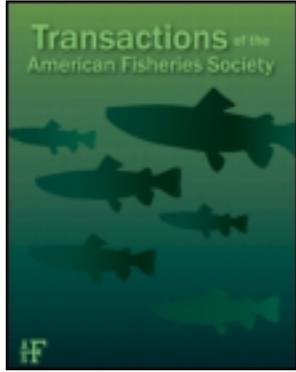


This article was downloaded by: [North Carolina State University]

On: 11 December 2013, At: 09:32

Publisher: Taylor & Francis

Informa Ltd Registered in England and Wales Registered Number: 1072954 Registered office: Mortimer House, 37-41 Mortimer Street, London W1T 3JH, UK



Transactions of the American Fisheries Society

Publication details, including instructions for authors and subscription information:

<http://www.tandfonline.com/loi/utaf20>

White Perch in Small North Carolina Reservoirs: What Explains Variation in Population Structure?

Bethany J. Bethke^{a b}, James A. Rice^a & D. Derek Aday^a

^a Department of Biology, North Carolina State University, Campus Box 7617, Raleigh, North Carolina, 27695, USA

^b Minnesota Department of Natural Resources, 5351 North Shore Drive, Duluth, Minnesota, 55805, USA

Published online: 11 Dec 2013.

To cite this article: Bethany J. Bethke, James A. Rice & D. Derek Aday (2014) White Perch in Small North Carolina Reservoirs: What Explains Variation in Population Structure?, Transactions of the American Fisheries Society, 143:1, 77-84

To link to this article: <http://dx.doi.org/10.1080/00028487.2013.830989>

PLEASE SCROLL DOWN FOR ARTICLE

Taylor & Francis makes every effort to ensure the accuracy of all the information (the "Content") contained in the publications on our platform. However, Taylor & Francis, our agents, and our licensors make no representations or warranties whatsoever as to the accuracy, completeness, or suitability for any purpose of the Content. Any opinions and views expressed in this publication are the opinions and views of the authors, and are not the views of or endorsed by Taylor & Francis. The accuracy of the Content should not be relied upon and should be independently verified with primary sources of information. Taylor and Francis shall not be liable for any losses, actions, claims, proceedings, demands, costs, expenses, damages, and other liabilities whatsoever or howsoever caused arising directly or indirectly in connection with, in relation to or arising out of the use of the Content.

This article may be used for research, teaching, and private study purposes. Any substantial or systematic reproduction, redistribution, reselling, loan, sub-licensing, systematic supply, or distribution in any form to anyone is expressly forbidden. Terms & Conditions of access and use can be found at <http://www.tandfonline.com/page/terms-and-conditions>

NOTE

White Perch in Small North Carolina Reservoirs: What Explains Variation in Population Structure?

Bethany J. Bethke,*¹ James A. Rice, and D. Derek Aday

Department of Biology, North Carolina State University, Campus Box 7617, Raleigh,
North Carolina 27695, USA

Abstract

White Perch *Morone americana* have been introduced into many inland systems throughout the United States. To determine factors affecting White Perch abundance and size structure, we compared White Perch growth, timing of maturity, and trophic level; the abundance of a predator (Largemouth Bass *Micropterus salmoides*); the abundance of an ecologically significant mid-level omnivore (Gizzard Shad *Dorosoma cepedianum*); prey availability (chironomid and zooplankton abundances); and environmental variables (specific conductivity, Secchi depth, dissolved oxygen concentration, and temperature) among four reservoirs (two with high White Perch abundance and two with low abundance). White Perch size structure was closely tied to abundance, with truncated size structure as abundance increased. Among the other variables we tested, only Largemouth Bass abundance had a significant (negative) relationship with White Perch abundance. White Perch size structure appeared to be highly density dependent, and variables that commonly explain variation in abundance of introduced fishes did not explain differences in the four White Perch populations we studied. Further study of the competitive and predatory interactions of White Perch and Largemouth Bass over ontogeny could shed light on the mechanism(s) potentially shaping population structure of the two species where they coexist.

Introductions of White Perch *Morone americana* have been problematic for freshwater fisheries managers (Madenjian et al. 2000; Gosch et al. 2010b). Since the 1950s, White Perch have been intentionally and unintentionally moved from their native range (i.e., North America's Atlantic coastal estuaries and river tributaries) into freshwater lakes, inland rivers, and reservoirs of the eastern and central United States (Scott and Christie 1963; Irons et al. 2002; Harris 2006). Studies in these areas have indicated detrimental impacts of White Perch on native species, primarily through competition (Schaeffer and Margraf 1986; Parrish and Margraf 1990, 1994; Prout et al. 1990) and egg

predation (Schaeffer and Margraf 1987; Hartman and Margraf 1992; Madenjian et al. 2000).

White Perch are excellent competitors and invaders due to a variety of life history traits, including their tolerance of a wide range of environmental conditions (Stanley and Danie 1983; Johnson and Evans 1990); their role as omnivorous, opportunistic feeders (Reid 1972; Hines 1981; Schaeffer and Margraf 1987; Hurley 1992; St-Hilaire et al. 2002; Couture and Watzin 2008; Gosch et al. 2010b); and their reproductive flexibility, with maturation occurring as early as age 1 or as late as age 3 (Sheri and Power 1968; Bur 1986; Schaeffer and Margraf 1986; Chizinski 2007; Feiner et al. 2012). Population dynamics of native and introduced White Perch have been linked to a variety of abiotic and biotic factors (Feiner et al. 2012, 2013), such as turbidity, dissolved solids, and specific conductivity (Hawes and Parrish 2003; North and Houde 2003) as well as predation (Ward and Neumann 1998; Margulies 1990; Vrtiska et al. 2003; Gosch et al. 2010a) and competition with other fish (Hawes and Parrish 2003). Finally, intraspecific competition in high-density White Perch populations may structure those populations through density-dependent mechanisms (Sheri and Power 1972; Schaeffer and Margraf 1986; Hurley 1992).

White Perch are widely distributed in North Carolina reservoirs, and the population abundance and size structure of White Perch vary among these systems (Wong 2002; Feiner et al. 2012). Anecdotal evidence indicates that White Perch attain a large adult body size in some reservoirs. Conversely, White Perch can also dominate reservoir fish communities via high densities of small individuals. A better understanding of the mechanisms driving this variability in abundance and size structure is important for managing present and future introductions of White Perch. Thus, we quantified the abundance and size structure of White Perch in four small North Carolina reservoirs

*Corresponding author: bethany.bethke@state.mn.us

¹Present address: Minnesota Department of Natural Resources, 5351 North Shore Drive, Duluth, Minnesota 55805, USA.

Received June 28, 2013; accepted July 24, 2013

and compared life history traits among the populations. We examined a variety of potential mechanisms to explain the disparity in White Perch body size across these reservoirs, including growth, timing of maturity, trophic interactions, lake productivity, and predator and prey abundances. By including many abiotic and biotic variables in our analysis, our intention was to take a comprehensive approach to understanding White Perch population dynamics in small southeastern reservoirs.

METHODS

Study reservoirs.—We sampled four reservoirs ranging from 137 to 662 ha in North Carolina's Piedmont region, including two systems with relatively high-abundance White Perch populations and two systems with low-abundance populations based on unpublished data from the North Carolina Wildlife Resources Commission (NCWRC). Lake Holt (Granville County; 137 ha) and Lake Reece (Randolph County; 242 ha) had low-abundance White Perch populations; Oak Hollow Lake (Guilford County; 280 ha) and Lake Townsend (Guilford County; 662 ha) had high-abundance White Perch populations. All four systems were municipal reservoirs with water levels that were stable throughout the study period. White Perch have been established in each of the reservoirs for over 30 years, but their origin is unknown except in Lake Townsend, where they were introduced intentionally by an angler during the 1970s (S. Davis, City of Greensboro, personal communication).

Fish collection.—Fish collection took place in April, August, and October 2010 and April, June, and July 2011. We collected White Perch, Largemouth Bass *Micropterus salmoides*,

and Gizzard Shad *Dorosoma cepedianum*. Largemouth Bass were chosen because they are the most common top predator in all of our study systems; Gizzard Shad were selected because they can significantly impact fish communities and may be an important source of prey for piscivores (e.g., Stein et al. 1995). In each reservoir, we collected fish during one 24-h period of each sampling month using nighttime electrofishing and gill-netting at four randomly selected sites distributed throughout the reservoir. Sampling took place at the same sites on each sampling date. Electrofishing began at least 0.5 h after sunset and was conducted in 1,200-s (about 200-m) shoreline transects at each site at an amperage output of 3.8–4.8 A. Gill nets were set perpendicular to the shoreline in at least 2.5 m of water 1 h before sunset and were soaked for 6 h. At two of the four gill-net sampling sites, we set a 2- × 50-m net with 25.4-mm bar mesh. At the other two sites, we set a 2- × 100-m net consisting of two 50-m panels (50.8- and 63.5-mm bar mesh). In the summer months, when much of the lower water column was hypoxic in each reservoir, we suspended gill nets at a depth that ensured placement in habitat with a dissolved oxygen (DO) concentration of at least 3 mg/L.

On each sampling date, we kept a maximum of 20 White Perch per gear and site from each of four size categories (<120, 120–179, 180–229, and >230 mm TL) and placed them on ice for laboratory processing. Length categories for White Perch were based on *a priori* information from previous collections conducted by the NCWRC. In June and July 2011, we also kept White Perch and Largemouth Bass for stable isotope analysis (SIA) and stomach content analysis (Table 1). Largemouth Bass from two size categories (<200 and ≥200 mm TL) based

TABLE 1. Mean (SE in parentheses) trophic level, TL, and sample size (*n*) of small White Perch (WHP; <150 mm TL), large WHP (≥150 mm TL), small Largemouth Bass (LMB; <200 mm TL), and large LMB (≥200 mm TL) that were sampled from four North Carolina reservoirs in June and July 2011 and used for stable isotope analysis.

Variable	Lake Holt	Lake Reece	Oak Hollow Lake	Lake Townsend
Small WHP				
Trophic level		3.6 (0.04)	3.7 (0.06)	4.1 (0.08)
TL (mm)		125 (9)	145 (2)	115 (12)
<i>n</i>		13	6	10
Large WHP				
Trophic level	3.8 (0.06)	4.1 (0.02)	3.9 (0.07)	4.0 (0.10)
TL (mm)	182 (4)	207 (5)	155 (5)	177 (7)
<i>n</i>	4	11	3	5
Small LMB				
Trophic level	4.2 (0.10)	4.2 (0.06)	3.8 (0.06)	4.4 (0.32)
TL (mm)	123 (13)	99 (10)	105 (11)	123 (12)
<i>n</i>	12	15	10	3
Large LMB				
Trophic level	4.2 (0.04)	4.3 (0.03)	4.0 (0.09)	4.6 (0.11)
TL (mm)	420 (17)	386 (7)	413 (13)	434 (22)
<i>n</i>	6	10	8	8

on stock length (Gabelhouse 1984) were retained for analyses. For each gear at each site, we weighed (g wet weight), measured (mm TL), and released up to 20 additional White Perch and Largemouth Bass. Gizzard Shad were counted and weighed in aggregate. All other collected fish were counted and released.

Prey collection.—We collected zooplankton and benthic invertebrates from each reservoir in August and October 2010 and April–July 2011 to assess prey availability. On each sample date, we collected zooplankton at three sites by using a 1.5-m conical net with a 0.5-m-diameter opening and 250- μ m mesh. We sampled zooplankton from the littoral zone using a vertical tow from twice the Secchi depth to the surface; samples were preserved with Lugol's iodine solution. We sampled benthic invertebrates by using a petite Ponar dredge at four sites throughout the littoral zone of each reservoir; an area of 0.023 m² was sampled at each site, and sediment was rinsed through a 1,000- μ m-mesh wash bucket. Benthos samples were preserved in ethanol and stained using rose bengal. Additional benthos samples were taken in August and October 2011 and were frozen (not preserved with ethanol) for baseline SIA (see below). Frozen benthos samples were later thawed, and chironomid larvae were separated from the sediment and refrozen until processed for SIA.

Abiotic measurements.—We measured DO (mg/L) and temperature ($^{\circ}$ C) on each sampling date using a Quanta Hydrolab (Hydrolab Corp., Loveland, Colorado) at the deepest accessible part of each reservoir. We measured specific conductivity (mS/cm) 1 m below the water's surface and 1 m above the reservoir bottom and then averaged the two values for comparisons. Temperature and DO concentrations were measured at 1-m intervals from the surface to the bottom; epilimnetic measurements (top 4 m of the water column, not including the surface) of temperature and DO were averaged and compared across systems. Secchi depth (m), which was used as a proxy for turbidity and productivity within each reservoir, was measured with a Secchi disk. All measurements were taken at least 2 h prior to sunset on each sampling date.

Laboratory methods.—Sampled fish were frozen at -20° C until laboratory processing. We used macroscopic visual inspection of the gonads to determine sex and stage of maturity for all White Perch collected in the April samples. Stage of maturity was determined using a four-point scale (1 = immature; 2 = developing; 3 = mature; 4 = spent) adapted from Núñez and Duponchelle (2009). Fish with a score of 3 or 4 were considered mature; in contrast to Núñez and Duponchelle (2009), we did not further subdivide scores for female fish. Dorsal muscle tissue (\sim 1 g) was removed from White Perch and Largemouth Bass sampled in June and July 2011 and was frozen for SIA (Table 1). Sagittal otoliths were removed, sectioned, and aged independently by two readers. If the two readers disagreed, the otolith was examined by a third reader; in all cases, the age determined by the third reader was in agreement with the age estimated by one of the first two readers, and that age was assigned to the fish.

Benthic invertebrates and zooplankton were identified to family and enumerated by using a dissecting microscope (zooplankton were subsampled; at least 5% of the sample volume was examined). Chironomid larvae were the most common benthic invertebrate (present in $>90\%$ of benthos samples) and are also known to be an important component of White Perch diets (Gosch 2010b; Feiner et al. 2012). Therefore, we used mean densities of chironomid larvae (number/m²) in data analysis as a measure of available benthic prey. For each sampling date, we averaged the total density of all zooplankton (number/m³) collected from each site.

Diet and stable isotope analysis.—Frozen muscle tissue and chironomid larvae were sent to the Stable Isotope Laboratory at Cornell University, where the samples were dried with a Viris Freezemobile 25SL freeze dryer, homogenized with a Spex CertiPrep 6750 freezer/mill, weighed to the nearest 1 mg with a Sartorius MC5 microbalance, and analyzed for nitrogen stable isotope ratios (δ^{15} N) with a Finnigan MAT Delta Plus mass spectrometer. Stable isotope values were compared with the atmospheric nitrogen standard. Measured δ^{15} N values were standardized relative to the baseline for each reservoir and were used to calculate trophic level (Vander Zanden and Rasmussen 2001), with benthic invertebrates assumed to have a trophic level of 2 (Vander Zanden and Rasmussen 2001; Post 2002). For both Largemouth Bass and White Perch, δ^{15} N values measured in June and July were not significantly different ($F_{1, >50} < 0.07$, $P > 0.08$), so for each species the SIA results from June and July were grouped for analysis. Grouping of SIA samples taken within a month of each other is acceptable because the turnover rate of stable isotopes in fish muscle tissue is more than 30 d (Buchheister and Latour 2010; Weidel et al. 2011).

Conversely, due to the fine time scale of stomach content sampling, we analyzed the diet data from June and July separately. Prey were grouped into five categories: benthic invertebrates, fish, suspended invertebrates, zooplankton, and other. Each prey group's contribution to the diet of each size-group within each species was quantified using the index of relative importance, an integrated measure of diet that incorporates prey weight, number, and frequency of occurrence (Cortés 1997). Diet overlap was then determined among size-classes and species by using Schoener's overlap index (D ; Schoener 1968); Schoener's D -values greater than 0.6 were considered to indicate ecologically significant diet overlap (Wallace 1981). The number of stomach content samples from White Perch caught in June was insufficient for comparison; therefore, Schoener's D was only used to compare July diets.

Data analysis.—We used ANOVA to compare White Perch and Largemouth Bass CPUE, individual size, and trophic level among reservoirs. We divided White Perch and Largemouth Bass into two size categories for analysis based on the onset of piscivory (Mittelbach and Persson 1998). We calculated the mean CPUEs of White Perch, Largemouth Bass, and Gizzard Shad by summing the total number of fish from each species caught with both gears at each site and then averaging among

sites sampled on each date. We estimated White Perch growth by fitting length and age data from each lake to the von Bertalanffy growth equation (von Bertalanffy 1938). We used the Kruskal–Wallis extension of the Wilcoxon–Mann–Whitney test, based on the normal (Z) distribution to compare White Perch length frequency distributions across populations. Using linear regression, we tested six variables to assess whether there was a relationship with White Perch CPUE: Largemouth Bass CPUE, Gizzard Shad CPUE, mean density of chironomid larvae, mean total zooplankton density, mean Secchi depth, and mean specific conductivity. Fish CPUE was \log_{10} transformed for linear regression analysis. All data analyses were carried out using the Statistical Analysis System version 9.2 (SAS Institute, Cary, North Carolina), with α set at 0.05.

RESULTS

White Perch Abundance, Size Structure, and Age Structure

White Perch displayed a gradient of abundance from low to high across the four reservoirs, and CPUE was statistically different among reservoirs ($F_{3, 16} = 18.79, P < 0.0001$). Size structure differed among the four White Perch populations and was

strongly related to White Perch abundance (Figure 1; Table 2). High-abundance White Perch populations had a truncated size structure and smaller maximum size than low-abundance populations ($Z_1 = 439.2, P < 0.0001$). Length frequency distributions were not significantly different between the reservoirs with high White Perch abundance ($Z_1 = -1.37, P = 0.1723$) but were statistically different between the reservoirs with low White Perch abundance ($Z_1 = 5.86, P < 0.0001$). Mean TL of White Perch was significantly lower in high-abundance populations than in low-abundance populations ($F_{1, 3} = 4.41, P < 0.0001$). Age frequency distributions were generally similar among White Perch populations; maximum age ranged from 9 to 14 years, and there were no missing year-classes in any population from ages 0 to 9.

White Perch Growth and Maturity

Growth of White Perch differed among populations; asymptotic maximum length (L_∞) estimates from the von Bertalanffy growth function were 60–100 mm larger for the two low-abundance populations (Lakes Holt and Reece) than for the two high-abundance populations (Oak Hollow Lake and Lake Townsend). The growth curves for Lake Townsend and Oak Hollow Lake overlapped, whereas growth estimates were significantly different between Lakes Reece and Holt. White Perch in

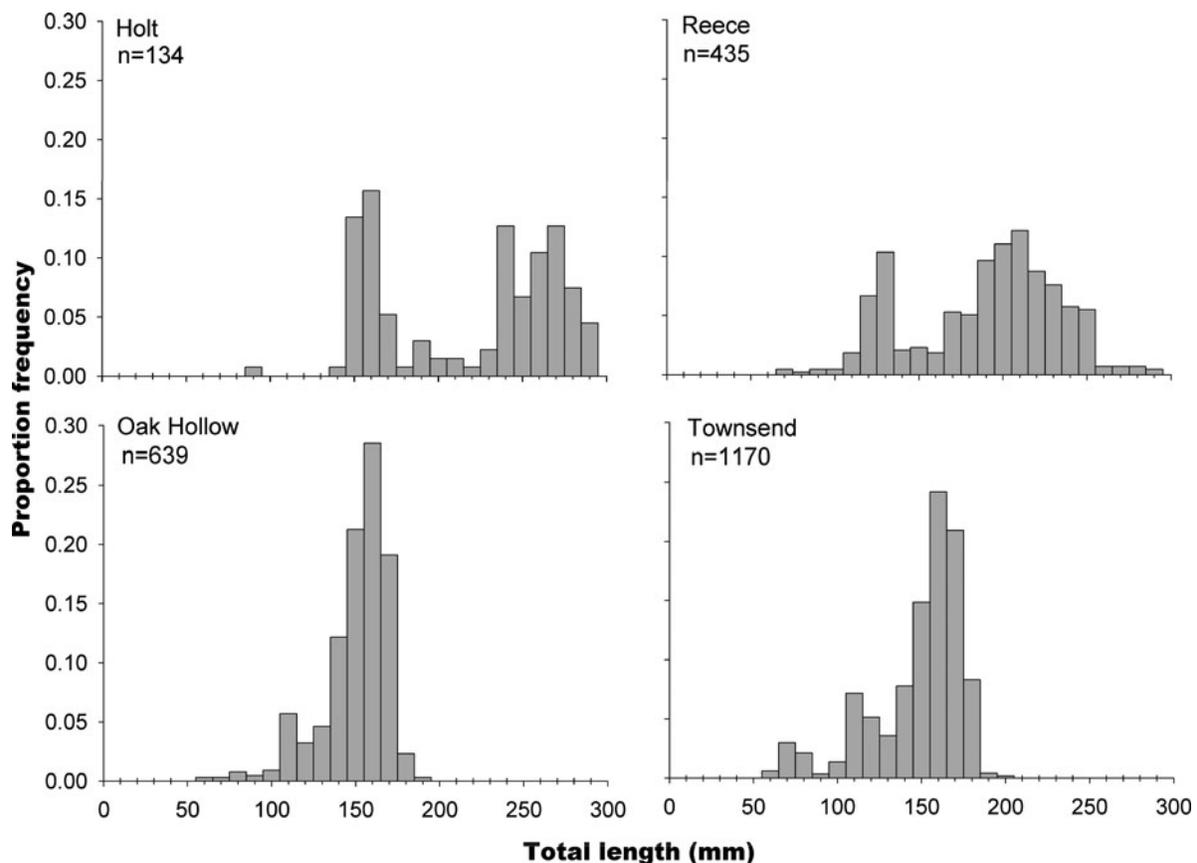


FIGURE 1. Length frequency distributions of White Perch sampled from four North Carolina reservoirs in 2010 and 2011 (n = number of fish sampled). Lakes Reece and Holt have low-abundance White Perch populations; Lake Townsend and Oak Hollow Lake have high-abundance White Perch populations.

TABLE 2. Mean (SE in parentheses) White Perch, Largemouth Bass, and Gizzard Shad CPUEs (combined average for gill net and boat electrofishing sampling); chironomid and zooplankton densities; Secchi depth; specific conductivity; epilimnion temperature; and epilimnion dissolved oxygen (DO) measured in four small North Carolina reservoirs during 2010 and 2011. Lakes Holt and Reece have low-abundance White Perch populations with large size structures; Oak Hollow Lake and Lake Townsend have high-abundance White Perch populations with truncated size structures. Linear regression was used to test for a relationship between White Perch CPUE and each of the other variables; summary statistics (P and R^2) from these tests are provided.

Variable	Lake Holt	Lake Reece	Oak Hollow Lake	Lake Townsend	P	R^2
White Perch CPUE	1.9 (1.6)	23.3 (5.7)	44.1 (20.4)	127.2 (52.4)		
Largemouth Bass CPUE	22.2 (7.9)	6.8 (2.4)	2.6 (0.9)	2.4 (0.9)	0.032	0.94
Gizzard Shad CPUE	0.0 (0.0)	26.7 (12.5)	17.6 (8.0)	34.2 (20.2)	0.071	0.87
Chironomid density (number/m ³)	54.6 (17.3)	97.9 (47.6)	78.2 (13.5)	59.6 (18.1)	0.879	0.02
Zooplankton density (number/m ³)	9.7×10^4 (2.6×10^4)	2.1×10^5 (6.8×10^4)	1.8×10^5 (6.5×10^4)	1.8×10^5 (4.0×10^4)	0.256	0.55
Secchi depth (m)	1.7 (0.2)	1.1 (0.2)	1.0 (0.1)	0.9 (0.1)	0.196	0.65
Specific conductivity (mS/cm)	0.06 (0.02)	0.10 (0.01)	0.11 (0.01)	0.10 (0.01)	0.228	0.60
Temperature (°C)	15.5 (1.2)	21.1 (1.3)	23.5 (1.4)	20.6 (1.0)	0.194	0.65
DO (mg/L)	8 (0.2)	7.2 (0.4)	7.7 (0.5)	8.7 (0.4)	0.708	0.85

Lake Holt grew faster and to a larger maximum size than White Perch from Lake Reece. Contrary to differences in growth rate, the timing of maturity was fairly consistent among study populations; at least 78% of males and females from all populations were sexually mature by age 2.

White Perch Abundance in relation to Biotic and Abiotic Variables

White Perch CPUE was inversely related to Largemouth Bass CPUE (Table 2). White Perch CPUE was not significantly related to Gizzard Shad CPUE, invertebrate prey densities (chironomids and zooplankton), or abiotic variables (Secchi depth and specific conductivity; Table 2). Temperature and DO measurements were similar among systems except Lake Holt, which had a lower mean temperature than the other reservoirs (Table 2). Only Oak Hollow Lake, which is aerated, did not exhibit a summer oxycline.

Largemouth Bass CPUE was higher ($F_{1,3} = 8.06, P = 0.013$) in reservoirs with low White Perch abundance than in reservoirs with high White Perch abundance (Table 2). Reservoirs with low-abundance White Perch populations had a higher proportion of small Largemouth Bass than reservoirs with high-abundance White Perch populations (Figure 2). Mean TL of Largemouth Bass was higher ($F_{1,426} = 14.23, P = 0.0002$) in Oak Hollow Lake and Lake Townsend than in Lakes Holt and Reece, primarily due to differences in the abundance of small Largemouth Bass in the latter two lakes. Largemouth Bass maximum TL was similar among reservoirs (Figure 2).

Diets and Stable Isotope Analysis

There were significant among-reservoir differences in the trophic level of each species and size-group, but differences were not correlated with the abundance of White Perch (Table 1). Trophic level of small White Perch was higher in Lake Townsend than in Lake Reece and Oak Hollow Lake ($F_{1,26} = 12.08, P = 0.0002$); the trophic level of large White Perch

was higher in Lake Reece than in Lake Holt ($F_{1,19} = 8.41, P = 0.0009$; Table 1) but was similar among the other reservoirs. Small Largemouth Bass from Oak Hollow Lake had a lower trophic level than small Largemouth Bass from the other three reservoirs ($F_{1,36} = 6.02, P = 0.0020$). Large Largemouth Bass from Oak Hollow Lake also had a lower trophic level than large Largemouth Bass from the other reservoirs but to a lesser degree, and large Largemouth Bass from Lake Townsend had the highest trophic level ($F_{1,28} = 10.08, P = 0.0001$; Table 1).

We documented only one instance of Largemouth Bass predation on White Perch (in Lake Reece; June 2011) and one instance of White Perch predation on Largemouth Bass (also in Lake Reece; August 2010). We detected significant diet overlap between small Largemouth Bass and both size categories of White Perch in all comparisons that had sufficient sample sizes (Table 3). Large Largemouth Bass exhibited low diet overlap with both size-classes of White Perch in the three reservoirs for which sample size allowed comparisons (Table 3).

DISCUSSION

White Perch size structure in our study populations was strongly linked to White Perch abundance; this result suggests the importance of density-dependent mechanisms, consistent with previous investigations (Busch et al. 1977; Zuerlein 1981; Gosch et al. 2010a). Although we can attribute the differences in size structure to intraspecific abundance, the factors affecting White Perch abundance in our study systems remain unclear. Despite differences in growth, White Perch from high-abundance and low-abundance populations occupied similar trophic niches. Furthermore, although early timing of maturity has been linked to decreases in size structure for some White Perch populations (Chizinski 2007; Feiner et al. 2012), maturity timing did not vary among the White Perch populations we studied. In addition, abiotic variables have been useful predictors of White

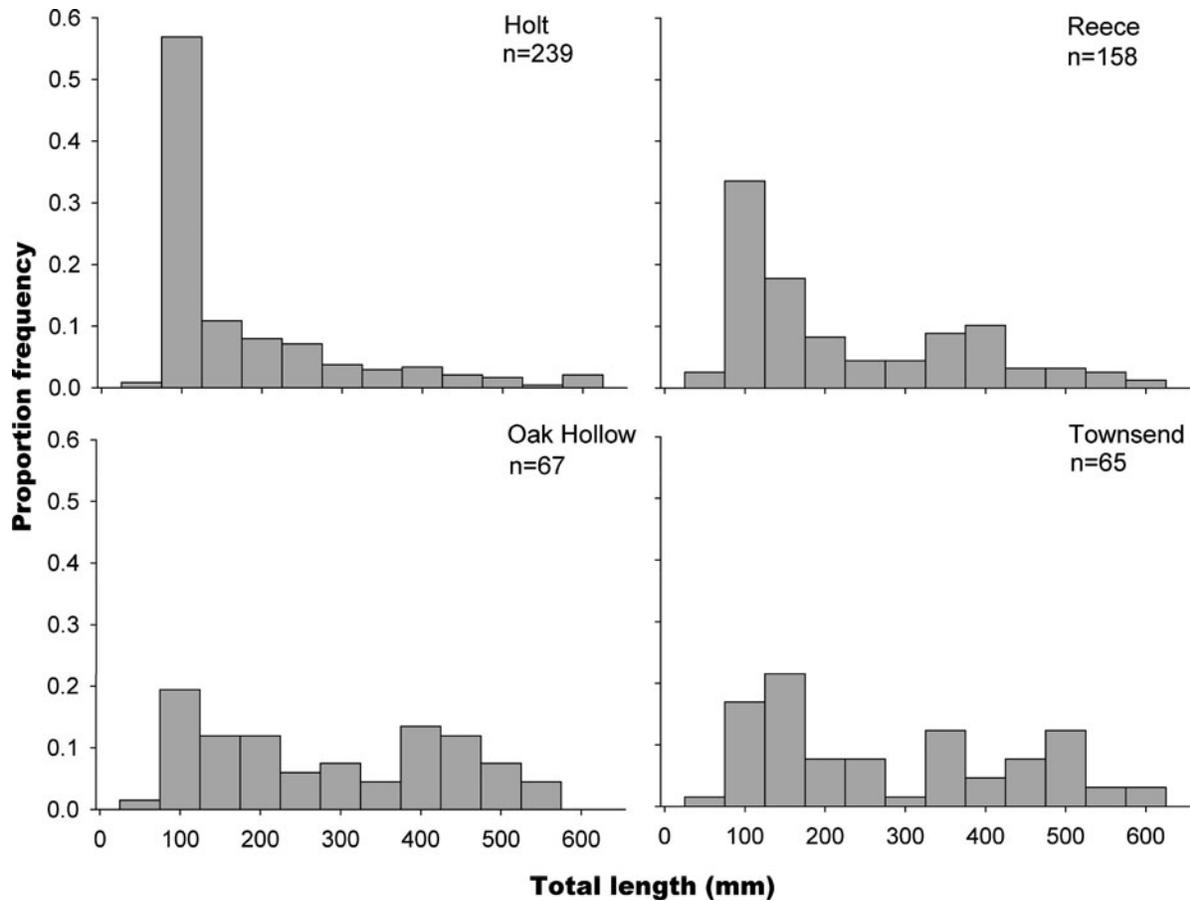


FIGURE 2. Length frequency distributions of Largemouth Bass sampled from four small (<700 ha) North Carolina reservoirs in 2010 and 2011. Lakes Reece and Holt have low-abundance White Perch populations; Lake Townsend and Oak Hollow Lake have high-abundance White Perch populations.

Perch abundance in previous studies (Hawes and Parrish 2003; North and Houde 2003), but we found no relationship between White Perch abundance and Secchi depth, specific conductivity, temperature, or DO concentration.

TABLE 3. Schoener's overlap index (D) values based on percent index of relative importance and trophic level of small White Perch (WHP; <150 mm TL), large WHP (≥ 150 mm TL), small Largemouth Bass (LMB; <200 mm TL), and large LMB (≥ 200 mm TL). Schoener's D -values greater than 0.6 (in bold italics) were considered to indicate significant diet overlap. A dash (–) signifies that the sample sizes were insufficient ($n < 5$) for analysis.

Lake	WHP size	Small LMB	Large LMB
Holt	Small WHP	–	–
	Large WHP	–	–
Reece	Small WHP	0.64	0.23
	Large WHP	0.77	0.23
Oak Hollow	Small WHP	0.77	0.29
	Large WHP	0.75	0.53
Townsend	Small WHP	–	0.00
	Large WHP	–	0.00

Other organisms in the reservoirs had mixed or nonexistent relationships with White Perch abundance. Studies have linked prey availability to population dynamics in fish (e.g., Deelder 1951; Jansen and MacKay 1992), but in the present study White Perch abundances were not related to invertebrate densities. Gizzard Shad abundance had a marginally significant positive relationship with White Perch abundance, providing weak evidence that the abundances of the two species may be related. High abundances of Gizzard Shad may alleviate predation pressure on White Perch if piscivorous fish select Gizzard Shad over White Perch (Aday et al. 2003; Gosch et al. 2010a).

White Perch abundance has been directly linked to predation (Margulies 1990; Hartman and Margraf 1992; Vrtiska et al. 2003). Gosch and Pope (2011) found that predation may increase stunting in White Perch populations if large predators remove older, larger (rather than younger, smaller) individuals from the population, thereby decreasing the overall size structure. Contrary to this pattern, Largemouth Bass in the present study did not consume many White Perch. Our study focused on Largemouth Bass because they were the most abundant predator in all four study systems, but other piscivores may also interact with White Perch (Schaeffer and Margraf 1987; Prout et al.

1990; Parrish and Margraf 1994; Couture and Watzin 2008). Limited availability of other predators in one or more of the study systems prevented us from including broader comparisons.

Our ability to draw inferences about trophic interactions was limited by a lack of historical data and the coarse time scale at which we collected data on prey availability. Without data describing the state of Largemouth Bass populations before the introduction of White Perch, it is difficult to interpret whether Largemouth Bass abundances have shaped White Perch abundances (or vice versa). It is also possible that more intensive sampling effort (e.g., bimonthly invertebrate sampling throughout the year) could permit the detection of important seasonal differences in prey abundance that affect White Perch abundance at key ontogenetic stages. Furthermore, data from a greater number of reservoirs would have strengthened our ability to draw conclusions. Despite these limitations, we were able to detect a strong density-dependent response in White Perch growth and an interesting relationship between White Perch and Largemouth Bass abundances.

Overall, density-dependent mechanisms drove differences in size structure among the White Perch populations we studied, and our results suggest that White Perch density is a function of Largemouth Bass density. Although we evaluated a suite of common factors that are widely assumed to drive fish abundance, the factors ultimately affecting White Perch abundance in these small reservoirs remain unclear. More research into the competitive and predatory relationships between Largemouth Bass and White Perch, especially at the juvenile stage, may provide insight into the mechanisms that determine White Perch abundance and thus size structure.

ACKNOWLEDGMENTS

This research was funded by the NCWRC through Federal Aid in Sport Fish Restoration Grant F-68. We thank D. Dickey for his assistance with statistical analysis, members of the Fisheries Aquatic Ecology Sciences Laboratory at North Carolina State University for assistance with field collections, and Z. S. Feiner for logistic and editorial support.

REFERENCES

- Aday, D. D., R. J. H. Hoxmeier, and D. H. Wahl. 2003. Direct and indirect effects of Gizzard Shad on Bluegill growth and population size structure. *Transactions of the American Fisheries Society* 132:47–56.
- Buchheister, A., and R. J. Latour. 2010. Turnover and fractionation of carbon and nitrogen stable isotopes in tissues of a migratory coastal predator, Summer Flounder (*Paralichthys dentatus*). *Canadian Journal of Fisheries and Aquatic Sciences* 67:445–461.
- Bur, M. T. 1986. Maturity and fecundity of the White Perch, *Morone americana*, in western Lake Erie. *Ohio Journal of Science* 86:205–207.
- Busch, W. D. N., D. H. Davies, and S. J. Nepszy. 1977. Establishment of White Perch, *Morone americana*, in Lake Erie. *Journal of the Fisheries Research Board of Canada* 34:1039–1041.
- Chizinski, C. J. 2007. Variation in life-history traits and morphology of stunted and non-stunted fish. Doctoral dissertation. Texas Tech University, Lubbock.
- Cortés, E. 1997. A critical review of methods of studying fish feeding based on analysis of stomach contents: application to elasmobranch fishes. *Canadian Journal of Fisheries and Aquatic Sciences* 54:726–738.
- Couture, S. C., and M. C. Watzin. 2008. Diet of invasive adult White Perch (*Morone americana*) and their effects on the zooplankton community in Missisquoi Bay, Lake Champlain. *Journal of Great Lakes Research* 34:485–494.
- Deelder, C. L. 1951. A contribution to the knowledge of the stunted growth of perch (*Perca fluviatilis* L.) in Holland. *Hydrobiologia* 3:357–378.
- Feiner, Z. S., D. D. Aday, and J. A. Rice. 2012. Phenotypic shifts in White Perch life history strategy across stages of invasion. *Biological Invasions* 14:2315–2329.
- Feiner, Z. S., J. A. Rice, and D. D. Aday. 2013. Trophic niche of invasive White Perch and potential interactions with representative reservoir species. *Transactions of the American Fisheries Society* 142:628–641.
- Gabelhouse, D. W. Jr. 1984. A length-categorization system to assess fish stocks. *North American Journal of Fisheries Management* 4:273–285.
- Gosch, N. J. C., L. L. Pierce, and K. L. Pope. 2010a. The effect of predation on stunted and nonstunted White Perch. *Ecology of Freshwater Fish* 19:401–407.
- Gosch, N. J. C., and K. L. Pope. 2011. Using consumption rate to assess potential predators for biological control of White Perch. *Knowledge and Management of Aquatic Ecosystems* 403:article 02.
- Gosch, N. J. C., J. R. Stittle, and K. L. Pope. 2010b. Food habits of stunted and non-stunted White Perch (*Morone americana*). *Journal of Freshwater Ecology* 25:31–39.
- Harris, J. L. 2006. Impacts of the invasive White Perch on the fish assemblage of Kerr Reservoir, Virginia. Master's thesis. Virginia Polytechnic Institute and State University, Blacksburg.
- Hartman, K. J., and F. J. Margraf. 1992. Effects of prey and predator abundances on prey consumption and growth of Walleyes in western Lake Erie. *Transactions of the American Fisheries Society* 121:245–260.
- Hawes, E. J., and D. L. Parrish. 2003. Using abiotic and biotic factors to predict the range expansion of White Perch in Lake Champlain. *Journal of Great Lakes Research* 29:268–279.
- Hines, R. 1981. The ecological significance of a stunted White Perch population in an eutrophic Maine pond. Master's thesis. University of Maine, Orono.
- Hurley, D. A. 1992. Feeding and trophic interactions of White Perch (*Morone americana*) in the Bay of Quinte, Lake Ontario. *Canadian Journal of Fisheries and Aquatic Sciences* 49:2249–2259.
- Irons, K. S., T. M. O'Hara, M. A. McClelland, and M. A. Pegg. 2002. White Perch occurrence, spread, and hybridization in the middle Illinois River, upper Mississippi River system. *Transactions of the Illinois State Academy of Science* 95:207–214.
- Jansen, W. A., and W. C. Mackay. 1992. Foraging in Yellow Perch, *Perca flavescens*: biological and physical factors affecting diel periodicity in feeding, consumption, and movement. *Environmental Biology of Fishes* 34:287–303.
- Johnson, T. B., and D. O. Evans. 1990. Size-dependent winter mortality of young-of-the-year White Perch: climate warming and invasion of the Laurentian Great Lakes. *Transactions of the American Fisheries Society* 119:301–313.
- Madenjian, C. P., R. L. Knight, M. T. Bur, and J. L. Forney. 2000. Reduction in recruitment of White Bass in Lake Erie after invasion of White Perch. *Transactions of the American Fisheries Society* 129:1340–1353.
- Margulies, D. 1990. Vulnerability of larval White Perch, *Morone americana*, to fish predation. *Environmental Biology of Fishes* 27:187–200.
- Mittelbach, G. G., and L. Persson. 1998. The ontogeny of piscivory and its ecological consequences. *Canadian Journal of Fisheries and Aquatic Sciences* 55:1454–1465.
- North, E. W., and E. D. Houde. 2003. Linking ETM physics, zooplankton prey, and fish early-life histories to Striped Bass *Morone saxatilis* and White Perch *M. americana* recruitment. *Marine Ecology Progress Series* 260:219–236.

- Núñez, J., and F. Duponchelle. 2009. Towards a universal scale to assess sexual maturation and related life history traits in oviparous teleost fishes. *Fish Physiology and Biochemistry* 35:167–180.
- Parrish, D. L., and F. J. Margraf. 1990. Interactions between White Perch (*Morone americana*) and Yellow Perch (*Perca flavescens*) in Lake Erie as determined from feeding and growth. *Canadian Journal of Fisheries and Aquatic Sciences* 47:1779–1787.
- Parrish, D. L., and F. J. Margraf. 1994. Spatial and temporal patterns of food use by White Perch and Yellow Perch in Lake Erie. *Journal of Freshwater Ecology* 9:29–35.
- Post, D. M. 2002. Using stable isotopes to estimate trophic position: models, methods, and assumptions. *Ecology* 83:703–718.
- Prout, M. W., E. L. Mills, and J. L. Forney. 1990. Diet, growth, and potential competitive interactions between age-0 White Perch and Yellow Perch in Oneida Lake, New York. *Transactions of the American Fisheries Society* 119:966–975.
- Reid, W. F. Jr. 1972. Utilization of the crayfish *Orconectes limosus* as forage by White Perch (*Morone americana*) in a Maine lake. *Transactions of the American Fisheries Society* 101:608–612.
- Schaeffer, J. S., and F. J. Margraf. 1986. Population characteristics of the invading White Perch (*Morone americana*) in western Lake Erie. *Journal of Great Lakes Research* 12:127–131.
- Schaeffer, J. S., and F. J. Margraf. 1987. Predation on fish eggs by White Perch, *Morone americana*, in western Lake Erie. *Environmental Biology of Fishes* 18:77–80.
- Schoener, T. W. 1968. The *Anolis* lizards of Bimini: resource partitioning in a complex fauna. *Ecology* 49:704–726.
- Scott, W. B., and W. J. Christie. 1963. The invasion of the lower Great Lakes by the White Perch, *Roccus americanus* (Gmelin). *Journal of the Fisheries Research Board of Canada* 20:1189–1195.
- Sheri, A. N., and G. Power. 1968. Reproduction of White Perch, *Roccus americanus*, in the Bay of Quinte, Lake Ontario. *Journal of the Fisheries Research Board of Canada* 25:2225–2231.
- Sheri, A. N., and G. Power. 1972. Effects of density on the growth of White Perch, *Roccus americanus* (Gmelin), in the Bay of Quinte, Lake Ontario. *Pakistan Journal of Zoology* 4:109–132.
- Stanley, J. G., and D. S. Danie. 1983. Life histories and environmental requirements of coastal fishes and invertebrates (North Atlantic): White Perch. U.S. Fish and Wildlife Service Biological Services Program FWS/OBS-82/11.7.
- Stein, R. A., D. R. DeVries, and J. M. Dettmers. 1995. Food-web regulation by a planktivore: exploring the generality of the trophic cascade hypothesis. *Canadian Journal of Fisheries and Aquatic Sciences* 52:2518–2526.
- St-Hilaire, A., S. C. Courtenay, F. Dupont, and A. D. Boghen. 2002. Diet of White Perch (*Morone americana*) in the Richibucto estuary, New Brunswick. *Northeastern Naturalist* 9:303–316.
- Vander Zanden, M. J., and J. B. Rasmussen. 2001. Variation in $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ trophic fractionation: implications for aquatic food web studies. *Limnology and Oceanography* 46:2061–2066.
- von Bertalanffy, L. 1938. A quantitative theory of organic growth. *Human Biology* 10:181–213.
- Vrtiska, L. A. Jr., E. J. Peters, and M. T. Porath. 2003. Flathead Catfish habitat use and predation on a stunted White Perch population in Branched Oak Reservoir, Nebraska. *Journal of Freshwater Ecology* 18:605–613.
- Wallace, R. K. Jr. 1981. An assessment of diet-overlap indexes. *Transactions of the American Fisheries Society* 110:72–76.
- Ward, S. M., and R. M. Neumann. 1998. Seasonal and size-related food habits of Largemouth Bass in two Connecticut lakes. *Journal of Freshwater Ecology* 13:213–220.
- Weidel, B. C., S. R. Carpenter, J. F. Kitchell, and M. J. Vander Zanden. 2011. Rates and components of carbon turnover in fish muscle: insights from bioenergetics models and a whole-lake ^{13}C addition. *Canadian Journal of Fisheries and Aquatic Sciences* 68:387–399.
- Wong, R. K. 2002. White Perch expansion and life history within a southern reservoir. Master's thesis. North Carolina State University, Raleigh.
- Zuerlein, G. 1981. The White Perch in Nebraska. Nebraska Game and Parks Commission, Nebraska Technical Series 8, Lincoln.