

FORAGING OF JUVENILE CRAPPIES IN TURBIDITY: THE DIFFERENCE IS BLACK
AND WHITE

BY

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THESIS

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ABSTRACT

Environmental conditions like turbidity can fluctuate rapidly during the early life of fishes and can impact foraging behaviors, and thus growth and survival. Black (*Pomoxis nigromaculatus*) and white (*P. annularis*) crappies have been hypothesized to respond strongly and distinctly to changes in turbidity, with black crappies often thought to respond more negatively than white crappies. To compare effects of three representative turbidity levels (0, 25, and 50 NTU) on juvenile crappie foraging, controlled experiments were used to quantify 1) overall consumption and size selectivity of a single prey type (*Daphnia*) and 2) prey type selection, total consumption, and energetic value of diets when three distinct prey types (*Daphnia*, *Chaoborus*, and *Chironomus*) were offered. Unexpectedly, black crappies exhibited universally greater diet biomass than white crappies. Black crappies displayed relatively higher prey consumption and were more size selective of a single prey type, whereas white crappies were less size selective and maintained similar overall consumption with increasing turbidity levels. Both species showed similar selection patterns among three prey types at all turbidity levels, preferring *Chaoborus* and avoiding *Chironomus*. However, black crappies also avoided *Daphnia*, whereas white crappies consumed them without preference. Overall, turbidity did not appear to impair the foraging of juvenile crappies.

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Introduction

Events during early ontogeny are widely recognized as strong influences on the growth and survival of fishes to population recruitment (defined here as survival to age-1; Fuiman & Higgs 1997; Houde 1989). Ultimately, survival of juvenile fish can depend largely upon size at the end of the first growing season, with larger individuals often experiencing increased recruitment success. Large size results in relatively lower vulnerability to predation (Houde 1989; Post & Prankevicius 1987), lower size-specific metabolic rates, and comparatively better ability to resist starvation, often facilitated by a switch from invertebrate to fish prey (Ludsin & DeVries 1997; Buijse & Houthuijzen 1992). Individual performance and growth during the first year of life are largely influenced by the ability to locate and capture suitable prey, and these behaviors are potentially affected by environmental conditions (Hoxmeier, Aday, and Wahl 2009; Ellison 1984). Turbidity is one abiotic factor that has been observed to significantly affect both growth (Pope 1996; Hall, Jenkins, & Finnell 1954) as well as foraging behavior (Pangle, Malinich, Bunnell, DeVries, & Ludsin 2012; Shoup & Wahl 2009), and thus potentially recruitment and survival of many fish species.

Turbidity is a dynamic environmental variable that changes seasonally (Dirnberger & Weinberger 2005) and is subject to sudden fluctuations driven by a variety of factors, many of which are anthropogenic. Runoff from residential and agricultural sources can increase inorganic turbidity through the addition of sediment, as well as organic turbidity via increased nutrient loading and subsequently increased primary production (Chow-Fraser 1999). Boat traffic has also been shown to contribute to bottom sediment resuspension (Anthony & Downing 2003), as has foraging activity of introduced species such as common carp *Cyprinus carpio* (Chow-Fraser 1999; Parkos et al. 2003). Perhaps most drastically, intentional water level manipulation in

reservoirs can increase turbidity to a greater extent than natural processes such as rain events (Dirnberger & Weinberger 2005). It is likely that such levels of environmental variation can affect the behavior of resident fish species.

Although turbidity has been observed to affect both overall growth and foraging strategies of fishes, the strength and direction of these effects is not uniform. Studies on crappies (*Pomoxis* spp.) (Pope 1996; Hall et al. 1954) and bluegill sunfish (*Lepomis macrochirus*) (Hoxmeier et al. 2009) in experimental ponds have observed reduced growth associated with higher turbidity. Yet other evidence suggests that turbidity may not always affect growth (Spier & Heidinger 2002), and that fish may continue to select larger and more energetically profitable prey despite increased turbidity (Gardner 1981). Moreover, for species that undergo an ontogenetic shift from planktivory to piscivory (e.g. most sportfish species) the effect of turbidity on foraging behavior may be variable throughout progressive life stages (Maceina 1992).

Although contrast degradation theory predicts a negative effect of turbidity on piscivores (Utne-Palm 2002), it may be advantageous for planktivores. Previous experiments on juvenile salmonids (De Robertis, Clifford, Veloza, & Brodeur 2003; Gregory & Northcote 1993) have indicated that moderate levels of turbidity can increase foraging activity due to both increased contrast of zooplankton against the water column and decreased visibility to potential predators. Turbidity may also alter not only overall foraging activity of fishes, but also prey type selection.

Optimal foraging theory predicts that fish will select the most energetically profitable prey items available, with regard to prey size, search and capture time, and handling efficiency (Werner & Hall 1974; Schoener 1971). However, prey selection is rarely inflexible, and can be influenced by a suite of biotic and environmental variables. This may result in selection of prey that are less than energetically optimal, but may be preferable due to comparatively lower search

and handling time (Werner & Hall 1974; Schoener 1971). Turbidity has been shown to affect prey selection in adult largemouth (*Micropterus salmoides*) (Shoup & Lane 2015; Shoup & Wahl 2009) and smallmouth bass (*Micropterus dolomieu*) (Carter et al. 2010) but less attention has been given to juvenile fish, who represent a pivotal transition phase of body size and gape limitations that affect foraging. Thus, the interaction between turbidity and foraging behaviors such as prey selection, especially during early ontogeny when growth is rapid and critical to survival of subsequent life stages (Houde 1989; Post & Prankevicus 1987), merits attention as a potentially important factor driving juvenile survival and recruitment of many fish species.

Black crappie (*Pomoxis nigromaculatus*) and white crappie (*Pomoxis annularis*) are two widely distributed and recreationally important species for which determining the effects of increased turbidity may be particularly appropriate. A historical component of the management of crappie populations has been understanding the highly variable recruitment of these species, and identifying factors that may influence the development of successful cohorts (Boxrucker & Irwin 2002). However, many past studies have examined crappies in general, without differentiating between species (e.g. Claramunt & Wahl 2000; Gablehouse 1984). In fact, few have addressed the increasingly apparent differences in feeding behavior between the two, especially in juveniles (which are often difficult to distinguish in the field; Smith et al. 1995). In recent decades, it has also been postulated that there are fundamental differences between the species in their response to environmental conditions (Olive, Miranda, & Hubbard 2005; Maceina 2003), in diet composition, and ultimately in growth trajectories (Heidinger et al 1995; Ellison 1984). In general, black crappie are thought to be less tolerant of turbid conditions, often evidenced by reduced growth and survival in high turbidity (Dockendorf & Allen 2005; Pope 1996), and white crappie often dominate in systems where both species persist (Maceina 2003;

Hall et al. 1954). Yet, others have found turbidity to have no apparent effect on growth (Spier & Heidinger 2002) suggesting that turbidity alone may not be what drives observed differences in ecology and recruitment of these two species.

Black and white crappies also appear to adopt distinct progressions of foraging strategies through ontogeny. Although both species commonly rely on zooplankton prey during early life, black crappie typically consume insect prey for a protracted duration, and often do not become fully piscivorous (Ellison 1984; Hanson & Qadri 1984; Keast 1968). Conversely, white crappies often switch rapidly from planktivory to piscivory, with minimal reliance on macroinvertebrates as prey. This could offer them a competitive advantage in turbid conditions where smaller prey are more difficult to locate (Ellison 1984). Conversely, as some previous work suggests (Utne-Palm 2002), piscivorous white crappies may be more limited by turbidity. Additionally, this strategy could be a disadvantage in situations where invertebrate prey are the most available and accessible option or where piscivory imposes increased risk due to the presence of larger predators. Considering the innately different foraging patterns of these species (Ellison 1984; Hanson & Qadri 1984; Keast 1968), it is likely that the response of black and white crappies to changing environmental conditions also differs, which can have long term effects on individual growth and survival. It is possible that differences in prey selection offer a mechanism providing some explanation for the contradictory results of previous studies that sought to relate crappie growth and survival to turbidity (Pope 1996; Ellison 1984; Hall et al. 1954).

Black and white crappies present a unique pair of species for investigating the effects of environmental variation such as turbidity on foraging behavior, particularly during critical early life stages. If foraging habits are an important mechanism driving observed differences in growth and abundance of these species with turbidity, black crappie would be hypothesized to forage

less effectively than white crappie at higher levels of turbidity, as evidenced by lower prey consumption or selection of less energetically profitable prey. For a single prey type, black crappies should be expected to forage less effectively than white crappies with increasing turbidity. Similarly, black crappie diets with a mixed prey base would be hypothesized to be either less energy-dense and/or show selection for less energetically valuable prey types in increased turbidity. To investigate these hypotheses, the objectives of this study were to quantify and compare 1) total prey consumption and prey size selection foraging on a single prey type, 2) prey type selection among three functionally distinct prey types, 3) relative and total prey biomass consumed, and 4) energy density of diets among a range of turbidity levels by both black and white crappies.

Methods

Fish collection and preparation

Adult black crappies to be retained as broodstock were collected from natural populations from Weldon Springs Lake (Clinton, IL) and white crappies were collected from Forbes Lake (Kinmundy, IL) during 2013 and 2014. Fish were then held in 0.4 ha ponds at the Sam Parr Biological Station, Kinmundy IL, where they were allowed to spawn and produce young. Each of the lakes from which adults were obtained contained only one crappie species, ensuring the absence of hybrid individuals. Juvenile crappies used in single prey foraging trials were collected from ponds using a beach seine, beginning in mid-June 2015, as soon as juveniles were observed after spawning. Seining was repeated monthly throughout the growing season, with the final collection taking place in late October. A range of fish sizes was included in order to test for potential differences in the effect of turbidity among fish sizes typical throughout the first growing season. However, because no such effect was observed (see *Statistical Analyses* section for more detail), a narrower size range of crappies was included in multiple prey trials conducted in 2016. Additionally, although preliminary laboratory observations indicated that both black and white crappies as small as 30mm were capable of consuming all prey types offered in this experiment, there is some published evidence to suggest that, in the field, black crappies below 50mm TL may not feed on *Chaoborus* (Hanson & Qadri 1984). To accommodate this possibility and avoid any biases from fish size, the target length for juveniles of both species included in the multiple-prey type trials was 40-60mm. Although juveniles were collected throughout summer, the majority of fish included in these experiments were obtained in July and August.

After collection, fish were transported immediately to the Kaskaskia Biological Station, Sullivan IL, and acclimated to ambient laboratory conditions (~22°C, within the optimal

temperature range for crappie; Hayward & Arnold 1996), and housed in 75L aquaria in clear (<1 NTU), dechlorinated, aerated water for at least one week prior to use in trials. During this time, fish were fed a mixed diet of *Daphnia*, *Chaoborus*, and *Chironomus*. Fish were moved to 38L aquaria and acclimated at desired turbidity levels and prey were withheld for 24 hours before beginning each trial, to ensure similar levels of hunger and experience with experimental turbidity levels.

Single prey feeding trials

Twenty replications of three turbidity levels and two fish species were conducted in random order, for a total of 6 treatment combinations and 120 total trials. Feeding trials were conducted in 19L aquaria in the laboratory, maintained at 22(\pm 0.5) °C. Turbidity levels tested were 0 (low), 25 (moderate), and 50 (high) NTU, as measured by a nephelometric turbidimeter (LaMotte model 2020, calibrated with a 10NTU Formazin standard) just prior to feeding trials, with actual NTU measurements maintained at no more than a 10% deviation from target levels (Shoup & Lane 2015; Carter, Shoup, Dettmers, & Wahl 2010). This range of turbidity represents typical low, moderate and high levels for impoundments and lakes throughout Illinois and much of the Midwestern U.S. (U.S. EPA 2013), and past studies have considered similar levels (Carter et al. 2010; De Robertis et al. 2003). Desired turbidity levels were achieved using a slurry of bentonite clay added to dechlorinated tap water (Shoup & Lane 2015; Shoup & Wahl 2009), and turbid water of each desired level was mixed and maintained in the laboratory at least two days prior to feeding trials, to more easily maintain desired water temperature. Aquaria were aerated during acclimation of fish immediately prior to trials to maintain desired turbidity, but were not aerated during trials.

Daphnia, a common zooplankton prey item of many freshwater fishes including crappie (Ellison et al. 1984; O'Brien, Loveless, & Wright 1984) were collected from on-site cultures and added to aquaria at a density of 25L⁻¹. This density was chosen as a typical moderate *Daphnia* density of lakes in Illinois and surrounding areas (Claramunt & Wahl 2000), and because preliminary trials revealed that juvenile crappie were able to feed to apparent satiation (consuming >100 *Daphnia* in some cases) in less than 10 minutes in low turbidity. Thus, the 25L⁻¹ density was determined to be sufficiently high to pose no inherent obstacle to juvenile crappie feeding. *Daphnia* were enumerated by hand and added via pipette to aquaria at least 15 minutes before trials began to allow acclimation and dispersion. The full range of naturally occurring sizes of *Daphnia* were included in feeding trials. Each day experiments were conducted, a subsample of 50 *Daphnia* was collected from the same population used in trials. Subsamples of prey were stored in 70% ethanol, and lengths were later compared to those of prey consumed by crappies to assess whether size-dependent selection of prey items occurred.

Fish were allowed to acclimate in semi-opaque holding chambers within the aquaria for 1 hour prior to trials, and were then released into the aquaria and allowed to feed for 10 minutes. After 10 minutes, fish were removed by netting, euthanized in MS222, and total length (to nearest mm) and mass (to nearest 0.01 g) were measured. Because black crappie and white crappie showed some morphological differences in early growth, fish mass was used in analyses instead of length, to ensure a homogenous size range between species. Stomach and buccal cavity contents were removed and diet items enumerated within 1 hour of euthanasia, and diet items were then preserved in 70% ethanol for further processing.

Multiple prey feeding trials

Prey species included in this study were two morphologically different pelagic invertebrates, *Daphnia magna* and *Chaoborus flavicans* larvae, and *Chironomus* larvae, a benthic invertebrate. As before, *Daphnia* were chosen for this experiment because they are a typically available zooplankton prey, and are commonly consumed by invertivorous fishes, including crappies (Ellison 1984; O'Brien et al. 1984). *Chaoborus* larvae are another common component of crappie diets (Ellison 1984; O'Brien 1984), and, like *Daphnia*, are pelagic. However, *Chaoborus* larvae are nearly transparent, and are more mobile than crustacean zooplankton (Spitze 1985). *Chaoborus* are also of a much higher energy density than *Daphnia* (~21kJ/g vs ~4kJ/g, respectively; Galis & de Jong 1988; Cummins & Wuycheck 1971), and are thus a more energetically profitable prey option if search, capture, and handling time are equal. *Chironomus* larvae are another almost ubiquitous and often important prey option for many fish species throughout the U.S. (Oliver 1971). Chironomids have a similar energy density to *Chaoborus* (~22kJ/g; Cummins & Wuycheck 1971), but present a distinct foraging experience because they are benthic, largely immobile insects (Oliver 1971) and are highly pigmented rather than transparent. Thus crappie were given a choice between two pelagic predators with minimal handling time but varied search and pursuit times, and a benthic prey option with presumably low search time, yet longer handling time.

All prey species were collected from local ponds and cultures. For this experiment, small *Daphnia* were not included in trials, to ensure a more homogenous offering of this prey type and minimize potential effects of *Daphnia* size on prey type selection. Similarly, only mature instars of macroinvertebrates were included, to increase size homogeneity within prey types and ensure distinct differences in energy content between zooplankton and insect prey. *Daphnia* were provided at a density of 25L⁻¹, whereas *Chironomus* and *Chaoborus* were each offered at

densities of 200m⁻². These densities represent moderate to high levels in nature (Claramunt & Wahl 2000; Pope, Carter, & Power 1973), and were intended to ensure that prey availability would be high for all taxa. Prey items were enumerated by hand, and introduced into tanks via pipette (for *Daphnia*) or using forceps (for Dipterans), at least 30 minutes prior to trials, to allow time for the invertebrates to acclimate and disperse.

Number of trials, turbidity treatments, acclimation, starvation, euthanasian, and diet collection procedures used in this experiment were identical to those described for the single prey experiment. However, because Chironomids typically attach themselves to substrates in natural settings, sand was added to the bottom of each tank, to a depth of 20-30mm to imitate natural conditions and potential influences on handling time. Coarse sand was used to help ensure that the substrate settled fully before beginning trials and did not strongly influence turbidity levels. Additionally, due to potentially longer handling times of prey included in this experiment, fish were allowed to forage for 30 minutes.

Diet analysis

All diet items from both experiments were counted and processed within 6 months of collection. Prey were photographed using a compound microscope and imaging software, OCVIEW7, at 60x magnification, then measured to the nearest 0.001mm using ImageJ software. *Daphnia* were measured from the top of the helmet to the base of the anal spine (Gardner 1981), *Chaoborus* were measured from the tip of the head capsule to the origin of the anal papillae (Fedorenko and Swift 1972), and *Chironomus* were measured from the base of the antennae to the procercus (Nolte 1990). For the single prey experiment, lengths of prey consumed were compared to prey offered to investigate prey size selectivity. The difference between average

prey size consumed (mm) and average prey size offered (mm) was calculated for each fish as a measure of prey size selection, and these differences were then compared using ANOVA.

Statistical Analyses

Initially, ANOVA was used to model total prey consumption in the single prey experiment, with the ratio of diet biomass / fish biomass (g) as the response variable, and with fish species and turbidity level, as well as their interaction included as explanatory variables. To control for differences in fish size, the ratio of diet biomass to fish biomass was used instead of raw diet biomass. To test for prey size selection, the difference between mean prey length consumed and mean prey length offered (mm) was calculated for each fish and used as the response variable in a full-factorial ANOVA, with fish species, turbidity level, and the two-way interaction as explanatory variables. Results of all analyses were considered significant at $p = 0.05$.

To evaluate prey type preference in the multiple prey experiment, Chesson's selectivity index (α) was calculated for each prey type, for each fish (Chesson 1983). Because data were obtained from known, finite populations in controlled experiments, the following "Case 2" formula assuming food depletion was used:

$$\hat{\alpha}_i = \frac{\ln((n_{i0} - r_i)/n_{i0})}{\sum_{j=1}^m \ln((n_{j0} - r_j)/n_{j0})}$$

where r_i = the number of individuals of a given prey type (i) in the diet, n_{i0} = the number of individuals of that prey type offered, n_{j0} and r_j are measurements of (respectively) number of a prey type offered and number of a prey type in the diet for all other prey types, and m = the total number of prey types offered. Neutral selection was calculated as $\frac{1}{m} = 0.333$ for all trials.

Selection values significantly greater than 0.333 indicated that fish depleted that prey resource at a rate greater than that expected for neutral consumption (i.e., selection of that prey type

occurred), and values significantly lower than 0.333 indicated that fish depleted that prey type at a rate lower than that expected for neutral consumption (i.e. avoidance of that prey type occurred). The mean α value and 95% confidence interval were calculated for each prey type and treatment group, and a set of Bonferroni-corrected t-tests (Galarowicz, Adams, & Wahl 2006) were used to determine whether observed distributions for each treatment group differed significantly from neutral selection.

To evaluate the implications of prey type selection, biomass estimates (total and per prey type) for each diet were determined using literature taxon-specific values for each prey type (Benke, Huryn, Smock, & Wallace 1999; Johnston & Cunjak 1999; Dumont & Balvay 1979). Biomass was then used to estimate total energy content of each diet using species-specific energy density estimates (Galis & de Jong 1988; Cummins & Wuycheck 1971). Diet biomass metrics were analyzed using one-way MANOVA, with total biomass, *Chaoborus* biomass, *Chironomus* biomass, and *Daphnia* biomass as response variables and with species, turbidity, and the two-way interaction term included as explanatory variables. Total energy density was described using a full-factorial ANOVA with energy density as the response variable and species, turbidity, and the species by turbidity interaction as explanatory variables. To ensure normality, total energy density values were log transformed prior to analysis.

Results

Total Diet Biomass and Size Selection of Daphnia

Black crappie diet biomass was not significantly different from that of white crappies at low turbidity (0 NTU), but was different at high turbidity (50 NTU), and was intermediate in moderate turbidity (25 NTU) (Fig. 1). Diet biomass was significantly influenced by turbidity (ANOVA $F = 4.27$, $P = 0.02$), fish species ($F = 11.8$, $P < 0.001$), and the turbidity by species interaction term ($F = 3.262$, $p = 0.04$). Black crappie diet biomass increased with higher turbidity, whereas white crappie diet biomass remained constant among turbidity levels (Fig. 1). Black crappies in high turbidity (50 NTU) had significantly higher diet biomass than white crappies at all turbidities (Tukey HSD post-hoc test), as well as black crappies in low turbidity (0 NTU). Black crappies in moderate turbidity (25 NTU) had intermediate diet biomass which did not differ significantly from any other treatment group (Fig. 1).

Both species (ANOVA $F = 43.634$, $p < 0.001$) and species by turbidity ($F = 12.964$, $P < 0.001$) significantly influenced prey size selection, resulting in the selection of larger than average *Daphnia*; however, the main effect of turbidity was not significant ($F = 0.065$, $P = 0.94$). Black crappies in low turbidity (0 NTU) were significantly less size selective than any other treatment combination (Tukey HSD post-hoc test, Fig. 2). Conversely, white crappies in low turbidity were more size selective than any other treatment combination, with the size of *Daphnia* consumed averaging near 0.5 mm larger than what was offered. Size selectivity for both species in moderate and high turbidity was intermediate, differing significantly from low turbidity treatments but not between moderate and high turbidity treatments (Fig. 2).

Prey Selectivity

Both black and white crappies selected *Chaoborus* and avoided *Chironomus* at all turbidity levels (Fig. 3). Black crappies showed significant positive selection of *Chaoborus* at all turbidity levels (t-test, $P < 0.001$), whereas selection by white crappies was similarly high, but significantly different from neutral selection only in moderate (25 NTU) and high (50 NTU) turbidity. Similarly, black crappie avoidance of *Chironomus* was significantly different from neutral selection in moderate and high turbidity, whereas white crappie avoidance of *Chironomus* was significant in all treatments. The most obvious difference in foraging preference between species was in the selection of *Daphnia*. Black crappies showed significant avoidance of *Daphnia* in all treatments (t-test, $P < 0.001$), whereas white crappies displayed neutral selection in all treatments (t-test, $P < 0.001$; Fig. 3).

Prey biomass and total energy density

Species was the only variable that significantly affected total biomass and per species biomass among treatments (MANOVA $F = 8.98$, $P < 0.001$), with black crappie consuming about twice the total biomass of white crappie in all treatments (Fig. 4). As observed for biomass, energy density of diets was significantly higher (up to ~8x) for black crappies than for white crappies (ANOVA $F = 111.26$, $P < 0.001$; Fig. 5), and no significant differences were observed within species among turbidity levels ($F = 0.606$, $P = 0.55$).

Discussion

Our results support the hypothesis that foraging habits differ between crappie species, however the way in which each species responded to turbidity was not entirely as predicted. Black crappies, foraged more in turbidity when a single prey type was offered, but did not when offered a mixed prey assemblage. As predicted, white crappies appeared less responsive to changes in turbidity when foraging only on zooplankton, maintaining consistent prey intake among all turbidity levels. Although black crappies also consumed more prey than white crappies in multiple prey trials, observed differences in prey selection were not as dramatic as those observed for prey size selection of *Daphnia*. Turbidity appeared to affect foraging of juvenile crappies in some situations, although differences between species were much greater than differences in response to turbidity.

Past studies have shown decreased growth of black crappies in turbidity (Dockendorf & Allen 2005; Pope 1996), and observed decreased abundance compared to that of white crappies in turbid lakes (Hall et al. 1954), contributing to the assumption that black crappies may be less able to adapt to turbidity. However, reduced growth of both black and white crappies in turbidity has also been observed (Hall et al. 1954), whereas others have found little effect of turbidity on the growth of either species (Spier and Heidinger 2002). The positive relationship between black crappie consumption of zooplankton prey and turbidity observed in our study contrasts with many previous observations and indicates that any reduction in growth and success of black crappies is not likely driven by an inability to successfully capture prey in turbidity. The consistently greater prey consumption of black crappies than white crappies was also unexpected. The two species are morphologically similar and no inherent differences in metabolism have been observed (Gring 2015) which might indicate different energy intake

requirements. Neither species suffered any reduction in overall foraging ability in turbidity. Thus, observed differences in growth and abundance in natural settings are likely the result of more complex physiological or behavioral processes.

Prey size selection differed in turbid treatments for both species, but in opposite directions. White crappies became less size selective in turbidity while maintaining similar overall diet biomass, indicating the need to consume a greater number of smaller prey in turbidity to maintain similar energetic intake. However, black crappies became more size selective in turbid treatments, again contrasting the expectation that black crappies would show evidence of decreased foraging ability in turbidity. Differences in prey size selection of a single prey type may be the result of several potential mechanisms. For white crappies, reactive distance has been demonstrated to decrease in turbidity (Wright & O'Brien 1984). White crappies strongly selected larger than average prey in clear water, but became less selective in turbidity. Given previous knowledge of the effects of turbidity on reactive distance of this species, it is possible that white crappies were less able to perceive their prey in turbidity, and so chose to compensate by consuming a greater proportion of smaller, less energetically valuable *Daphnia*. Reactive distance has yet to be similarly quantified for black crappies, making direct comparison impossible. Turbidity may not reduce the reactive distance of black crappies as strongly as it does that of white crappies, enabling black crappies to locate a greater number of prey, even in turbidity. However, this possibility does little to explain increased selection of larger than average prey of black crappie in turbid treatments, nor the positive relationship between black crappie diet biomass and turbidity. More likely, species-specific differences in foraging response to turbidity are driven by diverging behaviors, and effects may be less pronounced in natural systems where a variety of prey types are available.

In multiple prey trials, both black and white crappies avoided *Chironomus* in all turbidity levels, indicating that neither species selects benthic prey when pelagic prey options are readily available, and that this preference does not vary greatly in response to turbidity. Both species tended to select *Chaoborus*, the more energetically valuable pelagic prey type offered, in all levels of turbidity. The preference for *Chaoborus* over *Chironomus* implies an advantage in search time, handling time, or both, that may be independent from environmental conditions such as turbidity. Because *Chaoborus* are highly cryptic (i.e. transparent), it was expected that this prey might become easier for crappies to locate in turbidity, via increasing contrast (De Robertis et al. 2003; Gregory & Northcote 1991). The observation that white crappie selection of *Chaoborus* increased slightly and became significantly different from neutral selection only in turbid treatments somewhat supports this hypothesis. Yet, no similar effect was observed for black crappies. Alternatively, because little overall variation in prey choice was observed for either species relative to turbidity, it is possible that all prey types were sufficiently visible in all treatments, and crappies generally preferred *Chaoborus* because of relatively lower handling time due to their position higher in the water column rather than attached to bottom substrate. In any case, turbidity did not appear to impair the ability of either species to forage effectively in either single or multiple prey experiments.

The greatest difference in prey selectivity was for *Daphnia* at all turbidity levels. In single prey experiments, black crappies consumed a much greater amount of *Daphnia* than white crappies in all treatments. A number of possible explanations exist for this disparity, but one possibility is that black crappies are simply more adept at, or more inclined toward foraging on zooplankton, whereas white crappies may prefer larger, more energetically profitable prey options. In that case, white crappies would be expected to show stronger avoidance of *Daphnia*

than black crappies in a scenario including multiple prey types, but this did not occur. Black crappies strongly avoided *Daphnia* in all treatments, whereas white crappies exhibited neutral selection. These findings seem counterintuitive, but support previous field data (Ellison 1984; Hanson & Qadri 1984) suggesting that black crappies tend to utilize a greater proportion of macroinvertebrate prey than do white crappies. White crappies tend to rely more heavily on zooplankton before abruptly switching to fish prey early in ontogeny (Olive et al. 2005; Ellison 1984). The lack of difference in *Daphnia* utilization of either species among turbidity levels indicates that foraging preferences do not appear to be affected by the turbidity levels tested in this study. Despite some small differences in prey selection among treatments, within-species variation in total prey consumption and total energetic value of diets varied little.

In contrast to trials offering only *Daphnia* as prey, no significant influence of turbidity on overall prey consumption was apparent when a mixed prey assemblage was available. Crappies were able to maintain a constant level of prey consumption among turbidity levels without any apparent need to switch foraging strategies. These results were somewhat unexpected, both in light of previous studies on both largemouth (Shoup & Lane 2015; Shoup & Wahl 2009) and smallmouth bass (Carter et al. 2010), and because turbidity was observed to affect foraging of black crappies on a single prey type. Lack of response in multiple prey experiments may be due to a number of factors. These experiments included larger and more nutritious insect prey, and because the duration of feeding trials was longer, crappies may have been able to feed to satiation in all levels of turbidity. It is also possible that for planktivorous fishes, tradeoffs in search/handling effort and energy content among a variety of invertebrate prey at moderate to high densities are simply not strong enough to result in changes in foraging behavior in response to turbidity. Indeed, previous experiments considering prey selectivity have focused on adult fish

foraging on prey types that were highly distinct from one another (e.g. Gizzard Shad *Dorosoma cepedianum*, bluegill, and Northern crayfish *Oronectes virilis*; Shoup and Wahl 2009). In comparison, most all previous evaluations of the foraging of juvenile and planktivorous fishes in turbidity have included only a single prey type (De Robertis et al. 2003; Gregory & Northcote 1993; Gardner 1981). Our results may be some of the first to indicate that turbidity-induced changes in prey type selectivity are less likely to occur in fish that are primarily planktivorous or insectivorous.

Crappies were offered relatively high densities of prey in the absence of predators. However, in natural systems the comparatively higher foraging rate of black crappies might result in some detrimental effects. Growth rates of brook trout in turbidity were reduced despite increased foraging, likely due to increased energy expended by more active foraging strategies (Sweka and Hartman 2001). Possibly, black crappies did not experience a similar effect, and had no trouble finding prey even in turbid treatments. However, if black crappies maintained similar prey intake only by increasing foraging activity in turbidity, it is possible that ultimate effects on growth may have been similar to those observed for brook trout (Sweka and Hartman 2001). In natural systems, if black crappies increase foraging activity in turbidity while focusing on invertebrate prey (Ellison 1984; Keast 1968), the result may be proportionally higher energy expenditure relative to energetic value of captured prey, resulting in lower growth rates in turbid systems, as has been previously observed (Dockendorf & Allen 2005; Pope 1996). Increased activity levels might also result in increased susceptibility to predation in turbid systems via reduced ability to outgrow predators' gape limits (Houde 1989; Post & Prankevicus 1987), decreased energy available to avoid predators (Ludsin & DeVries 1997; Buijse & Houthuijzen 1992), and increased exposure to predators while foraging (DeRobertis et al. 2003). Conversely,

if white crappies maintain lower levels of foraging activity in all turbidity levels, such effects may be minimized, leading to ultimately higher growth and survival compared to white crappies in turbid systems.

Attempting to quantify the effects of turbidity on juvenile fishes whose diet is expected to change throughout ontogeny would benefit from the addition of field data from natural systems, as most previous research has been conducted in the laboratory and it is increasingly clear that the response of individual organisms to turbidity may differ widely with respect to fish species (Shoup and Wahl 2009; DeRobertis et al. 2003; Ellison 1984), trophic position (Pangle et al. 2012; Boehlert and Morgan 1985), and life stage (Maceina et al. 1992). However, crappie populations can be difficult to sample in the field (Binion, Allen, Catalano, & Pine 2009), and identification between species of juveniles can often be difficult (Smith et al. 1995), making such studies logistically challenging, though not impossible. Studies considering juvenile crappies as not only predators but prey to piscivores may also be valuable (Pangle et al. 2012; DeRobertis et al. 2003), as predator-prey interactions may still be affected by turbidity at higher trophic levels, even where effects on foraging of planktivores are not apparent.

Mechanisms driving perceived negative responses of fish populations to turbidity are likely complex, and may result from behavioral changes rather than physiological limitations. Here, turbidity was not determined to be a strong driver of differences in total prey consumption or prey type selection of juvenile crappies. However, it may still impact the overall recruitment success of these and other fish species through other mechanisms not studied here. Based on some past literature (Boxrucker & Irwin 2002; Ellison 1984; Hall et al. 1954) managers may be inclined to consider turbidity as a strictly detrimental source of environmental variation in natural systems. However, as shown here, turbidity alone may not always be detrimental and in

some studies may be a beneficial (De Robertis 2003; Gregory & Northcote 1993) or insignificant contributor to foraging success, and thus potentially growth and abundance of some sportfish species, at least during early life. The challenge for managers may then be to incorporate the highly variable impact of turbidity into a larger framework considering not only the potential effects of environmental factors, but species- and community-wide interactions that influence the strength and direction of such effects.

Conclusions

Although turbidity was expected to elicit a decrease in foraging success for black crappies, the opposite was observed in experiments including only *Daphnia* as prey. Black crappies not only consumed a greater overall diet biomass in turbid vs non-turbid treatments, but became more size-selective. White crappies, somewhat more intuitively, maintained similar levels of consumption among treatments, but became less size selective in turbidity. In another experiment including three distinct prey types (*Daphnia*, *Chironomus* and *Chaoborus*), little difference was observed in prey type selection between species or among treatments. *Chaoborus* were preferred by both black and white crappies, while *Chironomus* were avoided. Black crappies tended to avoid *Daphnia*, while white crappies consumed them without preference. In general, black crappies still consumed a significantly higher prey biomass than white crappies, and overall energetic value of diets was higher for black crappies than white crappies, varying little among turbidity levels for either species.

Overall, the results of this study were somewhat as expected: foraging activity levels and to some extent prey type selection differed between crappie species. However, a negative foraging response of either species to turbidity was not observed, indicating that any negative effects of turbidity on the growth and survival of crappies in wild populations is not the direct result of an inability to locate prey, at least at the juvenile stage. More likely, observed differences in growth and survival are the result of differences in foraging behavior resulting in increased energy expenditure while foraging which may lead to a number of indirect, negative effects such as reduced growth and increased exposure to predators. Managers considering stocking crappies in turbid systems should not be deterred automatically, based on the results of

this study, but should consider other factors such as prey availability and potential predator densities which may interact with turbidity to influence the success of crappie populations.

Figures

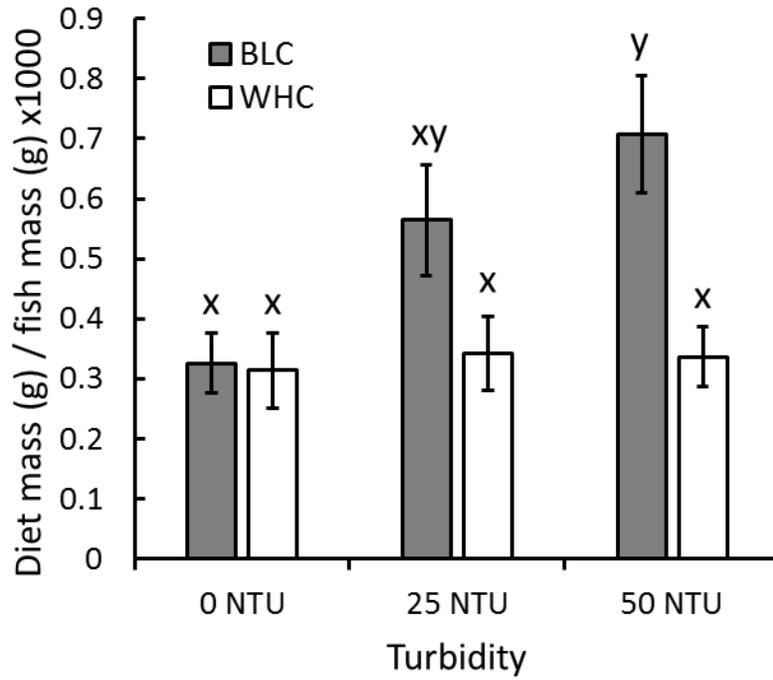


Figure 1. Mean ratio of diet biomass to fish biomass for black (BLC) and white (WHC) crappies among three turbidity levels (g). Bars indicate standard error for each treatment and letters above bars indicate Tukey HSD groupings.

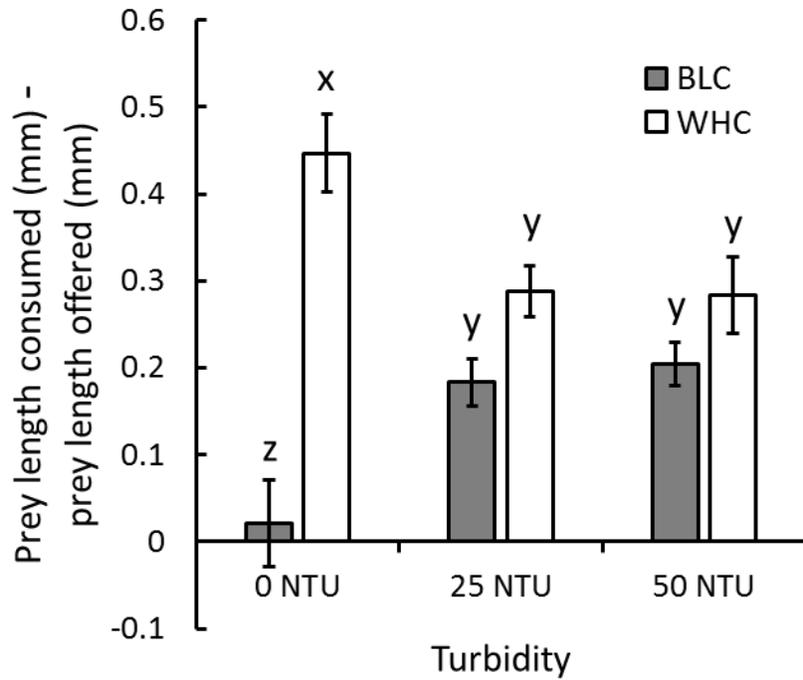


Figure 2. Prey size selection as measured by the difference between mean prey size observed in diets (mm) and mean prey size offered (mm) for both black (BLC) and white (WHC) crappies among three turbidity levels. Bars are standard error bars, and letters are Tukey HSD groupings.

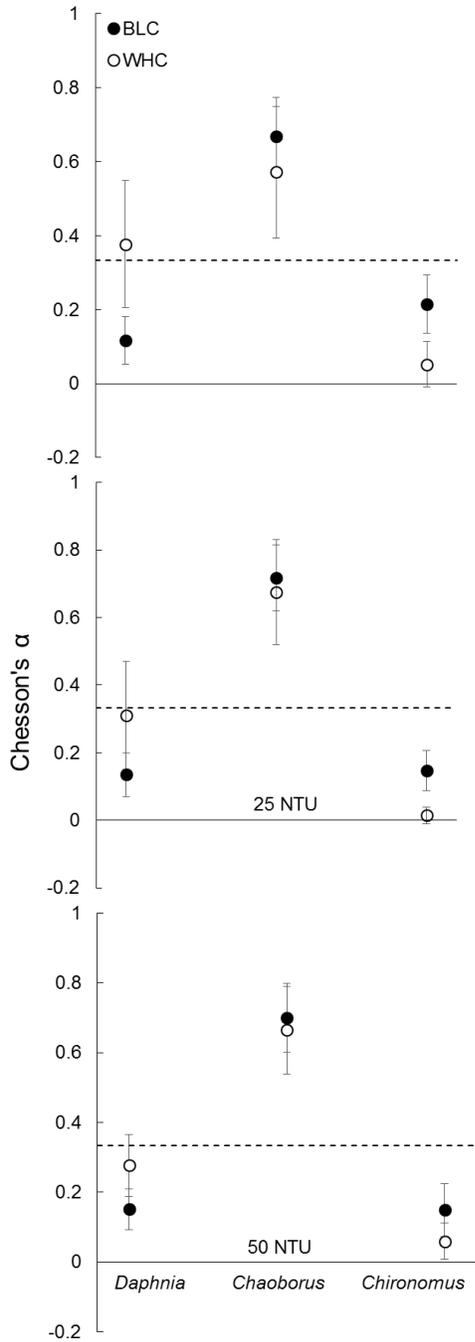


Figure 3. Chesson's selectivity index (α) for black (BLC) and white (WHC) crappies among 0 NTU, 25 NTU, and 50 NTU turbidity treatments. Bars indicate 95% confidence intervals. Dashed lines indicate neutral selection; points below the line indicate negative selection of a prey type, and points above the line indicate positive selection. Asterisks (*) indicate α values significantly different from random feeding (neutral selection), based on t tests with Bonferroni correction for multiple hypothesis tests.

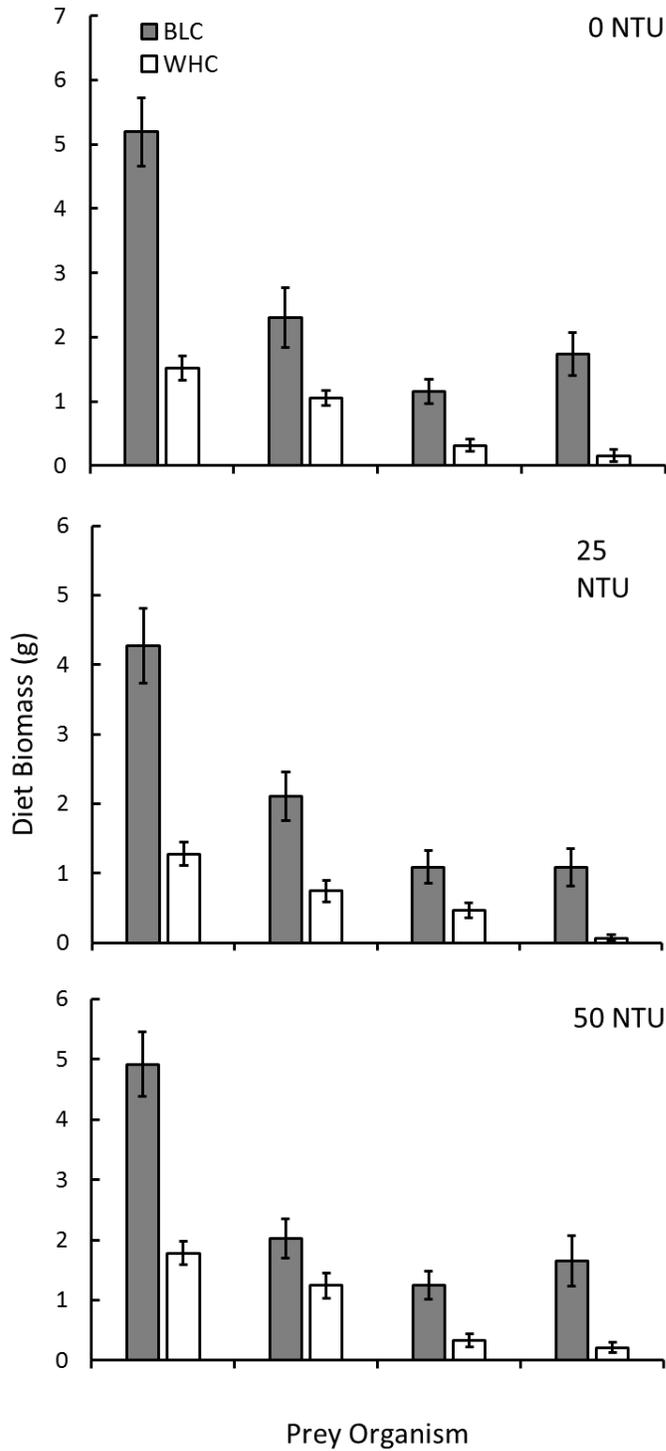


Figure 4. Mean biomass (mg) of *Chironomus*, *Chaoborus*, and *Daphnia* in crappie diets, as well as total diet biomass of black (BLC) and white (WHC) crappies in 0 NTU (A), 25 NTU (B), and 50 NTU (C) turbidity treatments. Bars represent standard error.

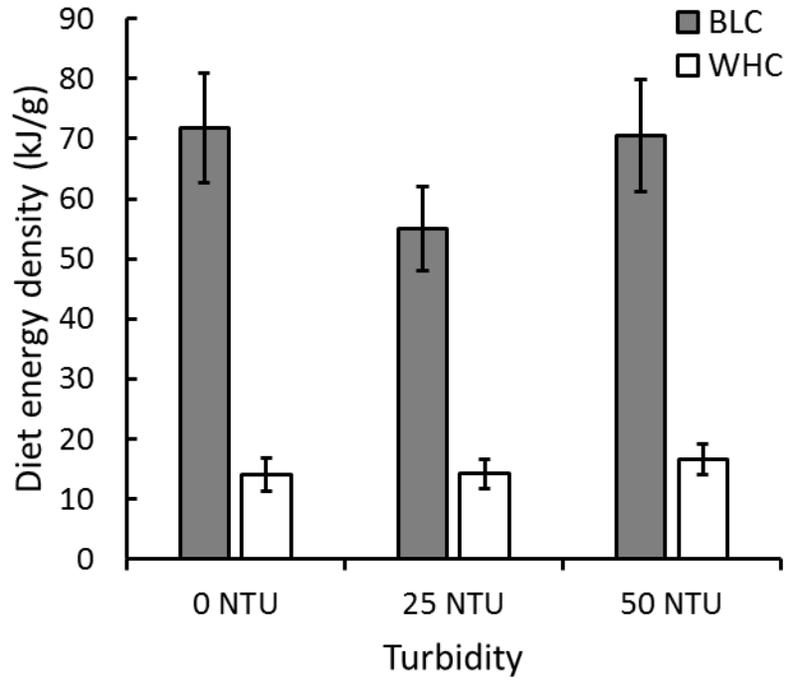


Figure 5. Total energy density (kJ/g) of black crappie (BLC) and white crappie (WHC) diets, among three turbidity levels. Bars represent standard error.

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