

Effects of changes in alternative prey densities on predation of drifting lake sturgeon larvae (*Acipenser fulvescens*)

Justin Waraniak ^a, Shaley Valentine^{a,b} and Kim Scribner ^a

^aDepartment of Fisheries and Wildlife, Michigan State University, East Lansing, MI, USA; ^bDepartment of Watershed Sciences, Utah State University, Logan, UT, USA

ABSTRACT

Predator–prey interactions including prey switching, predator swamping, and size-selectivity are important in maintaining multi-species systems. In fishes, early life stages are often recruitment bottlenecks due to high mortality partially caused by predation. High mortality is of particular concern for threatened species such as lake sturgeon (*Acipenser fulvescens*). Effects of different relative prey densities were examined using two predatory fishes [rock bass (*Ambloplites rupestris*) and hornyhead chub (*Nocomis biguttatus*)] and two density treatments of three prey [lake sturgeon, mayflies (Family: Heptageniidae), and suckers (Family: Catostomidae)]. Treatments consisted of prey introduced to predators in a series of pulses 30 min apart. In the initial low-density treatment, predators were offered prey at a pulse of prey at a 13:13:4 ratio of mayfly, suckers, and lake sturgeon, and a second pulse with a 1:1:1 prey ratio during the second pulse. In the equal-density treatment prey numbers were equivalent during both pulses. Larval sturgeon survival, predator preference, and size selection were measured for each trial. Lake sturgeon were the least preferred prey species while mayflies were positively selected. Hornyhead chub preference for lake sturgeon was higher in the equal-density treatment than in the low-density, indicating initial prey availability affected predator foraging behaviour. High densities of preferred macroinvertebrate prey could protect threatened lake sturgeon larvae from predation.

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Introduction

Predator–prey interactions play a crucial role in structuring communities, through both direct and indirect effects. Direct effects of predation include higher mortality rates and altered densities of prey populations. Indirect effects can manifest as changes in prey behaviour while in the presence of predators (e.g. shifts in foraging behaviour; Semlitsch 1987; Schmitz 1998; Creel and Christianson 2008), but can also include reduced predation pressure on one prey species caused by high abundance of another prey species (Pepin and Shears 1995). Reduction of predation pressure can be due to density-dependent predator preference (prey switching; Murdoch 1969; Ims 1990; Sundell et al. 2003) for certain prey items, as well as reduced predator effectiveness for capturing preferred prey when there is high relative abundance of other prey (multi-species predator swamping; Ims 1990; Aukema and Raffa 2004). Predator preference, prey switching, and predator swamping help maintain the coexistence of multiple prey species in an environment and could be important factors affecting successful recruitment in some fisheries (Fryxell and Lundberg 1994; Godiksen et al. 2006).

CONTACT Justin Waraniak  jmwara@umich.edu

High abundance of alternative prey can reduce predation pressure on a target prey species through prey switching or predator swamping (Ims 1990).

Switching occurs when one prey item becomes more abundant, and the feeding habits of the predator change so that they consistently preferentially consume the more abundant prey species (Kean-Howie 1988; Sundell et al. 2003). Prey switching is particularly pronounced when alternative prey species require different feeding strategies (Murdoch et al. 1975; Humphries et al. 2016). How predator foraging behaviour is mediated over short timescales is particularly important for predator–prey dynamics of larval fishes and their predators, as some larval fishes undergo diel vertical migrations or lotic drifting behaviours, causing their availability to predators to temporally fluctuate (Johnson and McKenna 2007; Humphries et al. 2016).

Predator swamping dilutes direct predation effects on a prey species through a high abundance of prey items. Typically, predator swamping is associated with synchronous reproduction events (Ims 1990) or schooling prey (Major 1978; Stier et al. 2013). The high abundance of prey items as a short-term pulse reduces the chance that any one prey item will be eaten. In addition, the high overall prey abundance may reduce the predation rate on relatively rare prey taxa, making preferred but rare prey more difficult or relatively less advantageous to selectively forage for (prey shielding; Kean-Howie et al. 1988; Aukema and Raffa 2004; Koss et al. 2004). The potential for high numbers of prey items to reduce overall predation on a single prey species is crucial to understand in dynamic environments, particularly for threatened and rare species.

The larval stage of fishes is a critical period in determining population levels of recruitment, and predation has a prodigious effect on larval mortality for many fish species (Bailey and Houde 1989; Legget and DeBlois 1994). In some systems, predation is the driving factor affecting larval recruitment, as exemplified by alewife (*Alosa pseudoharengus*) predation on mortality rates of larval yellow perch (*Perca flavescens*; Mason and Brandt 1996), and the effect predator density has on the recruitment of larval capelin (*Mallotus villosus*; Gjørseter et al. 2016). It can be difficult to investigate predation effects in natural systems as fish larvae often require specialized techniques to be detected in predator diet analysis (e.g. molecular genetic assays, stable isotope analysis; Schooley et al. 2008; Carreon-Martinez et al. 2011; Waraniak et al. 2017). However, experimental studies can simplify complex systems and offer direct evidence of how specific ecological factors can influence the predation of larval fishes (Stier et al. 2013). Quantifying predator–prey relationships in ecological systems where these relationships control population dynamics and recruitment is critical for species of conservation concern.

Sturgeons (Family: Acipenseridae) are of global conservation concern as the majority of species are threatened (Duncan and Lockwood 2001). Predation may be an important factor in the recruitment of multiple sturgeon species (Parsley 2002; Gadomski and Parsley 2005a, 2005b; Duong et al. 2011; Flowers et al. 2011). At the larval stage, lack of protective scutes and drifting behaviour leaves larval sturgeons susceptible to predation (Auer and Baker 2002; Peterson et al. 2007). Predator preference for juvenile sturgeons has been studied in pallid sturgeon (*Scaphirhynchus albus*; French et al. 2014) and white sturgeon (*Acipenser transmontanus*; Gadomski and Parsley 2005a, 2005b). However, comparatively little information is available on the predator–prey interactions for other sturgeon species (Parsley et al. 2002), including the lake sturgeon (*Acipenser fulvescens*).

Lake sturgeon is a species of conservation concern in the Laurentian Great Lakes region (Peterson et al. 2007). Adults are highly fecund, but early life-stage mortality can be high, leading to variable recruitment (Smith and King 2005; Caroffino et al. 2010a). Alterations to river systems, including impoundments, pollution, and reduced spawning habitat have affected lake sturgeon recruitment (Peterson et al. 2007). In addition, reductions in populations of co-distributed prey species may expose larval lake sturgeon to high levels of predation. Lake sturgeon larvae are susceptible to predation by a variety of predator taxa, including fishes (Waraniak et al. 2017) and crayfish (Crossman 2008). Research has quantified egg predation, but information on losses due to predation during the larval stage is lacking (Crossman 2008; Caroffino et al. 2010b). Predation has been a major factor affecting recruitment of other sturgeon species (Parsley et al. 2002; Steffenson et al.

2015), and may be an important factor contributing to the lack of natural lake sturgeon recruitment. Understanding the predator–prey relationships between lake sturgeon, other prey species, and their potential predators will prove useful in understanding why natural recruitment is low. Furthermore, possible management actions to increase populations of co-occurring alternative prey in spawning rivers may have indirect benefits to larval sturgeon survival.

In this study, experiments were conducted with two common riverine predators and three prey taxa from the Upper Black River (UBR) in Cheboygan County, Michigan, USA. Rock bass (*Ambloplites rupestris*) and hornyhead chub (*Nocomis biguttatus*) were used as predators; and lake sturgeon larvae, larval suckers (Family: Catostomidae), and mayfly larvae (Family: Heptageniidae) were used as prey. Densities of prey taxa were manipulated to address two primary objectives. First, the experiment assessed whether short-term prey switching behaviour influenced the predation rate on larval lake sturgeon. Second, the study tested whether elevated alternative prey abundances provided a shielding effect for lake sturgeon larvae. Additionally, analysis of predator size-selectivity was conducted.

Materials and methods

Study site and experimental enclosures

The UBR in Cheboygan County, Michigan, USA is the largest tributary of Black Lake and is used as spawning grounds for a well-studied population of lake sturgeon (~1200 adults; Pledger et al. 2013). The UBR is a wadeable stream with an average discharge rate of $8.3 \text{ m}^3 \text{ s}^{-1}$ during the lake sturgeon spawning season (Forsythe et al. 2012). The spawning grounds are composed primarily of cobble and gravel substrate. One river kilometre below the spawning grounds, UBR downstream elevational changes decrease and substrate transitions to sand and silt (Waraniak 2017). Water depth can be highly variable, but is typically $<1.5 \text{ m}$ (Forsythe et al. 2012). This study was conducted in spring 2016 at the Black River Streamside Rearing Facility (BR-SRF) near Kleber Dam. Water supplied to the BR-SRF was taken directly from the UBR (Kleber Reservoir).

Experiments were conducted in two $12.2 \text{ m} \times 0.5 \text{ m}$ flow-through fibreglass raceways (Figure 1). No substrate was added to raceways. Raceways were filled with UBR water to a depth of 0.27 m . Recirculating pumps were used to generate a laminar flow rate of $0.10\text{--}0.14 \text{ m/s}$, a relatively slow but realistic flow in the UBR (Smith and King 2005). Predator exclusion areas were created for the introduction and collection of prey at both ends of the raceways with $1.5 \text{ cm} \times 1.5 \text{ cm}$ steel mesh. Aquarium dip nets were placed over the outflows during each trial to capture prey that had travelled

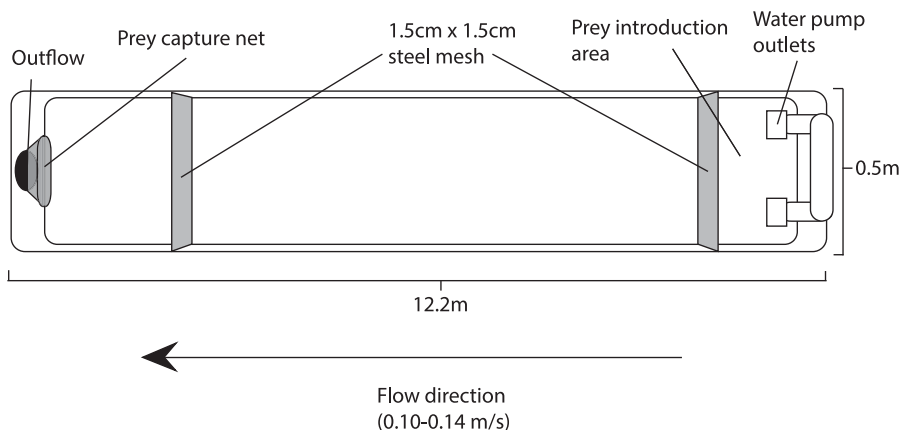


Figure 1. Diagram of experimental raceways used in predation trials.

the length of the raceway and were not consumed by predators. Trials were conducted in dark conditions to mimic nighttime light levels when prey drift (Smith and King 2005). A vinyl tarp was erected around the raceways to reduce the risk of disturbances that might affect prey and predator behaviours during the experimental trial.

Predator and prey collection and holding

Rock bass and hornyhead chub predators were collected near the lake sturgeon spawning grounds in the UBR and retained at the BR-SRF for experimental trials. These species were chosen because they were known to consume larval lake sturgeon in an experimental setting based on previous research (Crossman 2008) or molecular diet analysis had detected numerous instances of lake sturgeon predation from wild-caught fish (Waraniak et al. 2017). A barge electrofisher with a three-person crew (settings – 18 V, 4A) was used to collect predator fish. To maintain similar ratios of predator and prey biomass between trials and reduce the chance gape limitation or ontogenetic diet shifts could affect results, only predators of a certain size class were collected. All rock bass were between 123 and 209 mm total length (TL; mean \pm SD, 154 mm \pm 21.7 mm), and all hornyhead chub were between 80 and 157 mm TL (mean \pm SD, 111 mm \pm 19.3 mm).

Predators were maintained in covered, outdoor flow-through fibreglass raceways before trials were conducted. All predators were naive to trials. Food was withheld from predators for 24–26 h before being used in a trial. Four hours before trials began, predators were moved to the indoor trial raceways for acclimation. Recirculating pumps were turned on only one hour before the start of trials so predators could be acclimated to the higher flow conditions but not become fatigued from prolonged swimming in laminar flow without cover. After trials were completed, predators were released and new naive predators were collected for the next trials.

Individual prey items were collected similarly to one another from the UBR and retained at the BR-SRF. Larval sucker [white sucker (*Catostomus commersoni*), silver redhorse (*Moxostoma nigricum*)] and mayflies (Family: Heptageniidae) were selected as alternative prey because of their high abundance throughout the majority of the lake sturgeon drift period (mid-May to early July; Scribner, unpublished data). Lake sturgeon, sucker, and mayfly larvae were collected during nightly surveys using D-frame drift nets as described by Auer and Baker (2002) and Smith and King (2005). As needed, mayfly larvae were also collected in the UBR during the day using kick-nets. Wild lake sturgeon larvae were used, rather than hatchery produced larvae, to increasing applicability of results to the UBR system and because hatchery-reared larvae may be more susceptible than wild larvae to predation (Fritts et al. 2007). Sucker and mayfly larvae were retained in a covered flow-through outdoor fibreglass raceway, and lake sturgeon larvae were kept in 3.0-L polycarbonate flow-through aquaria. All prey were naive to trials and used in trials within three days of capture to reduce the possible effect captivity could have on prey behaviour and to most accurately reflect the sizes of prey in the environment.

Density treatment design

Two treatments were included in experimental trials: (i) initial low number of lake sturgeon (low) and (ii) even numbers of all three prey taxa (even). Six trials per treatment ($n = 6$ experimental units) were conducted for each predator species in a randomized complete block design. Trials were blocked by raceways to account for possible variation caused by the differences between the two different raceways, with treatment type alternating between the two raceways each time a new trial was conducted.

Each trial lasted a total of 60 min and consisted of two pulses of prey introduced to raceways 30 min apart. For the low-density treatment, the species composition of the first pulse was a 13:13:4 ratio of sucker larvae, mayfly larvae, and lake sturgeon larvae, respectively. The second pulse for the low-density treatment and both pulses for the even-density treatment had equal densities of the

three prey species. For trials with rock bass as the predator, 60 prey items per pulse were used (120 prey items total). For trials with hornyhead chub as the predator, 30 prey items per pulse were used (60 prey items total). The number of prey items for rock bass was double the number of prey for hornyhead chub to ensure some prey was recovered as previous research suggested rock bass were capable of consuming more prey than hornyhead chub (Gezon, unpublished data; Waraniak, unpublished data). One rock bass or two to three hornyhead chubs were used per trial. Multiple hornyhead chubs were used because some cyprinids will not feed unless in the presence of conspecifics (Persson 1982).

At the end of each trial, predators and prey were removed from each raceway and data was collected. Total length (TL) was measured for each predator, and predators were released back into the UBR. Prey were collected from raceways using dip nets after predators were removed. The number of prey recovered was subtracted from the number of introduced prey during the trial to estimate the number of prey consumed by the predator. A control trial was run without a predator, and >97% of prey items were recovered, suggesting loss due to causes other than predation was minimal.

To analyze predator size-selectivity, digital photographs of prey items were taken before and after trials with a reference ruler. For each prey item, TL was measured from photographs using ImageJ 1.49 (US National Institutes of Health; <http://rsb.info.nih.gov/nih-image/>). The average TL for each species group was calculated before release in trials and following collection after trials based on measurements using ImageJ.

Statistical analyses

To analyze the prevalence of prey switching behaviour, predator preference for each trial was calculated using Chesson's selectivity index (Equation (1); Chesson 1978).

$$\alpha = \frac{p_i/n_i}{\sum_{i=1}^3 p_i/n_i}, \quad (1)$$

where p_i is the proportion of the i th prey type in a predator diet and n_i is the proportion of the i th prey type in the environment. Chesson's selectivity index (α) is given on a scale from 0 to 1 with values under 0.33 indicating negative selection for a prey item, values over 0.33 indicating positive selection, and values near 0.33 indicating no preference in a system with three types of prey. The selectivity index compared the predator preference for each prey between the two density treatments. Each predator species was analyzed separately in a one-factor ANOVA. Chesson's selectivity index values ($n = 12$ for each predator species) were fit to a linear mixed effects model with the prey density treatment as a fixed factor, the raceway identity as a block, and the interaction between the fixed factor and block as a random factor. The ratio of number of predators to total number of prey introduced was also included as a fixed factor in the models for hornyhead chub to account for the possibility using different numbers of predators affected the results. The model fit between models with and without this factor were compared with Akaike's information criteria (AIC), and the model with the lowest AIC value was used for further analysis. The statistical significance of factors and interactions were calculated by approximating likelihood ratios of models with and without variables and interactions to a χ^2 distribution. Mixed models were fit and analyzed with the lme4 package in R (Bates et al. 2015).

To test the effects of predator swamping, the proportions of larval lake sturgeon that survived trials ($n = 12$ for each predator species) were compared between the two density treatments for each predator species. Linear mixed effects models were fit and significance of factors and interactions were calculated using the same methods as described previously. Models focused on hornyhead chub were analyzed with and without predator-prey ratios using AIC to decide whether or not to include that factor in final analyses.

To test predator size-selectivity, the size distributions of each prey taxa before and after trials were compared using a Kolmogorov–Smirnov (KS) test. Holm–Bonferroni corrections adjusted for type-I error with multiple comparisons for each predator species. All statistical analyses were conducted using R statistical software (v. 3.2.2, R Core Team).

Results

Chesson's selectivity index and prey switching

Lake sturgeon was the least preferred prey item (mean Chesson's alpha = 0.14 for rock bass, 0.11 for hornyhead chub; Table 1). Overall, preference for larval catostomids was slightly higher than preference for lake sturgeon larvae but still negative (mean Chesson's alpha = 0.16 for rock bass, 0.15 for hornyhead chub). Heptageniid mayfly larvae were the most preferred prey for both species, with both predator species exhibiting a positive preference (mean Chesson's alpha = 0.70 for rock bass, 0.79 for hornyhead chub).

The ratio of predators to total number of prey did not have a significant effect on results in hornyhead chub, and hence this predator–prey ratio factor was not included in further analyses. Hornyhead chub exhibited a significantly higher preference for lake sturgeon in the equal-density treatment than the low-density treatment ($\chi^2 = 5.642$, $P = 0.018$), even though hornyhead chub still negatively selected lake sturgeon in both treatments (Figure 2). Hornyhead chub consumed lake sturgeon larvae only once in the low-density treatment and still showed strong negative selection against lake sturgeon in the equal-density treatment (mean Chesson's alpha = 0.11). Rock bass did not exhibit a difference in preference for lake sturgeon between the two treatments ($\chi^2 = 0.224$, $P = 0.636$; mean Chesson's alpha = 0.14; Figure 2).

Proportional survival and predator swamping

Predator–prey ratio had no significant effect in the proportional lake sturgeon survival model for hornyhead chub and was not included in the model used for final analysis. In predator trials, there was no significant difference in the proportion of surviving lake sturgeon between the two density treatments for either rock bass ($\chi^2 = 1.237$, $P = 0.266$) or hornyhead chub ($\chi^2 = 3.629$, $P = 0.057$; Figure 3).

Size-selectivity

Across all trials, lake sturgeon were the largest prey (mean TL \pm SD, 22.7 \pm 2.7 mm) followed by catostomids (mean TL \pm SD, 15.2 \pm 1.0 mm) and heptageniid mayflies (mean TL \pm SD, 7.9 \pm

Table 1. Mean (\pm SE) of Chesson's alpha and proportional survival for larval lake sturgeon in each density treatment, even number of prey items in both pulses (even) and initial low number of sturgeon in the first pulse followed by an even number of prey items in the second pulse (low sturgeon) for each predator species.

Predator species	Prey type	Density treatment	Mean Chesson's α	Mean proportional survival
Rock bass	Lake sturgeon	Even	0.164 (\pm 0.097)	0.842 (\pm 0.159)
		Low sturgeon	0.121 (\pm 0.141)	0.923 (\pm 0.094)
	Catostomid	Even	0.167 (\pm 0.153)	0.808 (\pm 0.221)
		Low sturgeon	0.152 (\pm 0.096)	0.888 (\pm 0.093)
	Heptageniid	Even	0.667 (\pm 0.228)	0.488 (\pm 0.193)
		Low sturgeon	0.726 (\pm 0.117)	0.554 (\pm 0.189)
Hornyhead chub	Lake sturgeon	Even	0.110 (\pm 0.091)	0.950 (\pm 0.032)
		Low sturgeon	0.009 (\pm 0.021)	0.988 (\pm 0.029)
	Catostomid	Even	0.109 (\pm 0.128)	0.883 (\pm 0.175)
		Low sturgeon	0.194 (\pm 0.160)	0.804 (\pm 0.221)
	Heptageniid	Even	0.781 (\pm 0.097)	0.500 (\pm 0.297)
		Low sturgeon	0.797 (\pm 0.171)	0.370 (\pm 0.188)

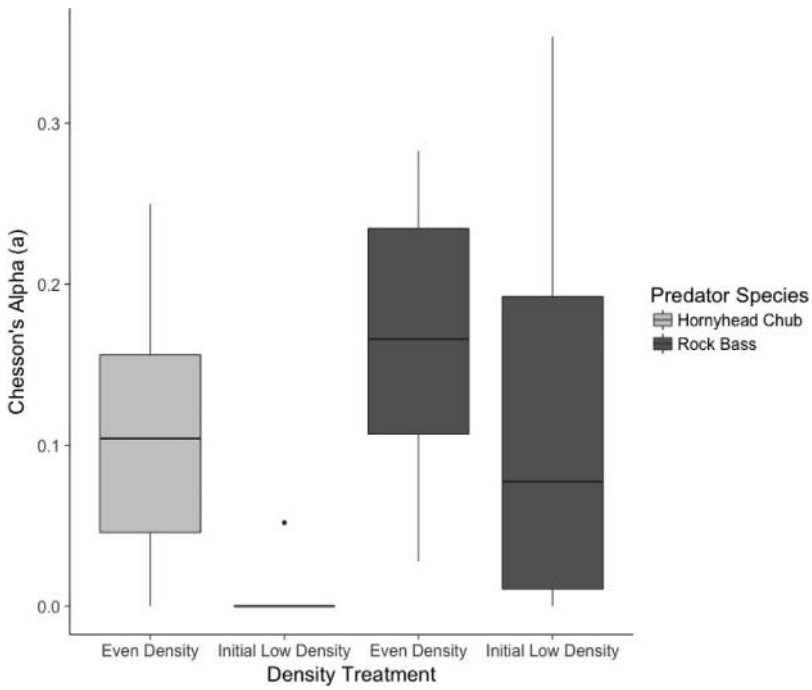


Figure 2. Boxplot of Chesson's alpha showing level of preference for larval lake sturgeon from trials with each predator species (shade) and each prey density treatment.

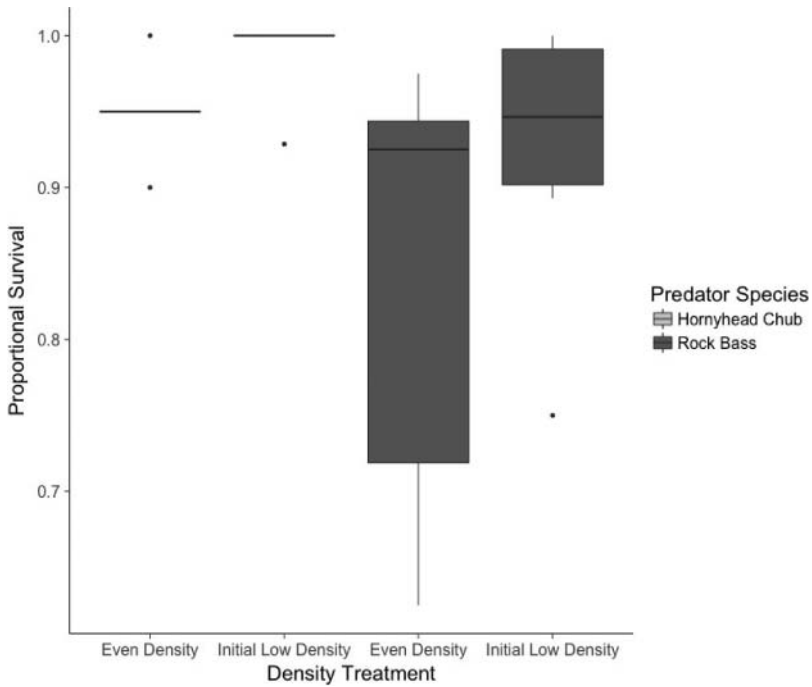


Figure 3. Boxplot of proportional survival of larval lake sturgeon in trials with each predator species (shade) and prey density treatment.

1.4 mm). Hornyhead chub did not exhibit size-selectivity for prey. However, rock bass selected for small and mid-size catostomid larvae (KS test; $D_{low} = 0.208$, $P < 0.001$, corrected alpha = 0.008; $D_{even} = 0.184$, $P < 0.01$, corrected alpha = 0.01; Figure 4(c,d)). Rock bass did not select for mayfly larvae on the basis of size, and small lake sturgeon larvae were nearly significantly selected for ($D = 0.144$, $P = 0.039$, corrected alpha = 0.013).

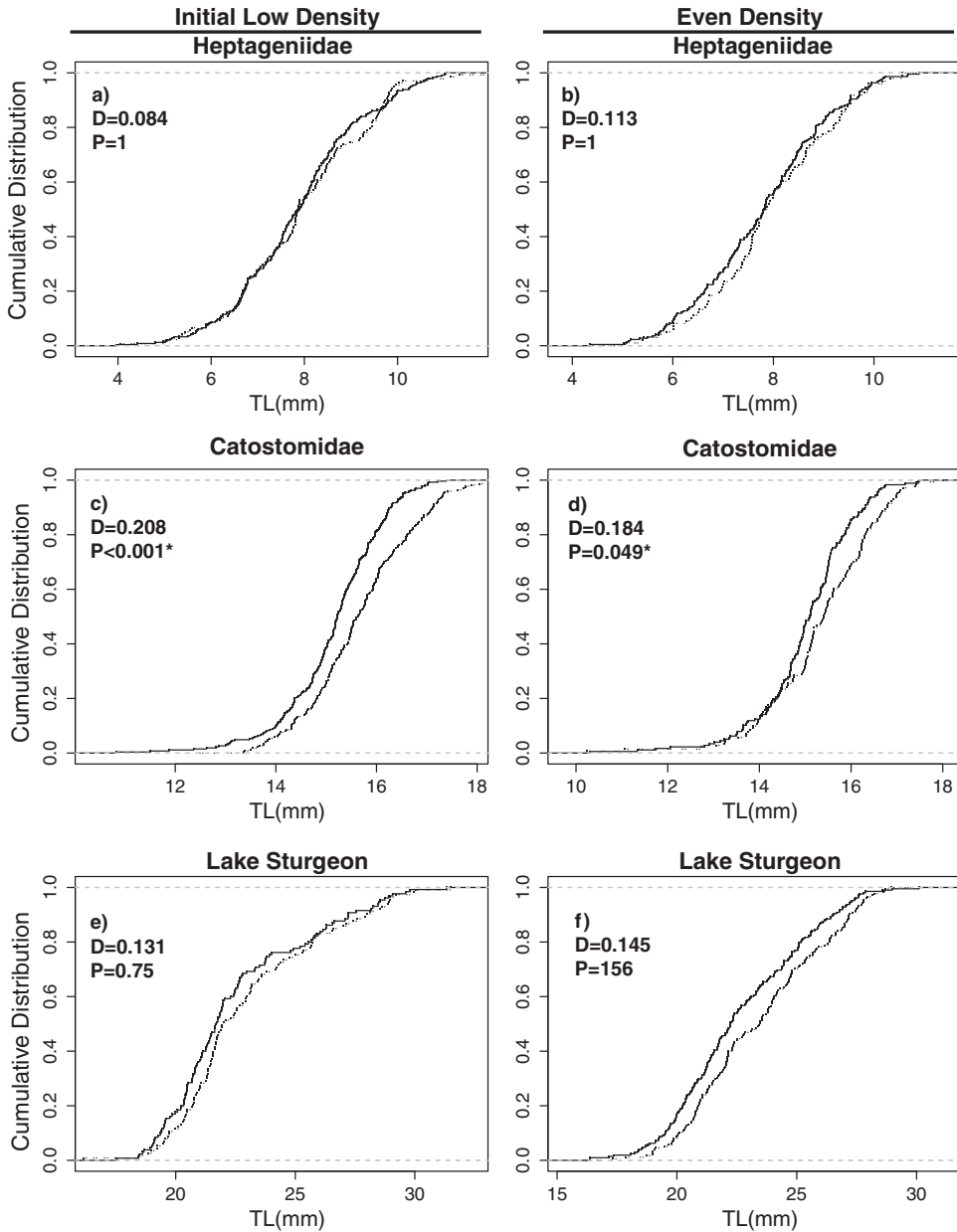


Figure 4. Cumulative distribution functions showing the distribution in total length (TL) of prey items before (solid line) and after (dotted line) predation trials with rock bass predators ($P =$ Holm–Bonferroni corrected significance of Kolmogorov–Smirnov test comparing prey size distributions before and after predator trials). Prey size data were pooled for each treatment for all trials in which the predator consumed at least one of a certain prey item.

Discussion

Experimental evidence indicated changes in predator preference due to exposure to different prey densities and size-selectivity among predators and prey types. However, there was no substantial evidence of predator swamping on larval lake sturgeon predation rate at the number of predators and prey densities used in trials. Studies including these predator–prey interaction behaviours are lacking for lake sturgeon. Data provide useful insights into predator–prey dynamics, showing how alternative prey can mediate predation pressure on lake sturgeon larvae. Recovery of many lake sturgeon populations is limited because of limited natural recruitment due to a variety of environmental and biological factors (Baker and Borgeson 1999; Caroffino et al. 2010a). Predator–prey interactions among lake sturgeon, other prey species, and predators may inform management decisions regarding lake sturgeon recruitment problems. Additionally, this study showed how short-term changes in prey communities can have demonstrable effects on predator foraging behaviour.

The consistent negative selection of lake sturgeon as a food source given the presence of alternate prey and high preference for heptageniid mayfly larvae indicates little evidence of strong prey switching for the densities tested. Mayfly larvae were preferred by both predator species while lake sturgeon and catostomid larvae were selected against. Both rock bass (Elrod et al. 1981) and hornyhead chub (Poff and Allan 1995) are known to display generalist feeding habits. Hornyhead chub diets consist primarily of benthic macroinvertebrates, with some piscivory and herbivory (Scott and Crossman 1973). Rock bass diets typically consist of benthic macroinvertebrates and crayfish, with piscivory common in larger adults (Paterson et al. 2006). Molecular diet analyses of these species also show that benthic macroinvertebrates are more commonly exploited prey than larval fishes in the UBR system (Waraniak 2017). Pallid sturgeon (*Scaphirhynchus albus*) juveniles have also been shown to be neutrally or negatively selected by a number of predator species, including channel catfish (*Ictalurus punctatus*), smallmouth bass (*Micropterus dolomieu*), walleye (*Sander vitreus*), and flathead catfish (*Pylodictis olivaris*) in the presence of fathead minnow (*Pimephales promelas*) alternative prey (French et al. 2010, 2014).

Some evidence suggested that varying prey densities had an effect on predator preference, at least for one of the predator species in this study. Rock bass did not exhibit a difference in preference for lake sturgeon in the two treatments. Instead, rock bass matched consumption with the abundance of prey within the environment, so some prey switching may have occurred following changes in prey availability. However, a greater range of prey densities should be considered to better quantify degree of prey switching behaviour. When hornyhead chub were initially offered low numbers of lake sturgeon with high numbers of alternative prey, they continued to consume the alternative prey at higher rates even after more lake sturgeon larvae were available. Thus, hornyhead chub did not exhibit prey switching, maintaining preferences for prey items even as relative prey availability changed. Only one lake sturgeon larvae was consumed in all initial low-density treatment trials combined for hornyhead chub, whereas at least one lake sturgeon larvae was consumed in all but one of the even prey availability treatments. This modest disparity appears to support the hypothesis that the prey selection of some predators is affected by the prey items they are initially exposed to. These predators appear to target prey items that were previously more abundant even if availability of other prey items increases over short timescales. Experiments using fifteen-spined stickleback (*Spinachia spinachia*) showed switching behaviour could change diet preferences on a similar short-term timescale (30 min; Ringler 1985; Hughes and Croy 1993). It is also possible initial exposure could affect foraging behaviour over longer timescales, for example, across multiple nights (Ringler 1985).

In this study, the observed pattern could have been created by satiation of the predators. Predators could have been satiated in the first pulse causing them to appear to more preferentially consume the abundant alternative prey species in the low-density treatment, when in fact preferences were not different between treatments. If predators simply stopped feeding before the second pulse was introduced, preference for larval lake sturgeon would have been underestimated in the low-density

treatment. However, it seems unlikely that predators were satiated by consuming prey in the first pulse, as both predator species routinely consumed more mayfly larvae than were initially offered.

From the perspective of lake sturgeon, predator swamping did not occur at the densities of prey used in the experiment. The proportions of surviving lake sturgeon were not significantly different between the two treatments for each predator species, though the lake sturgeon survival was slightly higher in the low-density treatment. There may have been a small improvement in lake sturgeon survival in the low-density treatment due to predator swamping, but the small sample size could have precluded observation of a significant difference. Additionally, a greater difference in the ratios of prey items could lead to a more prominent swamping effect. The reduction of predation through dilution effects has been hypothesized as a possible evolutionary benefit of synchronicity in drifting behaviour (Frank and Leggett 1984; Ims 1990). Potential for predator swamping in downstream drift is high, as larvae of many different species initiate drift in response to similar environmental conditions and at similar times (Brown and Armstrong 1985; Carter et al. 1986; Lechner et al. 2014).

Experimentally, it has been shown that high densities of alternative prey can reduce predation on a preferred prey species (Kean-Howie et al. 1988; Pepin and Shears 1995). In contrast, other experiments have shown that the presence of alternative prey items did not change the consumption rate of the species of interest (Goodsell and Kats 1999; Drake et al. 2014). In addition, some species prey on the most consistently abundant prey items, regardless of alternative prey species present (Worischka et al. 2015). Whether a predator switches prey may depend on the identities and behaviours of the interacting predator and prey species. For example, Elliot (2004) found that perlid stoneflies (Family: Perlidae) did not exhibit prey switching, while perlode stoneflies (Family: Perlodidae) did.

Evidence for predator size selection of prey was observed. No size selection was exhibited by hornhead chub, but rock bass selected smaller catostomid larvae (Figure 4(c,d)). Further evidence, although not significant, indicated rock bass also selected for small lake sturgeon larvae (Figure 4(e, f)). The distribution of surviving larval catostomids corroborates the observation made by Paradis et al. (1996) that determined vulnerability to predation was maximized when larval size is 1/10th that of predator size. The greatest difference in the size distributions of catostomid larvae before and after trials with rock bass (the KS test D statistic) is located around 15–16 mm, close to 1/10th the mean TL of rock bass used in the experimental trials (154 mm). Predators select smaller prey items to save energy while foraging as larger prey items require more energy to capture and handle (Floeter and Temming 2005). The preferred prey taxa (heptageniid mayflies) exhibited little size variation, and relatively few larval fishes were consumed. Preferences were affected by species-specific characteristics of prey and predators (Worischka et al. 2015).

The three prey species used in this study are behaviourally and morphometrically dissimilar to one another, which may affect the ability of predators to detect and capture them. Heptageniid larvae are grazers that cling to rocks and other hard surfaces to feed and are relatively poor swimmers compared to larval fishes (Wellnitz and Poff 2006). The two larval fishes also have different drifting behaviours. Catostomid larvae typically drift near the surface or the middle of the water column (Clifford 1972; Gale and Mohr 1978; Corbett and Powles 1986), whereas lake sturgeon larvae are benthic drifters, especially at relatively low flow rates, similar to conditions used in this study (Kempinger 1988; D'Amours et al. 2000; Smith and King 2005). Additionally, there are apparent qualitative differences between the swimming locomotion of larval catostomids and larval lake sturgeon. Catostomid larvae exhibit a sub-carangiform swimming movement, enabling short, fast bursts of speed, while larval lake sturgeon swim with a slower anguillid motion (personal observation). These differences in movement may affect the ability of predators to capture either type of larvae. Catostomid larvae are semi-transparent while larval sturgeon and heptageniid mayflies are opaque and provided a greater contrast against the surface of the experimental raceways, possibly increasing the ability of predators to identify them as prey items (Utne-Palm 1999; Hansen and Beauchamp 2014). In the case of this experiment, the differences between preferences for the different prey types were likely due to the differing morphologies and behaviour of the prey types than the different density treatments, as changes in preference due to density were relatively minor compared to the

differences in preference for the different prey types. Some freshwater fish predators have an affinity toward slower moving, benthic prey species, such as the mayflies used in this study (Specziár 2011). Prey densities may have a stronger effect on predator preference if prey items are more functionally similar, as there would be fewer differences in handling time, energy density, or other factors influencing predator preference. Yet, these three prey species are simultaneously abundant in the UBR (Waraniak 2017), so understanding the indirect effects these prey may have on each other may have important implications for predation of larval lake sturgeon during the drift period.

Other limitations to the applicability of this experimental study to the natural stream exist. First, only two predator species and two alternate prey species were used, which greatly simplifies the UBR ecosystem. Logperch (*Percina caprodes*), another common predator in the UBR, may exhibit a higher preference for lake sturgeon than hornyhead chub or rock bass (Waraniak 2017), so different alternative prey combinations and predator species may alter results. Second, predator species were used in separate trials, not together, so the effect of interspecific interactions at the predator–guild was not tested. Exploitative competition does affect predator–prey systems, yielding different numbers of prey items ingested per capita (Raborn et al. 2004). Third, the flowing experimental raceway streams were shallower than much of the UBR. Due to differences in the vertical distributions of the prey in the natural system, this may have artificially homogenized the encounter rate predators experienced during the trials compared to the river. Importantly, the densities for all three prey species used in this study were determined using data from the same D-frame drift net surveys (Waraniak 2017). Fourth, the duration of trials was short term (60 min), and predatory cues based on biomass or relative abundance of prey items may develop over longer time spans (days; Ringler 1985). Fifth, the number of prey items used in trials was fixed. Varying the number of prey and prey ratios could reveal a threshold level of abundance that may trigger prey switching or alter selectivity for prey (Gismervik and Andersen 1997). Finally, this experiment could only evaluate predator preference over the course of an entire trial, not how predator preference might have changed during each pulse. Predation rates were not measured using direct observations to prevent researchers from disturbing foraging predators, which could alter predator behaviour. Instead, recovered numbers of larvae were used as a proxy of the number of predation events per prey species. Video or another method that would avoid disturbing predators could be used in future studies to obtain direct observation data and estimate more instantaneous changes in predator diet preference as prey availability changes.

Results from this study have important implications for predator–prey dynamics between larval fishes, macroinvertebrates, and larger predatory fishes in riverine systems. Species appear to maintain diet preferences over the short term even as relative availability of different prey changes. Additionally, this study highlighted the importance of aquatic macroinvertebrates in the diets of two common native stream predators, indicating that high abundance of macroinvertebrate taxa could be important in reducing predation pressure on the larval stage of fishes. Predation is often a major factor affecting recruitment, especially at the pre-larval and larval stages, and thus investigating predator–prey dynamics at these life stages is critical. Furthermore, for species of conservation concern such as lake sturgeon, early life-stage mortality may be a leading factor that exposes a species to risk due to insufficient recruitment to maintain populations, potentially leading to extirpation. How foraging strategies and decisions of predators change in dynamic environments can have significant implications for larval fish that experience increased exposure to predators over short timescales. Conservation and management efforts can benefit from this knowledge, possibly using the presence of alternative prey species to promote the survival of species of interest, including lake sturgeon.

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Disclosure statement

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Notes on contributors


Justin Waraniak was a graduate student at Michigan State University at the time of this research interested in molecular and community ecology in aquatic systems.

Shaley Valentine was a field technician at the time of this research interested in community ecology and trophic level interactions.

Kim Scribner is an evolutionary ecologist with broad interests in population genetics, community ecology, and animal behaviour.

ORCID

Justin Waraniak  <http://orcid.org/0000-0002-6653-2021>

Kim Scribner  <http://orcid.org/0000-0003-3416-2828>

References

- Auer NA, Baker EA. 2002. Duration and drift of larval lake sturgeon in the Sturgeon River, Michigan. *J Appl Ichthyol.* 18:557–564.
- Aukema BH, Raffa KF. 2004. Does aggregation benefit bark beetles by diluting predation? Links between a group-colonisation strategy and the absence of emergent multiple predator effects. *Ecol Entomol.* 29:129–138.
- Bailey KM, Houde ED. 1989. Predation of eggs and larvae of marine fishes and the recruitment problem. *Adv Mar Biol.* 25:1–83.
- Baker EA, Borgeson DJ. 1999. Lake sturgeon abundance and harvest in Black Lake, Michigan. *N Am J Fish Manage.* 19:1080–1088.
- Bates D, Mächler M, Bolker B, Walker S. 2015. Fitting linear mixed-effects models using lme4. eprint arXiv:1406.5823:51.
- Brown AV, Armstrong ML. 1985. Propensity to drift downstream among various species of fish. *J Freshw Ecol.* 3:3–17.
- Caroffino DC, Sutton TM, Elliott RF, Donofrio MC. 2010a. Early life stage mortality rates of lake sturgeon in the Peshigo River, Wisconsin. *N Am J Fish Manage.* 30:295–304.
- Caroffino DC, Sutton TM, Elliott RF, Donofrio MC. 2010b. Predation on early life stages of lake sturgeon in the Peshigo River, Wisconsin. *Trans Am Fish Soc.* 139:1846–1856.
- Carreon-Martinez L, Johnson TB, Ludsin SA, Heath DD. 2011. Utilization of stomach content DNA to determine diet diversity in piscivorous fishes. *J Fish Biol.* 78:1170–1182.
- Carter JG, Lamarra VA, Ryel RJ. 1986. Drift of larval fishes in the Upper Colorado River. *J Freshw Ecol.* 3:567–577.
- Chesson J. 1978. Measuring preference in selective predation. *Ecology.* 59:211–215.
- Clifford HF. 1972. Downstream movements of white sucker, *Catostomus commersonii*, in a brown-water stream of Alberta. *J Fish Res Board Can.* 29:1091–1093.
- Corbett BW, Powles PM. 1986. Spawning and larval drift of sympatric walleyes and white suckers in an Ontario stream. *Trans Am Fish Soc.* 115:41–46.
- Creel S, Christianson D. 2008. Relationships between direct predation and risk effects. *Trends Ecol Evol.* 23:194–201.
- Crossman JA. 2008. Evaluating collection, rearing, and stocking methods for lake sturgeon (*Acipenser fulvescens*) restoration programs in the great lakes. East Lansing (MI): Michigan State University.
- D'Amours J, Thibodeau S, Fortin R. 2000. Comparison of lake sturgeon (*Acipenser fulvescens*), *Stizostedion* spp., *Catostomus* spp., *Moxostoma* spp., quillback (*Carpionodes cyprinus*), and mooneye (*Hiodon tergisus*) larval drift in Des Praires River, Quebec. *Can J Zool.* 79:1472–1489.

- Drake DL, Anderson TL, Smith LM, Lohraff KM, Semlitsch RD. 2014. Predation of eggs and recently hatched larvae of endemic ringed salamanders (*Ambystoma annulatum*) by native and introduced aquatic predators. *Herpetologica*. 70:378–387.
- Duncan JR, Lockwood JL. 2001. Extinction in a field of bullets: a search for causes in the decline of the world's freshwater fishes. *Biol Conserv*. 102:97–105.
- Duong TY, Scribner KT, Crossman JA, Forsythe PS, Baker EA, Kanefsky J, Homola JJ, Davis C. 2011. Relative larval loss among females during dispersal of lake sturgeon (*Acipenser fulvescens*). *Environ Biol Fish*. 91:459–469.
- Elliott JM. 2004. Prey switching in four species of carnivorous stoneflies. *Freshw Biol*. 49:709–720.
- Elrod JH, Busch WN, Griswold BL, Schneider CP, Wolfert DR. 1981. Food of white perch, rock bass and yellow perch in eastern Lake Ontario. *N Y Fish Game J*. 28:191–201.
- Floeter J, Temming A. 2005. Analysis of prey size preference of North Sea whiting, saithe, and grey gurnard. *ICES J Mar Sci*. 62:897–907.
- Flowers HJ, Bonvecchio TF, Peterson DL. 2011. Observation of Atlantic sturgeon predation by a flathead catfish. *Trans Am Fish Soc*. 140:250–252.
- Forsythe PS, Crossman JA, Bello NM, Baker EA, Scribner KT. 2012. Individual-based analyses reveal high repeatability in timing and location of reproduction in lake sturgeon (*Acipenser fulvescens*). *Can J Fish Aquat Sci*. 69:60–72.
- Frank KT, Leggett WC. 1984. Selective exploitation of capelin (*Mallotus villosus*) eggs by winter flounder (*Pseudopleuronectes americanus*): capelin egg mortality rates, and contribution of egg energy to the annual growth of flounder. *Can J Fish Aquat Sci*. 41:1294–1302.
- French WE, Graeb BDS, Chipps SR, Bertrand KN, Selch TM, Klumb RA. 2010. Vulnerability of age-0 pallid sturgeon *Scaphirhynchus albus* to fish predation. *J Appl Ichthyol*. 26:6–10.
- French WE, Graeb BDS, Chipps SR, Klumb RA. 2014. Vulnerability of age-0 pallid sturgeon *Scaphirhynchus albus* to predation; effects of predator type, turbidity, body size, and prey density. *Environ Biol Fish*. 97:635–646.
- Fritts AL, Scott JL, Pearsons TN. 2007. The effects of domestication on the relative vulnerability of hatchery and wild origin spring Chinook salmon (*Oncorhynchus tshawytscha*) to predation. *Can J Fish Aquat Sci*. 64:813–818.
- Fryxell JM, Lundberg P. 1994. Diet choice and predator–prey dynamics. *Evol Ecol*. 8:407–412.
- Gadomski DM, Parsley MJ. 2005a. Effects of turbidity, light level, and cover on predation of white sturgeon larvae by prickly sculpins. *Trans Am Fish Soc*. 134:369–374.
- Gadomski DM, Parsley MJ. 2005b. Laboratory studies on the vulnerability of young white sturgeon to predation. *N Am J Fish Manage*. 25:667–674.
- Gale WF, Mohr HW. 1978. Larval fish drift in a large river with a comparison of sampling methods. *Trans Am Fish Soc*. 107:46–55.
- Gismervik I, Andersen T. 1997. Prey switching by *Acartia clausi*: experimental evidence and implications of intraguild predation assessed by a model. *Mar Ecol Prog Ser*. 157:247–259.
- Gjøsaeter H, Hallfredsson EH, Mikkelsen N, Bogstad B, Pedersen T. 2016. Predation of early life stages is decisive for year-class strength in the Barents sea capelin (*Mallotus villosus*) stock. *ICES J Mar Sci*. 73:182–195.
- Godiksen JA, Hallfredsson EH, Pedersen T. 2006. Effects of alternative prey on predation intensity from herring *Clupea harengus* and sandeel *Ammodytes marinus* on capelin *Mallotus villosus* larvae in the Barents Sea. *J Fish Biol*. 69:1807–1823.
- Goodsell JA, Kats LB. 1999. Effect of introduced mosquitofish on pacific treefrogs and the role of alternative prey. *Conserv Biol*. 13:921–924.
- Hansen AG, Beauchamp DA. 2014. Effects of prey abundance, distribution, visual contrast, and morphology on selection by a pelagic piscivore. *Freshw Biol*. 59:2328–2341.
- Hughes RN, Croy MI. 1993. An experimental analysis of frequency dependent predation (switching) in the 15-spined stickleback, *Spinachia spinachia*. *J Anim Ecol*. 62:341–352.
- Humphries NE, Schaefer KM, Fuller DW, Phillips GEM, Wilding C, Sims DW. 2016. Scale-dependent to scale-free: daily behavioural switching and optimized searching in a marine predator. *Anim Behav*. 113:189–201.
- Ims RA. 1990. On the adaptive value of reproductive synchrony as a predator-swamping strategy. *Am Nat*. 136:485–498.
- Johnson JH, McKenna JE. 2007. Diel periodicity of drift of larval fishes in tributaries of Lake Ontario. *J Freshw Ecol*. 22:347–350.
- Kean-Howie JC, Pearre S, Dickie LM. 1988. Experimental predation by sticklebacks on larval mackerel and protection of fish larvae by zooplankton alternative prey. *J Exp Mar Biol Ecol*. 124:239–259.
- Kempinger JJ. 1988. Spawning and early life history of the lake sturgeon in the Lake Winnebago system, Wisconsin. *Am Fish Soc Symp*. 5:104–109.
- Koss AM, Chang GC, Snyder WE. 2004. Predation of green peach aphids by generalist predators in the presence of alternative, Colorado potato beetle egg prey. *Biol Control*. 31:237–244.
- Lechner A, Keckeis H, Schludermann E, Humphries P, Mccasker N, Tritthart M. 2014. Hydraulic forces impact larval fish drift in the free flowing section of a large European river. *Ecohydrology*. 7:648–658.
- Leggett WC, DeBlois E. 1994. Recruitment in marine fishes: is it regulated by starvation and predation in the egg and larval stages?. *Neth J Sea Res*. 32:119–134.

- Major PF. 1978. Predator–prey interactions in two schooling fishes, *Caranx ignobilis* and *Stolephorus purpureus*. *Anim Behav.* 26:760–777.
- Mason DM, Brandt SB. 1996. Effect of alewife predation on survival of larval yellow perch in an embayment of Lake Ontario. *Can J Fish Aquat Sci.* 53:1609–1617.
- Murdoch WW. 1969. Switching in general predators: experiments on predator specificity and stability of prey populations. *Ecol Monogr.* 39:335–354.
- Murdoch WW. 1975. Switching in predatory fish. *Ecology.* 56:1096–1105.
- Paradis AR, Pepin P, Brown JA. 1996. Vulnerability of fish eggs and larvae to predation: review of the influence of the relative size of prey and predator. *Can J Fish Aquat Sci.* 53:1226–1235.
- Parsley MJ, Anders PJ, Miller A, Beckman LG, McCabe GTJ. 2002. Recovery of white sturgeon population through natural production: understanding the influence of abiotic and biotic factors on spawning and subsequent recruitment. *Am Fish Soc S.* 28:55–66.
- Paterson G, Drouillard KG, Haffner GD. 2006. Quantifying resource partitioning in centrarchids with stable isotope analysis. *Limnol Oceanogr.* 51:1038–1044.
- Pepin P, Shears T. 1995. Influence of body size and alternate prey abundance on the risk of predation to fish larvae. *Mar Ecol Prog Ser.* 128:279–285.
- Persson L. 1982. Rate of food evacuation in roach (*Rutilus rutilus*) in relation to temperature, and to the application of evacuation rate estimates for studies on the rate of food consumption. *Freshw Biol.* 12:129–142.
- Peterson DL, Vecsei P, Jennings CA. 2007. Ecology and biology of the lake sturgeon: a synthesis of current knowledge of a threatened North American Acipenseridae. *Rev Fish Biol Fish.* 17:59–76.
- Pledger S, Baker E, Scribner K. 2013. Breeding return times and abundance in capture-recapture models. *Biometrics.* 69:991–1001.
- Poff N, Allan JD. 1995. Functional organization of stream fish assemblages in relation to hydrological variability. *Ecology.* 76:606–627.
- Raborn SW, Miranda LE, Driscoll MT. 2004. Diet overlap and consumption patterns suggest seasonal flux in the likelihood for exploitative competition among piscivorous fishes. *Ecol Freshw Fish.* 13:276–284.
- R Core Team. 2015. R: a language and environment for statistical computing. Vienna: R Foundation for Statistical Computing.
- Ringler NH. 1985. Individual and temporal variation in prey switching by brown trout, *Salmo trutta*. *Copeia.* 12:918–926.
- Schmitz OJ. 1998. Direct and indirect effects of predation and predation risk in old-field interaction webs. *Am Nat.* 151:327–342.
- Schooley JD, Karam AP, Kesner BR, Marsh PC, Pacey CA, Thornbrugh DJ. 2008. Detection of larval remains after consumption by fishes. *Trans Am Fish Soc.* 137:1044–1049.
- Scott WB, Crossman EJ. 1973. Freshwater fishes of Canada. *Bull Fish Res Board Can.* 184:1–966.
- Semlitsch RD. 1987. Interactions between fish and salamander larvae: costs of predator avoidance or competition? *Oecologia.* 72:481–486.
- Smith KM, King DK. 2005. Dynamics and extent of larval lake sturgeon *Acipenser fulvescens* drift in the Upper Black River, Michigan. *J Appl Ichthyol.* 21:161–168.
- Specziár A. 2011. Size-dependent prey selection in piscivorous pikeperch *Sander lucioperca* and Volga pikeperch *Sander volgensis* shaped by bimodal prey size distribution. *J Fish Biol.* 79:1895–1917.
- Steffensen KD, Lundgren SA, Huenemann TW. 2015. Documented predation of pallid sturgeon *Scaphirhynchus albus* (Forbes & Richardson, 1905) by flathead catfish *Pylodictis olivaris* (Rafinesque, 1818). *J Appl Ichthyol.* 31:843–845.
- Stier AC, Geange SW, Bolker BM. 2013. Predator density and competition modify the benefits of group formation in a shoaling reef fish. *Oikos.* 122:171–178.
- Sundell J, Eccard JA, Tiilikainen R, Yionen H. 2003. Predation rate, prey preference and predator switching: experiments on voles and weasels. *Oikos.* 101:615–623.
- Utne-Palm AC. 1999. The effect of prey mobility, prey contrast, turbidity, and spectral composition on the reaction distance of *Gobiusculus flavescens* to its planktonic prey. *J Fish Biol.* 54:1244–1258.
- Waraniak J. 2017. Barcoding, metabarcoding, and experimental analysis of community dynamics and environmental conditions affecting predation of larval lake sturgeon in the Black River, Michigan. East Lansing (MI): Michigan State University.
- Waraniak JM, Blumstein DM, Scribner KT. 2017. Barcoding PCR primers detect larval lake sturgeon (*Acipenser fulvescens*) in diets of piscine predators. *Conserv Genet Resour.* doi:10.1007/s12686-017-0790-5
- Wellnitz T, Poff NL. 2006. Herbivory, current velocity and algal regrowth: how does periphyton grow when the grazers have gone? *Freshw Biol.* 51:2114–2123.
- Worischka S, Schmidt SI, Hellmann C, Winkelmann C. 2015. Selective predation by benthivorous fish on stream macroinvertebrates - the role of prey traits and prey abundance. *Limnologia.* 52:41–50.

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