JUVENILE CRAPPIE GROWTH AND BIOENERGETICS: IMPLICATIONS FOR MANAGEMENT USING BLACKNOSE CRAPPIE

BY

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THESIS

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Abstract

Collectively, black crappie *Pomoxis nigromaculatus* and white crappie *P. annularis* make up important harvest-oriented sport fisheries across North America, especially in the Midwest. Over the past several decades, the major management issues facing crappie populations have been identified as poor size structure and highly variable recruitment. Although stocking programs have not been historically common for crappie, some recent examples have been successful in supplementing year classes in systems with poor recruitment. In order to differentiate stocked from naturally occurring individuals for evaluations of stocking programs, several management agencies have cultured and stocked blacknose crappie, a phenotypic variant of black crappie. Continued use of blacknose crappie by managers has also stemmed from perceived differences in growth and survival relative to black crappie in rearing environments. My thesis evaluates growth-related differences among juvenile black, white, and blacknose crappies in both experimental ponds and the laboratory. In a common garden pond experiment, I found no differences in survival among strains or ponds. Blacknose crappie outgrew black and white crappies in both length and weight and black crappie outgrew white crappie in just weight. Growth was pond-dependent for all strains, with growth rates being highest in ponds with high zooplankton density, low macroinvertebrate density, and low vegetation density. Turbidity also may have had indirect effects on the growth of black and blacknose crappies, but not white crappie. Across a range of temperatures in the laboratory, I found no differences in metabolic rate among the strains. I also observed superior growth characteristics of blacknose crappie in the laboratory, as they exhibited higher relative growth rates and food conversion efficiencies than black and white crappies. Black and blacknose crappies also had higher maximum food consumption rates than white crappie. No strain-temperature interactions were detected for the suite of parameters measured, suggesting a lack of differential thermal adaptations among black, white, and blacknose crappies. Differences in growth and food conversion efficiency between blacknose and black crappies may be attributable to selective pressures associated with the multi-decadal culture of the strain, especially in a species where survival and handling mortality are highly size-dependent. My laboratory results indicated ontogenetic shifts in thermal optima for juvenile crappies when compared to previous studies with adult white crappie. Results of my thesis can improve future juvenile crappie bioenergetics models and advise management decisions using blacknose crappie. Blacknose crappie may provide a better alternative to other crappies for stocking programs, but potential negative impacts on resident crappie populations need to be investigated in the future due to the origin of the strain coming from a single source population. Blacknose crappie exhibit superior growth characteristics over black and white crappies in rearing environments and these relationships should be evaluated further at larger spatial scales and across varying environmental conditions.

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Chapter 1: Factors affecting growth and survival of juvenile black, white, and blacknose crappies

Abstract

Although stocking of crappie is not historically widespread, it has recently gained popularity for managing populations in systems with poor recruitment and/or high harvest rates. Anecdotal evidence suggests that blacknose crappie, a phenotypic variant of black crappie *Pomoxis nigromaculatus* used for stocking, grow and survive better than black crappie in hatchery environments. We compared age-0 growth and survival of black, white *P. annularis*, and blacknose crappies in 0.04-ha experimental ponds using a common garden approach. Throughout the three-month experiment, a suite of variables was measured in each pond in order to associate between-pond variation in growth rates with environmental conditions. There were no differences in survival among the strains, but the blacknose crappie outgrew black and white crappies in both length and weight. Black crappie also grew faster than white crappie in weight but not length. Environmental variables affected the three strains similarly, as ponds with high zooplankton density, low macroinvertebrate density, and low vegetation density had the highest growth rates. Turbidity may have had indirect effects on the growth of black and blacknose crappies, but not white crappie. Differences in growth among juvenile black, white, and blacknose crappies have implications for management and stocking of crappie populations.

Introduction

Supplemental stocking of a multitude of species to enhance sport fish populations has been widely used across North America (Halverson 2008). White crappie (*Pomoxis annularis*) and black crappie (*P. nigromaculatus*) are collectively two of the most sought after sport fish species in North America (Hooe 1991; Boxrucker and Irwin 2002). Although historical stocking of crappies *Pomoxis* spp. has not been widespread, it has recently gained popularity for managing populations in systems with poor recruitment and/or high harvest rates (Myers et al. 2000; Isermann et al. 2002). The success of fish stocking programs often hinges upon initial poststocking growth and survival, especially for juveniles (Mather and Wahl 1989; Wahl 1999). Poststocking survival has been described as a function of pre- and poststocking environment and the size, condition, genetics, and handling of stocked individuals (Isermann et al. 2002). Poststocking evaluations are essential for understanding the effects of the stocking program on fish populations, but the success of crappie stocking programs has only been evaluated in a few studies (Myers et al. 2000; Myers and Rowe 2001; Isermann et al. 2002). Furthermore, no studies have compared black and white crappies with respect to early growth and stocking utility.

Because of the need to differentiate stocked from naturally produced individuals to evaluate stocking success, management agencies began culturing and stocking blacknose black crappie (hereafter blacknose crappie), a phenotypic variant of *P. nigromaculatus* (Isermann et al. 2002). Blacknose crappie are characterized by a dominant, predorsal black stripe and have been found to occur naturally in at least 13 states, from Wisconsin to Florida (Buchanan and Bryant 1973; Gomelsky et al. 2005). The production and use of blacknose crappie for stocking programs has been proliferated by the Tennessee Wildlife Resources Agency (TWRA), who initially obtained their broodstock from a black crappie population in Beaver Lake, Arkansas with a high occurrence of the blacknose trait (Isermann et al. 2002). Continued use of blacknose crappie by the TWRA and other agencies has occurred not only for identification purposes but also because of perceived increased survival and growth in hatchery environments (M. Smith, TWRA, personal communication), although these claims have not been formally evaluated. From the hatchery strain, the TWRA has supplied blacknose crappie to other states for stocking purposes, including Illinois.

Previous studies suggest crappie stocking success to be variable across species and systems. Poststocking survival of fingerling blacknose crappie in several Tennessee reservoirs was high (87%) but first-year contribution was highly variable and lake-dependent, ranging from 0 to 93% (Isermann et al. 2002). Short-term survival of black crappie fingerlings was estimated at 70 to 100% in a large (2000-ha) Florida lake (Myers and Rowe 2001). Initial poststocking survival of microwire tagged black crappie was much lower in a smaller (60-ha) Florida lake, ranging from 13 to 34% (mean = 26%) and contribution at age-1 was estimated at 4.8% (Myers et al. 2000). Year-class contribution of stocked fingerling white crappie was also low (0-3.8%) in Lake Chicot, Arkansas and mean 24-hour handling mortality was estimated at 27% (Racey and Lochmann 2002). These three studies suggest the potential of higher survival and year class contribution of stocked fingerling blacknose crappie relative to black and white crappies, although stocking success appears to be strongly lake- and region-dependent. Stocking period, size at stocking, and littoral predation rates have all been suggested as potentially important factors affecting year class contribution of stocked crappie (Isermann et al. 2002).

Several field studies have examined the effect of environmental factors on early crappie growth, with little agreement across systems. Zooplankton biomass had a positive effect on growth of larval black crappie in four Ohio reservoirs (Bunnell et al. 2003), but no effect on growth of age-0 black crappie in several Florida lakes (Dockendorf and Allen 2005). For larval white crappie, zooplankton density positively influences early growth (Sammons et al. 2001). Other factors with varying effects on early crappie growth are conspecific density (Myers and Rowe 2001; Sammons et al. 2001; Dudenhoeffer et al. 2014), benthic prey characteristics (Mathur and Robins 1971; Tuten et al. 2008), temperature (Pine and Allen 2001), turbidity (Dockendorf and Allen 2005; Spier and Heidinger 2002), larval gizzard shad abundance (Pope and Devries 1994), and reservoir hydrology (Sammons et al. 2001). All of these studies have examined either black or white crappies independently without comparing them or pooled the two species due to difficulties distinguishing the two as larvae and juveniles. Differences in adult growth rates have been documented between black and white crappies in both lake and pond environments, with white crappie typically exhibiting greater lengths-at-age than black crappie due to earlier shifts to piscivory (Buck and Hooe 1996; Jackson and Hurley 2005), but little research exists comparing the two at the juvenile life stage. White crappie outgrew black crappie through the age of 10 days but not 20 or 30 days in Weiss Lake, Alabama (Travnichek et al. 1996), but in ponds, early growth of black and white crappies was not different in either length or weight (Spier and Heidinger 2002).

There is a need for comparisons between juvenile black and white crappies, especially with respect to early growth. Furthermore, no research has compared blacknose crappie with black and white crappies. The objectives of our study were to 1) compare growth and survival of juvenile black, white, and blacknose crappies in a common environment and 2) evaluate what environmental factors drive juvenile growth among the three strains. We evaluated growth and survival of juvenile black, white, and blacknose crappies in experimental ponds, measuring a suite of environmental variables. We hypothesized that blacknose crappie would exhibit greater growth and survival compared to black and white crappies. We also expected to observe significant variation in growth among ponds with environmental conditions differentially affecting the three strains.

Methods

Fish Sources and Handling

All juvenile crappie were produced in 0.4-ha rearing ponds at the Sam Parr Biological Station (Kinmundy, IL). Brood fish were collected from Weldon Springs Lake (Clinton, IL) and Dawson Lake (Dawson, IL) for black crappie; Lake Paradise (Mattoon, IL), Forbes Lake (Kinmundy, IL), and Sam Dale Lake (Johnsonville, IL) for white crappie; and Clinton Lake (Clinton, IL) for blacknose crappie. For black and white crappies, lakes containing only one species of crappie were used. All brood fish were collected in February and March of 2013 via alternating current (AC) electrofishing and trap netting and approximately 40 individuals of each strain were stocked into strain-specific rearing ponds for production of juvenile crappie. Black, white, and blacknose crappies will be referred to as different strains, although white crappie are a different species.

Experimental Design and Sampling Methods

Growth and survival were compared among age-0 black, white, and blacknose crappies in ten 0.04-ha experimental ponds at the Sam Parr Biological Station using a common garden approach. All ponds were filled with water from Forbes Lake and filtered with a 300 µm mesh sock to prevent the introduction of larval fish. Two weeks were allowed for natural colonization and development of populations of phytoplankton, zooplankton, and macroinvertebrates. Prior to experimental set-up, rearing ponds were drained and all age-0 crappies were dip-netted from a drain basin and held in strain-specific circular tanks (1325 L polyethylene tanks) for approximately 72-hours to allow initial handling mortality to take its course. Rearing ponds were drained and juveniles were transferred to 0.04-ha experimental ponds on cool days in August of 2013 (mean air temperature < 24^{o} C) to minimize stress-induced mortality. The number of fish and biomass of age-0 fish of each strain were held constant for all ponds (N = 50 of each strain, 3,750 fish/ha), within the range of natural juvenile crappie densities (173-10,456 fish/ha; Mitzner 1981).

Initial weight (g) and total length (mm) for each strain were determined based on a subsample (N = 30) to reduce handling of all experimental fish. Mean ± SE initial TL (total length) was 44 ± 0.63 mm for black crappie, 46 ± 0.87 mm for blacknose crappie, and 46 ± 0.81 mm for white crappie, with no statistical differences among the strains (ANOVA: $F_{2,87} = 1.45$, $P = 0.24$). Initial weight (mean ± SE) was 0.93 ± 0.04 g for black crappie, 1.10 ± 0.06 g for blacknose crappie, and 0.92 ± 0.08 g for white crappie, and was also not significantly different among the strains (ANOVA: $F_{2,87} = 2.61$, $P = 0.07$). After three months, ponds were drained and final weight and length were determined by measuring all fish. Survival for each strain was calculated as the number of fish at draining divided by the number of fish initially stocked.

All experimental ponds were sampled to account for potential interactions between the growth and survival of each strain and environmental characteristics. Phosphorous, chlorophyll-a, temperature, dissolved oxygen, and turbidity were sampled every three weeks, whereas zooplankton, vegetation, and macroinvertebrates were sampled at the beginning, middle, and end of the experiment. Total phosphorous concentration was determined from two 45 mL water samples taken with a depth-integrated water sampler and frozen immediately. Phosphorous samples were processed by persulfate oxidation, addition of a molybdate reagent, and measuring absorbance with a spectrophotometer (Wetzel and Likens 1991). Chlorophyll-a concentration was determined from a depth-integrated water sample by filtering 100 mL of water through 0.7 µm glass fiber filter paper, extracting the chlorophyll-a in 90% acetone for 24 hours, and then determining fluorescence in a fluorometer (Turner Design, model TD700, Sunnyvale, California, USA; Welschmeyer 1994). Temperature and dissolved oxygen were measured with a handheld meter YSI model-55 at a depth of 0.5 m below the surface. Finally, turbidity was measured from a depth-integrated water sample, using an electronic turbidimeter.

Zooplankton samples were taken at five random locations within each pond using a 3 L vertical tube sampler. Samples were combined (total volume = 15 L), filtered through 64 µm mesh, and then stored in a 4% Lugol's solution. Zooplankton samples were processed in the laboratory by adjusting all samples to a constant volume (100 mL) and then processing in 1 mL aliquots. Whole samples were processed until at least 200 individuals from the most abundant taxonomic groups were counted or until 10% of the total sample volume was processed (Welker et al. 1994). Littoral vegetation was surveyed and quantified at five random locations in each pond by deploying a 0.5 m diameter ring and quantifying the species present within the ring by weight (g). Macroinvertebrate samples were taken at five random locations in each pond with a modified stovepipe sampler (Turner and Trexler 1997), combined, and preserved in an ethanol and rose Bengal solution. Macroinvertebrate samples were processed by identifying and enumerating individuals to family.

Statistical Analyses

Mixed-model analysis of variance (ANOVA, $\alpha = 0.05$) with fixed strain and random pond effects was used to test the overall strain effects on growth and survival. A Tukey's studentized range test was used to test differences in growth and survival among black, white, and blacknose crappies ($\alpha_e = 0.05$). Multivariate analyses were used to determine which environmental variables had the greatest effect on strain-specific growth and accounted for the majority of between-pond variation. Prior to multivariate analyses, all environmental variables were square root transformed to normalize errors, except a reciprocal transformation for turbidity. A principal component analysis (PCA) was used to reduce the number of overall variables for final analysis, utilizing the "B4-broken-stick" method for variable selection (King and Jackson 1999). Multiple linear regression analyses were used to associate final weight (final length followed similar trends) with the reduced environmental variable set. Multiple linear regression analysis was not performed on percent survival using environmental variables because no significant pond effect was detected. Akaike information criterion (AIC) scores were used to select the best model(s), with the best model having the lowest AIC score. Models within two AIC units of the best model were considered of equal predictive power (Burnham and Anderson 2002). Simple linear regression analysis was then performed separately on final weight of each strain and each environmental variable from our reduced variable subset. All analyses were conducted using the SAS® system (Statistical Analysis System Version 9.3; SAS Institute, Cary, North Carolina).

Results

Percent survival was estimated for nine of the ten experimental ponds; the tenth pond lost some fish from the catch basin during draining and was excluded from analyses. Survival of all age-0 crappies varied from 42-80% and was not pond-dependent (ANOVA: $F_{2,16} = 0.15$, $P = 0.38$). Mean survival for all strains was 68%, and was not significantly different among the strains (ANOVA: $F_{2,16} = 0.14$, $P = 0.87$)(Figure 1A). Final length was variable by pond (ANOVA: $F_{9,18} = 27.8$, $P < 0.0001$)(Figure 2A) and a significant strain effect was observed, with blacknose crappie growing more in length than both black and white crappies (ANOVA: $F_{2,18} = 7.19$, $P = 0.005$)(Figure 1B). Final weight was also variable by pond (ANOVA: $F_{9,18} = 24.60$, $P < 0.0001$)(Figure 2B) and a significant strain effect was detected, with blacknose crappie gaining more weight than black crappie followed by white crappie (ANOVA: $F_{2,18} = 29.80$, $P = <0.0001$)(Figure 1C).

Ponds were fairly diverse in terms of the environmental variables measured, except for temperature and dissolved oxygen (Table 1). Variable selection via PCA reduced the initial six variable set to a reduced variable set (N = 3) that included turbidity, phosphorous, and total zooplankton density. Mean turbidity ranged from 6.28 to 25.20 NTU (Nephelometric Turbidity Units; mean = 11.35) and phosphorous ranged from 33.7 to 92.1 $\mu g \cdot L^{-1}$ (mean = 55.1) for all ponds. Total zooplankton density for all ponds (442 ± 33 (mean ± SE) $\# \cdot L^{-1}$) was comprised mainly of rotifers and copepods (Table 1). Total zooplankton density was highly negatively correlated with total macroinvertebrate density ($r^2 = 0.49$, $P < 0.0001$) and total vegetation density ($r^2 = 0.63$, $P < 0.0001$) in the experimental ponds. Factor loadings from the first principal component indicate a negative relationship between zooplankton density, turbidity, and chlorophyll-a, and vegetation and macroinvertebrate density. Factor loadings from the second principal component indicate a positive relationship between phosphorous and chlorophyll-a. Finally, factor loadings from the third principal component indicate a positive relationship between turbidity and macroinvertebrate density (Table 1).

The best model for black crappie growth included total zooplankton density and turbidity ($r^2 = 0.74$), with one alternative model being within two AIC units (Table 2). Similarly, the best model for blacknose crappie included total zooplankton density and turbidity ($r^2 = 0.51$), with two alternative models being within two AIC units (Table 2). The best model for white crappie included only total zooplankton density ($r^2 = 0.51$), with two alternative models being within two AIC units (Table 2). For white crappie, the addition of turbidity or phosphorous to the model was no better than total zooplankton alone in predicting growth. Growth of juvenile black and blacknose crappies, however, appeared to be determined by the combination of zooplankton and turbidity, with no benefit of including phosphorous in the model.

Simple linear regression analyses indicated significant, positive relationships between total zooplankton density and final weight of black ($r^2 = 0.64$, $P = 0.006$), white ($r^2 = 0.56$, $P = 0.01$), and blacknose ($r^2 = 0.48$, $P = 0.03$) crappies (Figure 3). Linear regression analyses did not indicate significant relationships between final weight and either turbidity or phosphorous for any of the strains ($r^2 < 0.1$ for all relationships). Across all strains, fastest growth occurred in ponds with high zooplankton densities and low vegetation and macroinvertebrate densities.

Discussion

In agreement with the hypothesis, we observed faster growth of blacknose crappie than both black and white crappies in both length and weight. Because of differing length-weight relationships between black and white crappies (Neumann and Murphy 1991), black crappie also outgrew white crappie in weight, but not length. This is contrary to growth comparisons in an aquaculture setting, where no differences were observed between juvenile black and white crappies fed commercial feed (Dudenhoeffer et al. 2014), suggesting differences in behavior, foraging efficiency, and/or resource utilization in larger systems. Our results are consistent with anecdotal reports of faster growth of blacknose crappie in lakeside and hatchery rearing ponds. Although blacknose crappie are genetically identical to black crappie in terms of mapped loci used for species differentiation, the strain originated from a genetically unique population of black crappie in Beaver Lake, Arkansas with a high occurrence of the predorsal black stripe. Since the 1980's, the phenotype associated with the unique genetic identity of these fish has been selected for in hatcheries and rearing ponds to produce the current strain of crappie (Isermann et al. 2002; Gomelsky et al. 2005). We suggest two potential mechanisms for these differences among strains: local adaptation and selection in hatcheries and rearing ponds. Because the origin of the blacknose crappie used in stocking programs in Tennessee and Illinois was a single reservoir, differences in genetic variability and historical selective pressures could account for differences in growth and/or survival. The genetic origin of a population can significantly affect its growth and survival in different environments (Schultz et al. 1998; Mandiki et al. 2004; Slaughter et al. 2008). Previous research on regional adaptations has investigated within-species adaptations to different thermal regimes and latitudes. With respect to fishes, differences in growth, metabolism, and thermal tolerance have been documented between both conspecifics from different thermal regimes (e.g., Clapp and Wahl 1996; Galarowicz and Wahl 2003; Jonassen et al. 2000) and between closely related species in sympatry (e.g., Dent and Lutterschmidt 2003). Differences in growth and behavior have also been found between subpopulations of white crappie in the same system that were attributed to differences in resource utilization (Heidinger et al. 1985). Several studies have argued that genetic lineage, especially with respect to thermal adaptations, should be considered when managing sport fish populations (Phillip et al. 1981; Koppelman and Phillip 1986; Clapp and Wahl 1996).

The observed differences in growth among strains could also be the product of multi-decade rearing of blacknose crappie for stocking purposes. The TWRA began producing and stocking blacknose crappie in the late 1980's (Isermann et al. 2002). Use and production of blacknose crappie in Illinois began in early 2000's from the same strain utilized in Tennessee. During this time, the strain has been produced in hatcheries or rearing ponds, with selection for the blacknose trait and potential selection for individuals with better fitness in these environments. A number of previous studies have found differing growth rates, survival, and genetic variability between hatchery and wild strains of fishes in different environments (Garcia-Marin et al. 1991; Araki and Schmid 2010). In steelhead trout (*Salmo gairdneri*), hatchery strains exhibited increased growth but decreased survival when compared to wild fish in streams but had higher survival in hatchery scenarios (Reisenbichler and McIntyre 1977). Furthermore, decreased long-term growth and survival of stocked northern pike (*Esox lucius*) to wild individuals has been attributed to carry over hatchery effects and genetic-based local maladaptation among stocked fish (Skov et al. 2011). Selective pressures associated with the production of blacknose crappie over the past several decades in rearing environments may be responsible for their observed faster growth than black crappie in these environments. Faster growth of blacknose crappie than black crappie may be the result of physiological differences (e.g. lower metabolic rate, higher food conversion efficiency, higher food consumption, etc.), behavioral differences (e.g. higher aggression, different prey or habitat selection, etc.), or a combination of other factors related to recent or historical selective pressures.

Environmental conditions in the ponds were comparable to meso- and eutrophic systems in terms of phosphorous, chlorophyll-a, and turbidity (Wetzel 2001). Total zooplankton density was the single most important factor driving among-pond variation in growth rates across all strains. These results are not surprising, as zooplankton are the primary food source for juvenile crappies up to approximately 65 mm, and remain an important part of their diet (along with benthic macroinvertebrates) until they eventually transition to piscivory at 150 - 200 mm (Ellison 1984; O'Brien 1984; Pine and Allen 2001; Dockendorf and Allen 2005). Ontogenetic diet shifts vary between systems and individuals, as both black and white crappies continue to feed on zooplankton at sizes over 150 mm in some systems (Ellison 1984; Heidinger et al. 1985; Muoneke et al. 1992). Zooplankton density driving early crappie growth in our ponds is consistent with several studies at larger spatial scales. A positive correlation between growth of age-0 white crappie and zooplankton density was found in Normandy Reservoir, Tennessee (Sammons et al. 2001). Black crappie in five Ohio reservoirs showed increased growth of first-feeding larvae with increasing zooplankton biomass (Bunnell et al. 2003). In contrast, Dockendorf and Allen (2005) observed no direct effect of zooplankton density on fall abundance and growth of age-0 black crappie in three Florida lakes but suggested that reduced water clarity due to high chlorophyll-a levels and wind resuspension of sediment may have reduced foraging efficiency where zooplankton densities were high. Our results confirm the importance of zooplankton prey in determining growth rates of juvenile crappie across a range of sizes (45-100 mm TL).

Although zooplankton affected growth similarly for all three strains, our multiple regression analyses suggested that turbidity might also be important in determining growth of black and blacknose crappies, but not for white crappie. The two best models for black crappie and blacknose crappie final weight both included zooplankton and turbidity. Several previous studies have suggested differences between black and white crappies with respect to effects of turbidity. Comparisons of species composition relative to water clarity have found black crappie to be less tolerant of turbidity than white crappie (Hall et al. 1954 and Goodson 1966). Also, decreased visibility limited capture efficiency and resulted in high mortality rates for black crappie but not for white crappie in a Nebraska lake (Ellison 1984). The ability of white crappie to shift to fish prey allowed them to avoid the summer energy shortage experienced by zooplanktivorous black crappie. The effect of turbidity on black and white crappies has only been examined in two controlled studies. Feeding rates of small (100-150 mm) black and white crappies on *Daphnia pulex* were similar at multiple turbidities (80 and 160 NTU; Barefield and Ziebell 1986) and turbidity had similar effects on growth rates of juvenile black and white crappies in experimental ponds (Spier and Heidinger 2002). Similar to Spier and Heidinger (2002), we believe that factors correlated with turbidity (e.g., vegetation, flow, and primary production) rather than turbidity directly, may be more influential in dictating crappie dynamics. Based on the factor loadings in the first principal component of our PCA, growth for all three strains was maximized in ponds with high zooplankton density and low vegetation and macroinvertebrate densities. Juvenile crappies appeared to rely more on pelagic production than littoral-benthic resources in our ponds. These relationships may, however, be less important in larger systems with more depth and greater surface area to shoreline ratios, resulting in higher availability of pelagic resources.

Contrary to our hypothesis, we observed no survival differences among the three strains, with blacknose crappie surviving similarly to black and white crappies. Despite no survival differences observed in our experimental ponds, differences in long-term survival and stocking success still might be observed among the strains. Long-term survival, and eventual recruitment, of larval and juvenile fishes has been shown to be directly related to growth (Houde 2008). Faster growing larvae and juveniles exhibit increased overwinter survival for a number of species due to decreased risks of size-dependent predation (e.g., Miranda and Hubbard 1994), osmoregulatory failure (e.g., Johnson and Evans 1996), and starvation (e.g., Oliver et al. 1979), factors that we were not able to assess. No evidence of size-specific mortality in juvenile white crappie due to starvation or osmoregulatory failure was found previously in lakes or laboratory experiments, but size in the spring was set by the fall, as fish did not grow during the winter (McCollum et al. 2003). Because of faster growth rates, our results suggest that juvenile blacknose crappie could exceed the gape of predators before black or white crappies, potentially influencing long-term survival.

Many factors contribute to the success of stocking programs, including both short- and long-term poststocking survival (Murphy and Kelso 1986). Poststocking survival has been linked to size at stocking for a number of species (Serns and Andrews 1986; Hume and Parkinson 1988; Szendry and Wahl 1996), including crappies (Isermann et al. 2002). Given that blacknose crappie grew the fastest in our experiment, these growth rates should translate to larger size at stocking relative to black and white crappies reared under similar conditions. After three months, blacknose crappie outgrew black crappie by 8% in length and 14% in weight and white crappie by 10% in length and 41% in weight. Black crappie also added 24% more mass than white crappie despite no differences in length. If poststocking survival is influenced by differences in mass and not length, then black crappie fingerlings may be a better option for stocking than white crappie.

Growth of juvenile crappies was extremely pond-dependent in our study. While total zooplankton density was the most important factor driving growth of all three strains, our multiple regression analyses indicate that turbidity might also be an important factor dictating growth of black and blacknose crappies (although turbidity effects appeared to be indirect). Ponds with the fastest growth rates of all juvenile crappies were characterized by high zooplankton densities, low vegetation densities, and low macroinvertebrate densities. These environmental factors should be considered when trying to predict or evaluate crappie year-class strength, especially in systems where recruitment is determined by early growth. Before informed management decisions can be made regarding the use of blacknose crappie for stocking, future studies need to evaluate long-term poststocking growth and survival of black, white, and blacknose crappies in larger systems and across differing environmental conditions (e.g., different turbidities, thermal regimes, etc.). Although blacknose crappie grew fastest in our ponds, this faster growth did not translate into better short-term survival. In addition, genetic differences between blacknose and black crappies need to be assessed for the potential for outbreeding depression when stocking blacknose crappie in systems with resident crappie populations (Philip et al. 2002; Stockwell and Leberg 2002; Huff et al. 2011). One limitation of our study is that our blacknose crappie brood fish came from a single lake. A further examination of growth and survival characteristics of blacknose crappie from different sources (lakes, hatcheries, etc.) needs to be conducted to determine if growth differences are consistent among all blacknose crappie being used for stocking, or only those with certain production histories. In the meantime, we caution that use of blacknose crappie for stocking should be limited to isolated systems without existing crappie populations to reduce the risk of potentially introducing maladaptive genes.

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Tables

Variable	Mean (Range)	Standard Error	Principal Component		
			1	2	3
Temperature (^{o}C)	16.6 (16.1-17)	0.08	--	--	--
Dissolved oxygen (mg · L^{-1})	7.04 (6.44-7.80)	0.15	--	--	--
Turbidity (NTU)^{b}	11.35 (6.28-25.20)	1.19	0.678	0.175	<u>0.681</u>
Phosphorous (µg · L^{-1})^{a}	55.1 (33.7-92.1)	2.99	-0.466	<u>0.796</u>	-0.190
Chlorophyll-a (µg · L^{-1})^{a}	8.95 (3.88-16.84)	0.76	-0.701	0.650	0.002
Total littoral vegetation (g · m^{2})^{a}	431 (154-705)	31	0.777	0.560	0.138
Total macroinvertebrate density (# · m^{3})^{a}	9,021 (2,748-13,492)	700	0.762	-0.082	-0.601
Total dipteran larva density (# · m^{3})	5,917 (1,797-9,318)	477	--	--	--
Total zooplankton density (# · L^{-1})^{a}	442 (204-827)	33	<u>-0.831</u>	-0.405l	0.239
Rotifer density (# · L^{-1})	203 (32-656)	31	--	--	--
Copepod density (# · L^{-1})	127 (78-166)	5	--	--	--
Cladoceran density (# · L^{-1})	13 (2-33)	2	--	--	--
Percent of variance explained	--	--	50.7	26.2	15.6

[a] Square-root transformed.
[b] Reciprocal transformed.

Table 1: Environmental variables averaged across all ponds and sampling dates for ten experimental ponds used to evaluate growth and survival of white, black, and blacknose crappies. Range is based on pond averages across sampling dates. Factor loadings for the first three principal components are based on transformed data. The highest loading variable for each component is underlined.

Model	RMSE	Adjusted R^2	Δ AIC
Black Crappie			
Zooplankton + Turbidity	1.39	0.738	--
Zooplankton + Turbidity + Phosphorous	1.43	0.726	0.9
Zooplankton	1.82	0.553	4.7
Zooplankton + Phosphorous	1.95	0.490	6.7
Phosphorous	2.88	-0.119	13.8
Blacknose Crappie			
Zooplankton + Turbidity	2.69	0.509	--
Zooplankton + Turbidity + Phosphorous	2.72	0.500	0.6
Zooplankton	2.95	0.411	1.2
Zooplankton + Phosphorous	3.11	0.344	2.9
Phosphorous	4.02	-0.096	7.6
White Crappie			
Zooplankton	2.28	0.507	--
Zooplankton + Phosphorous	2.38	0.461	1.6
Zooplankton + Turbidity	2.39	0.457	1.6
Zooplankton + Turbidity + Phosphorous	2.49	0.412	2.9
Turbidity	3.38	-0.087	7.7

Table 2: Strain-specific multiple regression models for final weight of juvenile black, blacknose, and white crappies in experimental ponds as determined by Δ AIC model selection. Available variables for inclusion were total zooplankton density ($\# \cdot L^{-1}$), turbidity (NTU), and phosphorous ($\mu g \cdot L^{-1}$).

Figures

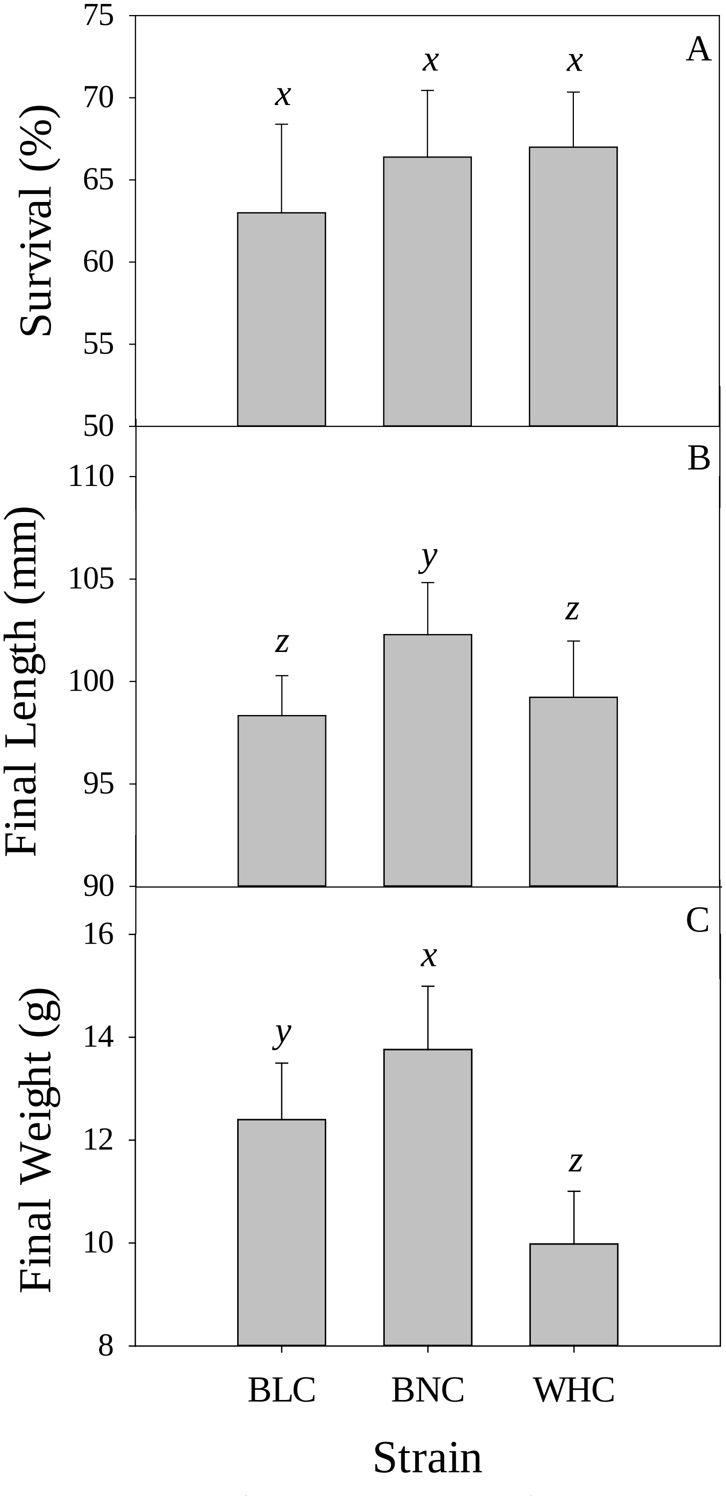

Figure 1. Mean survival (A), final length (B), and final weight (C) of juvenile black (BLC), blacknose (BNC), and white (WHC) crappies across all ponds. Error bars represent standard errors and lowercase letters indicate significant differences among strains.

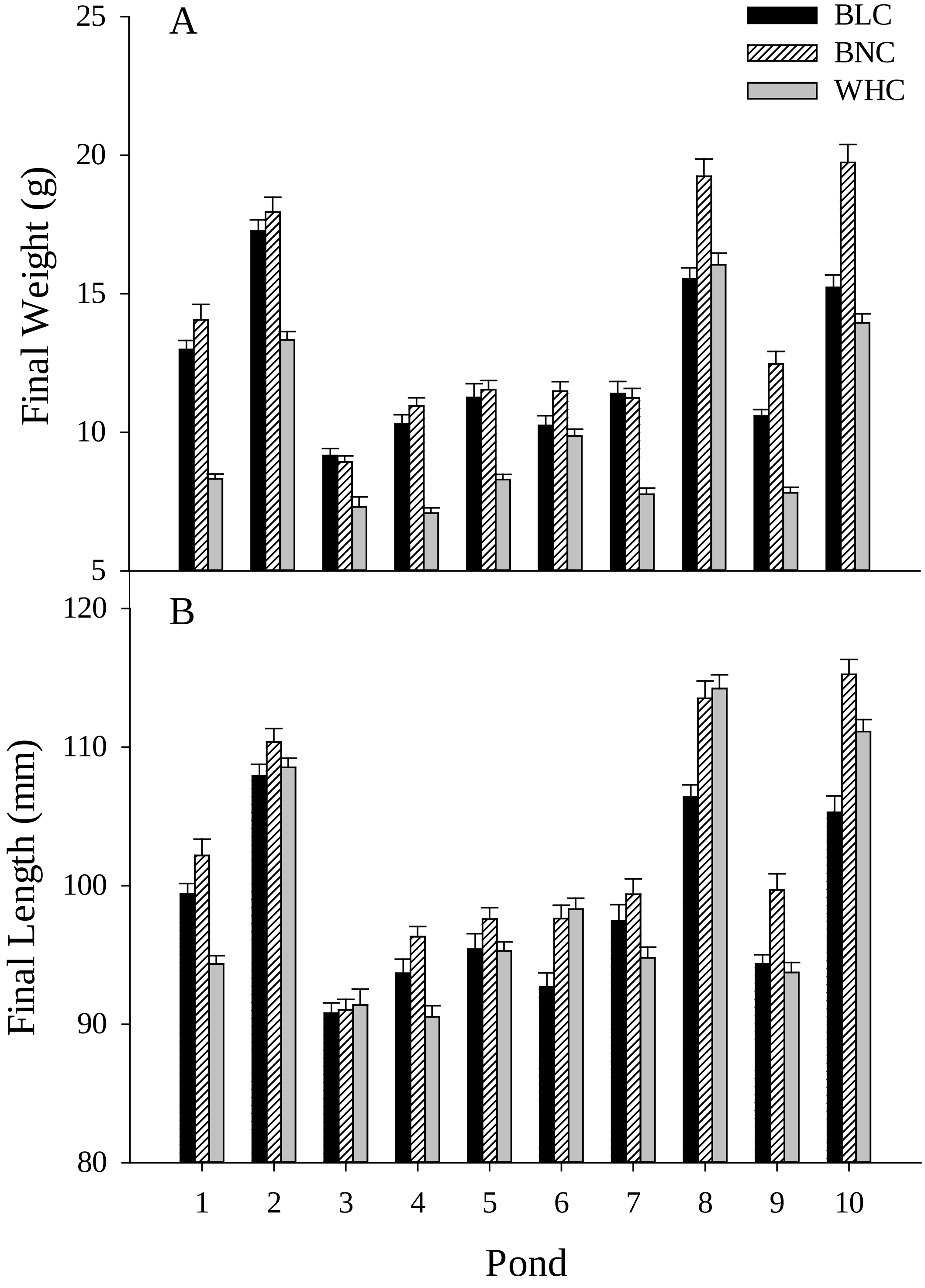

Figure 2. Final length (A) and weight (B) of juvenile black (BLC), blacknose (BNC), and white (WHC) crappies stocked into each of ten experimental pond after three months. Error bars represent standard errors.

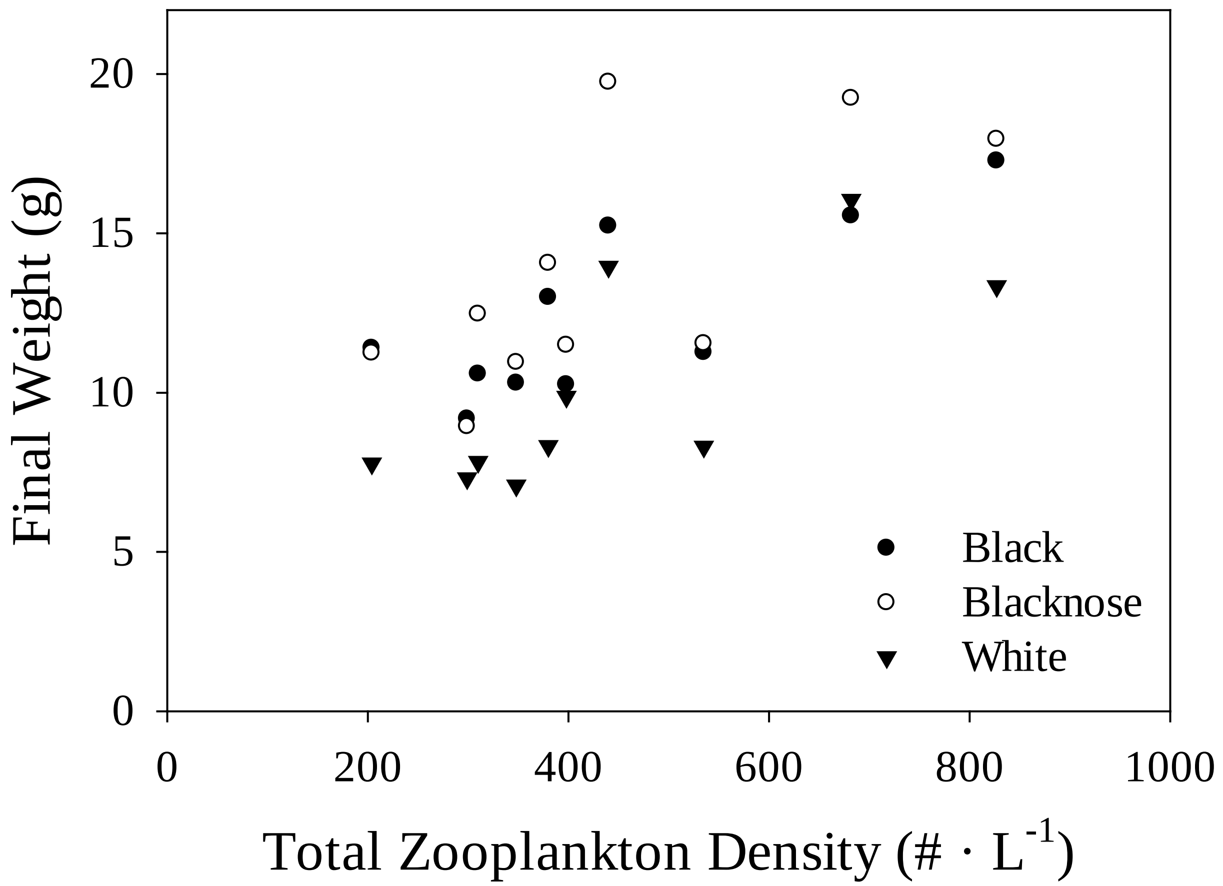

Figure 3. Relationship between final weight (g) and total zooplankton density (# · L^{-1}) for black, blacknose, and white crappies.

Chapter 2: Bioenergetic differences among juvenile black, white, and blacknose crappies

Abstract

Black and white crappies are two closely related species that differ in several life history characteristics. Blacknose crappie, a phenotypic variant of black crappie, have been used for evaluating stocking success and anecdotally have greater growth and survival in rearing environments. We evaluated effects of temperature on bioenergetics parameters of black, white, and blacknose crappies by conducting respirometry (computerized intermittent-flow) and consumption and growth experiments. No strain-temperature interactions were detected for any of the physiological response variables measured, suggesting a lack of differential thermal adaptations among the strains. No differences in metabolic rates were observed among the strains, but faster growth was observed for blacknose crappie compared to black and white crappies. Black and blacknose crappies had greater maximum food consumption rates than white crappie. Blacknose crappie also exhibited faster relative growth rates and higher food conversion efficiencies than black and white crappies. We believe these differences stem from the unique rearing history of blacknose crappie over the past several decades. Our results indicated ontogenetic shifts in thermal optima for juvenile crappies when compared to previous studies with adult white crappie, with maximum juvenile growth occurring at higher temperatures.

Introduction

Temperature is among the most influential factors on the survival and growth of fishes and has been shown to significantly affect behavior, growth rates, and physiological demands of several species, including crappie (Fry et al. 1971; Hayward and Arnold 1996; Taniguchi et al. 1998). Physiological adaptations have been documented among conspecifics from different latitudes for a number of freshwater species, including walleye (*Stizostedion vitreum*, Galarowicz and Wahl 2002) and muskellunge (*Esox masquinongy*, Clapp and Wahl 1996). Temperature-dependent responses of physiological characteristics (e.g. thermal tolerance and metabolic rate) have also been used to compare habitat use and performance of closely related species in sympatry, such as bluegill (*Lepomis machrochirus*) and longear sunfish (*L. megalotis*) (Dent and Lutterschmidt 2003). Latitudinal variation in growth rates has been explained in fish by two competing hypotheses: local thermal adaptation (Levinton 1983) and countergradient variation in growth (Conover and Present 1990). As the result of widespread introductions, black crappie *Pomoxis nigromaculatus* and white crappie *P. annularis* are broadly distributed across North American latitudes and thermal regimes but little is known about the differential effects of temperature on the two species.

Although supplemental stocking programs are not a historically popular management technique for crappies, successful applications in larger systems with poor recruitment are becoming increasingly common. Because of the need to identify stocked individuals in order to evaluate the success of stocking programs, several agencies (e.g. Tennessee Wildlife Resources Agency, TWRA; Illinois Department of Natural Resources, IDNR) have been using blacknose black crappie (hereafter blacknose crappie) for stocking programs. Blacknose crappie are a phenotypic variant of black crappie, exhibiting a genetically dominant predorsal black stripe

(Gomelsky et al. 2005). Although this phenotype occurs naturally (Buchanan and Bryant 1973), it has been cultured in hatcheries and lakeside rearing ponds since the late 1980s, with original brood fish coming from Beaver Lake, Arkansas due to a naturally high occurrence of the trait in that system (Isermann et al. 2002; M. Smith, TWRA, personal communication). Continued use of blacknose crappie in stocking programs has also stemmed from anecdotal evidence that they grow, handle, and survive better than other crappies in hatcheries and rearing ponds (M. Smith, TWRA, personal communication).

There is currently a lack of direct growth comparisons between juvenile black and white crappies and only one previous study comparing the two with blacknose crappie. Juvenile blacknose crappie outgrew black and white crappies in length and weight and black crappie outgrew white crappie in weight in experimental ponds (Gring and Wahl in review). Other studies comparing early growth of crappies have found either no growth difference between juvenile black and white crappies (Spier and Heidinger 2002) or that white crappie outgrew black crappie in length (Travnichek et al. 1996). Given that blacknose crappie originally came from Arkansas and were subsequently reared in Tennessee for several decades, there is potential for differences in thermal adaptations between these stocked fish and resident black and white crappies in systems where they have been introduced (e.g. Illinois lakes). Improving our knowledge of growth differences among juvenile black, white, and blacknose crappie would have important management implications, as crappie populations are notorious for exhibiting undesirable growth rates in many fisheries, failing to meet anglers' expectations.

Suboptimal growth rates in crappies have been explained by overcrowding (e.g. Boxrucker 2002; Pope et al. 2004) , inadequate prey resources (e.g. Bunnell et al. 2003; Tuten et al. 2008), high summer water temperatures (e.g. Ellison 1984; Hayward and Arnold 1996), and heredity (Buck and Hooe 1996; Travnichek et al. 1996; Miller et al. 2008), as well as other environmental factors. A combination of "boom-bust" recruitment patterns and high fecundity can lead to overabundant year-classes in crappie populations. In systems lacking a sufficient forage base, whether an issue of quantity or quality of prey, suboptimal growth rates are often the result. Combined effects of inadequate prey resources and adverse temperatures have been linked to poor growth in adult black (Ellison 1984) and white crappies (Michaletz et al. 2012).

Differences in adult growth rates have also been documented between black and white crappies (Buck and Hooe 1996; Jackson and Hurley 2005) with white crappie typically exhibiting greater lengths-at-age than black crappie. The effect of heredity on growth of crappies has been examined, specifically growth rates of parental black and white crappies with their hybrid offspring. F_1 hybrids outgrew both parental species in ponds (Buck and Hooe 1996) and lakes (Travnichek et al. 1996) in their first-year and have been shown to inflate back-calculated lengths for black crappie in Minnesota lakes (Miller et al. 2008). For management purposes, black and white crappies are frequently treated as a single entity due to issues of hybridization and difficulties distinguishing the two at the larval and juvenile stages. In studies focusing on subadult crappies, the two species are typically pooled, resulting in a lack of information directly comparing black and white crappies with respect to basic biological characteristics.

Bioenergetics models (BEMs) are commonly used to investigate differences between species or stocks, especially with respect to differing effects of environmental factors, such as temperature, that affect fish growth, consumption, and metabolism (Kitchell et al. 1977; Bevelhimer et al. 1985; Clapp and Wahl 1997; Galarowicz and Wahl 2003). Bioenergetics models are mass-balance equations used to represent resource allocation and energy flow through an organism (Kitchell et al. 1974). In order to construct a BEM for a species or stock, laboratory experiments must be conducted to calculate the various parameters that make up the model. While a BEM for adult white crappie has been developed (Bajer et al. 2004; Bajer and Hayward 2006), no such model exists for black crappie or juvenile crappie of either species. When a complete BEM does not exist for a species, parameters are often borrowed from similar species to create a model, resulting in inaccurate BEMs being used to manage fish populations (Ney 1993; Chipps and Wahl 2008). Furthermore, BEM parameters are often estimated over a limited size range and then applied to other life stages even though ontogeny often affects physiological characteristics. Knowledge of physiological characteristics of black, blacknose, and juvenile white crappies will improve our understanding of crappie energetics.

The first objective of our study was to compare a suite of physiological characteristics among black, white, and blacknose crappies (hereafter referred to as different strains for ease of communication, white crappie are a different species) across a range of temperatures. We were especially interested in temperature-strain interactions for metabolic rate, growth, maximum daily food consumption, and food conversion efficiency to assess differences in thermal adaptations among the strains. Our second objective was to compare the parameters of juvenile crappies with those previously published for adult white crappie to evaluate ontogenetic differences in thermal optima.

Methods

Fish Sources and Maintenance

For all laboratory experiments, age-0 crappies were produced in 0.4-ha rearing ponds at the Sam Parr Biological Station (Kinmundy, IL) during the spring of 2013. All brood fish were collected in the late winter and early spring (late February-early March) of 2013 via alternating current (AC) electrofishing and trap netting from Weldon Springs Lake (Clinton, IL) and Dawson Lake (Dawson, IL) for black crappie (BLC) Lake Paradise (Mattoon, IL), Forbes Lake (Kinmundy, IL), and Sam Dale Lake (Johnsonville, IL) for white crappie (WHC) and Clinton Lake (Clinton, IL) for blacknose crappie (BNC) and placed into rearing ponds during late February and early March. For black and white crappies, only lakes containing single species of crappie were used. In July and August of 2013, all experimental fish were collected from ponds via seines or modified mini-fyke nets and maintained in the laboratory for at least 14 days prior to any further experiments. During this 14-day period, fish were held in groups of approximately 20 in 114-L aquaria at 18-22˚ C (ambient lab temperature) and fed frozen brine shrimp to satiation every other day.

Consumption and Growth Experiment

Prior to consumption experiments, all fish were acclimated to experimental temperature, photoperiod, and prey source (live California blackworms, *Lumbriculus variegatus*) for an additional 14 days. Temperature changes between experiments did not exceed 2˚ C per day, and no fish were reused during the study. Ten juvenile crappies of each strain were held individually in 35-L aquaria at five different temperatures (10, 15, 20, 25, and 30˚ C), held constant in an environmental control chamber. Photoperiod was also held constant at 10 h light/14 h dark for 10 and 15˚ C and 12 h light/12 h dark at 20, 25, and 30˚ C. Experiments were conducted from August 2013 to February 2014 and experimental temperatures followed ambient water temperatures to avoid confounding seasonal effects (Chipps et al. 2000, Chipps and Wahl 2008). Initial wet weight (g) and total length (mm) were determined for each fish after a 24-hour fasting period. Known weights of live California blackworms were fed ad libitum to each fish and any uneaten prey were siphoned from the tanks the following day, blotted dry, weighed, and then subtracted from the initial weight to estimate of daily food consumption. Following the 14-day trial, final wet weight and total length were determined for each fish after a 24-hour fasting period. Maximum daily food consumption (C_{max}), relative growth rate (RGR), and food conversion efficiency (FCE) were calculated for each strain at each experimental temperature. C_{max} was determined as the grams of food consumed per mean weight of the individual fish per day ($g \cdot g^{-1} \cdot day^{-1}$), RGR as weight gained per day relative to the mean weight of the individual fish ($g \cdot g^{-1} \cdot day^{-1}$), and FCE as the change in fish weight per gram of food consumed ($g \cdot g^{-1}$).

Respirometry Experiment

As in the consumption experiments, all fish were acclimated to experimental temperatures and photoperiods for at least 14 days prior to respirometry trials, with changes in temperature not exceeding the rate of 2˚ C per day. Fish were held individually in 35-L aquaria and fasted for 24 hours prior to trials to minimize effects of specific dynamic action on measurements (Brett 1962; Murchie et al. 2011). Standard metabolic rate (SMR) was calculated for a minimum of 10 juvenile black, white, and blacknose crappies at six different temperatures (5, 10, 15, 20, 25, and 30˚ C) using a computerized intermittent-flow respirometry system consisting of four 135 mL glass chambers connected to fiber optic oxygen sensors via recirculating pumps (Loligo Systems, Tjele, Denmark). Respirometry trials lasted for 20 hours, consisting of sequential loops ranging from 15 to 54.5 minutes. Each loop was broken down into a 180-second flush period to maintain respirometer water quality, followed by a 90-second waiting period and then a measurement period for the remainder of the loop (10.5 min at 25 and

30˚ C, 12 min at 20˚ C, 15 min at 15˚ C, 20-30 min at 10˚ C, and 40-50 min at 5 ˚ C). Measurement periods were adjusted based on water temperature and fish size to maximize reading accuracy while still maintaining sufficient oxygen concentrations. Water in each chamber was continuously recirculated over the oxygen sensor during the measurement period to ensure adequate mixing and accurate readings. Oxygen consumption rate (MO_2, mg $O_2 \cdot kg^{-1} \cdot h^{-1}$) was calculated after each measurement period as a function of the change in oxygen concentration ($\alpha = \Delta O_{2saturation} / \Delta t$), the volume of the chamber ($V_{chamber}$), the oxygen solubility at the current temperature and barometric pressure (β), and the mass of the fish (M_b):

$$MO_2 = \alpha V_{chamber} \beta M_b^{-1}$$

MO_2 and the coefficient of determination (r^2) of MO_2 during each measurement period were calculated and recorded using AutoResp software (Version 1.4, Tjele, Denmark). Blanks (chambers containing no fish) were run for 1.5 hours before and after each trial to get an estimate of background microbial respiration for a given chamber and trial. The average change in oxygen of both blanks (representing the average blank value in the middle of the trial) was then converted to an MO_2 value based on fish mass in the corresponding trial and was subtracted from the MO_2 estimate obtained for that fish (Facey and Grossman 1990). The first three hours of each 20-hour trial were excluded from analysis because MO_2 values for fish were noticeably elevated due to handling stress (Herrmann and Enders 2000). Standard metabolic rate (SMR) for each fish was then calculated as the average of the six smallest MO_2 values (Murchie et al. 2011) with an $r^2 \geq 0.75$.

Data Analysis

Even though there were no differences in mean size among the strains, all metabolic rates were rescaled to the median mass of all experimental fish (1.56 g) using common allometric scaling equations because of the importance of mass when calculation metabolic rate as a function of mass (e.g. MO_2, Gillooly et al 2001; Dwyer et al. 2014). Following Dwyer et al. (2014), metabolic rates were rescaled using the following equation:

$$MO_{2,1.56} = MO_{2,obs}\left(\frac{1.56}{\mathrm{M_{obs}}}\right)^{\beta}$$

where the standardized metabolic rate at 1.56 g ($MO_{2,1.56}$) is a function of the observed metabolic rate of a given fish ($MO_{2,obs}$), the median mass used for standardization (1.56 g), the mass of the individual fish (M_{obs}), and the mass-specific allometric scaling exponent (β). We selected the common scaling exponent of β = -0. 247 for all strains (Downs et al. 2008, Dwyer et al. 2014). Although some recent examples suggest variation in β among taxa (Glazier 2005, Killen et al. 2010), we were unable to estimate strain-specific scaling exponents due to insufficient size ranges. Our response variable used for analysis was the mass-standardized standard metabolic rate ($SMR_{1.56}$).

Prior to analysis, $SMR_{1.56}$ was $\log_{10}$ transformed to normalize the residuals. Following transformation, all response variables ($SMR_{1.56}$, C_{max}, RGR, and FCE) were examined for each strain at each temperature for outliers using Grubbs' outlier test ($\alpha = 0.05$) and examination of box plots and all outliers were removed from further analysis. Inclusion or exclusion of these outliers did not change the interpretation of our results. For our respirometry experiments, length of measurement periods were adjusted based on temperature and fish size for 5-20 ˚ C in order to maximize oxygen consumption (and subsequently r^2 values) without depleting oxygen levels to the point where they would affect the fish. Adjustments at 10˚ C were inadequate and our values obtained at 10° C were less reliable than those obtained at other temperatures as indicated by lower r^2 values. We chose to exclude this temperature from our analysis even though our overall ANOVA interpretation did not differ whether those values were included or not. These changes to our data were made to improve the accuracy of our parameter estimates for future application to bioenergetics models. Two-way analysis of variance (ANOVA) was used to evaluate strain and temperature effects on $SMR_{1.56}$, C_{max}, RGR, and FCE. Following the overall ANOVA, mean comparisons of $SMR_{1.56}$, C_{max}, RGR, and FCE were made among strains using Fisher's protected least significant difference (LSD) test because we were only comparing three strains.

Results

Consumption Experiment

Following the removal of outliers (N = 10 across all strains and temperatures), all strain-specific response variables were estimated based on 7-10 individuals at each temperature. Average initial fish mass (mean ± SE) did not differ by strain (ANOVA: $F_{2,145} = 0.237$, $P = 0.79$) or temperature ($F_{4,145} = 0.159$, $P = 0.96$) and was 1.61 ± 0.11 g for black crappie, 1.68 ± 0.11 g for blacknose crappie, and 1.62 ± 0.11 g for white crappie. No strain by temperature interactions were detected for C_{max} ($F_{8,118} = 0.574$, $P = 0.80$), RGR ($F_{8,118} = 0.483$, $P = 0.87$), or FCE ($F_{8,118} = 1.526$, $P = 0.16$) so we removed the interaction terms from our models and compared response variables among strains across all temperature and not within each temperature. Maximum food consumption increased with temperature (ANOVA: $F_{4,126} = 446.2$, $P < 0.0001$) and ranged from $0.032\ g \cdot g^{-1} \cdot day^{-1}$ (WHC) at 10° C to $0.278\ g \cdot g^{-1} \cdot day^{-1}$ (BNC) at 30° C (Table 3, Figure 4A). Strain ($F_{2,126} = 5.42$, $P = 0.006$) significantly affected C_{max} with black and blacknose crappies consuming more than white crappie, but no differences between black and blacknose crappies (Figure 2A). Relative growth rate also increased with temperature (ANOVA: $F_{4,126} = 289.26$, $P < 0.0001$) and ranged from $0.006\ g \cdot g^{-1} \cdot day^{-1}$ (WHC) at 10˚ C to $0.068\ g \cdot g^{-1} \cdot day^{-1}$ (BNC) at 30˚ C (Table 3, Figure 4B). Relative growth rate was also affected by strain (ANOVA: $F_{2,126} = 5.52$, $P = 0.005$) with blacknose crappie growing faster than both black and white crappies (Figure 5B). Food conversion efficiency was calculated as a function of consumption and growth and ranged from $0.169\ g \cdot g^{-1}$ (15˚ C, BLC) to $0.29\ g \cdot g^{-1}$ (25˚ C, WHC) (Table 3, Figure 5C). Significant strain (ANOVA: $F_{2,126} = 7.26$, $P = 0.001$) and temperature ($F_{4,126} = 16.04$, $P < 0.0001$) effects were detected for FCE with blacknose crappie converting food more efficiently than black crappie and white crappie and no differences between black and white crappies (Figure 5C). The effects of temperature on FCE were slightly different than C_{max} and RGR. Food conversion efficiency increased with temperature but declined between 25 and 30˚ C. Although no strain-temperature interactions were detected, strain differences were more apparent at lower temperatures for C_{max}, RGR, and FCE (Figure 4). The most apparent of these trends was FCE, with blacknose crappie exhibiting noticeably higher FCE than black or white crappies at 10-20˚ C with less separation observed at 25 and 30˚ C (Figure 4C).

Respirometry Experiment

Following the removal of outliers (N = 2 across all strains and temperatures), $SMR_{1.56}$ was determined for each strain based on 8-13 individuals. As in the consumption and growth experiments, inclusion of these data in our analyses did not change the interpretation of our results. Average fish mass (mean ± SE) did not differ by strain (ANOVA: $F_{2,126} = 0.076$, $P = 0.927$) or temperature ($F_{2,126} = 0.021$, $P = 0.999$) and was 1.62 ± 0.09 g for black crappie, 1.65 ±

0.09 g for blacknose crappie, and 1.65 ± 0.10 g for white crappie. Metabolic rates ranged from 44.3 mg $O_2 \cdot kg^{-1} \cdot h^{-1}$(WHC) at 5˚ C to 212 mg $O_2 \cdot kg^{-1} \cdot h^{-1}$(BLC and BNC) at 30˚ C and were positively related to temperature (Table 3, Figure 6). The strain-temperature interaction was non-significant ($F_{8,140}$ = 0.422, P = 0.9063) so the term was removed from the model. There was no observed strain effect on $SMR_{1.56}$ (ANOVA: $F_{2,145}$ = 0.62, P = 0.54) with no mean separations among the strains. Overall strain averages (mean ± SE) were 124.8 ± 4.65 mg $O_2 \cdot kg^{-1} \cdot h^{-1}$ for black crappie, 124.2 ± 4.57 mg $O_2 \cdot kg^{-1} \cdot h^{-1}$ for blacknose crappie, and 121.4 ± 4.55 mg $O_2 \cdot kg^{-1} \cdot h^{-1}$ for white crappie. Across all strains, $SMR_{1.56}$ was significantly affected by temperature (ANOVA: $F_{4,145}$ = 472.66, < 0.0001) and increased significantly between each temperature from 5-30˚ C.

Discussion

Temperature is a major driver in growth-related physiological responses of fishes (Fry et al. 1971). For juvenile black, white, and blacknose crappies, maximum food consumption increased from 5 through 30˚ C. For adult white crappie fed live fathead minnows, consumption increased from 18 to 24˚ C and then declined by two-thirds at 27˚ C (Hayward and Arnold 1996). For juveniles of all three strain, we observed a 26-30% increase in food consumption between 25 and 30˚ C which was also accompanied by faster growth rates, suggesting optimal temperatures for growth and consumption exceeded 25˚ C. With a decline in prey size relative to the size of the predator, growth efficiency is expected to decrease as crappie grow until ontogenetic diet shifts take place (Ellison 1984). Ontogenetic shifts in thermal preferenda have been observed in several cool- and coldwater fish species, with younger fish typically preferring warmer temperatures than conspecific adults (McCauley and Huggins 1979). In post-smolt Atlantic salmon, optimal temperatures for feed conversion efficiency decrease with size (70-150 g to 170-300 g), while optimal temperatures for growth increase across the same size classes (Handeland et al. 2008). Optimal temperature has also been suggested to decline with maturation in Chinook salmon, as thermal preferenda has been observed to shift during smoltification (Sauter et al. 2001).

High summer water temperatures have been implicated as a cause of suboptimal growth in black (Ellison 1984) and white crappies (Hayward and Arnold 1996, Hale 2001; Michaletz et al. 2012). Increased metabolic demand combined with inadequate prey resources and habitat-limiting summer stratification can result in slow growth rates and increase mortality in adult crappies. Black crappie greater than 200 mm, when unable to switch to piscivory, suffered from slow growth rates and high mortality rates during the summer in a Nebraska lake (Ellison 1984). When coupled with diet data, these high summer mortality rates suggested an inability of larger black crappies to meet their metabolic requirements. Similarly, decreased or negative growth rates have been observed in adult white crappie in Missouri systems with summer temperatures exceeding 27˚ C and a lack of available prey fish (Michaletz et al. 2012). For age-0 white crappie, we found relative growth rate to increase through 30˚ C when fed ad libitum rations. The increase in growth rate between 25 and 30˚ C slowed, suggesting an asymptote in growth around 30˚ C. Food conversion efficiency peaked at around 25˚ C and maximum daily food consumption continued increasing through 30˚ C. Positive growth rates for juveniles above 27˚ C contrast with previous laboratory experiments with adult white crappie, highlighting differences in energetic constraints across size classes. High summer water temperatures may not be as consequential to age-0 crappies as they are for older conspecifics. For adult crappie, high-quality prey items can be limited during summer months of lake stratification due to low benthic dissolved oxygen levels. If, however, age-0 fish have access and utilize alternate high-quality food sources (e.g. dipteran larvae, annelids, mysid shrimp, etc.), growth rates have the potential to increase at summer water temperatures unfavorable at later life stages.

Differences in physiological responses to different thermal environments have been shown between closely related species, as well as among isolated populations of conspecifics. At extreme temperatures, walleye populations exhibit latitudinal adaptations in growth, with southern stains growing faster at 25˚ C and northern strains growing faster at 5˚ C (Galarowicz and Wahl 2003). Differences in food consumption and metabolic rate were also observed at temperature extremes. Southern populations exhibited increased metabolic demands at higher temperatures that were compensated for by increased food consumption, resulting in faster growth rates. Although temperature significantly affected a suite of physiological responses in juvenile crappies, it did not differentially affect black, white, or blacknose crappies. The lack of temperature-strain interactions for metabolic rate, maximum food consumption, relative growth rate, and food conversion efficiency suggests a lack of differential thermal adaptation among the strains. Although temperature-strain interactions were not significant, strain differences in C_{max}, RGR, and FCE were more apparent at lower temperatures (10-20˚ C). Differences in energetic responses of black and white crappies to temperature have not been previously studied in the laboratory. Cold acclimation strategy was examined in the laboratory and found to be similar between black and white crappies in terms of heart hypertrophy, but differed significantly in enzymatic and swimming activity between the two species (Tschantz et al. 2002). Despite these differences in enzymatic response to temperature acclimation between black and white crappies, we did not detect differences in metabolic rate between the two. Overall, temperature was extremely influential on the suite of physiological characteristics we measured, highlighting the importance of temperature on energetics of juvenile crappies.

Although no interactions with temperature were observed among the strains, we did find some differences among strains in maximum food consumption, relative growth rate, and food conversion efficiency, but not metabolic rate. Both black and blacknose crappies consumed more than white crappie. This could be the related to differences in adaptations to prey between the species. Macroinvertebrates are commonly a more important food source for juvenile black crappie, as white crappie will often switch from zooplankton directly to fish as they grow (e.g. Ellison 1984). The differences in consumption between species found in our study may differ with zooplankton prey. Blacknose crappie exhibited superior growth characteristics, both in relative growth rate and food conversion efficiency, over both black and white crappies. The faster growth rate and higher food conversion efficiency of blacknose crappie compared to black and white crappies is consistent with growth of the three strains in ponds (Gring and Wahl in review). In a common garden pond experiment, faster growth of age-0 blacknose crappie was observed than for black and white crappies in both length and weight. However, we do not believe these differences to be related to differences in thermal adaptation, but rather other unique aspects of their rearing history.

Since the late 1980s, blacknose crappie have been produced in hatcheries and lakeside rearing ponds for stocking programs. Selective pressures on fish from hatchery or other rearing environments have been examined in numerous studies (Kinghorn 1983; Huntingford 2004). Hatchery fish have frequently been observed to be more aggressive than their wild counterparts, which can be energetically beneficial or detrimental depending on the availability of prey (Swain and Riddell 1990). Effects of the hatchery environment have been shown to affect risk-taking in rainbow trout (*Oncorhynchus mykiss*, Pottinger and Carrick 2001) as well as stress response and behavioral differences (e.g. aggression) in common carp (*Cyprinus carpio*, Tanck et al. 2002). Differences in risk-taking and aggression (or other behavioral characteristics) between blacknose crappie and other crappies could result in the differences in food consumption, and subsequently growth rates. These behavioral differences could benefit blacknose crappie in some management scenarios, such as rearing ponds and hatcheries, where food is abundant. In larger natural systems, however, where food is spatially and temporally dispersed, such differences could be energetically costly.

In fish, food conversion efficiency is influenced by many factors including temperature (Handeland et al. 2008), fish size (Handeland et al. 2008), food quality (Winfree and Stickney 1981), ration level (Wurtsbaugh and Davis 1977), latitudinal adaptations (Jonassen et al. 2000), and other genetic characteristics (Venugopal et al. 2004). The increased food conversion efficiency of blacknose crappie over black and white crappies suggest physiological, and not just behavioral, differences among strains. Behavioral differences could account for differences in consumption rate and growth, but not in the efficiency by which consumed calories are converted to somatic tissue. Juvenile crappies are known to exhibit low survival and high handling mortality in aquaculture settings. Handling mortality of fingerling black crappie (25-35 mm) was 80-100% just 3 hours after harvesting rearing ponds (Smeltzer and Flickinger 1991). In contrast, relatively successful handling and stocking of large fingerling black crappie (> 76 mm) with high estimated short-term post-stocking survival (70-100%) has been observed (Myers and Rowe 2001). If handling mortality in aquaculture settings is size-dependent, handling could be a strong selective pressure on growth of cultured crappies. Selection would favor larger individuals at the time of pond harvest, resulting in better survival of faster growing individuals.

For other fish species, intentional selection for faster growth rates has been successful in hatchery environments in as few as three generations (e.g. Kincaid et al. 1977). Although the size of crappies in rearing ponds is highly density-dependent, significant variability in size does occur (Myers and Rowe 2001) making selection for larger individuals plausible.

Our study highlights ontogenetic shifts in thermal optima for at least white crappie as well as differences among black, white, and blacknose crappies in a suite of physiological characteristics. Despite a significant increase in metabolic rate and decrease in food conversion efficiency from 25 to 30˚ C, relative growth rate still increased for all strains, suggesting that consumption rates increased enough to offset metabolic demands at temperatures exceeding 25˚ C. Our results can be used to improve the accuracy of crappie bioenergetics models for juvenile fish. When a complete bioenergetics model does not exist for a species or stock, parameters are borrowed from other species, compromising the accuracy of model outputs (Ney 1993; Chipps and Wahl 2008). Incorporation of our strain-specific parameters for juvenile crappie in bioenergetics models can improve estimates of consumptive demand on prey resources, as well as species- or strain-specific growth rates. We found a lack of evidence to support differences in thermal adaptations among the strains, but suspect multi-decadal production of blacknose crappie in hatcheries and rearing ponds have resulted in adaptations to rearing environments, potentially effecting growth characteristics. Blacknose crappie may provide a better alternative for culture and stocking, given the size-dependence of poststocking survival in crappies. These relationships should be evaluated further at larger spatial scales and across different environmental conditions to elucidate differences between blacknose and black crappies. Hatchery adaptations often have negative consequences in natural systems, such as decreased survival of hatchery-produced fish (Olla et al. 1998) and negative impacts on native conspecifics (Koppelman and Phillipp 1986) that need to be assessed.

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Tables

Strain		Temperature (˚ C)					
		5	10	15	20	25	30
C_{max} (g ·g^{-1} · day^{-1})							
BNC	A	--	0.047 (10)	0.074 (9)	0.147 (9)	0.215 (8)	0.278 (9)
BLC	A	--	0.039 (9)	0.069 (10)	0.157 (9)	0.205 (9)	0.267 (7)
WHC	B	--	0.032 (8)	0.058 (10)	0.125 (7)	0.205 (9)	0.259 (10)
RGR (g ·g^{-1} · day^{-1})							
BNC	A	--	0.018	0.016	0.039	0.059	0.068
BLC	B	--	0.007	0.012	0.032	0.057	0.065
WHC	B	--	0.006	0.010	0.028	0.059	0.064
FCE (g · g^{-1})							
BNC	A	--	0.247	0.211	0.266	0.278	0.244
BLC	B	--	0.182	0.169	0.191	0.280	0.241
WHC	B	--	0.186	0.180	0.217	0.290	0.247
$SMR_{1.56}$ (mg O_2 · kg^{-1} · h^{-1})							
BNC	A	45.8 (11)	--	56.2 (10)	134 (9)	174 (10)	212 (10)
BLC	A	46.9 (10)	--	56.2 (9)	118 (8)	176 (11)	212 (10)
WHC	A	44.3 (11)	--	59.9 (9)	121 (11)	161 (13)	208 (10)

Table 3. Laboratory derived values of maximum daily food consumption (C_{max}), relative growth rate (RGR), food conversion efficiency (FCE), and mass-standardized standard metabolic rate ($SMR_{1.56}$) for juvenile black (BLC), blacknose (BNC), and white (WHC) crappies at a range of temperatures. The absence of a shared letter (A or B) between strains indicates a statistically significant difference and the number in parentheses following estimates represents the sample size used in that calculation. Sample sizes for RGR and FCE are the same as C_{max} for the corresponding strain-temperature combination.

Figures

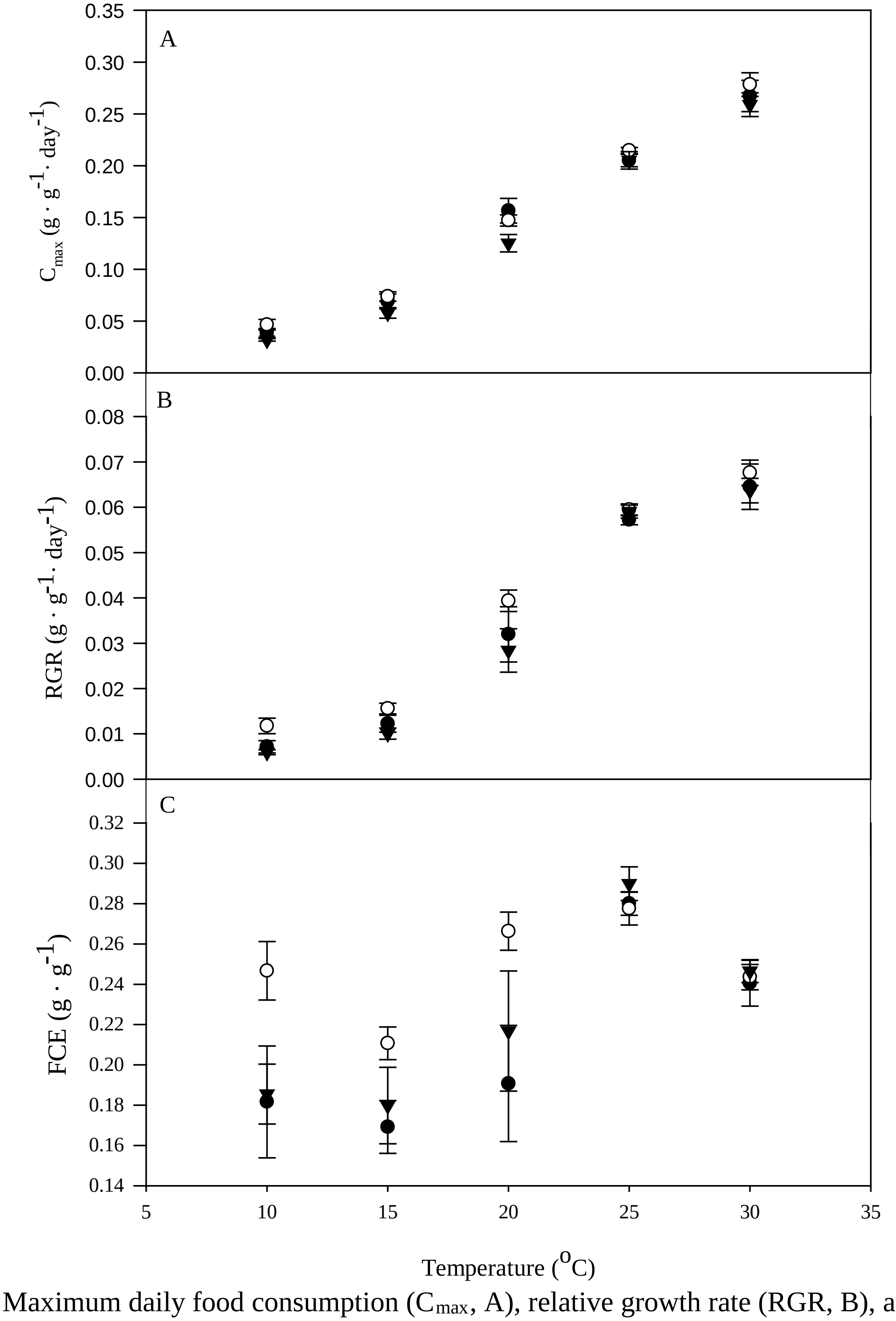

Figure 4. Maximum daily food consumption (C_{max}, A), relative growth rate (RGR, B), and food conversion efficiency (FCE, C) of black (filled circles), blacknose (open circles), and white (filled triangles) crappies at each experimental temperature. Error bars represent standard errors.

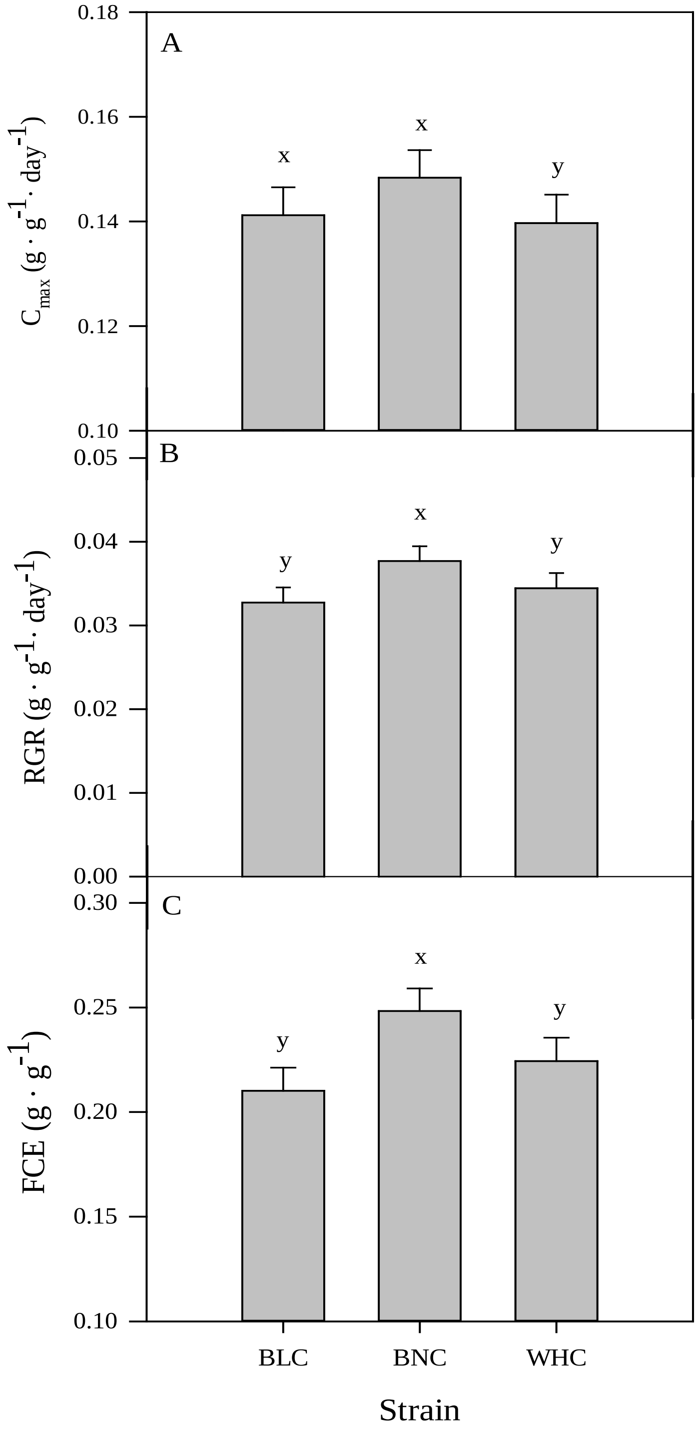

Figure 5. Mean maximum food consumption (A), relative growth rate (B), and food conversion efficiency (C) of juvenile black (BLC), blacknose (BNC), and white (WHC) crappies across all temperatures. Error bars represent standard errors and lowercase letters indicate significant differences among strains.

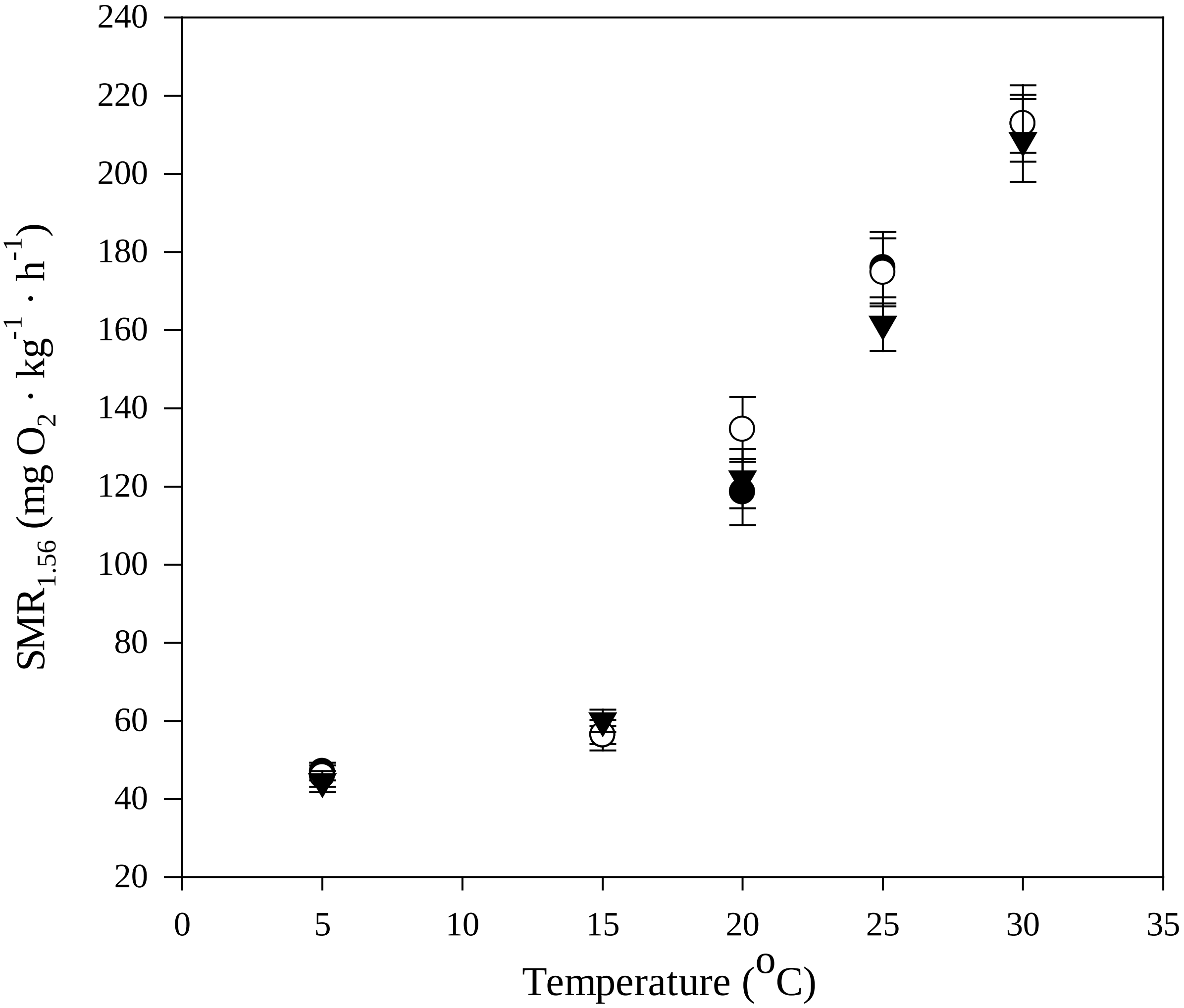

Figure 6. Mass-corrected standard metabolic rate ($SMR_{1.56}$,) of black (filled circles), blacknose (open circles), and white (filled triangles) crappies at each experimental temperature. Error bars represent standard errors.

Conclusions

Black and white crappies are two closely related species that differ in several life history characteristics. Across North America, recent crappie stocking programs have been met with varying success with survival often relating to size at stocking. Several management agencies have observed differences in growth and survival between black and blacknose crappies produced in hatcheries and lakeside rearing ponds although no formal comparisons had been made prior to my studies. I examined growth differences among juvenile black, white, and blacknose crappies via controlled studies at multiple spatial scales. In ponds set up using a common garden approach, blacknose crappie outgrew black and white crappies in both length and weight after a three month growth period. Juvenile black crappie also outgrew white crappie in weight but not length, which may be attributable to slight differences in morphology between black and white crappies (black crappie are typically deeper bodied). Ponds with high zooplankton density, low macroinvertebrate density, and low vegetation density were associated with the highest growth rates of all three crappie strains and my analyses indicated possible indirect effects of turbidity on the growth of black and blacknose crappies but not white crappie. No differences in survival were detected among the stains or between ponds which indicates that poststocking survival may be influenced more by size at stocking than environmental variables since all fish were stocked at the same size.

Temperature is one of the most influential factors affecting physiological characteristics in fishes, such as growth. Prior to my study, little previous research existed examining differential effects of temperature on black and white crappies and no previous studies had compared the two with blacknose crappie. I compared a suite of physiological characteristics (metabolic rate, maximum food consumption, relative growth rate, and food conversion efficiency) among juvenile black, white, and blacknose crappies across a range of temperatures in the laboratory. For all parameters, I did not detect strain-temperature interactions, suggesting a lack of differential thermal adaptations among black, white, and blacknose crappies. Across all temperatures, no differences among strains were detected for metabolic rate but black and blacknose crappies had higher maximum food consumption rates than white crappie and blacknose crappie exhibited higher relative growth rates and food conversion efficiencies than both black and white crappies. When compared to previous research on adult white crappie, juvenile white crappie showed ontogenetic differences in thermal optima for growth characteristics, with optima occurring at higher temperatures. Juvenile crappie bioenergetics models should be improved by including the strain-specific parameters determined in my study, resulting in more accurate estimates of growth rates, consumptive demand on the prey community, etc.

I believe the faster growth of blacknose crappie over black and white crappies in both of my studies is the result of multi-decadal culture of the strain in hatcheries and lakeside rearing ponds. In other fish species, production in aquaculture settings has led to both behavioral (e.g. increased aggression, increased boldness, and higher food consumption rates) and physiological differences (e.g. selection for higher food conversion efficiencies and more/less abdominal fat). Given that handling mortality and poststocking survival is highly size-dependent in crappies, I believe selection for improved growth characteristics in rearing environments is probable. Blacknose crappie exhibit superior growth characteristics over black and white crappies in rearing environments and these relationships should be evaluated further at larger spatial scales and across varying environmental conditions. In addition, genetic differences between blacknose and black crappies need to be assessed for the potential for outbreeding depression when stocking blacknose crappie in systems with resident crappie populations. Because our studies included blacknose crappie from one lake, a further examination of growth and survival characteristics of blacknose crappie from different sources (lakes, hatcheries, etc.) needs to be conducted to determine if growth differences are consistent among all blacknose crappie being used for stocking, or only those with certain production histories. In the meantime, we caution that use of blacknose crappie for stocking should be limited to isolated systems without existing crappie populations to reduce the risk of potentially introducing maladaptive genes.