to their wide salinity, oxygen and temperature tolerances, and their ability to exist at high population density (Stickney 1986; McKaye et al. 1995; Coward and Little 2001). These fishes are reproductively prolific, able to feed at

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multiple trophic levels, and can significantly alter the aquatic community (Canonico et al. 2005), all of which further enables them to thrive outside their native range.

Tilapia are indigenous to Africa and the Middle East (Canonico et al. 2005). Historically, accidental and purposeful introductions of tilapia were generally the result of aquarium releases and live-transportation of food sources for the Japanese during World War II (Canonico et al. 2005). More recently tilapia have become popular for stocking in private and public waters as biological control for nuisance vegetation and as forage fish for sport species (Mallin 1985; Canonico et al. 2005). They are also one of the most popular and widespread groups of species in the aquaculture trade (El-Sayed 2006), and selective breeding for more tolerant and productive strains of tilapia in the aquaculture environment strengthens their invasion potential (Dey et al. 2000). In fact, researchers suspect that the only factor limiting the spread of Blue Tilapia *Oreochromis aureus* in the United States is temperature (Shaf-land and Pestrak 1982; Zale 1984).

In North Carolina there are presently two tilapia species in some freshwater systems across the state, Blue Tilapia and Redbelly Tilapia *Tilapia zillii*. The U.S. Geological Survey reported that with the exception of Virginia, these two species have established populations in every state in the southeastern region of the United States (Nico et al. 2016). These invasions are a cause for concern because of the potential influence on co-occurring sport fish species (e.g., Largemouth Bass *Micropterus salmoides* and Spotted Bass *M. punctulatus*, Bluegill *Lepomis macrochirus*, and Black Crappie *Pomoxis nigromaculatus*). Relatively few studies have considered possible interactions among invasive tilapia and sport fishes, and literature that is available has produced equivocal outcomes indicating positive, negative, and no influence of tilapia on various sport species. For example, Martin et al. (2010) determined that invasive tilapia have negative impacts on Redspotted Sunfish *L. minutus*, as the Redspotted Sunfish spend less time in their preferred habitats when tilapia are present. In addition, tilapia can negatively influence growth and survival of Largemouth Bass (Zale 1987; Traxler and Murphy 1995). Conversely, studies have indicated that Bluegills will consume tilapia fry (Bickerstaff et al. 1984) and small tilapia can serve as the optimal and preferred prey (over Bluegill) of Largemouth Bass (Schram and Zale 1985). Somewhat contradictory data suggest that Largemouth Bass will choose Redspotted Sunfish over tilapia as prey (in structured habitats) (Martin et al. 2010) and that Largemouth Bass and Black Crappies do not consume invasive tilapia (Gu et al. 1996). Finally, previous studies have found that tilapia both compete (Crutchfield 1995) and do not compete (Mallin 1985; Peterson et al. 2006) with native fishes for resources. This mix of

results prevents natural resource managers from developing effective policy and mitigation strategies (or determining if any are warranted at all).

In this investigation, we assessed interactions between tilapia and sport fish species in two different freshwater reservoirs through quantification of diets, stable isotope analyses, and relative abundance analyses. Gut content analyses (GCA) can be used in combination with stable isotope analyses (SIA) to understand trophic niche use and potential resource-based overlap between tilapia and sport species (Montaña and Winemiller 2013). Stable isotope analysis provides a more integrated signature of food habits than GCA and can be used to explore longer-term food web interactions (Vander Zanden et al. 1997; Rybczynski et al. 2008). The stable isotope  $\delta^{13}\text{C}$  can be used to determine original sources of carbon (e.g., benthic versus pelagic) in the diet of an individual, and  $\delta^{15}\text{N}$  is indicative of their trophic position (Layman et al. 2012). Although a variety of biotic and abiotic factors can be drivers of fish abundance in particular systems (Middaugh et al. 2013), it is unclear how the presence of tilapia might be influencing the relative abundance of sport species following invasion of our study systems. In the present study we use multimodel inference in the form of Akaike's information criterion (AIC; Burnham and Anderson 2002) to assess the influence of tilapia relative to other biotic and abiotic factors on relative abundance of co-occurring sport fishes. Our goal was to collect fundamental information about tilapia-sport species interactions to address concerns about how these common invaders might be affecting sport fish species in the study reservoirs and similar systems.

## METHODS

*Study area.*—There are currently two lakes in North Carolina, Hyco Lake (Roxboro, North Carolina) and Lake Julian (Arden, North Carolina), that host established populations of tilapia. Both lakes are cooling reservoirs for steam-generated electrical power plants, which provide heated effluent to the lakes. The heated effluent is suspected to allow tilapia to persist and overwinter in an otherwise intolerable North Carolina winter climate (Crutchfield 1995). In 1984, both Redbelly Tilapia and Blue Tilapia were accidentally introduced to Hyco Lake during an onsite experiment (Crutchfield 1995). In 1965, Blue Tilapia were purposefully introduced to Lake Julian to serve as aquatic plant control and as forage fish for black bass populations (Corey Oakley, North Carolina Wildlife Resources Commission, personal communication). The lakes differ dramatically in size, structure, and use and are not offered as a comparison in the present investigation, but rather as an

opportunity to examine tilapia–sport fish interactions in two very different study systems.

Hyco Lake (Figure 1) is 1,520 ha in area and has an average depth of 6 m and a maximum depth of 9 m. It was constructed on the Hyco River at the confluence of three main tributaries: North Hyco Creek, South Hyco Creek, and Cobbs Creek. The single, heated-effluent source is centrally located and creates a heated pool that cools as distance from the effluent source increases. Water quality is heterogeneous with variable temperatures across the lake. Ongoing fisheries assessments suggest that the dominant fish species are Bluegill, Largemouth Bass, Black Crappie, Gizzard Shad *Dorosoma cepedianum*, and the two tilapia species. Lake Julian (Figure 2) is a bowl-shaped lake of 87 ha surface area, with an average depth of 9 m and maximum depth of 33 m. The lake does receive heated effluent, but due to the shape and size of the lake, dissolved oxygen and temperature are essentially homogenous within season. Much like the species found in Hyco Lake, centrarchids dominate the fish community

(in this case Bluegill, Largemouth Bass, and Spotted Bass).

*Field sites and fish collection.*—Hyco Lake experiences strong heterogeneity in temperature due to lake morphology and the heated effluent, so we classified the lake into three different zones in an effort to understand fish distributions and potential interactions. Using preliminary temperature data from a pilot study we delineated three temperature zones: “hot,” which extends roughly 0.8 km from the heated effluent outfall; “intermediate,” from the edge of the hot zone extending outward approximately 3 km; and “cold,” which includes all areas of the lake beyond the intermediate zone (Figure 1). Preliminary data collection indicated that the cold zone is outside the influence of the heated effluent and experiences ambient temperatures. We established three replicate study sites within each zone for a total of nine throughout the lake (Figure 1). Sampling was conducted bimonthly from July 2014 through November 2015. At each site ( $N = 9$ ) a sampling occasion consisted of one trap net set for approximately

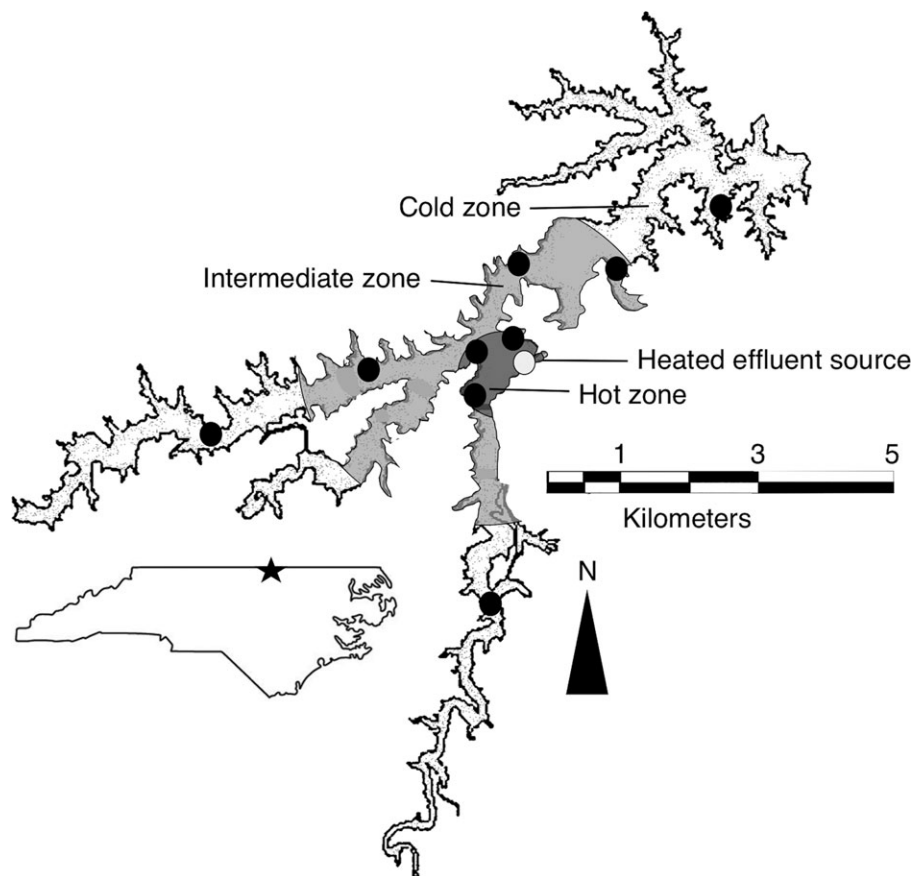


FIGURE 1. Hyco Lake and its location in North Carolina. Heated effluent influence on lake temperature is delineated into “hot,” “intermediate,” and “cold” zones (temperature trends are shown in Figure 3). Hot zone is defined as the central thermal pool within 0.8 km of the heated effluent source, the intermediate zone extends 3 km beyond the edge of the hot zone, and the remainder of the lake is the cold zone and considered ambient. Zones were determined based on a pilot study. Three replicate sampling sites within each zone of the lake are indicated by black circles.

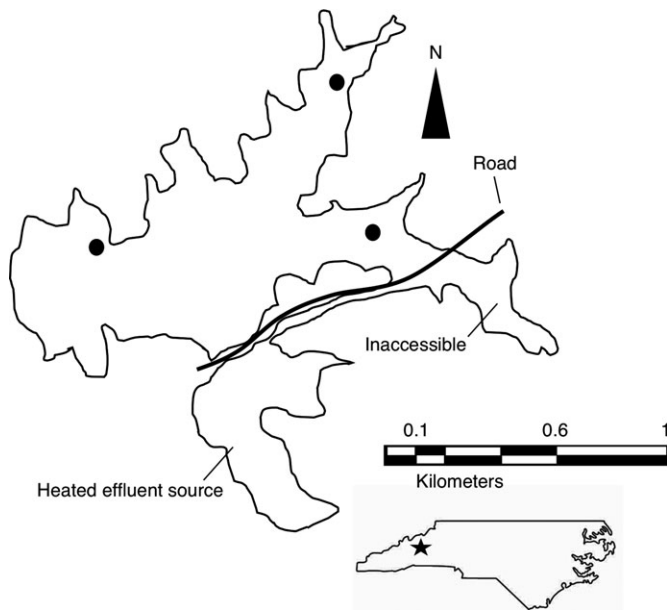


FIGURE 2. Lake Julian and its location in North Carolina. Black circles indicate three replicate sample sites.

24 h, followed by a 10-min boat electrofishing sample. Trap nets consisted of two rectangular frames (182 cm width  $\times$  92 cm height), a center upright crosspiece, and six round hoops (76 cm diameter) and had 2.5-cm knotted bar mesh. Nets were set perpendicular to shore at depths of less than 3 m with a 15-m leader extending from the shoreline. Boat electrofishing was conducted along the shoreline using pulsed DC standardized to produce a 3,000-W power transfer to fish (Burkhardt and Gutreuter 1995; Fischer and Quist 2014). Samples were defined by exactly 10 min of applied pedal time, typically covering about 250 m of shoreline. Electrofishing samples and trap-net locations within each site were separated by 300–500 m to ensure no interference between gears. Each site also had a string of temperature loggers (Onset HOBO 8K Pendant UA-001-08; accuracy,  $\pm 0.14^\circ\text{C}$ ) to collect temperature readings every 30 min at depths of 0.5, 1.5, 2.5, and 3.5 m. Fish collected at each site were weighed (g) and measured (mm TL) and immediately released on site after processing, except for a subset of fish collected in September 2014, March 2015, and September 2015 that were euthanized and frozen for later GCA and SIA analyses. To explore interactions between sport species and tilapia we focused on Largemouth Bass, Bluegill, Black Crappie, and both tilapia species in Hyco Lake for GCA, SIA, and relative abundance analyses. Due to bimodal size distributions in catch and possible differential influences on sport species, each tilapia species was divided into two size-classes (Blue Tilapia: small,  $\leq 120$  mm TL; large,  $>120$  mm TL. Redbelly Tilapia: small,  $\leq 150$  mm

TL; large,  $>150$  mm TL). The remaining sport species were also split into size-classes to account for size-based ontogenetic diet shifts (Bluegill: small,  $\leq 100$  mm TL; large,  $>100$  mm TL. Largemouth Bass (and Spotted Bass in Lake Julian): small,  $\leq 130$  mm TL; large,  $>130$  mm TL). To comprehensively assess GCA and SIA in each lake we aimed to capture a minimum of seven individuals of each size-class of our study species during each sampling occasion.

Lake Julian is much smaller and more abiotically homogenous, so we sampled three replicate sites across the entire lake (Figure 2). Fish were collected using the methodology described above in September 2014, March 2015, and September 2015. We conducted supplemental night boat electrofishing transects to meet sample size goals due to the low turbidity of the lake and associated challenges of electrofishing during the day. In Lake Julian we conducted GCA and SIA on the same size-classes of black bass (Largemouth Bass and Spotted Bass), Bluegill, and Blue Tilapia (Redbelly Tilapia are not present in Lake Julian) and attempted to collect at least seven individuals of each size-class.

*Sport species relative abundance.*—We constructed a priori Poisson regression models and used Akaike's information criterion (AIC; Burnham and Anderson 2002) to assess relative abundance of sport fish species based on the influence of tilapia and other potential drivers (e.g., temperature) in Hyco Lake. Although not a primary goal of this investigation, we were able to use the same data and approach to assess drivers of tilapia relative abundance in Hyco Lake. We did not conduct relative abundance analyses on Lake Julian because of the small size and homogenous nature of abiotic conditions in that system.

Our primary interest in model development was to assess ways in which tilapia might influence relative abundance of sport fishes through potential competitive or predatory interactions. First, we measured abundances of sport species at specific life stages that might be affected by competitive interactions with tilapia for food resources: Bluegill trap-net CPUE (number per 24-h trap-net set), Bluegill electrofishing CPUE (number per 10 min of electrofishing), and small Largemouth Bass electrofishing CPUE (Zale 1987; Crutchfield 1995; Traxler and Murphy 1995). Because tilapia may compete with each other as well as with sport species, our model suite included four additional species variables in the competitor category: Redbelly Tilapia trap-net CPUE, Redbelly Tilapia electrofishing CPUE, Blue Tilapia trap-net CPUE, and Blue Tilapia electrofishing CPUE. Next, we identified two variables that may indicate whether tilapia availability as prey is important to piscivorous predators: large Largemouth Bass electrofishing CPUE and Black Crappie trap-net CPUE.



For model construction we used relative abundance estimates separated by our two collection methods (trap nets and electrofishing), as it would be inappropriate to combine them. Trap-net data and electrofishing data were used separately for Redbelly Tilapia, Blue Tilapia, and Bluegill; only trap-net data were used for Black Crappie relative abundance estimation (electrofishing for Black Crappie was inefficient and produced very small sample sizes). Largemouth Bass were primarily collected via electrofishing; trap-net data were not included for Largemouth Bass due to insufficient sample size. Small and large individuals may have different roles in the food web, so we separated Largemouth Bass into small ( $\leq 130$  mm TL) and large ( $> 130$  mm TL) size-classes based on approximate sizes associated with ontogenetic diet shifts (Garcia-Berthou 2002).

Using these data we developed sets of a priori candidate models predicting abundance indices of sport fishes that may be potential competitors with tilapia (Bluegill, small Largemouth Bass). Each set included models based on (1) relative abundances of tilapia only, (2) all possible competitors (native sport species and tilapia), (3) possible predators, (4) abiotic factors only (zone, temperature), and (5) combinations of these groups (Table 1). For potential predators on tilapia (large Largemouth Bass, Black Crappie) our approach was to build candidate models using (1) relative abundances of tilapia only, (2) the native species community (native sport fish species), (3) abiotic factors only, and (4) combinations of these groups (Table 2). The modeling approach that we used allowed us to include correlated variables as we assessed functional relationships between abiotic factors and relative abundance of each fish species (McDonald 2014).

Temperature in Hyco Lake was assessed in two ways: categorically (hot, intermediate, cold zones) and numerically (direct quantification of temperature at each sample site calculated using the average temperature recorded by HOBO loggers at the surface and at 1.5-, 2.5-, and 3.5-m depths during each week of sampling). It was necessary to include both temperature variables as they convey different aspects of thermal history; temperature differences were relatively consistent among zones throughout the year, but there was substantial variation within and among seasons within zones (Figure 3).

We used AIC corrected for small sample size ( $AIC_c$ ) to assess all a priori candidate models within each set simultaneously. A Poisson distribution was used for abundances in the models. The best model was determined by the lowest  $AIC_c$  value and the highest model weight ( $w_i$ ; Burnham and Anderson 2002).

*Stable isotope and diet processing.*—Processing for SIA followed the procedure of Vander Zanden et al. (2006). We removed a tissue sample (approximately 2 g) from the dorsolateral region of all collected fish. Each tissue sample

was dried at 60°C for at least 72 h and then ground to a fine powder using a mortar and pestle. Subsamples of the dried, ground powder were placed into tin capsules (Costech). We sent the samples to the Stable Isotope Ecology Laboratory in the Center for Applied Isotope Studies at the University of Georgia, where  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  isotopes were measured with an isotope ratio mass spectrometer.

Fish collected for SIA were also used for GCA. Stomachs were removed after whole fish were partially thawed in the laboratory. We preserved stomach contents of each fish in 95% ethanol. Using a dissection microscope (10 $\times$  magnification), we examined and identified all food items present to the lowest feasible taxonomic level (Winemiller 1990; Montaña and Winemiller 2013). These lowest taxonomic units of food items were then simplified into eight categories: terrestrial insects (Coleoptera, Hemiptera, Hymenoptera), benthic macroinvertebrates (Ephemeroptera, Odonata, Trichoptera, Diptera, Mollusca, Hydrachnidia), small zooplankton (included Cladocera,  $0.55 \pm 0.3$  mm [mean  $\pm$  SD]; Rotifera,  $0.46 \pm 0.3$  mm; Ostracoda,  $0.21 \pm 0.05$  mm), large zooplankton (Copepoda,  $1.04 \pm 0.4$  mm), detritus, fish, eggs, and crayfish. The volumetric proportion of each category was estimated using water displacement in a graduated cylinder (Winemiller 1990).

*Analysis of stable isotope and diet overlap.*—To assess isotopic niche overlap between tilapia and sport fish species for each lake independently we used Stable Isotope Bayesian Ellipses in R (SIBER). This approach allowed us to plot calculated Bayesian standard ellipse areas that represent the isotopic niche area of the species of interest (Jackson et al. 2011). We used the  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  data for each species to inform the standard ellipse area corrected for small sample size ( $SEA_c$ ). The ellipse created is an estimate containing approximately 40% of the data based on bivariate normal distributions (Jackson et al. 2011). These estimated ellipses were then plotted and used to visually identify trophic niche position and patterns, as well as to calculate the overlap between species of interest in each lake. For Hyco Lake we compared Blue Tilapia, Redbelly Tilapia, Bluegill, Largemouth Bass, and Black Crappie. For Lake Julian we compared Blue Tilapia, Bluegill, Largemouth Bass, and Spotted Bass. As we were interested in general trophic niche patterns and there were no noteworthy differences across seasonal sampling occasions, we compared pooled data across the three sampling occasions (September 2014, March 2015, September 2015) in each lake (Layman et al. 2005).

To evaluate diet overlap between tilapia and sport fishes for each lake independently, we calculated Pianka's (1973) index of symmetrical niche overlap using the volumetric proportions of the food items consumed by each species of interest. Any individuals with empty stomachs were excluded from analysis. This method of analysis is an index ranging from 0 (no overlap) to 1 (absolute

TABLE 1. Sets of a priori candidate models estimating relative abundance of sport species (Bluegill trap-net CPUE, Bluegill electrofishing CPUE, small Largemouth Bass electrofishing CPUE) potentially affected by competition with tilapias and their corresponding number of covariates (*K*), AIC<sub>c</sub> value, ΔAIC<sub>c</sub>, and model weight (*w<sub>i</sub>*). Gear type for each covariate CPUE is indicated by (T) for trap net or (E) for electrofishing; species are defined as follows: Blue Tilapia (BT), Redbelly Tilapia (RT), Bluegill (BLG), Largemouth Bass (LMB), and Black Crappie (BC). Covariates used in each candidate model are indicated by the letter X, abiotic factors (AF) are Zone, which represents hot, intermediate or cold, and Temp, which is the average temperature (°C) during the week of sampling. The top-ranking model is indicated by bold text.

A priori candidate models	Covariates included in candidate model										AIC <sub>c</sub> output				
	Zone	Temp	BT (T)	BT (E)	RT (T)	RT (E)	BLG (T)	BLG (E)	Small LMB (E)	Large LMB (E)	BC (T)	<i>K</i>	AIC <sub>c</sub>	ΔAIC <sub>c</sub>	<i>w<sub>i</sub></i>
<b>Bluegill trap-net abundance</b>															
<b>Global</b>	<b>X</b>	<b>X</b>	<b>X</b>	<b>X</b>	<b>X</b>	<b>X</b>			<b>X</b>	<b>X</b>	<b>X</b>	<b>11</b>	<b>1,041.5</b>	<b>0</b>	<b>1</b>
Competitors + AF	X	X	X	X	X	X			X			9	1,077.4	35.89	0
Tilapias + AF	X	X	X	X	X	X						6	1,119.23	77.73	0
Competitors			X	X	X	X			X			6	1,155.97	114.47	0
Tilapias			X	X	X	X						3	1,231.27	189.76	0
Predators + AF	X	X								X	X	6	1,373.54	333.03	0
AF	X	X										4	1,427.18	385.67	0
Temperature		X										3	1,483.06	441.56	0
Predators										X	X	3	1,542.21	500.71	0
Zone	X											2	1,594.93	553.43	0
<b>Bluegill electrofishing abundance</b>															
<b>Global</b>	<b>X</b>	<b>X</b>	<b>X</b>	<b>X</b>	<b>X</b>	<b>X</b>			<b>X</b>	<b>X</b>	<b>X</b>	<b>11</b>	<b>2,009.6</b>	<b>0</b>	<b>1</b>
Competitors + AF	X	X	X	X	X	X			X			9	2,038.64	29.04	0
Tilapias + AF	X	X	X	X	X	X						8	2,156.46	146.86	0
Competitors			X	X	X	X			X			6	2,284.55	274.95	0
Tilapias			X	X	X	X						5	2,379.65	370.05	0
Predators + AF	X	X								X	X	6	2,612.28	602.68	0
AF	X	X										4	2,689.78	680.18	0
Temperature		X										3	2,701.28	691.68	0
Predators										X	X	3	2,860.86	851.26	0
Zone	X											2	2,936.54	926.94	0
<b>Small Largemouth Bass electrofishing abundance</b>															
<b>Global</b>	<b>X</b>	<b>X</b>	<b>X</b>	<b>X</b>	<b>X</b>	<b>X</b>	<b>X</b>	<b>X</b>		<b>X</b>	<b>X</b>	<b>12</b>	<b>250.31</b>	<b>0</b>	<b>0.75</b>
Competitors			X	X	X	X	X	X				7	253.01	2.7	0.19
Predators + AF	X	X								X	X	6	256.06	5.76	0.04
AF	X	X										4	259.55	9.24	0.01
Tilapias + AF	X	X	X	X	X	X						8	260.99	10.68	0
Competitors + AF	X	X	X	X	X	X	X	X				8	260.99	10.68	0
Zone	X											3	261.07	10.76	0
Tilapias			X	X	X	X						5	263.74	13.43	0
Temperature		X										2	263.79	13.48	0
Predators										X	X	2	457.73	207.43	0

overlap) where 0.6 or higher represents meaningful overlap (Montaña and Winemiller 2013). Gut content analyses provide an immediate record of food consumption while SIA delivers a more integrated assessment of niche overlap. Because of the finer resolution of GCA, we were able to compare species using the size-classes delineated in our collection methods. Each size-class of a sport species category was compared with the available tilapia species size-classes in that lake by season.

**RESULTS**

**Relative Abundance**

In Hyco Lake, the only system for which distribution and relative abundance analyses were conducted, we captured 810 fish across the five species of interest over nine bimonthly sampling occasions (Henson 2017). The CPUE varied widely among sites and seasons (Redbelly Tilapia, 0–51; Blue Tilapia, 0–42; Bluegill, 0–159; Largemouth

TABLE 2. Sets of a priori candidate models estimating relative abundance of sport fish species that are potential predators on tilapia (large Largemouth Bass electrofishing CPUE, Black Crappie trap-net CPUE), and their corresponding number of covariates (*K*), AIC<sub>c</sub> value, ΔAIC<sub>c</sub>, and model weight (*w<sub>i</sub>*). Gear type for each covariate CPUE is indicated by (T) for trap net or (E) for electrofishing; species are defined as follows: Blue Tilapia (BT), Redbelly Tilapia (RT), Bluegill (BLG), Largemouth Bass (LMB), and Black Crappie (BC). Covariates used in each candidate model are indicated by the letter X, abiotic factors (AF) are Zone, which represents hot, intermediate or cold, and Temp., which is the average temperature (°C) during the week of sampling. The top-ranking model is indicated by bold text.

A priori candidate models	Covariates included in candidate model										AIC <sub>c</sub> output				
	Zone	Temp.	BT (T)	BT (E)	RT (T)	RT (E)	BLG (T)	BLG (E)	Small LMB (E)	Large LMB (E)	BC (T)	<i>K</i>	AIC <sub>c</sub>	ΔAIC <sub>c</sub>	<i>w<sub>i</sub></i>
<b>Large Largemouth Bass electrofishing abundance</b>															
AF	X	X										<b>4</b>	<b>262.68</b>	<b>0</b>	<b>0.49</b>
Temperature		X										2	262.84	0.17	0.45
Tilapias + AF	X	X	X	X	X	X						8	268.17	5.5	0.03
Native community + AF	X	X					X	X	X		X	8	268.6	5.92	0.03
Global	X	X	X	X	X	X	X	X	X		X	12	274.74	12.06	0
Native community							X	X	X		X	5	303.45	40.77	0
Zone	X											3	307.86	45.18	0
Tilapias			X	X	X	X						5	309.46	46.78	0
<b>Black Crappie trap-net abundance</b>															
<b>Global</b>	<b>X</b>	<b>X</b>	<b>X</b>	<b>X</b>	<b>X</b>	<b>X</b>	<b>X</b>	<b>X</b>	<b>X</b>	<b>X</b>	<b>12</b>	<b>759.17</b>	<b>0</b>	<b>1</b>	
Native community + AF	X	X					X	X	X	X	8	796.06	36.9	0	
Tilapias + AF	X	X	X	X	X	X						8	867.2	108.04	0
AF	X	X										4	997.32	238.15	0
Zone	X											3	1,021.95	262.79	0
Native community							X	X	X	X		5	1,069.1	309.94	0
Tilapias			X	X	X	X						5	1,078.82	319.66	0
Temperature		X										2	1,137.93	378.76	0

Bass, 0–19; Black Crappie, 0–60). Within each set of candidate models we developed for predicting the relative abundance of sport species with which tilapia may potentially compete, Bluegill (trap-net and electrofishing CPUE) and small Largemouth Bass (electrofishing CPUE) abundance were best fit by the global model (Table 1). For both Bluegill relative-abundance metrics only the global model had any model weight; no submodels with only tilapia or tilapia in combination with abiotic factors had any model weight. The global model also best fit the relative abundance of small Largemouth Bass and had 75% of the weight. The only other model with substantial weight contained competitors, which included both tilapia and Bluegill (Table 1).

Tilapia relative abundance was also not a prominent component of models that best fit the relative abundance of their possible predators, Black Crappie and large Largemouth Bass. Black Crappie abundance was best fit by the global model, which had all of the model weight (Table 2). For large Largemouth Bass abundance, two

models including only abiotic factors had 94% of the model weight. The best model contained only abiotic factors (temperature and zone), and the second-best model contained only temperature. A model that contained tilapia and abiotic factors had substantially lower model weight (0.03) than the model with abiotic factors alone (0.49), indicating that the presence of tilapia had little or no value in terms of describing Largemouth Bass relative abundance (Table 2).

**Stable Isotopes and Diet Overlap**

We collected 406 individuals of the five species of interest in Hyco Lake for SIA; of those, 335 with nonempty stomachs were analyzed in GCA. Bayesian standard ellipse areas estimated using δ<sup>13</sup>C and δ<sup>15</sup>N concentrations exhibited some overlap in isotopic niche space among species (Figure 4). However, the only ellipse overlap between tilapia and sport species occurred between Redbelly Tilapia and Bluegill. Gut content analyses indicated that none of the sport species except small Bluegill exhibited any

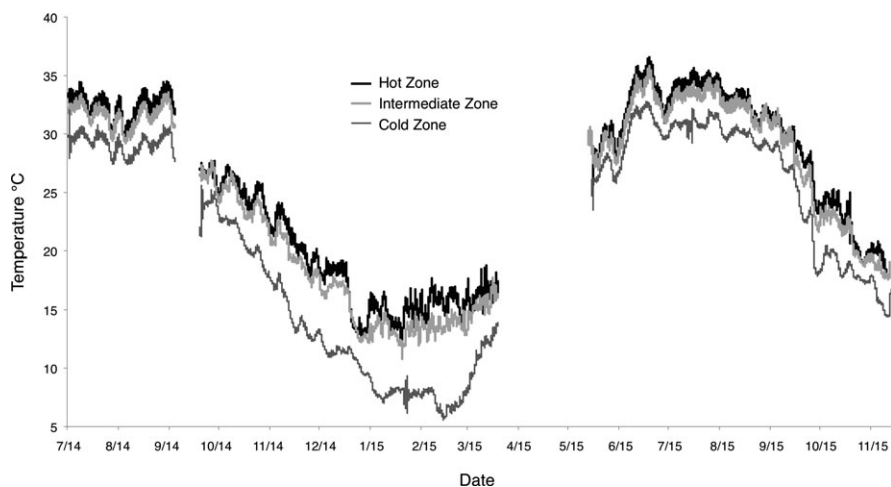


FIGURE 3. Temperature (°C) trends in Hyco Lake during the 2014–2015 sampling period. Temperatures were averaged from temperature logger data collected at the surface and at 1.5-, 2.5-, and 3.5-m depths at each of the three replicate sites in each zone (hot, intermediate, cold). Gaps in the data were due to equipment malfunctions.

significant diet overlap with Redbelly Tilapia or Blue Tilapia in Hyco Lake (Table 3). Diets of small Bluegill overlapped substantially with diets of both small and large Blue Tilapia and Redbelly Tilapia in spring of 2015, but not in fall of either year. Overlap among these species was driven by the detritus diet category in small Bluegill and in both sizes of Blue Tilapia and Redbelly Tilapia (Figure 5). Redbelly Tilapia and Blue Tilapia of all sizes had high diet overlap with each other during all seasons (Table 3; Figure 5).

We collected 274 individuals of the three species of interest in Lake Julian for SIA; of those, 253 with non-empty stomachs were used for GCA. The Bayesian standard ellipse area estimated for Blue Tilapia overlapped with that of Bluegill, but not that of Largemouth Bass (Figure 6). In the 2015 sampling periods (spring and fall) we did not collect enough small Blue Tilapia for GCA so diet overlap was only evaluated between large Blue Tilapia and small black bass, large black bass, small Bluegill, and large Bluegill. In both years and seasons there was almost no diet overlap between small or large Largemouth Bass with either size of Blue Tilapia (Table 4). In contrast, small Bluegill in both fall and spring 2015 exhibited strong diet overlap with large Blue Tilapia, as did large Bluegill in fall 2015. The considerable overlap was caused by the high proportion of detritus in the diets of Bluegill and large Blue Tilapia (Figure 5).

**DISCUSSION**

Our results indicate that tilapia are likely not affecting the abundance of sport fish species in Hyco Lake and that the potential for diet and niche overlap between tilapia and native sport species is limited. In Hyco Lake we

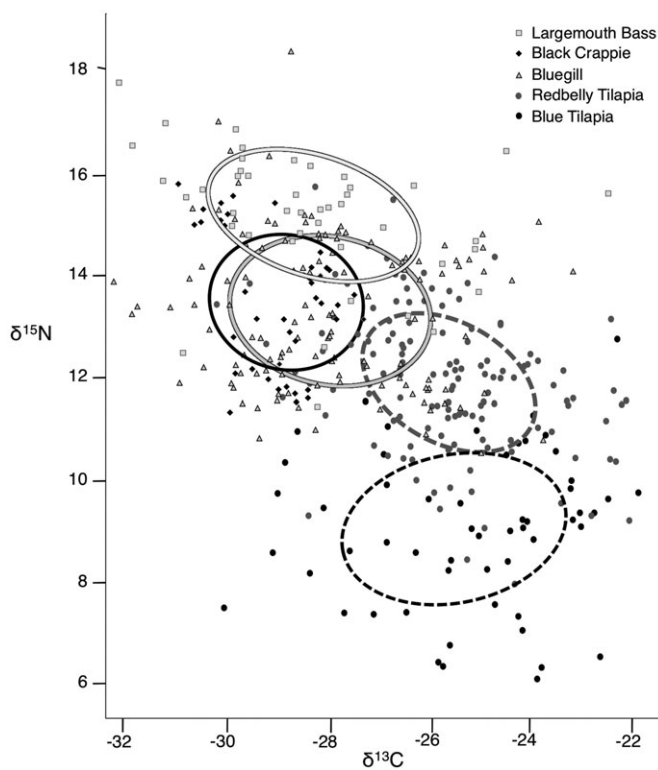


FIGURE 4. Bayesian standard ellipse areas calculated using  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  for invasive Blue Tilapia and Redbelly Tilapia and the native sport species—Largemouth Bass, Bluegill, and Black Crappie—from three collections in fall 2014, spring 2014, and spring 2015 in Hyco Lake. Black circles with a dashed black ellipse represent Blue Tilapia, gray circles with a dashed gray ellipse represent Redbelly Tilapia, gray triangles with a solid gray ellipse represent Bluegill, black diamonds with a thick solid black ellipse represent Black Crappie, and Largemouth Bass are represented by open gray squares and the thin solid black ellipse.



TABLE 3. Estimates of diet overlap quantified with Pianka’s index of symmetrical niche overlap using the invasive tilapias in Hyco Lake (Blue Tilapia and Redbelly Tilapia) and the native sport species (Bluegill, Largemouth Bass, and Black Crappie) separated by size-class (Blue Tilapia: small, ≤120 mm TL; large, >121 mm TL; Redbelly Tilapia: small, ≤150 mm TL; large, >151 mm TL; Bluegill: small, ≤100 mm TL; large, >100 mm TL; Largemouth Bass: small, ≤130 mm TL; large, >130 mm TL). Relationships that show high overlap (>0.60) are indicated with values in bold text.

Compared species	Fall 2014			Fall 2015				Spring 2015			
	Redbelly Tilapia		Blue Tilapia	Redbelly Tilapia		Blue Tilapia		Redbelly Tilapia		Blue Tilapia	
	Small	Large	Large	Small	Large	Small	Large	Small	Large	Small	Large
Small LMB	0.12	0.08	0.06	0.37	0.50	0.47	0.47	0.02	0.00	0.00	0.00
Large LMB	0.19	0.12	0.09	0.01	0.07	0.03	0.03	0.03	0.02	0.03	0.03
Black Crappie	0.26	0.19	0.16	0.44	0.05	0.05	0.04	0.20	0.19	0.19	0.19
Small Bluegill	0.57	0.55	0.52	0.31	0.35	0.36	0.35	<b>0.70</b>	<b>0.70</b>	<b>0.70</b>	<b>0.70</b>
Large Bluegill	0.30	0.12	0.22	0.37	0.50	0.47	0.47	0.44	0.40	0.40	0.40
Small Redbelly Tilapia			<b>0.99</b>			<b>0.82</b>	<b>0.82</b>			<b>0.98</b>	<b>0.99</b>
Large Redbelly Tilapia			<b>0.99</b>			<b>0.99</b>	<b>0.99</b>			<b>0.99</b>	<b>0.99</b>
Small Blue Tilapia				<b>0.82</b>	<b>0.99</b>			<b>0.99</b>	<b>0.99</b>		
Large Blue Tilapia	<b>0.99</b>	<b>0.99</b>		<b>0.82</b>	<b>0.99</b>			<b>0.99</b>	<b>0.99</b>		

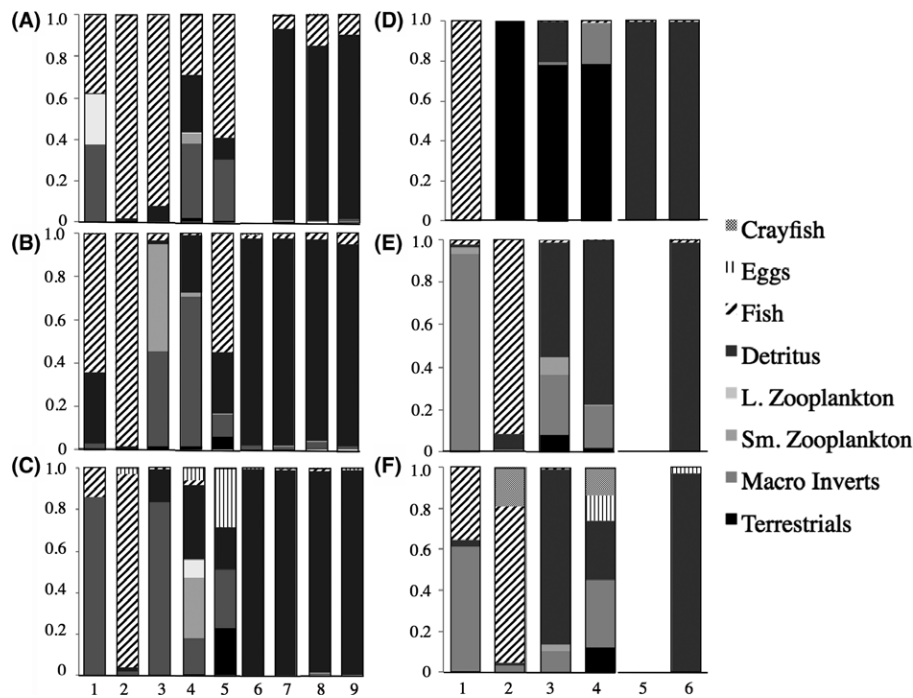


FIGURE 5. Proportion by volume of the eight prey categories used in the stomach content analyses. The left column represents Hyco Lake samples from (A) September 2014, (B) September 2015, and (C) March 2015, while the right column represents Lake Julian samples from (D) Fall 2014, (E) Fall 2015, and (F) Spring 2015. The species in (A–C) are represented using numbers: (1) small Largemouth Bass, (2) large Largemouth Bass, (3) Black Crappie, (4) small Bluegill, (5) large Bluegill, (6) small Blue Tilapia, (7) large Blue Tilapia, (8) small Redbelly Tilapia, and (9) large Redbelly Tilapia. The species in (D–F) are represented using numbers: (1) small black bass, (2) large black bass, (3) small Bluegill, (4) large Bluegill, (5) small Blue Tilapia, and (6) large Blue Tilapia. Missing data indicate a lack of availability of that size class during sampling.

found that the relative abundance of important sport species—both as potential predators of and competitors with tilapia—was driven by a complex combination of biotic

and abiotic interactions rather than by the presence of tilapia in the system. Previous research addressing similar relationships between native sport species and invasive

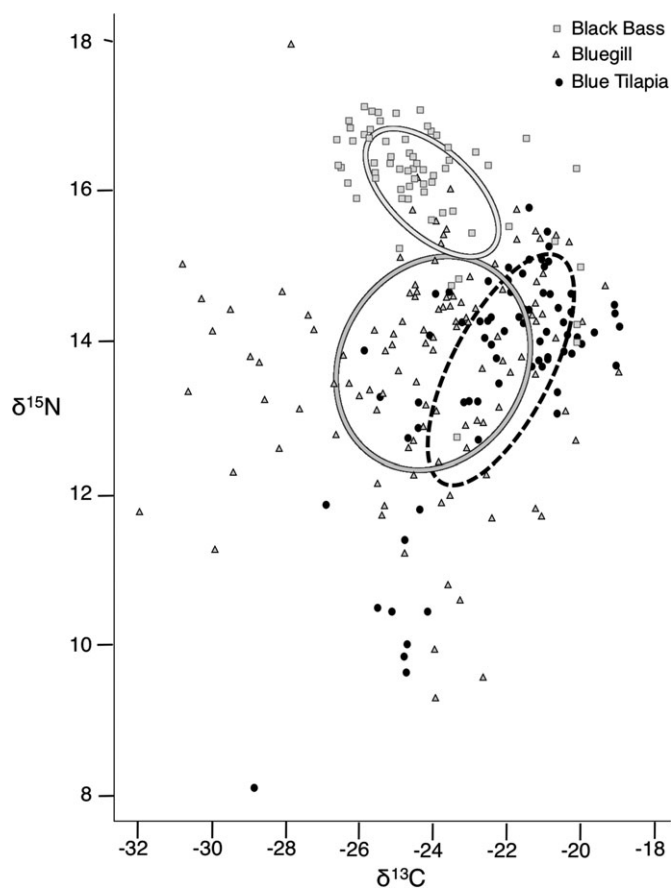


FIGURE 6. Bayesian standard ellipse areas calculated using  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  for invasive Blue Tilapia and the native sport species, Bluegill and black basses (Largemouth Bass and Spotted Bass), summarized from three collections in September 2014, March 2014, and September 2015 in Lake Julian. Black circles with a dashed black ellipse represent Blue Tilapia, triangles and solid gray ellipse represent Bluegill, and black bass (Largemouth Bass and Spotted Bass) are represented by open gray squares and the thin solid black ellipse.

tilapia has provided conflicting results (e.g., Traxler and Murphy 1995; Martin et al. 2010). Our findings are consistent with those that indicate tilapia influence is relatively minor (e.g., Gu et al. 1996; Peterson et al. 2006). This is an important result given the general assumption that invaders are typically strong interactors with native species (Canonico et al. 2005).

We found no evidence for strong influence of tilapia on piscivorous sport species in measures of abundance or food habits. Rather, our results indicated that the abundance of large Largemouth Bass is primarily a function of abiotic factors including temperature and lake zone, a correlate of temperature. This result is not particularly surprising given the large body of literature describing the general effect of temperature on fish abundance, including Largemouth Bass (e.g., Hasler et al. 2009; Peat et al. 2016), but it is important to note that the presence of

TABLE 4. Estimates of diet overlap quantified with Pianka's index of symmetrical niche overlap between invasive Blue Tilapia in Lake Julian and the native sport species (Bluegill and black bass [i.e., Largemouth Bass and Spotted Bass]) separated by size-class (Blue Tilapia: small,  $\leq 120$  mm TL; large,  $>120$  mm TL; Bluegill: small,  $\leq 100$  mm TL; large:  $>100$  mm TL; black bass, small,  $\leq 130$  mm TL; large,  $>130$  mm TL). Relationships that show high overlap ( $>0.60$ ) are indicated with values in bold text.

Compared species	Fall 2014		Fall 2015	Spring 2015
	Blue Tilapia		Blue Tilapia	Blue Tilapia
	Small	Large	Large	Large
Small black bass	0.000	0.000	0.021	0.051
Large black bass	0.024	0.023	0.101	0.019
Small Bluegill	0.000	0.001	<b>0.873</b>	<b>0.983</b>
Large Bluegill	0.251	0.554	<b>0.969</b>	0.554

tilapia, a potential prey, had no meaningful influence on relative abundance of large Largemouth Bass, which are typically those most sought by anglers (Barnhart 1989; Noble 2002). Although we are not aware of other published research linking the presence of tilapia with Largemouth Bass abundance, our results are consistent with previous investigations that have indicated limited effects of interactions among these species (e.g., Gu et al. 1996; Peterson et al. 2006). Likewise, our results indicated that tilapia have no substantial effect on the abundance of Black Crappie; no submodel containing only tilapia or tilapia plus abiotic factors had any model weight. The only model with weight was the global model, indicating that a complex mixture of biotic and abiotic factors is driving Black Crappie abundance. This is the first study that we are aware of to examine impacts on relative abundance between these species.

Our ranked abundance models for the piscivores were supported by diet and SIA analyses, which indicated no influence of tilapia on trophic niche use of the piscivorous sport species in our study. We anticipated that diet-associated effects of tilapia on piscivorous species would be primarily through the consumption of tilapia, but this pattern was not apparent in our data. Interpretation of the SIA ellipses suggests that piscivorous Black Crappie and black basses in both study lakes are consuming few, if any, tilapia, a pattern confirmed by our diet analyses. With each trophic transfer the  $\delta^{15}\text{N}$  of consumers typically increases by  $\sim 3\text{‰}$  and their  $\delta^{13}\text{C}$  increases by  $\sim 1\text{‰}$ . However, neither tilapia species falls within the isotopic niche space one trophic transfer level below those of the piscivores. These results are consistent with previous research that has suggested tilapia are rarely consumed by these

apex predators (Gu et al. 1996). Conversely, the patterns we observed are inconsistent with studies that have indicated that tilapia can, in fact, serve as an important forage species for black basses, depending on prey size and habitat characteristics (Schram and Zale 1985). In summary, the combination of abundance analyses and trophic niche data from two very different reservoir systems reveals only minor, if any, influence of tilapia on Largemouth Bass and Black Crappie.

We also found little influence of tilapia on the relative abundance of the sport fishes that could potentially compete with them. The best model for predicting abundance of Bluegill and small Largemouth Bass was the global model, and in the case of Bluegill (collected both by electrofishing and trap nets), the global model had all of the model weight. In the case of small Largemouth Bass, there was substantial weight in a submodel that included all potential competitors (Blue Tilapia, Redbelly Tilapia, and Bluegill). However, as none of the submodels that included only tilapia or tilapia plus abiotic factors had any weight, it is reasonable to conclude that the model weight of this competitor submodel was driven primarily by the inclusion of Bluegill. As in the case with Black Crappie, this pattern suggests that the abundance of Bluegill and small Largemouth Bass in our study system is best described by interactions among multiple biotic and abiotic factors, and there is no evidence for strong influence of tilapia presence on abundance of either species. This lack of influence conflicts with previous research suggesting that tilapia has a negative influence on growth and survival of young Largemouth Bass (Zale 1987) and on sunfish habitat use and survival in the presence of piscivores (Martin et al. 2010).

Although we found little evidence of tilapia affecting abundance of potential competitor sport species, we did find substantial diet and niche overlap between tilapia and Bluegill in both study systems; there was considerable diet overlap between Bluegill (especially small Bluegill) and both species of tilapia in Hyco Lake and between Bluegill and Blue Tilapia in Lake Julian. In addition, these overlap patterns were apparent in all of our stable isotope Bayesian ellipse analyses, with the exception of Blue Tilapia and Bluegill in Hyco Lake. Although assessing consequences of this interaction is beyond the scope of this investigation, our results do indicate the potential for competitive interactions between Bluegill and invasive tilapia that might lead to decreases in Bluegill growth or population size structure, as has been observed in other cases (Garvey and Stein 1997; Wolfe et al. 2009; Kaemingk et al. 2012).

Despite evidence suggesting that Bluegill may opportunistically forage on tilapia (Bickerstaff et al. 1984), we found no evidence of that in our diet and SIA data. In

addition, we expected based on previous work (Zale 1987; Traxler and Murphy 1995) that tilapia would overlap with small Largemouth Bass in terms of diet and trophic niche, but once again we found no evidence for that in our study. The wide variation in the SIA data of both the tilapia species, despite their diets of mainly detritus, also suggests that either individuals are foraging in different benthic habitats in the lakes or that they undergo different assimilations of these isotopes.

While our study provides useful information about the influence of tilapia relative to other common drivers of sport fish abundance, it is important to note that relative abundance of all our target species is clearly a function of many factors, some of which we likely did not capture in our analyses. The contribution of our study, however, is in the assessment of relative rather than absolute importance of an increasingly common invasive species in warmwater reservoir systems. Further, the general lack of strong tilapia effects on sport species abundance was supported by our trophic niche analyses, which indicated no significant diet or SIA overlap except in the case of Bluegill. It is worth pointing out that tilapia could be influencing sport species in ways that we did not assess in this investigation. For example, there might be competition at earlier life stages or for access to spawning sites (Zale 1987; Canonico et al. 2005). Tilapia can be aggressive, and their large nests occupy habitat that might otherwise be used by sport fishes. However, it was not clear in our study that spawning habitat was limiting; in both reservoirs there were substantial areas suitable for spawning by sport species that had no tilapia nests. Despite little evidence in our study of strong interactions between tilapia and sport fishes, the wide variety of habitats suitable for tilapia invasion and their broad usage (Mallin 1985; Canonico et al. 2005) suggests that continued monitoring and assessment will be necessary to prevent further invasion risk and threat to native biodiversity.

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