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RESEARCH ARTICLE

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Experimental evidence quantifying effects of nocturnal light conditions on predation levels by riverine predators on larval prey

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ABSTRACT

Larval fish and aquatic macroinvertebrates are believed to be at greater predation risk by visual riverine predators during periods of higher lunar illumination. Predation rates may also be affected by the taxonomic composition and relative abundance of alternative co-distributed prey. We experimentally tested whether differences in larval lake sturgeon (*Acipenser fulvescens*) predation levels were attributed to changes in prey selectivity, or to an overall decrease in consumption of co-distributed and dispersing prey consumed by predatory riverine species under different light conditions. Larvae from three common riverine prey taxa observed nocturnally dispersing together (lake sturgeon, white suckers (*Catostomus commersonii*), and Hetptageniid mayflies) were released concurrently into raceway mesocosms. Raceways contained one of two abundant predacious riverine fishes [either rock bass (*Ambloplites rupestris*) or hornyhead chub (*Nocomis biguttatus*)]. Trials were conducted in light conditions simulating a full or new moon. Both predators consumed fewer prey under new moon relative to full moon light conditions. In full moon conditions, rock bass selected for mayflies and against white suckers, but in new moon conditions rock bass selectivity was similar for all prey. Hornyhead chub selected for mayflies under both light conditions. Results indicate rock bass and hornyhead chub rely on visual cues to detect prey. Rock bass also appeared to visually differentiate between prey taxa, whereas hornyhead chub may use alternative senses to select prey. Variation in larval lake sturgeon mortality during the downstream drifting period was a function of the taxonomic composition and size distribution of predators, and composition and relative abundance of alternative co-distributed prey. Nocturnal light levels likely also influence predation rates in natural populations of nocturnally dispersing aquatic larvae. Light levels during larval dispersal should be considered when interpreting intra- and inter-annual variation in recruitment in species of regional conservation concern.

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KEY POLICY HIGHLIGHTS

- Experimental mesocosm studies demonstrated that larval prey of all species evaluated that dispersed under higher nocturnal light conditions incurred greater levels of predation by taxonomically diverse stream predators than larvae dispersing under low light conditions.
- Lunar phase and physical environmental factors including stream temperature and discharge are widely used by adults as cues to initiate spawning. Cues are increasingly mismatched to conditions experienced by larvae subsequently, which can incur substantial costs to offspring survival.
- The impacts of nocturnal light level and prey community abundance and composition to larval mortality is of importance to managers to forecast population levels of recruitment.

1. Introduction

Most fish populations experience high mortality among individuals of early life stages (Demetrius 1978). Larval fish are susceptible to predation because small size and restricted mobility limit their ability to evade predators (Almany and Webster 2006; Durant et al. 2007). Annual variation in early life mortality in larval fish can influence population levels of recruitment (Osman and Whitlatch 1995; Gagliano et al. 2007; Doropoulos et al. 2016). Consequently, sources and levels of early life mortality remain heavily investigated topics (Li and Mathias 1982; Houde 1989; Berkeley et al. 2004; Johnson et al. 2014). Behaviors expressed during early life stages of many fish species such as dispersal from adult spawning areas to larval rearing areas expose individuals to high levels of mortality through predation (Radinger and Wolter 2014; Almany et al. 2017). Understanding how environmental and biotic factors influence mortality during dispersal is critical to understand and predict mortality levels during the vulnerable larval stage (Houde 1989).

Many studies focusing on impacts of environmental factors on larval fish mortality have examined commercially harvested species (Houde 1989; Johnson et al. 2014; Garrido et al. 2015) and are of particular importance for species of conservation concern. In this study, we examined how environmental factors influence the larval mortality rates of lake sturgeon (*Acipenser fulvescens*), a regionally threatened species (Léonard et al. 2004). Adult lake sturgeon generally inhabit the benthic zone of lakes and large rivers, and forage over sand and silt substrate. Sexually mature adults are adfluvial and migrate up rivers to spawn on rocky substrate (Harkness and Dymond 1961; Haxton et al. 2008). Like many river-spawning species, lake sturgeon larvae passively disperse downstream following hatch after yolk sac reserves have been depleted and sensory abilities have developed (Auer and Baker 2002). Larval lake sturgeon disperse along with larvae from other taxa, including co-distributed fish species and immature macroinvertebrate taxa, and are consumed by predators (Waraniak et al. 2019; Receveur et al. 2022).

Previous research on larval lake sturgeon dispersal has shown that as nightly lunar illumination increases, the probability of detecting lake sturgeon in the diets of predatory fish increases (Waraniak et al. 2018). Findings imply that lake sturgeon are more easily detected by predators during periods of higher lunar illumination, but population-level effects of nocturnal lunar illumination on lake sturgeon survival have not been documented. Other stream features including high turbidity during larval dispersal have been associated with higher larval fish survival rates (Fiksen et al. 2002; Carreon-Martinez et al. 2014), further demonstrating that impediments to predator visual acuity are associated with higher larval survival.

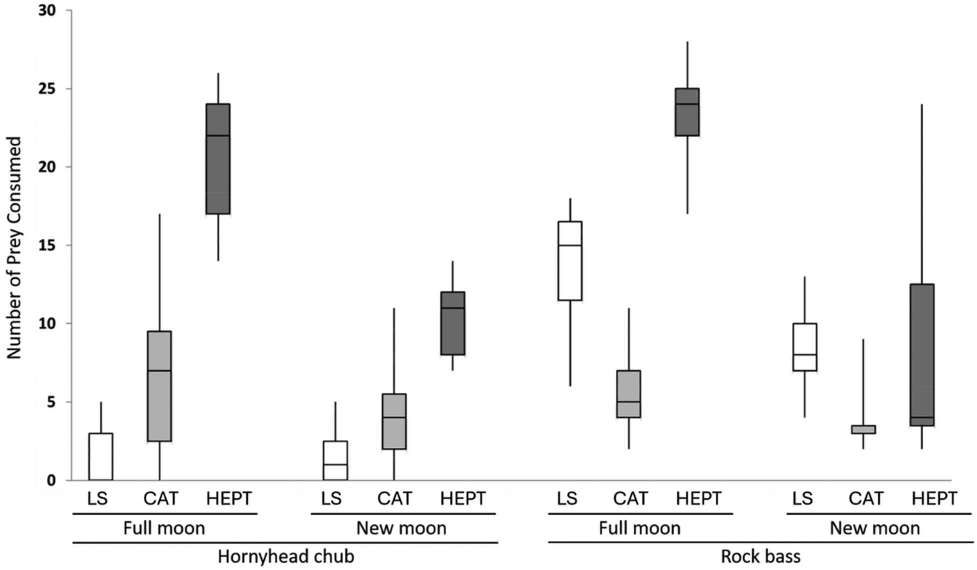

Figure 1. Boxplot showing the number of lake sturgeon (LS), catostomid (CAT), and heptageniid (HEPT) larvae consumed in trials with either full moon or new moon light conditions, and with either hornyhead chub (HHC) or rock bass (RB) as the predatory species.

Our objective in this study was to experimentally quantify the impact of night light level on larval lake sturgeon mortality rates. Because of the high level of complexity in natural stream environments, we used replicated experimental raceways to simulate flowing stream habitats to evaluate three hypotheses: (H1) larval lake sturgeon mortality rates increase with higher lunar illumination consistently over time, (H2) predation preference for different prey species changes under lower light levels based on the ability of predators to differentiate between different types of prey, and as a consequence, (H3) larval lake sturgeon mortality rates are affected by lower levels of detection in low light and altered predation risk due to predator selectivity for alternate co-distributed prey.

2. Methods

2.1. Study site and subject

All experiments were conducted at the Black River Streamside Rearing Facility, a lake sturgeon hatchery and research facility on the Upper Black River (UBR) in Cheboygan County, MI (USA). A well-characterized population of lake sturgeon inhabiting Black Lake spawn annually in the UBR during late April through early June (Forsythe et al. 2012a). This population has been restricted to Black Lake and the lower reaches of the Upper Black River since 1903 due to the construction of a hydroelectric dam on the Lower Black River, located downstream of Black Lake (Smith and Baker 2005). Lake sturgeon spawn over rock and gravel substrate, where eggs and yolk sac larvae remain until yolk sacs have been absorbed, at which point the larvae enter the water column at night and disperse downstream to foraging areas in the river (Auer and Baker 2002). During this dispersal stage, lake sturgeon larvae are highly susceptible to predation by a taxonomically diverse group of predators (Waraniak et al. 2018, 2019).

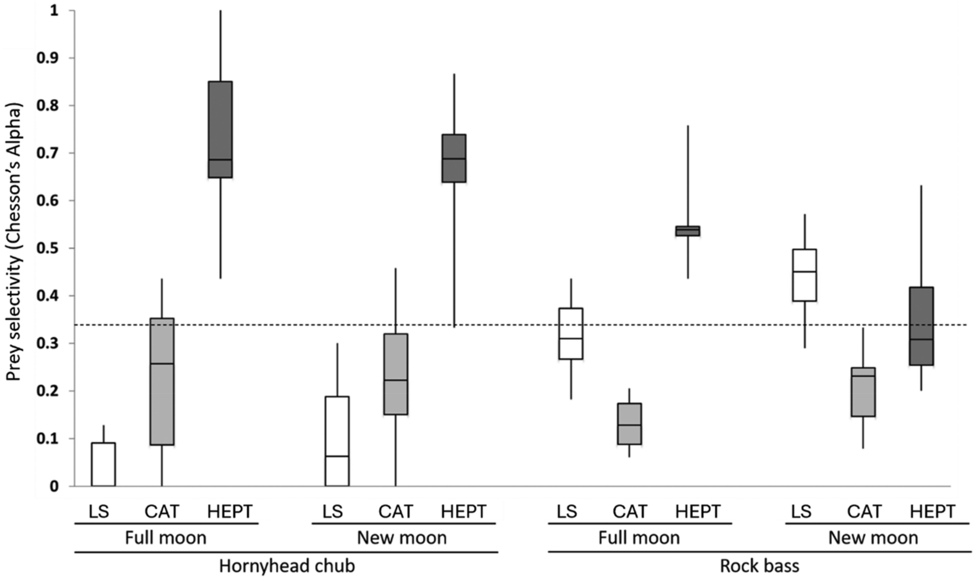

Figure 2. Boxplot showing the prey selectivity of hornyhead chub (HHC) and rock bass (RB) for lake sturgeon (LS), catostomid (CAT), and heptageniid (HEPT) larvae in trials with either full moon or new moon light conditions. Dotted line indicates chesson's alpha value of 0.333, indicating neutral selectivity.

Lake sturgeon larvae in the UBR have been observed drifting concurrently with larval Catostomids including white sucker (*Catostomus commersonii*) and river redhorse (*Moxostoma carinatum*), as well as a diverse community of macroinvertebrates (Waraniak et al. 2019). To simulate natural stream conditions, prey taxa used in this experiment included naturally occurring lake sturgeon (LS) larvae, Catostomid (CAT) silver redhorse larvae, and Heptageniid mayfly (HEPT) larvae. Prey species were captured from the UBR using D-frame drift nets deployed nightly downstream of sturgeon spawning grounds. Prey items were held in 3 L or 5 L tanks with filtered UBR water before being used in experimental raceway trials and all prey items were used within 24 h of collection to maintain vigor.

Two abundant predatory species inhabiting the UBR are rock bass (*Ambloplites rupestris*, RB) and hornyhead chub (*Nocomis biguttatus*, HHC). Both predator species were selected because they have been shown to consume a taxonomically diverse number of prey species under natural stream conditions and in previous experiments (Waraniak et al. 2017) including larval lake sturgeon, macroinvertebrates, and other larval fishes that are co-distributed in the drift. Individuals of both predator species used in experiments were collected by barge electroshocking in the UBR and were housed in covered tanks with filtered UBR water. Predators represent a range of sizes characteristic of stream populations (Waraniak et al. 2019). RB total length (TL) ranged from 9.3 to 13.1 cm. HHC TL ranged from 8.8 to 11.5 cm. Individuals of both species were held for 24–32 h before being used in a trial. Collection, handling, and experimental protocols were all performed under conditions approved by the Michigan State University Animal Use and Care Committee.

2.2. Experimental design

All experimental trials were conducted in one of two flow-through raceway mesocosms with dimensions 7.15 m x 0.5 m (length by width), housed in a darkened Quonset hut.

Six hours prior to the start of a trial, two predators (either RB or HHC) were placed in 5 m x 0.5 m gated areas sequentially within the raceway to eliminate the potential for predator interactions that could have affected experimental outcomes. The gates allowed larval LS, CAT, and HEPT to pass downstream freely but did not allow RB or HHC to move further upstream or downstream. For the first five hours of predator acclimation, sand-filtered water from the UBR was pumped at a flow velocity of approximately 0.085 m/s. One hour prior to the start of a trial, recirculating water pumps were activated to increase water velocity to 0.134 ± 0.003 m/s, which is commonly observed in the stream regardless of timing of the lunar cycle (Riedy 2022). Recirculating pumps were not employed for the duration of the acclimation period to limit fatigue of predators (Waraniak et al. 2017). Light conditions were adjusted so that light at the water surface in the center of the raceways measured either 0.20 or 0.00 lux conditions. 0.20 and 0.00 lux were chosen for light and dark trials, respectively, because 0.20 lux is a plausible brightness of a relatively bright full moon and 0.00 lux is characteristic of a new moon (Kyba et al. 2017). Flow rates were measured with a Marsh-McBirney Flo-Mate 2000 flow meter (Frederick, MD) and lux was measured with an Extech LT300 light meter (Waltham, MA). Both flow rate and lux were measured upstream of the predator gates, between the two gated areas, and downstream of the gates to ensure there were even flow rates and light levels across the length of the raceways. Downstream of the gated area, fine-mesh aquarium nets were placed over the raceway outflow to capture drifting prey items that were not consumed by the predator.

At the start of the trial, 10 individuals of each prey taxa (LS, CAT, HEPT) were released simultaneously in the raceway upstream from the gated section. Prey releases were repeated at 15, 30, and 45 min, for a total of 40 individuals of each prey species in each raceway and experimental trial. A similar study did not find evidence of predator satiation at this prey density (Waraniak et al. 2017). After 60 min, the trial ended, and the predatory fish were removed from the raceway. The entire raceway was searched for surviving prey. All surviving prey items were collected to determine counts of each prey taxa consumed during the trial. After each trial, predators were fin-clipped and released into Upper Black River to avoid using individuals in more than one trial. Eight replicate trials of each predator and light level combination were conducted.

2.3. Statistical analysis

Binomial generalized linear models were used to quantify sources of variation in the number of each prey taxa and the total number of prey consumed during a trial as a function of light level (lux), predator species, predator body size (total length; TL), and water temperature. The full model included interactions among all variables. Temperature and predator TL variables were nested within each predatory species. Temperature was included in the models because it influences the predator's metabolism, and potentially feeding rate (Volkoff and Rønnestad 2020). Predator body size likewise could affect rate feeding rate (Rall et al. 2012) and diet (Szedlmayer and Lee 2004). Competing models containing all combinations of variables and interactions in the full model were created and ranked *via* Akaike information criterion correction (AICc) using the dredge function of the MuMIn package in R (Bartoń 2022).

Chesson's selectivity or alpha values (Chesson 1983) were calculated to determine the degree to which each predator selected for or against each prey species. If Chesson's alpha exceeded or was less than one third, the predator selected for or against the prey item, respectively, because equal numbers of three taxa were introduced to the predator. Predators select neutrally for a prey item if Chesson's alpha is approximately one third.

Table 1. The top five AICc-ranked binomial generalize ranked models describing the total number prey taxa consumed during raceway trials.

Dependent variable	Independent variables included	Model selection criteria	
		AICc	ΔAICc
Total prey consumed	light * predator species* predator size	236.86	0.00
	light + predator species* predator size	239.39	2.53
	light + predator species* predator size* temperature	246.73	9.87
	light * predator species	260.60	23.20
	light + predator species	261.63	24.77

Binomial generalized linear models were used to explain prey selectivity (Chesson's alpha) for each of the three prey species as a function of light level (lux), predator species, predator TL, and water temperature, and the interactions between these factors. Similar to models detailed above describing the number of prey consumed, competing models containing all possible combinations of factors and interactions in the full model were created and ranked AICc using the dredge function of the MuMln package in R (Bartoń 2022). Competing models with a ΔAICc < 2 were averaged using the MuMln package as well.

3. Results

3.1. Total prey consumed

Across all trials, the average total number of individual prey consumed was higher in full moon (0.20 lux) than new moon (0.00 lux) trials (mean ± SE full moon: 36.69 ± 2.33; mean ± SE new moon: 19.6 ± 2.32) (Figure 1). The AICc top-ranked model explaining total prey consumed included light level, predator species, predator size, the interaction between light level and predator species, the interaction between light level and predator size, and the three-way interaction between light level, predator species, and predator size (Table 1). The top ranked model indicated the probability of an individual prey being consumed in a full moon trial was 0.16 (95% CI: 0.10–0.21) higher than that in new moon trials (p-value = 2.53e − 08).

3.2. Lake sturgeon consumed

The average number of LS consumed was higher in 0.20 lux trials than in 0.00 lux trials (mean ± SE full moon: 7.31 ± 2.33; mean ± SE new moon: 4.93 ± 1.00) (Figure 1). The AICc top-ranked model explaining the number of LS consumed included light level, predator species, predator size, and the interaction between predator species and predator size (Table 2). The AICc top-ranked model indicated the probability of an LS individual being consumed in a full moon trial was 0.11 (95% CI: 0.02–0.18) higher than that in new moon trials (p-value = 0.01). The average number of LS consumed in RB trials was higher than in HHC trials (mean ± SE RB: 10.44 ± 1.11; mean ± SE HHC: 1.81 ± 0.48). The top model also indicated that the probability of an individual LS being consumed in an RB trial was 0.39 (95%CI: 0.35–0.43) higher than in a HHC trials. The number of LS consumed in a trial was positively correlated with the size of the predator (Table 2). The top model indicated an increase in mean predator TL of 1 cm increased the probability of an individual LS being consumed by 0.16 (95% CI: 0.16–0.26) in HHC trials and 0.06 (95%CI: −0.06–0.15) in RB trials.

Table 2. The top five ranked models by AICc explaining the total number of each prey taxa consumed during raceway trials.

Dependent variable	Independent variables included	Model selection criteria AICc	Model selection criteria ΔAICc
Lake sturgeon consumed	light + predator species* predator size	147.03	0.00
	predator species* predator size	150.98	3.95
	light * predator species* predator size	155.76	8.73
	light + predator species* predator size* temperature	160.18	13.16
	predator species* predator size* temperature	161.85	162.78
Catostomids consumed	light * predator species* predator size	203.47	0.00
	light + predator species* predator size	206.92	3.44
	predator species* predator size	212.01	8.54
	light + predator species* predator size* temperature	212.40	8.93
	predator species* predator size* temperature	216.02	12.55
Heptageniids consumed	light * predator species* predator size	188.03	0.00
	light + predator species* predator size* temperature	198.38	10.36
	light + predator species* predator size	201.31	13.29
	light * predator species* predator size* temperature	221.78	33.76
	light * predator species	222.06	34.03

3.3. Catostomids consumed

The AICc top-ranked model indicated that the best supported model included effects of light level, predator species, predator size, the interaction between lux and predator species, the interaction between predator species and predator size, and the three-way interaction between lux, predator species, and predator size (Table 2). The effect of predator size on the number of CAT consumed was greater during full moon trials than new moon trials (Table 3). The probability an individual CAT would be consumed increased by 0.24 (95% CI: 0.15–0.34) for every 1 cm increase in mean predator TL in full moon trials, but 0.07 (95% CI: 0.00–0.15) for new moon trials ($p = 0.003$).

3.4. Heptageniids consumed

The number of HEPT consumed was higher in full moon trials than new moon trials (mean ± SE full moon: 22.31 ± 1.06 vs. mean ± SE new moon: 9.50 ± 1.43) (Figure 1). The AICc top-ranked model accounted for estimated effects of predator species, predator size, the interaction between predator species and predator size, the interaction between light level and predator species, the interaction between light level and predator size, and the three-way interaction between light level, predator species, and predator size (Table 2). The difference in magnitude of light level effects was greater for RB trials (mean ± SE RB full moon: 24.00 ± 1.35 vs. mean ± SE RB new moon: 8.5 ± 2.78) relative to the HHC trials; (mean ± SE HHC full moon: 20.63 ± 1.49, vs. mean ± SE HHC new moon: 10.5 ± 0.91). The probability a HEPT individual would be consumed in a full moon trial was 0.25 (95% CI: 0.18–0.30) and was higher than that in new moon trials (p-value = 2.76e − 10). The effect of light level was larger in RB trials than HHC trials. During RB trials, the probability a HEPT individual would be consumed in a full moon lit trial was 0.36 (95% CI: 0.28–0.41) higher than new moon lit trials, and in HHC trials, the probability an HEPT individual would be consumed in a full moon trail was 0.25 (95% CI: 0.17–0.30) higher than new moon trials ($p = 0.006$). The relationship between predator size and number of HEPT consumed is more strongly

Table 3. Parameter estimates included in the top AICc-ranked model describing the number of lake sturgeon, catostomids, and heptageniids consumed during raceway predation trials.

Lake sturgeon consumed	Parameter	Estimate	Std. error	P-value
	Intercept	−3.448	0.2438	<0.001
	Lux-0.2	0.4383	0.1693	0.009
	Predator species-RB	2.1423	0.2384	<0.001
	Mean predator size	0.6807	0.2309	0.003
	Predator species-RB: Predator size	−0.4222	0.2442	0.084
Catostomids consumed	Parameter	Estimate	Std. error	P-value
	Intercept	−1.8392	0.1669	<0.001
	Lux-0.2	0.2833	0.2328	0.223679
	Predator species-RB	−0.1767	0.2427	0.466699
	Pred_cm	0.309	0.152	0.042107
	Lux-0.2: Predator species-RB	0.1334	0.3319	0.687811
	Lux-0.2: Predator size	0.8239	0.2773	0.002971
	Predator species-RB:Pred_cm	−0.2359	0.1905	0.21566
	Lux-0.2: Predator species-RB: Predator size	−1.2786	0.3667	0.000489
Heptageniids consumed	Parameter	Estimate	Std. Error	P-value
	(Intercept)	−1.0308	0.1272	<0.001
	Lux-0.2	1.075	0.1703	<0.001
	predatorRock bass	−0.3073	0.1976	0.11995
	Pred_cm	−0.0945	0.1181	0.42359
	Lux-0.2:predatorRock bass	0.7006	0.2586	0.00674
	Lux-0.2: Predator size	−0.3103	0.1928	0.10745
	Predator species-RB:Pred_cm	0.6731	0.154	<0.001
	Lux-0.2: Predator species-RB: Predator size	−0.367	0.2542	0.1489

negative in HHC trials than in RB trials (Table 3). Across HHC trials, as mean predator TL increased by 1 cm, the probability of a HEPT being consumed decreased by 0.02 (95% CI: −0.08–0.03) whereas across RB trials, as mean predator TL increased by 1 cm, the probability of a HEPT being consumed increased by 0.14 (95% CI: 0.07–0.21; p-value = 1.25e − 5). Although other covariates were included in the top model, no other co-variate was found to have a significant influence on the probability of HEPT consumption.

3.5. Lake sturgeon selectivity

Lake sturgeon larvae were selected against by HHC and were neutrally selected for by RB (Figure 2). The average of top ranked models (ΔAICc < 2) included the estimated effects of light level, predator size, and the interaction between predator species and predator size (Table 4). LS were selected for by RB more than by HHC (mean ± SE Chesson's alpha RB: 0.35 ± 0.03, mean ± SE Chesson's alpha HHC: 0.08 ± 0.02). The probability LS would be selected for in a RB trial was 0.87 (95% CI: 0.80–0.92) higher than that in HHC trials (p-value < 2e − 16). LS were more likely to be selected for in new moon trials than in full moon trials (mean ± SE new moon Chesson's selectivity: 0.26 ± 0.04; mean ± SE full moon Chesson's selectivity: 0.17 ± 0.04). The average of top ranked models indicated the probability LS would be selected for in new moon trials was 0.07 (95% CI: 0.01–0.18) higher than in full moon trials (p-value = 0.03). As predator size increased, selection for LS also increased in HHC trials, but not RB trials. For every 1 cm increase in predator TL, the probability LS would be selected for increases by 0.14 (95% CI: 0.02–0.24) in HHC trials and 0.01 (95% CI: −0.12–0.13) in RB trials (interaction p-value = 0.364).

Table 4. The top five ranked models by AICc explaining the selectivity for each prey taxa consumed during raceway trials.

		Model selection criteria	
Dependent variable	Independent variables included	AICc	ΔAICc
Sturgeon selection	light + predator species* predator size	144.70	0.00
	light + predator species	145.71	1.00
	predator species* predator size	146.60	1.90
	light + predator species* temperature	147.21	2.51
	light* predator species	148.79	3.24
Catostomid selection	light + predator species* predator size	165.97	0.00
	predator species* predator size	166.43	0.46
	light* predator species* predator size	168.14	2.16
	light + predator species* predator size* temperature	171.52	5.55
	predator species* predator size* temperature	171.63	5.65
Heptageniid selection	light* predator species* predator size	177.65	0.00
	predator species* predator size	178.08	0.43
	light* predator species* predator size	181.37	3.72
	light + predator species* predator size* temperature	186.91	9.26
	predator species* predator size* temperature	195.90	18.26

3.6. Catostomid selectivity

Catostomids were neutrally selected for by HHC and selected against by RB Figure 2. CAT were selected for by HHC more than by RB (mean ± SE Chesson's alpha HHC: 0.25 ± 0.04, mean ± SE Chesson's alpha HHC: 0.19 ± 0.03). The average of top ranked models (ΔAICc < 2) indicated, accounting for estimated effects of light level, predator size, and the interaction between predator species and predator size (Table 4), the probability CAT would be selected for in a HHC trial was 0.12 (95% CI: 0.04–0.20) higher than in an RB trial (p-value = 0.004). As predator size increased, selection for CAT also increased in HHC trials, but not RB trials. For every 1 cm increase in predator TL, the probability CAT would be selected for increased by 0.13 (95% CI: 0.07–0.19) in HHC trials and decreases 0.07 (95% CI: −0.15–0.02) in RB trials (interaction p-value = 4.24e − 06). The effect of light level was also included in the averaged top models but did not significantly impact selectivity for CAT.

3.7. Heptageniid selectivity

Heptageniids were selected for by HHC and RB (Figure 2), though levels of selection were dependent on light level, predator species, and predator size. HEPT were selected for by HHC more than by RB (mean ± SE Chesson's alpha RB: 0.45 ± 0.04, mean ± SE Chesson's alpha HHC: 0.67 ± 0.05). The average of top ranked models (ΔAICc < 2) indicated that when accounting for estimated effects of light level, predator size, and the interaction between predator species and predator size, light level and predator species, light level and prey size, and the three way interaction between light level, prey size and prey species (Table 4), the probability HEPT would be selected for in a RB trial was 0.19 (95% CI: 0.09–0.28) higher than that in HHC trials (p-value = 3.13e − 04). HEPT were more likely to be selected for in full moon trials than new moon trials (mean ± SE new moon Chesson's selectivity: 0.48 ± 0.05; full moon Chesson's selectivity: 0.63 SE: 0.04). The average of top ranked models indicated the probability HEPT would be selected for in new moon trials was 0.11 (95% CI: 0.02–0.21) higher than in full moon trials (p-value = 0.017). As predator size increased, selection for HEPT also increased in HHC trials, but not RB trials. For every 1 cm increase in predator TL, the probability LS would be selected for increased by 0.14 (95% CI: 0.02–0.24) in HHC trials and 0.01 (95% CI: −0.12–0.13) in RB trials (interaction p-value = 0.364).

4. Discussion

Results indicate both common stream predatory fishes evaluated in this study relied on light to locate prey. Total prey consumed was significantly less in trials reflecting new moon conditions than full moon conditions for both predators. Data further revealed that RB selected prey more efficiently under full moon conditions, whereas HHC prey selection was consistently focused on HEPT regardless of light level. Results explain the observed correlation between levels of lunar illumination and the probability of finding dispersing sturgeon in the diets of riverine predators (Waraniak et al. 2018). Findings suggest decreases in larval LS predation during nights of lower lunar illumination can be attributed to lower probability of predators detecting and consuming prey in low light conditions. Chesson's alpha was slightly higher in new moon trials for both RB and HHC indicating higher selection for LS in new moon conditions, but both predator species consumed fewer LS in new moon trials, confirming they were able to detect and consume prey, albeit in lower numbers during full moon light conditions.

4.1. Prey responses to environmental cues affect predation risk

Larvae of other fish species that are vulnerable to predation rely on the cue of the new moon to signal the beginning of their down-stream dispersal from spawning grounds. For example, Coho salmon (*Oncorhynchus kisutch*) smolts were more likely to migrate downstream during the new moon, though the strength of this relationship varied by population (Spence and Dick 2014). The relationship between Coho smolt outmigration and new moon is thought to increase smolt survival due to the difficulty visual predators have locating smolts (Grau et al. 1981). There is evidence that Coho smolts released during a new moon have higher recruitment rates than those released at a random date (Nishioka et al. 1989). However, larval LS migrate downstream passively when their yolk-sac energy reserve is exhausted, therefore outmigration timing strongly is dependent on the timing of spawning, and water temperature (Duong et al. 2011), which influences their metabolic rate.

It is common for fish populations to rely on environmental cues to initiate spawning. Lunar phase and temperature have been shown to be predictive of the onset of spawning for several species including European eel (*Anguilla anguilla*; Miyai et al. 2004), Japanese eels (*Anguilla japonica*; Sudo et al. 2014), coral trout (*Plectropomus leopardus*; Samoilys 1997), multi-species coral reef aggregations (Fisher et al. 2018), and honeycomb grouper (*Epinephelus merra*; Lee et al. 2002). The onset of spawning in LS can be predicted based upon lunar phase, temperature, and river discharge. Spawning generally begins during a new moon and when water temperature warms to 10 °C (Forsythe et al. 2012a). Temperatures early in the spawning season result in larval lake sturgeon consuming the last of their yolk-sac and beginning to drift approximately 25–30 days (total observed range 21–36 days) after fertilization (Duong et al. 2011). If an egg is fertilized during the new moon and the larva disperses 25–30 days afterwards, the larva will be drifting near the next new moon, in the darkest conditions. Results in this study indicate that the larval sturgeon drifting during the lowest light levels have the highest survival rates during this vulnerable dispersal period. This means adult LS spawning during a new moon at the beginning of the spawning season may realize higher probabilities of offspring surviving, and therefore higher reproductive success.

Previous research has shown that there is a high repeatability of the timing of the onset of LS spawning for individuals, suggesting it is a heritable trait (Forsythe et al. 2012b). Taken together, results from this study along with known characteristics of LS spawning ecology indicate that the timing of lake sturgeon spawning could be a heritable trait that is selected for through higher survival rates of larval lake sturgeon drifting in lower light levels. More research into the heritability of spawning time, the relative survival of larvae under different environmental conditions, and the replication of studies across numerous lake sturgeon populations is needed to make definitive conclusions as to whether selection has acted on the timing of the first LS spawning period.

4.2. Predator features associated with prey mortality risk

Examination of the morphology of RB and HHC may explain why RB appeared to depend on sight to select prey, whereas HHC were able to strongly select for HEPT in both high and low light conditions. Centrarchids in general have eyes with a higher cone density than other groups, and RB in particular have larger eyes and larger cone surface area than other Centrarchids, allowing RB to see in low levels of light (Williamson and Keast 1988). This trait likely allows Centrarchids and especially RB to rely on using sight to detect and select prey, even in low-light conditions. Likewise, we found that RB were able to capture more prey and select for prey in full moon conditions. In new moon conditions, where no light was detected by lux meter, RB consumed less total prey and did not exhibit the same selectivity displayed in full moon conditions, suggesting low light levels are required for RB prey detection and identification. Previous studies have also found Centrarchid's are capable of prey detection and identification in low visibility conditions. Andree and Wahl (2019) found both black crappie (*Pomoxis nigromaculatus*) and white crappie (*Pomoxis annularis*), both Centrarchid visual predators, were able to select for prey species similarly in water of 0–50 nephelometric turbidity units (NTU), though selectivity for size of prey diminished as turbidity increased.

Conversely, HHC, which does not possess eyes highly-adapted for low-light conditions, exhibited positive selection for HEPT and negative selectivity for LS under low light conditions. HHC belong to the super-group Ostariophysi, which also includes Cypriniformes (minnows, suckers, and carp), Characiformes (characins), Gymnotiformes (electric eels), and Siluriformes (catfish). A major synapomorphy of this group is the Weberian Apparatus, a bony structure connecting the swim bladder to the inner ear, which effectively uses the swim bladder to amplify sounds to improve hearing ability. The Weberian Apparatus has divergently evolved in families of fish, allowing each optimal hearing in their environment (Bird and Hernandez 2007). HHC likely use their Weberian Apparatus to select for prey when they cannot see the prey. Cyprinids have been documented using hearing alone to find prey. Holt and Johnston (2011) found that when sounds mimicking prey were played on underwater speakers, several Ostariophysi species, mainly Cyprinids, approached the speakers, but no species without a Weberian Apparatus approached speakers, displaying the efficacy of Cyprinids relying on hearing or vision to hunt prey.

Predator size was included in all top ranked models for number of each prey taxa consumed and prey selection. Across all trials, as predator size increased, the number of LS consumed increased, and the number of HEPT consumed decreased, with the exception of HEPT consumed by RB in new moon trials. These trends are expected, as generalist diets tend to shift through ontogeny from zooplankton, to invertebrates, and to small fish, and often continues to larger fish as the generalists grow (Kitagawa and Fujioka 2017; Jacobson et al. 2019). Ontogenetic diet shifts to piscivory have been documented in Centrarchids (Probst et al. 1984; Dauwalter and Fisher 2008). Larger RB may consume more HEPT in darker conditions because larger predators consume more prey, but RB cannot efficiently differentiate between prey types in new moon conditions. It is relatively rare for Cyprinids to become piscivorous (Vejřík et al. 2016; Özdilek 2017). However, LS in the drifting period are relatively small (16.0–24.4 mm; Auer and Baker 2002), similar to the size of aquatic macroinvertebrates, so HHC are not gape-limited. One study detected LS in diets of 5 Cyprinid species during the larval LS drifting period, including 9% of HHC sampled (Waraniak et al. 2019). Results in this study indicate RB and HHC may be important predators of LS, particularly when predators are relatively large.

4.3. Lake sturgeon predation risk

Mortality rates of larval aquatic macroinvertebrate species and lake sturgeon have been thought to have high inter-annual variation (McElravy et al. 1989; Caroffino et al. 2010a). Numerous biotic and abiotic variables, including river discharge, temperature, competition, and predation have been shown to affect macroinvertebrate mortality (Gasith and Resh 1999). Results of this study suggest that macroinvertebrate mortality rates may also be influenced by lunar illumination, as both RB and HHC consumed more HEPT, and both predators selected for HEPT in full moon light conditions. Predation rates of larval Heptageniid populations are likely more influenced by lunar illumination than predation on larval lake sturgeon populations.

Survival of LS during early life stages and subsequent recruitment has been studied across several populations (Caroffino et al. 2010a, 2010b; McDougall et al. 2014; Pratt et al. 2014; Waraniak et al. 2018, 2019; Barth et al. 2020). LS population survival across ontogeny is an important metric for managers to model to allocate resources to conserve threatened populations. Evidence of the impact of nightly lunar illumination on predation rates of LS exemplifies the need for lunar illumination during the drift period to be included in future models describing larval LS survival. However, lunar phase is not the only factor influencing available light at night for visual predators; the timing of moonrise, local weather conditions, depth, and turbidity (Fiksen et al. 2002; Carreon-Martinez et al. 2014; Andree and Wahl 2019) will all influence the amount of light and therefore prey detectability.

Population sizes of invertebrates likely influence LS predation rates. In this study, as well as others in the Black River system by Waraniak et al. (2017) and Waraniak et al. (2019), found that most fish species do not select for LS larvae and instead exhibit positive selectivity for drifting macroinvertebrates, particularly HEPT. This suggests that if there were an abundance of more desirable prey drifting with LS larvae, predation rates on LS are likely to decrease. Although HHC and RB did not select for LS, both predator species did consume LS in the majority of trials, and there is evidence for prey-switching in this community (Waraniak et al. 2017), suggesting predation during drift does affect LS larval survival rate. This is especially likely during periods when LS larvae are abundant relative to other drifting larvae, which is has been regularly documented in our study system (Waraniak et al. 2019; Receveur et al. 2022). Managers interested in increasing lake sturgeon survival rates during critical early life stages may benefit from managing river ecosystems to promote high population abundance of taxa such as mayflies that are selected by riverine predators but are sensitive to poor water quality.

The impact of nocturnal light level on larval mortality of all prey species evaluated is of interest to ecologists and managers with the goals of modelling sources and levels of larval fish and aquatic macroinvertebrate recruitment. Variation in a predators' ability to see prey is influenced by lunar phase but is also likely dependent on the height of the moon, local cloud cover, forest canopy cover of the river, and turbidity of the water.

These are likely relevant parameters for all larval fish and invertebrate mortality estimations, as light level was shown not only to affect survival of lake sturgeon, our species of interest, but also overall predation rates over all potential prey species. Importantly, predation rates evaluated experimentally here and encountered in natural stream situations will likely be most closely predicted by the covariation of nocturnal light levels with the taxonomic diversity and relative abundance of co-distributed prey as well as the size and species composition of predators.

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Author contributions

K. Scribner and E. Baker secured funding for the project. J. Riedy was responsible for study conception and design and led data collection and analyses with assistance from K. Scribner and E. Baker. J. Riedy prepared the first draft of the article. All authors contributed to writing revision.

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Data availability statement

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