

# Ontogenetic Diet Shift, Feeding Ecology, and Trophic Niches of the Redspot Chub (Cypriniformes: Cyprinidae: *Nocomis asper*)

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**Redspot Chub (*Nocomis asper*) are a keystone species in Ozark Highland streams of the Arkansas River drainage because their unique mound-building reproductive behavior facilitates recruitment of nest associates. Data contributing to an increased understanding of Redspot Chub natural history is required for the conservation of this species as it is listed as a species of concern throughout most its range. The findings presented within thoroughly describe Redspot Chub feeding ecology by documenting an ontogenetic diet shift, patterns of seasonal resource use, important prey taxa, estimates of trophic position and dietary niche breadth, as well as documenting feeding strategies at population and individual levels. Diet collections were conducted seasonally in 2018 and 2019 at four sites on Spavinaw Creek in Arkansas and Oklahoma. Logistic regression provided evidence for a previously undescribed ontogenetic diet shift, which split Redspot Chub into two functionally different species from a dietary perspective. Redspot Chub  $\geq 162$  mm total length (TL, RSCB) occupied a significantly higher trophic level than Redspot Chub  $< 162$  mm TL (RSCS). In terms of caloric contribution, Ringed Crayfish (*Faxonius neglectus neglectus*) nearly accounted for the entire diet of RSCB, regardless of season. This specialization led to a much lower overall dietary niche breadth when compared to RSCS. Furthermore, Amundsen plots clearly depicted RSCB population specialization on crayfish. Conversely, Trichoptera were the most important prey across seasons for RSCS. Coleoptera, Ringed Crayfish, and Ephemeroptera ranked second in importance at different times seasonally. RSCS also possessed a relatively narrow niche width, but Amundsen plots exhibited a pattern where seasonally the two most important prey types were specialized on by approximately half the population, while smaller proportions of the population specialized on less commonly used prey resources. Species' diets reflect an integration of numerous ecological components; therefore, our aim was to provide a greater understanding of Redspot Chub feeding ecology that may be useful for informing future conservation assessments and management decisions.**

**K**NOWLEDGE of species' basic biology and fundamental ecology is critical for conservation. Biological data provide the backbone for "state fish book" species accounts, syntheses, meta-analyses, and species conservation assessments (Miller and Robison, 2004; Ptacek et al., 2005; Kornis et al., 2012; Matthews, 2015). Matthews (2015) noted the need for high-quality natural history information remains for many fish species and encouraged researchers to publish papers that fill data gaps. The study of food webs may provide important insight into trophic relations, predator-prey dynamics, habitat use, and energy flow within aquatic ecosystems. Understanding the diet of a species is considered central to its conservation and management because diets reflect an integration of these ecological components (Chipps and Garvey, 2007; Garvey and Chipps, 2012). Furthermore, baseline dietary data are necessary to test hypotheses examining how stressors such as climate change, invasive species, habitat degradation, or changes in prey resources may affect a particular species' dietary niche and feeding ecology (Heisey et al., 1980; Baxter et al., 2004; Pilger et al., 2010; Crane and Einhouse, 2016; Civiello et al., 2018; Middaugh et al., 2018).

The Redspot Chub (*Nocomis asper*) is one member of the genus *Nocomis*, which is known for building large gravel mound nests in streams (Lachner and Jenkins, 1971; Pflieger, 1997; Miller and Robison, 2004). Members of this genus are considered ecosystem engineers and keystone species because their populations and nest building behaviors are tied directly into the reproduction, range, and persistence of species characterized as obligate nest associates (Jones et al., 1994; Pendleton et al., 2012; Frimpong, 2018; Robison and

Buchanan, 2020). The species' range is comprised of three disjunct populations: the Blue River in Oklahoma, the upper Ouchita River in Arkansas, and the Ozark Highlands region of northeast Oklahoma, southeast Kansas, southwest Missouri, and northwest Arkansas (Miller and Robison, 2004; Robison and Buchanan, 2020; Whitney et al., 2020). Kansas lists the Redspot Chub as state threatened because it is restricted to six river kilometers of habitat in the state, and both Oklahoma and Arkansas designate it as a species of greatest conservation need (Haslouer et al., 2005; ODWC, 2016; Robison and Buchanan, 2020; Whitney et al., 2020). Thus, collection and communication of biological data are imperative to inform conservation initiatives, management actions, and listing decisions regarding Redspot Chub.

Currently, detailed natural history information regarding the feeding ecology of Redspot Chub is lacking. Pflieger (1997) assumed habits and life history of Redspot Chub are similar to Hornyhead Chub (*N. biguttatus*), and Miller and Robison (2004) generally stated Redspot Chub feed on invertebrates, but they may occasionally ingest plant material. Other published accounts characterize Redspot Chub as carnivorous sight feeders that primarily feed on benthic invertebrates (Davis and Miller, 1967; Felley and Hill, 1983; McNeely, 1987; Cross and Collins, 1995; German et al., 2010). However, previous research did not assess potential ontogenetic diet shifts, seasonal patterns in resource use, trophic position, feeding strategies, or the dietary niche breadth of Redspot Chub. Therefore, the objective of this study was to perform a suite of diet analyses that thoroughly describe Redspot Chub feeding ecology within a representative Ozark Highland stream.

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## MATERIALS AND METHODS

**Study site.**—Redspot Chub were collected from Spavinaw Creek in northeastern Oklahoma and northwestern Arkansas. The entire length of Spavinaw Creek flows through the Ozark Highlands ecoregion. Streams in this region are often influenced by karst features such as springs and underground caves, which can lead to increased groundwater exchange and thermal patchiness (Mollenhauer et al., 2019, 2020). Spavinaw Creek is characteristic of Ozark Highland streams in that it has well-defined riffle–pool sequences with relatively clear, cool water and gravel substrate.

**Field methods.**—Fish collections were conducted seasonally in 2018 and 2019 at three sites in Oklahoma and one site in Arkansas. Seasons were defined by sampling date and water temperature to ensure consistency between years. Winter, spring, summer, and fall surveys were primarily conducted from January to February, March to April, July to August, and October to November, respectively. However, sampling was not conducted in fall of 2019 due to flooding. All available habitats were sampled via single-pass electrofishing. In Oklahoma, Redspot Chub were collected using a tow-barge electrofishing unit (Stealth Mini-boat, Midwest Lake Management, Polo, MO) with an Infinity Control Box (Midwest Lake Management). Greater pool depth at the farthest upstream site in Arkansas necessitated the use of boat electrofishing (2.5 GPP, Smith-Root Inc., Vancouver, WA). Prior to sampling, ambient water conductivity was measured and voltage adjustments were made as necessary to maintain appropriate target power as outlined in Miranda (2009). Captured individuals were placed in flow-through enclosures prior to processing. Stomach contents were obtained using gastric lavage techniques with filtered water (Foster, 1977; Light et al., 1983; Kamler and Pope, 2001) on a handling device slightly modified from Fowler and Morris (2008). Gastric lavage is a non-lethal technique for collecting diet samples that has been successfully utilized on the morphologically similar Creek Chub (*Semotilus atromaculatus*) and numerous other species (Baker and Fraser, 1976; Foster, 1977; Light et al., 1983; Wasowicz and Valdez, 1994; Kamler and Pope, 2001; Waters et al., 2004; Hafs et al., 2011). Flushed prey items were placed in Whirl-Pak bags and preserved in 10% formalin. After diet removal, fish were moved back to flow-through enclosures to recover prior to release.

**Laboratory methods.**—Prey items were identified at least to order and then grouped by order prior to analyses, excepting snails and aquatic worms that were identified to Gastropoda and Oligochaeta, respectively. Redspot Chub preyed on one species of crayfish, Ringed Crayfish (*Faxonius neglectus neglectus*), so hereafter Ringed Crayfish and crayfish are synonymous. Prey counts were made using consistent body parts (e.g., heads, casings) when fragments of prey items were present. Prey measurements (nearest 0.01 mm) were taken with digital calipers. Measurements on a subsample of ten randomly selected individuals were completed in instances where stomachs contained large numbers of individual prey taxa. If accurate prey size measurements were precluded by digestion, the average size of that prey taxon for that season was applied. Invertebrate biomass estimates were derived using published length–dry mass equations (Benke et al., 1999; Sabo et al., 2002). Ringed Crayfish original size and biomass estimates were determined using the equations

provided in Rodger and Starks (2020). The use of energy values permits a more accurate quantitative measure of the nutritional benefit of prey than would be obtained from weights or counts because the caloric content of prey differs among species. (Probst et al., 1984; Pope et al., 2001; Chipps and Garvey, 2007). Thus, caloric densities were multiplied by the estimated dry weights of each prey item to calculate the energetic contribution of different prey types to Redspot Chub diets (Probst et al., 1984; Pope et al., 2001). Estimates of prey specific caloric values were obtained from published literature (Cummins, 1967; King and Ball, 1967; McDuffett, 1970; Kelso, 1973; Probst et al., 1984). Caloric values of macroinvertebrate prey with exoskeletons were reduced 17%, while all other prey types were given reductions of 6% to account for unassimilated energy fractions (Probst et al., 1984).

**Analyses.**—Anecdotal observations during field diet collections of stomach contents revealed a potential relationship between Redspot Chub size and crayfish consumption. Given that the existence of an ontogenetic diet shift could potentially obfuscate other dietary analyses, a logistic regression using binary response data was used to test the relationship between Redspot Chub total length (TL) and crayfish consumption. The potential ontogenetic diet shift to crayfish predation was determined as the length at which crayfish were predicted to occur in  $\geq 50\%$  of Redspot Chub stomachs (Guy et al., 2011; Schmitt et al., 2018).

Multiple diet indices were used to characterize Redspot Chub diets because no single diet index is robust enough to fully describe the complex nature of a species' feeding ecology. The utility and known biases associated with various indices are reviewed elsewhere in the literature (Hyslop, 1980; Pope et al., 2001; Chipps and Garvey, 2007). Percent empty stomachs (%E) were calculated seasonally to assess temporal trends in feeding activity. Frequency of occurrence ( $O_i$ ) denotes how often a prey category is consumed and is calculated by dividing the number of stomachs containing a specific prey item by the total number of stomachs containing food. Percent composition by number ( $N_i$ ) represents the total number of individuals of each prey type expressed as a proportion of the total number of individuals of all prey types consumed. Percent composition by calories ( $C_i$ ) is calculated in the same manner using caloric values in place of counts. These indices provide important summary data for the population, but they represent single measures with no corresponding variance estimate, thus they are not appropriate for use in statistical calculations (Pope et al., 2001; Chipps and Garvey, 2007). However,  $N_i$  and  $C_i$  can be calculated for individual fish and averaged for each prey type to generate mean estimates with variance for mean proportion by number ( $MN_i$ ) and mean proportion by calorie ( $MC_i$ ) indices. In this manner each stomach is standardized, and individual fish are assumed to represent independent, random samples (Chipps and Garvey, 2007). In addition to logistic regression,  $MC_i$  values of common prey types were compared across size classes to assess relationships between Redspot Chub size and prey importance.

Amundsen plots were used to graphically assess several important components of Redspot Chub feeding ecology including: prey importance, individual and population level feeding strategy (i.e., specialization or generalization), and

niche width contribution. This method plots individual prey types by their  $O_i$  on the x-axis and prey-specific abundance ( $P_i$ ) on the y-axis. Prey-specific abundance was calculated using the equation:

$$P_i = \left( \sum S_i / \sum S_{ii} \right) \times 100$$

where  $P_i$  is the prey-specific abundance of prey  $i$ ,  $S_i$  is the summed proportion of calories comprised of prey  $i$  in stomachs, and  $S_{ii}$  is the total caloric value of stomach contents in only those fish with prey  $i$  in their stomach. Graphically, prey importance generally increases from the lower left to upper right of the diagram as a function of  $P_i$  and  $O_i$ . Thus, rare or unimportant prey types are located in the bottom left of the graph. Because stomachs were standardized prior to analysis, the product of  $P_i$  and  $O_i$  is mathematically equivalent to  $MC_i$  and was used as a quantitative estimate of overall prey importance. The vertical axis designates whether prey types were specialized on or fed on more generally. Points in the upper half of the diagram depict prey items that were specialized on because they contributed more than 50% of the caloric value to stomachs in which they occurred. The diagonal axis running from the upper left to the lower right explains the difference in feeding strategies related to niche width contribution. Data points clustered in the upper left corner of the diagram suggest a predator population exhibits high between-phenotype component whereby individual predators specialize on different prey items. In a predator population with a high within-phenotype component, the majority of the population utilizes numerous prey resources simultaneously; therefore, prey items will be clustered in the lower right corner of the graph. A mixed strategy occurs when species feed on prey items with varying degrees of specialization and generalization (Amundsen et al., 1996).

Trophic position of Redspot Chub was calculated by using the equation:

$$T_a = \sum (V_i \times T_i) + 1$$

where  $T_a$  is mean trophic position of the  $a^{\text{th}}$  predator,  $V_i$  is the  $MC_i$  of prey  $i$ , and  $T_i$  is the trophic position of prey  $i$  (Adams et al., 1983). Trophic positions were calculated seasonally and then averaged to obtain an overall estimate. Values of prey trophic positions were obtained from Vander Zanden et al. (1997) and Pilger et al. (2010).

Diet breadth was calculated using the standardized Levins's index:

$$B = \frac{1}{S-1} \left( \frac{1}{\sum_{i=1}^S X_i^2} - 1 \right)$$

where  $B$  is a measure of diet breadth for species  $X$ ,  $S$  is the number of prey categories, and  $X_i$  is the  $MC_i$  of prey item  $i$  in species  $X$ . Values are bound from 0–1 with a value of zero indicating a predator consumed a single prey item and a value of one meaning all prey items were consumed in equal proportions (Levins, 1968; Hulbert, 1978; Feiner et al., 2013). Novakowski et al. (2008) qualitatively categorized values of diet breadth to be high when  $> 0.6$ , moderate between 0.4–0.6, and low when  $< 0.4$  (Sá-Oliveira et al., 2014).

## RESULTS

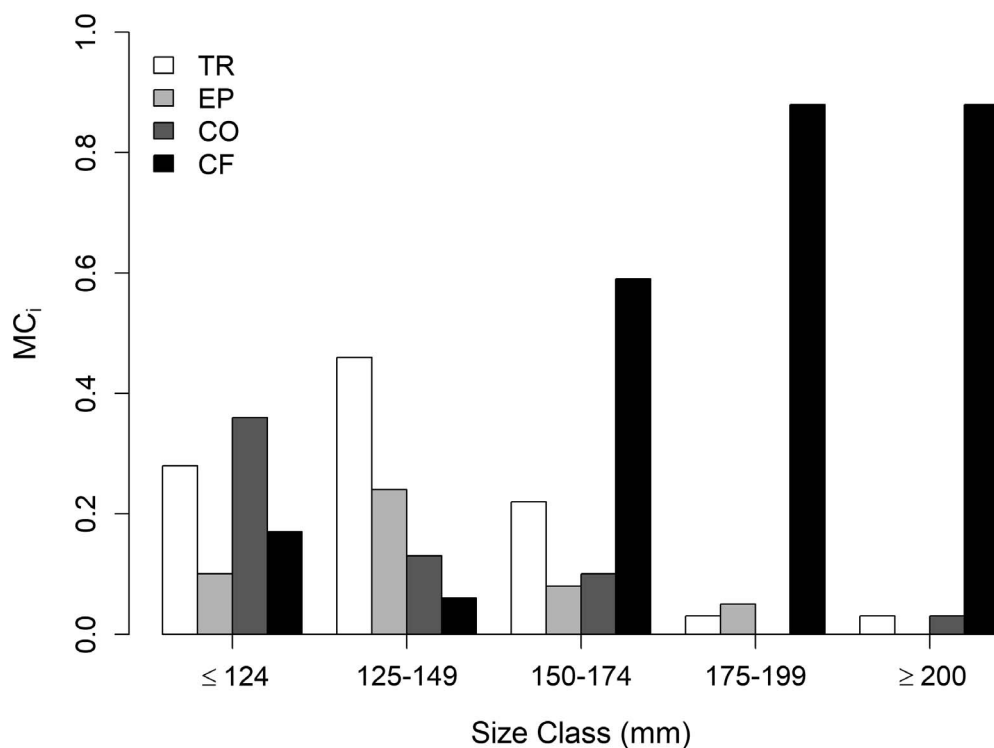
In total, 359 Redspot Chubs ranging in size from 78–241 mm TL were collected from Spavinaw Creek, and 158 individuals had stomach contents for an overall %E of 0.56. A positive relationship between the  $MC_i$  value of crayfish and Redspot Chub size was observed. The 150–174 mm size class marked an obvious transition to Redspot Chub consuming crayfish as their predominant prey (Fig. 1). Logistic regression revealed a significant ontogenetic diet shift ( $P < 0.01$ ) occurred at approximately 162 mm (95% confidence interval [CI] =  $\pm 8$  mm, Fig. 2) TL. Therefore, Redspot Chub were split into two groups for additional analyses with individuals  $\geq 162$  mm hereafter referred to as “big” Redspot Chub (RSCB,  $n = 88$ ) and individuals  $< 162$  mm as “small” Redspot Chub (RSCS,  $n = 70$ ). Size delineations were further corroborated by differences in trophic position and diet breadth between the size classes. Overall, RSCB ( $T_a = 3.9$ , 95% CI  $\pm 0.1$ ) occupied a significantly higher trophic position than RSCS ( $T_a = 3.2$ , 95% CI  $\pm 0.2$ ) based on non-overlapping 95% CIs. The average diet breadth value for RSCB ( $B = 0.15$ ) was much lower than RSCS ( $B = 0.59$ ) as well.

Winter values of %E stomachs were 63% and 62% for RSCS and RSCB, respectively. Small Redspot Chub utilized five prey categories (crayfish, Diptera, Ephemeroptera, Oligochaeta, and Trichoptera), while RSCB only fed on two: crayfish and Trichoptera. Winter diet breadth values were high for RSCS ( $B = 0.74$ ) but low for RSCB ( $B = 0.28$ ). During the winter, Ephemeroptera and Trichoptera were the most frequently encountered prey types in RSCS diets ( $O = 0.42$ ), while RSCB consumption of crayfish was nearly ubiquitous ( $O = 0.88$ ). The most important prey types for RSCS and RSCB were Trichoptera ( $MC = 0.36$ ) and crayfish ( $MC = 0.87$ ), respectively (Tables 1, 2). The winter RSCS Amundsen plot indicated crayfish and Oligochaeta were specialized on by a small proportion of the population, while Trichoptera made up a large proportion of the calories in nearly half of the RSCS stomachs. Ephemeroptera were encountered in the same number of stomachs as Trichoptera but contributed fewer calories (Fig. 3). For RSCB, the winter Amundsen plot denotes population specialization on crayfish (Fig. 4).

The %E value for spring RSCB decreased to 43%, but remained at 63% for RSCS. Spring prey resource use increased to five types for RSCB (crayfish, Diptera, Ephemeroptera, Lepidoptera, and Trichoptera). Small Redspot Chub utilized the same prey resources as winter, with the exception of Oligochaeta. Spring  $B$  values decreased from winter for both RSCS and RSCB. Diet breadths were moderate for RSCS ( $B = 0.58$ ) and low for RSCB ( $B = 0.11$ ). Trichoptera ( $O = 0.67$ ) and Ephemeroptera ( $O = 0.50$ ) remained the two most commonly encountered prey types in RSCS diets, and crayfish were consumed by 83% of RSCB. Trichoptera ( $MC = 0.46$ ) was the most important prey type for RSCS, followed by Ephemeroptera ( $MC = 0.37$ , Table 1). Crayfish ( $MC = 0.83$ ) was the most important prey for RSCB in the spring (Table 2). All prey types were specialized on by RSCS to varying degrees with a small percentage of the population consuming crayfish and Diptera, and a larger proportion of the population specializing on Trichoptera and Ephemeroptera (Fig. 3). Similar to winter, RSCB exhibited population specialization on crayfish (Fig. 4).

Summer values of %E stomachs were 53% and 54% for RSCS and RSCB, respectively. The diversity of prey types

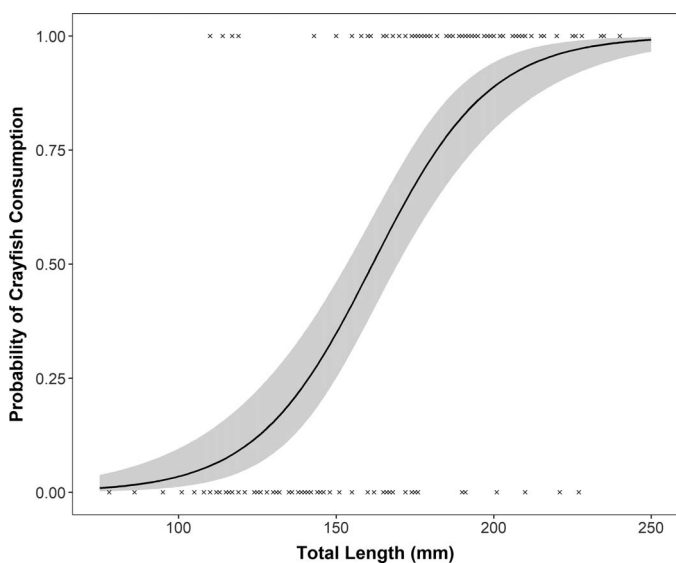




**Fig. 1.** Variation by size of prey mean proportion by calorie ( $MC_i$ ) values in the diets of 158 Redspot Chub. Prey types with  $MC_i$  values  $\geq 0.1$ , in at least one size bin, are displayed for comparison. Abbreviations for prey types are as follows: (CO) Coleoptera, (CF) crayfish, (EP) Ephemeroptera, and (TR) Trichoptera.

encountered in Redspot Chub diets was higher in summer than all other seasons for both RSCS and RSCB. The number of prey categories found in summer diets increased to ten for RSCS (Amphipoda, Coleoptera, crayfish, Diptera, Ephemeroptera, Gastropoda, Lepidoptera, Odonata, Plecoptera, and Trichoptera) and nine for RSCB (Coleoptera, crayfish, Diptera, Ephemeroptera, Gastropoda, Lepidoptera, Orthoptera, Plecoptera, and Trichoptera). Diet breadth was low for both RSCS ( $B = 0.31$ ) and RSCB ( $B = 0.09$ ). Trichoptera ( $O = 0.56$ ) and crayfish ( $O = 0.76$ ) had the highest  $O_i$  values for

RSCS and RSCB, respectively, but Coleoptera were encountered almost as frequently in RSCS diets ( $O = 0.49$ ). Trichoptera ( $MC = 0.36$ ) and Coleoptera ( $MC = 0.32$ ) were similar in prey importance for RSCS (Table 1), and crayfish was the most important prey for RSCB ( $MC = 0.76$ , Table 2). Summer Amundsen plots for RSCS reveal Amphipoda, Diptera, and Gastropoda were relatively unimportant, crayfish, Ephemeroptera, Lepidoptera, Odonata, and Plecoptera were specialized on by a small proportion of the population, and Trichoptera and Coleoptera were the two most important prey types (Fig. 3). While RSCB incorporated more prey types in their summer diets, all prey types, excluding crayfish, were relatively unimportant as crayfish dominated summer diets (Fig. 4).



**Fig. 2.** Logistic regression of Redspot Chub total length (mm) and the probability of crayfish in the diet (1 = crayfish present, 0 = crayfish absent). Redspot Chub underwent a significant ontogenetic diet shift (i.e., the probability of crayfish consumption was  $> 0.5$ ) at 162 mm (95% CI = 154–170 mm).

Fall %E values were 65% and 61% for RSCS and RSCB, respectively. The number of prey categories utilized in fall was limited to three (Coleoptera, crayfish, and Trichoptera) for RSCS and two (Coleoptera and crayfish) for RSCB. Fall diet breadth values were high for RSCS ( $B = 0.74$ ) and low for RSCB ( $B = 0.12$ ). Trichoptera remained the most frequently encountered prey item in RSCS stomachs ( $O = 0.57$ ), but crayfish consumption increased substantially relative to other seasons as they were found in 43% of the fall diets. Nearly every RSCB fed on crayfish in the fall ( $O = 0.94$ ). Trichoptera ( $MC = 0.45$ ) and crayfish ( $MC = 0.43$ ) had nearly equal values of prey importance for fall RSCS diets (Table 1), while crayfish dominated the diet of RSCB ( $MC = 0.94$ , Table 2). Fall RSCS Amundsen plots indicate all prey types were specialized on to varying degrees, and RSCB exhibited population specialization on crayfish (Figs. 3, 4).

**DISCUSSION**

Logistic regression demonstrated a significant relationship between Redspot Chub TL and crayfish consumption. The ontogenetic shift to crayfish predation was estimated to

**Table 1.** Summary of Redspot Chub <162 mm TL seasonal diet indices, where  $n$  is the number of stomachs containing prey,  $B$  is the standardized Levins's index, %E is the percent of empty stomachs,  $O_i$  is frequency of occurrence,  $N_i$  is percent composition by number,  $MN_i$  is mean proportion by number,  $C_i$  is percent composition by calories, and  $MC_i$  is mean proportion by calories. Prey items are listed in order of importance ( $MC_i$ ).

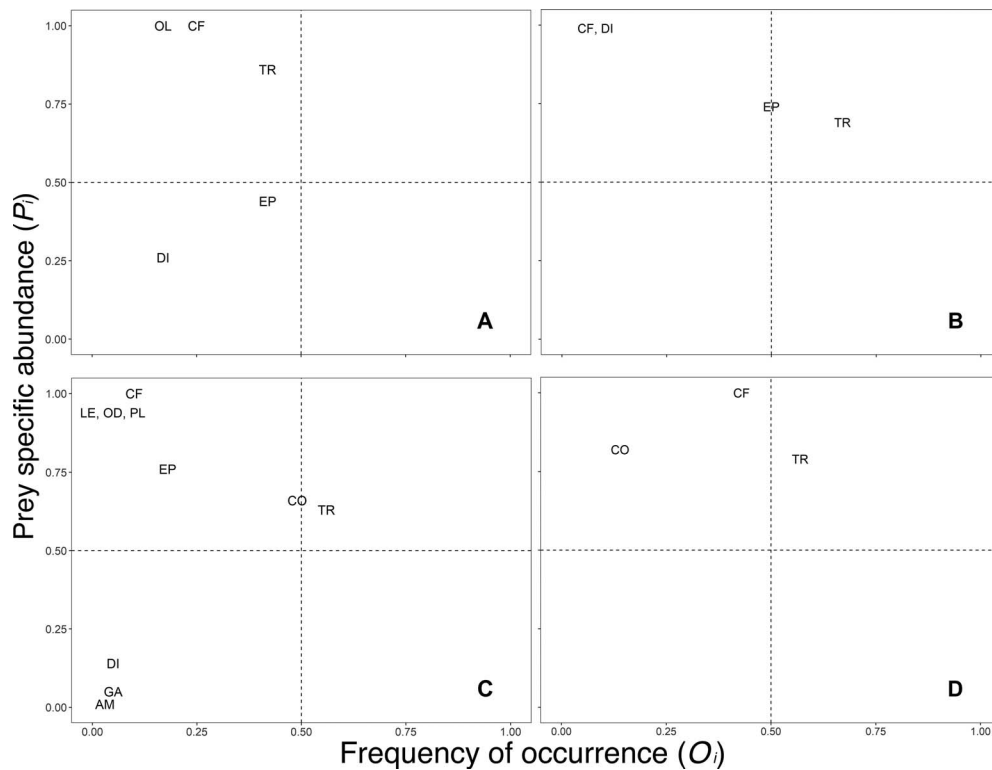
Season	$B$	%E	Prey	$O_i$	$N_i$	$MN_i$	$C_i$	$MC_i$
Winter $n = 12$	0.74	63	Trichoptera	0.42	0.19	0.26	0.01	0.36
			Crayfish	0.25	0.11	0.25	0.69	0.25
			Ephemeroptera	0.42	0.19	0.20	0.00	0.18
			Oligochaeta	0.17	0.11	0.17	0.30	0.17
Spring $n = 12$	0.58	63	Diptera	0.17	0.41	0.13	0.00	0.04
			Trichoptera	0.67	0.63	0.56	0.03	0.46
			Ephemeroptera	0.50	0.25	0.32	0.04	0.37
			Crayfish	0.08	0.04	0.04	0.93	0.08
Summer $n = 39$	0.31	53	Diptera	0.08	0.08	0.08	0.00	0.08
			Trichoptera	0.56	0.41	0.41	0.03	0.36
			Coleoptera	0.49	0.41	0.33	0.04	0.32
			Ephemeroptera	0.18	0.07	0.09	0.02	0.14
			Crayfish	0.10	0.03	0.07	0.84	0.10
			Lepidoptera	0.03	0.01	0.03	0.06	0.03
			Plecoptera	0.03	0.01	0.03	0.00	0.03
			Odonata	0.03	0.01	0.01	0.01	0.02
			Diptera	0.05	0.02	0.02	0.00	0.01
			Gastropoda	0.05	0.02	0.02	0.00	0.00
Fall $n = 7$	0.74	65	Amphipoda	0.03	0.01	0.01	0.00	0.00
			Trichoptera	0.57	0.44	0.48	0.02	0.45
			Crayfish	0.43	0.33	0.43	0.95	0.43
			Coleoptera	0.14	0.22	0.10	0.03	0.12

occur at 162 mm TL (Fig. 2). The transition to crayfish specialization appeared relatively abrupt as illustrated by the change in crayfish  $MC_i$  values once Redspot Chub reach 150 mm TL (Fig. 1). Although our description of an ontogenetic diet shift is a novel finding for Redspot Chub, it is not the first known ontogenetic diet shift described in the genus *Nocomis*. Cloe et al. (1995) described an ontogenetic diet shift from insects to molluscs for Bull Chub (*N. raneyi*) in the James River, Virginia, and Lachner (1950) reported differential habitat and food preferences between juvenile and adult

River Chub (*N. micropogon*) and Hornyhead Chub. The concept of an ontogenetic niche recognizes that fish populations are commonly size-structured such that different size classes display intraspecific variation in ecological roles related to resource use (Helfman et al., 1997). Consequently, the size-specific nature of ontogenetic niche shifts plays a vital role in shaping community structure, species' life histories, growth rates, and intra- and interspecific interactions (Werner and Gilliam, 1984; Winemiller, 1989; Osenberg et al., 1992; Mittelbach and Persson, 1998; Dauwalter

**Table 2.** Summary of Redspot Chub  $\geq 162$  mm TL seasonal diet indices, where  $n$  is the number of stomachs containing prey,  $B$  is the standardized Levins's index, %E is the percent of empty stomachs,  $O_i$  is frequency of occurrence,  $N_i$  is percent composition by number,  $MN_i$  is mean proportion by number,  $C_i$  is percent composition by calories, and  $MC_i$  is mean proportion by calories. Prey items are listed in order of importance ( $MC_i$ ).

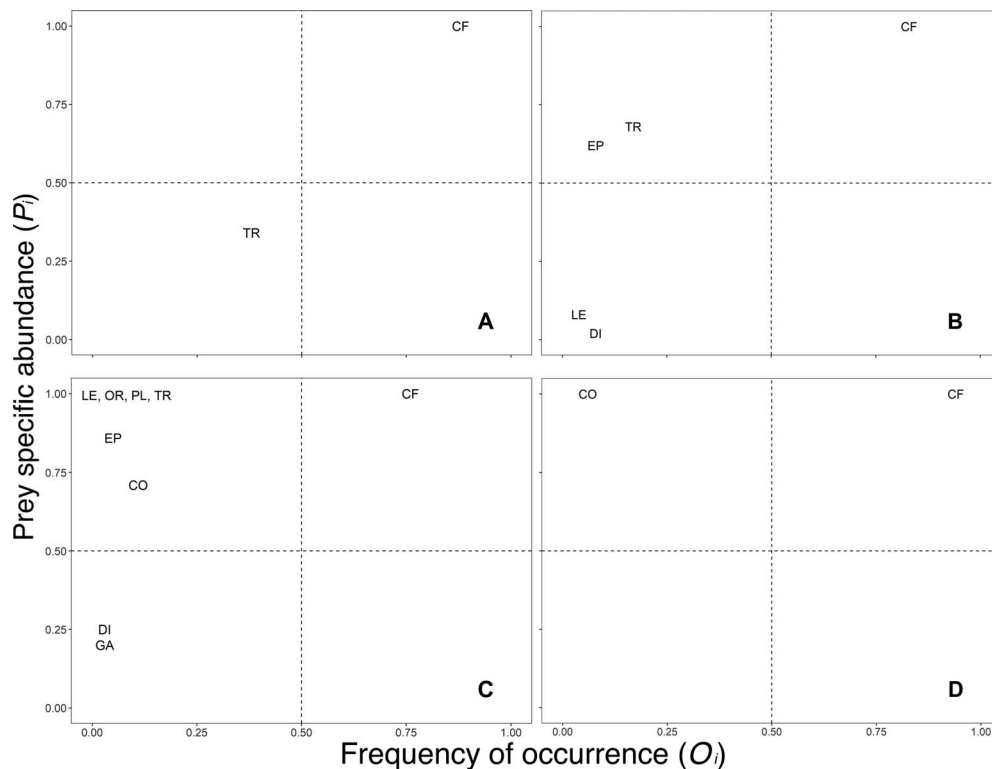
Season	$B$	%E	Prey	$O_i$	$N_i$	$MN_i$	$C_i$	$MC_i$
Winter $n = 8$	0.28	62	Crayfish	0.88	0.39	0.71	1.00	0.87
			Trichoptera	0.38	0.61	0.29	0.00	0.13
Spring $n = 24$	0.11	43	Crayfish	0.83	0.42	0.79	0.99	0.83
			Trichoptera	0.17	0.44	0.13	0.00	0.11
			Ephemeroptera	0.08	0.06	0.03	0.00	0.05
			Diptera	0.08	0.06	0.02	0.00	0.00
			Lepidoptera	0.04	0.02	0.02	0.01	0.00
Summer $n = 38$	0.09	54	Crayfish	0.76	0.62	0.76	0.99	0.76
			Coleoptera	0.11	0.19	0.07	0.00	0.07
			Ephemeroptera	0.05	0.06	0.04	0.00	0.05
			Lepidoptera	0.03	0.02	0.03	0.00	0.03
			Orthoptera	0.03	0.02	0.03	0.01	0.03
			Plecoptera	0.03	0.02	0.03	0.00	0.03
			Trichoptera	0.03	0.02	0.03	0.00	0.03
			Diptera	0.03	0.02	0.01	0.00	0.01
Fall $n = 18$	0.12	61	Gastropoda	0.03	0.02	0.01	0.00	0.01
			Crayfish	0.94	0.71	0.94	1.00	0.94
			Coleoptera	0.06	0.29	0.06	0.00	0.06



**Fig. 3.** Amundsen plots for small (<162 mm TL) Redspot Chub (RSCS) collected from Spavinaw Creek, OK in (A) winter ( $n = 12$ ), (B) spring ( $n = 12$ ), (C) summer ( $n = 39$ ), and (D) fall ( $n = 7$ ). Abbreviations for prey types are as follows: (AM) Amphipoda, (CO) Coleoptera, (CF) crayfish, (DI) Diptera, (EP) Ephemeroptera, (GA) Gastropoda, (LE) Lepidoptera, (OD) Odonata, (OL) Oligochaeta, (PL) Plecoptera, (TR) Trichoptera. Prey items separated by commas reside on the same coordinates.

and Fisher, 2008; Lattuca et al., 2008). Separating Redspot Chub by size class in this study highlighted functional differences in feeding ecology related to size within the species. Future research is necessary to determine the prevalence of ontogenetic diet shifts in the genus *Nocomis*, as well as to determine if ontogenetic diet shifts are stream specific.

Past descriptions of Redspot Chub as benthic carnivores held true for both size classes in our study (Fellely and Hill, 1983; McNeely, 1987; Miller and Robison, 2004; German et al., 2010). This is likely due to the fact that Redspot Chub are specially adapted to utilize chitin, the primary component of arthropod exoskeletons, as a source of nitrogen and energy due to their elevated levels of the digestive enzyme chitinase



**Fig. 4.** Amundsen plots for large ( $\geq 162$  mm TL) Redspot Chub (RSCB) collected from Spavinaw Creek, OK in (A) winter ( $n = 8$ ), (B) spring ( $n = 24$ ), (C) summer ( $n = 38$ ), and (D) fall ( $n = 18$ ). Abbreviations for prey types are as follows: (CO) Coleoptera, (CF) crayfish, (DI) Diptera, (EP) Ephemeroptera, (GA) Gastropoda, (LE) Lepidoptera, (OR) Orthoptera, (PL) Plecoptera, (TR) Trichoptera. Prey items separated by commas reside on the same coordinates.

and specialized pharyngeal teeth that pierce and shred invertebrate exoskeletons (German et al., 2010). However, by using a suite of diet analyses, major intraspecific differences in feeding ecology became obvious between the size classes. RSCS ( $T_a = 3.2$ , 95% CI  $\pm 0.2$ ) consumed a higher proportion of prey resources occupying lower trophic levels; therefore, they were estimated to occupy a significantly lower trophic position than RSCB ( $T_a = 3.9$ , 95% CI  $\pm 0.1$ ). In Spavinaw Creek, estimated trophic levels for RSCS and RSCB are similar to young of year and adult Neosho Smallmouth Bass (*Micropterus dolomieu velox*), respectively (Rodger, unpubl. data). This suggests Redspot Chub function as keystone predators alongside the native Smallmouth Bass. The average diet breadth value for RSCB ( $B = 0.15$ ) was much lower than RSCS ( $B = 0.59$ ) because RSCB get almost all of their calories from one prey resource. The low RSCB diet breadth estimate, high average prey importance value of crayfish across seasons ( $MC = 0.85$ ), and their feeding strategy revealed in the Amundsen plots (i.e., population specialization on crayfish) provides compelling evidence that RSCB exhibit a narrow niche width and incredibly specialized feeding ecology in Spavinaw Creek (Amundsen et al., 1996). For RSCS, Trichoptera were the most important prey throughout the year, but their lower average seasonal prey importance value ( $MC = 0.41$ ) demonstrates they did not dominate RSCS diets in the same manner crayfish dominated RSCB diets. Ephemeroptera, Coleoptera, and crayfish varied in their importance seasonally for RSCS. Crayfish ranked second in importance in the fall and winter, Ephemeroptera ranked second in the spring, and Coleoptera became the second most important prey type in summer (Table 1). Trichoptera, Ephemeroptera, and Coleoptera prey types in RSCS stomachs were most often represented by members of the families Helicopsychidae, Heptageniidae, and Elmidae, respectively. Based on the Amundsen plot, RSCS feeding strategy related to niche width contribution most closely aligns with populations that exhibit a high between-phenotype component. This can be observed in the feeding strategy diagrams as nearly all prey points, excluding unimportant prey types, are positioned in the upper half of seasonal Amundsen plots (Fig. 3). Species employing high between-phenotype component feeding strategies have relatively low intraspecific resource overlap because of individual specialization within the population. Additionally, most prey types would fall above a diagonal line running from the upper left to the lower right of the graph, which indicates a predator population with a narrow niche width (Amundsen et al., 1996). However, certain prey types were specialized on by a larger proportion of the RSCS population. For example, a pattern emerged where the two most important prey types were specialized on by approximately half the population, while smaller proportions of the population specialized on less commonly encountered prey types (Fig. 3). The specialist nature revealed in the Amundsen plots seemingly contradicts the moderate to high estimated values of seasonal diet breadth. The apparently disparate conclusions are driven by the fact that RSCS seasonal  $MC_i$  values for their two most important prey types are relatively similar (Table 1). This drives up the standardized Levins's index value, which assesses how evenly resources are consumed by a predator. Instead of concluding that RSCS are generalist consumers that utilize available resources evenly, we place the context of the diet breadth results within the framework of the niche width contribution results

to highlight the fact that RSCS are specialists that seasonally consume their two most important prey types in a similar manner.

Accurately describing predators' diets is a complex task that requires particular attention to study design (Garvey and Chipps, 2012); thus, it is important to keep a few points in mind in regard to the current study. In general, diet studies benefit from large sample sizes (Schmitt et al., 2018). Several factors increased the difficulty of obtaining larger sample sizes in this study including: splitting our overall sample into two size classes spread across four seasons, consistently high %E values, and fall flooding that prevented additional sampling. However, diet studies that fail to account for size-specific and/or seasonal differences in species' feeding ecology may obfuscate the seasonal importance of prey items to various life stages. Furthermore, Angermeier (1982) found seasonal differences in the diet of the closely related Hornyhead Chub. Thus, it was determined to be more beneficial to employ a study design that accounted for ontogenetic and seasonal differences in diets in order to gain insight that would otherwise have been lost if diets were pooled (Kelso, 1973; Winemiller, 1989; Dauwalter and Fisher, 2008). For example, McNeely (1987) studied the diets of Redspot Chub ranging from 40–150 mm SL in a different Oklahoma Ozark Highlands stream and reported that crayfish only made up 11% of their diets. German et al. (2010) did not list crayfish in their diet summary of Redspot Chub from Flint Creek, Arkansas, and no mention was made of the size of Redspot Chub included in the study. Consequently, because previous studies gave no attention to size-specific diet relationships, it is possible that the contribution of crayfish to Redspot Chub diets was misrepresented, especially for large individuals. Additionally, if RSCS and RSCB diets were pooled in the current study, the overall importance of smaller invertebrates like Trichoptera, Ephemeroptera, and Coleoptera would have been severely diminished as one large prey item (e.g., crayfish) can provide a much larger caloric contribution than numerous smaller prey items (Chipps and Garvey, 2007). Analyzing the diets seasonally also highlighted the increase in the diversity of prey items consumed by both size classes of Redspot Chub in the summer. Moreover, Coleoptera were important prey for RSCS in the summer even though they were not represented in the diets from the cooler water periods (i.e., winter and spring; Table 1). If diets were pooled over the course of the study, the seasonal importance of Coleoptera to RSCS would not have been detected. Ultimately, larger seasonal sample sizes and data from additional streams may be needed to generalize diet results for the species as a whole, but we believe our sample sizes are sufficient to describe the ontogenetic diet shift and the intraspecific differences in feeding ecology between the two size classes of Redspot Chub.

Another inherent difficulty within diet studies is the likelihood of underestimating the contribution of different prey types to predators' diets because it is common for prey items to be in advanced stages of digestion, and different taxa are digested at different rates (Bromley, 1994; Garvey and Chipps, 2012; Preston et al., 2017). To address this issue and provide more accurate estimates of the caloric contribution of prey types to Redspot Chub diets, additional effort was expended to measure prey items and utilize regression equations to obtain estimates of original prey size at ingestion (Benke et al., 1999; Sabo et al., 2002; Garvey and



Chipps, 2012; Rodger and Starks, 2020). Because Redspot Chub possess pharyngeal teeth that mechanically break down prey prior to entering the digestive track, it was sometimes difficult to differentiate prey. Therefore, care was taken not to inflate prey counts by relying on consistent body parts (e.g., heads, casings) and assigning the estimated seasonal average size for prey when accurate measurements were precluded by digestion. Lastly, we did not collect data on the relative abundance of prey types in Spavinaw Creek; therefore, one aspect of Redspot Chub feeding ecology that we cannot address in this study is prey preference or selectivity.

The conservation of Redspot Chub is a priority because it is designated as a species of concern in three of the four states in which it occurs (Haslouer et al., 2005; ODWC, 2016; Robison and Buchanan, 2020; Whitney et al., 2020). It has been demonstrated that specialist species are at a higher risk of population decline because their narrow niches make them especially susceptible to environmental change (McKinney, 1997; Munday, 2004; Biesmeijer et al., 2006; Wilson et al., 2008; Clavel et al., 2011). Redspot Chub distributions are tied to their strict habitat affinity for clear, spring-fed streams. Thus, increased sedimentation continues to put this species at risk (Robison and Buchanan, 2020; Whitney et al., 2020). Based on the data presented in this study, there is now evidence that in addition to being habitat specialists, Redspot Chub exhibit specialist feeding strategies as well. If the specialized diet of Redspot Chub documented in Spavinaw Creek is found to be consistent throughout the species' range, it further underscores the species' limited tolerance for environmental change, including perturbations that may detrimentally affect crayfish populations, which are among the most threatened of all aquatic taxa (Larson and Olden, 2010). Due to the conservation concern for Redspot Chub, it is imperative that research continues to fill critical data gaps regarding Redspot Chub biology and ecology to help predict how future stressors may affect population trends.

#### DATA ACCESSIBILITY

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