ABSTRACT

FEINER, ZACHARY SCOTT. Life History and Trophic Dynamics of Invasive White Perch Across Stages of Invasion in Large North Carolina Reservoirs. (Under the direction of Dr. D. Derek Aday and Dr. James A. Rice.)

Successful invasive species must pass through several invasion stages, and life history or trophic strategies allowing for successful transitions may change as the species advances from one stage to the next. To evaluate the role of life history shifts in the invasion success of white perch *Morone americana*, age- and size-at-maturity, gonadosomatic index (GSI), and growth were compared across three invasive reservoir populations ranging from 1, 11, and 21 years since initial detection. Individuals in the newly introduced population grew faster and had higher mean reproductive investment than the two established populations across both study years. Individuals in the new population also matured earlier than those in the older populations in 2009, but maturity schedules did not differ in 2010, possibly due to changes in environmental conditions causing life history shifts in both older populations. These results suggest that phenotypic plasticity in white perch life history traits plays an important role in successful invasions, not only in shifting life history strategy across the stages of an invasion, but also in adapting to local environmental conditions in the invaded system. I evaluated the trophic position and diet overlap of white perch and three established species, a littoral omnivore (bluegill *Lepomis macrochirus*), littoral piscivore (largemouth bass *Micropterus salmoides*), and a pelagic piscivore (striped bass *Morone saxatilis* or walleye *Sander vitreus*) using stable isotope and diet analyses. Small (<120 mm TL), medium (121-180 mm TL), and large (>181 mm TL) white perch occupied consistent trophic positions among reservoirs. Smaller sizes of white perch had the largest total niche areas of

any species and had strong diet overlap with bluegill, while large white perch had moderate overlap with striped bass. White perch appear to occupy a wide trophic niche that may be advantageous in establishing new invasive populations. However, they are not invading an empty niche; instead, they are using benthic resources shared by other species, which may negatively impact established species if these resources are limited.

Life History and Trophic Dynamics of Invasive White Perch in Large North Carolina
Reservoirs Across Stages of Invasion

by
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BIOGRAPHY

I was born in Baraboo, WI, and grew up in the small towns of Plain and Spring Green, WI, with my younger brothers Ben and Eric. I spent the majority of my childhood camping and fishing on the Wisconsin River and the countless sloughs, ponds, and lakes surrounding my home. I owe much of my interest in the natural world, especially in fish and aquatic ecology, to those fishing and hunting trips with my dad, Mike, my grandfather Dick, my uncles Mitch and Randy, and my step-father Chris. I owe my ambitions and academic successes through high school and college to my mom, Lori.

After graduating from River Valley High School in 2003, I moved on to the University of Wisconsin-Madison. There I had the privilege to march in the University of Wisconsin Marching Band for four years, one of the most rewarding experiences of my life. My interest in fisheries ecology was solidified after I worked a summer as a technician in the UW Center for Limnology under Dr. Emily Stanley, and took Ecology of Fishes, taught by Dr. Jake Vander Zanden and Dr. Jim Kitchell.

Technician positions with the Arizona Game and Fish Department and NC State gave me the experience I needed to pursue my master's degree in fisheries ecology. In 2008, I was accepted to a position working under Dr. Derek Aday and Dr. Jim Rice, who have been invaluable mentors over the past two and a half years. I have learned a lot and met some lasting friends in my time at NC State. In the future, I hope to continue on and earn my Ph.D. in aquatic ecology, researching interesting and exciting topics on invasive species, food web ecology, and native species conservation.

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INTRODUCTION

Currently, there is a rapidly growing literature of attempts to identify "invasive" characteristics and predict potentially detrimental invasions, ranging from local to global scales (Moyle and Light 1996, Kolar and Lodge 2002, Vander Zanden et al. 2004, Moyle and Marchetti 2006, Vatland and Budy 2007, Hayes and Barry 2008). However, identifying these characteristics has proven difficult, as there may be only a few universal predictors of invasion success (e.g., history of invasiveness; Ribeiro et al. 2008). It has been generally accepted that most invasions are comprised of a progression of stages, including introduction, establishment, and assimilation (Kolar and Lodge 2002, Coulatti and MacIsaac 2004). In many cases, failure to predict successful invasions can be attributed to lack of information associated with mechanisms and dynamics of the invader at each invasion stage, particularly because the earliest stages tend to be inconspicuous (Williamson 1999). Research that has analyzed the biological traits required for success within each stage suggests that unique suites of characteristics may be required for each successful transition (Kolar and Lodge 2002, Ribeiro et al. 2008). Successful invaders may exhibit varying combinations of these characteristics, and phenotypic plasticity, realized as the ability to optimally adapt to local conditions, is likely as important for many successful invaders as the traits themselves (Fox et al. 2007, Ribeiro et al. 2008, Valiente et al. 2010).

Recently, invasion ecology research has focused on assessing how aspects of invader life histories can be used to predict the success and consequences of potential invasions. Specifically, it has been recognized that research is needed to quantify the effects and

characteristics of invaders at the individual and population levels at all stages of invasion, in an effort to examine how these characteristics might change as a species moves from one stage to another (Williamson 1999, Sakai et al. 2001, Kolar and Lodge 2002). Measures of life history traits such as age and length at maturity, fecundity, reproductive energy investment, and growth have been used to define, compare, and predict the invasiveness of non-native populations at different stages, and to elucidate their relative importance to successful establishment and spread (Bøhn et al. 2003, Villenueve et al. 2005, Olden et al. 2006, Cucherousset et al. 2009). The resulting integration of invasion ecology and life history theory yields useful predictions about a population's life history dynamics as they are related to the stages of an invasion. Traits that have been theorized to promote survival during establishment, when populations are at low densities and resources do not appear to be limited, include fast individual growth (especially in juveniles), early maturation, and high reproductive investment (Hutchings 1993, Fox et al. 2007). In life history theory, these are common characteristics of opportunistic or r-selected life histories (Winemiller and Rose 1992, Olden et al. 2006). As the invader becomes more abundant and widespread during the establishment and assimilation stages, or as resources become limited via intra- or interspecific competition, traits that are predicted to promote survival include slow growth, late maturation, and low reproductive investment (Hutchings 1993, Fox et al. 2007). These traits would suggest a k-selected or equilibrium life history strategy (Winemiller and Rose 1992, Olden et al. 2006). The ability of an introduced species to shift between these respective strategic endpoints would seem to facilitate its successful invasion.

The objectives of this study were to quantify the life history traits of an introduced moronid, white perch (*Morone americana*), in three large reservoirs in North Carolina, USA, which represented a series of 1, 11, and 21 years since initial white perch detection. Invasive species have been especially problematic in reservoirs, which are thought to be more susceptible than natural lakes to invasion, more likely to hold multiple invaders, and to increase the probability of spread of invasive species across landscapes (Johnson et al. 2008). This increased susceptibility has been attributed to greater accessibility by the public, higher levels of disturbance, and more variability in resources in reservoirs than in natural systems (Havel et al. 2005, Johnson et al. 2008). However, recent research has shown that established reservoir fish communities appear to be resilient and relatively stable over long time periods (Gido et al. 2000) and species introduced into reservoirs are still required to pass through the stages of invasion in order to fully establish and assimilate into the community (Vatland and Budy 2007, Vander Zanden and Olden 2008). In addition, reservoirs are often managed for recreational angling, so thorough information on historic and current community assemblages and species introductions is more frequently available for reservoirs than for natural, less disturbed systems. In sum, because the biotic rules of invasion still apply in reservoirs, and because more complete information on species introductions can be obtained, reservoirs offer ideal sites for in-depth studies of invasion ecology.

We made two primary predictions based on life history and invasion stage theories: 1) a new population would occur in low abundance and follow an opportunistic life history strategy characterized by rapid growth, early maturation, and increased reproductive investment, and 2) older populations would occur in high abundance and switch to an

equilibrium life history strategy characterized by slow growth, late maturation, and low reproductive investment. To test these hypotheses, we quantified relative abundance, growth, age and length at maturation, and reproductive investment in three populations of white perch ranging from one to more than twenty years since initial detection. Through these analyses we sought to determine to what extent life history strategy and plasticity drives the invasion success of white perch in reservoir systems.

STUDY SPECIES

White perch are semi-anadromous, estuarine fish native to the Atlantic coast from South Carolina to northern Maine (McGrath and Austin 2009). They exhibit sexually dimorphic life history strategies, wherein males mature by age 2 and females mature at age 3 or 4 (Conover 1958, Mansueti 1961). White perch can be classified as capital spawners (i.e., they build up gonad material through time, as opposed to shunting energy to maturation just before the spawning period), exhibiting a biphasic increase in gonad development through the year. Peak gonad development and spawning occurs around 15-20°C, usually in April to early May in North Carolina reservoirs (Mansueti 1961, Jackson and Sullivan 1995, Stephens et al. 2009). White perch are highly fecund broadcast spawners that do not exhibit any apparent preference for spawning habitat or substrate (Foster 1919, Zuerlein 1981). Fecundity estimates range up to 300,000 eggs per female (Bur 1986, Chizinski 2007).

White perch have invaded lakes and reservoirs in New York (Prout et al. 1990), Nebraska (Hergenrader and Bliss 1971), Oklahoma (Kuklinski 2007), Maine (Hines 1981), Virginia (Harris 2006), North Carolina (Wong et al. 1999), Illinois (Irons et al. 2002), and all five Great Lakes (Scott and Christie 1963, Boileau 1985, Sierszen et al. 1996, Madenjian et

al. 2000). Though relatively little is known about white perch invasions, the period immediately following introduction has been exemplified by rapid population growth which eventually results in a stunted population, thought to be driven by high fecundity and ability to spawn on any substrate, as noted by Hergenrader and Bliss (1971) in Nebraska reservoirs. Data on white perch life histories have been collected long after initial white perch invasion (e.g., Bur 1986, Wong 2002, Chizinski 2007), but little else is known about white perch life history strategies during the early stages of invasion or how this might drive population dynamics as they advance through each invasion stage.

METHODS

Study Sites

White perch were collected from Lake James, Lake Norman, and Jordan Lake, NC, in order to cover a gradient in time since white perch invasion (Table 1.1). Lake James represents the newest population, as white perch were first discovered there by North Carolina Wildlife Resources Commission (NCWRC) biologists in 2008 and are still primarily localized to the northern arm of the lake in relatively low densities (JM Rash, NCWRC, personal communication, 2009). Sampling by the NCWRC and this study captured primarily one and two year old fish, with the maximum age represented by a single age-4 female. Because white perch in southern reservoirs commonly reach age-8 or older (Wong 2002, Harris 2006, this study), and white perch up to 13 years old have been found in other North Carolina reservoirs (B.J. Galster, unpublished data), this suggests white perch were first introduced to Lake James four years prior to detection. Therefore, we believe white perch are in the early establishment stage of invasion in Lake James. Lake Norman

represents the intermediate-age population in this study, as white perch were first discovered there in 1998 (BJ McRae, NCWRC, personal communication, 2010). The white perch population in Lake Norman is believed to still be expanding, and white perch are found throughout the lake, indicating that this population is probably in the early assimilation stage of invasion. Finally, Jordan Lake represents the oldest population of white perch in this study, with first discovery in 1988 (Wong et al. 1999). White perch are widespread and highly abundant in Jordan Lake, and their population expansion appears to have leveled off, as catches of white perch reported in this study are similar to those reported in 1998 by Wong et al. (1999). Thus, the white perch population in Lake Jordan is in a late assimilation invasion stage. Studying the white perch populations in each lake allowed us to examine the importance of shifts in life history strategy across stages of invasion ranging from early establishment (Lake James) to late assimilation (Jordan Lake).

Data Collection

White perch were collected in April of 2009 and 2010, when surface water temperatures reached 13-15°C, the average reported temperature at which white perch spawn (Jackson and Sullivan 1995). At this time, mature individuals were at peak gonad development just before spawning. Four sites in each lake were sampled (Figure 1.1). Each site consisted of two boat electrofishing transects, one nearshore gill net, and two offshore gill nets. Each electrofishing transect consisted of 1200 seconds of shocking time (approximately 275-325 m in length) using 120 volt DC current conducted at night, which has been shown to be the most effective method for white perch collection (Kuklinski 2007, Wong 2002). All white perch were netted and placed in a 190-liter live well.

Experimental gill nets were set at dusk each night and retrieved after fishing for 6 to 8 hours. Nearshore nets 2 m × 38 m, composed of five, 7.6-m panels (12.7, 19.1, 25.4, 38.1, and 50.8-mm bar mesh) were used to sample the littoral zone. They were set perpendicular to and away from shore starting in 2-2.5 m of water. Two different nets were used to sample the offshore zone; one 2 m × 50 m net with 25.4-mm bar mesh, and one 2 m × 100 m net consisting of 50 m of 50.8-mm and 50 m of 63.5-mm bar mesh. In 2010, the 100-m net was replaced by one new net, 2 m × 100 m, with 50 m of 38.1-mm and 50 m of 50.8-mm bar mesh. This reduction in mesh size allowed more effective sampling of large adult white perch, as 63.5-mm mesh was unsuccessful in sampling them. For both gears, white perch were sorted by size to ensure a representative sample of each population was collected, and a maximum of 15 fish from each of four size bins (<120, 121-180, 181-230, and >230 mm total length [TL]) were killed and immediately placed on ice.

Once returned to the lab, all fish were frozen until further processed. At processing, fish were thawed, measured to the nearest 1 mm TL, and weighed to the nearest 0.01 g. Sex and maturity level of all white perch was assessed via macroscopic inspection and scored on a 1-4 point scale (1=immature, 2=developing, 3=mature, 4=spent) adapted from Núñez and Duponchelle (2009). Only gonads scored as a 3 or 4 were considered mature. Wet weight of gonads was measured to determine gonadosomatic index (GSI), calculated as gonad mass/body mass×100. The GSI gives the percentage of the fish's body weight made up of gonad tissue, which can be used as a proximate measure of energetic investment into reproduction (Hutchings 1993). For age determination, saggital otoliths were sectioned, mounted on slides, and read by two independent readers with no knowledge of the fish length

or the other reader's age estimate. Any disagreements were resolved by a third, independent reader. Using this method, 1,035 fish were aged with 94.4% agreement between the first two readers. All disagreements were resolved by the third age estimate.

Data Analysis

Relative abundance was determined by comparing electrofishing catch per unit effort (CPUE, expressed as catch/electrofishing minute) among lakes. Electrofishing CPUE reflected the abundance of white perch in spring because white perch move nearshore to spawn, and all sizes of fish at all stages of maturation are susceptible to electrofishing at that time. Age and length at maturity and mean GSI were calculated and compared across populations using Bayesian analyses in OpenBUGS software v. 3.1.1 (© Free Software Foundation, Inc. 2007). Bayesian analyses provide estimates of the posterior distributions for model parameters based on prior information and current data (McCarthy 2007). Estimates are obtained iteratively using Markov chain Monte Carlo (MCMC) methods.

For our purposes, there were two major benefits to using Bayesian statistics. First, it allowed the generation of 95% credible intervals (defined as a 95% chance the true value is included in the specified interval) for means, individual model parameters, and calculated values, which allowed for easy and straightforward comparisons of life history traits among populations (McCarthy 2007). Second, we were able to use deviance information criterion (DIC) scores to aid in model selection. DIC scores operate on much the same principles as other information criteria, in which a model is tested for fit while being penalized for complexity (Spiegelhalter et al. 2002). Resulting DIC scores from multiple alternate models for the same dataset can be compared, and the lowest score suggests the best model

(Spiegelhalter et al. 2002, Van Der Linde 2005). Spiegelhalter et al. (2002) suggested that in using DIC for model selection, models that differ by one to two DIC units from the lowest DIC score should be considered useful, while models with differences of more than three DIC units are not supported. We used both DIC score and 95% credible interval analyses in comparing our data across lakes and times since invasion.

To estimate maturity schedules of each population, age and length at maturity curves were generated separately for males and females in each lake. Maturity was described as a categorical variable with values of 1 (mature) or 0 (immature). A logistic regression of age (years) or length (mm TL) versus maturity (0 or 1) was fitted to each individual dataset, yielding estimates for the intercept and slope of the logistic equation:

(1.1) $$Y(t) = 1/\left(1 + e^{(-(\alpha + \beta \times t))}\right)$$

where α represents the intercept, β is the slope, and $Y(t)$ equals the probability of a fish maturing at age or length t (Wang et al. 2009). Two models were constructed to test for differences in maturation schedule across populations each year; a full model, including separate slope and intercept parameters for each lake (DIC_{Full}) and a reduced model, including a single slope and intercept across all lakes ($DIC_{Reduced}$). To ensure a stable posterior distribution was reached, models were allowed to run for 50,000 updates (iterations) with a burn-in of the initial 2,500 updates discarded to remove any effects of the initial parameter values. Once a stable posterior distribution was reached, DIC scores were assessed from an additional 10,000 updates of the model. Maturity schedules were considered different among lakes when the full model DIC score was at least three units lower than the reduced model DIC (Spiegelhalter et al. 2002, He and Bence 2007, McCarthy

2007). Percent mature at age-2 was calculated as a useful metric for directly comparing age at maturity among populations.

Full and reduced model comparisons were also used to evaluate differences in white perch growth among lakes, which was calculated by fitting age at length data from each lake to the von Bertalanffy equation:

(1.2)
$$L_t = L_\infty\left(1 - e^{-k(t-t_0)}\right)$$

where L_t is the estimated total length at age t, k is the growth coefficient, L_∞ is the average maximum length for the population, and t_0 is the age where L_t equals 0 (Ricker 1975).

Sex-specific mean GSI was compared among populations using Bayesian analysis of variance (ANOVA), comparing the 95% credible intervals of each mean value and full- and reduced-model DIC scores. Means without overlapping credible intervals and with a difference of at least three DIC units between the full and reduced model scores were considered different (Spiegelhalter et al. 2002, McCarthy 2007).

RESULTS

In 2009, a total of 90 white perch were collected from Lake James, 274 from Lake Norman, and 280 from Jordan Lake (Table 1.2). In 2010, we collected 140 white perch from Lake James, 261 from Lake Norman, and 253 from Jordan Lake (Table 1.2). White perch occurred in the lowest relative abundance in the newest population (Lake James) in both 2009 and 2010 (Figure 1.2). In 2009, the oldest population (Jordan Lake) was twice as abundant as the intermediate population (Lake Norman; 4.42 vs. 2.43 fish/shocking minute) and almost nine times as abundant as the newest population (0.59 fish/minute; Lake James). In 2010, the intermediate population was most abundant, followed by the oldest and newest

populations (2.22, 1.32, and 0.37 fish/minute). Fewer white perch were caught in 2010 than

2009 in all three lakes, with the largest decline occurring in Jordan Lake, followed by Lake

Norman and Lake James (Figure 1.2).

       Mean GSI of mature female white perch was higher in the new population than in the

intermediate or old populations in both years, and the 95% credible intervals overlapped only

slightly between the new and oldest populations (Figure 1.3). In 2009 and 2010, slightly

lower DIC scores for the full models than for the reduced models (differences of 2.4 and 1.4

units) indicated that the GSIs were marginally different among populations, although both

models had some support. However, the new population exhibited higher reproductive

investment each year than either older population, and this trend was nearly identical across

years, which suggests that females in the new population do invest more in reproduction than

their counterparts in the older populations (Table 1.3, Figure 1.3a). For mature male white

perch, there was no difference in GSI among populations in 2009, evidenced by nearly

identical DIC scores (Table 1.3) and highly overlapping credible intervals (Figure 1.3b).

Male GSI was higher in the newest population than in the oldest population in 2010, as

evidenced by non-overlapping credible intervals (Figure 1.3b) and a DIC_{Full} score 9.8 units

lower than $DIC_{Reduced}$ (Table 1.3).

       White perch of both sexes grew faster and to larger sizes in the newest population

when compared to both the intermediate and old population in 2009 (Figure 1.4a, c). This

was supported by large differences in DIC scores for both females and males (Table 1.3). A

similar trend occurred in 2010, with the exception that the intermediate population appeared

to reach a slightly larger final size for both males and females (Figure 1.4b, d). The new

population continued to grow fastest among all populations and reach larger sizes than the oldest population (Figure 1.4b, d; Table1.3).

There was no difference among populations in female white perch length at maturity in 2009 (Table 1.3, Figure 1.5a). In 2010, female white perch matured at shorter lengths in the oldest and intermediate populations than in the new population (Table 1.3, Figure 1.5b). In males, there was no difference in length at maturity among lakes in either 2009 or 2010 (Table 1.3, Figure 1.5c, d). Both male and female white perch matured at younger ages in the new population compared to each older population in 2009 (Table 1.3, Figure 1.6a, b). This was best illustrated by the striking difference in percent of age-2 fish that were mature (Table 1.4). In the new population, 93% of females and 100% of males were mature, while only 37% and 24% of females and 80% and 71% of males were mature in the intermediate and older populations. However, in 2010, there was no difference in age at maturation in either females or males (Table 1.3, Figure 1.6c, d), again best exhibited by little difference the percentage of mature age-2 individuals among populations (Table 1.4). A post-hoc analysis to determine the cause of the shift from a difference in age at maturity in 2009 to no difference in 2010 revealed much higher proportions of age-2 fish maturing in 2010 in both the intermediate and old populations, with increases of about 60% in females and 25% in males (Table 1.4). In addition, mean length of both male and female age-2 fish was shorter in 2010 when compared to 2009 across all lakes.

DISCUSSION

Phenotypic plasticity, realized as the ability to optimize life history traits in response to biotic or abiotic conditions, has been postulated as a primary advantage to invasive species

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(Chun et al. 2007, Valiente 2010). This study used the combination of life history and invasion stage theories to form and test specific predictions about the life history strategies of white perch populations across the establishment and assimilation invasion stages. We predicted that a newly established population would occur in low abundance and follow an opportunistic life history strategy, exhibiting higher reproductive investment, faster individual growth, and earlier maturation than older, assimilated populations, which would follow an equilibrium life history strategy (Winemiller and Rose 1992, Olden et al. 2006). By quantifying the life histories of populations in both the establishment and assimilation stages of invasion, we sought to make inferences about how the invasion dynamics and success of this species may be governed by plasticity in life history traits.

Results from abundance, growth, and reproductive investment comparisons among populations supported our predictions in both years of the study. Each response variable differed in new versus established populations, and differences were in the direction predicted by theory. Our prediction that the newest population would occur in the lowest abundance was supported; white perch in Lake James occurred in localized areas and low abundances whereas the intermediate and old populations were widespread and in high abundance. The oldest population, in Jordan Lake, was by far the most abundant in 2009, and the intermediate population in Lake Norman was the most abundant in 2010. Our prediction that individuals in an establishing population would grow faster was also supported; fish in the newest population exhibited faster growth rates and larger final sizes than those in the two established populations in 2009. In 2010, the intermediate population appeared to reach similar final sizes as the new population, but individuals in the new

population continued to exhibit faster growth rates than both older populations and reach larger final sizes than the oldest population. Finally, our prediction that a new population would invest more in reproduction was partially supported. In both years, mature females in the new population exhibited higher GSI compared to the intermediate and old populations, the latter two being relatively similar. In the case of males, however, we saw no difference in GSI in 2009, but in 2010, mature males from the newest population exhibited higher GSI, followed by the intermediate and old populations. However, because the data from females in 2009 and both sexes in 2010 follow almost identical trends of increased GSI in the new population, it is likely that the new population is indeed investing more in gonadal development than either older population.

The maturity schedules of these populations, however, presented alternate narratives from one year of our study to the next. In 2009, we found no difference in length at maturity among populations. This was not entirely unexpected, as previous literature suggests that white perch may need to reach 120-140 mm TL prior to maturity (Sheri and Power 1968, Zuerlein 1981), lengths similar to what was found in this study at the onset of maturation. There were differences in age at maturity, with the newest population maturing earliest and reaching 100% maturity by age 2 in females and age 1 in males, followed by the intermediate (females and males 100% mature by age 3) and old (100% of females mature by age 5, males by age 3) populations. This pattern was consistent in both sexes, and is consistent with the notion of a physiological minimum size for maturity. Individuals in the faster growing, establishing population would reach that minimum at a younger age than the slower growing,

assimilated populations, thus enabling the individuals in the new population to mature relatively earlier.

Similar trends of life history differences across gradients of invasion stage have been found in other species, most notably in invasive vendace (*Coregonus albula*). Vendace populations exhibited decreasing size-at-maturity as population densities increased through the stages of invasion. This plastic maturity schedule, in conjunction with high fecundity rates, was implicated as the primary mechanism associated with the success of vendace invasions in European rivers, despite their specialist diet and habitat requirements (Bøhn et al. 2003). Cucherousset et al. (2009) used age-at-maturity and growth parameters to predict the invasiveness and define the invasion stage of pumpkinseed (*Lepomis gibbosus*) populations in European waters; pumpkinseed populations that exhibited fast juvenile growth and early maturity were predicted to be the most invasive populations of concern. Thus, the results of the 2009 portion of our study appear to present an important addition to the literature supporting r-selected life history strategies among highly invasive, newly established populations. As population densities increase in the later stages of invasion, resource limitation driven by intraspecific competition or other trophic interactions may limit the growth and maturation schedules of the invader, thus resulting in a shift toward equilibrium, k-selected life history strategy.

However, maturation schedules from the subsequent year of our study exhibited significant shifts when compared to 2009. Length at maturity, which did not differ among lakes for either sex in 2009, was different for both sexes in 2010, with the intermediate and old populations shifting to mature at smaller sizes while the new population did not change.

Conversely, age at maturity, which differed among populations for both sexes in 2009, was not different in 2010. The intermediate and old populations shifted toward younger ages at maturity, while the new population did not change, leading to overlapping age-at-maturity curves across lakes. Upon closer examination of the data to determine the mechanism behind these shifts in maturity, we found that in both older populations, the mean length of fish at age 2 had decreased while the percentage of fish maturing in that age class had increased, by as much as 60% in females and 27% in males. This dramatic shift in age-2 fish then led to the restructuring of each population's maturity schedule, with the result that both the intermediate and old populations of white perch exhibited traits similar to the new population.

Environmental variation may have caused these life history shifts. White perch are prone to suffer from winter mortality in cold weather, which has been negatively correlated to the number of degree days above 15°C and is associated with winter starvation (Johnson and Evans 1990, O'Gorman and Burnett 2001). North Carolina suffered from a historically cold winter in 2009-2010, leading to unusually cold water temperatures. For example, the mean surface water temperature in January and February 2010 in Lake Norman was 5.27°C with a low of 3.72°C, compared to a mean surface water temperature from January and February 2009 of 9.62°C with a low of 7.22°C. The severe winter in 2009-2010 could have resulted in decreased survival and growth of white perch, which may have affected their life histories. Relative abundance data support this hypothesis, showing decreases in white perch abundance in all three lakes from 2009 to 2010, most markedly in Jordan Lake, which is the shallowest of the three and presumably would have gotten the coldest. Cold conditions may

also have led to the decreased mean length of age-2 fish discussed earlier. Thus, adverse environmental conditions may have caused increased mortality of white perch in the older populations, or led to poor growing conditions that caused an adaptive response in these populations to shift back to more opportunistic, r-selected life history traits.

While the oldest populations shifted toward younger age at maturity and shorter size at maturity, the new population exhibited no change in its life history strategy from one year to the next. There is some evidence that newly establishing invasive populations may be less reactive to environmental or abiotic conditions than native species, but that after invaders become established, they adjust to local conditions similarly to other species in the community (Matern and Moyle 2002, Moyle and Marchetti 2006). The shifts in maturity schedule we have documented are consistent with this theory, as the new population exhibited no change in its maturity schedule from 2009 to 2010, while the maturity schedules of the intermediate and old populations shifted toward younger and smaller age and length at maturity. This relative non-reactivity to environmental conditions of the newest population may be due to the low densities of white perch in Lake James, which could alleviate resource deficiency connected with intraspecific competition for food that has negatively affected individual growth in other white perch populations (e.g., Hergenrader and Bliss 1971). Because they are not resource- or space-limited, white perch in Lake James could continue to grow quickly and to large sizes, have high reproductive investment, and mature at young ages, despite adverse environmental conditions. This differs from the older, assimilated populations, which due to their high abundance may be resource limited. Changes in abundance, growth, or resource availability brought on by stochastic environmental processes

could then elicit substantial changes in life history parameters of older, assimilated populations as they adjust to more optimal life history strategies.

It is important to recognize that physical and biotic differences between study lakes could potentially influence white perch life history strategies in ways that this study did not measure. The fish communities and productivity of each system are somewhat different, especially between the new population in Lake James (coolwater community, oligotrophic) and the intermediate and old populations in Lake Norman (warmwater community, oligo- to mesotrophic) and Jordan Lake (warmwater community, eutrophic). It is possible that differences in trophic factors (e.g., resource abundance, forage fish availability, or interspecific competition) or physical characteristics of each lake (e.g., habitat availability or water temperature regimes) could differentially affect the life history responses of white perch in each system. However, we believe our results are robust to these caveats. Were lake productivity or water temperature significant factors driving white perch life history strategy, we would expect fish in the cooler, less productive system (Lake James, new population) to grow more slowly and invest less in reproduction than fish in warmer, more productive systems, regardless of invasion stage. However, our results show just the opposite: fish in the coolest and least productive system (but in the earliest stage of invasion) grew the fastest and invested the most in reproduction across both years of the study. This trend is further supported by fish in the intermediate-age population (Lake Norman) growing faster than individuals in the oldest population (Jordan Lake), despite Lake Norman being much less productive than Jordan Lake.

It is also possible that differences in life history strategies are being driven by differences in population density among the three populations. However, population density is a trait that inherently differs among the stages of invasion, usually increasing as a population advances from introduction to establishment to assimilation. Thus, life history shifts attributable to increasing population densities are still intrinsically linked to the stage of an invasion.

This study suggests that white perch, a highly successful invader, can adjust its life history strategy as it progresses through stages of invasion, as well as in response to changes in environmental conditions in the invaded system. Other invasion research has shown that plasticity in species traits is as equally or more important to invasion success as the traits themselves. Valiente (2010) concluded that plasticity in spawning time and migratory behavior gave brown trout (*Salmo trutta*) a competitive advantage when invading South American systems. Wide tolerance to environmental change due to high phenotypic plasticity in Asian topmouth gudgeon (*Pseudorasbora parva*) was also determined to be more important to invasion success than individual, pre-adapted traits (Rosecchi et al. 2001). Our research supports these findings, and offers insights into the advantage phenotypic plasticity can confer when environmental conditions become sub-optimal. The ability to quickly shift life history strategies is likely to be advantageous to white perch as they invade and integrate into established systems.

This information yields further insight into the role of life history shifts not only from one stage to another, but also within a stage under different environmental conditions, in a highly successful invader. Our results show that invasion stage must be taken into account

when evaluating mitigation or management policy for invasive species, as the life history of the invader may vary greatly from system to system, stage to stage, or even year to year. Thus, biologists should attempt to discern what effects their management actions may have on target species' life history strategy, as it is likely to impact subsequent dynamics of the species in possibly unexpected or undesirable ways. Overall, it appears that life history plasticity confers an important advantage to invasive species, allowing them to adapt for successful transitions throughout the invasion process, as well as to local conditions within the invaded system once they become fully integrated into established communities.

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TABLES

Table 1.1. Physical and biotic characteristics of study lakes, including year white perch were first discovered in North Carolina Wildlife Resources Commission (NCWRC) samples.

Lake	Year Impounded	River Basin	Area (ha)	Mean Depth (m)	Max Depth (m)	Mean Chl-α (μg/L)	Year First Discovered
James	1923	Catawba	2,634[a]	13.5[a]	43[a]	4.63[a]	2008[b]
Norman	1964	Catawba	13,156[a]	10[a]	33.5[a]	7.28[a]	1998[c]
Jordan	1981	Cape Fear	5,720[d]	5[e]	16[e]	41.9[d]	1988[e]

[a]NCDENR 2008
[b]JM Rash, NCWRC, personal communication, 2009
[c]BJ McRae, NCWRC, personal communication, 2009
[d]NCDENR 2009
[e]Wong et al. 1999

Table 1.2. Numbers of immature and mature fish of either sex sampled from study lakes in April 2009 and 2010 that were used in life history trait analyses.

		2009		2010	
		Immature	Mature	Immature	Mature
James	Female	32	14	49	17
	Male	15	29	34	40
Norman	Female	79	70	35	110
	Male	29	96	15	101
Jordan	Female	89	65	34	56
	Male	41	85	26	137

Table 1.3. Life history trait comparisons, corresponding full and reduced model DIC scores (female scores above male scores), and associated interpretations with respect to trends predicted by invasion and life history theories.

Year	Trait	Prediction	DIC$_{Full}$	DIC$_{Reduced}$	Interpretation
2009	Reproductive Investment	New population higher	757.9 841.1	760.3 841	Partially supported
	Individual Growth	New population faster	1767 1263	1834 1338	Supported
	Length at Maturity	No difference	204.3 262.1	203.9 261.9	Supported
	Age at Maturity	New population younger	121.4 136.9	147.4 142.9	Supported
2010	Reproductive Investment	New population higher	700.4 972.8	701.8 982.6	Partially supported
	Individual Growth	New population faster	2611 2758	2729 3039	Supported
	Length at Maturity	No difference	190.5 115.8	228.4 123.3	Not supported
	Age at Maturity	New population younger	164.2 127.7	164.2 125.2	Not supported

Table 1.4. Mean total lengths (mm TL) with 95% credible intervals and percentage of mature age-2 white perch across all lakes and years.

		James		Norman		Jordan	
		2009	2010	2009	2010	2009	2010
Female	Mean TL	199.6	175.5	164.8	147.3	153.0	142.5
	95% CI	190.7, 208.5	166.6, 183.8	157.1, 172.4	147.3, 151.2	146.3, 159.6	135.8, 149.1
	% Mature	92.9	86.7	36.8	79.7	24.0	84.0
Male	Mean TL	185.1	173.6	161.0	135.0	149.9	131.8
	95% CI	175.8, 194.3	167.7, 179.5	152.4, 169.6	130.8, 139.2	141.8, 158.0	128.1, 135.4
	% Mature	100.0	100.0	80.0	98.4	70.6	97.6

FIGURES
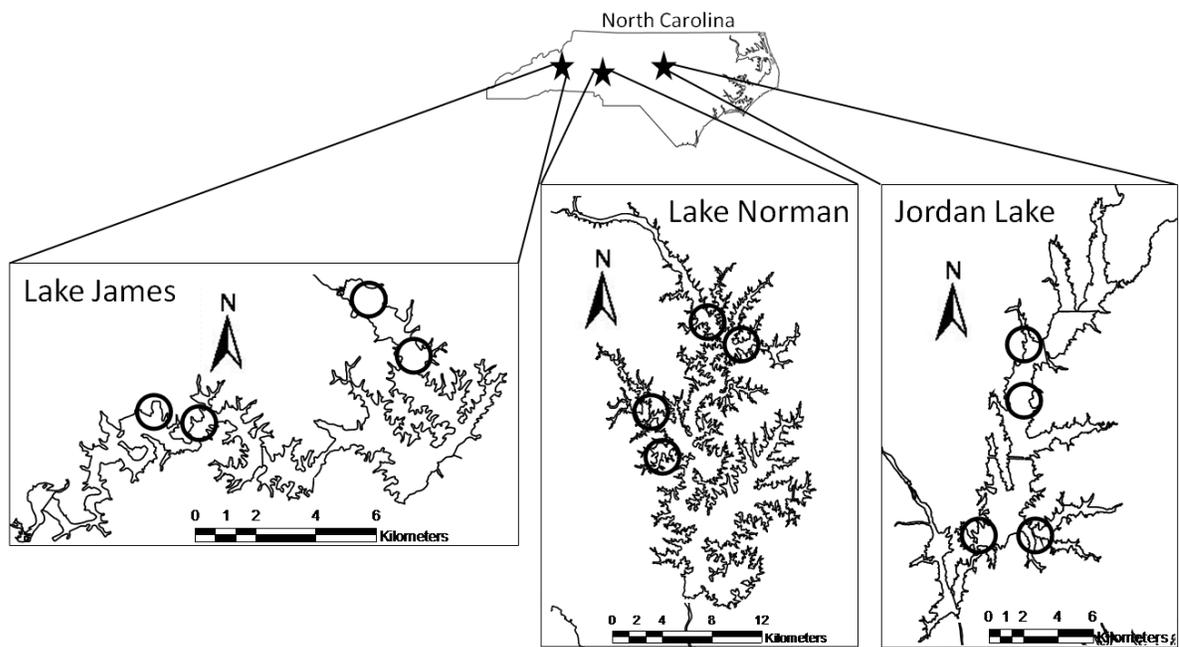
Figure 1.1. Locations of study lakes, from left to right: Lake James, Lake Norman, and Jordan Lake, NC. Sample sites are marked by circles.
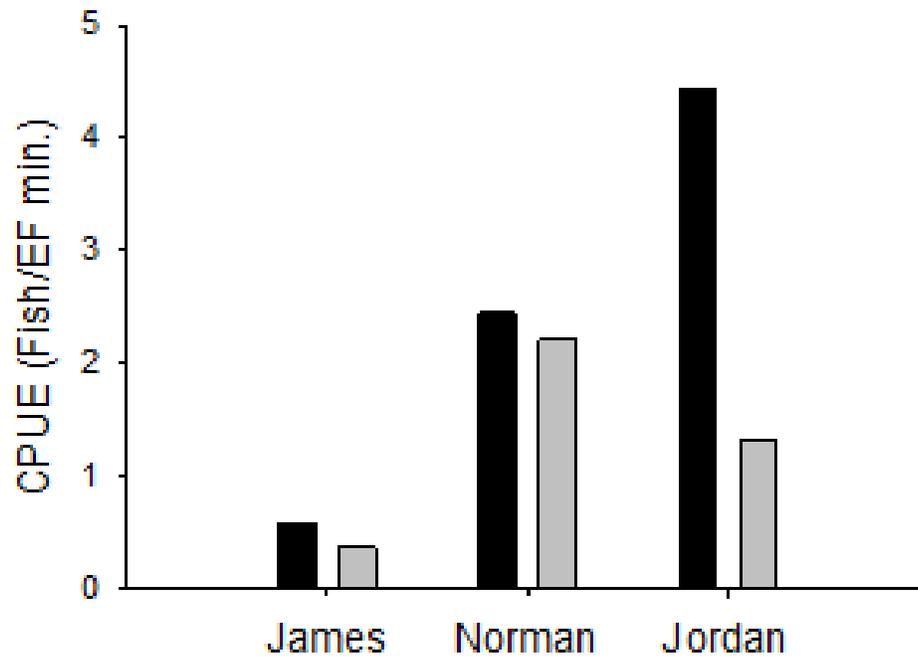
Figure 1.2. Electrofishing catch per unit effort (CPUE) of white perch by shoreline electrofishing in 2009 (black bar) and 2010 (gray bar).
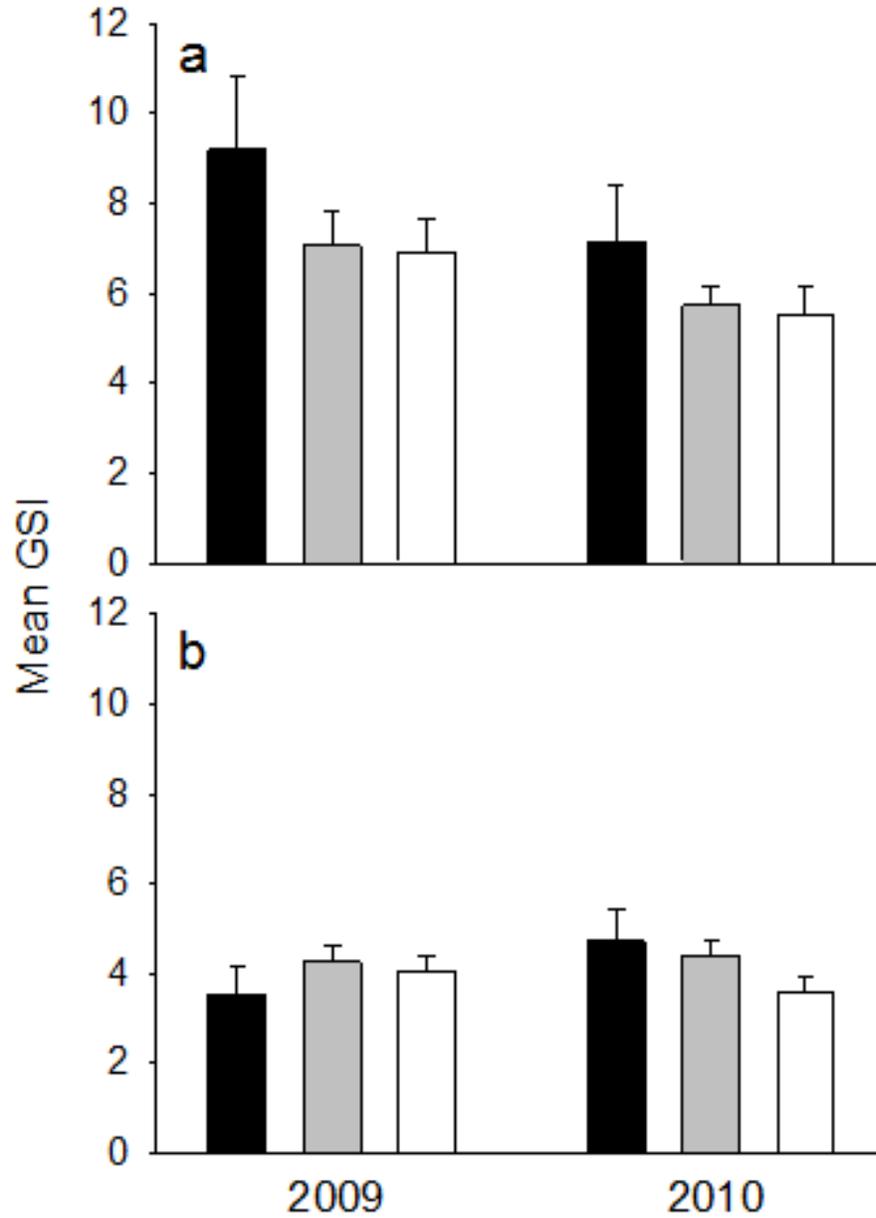
Figure 1.3. Mean gonadosomatic index (GSI) with 95% credible intervals of (a) mature female and (b) mature male white perch from new (black bars), intermediate (gray bars), and old (white bars) populations in 2009 and 2010.
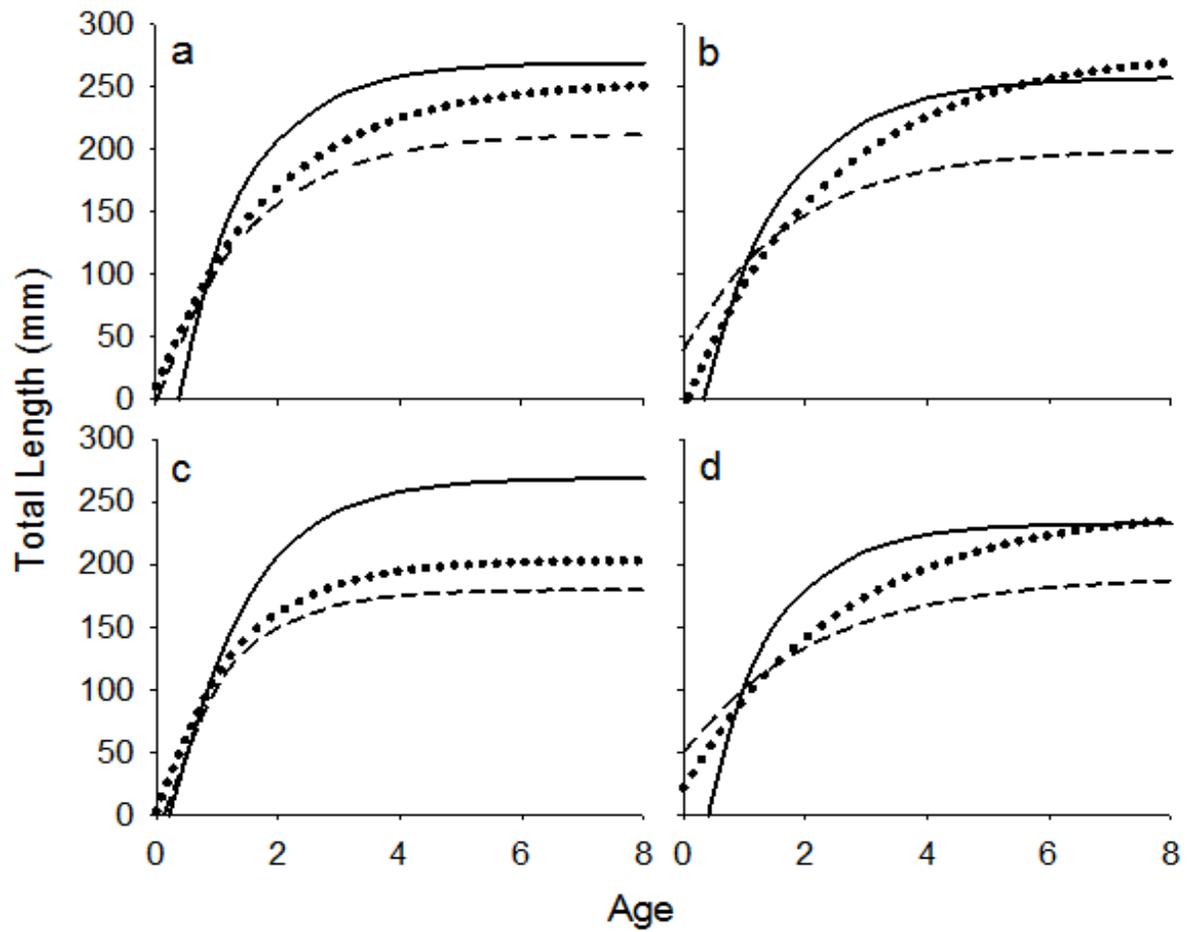
Figure 1.4. Sex-specific von Bertalanffy growth curves for new (solid line), intermediate (dotted line), and old (dashed line) populations of white perch for (a) 2009 females, (b) 2010 females, (c) 2009 males, and (d) 2010 males.
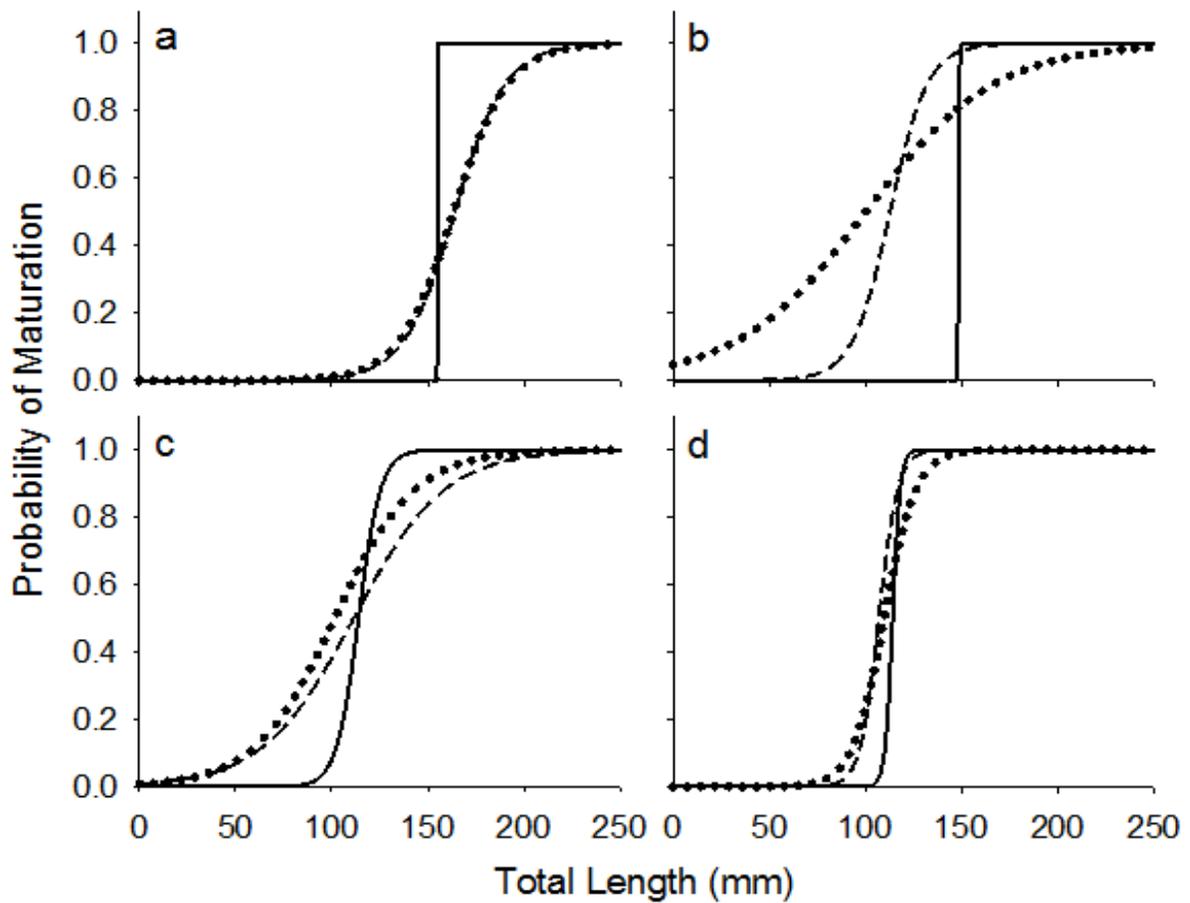
Figure 1.5. Sex-specific length-at-maturity curves for new (solid line), intermediate (dotted line), and old (dashed line) populations of white perch for (a) 2009 females, (b) 2010 females, (c) 2009 males, and (d) 2010 males.
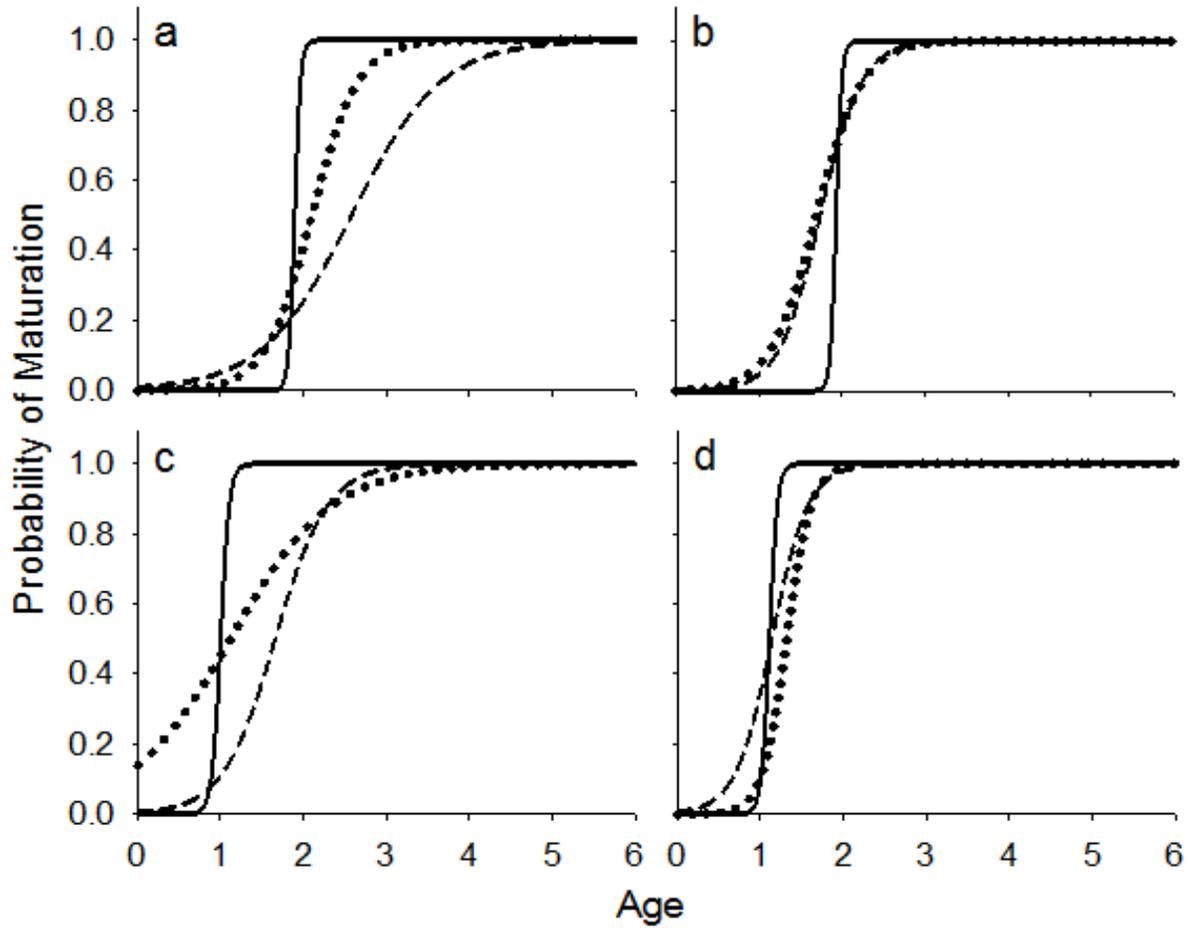
Figure 1.6. Sex-specific age-at-maturity curves for new (solid line), intermediate (dotted line), and old (dashed line) populations of white perch for (a) 2009 females, (b) 2010 females, (c) 2009 males, and (d) 2010 males.

CONSISTENT NICHE AND TROPHIC POSITION OF INVASIVE WHITE PERCH ACROSS STAGES OF INVASION

INTRODUCTION

Invasive species are one of the greatest threats to freshwater systems in North America (Jelks et al. 2008). The impact of invasive species on existing established communities can be drastic, often due to interspecific interactions such as competition, predation, and hybridization (Dowling and Childs 2002, Wilson et al. 2004, Kueffer et al. 2007). Current literature suggests most invasive species must survive through a series of stages, including transport (Stage I), introduction (Stage II), establishment (Stage III), and assimilation (Stages IV-V) (Kolar and Lodge 2002, Coulatti and MacIsaac 2004). However, the species characteristics that promote success at each transition often differ from stage to stage, and there are relatively few traits (e.g., history of invasiveness or human interactions) that are universal predictors of invasion success (Moyle and Light 1996, Ribeiro et al. 2008). This suggests that species or system-specific investigations are required to answer specific questions about the dynamics of invader success and impact (Williamson et al. 1999, Van Kleunen et al. 2010).

The trophic dynamics of invasive species in new habitats are important in predicting the success of potential invaders and evaluating their effects. Generally, it is assumed that most successful invasive species are trophic generalists, and several studies have found significant relationships between a species' trophic status as a generalist and its success across invasion stages. Marchetti et al. (2004) concluded that ecological generalists with wide physiological tolerances were most successful in the establishment and assimilation stages, and Kolar and Lodge (2002) found that species with a wide diet breadth were most

successful in establishing new populations. Integrating community ecology and invasion

stage theories, Shea and Chesson (2002) posited a pair of hypotheses related to community

niche space and invasibility. The empty-niche hypothesis states that in systems with

unexploited resources, opportunistic invaders may gain an advantage by utilizing these

resources, and thus would occupy a distinct niche space relative to the established

community. Alternatively, the sampling hypothesis is based on the idea that invasion success

depends on the invader being a better competitor than one or more of the established species,

either through exploitation of resources or other advantages; in this case the invader would be

expected to overlap in niche space with members of the established community. A

combination of these events may occur if the established competitor is only present at in low

densities or during short time periods (Shea and Chesson 2002). These strategies

(opportunistic or competitive) may lead to very different outcomes, and community effects

may play a role in determining the dispersal and abundance of an invader (Colautti and

MacIsaac 2004). Indeed, a number of investigations have illustrated trophic shifts forced

upon native species by new invaders (Vander Zanden et al. 1999, Eagles-Smith et al. 2008)

while others have found little impact (e.g., Kuklinski 2007). In addition, the trophic strategy

of an invader may shift over time as the species assimilates or causes shifts in the established

food web. How an invasive species integrates into the invaded food web can yield important

insights into how alterations will affect the overall community, which species are likely to be

most affected, and possible management strategies to mitigate negative effects (Shea and

Chesson 2002, Vander Zanden et al. 2004, Quevedo et al. 2009). This information is vital to

understanding both the consequences of the initial invasion and in predicting how the trophic structure of the community will change as the invasion progresses.

We examined the trophic status of invasive white perch (*Morone americana*), in three reservoirs in North Carolina, USA, that represent a gradient of one, 11, and 21 years since first discovery of white perch. Reservoirs are generally more accessible to the public than natural lakes, and therefore have higher levels of anthropogenic disturbance and more variability in resources (Havel et al. 2005, Johnson et al. 2008). Because of this, reservoirs are thought to be less resistant to invasion and more likely to support multiple invasive species than natural lakes (Johnson et al. 2008). However, established reservoir communities appear to be relatively stable over time following initial impoundment (Gido et al. 2000). Additionally, reservoirs tend to be managed for recreational angling opportunities, so they often have more and better information available on aquatic community structure and species introductions than many natural systems. Relatively stable communities, combined with information on recent introductions, can make reservoirs ideal systems in which to investigate the trophic dynamics of an invasive species such as white perch.

We used a combination of quantitative diet and stable isotope analyses to determine if shifts in trophic position occur as white perch populations move through the stages of invasion. We also examined potential trophic overlap or shifts between white perch and four established representative (hereafter established) species chosen for their widespread ranges, potential interactions with white perch, and representation of relative trophic end-points in lake and reservoir food webs: a littoral piscivore (largemouth bass *Micropterus salmoides*), littoral omnivore (bluegill *Lepomis macrochirus*), and pelagic piscivore (either striped bass

Morone saxatilis or walleye *Sander vitreus*, based on the availability of these species in each

reservoir). Whereas diet studies can yield important information on the types of prey

consumed, they only provide a snapshot of what that fish has eaten over the last 10 to 12

hours (Parrish and Margraf 1990). Stable isotopes, conversely, provide a much more

integrated estimate of food habits, have been successfully used to quantify the trophic

position of species over long time periods (e.g., six months to years; Hesslein et al. 1993),

can reliably identify shifts in diet, and allow inferences to be made about changes in food

web structure (Vander Zanden et al. 1999, Layman et al. 2007). Because benthic energy

sources in lakes and reservoirs are usually derived from allochthonous inputs and

autochthonous production by benthic algae in the littoral zone, the littoral carbon isotope

composition (δ^{13}C) can be attributed to benthic production, and is more enriched (less

negative) relative to the δ^{13}C value of phytoplankton at the energetic base of the pelagic

zone, which is ^{13}C depleted (more negative; France 1995). The distinct δ^{13}C signatures of

each zone allow carbon isotopic partitioning to be used to determine the proportion of energy

an individual fish derives from benthic or pelagic sources (Post 2002). Nitrogen isotope

composition (δ^{15}N) becomes enriched by approximately 3.4‰ with each increase in trophic

level within a food web, and thus can indicate the trophic level of an individual fish (Vander

Zanden et al. 1999, Fry 2006). The values of δ^{15}N and δ^{13}C can then be used in concert to

determine the relative trophic position of an organism in a food web (France 1995, Post

2002, Fry 2006). The combination of diet and stable isotope approaches allowed us to both

quantify diet overlap between white perch and the established species of interest and also

investigate the broader trophic structure of each reservoir community.

Study Species

White perch, a semi-anadromous, estuarine fish native to the Atlantic coast from South Carolina, USA, to Nova Scotia, Canada (McGrath and Austin 2009), have been recognized as a problematic invasive species since the 1950s. They have invaded lakes and reservoirs in New York (Prout et al. 1990), Nebraska (Hergenrader and Bliss 1971), Oklahoma (Kuklinski 2007), Maine (Hines 1981), Virginia (Harris 2006), North Carolina (Wong et al. 1999), and Illinois (Irons et al. 2002), as well as all five Great Lakes (Scott and Christie 1963, Boileau 1985, Sierszen et al. 1996, Madenjian et al. 2000). White perch have been implicated in the declines of many species throughout their invaded range, including bluegill, black bullhead (*Ameiurus melas*), flat bullhead (*Ameiurus platycephalus*), largemouth bass, walleye, yellow perch (*Perca flavescens*), and white bass (*Morone chrysops*) (Hurley and Christie 1977, Parrish and Margraf 1990b, Wong et al. 1999, Madenjian et al. 2000, Vrtiska et al. 2003). White perch are often considered opportunistic feeders that shift among seasonally available forage items, feeding primarily on zooplankton and larval insects (Schaeffer and Margraf 1986, Wong 2002, Harris 2006, Couture and Watzin 2008, Gosch 2008). Large adult white perch can become almost entirely piscivorous (Sierszen et al. 1996, Moring and Mink 2002). Previous research has also shown that white perch tend to have more food in their stomachs on average than established species in the same system such as white bass and yellow perch, indicating that they may be more effective foragers than native competitors (Gopalan et al. 1998). This broad diet, opportunistic feeding strategy, and ability to shift between benthic and pelagic food sources may contribute to their ability to successfully invade and impact many different systems and biotic communities.

Due to their frequent introductions and potential negative impacts on established communities, it is important to understand white perch trophic dynamics in reservoirs, particularly in the context of developing mitigation or management strategies. Unfortunately, white perch trophic dynamics are not well understood. Gosch (2008) concluded that white perch rise no higher on the food chain than forage fish such as gizzard shad. Conversely, Sierszen et al. (1996) found that the trophic status of white perch greater than 280 mm total length (TL) in Lake Superior was similar to that of the top piscivore in the system, northern pike (*Esox lucius*). These equivocal results suggest that white perch are capable of occupying very different trophic niches in different systems. Thus, in order to understand the role shifts in white perch trophic niche size and position play in successful invasions, we need to first quantify their trophic dynamics in the systems of concern, which has not been conclusively determined in reservoirs. This information could then shed light on the potential impacts white perch could have on established communities, and be used to develop management options for established populations.

METHODS

Study Sites

We studied white perch trophic dynamics in three large reservoirs in North Carolina that were chosen to represent a gradient of time since white perch invasion (Figure 2.1, Table 2.1). The newest population of white perch studied exists in Lake James, and was first discovered by the North Carolina Wildlife Resources Commission (NCWRC) in 2008 (J. M. Rash, NCWRC, Marion, NC, personal communication, 2009). The intermediate-age and oldest populations of white perch occur in Lake Norman and Jordan Lake, where they were

discovered in 1998 and 1988, respectively (Wong et al. 1999; B. J. McRae, NCWRC, Raleigh, NC, personal communication, 2009). Sampling by the NCWRC and a concurrent study revealed the white perch population in Lake James is very young, consisting of roughly 75% fish age ≤ 1 and 25% age-2 individuals. The oldest fish captured in Lake James in 2009 was a single age-4 female, while white perch in Lake Norman and Jordan Lake regularly reach age 7 or 8, similar to maximum ages for white perch found elsewhere (Chizinski 2007). These findings suggest the Lake James white perch population is in the early establishment stage of invasion, while the populations in Lake Norman and Jordan Lake are in the early and late assimilation stage, respectively, which allowed us to make inferences about white perch trophic dynamics across at least two stages of invasion (establishment and assimilation).

Lake James contains a coolwater fish assemblage and supports recreational fisheries for smallmouth bass (*Micropterus dolomieu*), largemouth bass, walleye, white bass, muskellunge (*Esox masquinongy*), and black crappie (*Pomoxis nigromaculatus*). Lake Norman and Jordan Lake each support warmwater communities typical of those found in reservoirs across the southeast, and support popular striped bass, black crappie, catfish (*Ictalurus* spp.), and largemouth bass fisheries. All three reservoirs also support large populations of sunfish (*Lepomis* spp.), gizzard shad (*Dorosoma cepedianum*), threadfin shad (*Dorosoma petenense*), and yellow perch.

Data Collection

To characterize the community structure of each reservoir, fish were collected at night in July 2010, when young-of-year white perch began to recruit to electrofishing gear. Each lake was sampled at four sites: a single site consisted of two shoreline boat

electrofishing transects, one nearshore gill net, and two offshore gill nets (Figure 2.1). Each electrofishing transect was 1,200 shocking seconds long (typically 275-325 m of shoreline), using 120 volt pulsed DC current. An experimental mesh nearshore gillnet 2 m x 38 m, composed of five 7.6 m panels of 12.7, 19.1, 25.4, 38.1, and 50.8-mm bar mesh was set on the bottom perpendicular to and away from shore beginning in 2-2.5 m of water. Two offshore gill nets were used, one 2 m x 50 m consisting of 25.4-mm bar mesh, and one 2 m x 100 m consisting of 50 m of 38.1-mm and 50 m of 50.8-mm bar mesh. Offshore gill nets were set at least 50 m from shore at depths of 7-20 m in Lake James, 10-18 m in Lake Norman, and 6-8 m in Jordan Lake, depending on the characteristics of each site. When the lake was not stratified, offshore gill nets were set on the bottom. When the lake was stratified, nets were suspended just above the oxycline. At each site a Hydrolab Quanta® Water Quality Monitoring System (Hydrolab Corporation, Austin, TX, USA) was used to measure temperature and oxygen concentration at 1 m intervals from surface to bottom.

A minimum of 10 and maximum of 20 individuals each of a established littoral piscivore (adult largemouth bass), littoral omnivore (adult bluegill), pelagic piscivore (adult striped bass in Lakes Norman and Jordan, walleye in Lake James), and three size classes of white perch were killed, placed on ice, and returned to the lab. These established species were chosen in order to develop a framework of the relative trophic structure of each lake so that the trophic position of each white perch size class could be compared relative to the positions of each representative species. Only adults of the established species were kept in an effort to eliminate likely trophic variation between juvenile and adult stages. Three size classes of white perch, small (<100 mm TL), medium (140-170 mm TL), and large (>200

mm TL) were kept in order to more closely examine their ontogenetic trophic shifts. In

addition, counts and aggregate weights of all species caught were recorded to calculate

relative abundances and evaluate differences in the fish communities of each lake.

To collect a littoral baseline for stable isotope analysis, benthic invertebrates were

collected with a Ponar sediment collector at depths of 0.5-1 m at each site. Invertebrates

such as Chironomidae and Ceratopogonidae larvae feeding on benthic material in the littoral

zone can be used to represent the baseline littoral signature of aquatic systems (Vander

Zanden and Rasmussen 1999). To serve as a pelagic baseline, filter-feeding Asian clams

(*Corbicula* spp.) were hand collected. Filter-feeding bivalves have been shown to accurately

represent an integrated pelagic signature of aquatic systems (Post 2002), and *Corbicula* in

particular have been used to determine pelagic baselines in other trophic studies (e.g., Garcia

et al. 2006, Kopp et al. 2009); therefore, we were confident that *Corbicula* were appropriate

to use as a pelagic baseline. All baseline organisms were immediately placed on ice and

transported to the lab for further processing.

In the laboratory, fish were thawed, measured to the nearest 1 mm TL, and weighed

to the nearest 0.01 g. Stomachs of all species were excised and stored in 95% ethanol.

Stomachs were weighed before and after content removal to estimate content weight. Diet

items were identified to the lowest possible taxon, counted under a dissecting microscope,

and weighed. For very small items (e.g., zooplankton), the combined weight of 100

individuals was recorded and used to determine an average individual weight. Because diet

items can often be partially digested, only one easily distinguishable body part of each taxon

(e.g., chironomid heads) was recorded in numerical diet analysis of each stomach. Complete

fish backbones were weighed (nearest 0.01 g) and the number of vertebrae counted for species identification. If a stomach contained multiple vertebral segments that may have been from more than one fish and were not easily pieced together, each segment was weighed and grouped as "unidentified fish."

For stable isotope analysis, benthic samples were sieved and all benthic invertebrates were removed and cleaned of particulate matter. A minimum weight of 1 mg of invertebrates, comprised of Chironomidae and Ceratopogonidae larvae, was removed from each sample. Foot and adductor muscle was removed from 6 -10 *Corbicula,* cleaned of debris, and aggregated for a 1 g sample. One gram of muscle tissue was excised from the dorsal area on the left side of each of 15 white perch per size class (small, medium, and large) and 10 individuals of the established species (adult bluegill, largemouth bass, and striped bass or walleye) per lake, except in those cases where slightly smaller sample sizes were caught (Table 2.2). These samples were frozen and sent to the Cornell University Stable Isotope Lab, Ithaca, NY, for further preparation and stable isotope analysis.

Data Analysis

Differences in species abundances were estimated from catch per unit effort (CPUE) in fish/shocking minutes for electrofishing or fish/net-night for gillnetting. Most species were grouped into general taxonomic categories: sunfish (*Lepomis* spp.), black bass (largemouth, smallmouth, and spotted bass), catfish (*Pylodictis*, *Ictalurus*, and *Ameiurus* spp.), and clupeids (gizzard shad, threadfin shad, and alewife). Species that were rare or occurred sporadically in small numbers (i.e., common carp (*Cyprinus carpio*), quillback (*Carpiodes cyprinus*), catostomid and cyprinid species, etc.) were grouped in an "other"

category. White perch, white bass, striped bass, yellow perch, and black crappie were measured individually. The relative abundance of white perch was also compared among lakes to determine if population density might be a factor driving trophic dynamics.

Trophic position of each established species and white perch size class was calculated using a series of equations. First, because lipids are ^{13}C-depleted relative to muscle, differences in tissue lipid content among species may lead to incorrect conclusions about the trophic positions of different species. Therefore, the δ^{13}C value for each fish was mathematically normalized for differences in lipid content following the linear regression formula:

(2.1)
$$\Delta\delta^{13}C = -3.32 + 0.99 \times C:N$$

based on the linear relationship of the C:N ratio of the sample (which is correlated to lipid content), and the expected change in δ^{13}C after lipid extraction of that sample (Post et al. 2007). We assumed there was no trophic fractionation of δ^{13}C, as previous studies have shown the actual fractionation rate to be ecologically indistinguishable from zero, and that the ultimate calculation of trophic position is insensitive to assumptions about δ^{13}C trophic fractionation (Post 2002, Vander Zanden and Vadeboncoeur 2002). Trophic position of each species and white perch size class was determined using a two-member mixing model (Post 2002), where the proportion of energy derived from the littoral base (α) was determined using:

(2.2)
$$\alpha = \left(\delta^{13}C_{fish} - \delta^{13}C_{pelagic\,baseline}\right) / \left(\delta^{13}C_{littoral\,baseline} - \delta^{13}C_{pelagic\,baseline}\right) \qquad .$$

Trophic level of each fish was then determined using:

(2.3)
$$Trophic\;Level = 2 + \left(\delta^{15}N_{fish} - \left[\delta^{15}N_{littoral\,baseline} \times \alpha + \delta^{15}N_{pelagic\,baseline} \times (1-\alpha)\right]\right) / 3.4$$

assuming a baseline trophic level of 2 and trophic fractionation of 3.4‰ (Vander Zanden et al. 1999). Trophic niches and potential overlaps were analyzed using $\delta^{15}N - \delta^{13}C$ biplots and three metrics for each species. Nitrogen range (the difference between the highest and lowest $\delta^{15}N$; NR), is a measure of the ability of that species to forage at different levels of the food web. Carbon range (the difference between the highest and lowest $\delta^{13}C$; CR), reflects the ability of individuals of that species to forage on both pelagic and littoral energy sources, except in the rare case where all individuals of a species rely roughly equally on both sources (i.e., alpha~0.5). However, this situation did not occur in our study. Finally, total niche area (the estimated convex hull area occupied on the $\delta^{15}N - \delta^{13}C$ biplot; TA), was used as a measure of the size of that species' trophic niche in the community, and overlap among convex hulls signifies potential trophic overlap between species (Layman et al. 2007, adapted by Zambrano et al. 2010).

All diet items discovered in fish stomachs were grouped into categories based on their body size and location in the water column (Table 2.3). Diets of each species were qualitatively described using frequency of occurrence of diet items in the stomach (%FO), average percent by number of each diet item within a species or size class (%N), and average percent by weight of each diet item (%W). Because each of these individual measures has biases (Hyslop 1980, Hart et al. 2002), an Index of Relative Importance (IRI; Pinkas et al. 1971) was calculated for each diet item, *i,* within each species and white perch size class, using the equation:

(2.4)
$$IRI_i = \%FO \times (\%N_i + \%W_i)$$

From the IRI, a percent IRI (%IRI) was calculated for each diet item i within species and white perch size class j as:

$$(2.5) \qquad \%IRI_{ij} = \frac{100 \times IRI_i}{\sum_{j=1}^{n} IRI_j}$$

where n is the number of individuals within that species or size class. This index has been suggested as the best method to balance the relative importance of frequency of occurrence, numerical abundance, and contribution by weight of diet items in fish stomachs, and has been used extensively in fish diet analyses both alone (Cortés 1997, Liao et al. 2001, Hart et al. 2002) and in assessing diet overlap (Golani 1994, Matić-Skoko et al. 2004, Figueroa et al. 2010). To measure diet overlap between species, we used %IRI in Schoener;s Index (Schoener 1968), a commonly used diet overlap index that previous research suggests is effective at minimizing bias in measuring diet overlap between species (Wallace 1981). We calculated Schoener's Index as:

$$(2.6) \qquad D = 1 - 0.5(\sum_{i=1}^{S} |X_i - Y_i|$$

where S is the number of food categories, X_i is the %IRI of diet item i in species or size class X, and Y_i is the %IRI of diet item i in species or size class Y. Overlap was considered ecologically significant when values of D were greater than 0.6 (Wallace 1981).

RESULTS

Fish Community Structure

Relative abundance of fish collected by shoreline electrofishing followed the gradient of productivity of each lake, as the CPUE for all fish combined was twice as high in eutrophic Jordan Lake as in less productive Lake Norman, and five times higher than in the least productive system, Lake James. However, the fish communities of each lake contained

proportionally similar amounts of most species and functional groups (Table 2.4). The

fewest white perch were caught in the newest population (Lake James), followed by the

intermediate population (Lake Norman) and the oldest population (Jordan Lake).

Gill-net catches were variable in each lake. Nearshore net catches of both total fish

and white perch mirrored electrofishing catch rates, with the highest catches in Jordan Lake,

followed by Lake Norman and Lake James (Table 2.4). Proportionally, nearshore net catches

were also similar among lakes, being dominated by white perch and clupeids, mainly gizzard

shad (Table 2.4). Catches in offshore nets were generally low and sporadic, and therefore not

a useful indication of relative abundance.

Stable Isotope Analysis

Lake James appeared to have two main trophic levels. Bluegill and all three size

classes of white perch were on the lower level at trophic positions ranging from 3.08 to 3.38,

whereas walleye and largemouth bass occupied the upper level with trophic positions of 4.08

and 4.14 (Figure 2.2). On the lower level, small white perch were the most dependent on

littoral energy sources, followed by medium and large white perch (Figure 2.2). Bluegill

were the most pelagic-based species on the lowest trophic level. On the upper level,

largemouth bass carbon isotope composition was shifted toward littoral resources compared

to walleye $\delta^{13}C$ values, which were similar to those of large white perch (Figure 2.2).

Convex hull estimation revealed that medium white perch and bluegill occupied much larger

trophic niches than any other species, and also exhibited the widest carbon and nitrogen

ranges, whereas walleye and large white perch had the smallest niche area, carbon range, and

nitrogen range (Table 2.2, Figure 2.3).

The Lake Norman community exhibited three main trophic levels. On the lowest trophic level, bluegill and medium white perch had relatively similar, intermediate $\delta^{13}C$ values and trophic positions (3.27 and 3.31), while small white perch had a highly littoral carbon isotope signature and occupied a slightly lower trophic position (2.94) (Figure 2.2). Largemouth bass and large white perch occupied similar trophic positions on the second level, with trophic positions of 4.07 and 3.97 and intermediate $\delta^{13}C$ values (Figure 2.2). The apex was occupied by striped bass, at a trophic position of 4.81 and strongly pelagic $\delta^{13}C$ values (Figure 2.2). As in Lake James, medium white perch and bluegill occupied the largest trophic niche area and had the widest nitrogen range, while small and medium white perch had the widest carbon range. Striped bass had the smallest trophic niche, carbon range, and nitrogen range of all species, reflecting a consistently high trophic position based heavily on pelagic resources (Table 2.2, Figure 2.3).

The Jordan Lake food web appeared to be composed of two primary trophic levels with striped bass (5.13), largemouth bass (4.81), and large white perch (4.81) on the highest level and medium white perch (4.21), bluegill (3.93), and small white perch (3.65) at a gradient of lower trophic positions on the second level (Figure 2.2). The range of Jordan Lake $\delta^{13}C$ values was restricted; there was little difference between the most pelagic, ^{13}C-depleted species (bluegill) and the most littoral, ^{13}C-enriched species (largemouth bass). Small and medium white perch had the largest trophic niche areas, nitrogen ranges, and carbon ranges, while striped bass had the smallest total niche area and nitrogen range, and largemouth bass the lowest carbon range (Table 2.2, Figure 2.3).

Diet Overlap

White perch diets supported the trends exhibited by our stable isotope analyses. Small and medium white perch diets were consistent within size classes across all three lakes (Figure 2.4). Small white perch diets were composed primarily of small benthic invertebrates (e.g., chironomid and ceratopogonid larvae) and large benthic invertebrates (e.g., Ephemeroptera and Megaloptera larvae), with smaller proportions of surface items and zooplankton. Medium white perch diets were mostly composed of small and large benthic invertebrates, surface items, and a small proportion of fish (Figure 2.4). The pattern of invertebrate groups in the diets of large white perch was not consistent across lakes, but they ate substantial proportions of fish in each lake (18-41%, mainly threadfin and gizzard shad). The established species studied also had consistent patterns in diet composition across all lakes (Figure 2.4). Bluegills ate mainly large and small benthic invertebrates and surface organisms (Diptera pupae), except in Lake Norman, where terrestrial insects made up a larger proportion of the diet. Largemouth bass ate primarily fish and crayfish in Lakes James and Norman, and fish in Jordan Lake. Walleyes in Lake James ate nearly all fish and a small proportion of large benthic invertebrates, and striped bass ate mainly fish in both Lake Norman and Jordan Lake (Figure 2.4).

In all three lakes, medium white perch and bluegill had the highest amount of dietary overlap, with significant overlap in Lake James and Jordan Lake, and moderate but insignificant overlap in Lake Norman (Table 2.5). Small white perch also had significant diet overlap with bluegill in Jordan Lake, and moderate but insignificant overlap in Lake Norman. There was also moderate overlap ($D = 0.414$) between large white perch and

striped bass in Lake Norman (Table 2.5). In no case was there significant overlap between largemouth bass and any size class of white perch, though there was some evidence for moderate overlap with large white perch.

DISCUSSION

This study used a combination of diet and stable isotope analyses to quantify the trophic niche of invasive white perch across a gradient of time since invasion. Small and medium white perch appear to exploit a wide range of prey resources in reservoirs during all stages of invasion. Medium white perch had among the largest niche size of any species in each lake, on par with the niche size of bluegill, the representative omnivore in this study. Small white perch niche size was driven by a wide carbon range, meaning individuals varied widely in their degree of foraging on pelagic and littoral prey sources, but were able to use both. However, their niche area appeared to be limited by a narrow nitrogen range, due to their apparent dietary focus on small benthic invertebrates and zooplankton, which generally represent the lowest level consumers in lakes and reservoirs. As white perch increased in size, they became more piscivorous and their total niche area generally declined, though not to the extent of walleye or striped bass. These results suggest that white perch, especially in the medium size class, occupy a very large trophic niche, and are able to opportunistically forage on a wide range of prey items. In addition, their niche does not change as the population becomes established and assimilated into the reservoir community.

Generalist feeding habits and a wide trophic niche are thought to be advantageous for the survival and success of invasive species (Kolar and Lodge 2002, Moyle and Marchetti 2006). Previous literature has supported this theory in a number of cases. For example,

Ribeiro et al. (2007) concluded that wide diet breadth and a generalist feeding strategy were likely promoting invasion success of the South American cichlid (*Australoheros facetus*) in Mediterranean rivers, and Gido and Franssen (2007) found that an omnivorous diet is important for invasion success of stream fishes. Hergenrader and Bliss (1971) concluded that an opportunistic diet and generalist feeding strategy was one of the reasons white perch were successful in invading and dominating Nebraskan reservoirs. Our results indicate that the ability of white perch to occupy large trophic niches, especially at small and intermediate sizes, may aid in their successful establishment, and lead to impacts on multiple levels of established food webs as their abundance increases throughout the establishment and assimilation stages of invasion.

In addition to their large niche sizes, small and medium white perch exhibited consistent patterns of resource use across new, intermediate, and old populations. In all lakes, small white perch occupied the lowest trophic level and were ^{13}C-enriched, indicating a heavier reliance on benthic-derived prey sources than bluegill or medium white perch. Medium white perch occupied a slightly higher trophic level, indicating the incorporation of trophically elevated prey items such as fish, and were ^{13}C-depleted, indicating a heavier reliance on pelagic-derived prey sources than the other lower trophic level species. The diets of these size classes, though only representative of one point in time, are generally consistent with the findings of our stable isotope analysis. In all three lakes, small and large benthic invertebrates made up roughly 90% of small white perch diets by %IRI, corresponding with their low trophic level and more littoral-based, ^{13}C-enriched isotopic compositions. Medium white perch diets were still composed of 70-80% benthic invertebrates, and also included

smaller proportions of fish, surface invertebrates (such as Hemiptera and Diptera pupae), and *Chaoborus* larvae and pupae, which may have resulted in their $\delta^{13}C$ values shifting toward a pelagic-based signature.

The main difference between the small and medium size classes across lakes was the level of ^{13}C-enrichment in small white perch. In Lake James and Jordan Lake, small white perch were only moderately reliant on littoral sources compared to other species in the community, while small white perch in Lake Norman appear to be heavily reliant on littoral food sources. Because this study only encompasses the diet of white perch from one season, we were unable to find an exact dietary cause. Differences in the amount of zooplankton consumed earlier in the year may have led to slightly different trophic positions (Parrish and Margraf 1994, Couture and Watzin 2008). However, the overall trend of small white perch trophic position remained consistent – small white perch were the most benthic-reliant species on the lower trophic level of all three lakes, which is congruent with their overwhelmingly benthic diet composition. Overall, small and medium white perch occupied markedly consistent trophic positions relative to other species in each lake, suggesting that resource use within size classes is consistent across lakes regardless of invasion stage, which is supported by their patterns of diet composition.

Large white perch diets were relatively consistent across all three lakes, with fish becoming a more important diet component than in the smaller size classes. Stable isotope analysis reflected these diet patterns in Lake Norman and Jordan Lake, but did not in Lake James, where stable isotopes showed that large white perch occupied the lower trophic level, as opposed to their position at higher trophic levels in Lake Norman and Jordan Lake. The

apparent disagreement between diet and stable isotope results in Lake James may stem from differences in life history traits of the newest population compared to the two older populations. Individuals in Lake James grew faster and to larger sizes than individuals in the two older populations (Chapter 1). As a result, a 200-mm TL white perch from Lake James was only two years old, and was roughly 100-120 mm TL one year before, while a 200-mm TL white perch from Jordan Lake or Lake Norman was about six years old, and was roughly the same size the previous year (Chapter 1). Thus, over most of the six months to one year during which the stable isotope composition of muscle was assimilated, a 200-mm TL white perch in Lake James had mostly been eating the diet of a small to medium white perch, while similar sized white perch in the other two lakes were consistently eating a diet typical of large white perch, leading to the discrepancy in isotope composition and apparent trophic position between the new and old populations. Because large white perch in all three lakes were eating similar diets at time of capture, and previous studies of white perch have found increases in trophic position with increasing size (Sierszen et al. 1996, Weinstein et al. 2010), it is likely that, given time to fully assimilate their new diet into muscle tissue, stable isotope analysis would show large white perch in Lake James occupying a similar trophic niche to those in Lake Norman or Jordan Lake. Regardless, each size class of white perch exhibited consistent patterns of resource use and wide trophic niches in both the establishment and assimilation stages of invasion.

Small and medium white perch and bluegill exhibited high diet overlap in all three lakes, and these results were supported by highly overlapping niche areas, as indicated by stable isotope analysis. The high trophic and diet overlap between white perch and bluegill

supports the notion that white perch have caused declines in bluegill and other centrarchid species in invaded systems (Hergenrader and Bliss 1971, Hurley and Christie 1977). While our study only tested for diet overlap with the adult stage of bluegill, diets of juvenile and adult bluegill are relatively similar (Rettig and Mittelbach 2002; Brey, unpublished diet data from Lake Norman). Therefore white perch may have high diet overlap with all life stages of bluegill, and competition for resources could lead to declines in bluegill abundance following white perch invasion. The reliance of white perch on benthic invertebrates may have negative effects on many other benthivorous species as well. For example, bullhead species have been found to decline after white perch invasion in Nebraska and North Carolina reservoirs, possibly due to competition with white perch for benthic resources (Hergenrader and Bliss 1971, Wong et al. 1999). Although our stable isotope analyses only evaluated trophic overlap between white perch and adult largemouth bass, walleye, and striped bass, the juvenile stages of many sportfish, including those studied here, are also benthivorous (Johnson et al. 1988, Matthews et al. 1992). In fact, Harris (2006) found some evidence for high diet overlap between white perch, juvenile striped bass, and largemouth bass smaller than 120 mm TL in a Virginia reservoir. Earlier in their ontogeny, all of these species may have significant trophic overlap with white perch before they shift to piscivory, which may lead to decreased growth or increased mortality of these species.

In addition to the potential for diet overlap with juvenile sportfish, we also found evidence for moderate diet overlap between large white perch and striped bass and largemouth bass in Lake Norman, where large white perch were the most piscivorous. This may mean large white perch compete with adult striped bass or other predators for forage

fish in resource limited systems. Because white perch occupy such wide trophic niches, managers should be aware that multiple levels of the food web, including the juvenile and adult stages of sportfish such as largemouth bass, walleye, and striped bass, may face increased competition for resources from invasive white perch which could lead to decreased survival and growth of these popular game fish (Mittelbach and Persson 1998).

The diet trends presented here are well supported by previous literature on invasive white perch (Prout et al. 1990, Parrish and Margraf 1990b, Kuklinski 2007). In some cases our diet sample sizes were small, due either to inability to catch large numbers of fish or a high proportion of empty stomachs. Small sample size has been shown to bias diet overlap indexes toward insignificant values, due to individual variation in diet contents (Randal and Meyers 2001). Despite this, our estimate for overlap between bluegill and medium white perch in Lake James, the most likely case where this would affect our conclusion due to a small sample of bluegill diets, was still significant. Thus, we believe our estimates are conservative. In the case of small sample sizes for predator diets (e.g., striped bass in Jordan Lake, largemouth bass in Lake James), a large body of previous research indicates that these species are reliably and consistently piscivorous at the sizes we collected (Matthews et al. 1988, Bettoli et al. 1992, Thompson 2006, Godbout 2009). Finally, because our conclusions from diet studies and stable isotope analysis are mutually supportive, we believe we were able to identify the relative niche of white perch in each lake and make inferences about their possible interactions within each community.

Overall, the reallocation of limited energy sources into a generalist invader such as white perch could have wide-ranging negative effects at all trophic levels of an established

community, which would be very difficult to control or mitigate from a management standpoint. The similar trophic position of white perch across systems, in conjunction with high overlap with bluegill, indicates that white perch may not be filling an empty niche in reservoirs. Instead, they are likely sharing resources with other benthivorous fish, such as bluegill and juvenile sportfish, supporting the sampling hypothesis of Shea and Chesson (2002). Because there does not appear to be a successful management strategy for controlling or eradicating white perch once they are introduced (Gosch 2008), management efforts should focus on educational and regulatory approaches to discourage further introductions. If white perch are introduced, it might be feasible to manage them as a recreational fishery. All three populations in this study reached sizes over 200 mm TL, large enough to be targeted by anglers. Educating the public on preventing introductions, while also advertising existing populations as a potential game fish, may be the best management strategy available for white perch in large reservoirs.

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TABLES

Table 2.1. Physical and biotic characteristics of study lakes, including year white perch were first discovered in North Carolina Wildlife Resources Commission (NCWRC) samples.

Lake	Year Impounded	Fish Assemblage	Area (ha)	Mean Depth (m)	Max Depth (m)	Mean Chl-α (µg/L)	White Perch Discovered
James	1923	Coolwater	2,634[a]	13.5[a]	43[a]	4.63[a]	2008[b]
Norman	1964	Warmwater	13,156[a]	10[a]	33.5[a]	7.28[a]	1998[c]
Jordan	1981	Warmwater	5,720[d]	5[e]	16[e]	41.9[d]	1988[e]

[a]NCDENR 2008
[b]J. M. Rash, NCWRC, personal communication 2009
[c]B. J. McRae, NCWRC, personal communication 2009
[d]NCDENR 2009
[e]Wong et al. 1999

Table 2.2. Sample sizes for stable isotope analysis (SIA) and diet analysis, mean total length, carbon range (CR), nitrogen range (NR), and total convex hull area (TA) for each established species and white perch size class in each lake.

Lake	Species	N (SIA)	N (Diets)	Mean TL (mm)	CR	NR	TA
Lake James	Small White Perch	15	20	61.9	5.92	1.81	5.62
	Medium White Perch	15	20	145.4	11.84	4.78	30.86
	Large White Perch	15	20	227.5	4.29	2.91	5.77
	Bluegill	9	9	140.6	6.76	4.68	18.84
	Largemouth Bass	8	8	372.8	6.06	3.68	8.30
	Walleye	10	20	387.6	3.32	1.17	2.36
Lake Norman	Small White Perch	15	29	59.0	5.96	2.09	6.17
	Medium White Perch	15	20	150.5	5.58	4.03	9.29
	Large White Perch	15	18	234.1	2.59	3.89	5.79
	Bluegill	10	20	145.8	4.36	7.96	18.75
	Largemouth Bass	10	11	375.8	3.08	3.24	3.93
	Striped Bass	10	20	545.0	0.91	1.24	0.79
Jordan Lake	Small White Perch	15	20	55.5	2.81	5.14	7.64
	Medium White Perch	15	20	154.7	2.45	4.55	6.01
	Large White Perch	11	11	212.0	1.84	3.49	3.98
	Bluegill	10	20	134.4	1.93	4.13	5.07
	Largemouth Bass	10	10	324.5	1.26	3.06	1.79
	Striped Bass	10	12	627.3	1.87	1.40	0.70

Table 2.3. Categorization of fish diet items (category names in bold) in July 2010 in Lake James, Lake Norman, and Jordan Lake, NC.

Zooplankton	Benthic Invertebrates	Other Invertebrates	Other Items
Cladocera	**Small**	**Surface**	**Fish**
Bosmina	Amphipoda	Diptera pupae	Threadfin Shad
Chydoridae	Hydrachnidia	Hemiptera	Gizzard Shad
Daphnia	Ceratopogonid larvae	Ephemeroptera adults	Alewife
Holopedium	Chironomid larvae	**Terrestrial**	*Lepomis* spp.
Sididae	Plumatellidae	Hymenoptera adults	Yellow Perch
Copepoda	Isopoda	Lepidoptera larvae	Cyprinid spp.
Calanoidea	Ostracoda	Coleoptera adults	Unidentified Fish
Cyclopoida	**Large**	Odonata adults	**Other**
	Mollusca	Orthoptera adults	Amphibian eggs
	Ephemeroptera larvae	***Chaoborus***	Fish eggs
	Odonata larvae	**Crayfish**	Insect eggs
	Trichoptera larvae		Fish hook
	Megaloptera larvae		Plant matter
			Rubber Worm
			Fish scale
			Detritus

Table 2.4. Catch per unit effort (CPUE) and percent total catch of fish species and taxonomic groups sampled from Lake James, Lake Norman, and Jordan Lake, NC, by electrofishing, nearshore gill nets, and offshore gill nets. Dashes (--) signify species does not occur in lake.

	Electrofishing (Catch/minute)					
	James		Norman		Jordan	
	CPUE	% Catch	CPUE	% Catch	CPUE	% Catch
White Perch	0.29	4.64	0.85	6.73	2.39	8.15
Lepomis spp.	1.75	27.77	2.90	22.83	5.93	20.23
Micropterus spp.	0.64	10.14	0.49	3.84	0.21	0.72
Clupeids	0.01	0.09	7.84	61.70	16.55	56.43
Yellow Perch	2.86	45.40	0.11	0.86	1.53	5.23
Catfish	0.08	1.33	0.05	0.38	0.14	0.47
White Bass	0.04	0.57	0.00	0.00	0.00	0.00
Black Crappie	0.01	0.09	0.03	0.24	0.16	0.55
Striped Bass	--	--	0.09	0.72	0.00	0.00
Other	0.63	9.95	0.34	2.69	2.41	8.21
Total	6.29	100	12.70	100.00	29.32	100.00
	Nearshore Gill Net (Catch/net-night)					
	James		Norman		Jordan	
	CPUE	% Catch	CPUE	% Catch	CPUE	% Catch
White Perch	11.00	29.93	31.50	62.07	43.25	41.69
Lepomis spp.	0.50	1.36	0.25	0.49	0.75	0.72
Micropterus spp.	0.25	0.68	4.25	8.37	0.00	0.00
Clupeids	15.25	41.50	9.75	19.21	26.50	25.54
Yellow Perch	0.00	0.00	0.00	0.00	0.75	0.72
Catfish	1.00	2.72	1.75	3.45	21.25	20.48
White Bass	6.00	16.33	0.00	0.00	0.00	0.00
Black Crappie	0.25	0.68	2.25	4.43	11.25	10.84
Striped Bass	--	--	0.00	0.00	0.00	0.00
Other	2.50	6.80	1.00	1.97	0.00	0.00
Total	36.75	100	50.75	100	103.75	100
	Offshore Gill Net (Catch/net-night)					
	James		Norman		Jordan	
	CPUE	% Catch	CPUE	% Catch	CPUE	% Catch
White Perch	29.00	67.84	0.75	30.00	13.25	39.55
Lepomis spp.	0.00	0.00	0.00	0.00	0.00	0.00
Micropterus spp.	0.00	0.00	0.00	0.00	0.00	0.00
Clupeids	12.50	29.24	0.00	0.00	8.50	25.37
Yellow Perch	1.00	2.34	0.00	0.00	0.00	0.00
Catfish	0.00	0.00	1.75	70.00	6.50	19.40
White Bass	0.00	0.00	0.00	0.00	0.00	0.00
Black Crappie	0.00	0.00	0.00	0.00	5.00	14.93
Striped Bass	--	--	0.00	0.00	0.25	0.75
Other	0.25	0.58	0.00	0.00	0.00	0.00
Total	42.75	100	2.50	100	33.50	100

Table 2.5. Schoener's and Morisita's Indices of diet overlap between white perch size classes and representative species in each lake. Overlap values in bold are considered ecologically significant.

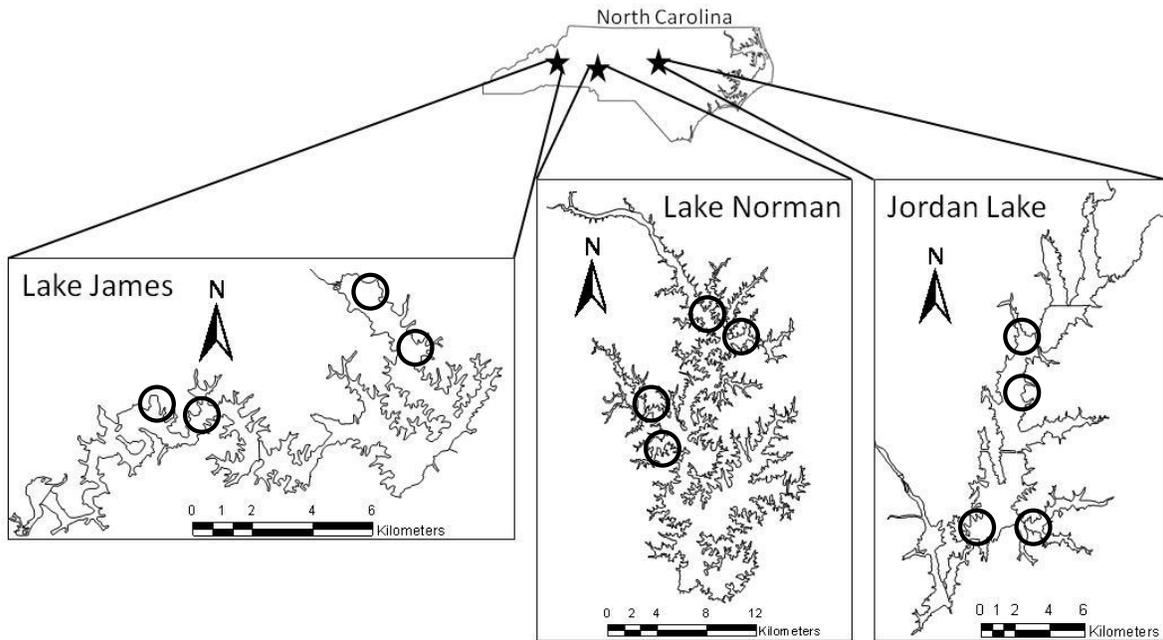| | | Schoener's Index | | |
		Small White Perch	Medium White Perch	Large White Perch
Lake James	Bluegill	0.173	**0.677**	0.255
	Largemouth Bass	0.015	0.033	0.294
	Walleye	0.009	0.021	0.287
Lake Norman	Bluegill	0.429	0.558	0.310
	Largemouth Bass	0.000	0.015	0.414
	Striped Bass	0.000	0.004	0.414
Jordan Lake	Bluegill	**0.639**	**0.794**	0.344
	Largemouth Bass	0.024	0.045	0.314
	Striped Bass	0.005	0.034	0.225

FIGURES

Figure 2.1. Locations of study lakes, from left to right: Lake James, Lake Norman, and Jordan Lake, NC. Sample sites in each lake marked by circles.
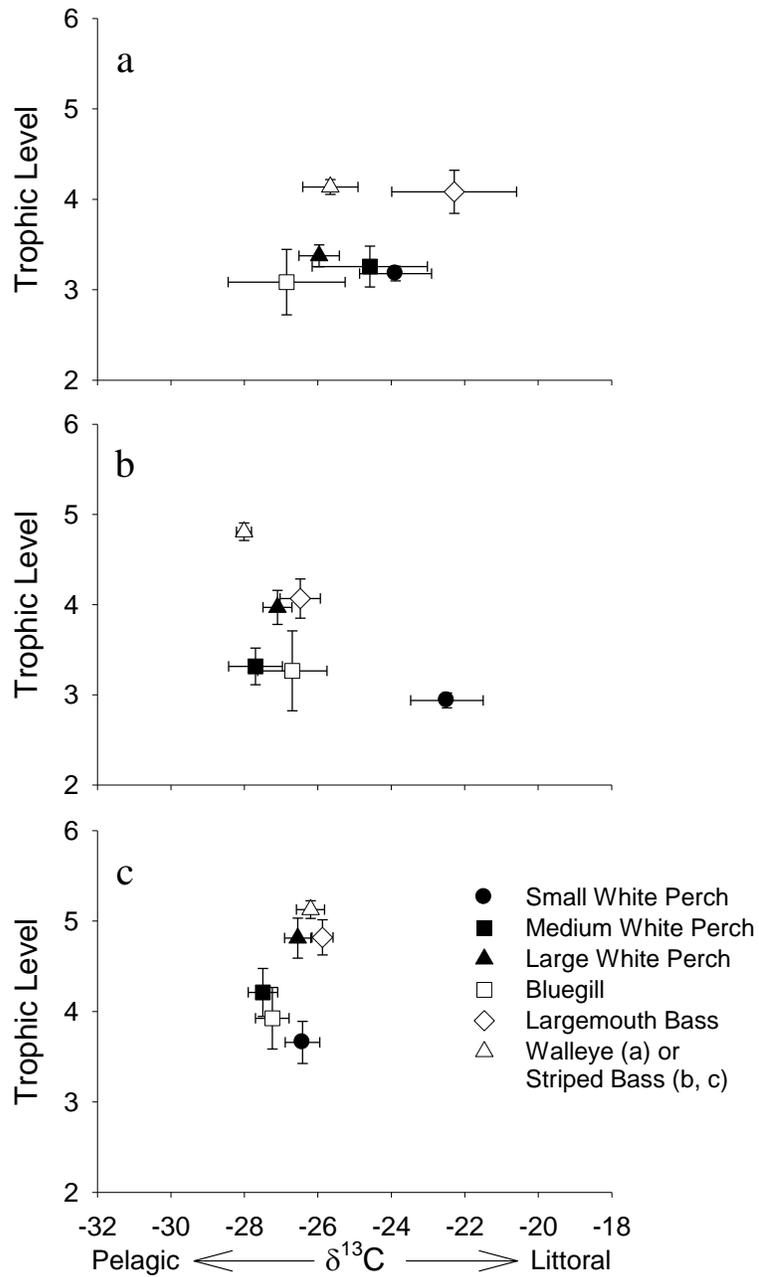
Figure 2.2. Mean trophic level (y-axis) and $\delta^{13}C$ isotopic composition (x-axis) with 95% confidence intervals of establsihed species and white perch size classes in (a) Lake James, (b) Lake Norman, and (c) Jordan Lake, NC.
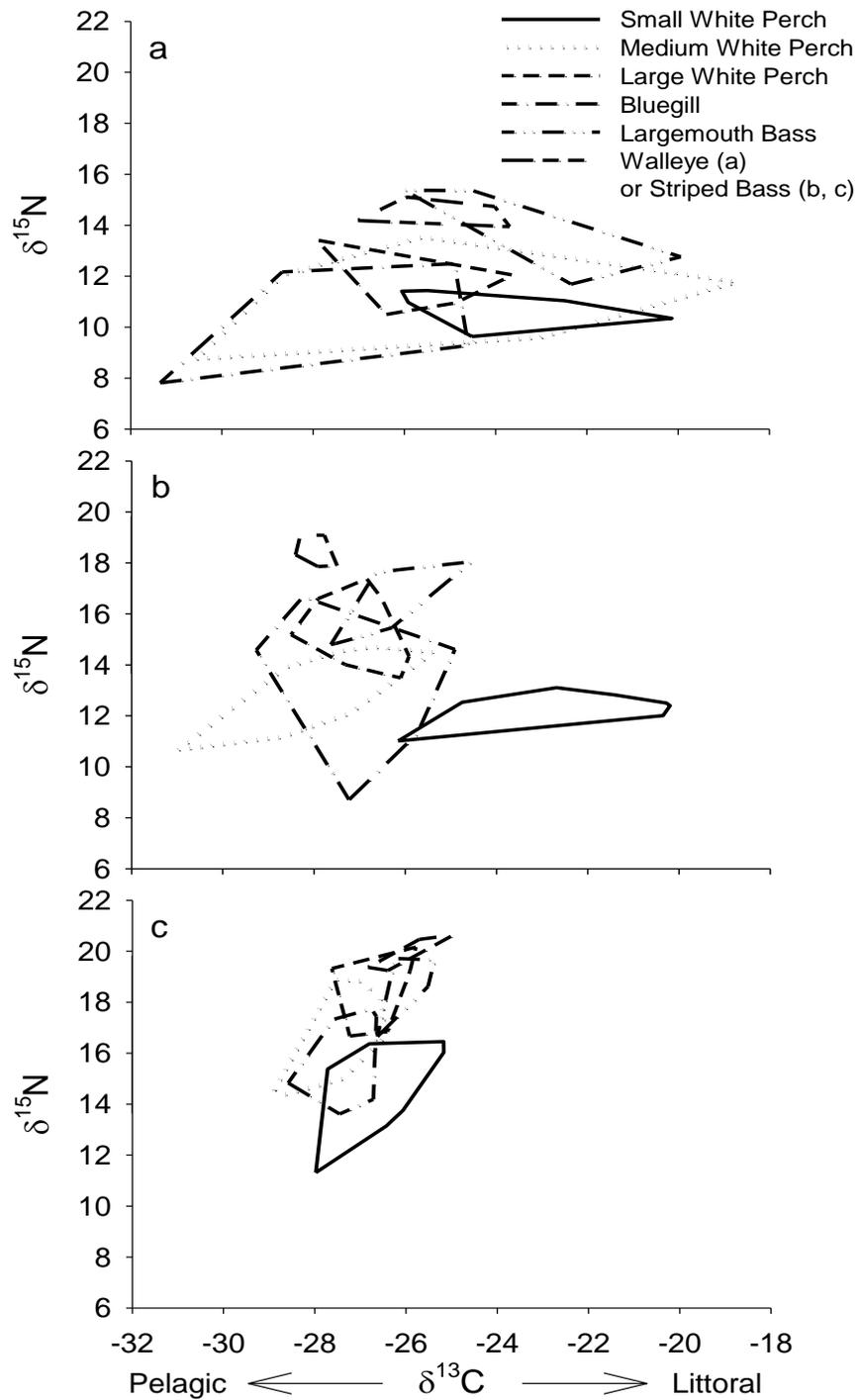
Figure 2.3. Convex hull areas of white perch size classes and representative species in (a) Lake James, (b) Lake Norman, and (c) Jordan Lake, NC.
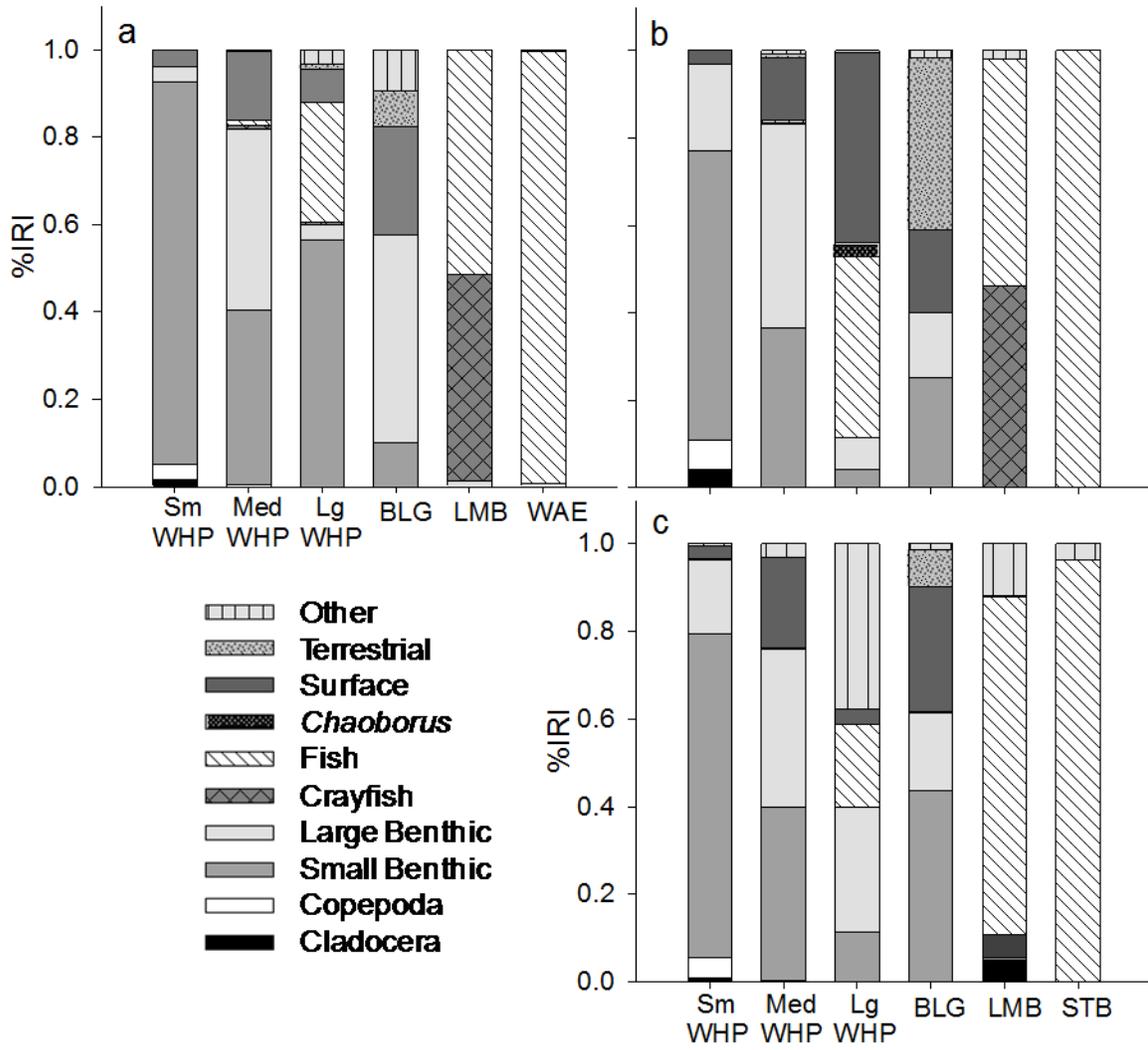
Figure 2.4. %IRI of diet items in stomachs of representative species and white perch size classes in (a) Lake James, (b) Lake Norman, and (c) Jordan Lake, NC.