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Molecular diet analysis reveals predator–prey community dynamics and environmental factors affecting predation of larval lake sturgeon *Acipenser fulvescens* in a natural system

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This study utilized molecular tools to quantify the prevalence of predation during the vulnerable drifting larval life-history stage of lake sturgeon *Acipenser fulvescens*. How predators, the co-distributed prey community and abiotic environmental conditions (*e.g.*, stream substrata) affected predation levels was quantified. Nightly D-frame drift net surveys were used to estimate the biomass of *A. fulvescens* and co-distributed prey. Gastrointestinal diet samples (n = 1,140) from 28 species of potential fish predators were collected during electrofishing surveys. Sampling was conducted for 17 days across 2015 and 2016. Based on DNA barcode analysis using sturgeon-specific mtDNA cytochrome oxidase I primers, *A. fulvescens* DNA was detected in 73 of 1,140 diet samples (6.40%) from 16 of the 28 predator species examined. A logistic regression model was used to analyse the effects of biotic and abiotic variables associated with the likelihood a predator had consumed larval *A. fulvescens*. Increasing lunar illumination and biomass of larval *A. fulvescens* increased predation rates on larval *A. fulvescens*. Higher discharge and greater biomass and proportions of alternative prey decreased predation rates of larval *A. fulvescens*. Predation rates were slightly higher in habitats with sand substrata. Most predator species preyed upon larval *A. fulvescens* at similar rates. The study revealed considerably higher incidence of predation on larval *A. fulvescens* than previous studies had documented using traditional morphological diet analysis. Co-distributed prey and abiotic environmental variables that affected the predation rates of a species of regional conservation concern can inform future management actions.

KEYWORDS

Acipenser fulvescens, barcoding, larval fish, lunar illumination, molecular diet analysis

1 | INTRODUCTION

The early life stages of many fishes are subject to high mortality rates and impose a bottleneck to recruitment for many species (Hjort, 1914; Houde, 2008). Egg and larval stages of many fishes are particularly vulnerable to predation (Gjøsæter *et al*., 2016; Mason & Brandt, 1996; Pine *et al*., 2001). Predation on the early life stages of fishes can influence recruitment of otherwise highly abundant populations (Silbernagel & Sorenson, 2013) and can inhibit recovery in populations already experiencing low natural recruitment (Dudley & Matter, 2000; Köster & Möllmann, 2000).

Predation of early life stages of fishes has been difficult to quantify in natural systems. Previous studies focused on larval fish recruitment have relied upon inferences drawn from the relationship between predator abundance and the number of successful recruits (Gjøsæter *et al*., 2016; Mason & Brandt, 1996) or results extrapolated from experimental studies showing predators readily consumed large numbers of fish larvae (Gadomski & Parsley, 2005; Silbernagel & Sorenson, 2013). Attempts to estimate predation rates of larval fishes from predator diet analyses often underestimate levels of predation on larval fish when morphological methods are used to identify prey in diets (Schooley *et al*., 2008). Larval fish have no long-lasting hard structures that can be identified when digested and are often unidentifiable beyond 2 h after consumption by piscivorous fishes (Hallfredsson *et al*. 2007; Legler *et al*., 2010; Schooley *et al*., 2008). An alternative method involves the use of molecular methods to identify

prey DNA in the gastrointestinal (GI) contents of predators (Carreon-Martinez *et al*., 2011; Jo *et al*., 2014; Rosel & Kocher, 2002). DNA of larval fishes has a much longer detection period in the GI tracts of piscivorous fishes, extending the detection period to 24–48 h using genetic techniques (Carreon-Martinez *et al*., 2011; Hunter *et al*., 2012; Ley *et al*., 2014). Molecular techniques have detected DNA from other prey species within similar time periods, though this depends on prey morphology (Corse *et al*., 2014) the predator species (Albaina *et al*., 2015; Corse *et al*., 2014; Ley *et al*., 2014) and amount of prey consumed (Thalinger *et al*., 2017). With more sensitive tools to identify larval fishes in the diets of predators, more rigorous field studies can be conducted to characterize factors affecting predation on larval fishes.

Species composition and size-classes of predatory fish in a community can have important effects on predation levels of larval prey (Chalcraft & Resetarits, 2003; Parke *et al*., 2009). Prey preferences (Silbernagel & Sorenson, 2013; Reiss *et al*., 2014), foraging efficiencies (Scharf *et al*., 2009) and consumption rates (Gosch & Pope, 2011) can vary greatly among predators. Recognition of certain species as important predators of larval fish can inform management decisions about harvest regulations, targeted removals, biological controls, or other strategies of predator control to improve recruitment of a target species (Carpenter & Mueller, 2008). Additionally, identifying predators improves understanding about the ecological importance of larval fish and how these predator–prey relationships affect prey abundance and structure the overall community (Gjøsæter *et al*., 2016).

Prey community composition has the potential to affect predation rates of larval fish through indirect effects. Indirect effects can be mediated by predator switching, which occurs as prey items change in density and predators focus foraging efforts on more abundant prey (McPhee *et al*., 2015; Murdoch, 1969; Murdoch *et al*., 1975; Reiss *et al*., 2014; Willette *et al*., 2001). Abundance and biomass of larval fishes is often highly variable through time and space (Kallasvuo *et al*., 2017; Reiss *et al*., 2002; Smith & King, 2005a), making prey switching behaviours in predator species likely, as the availability of prey fishes and encounter rates between predators and prey change spatially (*e.g*., among habitats) or temporally (*e.g*., seasonally). Overall abundance of prey species can also improve survival rates through predator swamping (Furey *et al*., 2016). Chronology of reproduction and offspring migration within a species and across species has been hypothesized as an adaptive strategy to swamp predators and improve survival of early life stages (Frank & Leggett, 1983; Ims, 1990). For example, the predation rate on relatively rare larval fishes may decline in the presence of more abundant co-distributed prey species by lowering the rate predators can find the rare species or causing predators to switch focus to the more abundant prey (Frank & Leggett, 1983; Kean-Howie *et al*., 1988).

Abiotic environmental conditions have important effects on predation rates of larval fishes, particularly environmental conditions that affect the foraging abilities of predators (Camp *et al*., 2012; Carreon-Martinez *et al*., 2014; Huusko *et al*., 1996). For example, turbidity can serve as cover from predators for larval fish, *e.g*., larval yellow perch *Perca flavescens* (Mitchill 1814) (Carreon-Martinez *et al*., 2014), juvenile Gila chub *Gila cypha* Miller 1946 (Dodrill *et al*., 2016), larval white sturgeon *Acipenser transmontanus* Richardson 1837 (Gadomski & Parsley, 2005). Similarly, light levels affect the foraging success of visual predators and prey behaviours coinciding with diel and lunar patterns in light levels can affect vulnerability to predation (Beauchamp *et al*., 1999; Gadomski & Parsley, 2005; Huusko *et al*., 1996; Prugh & Golden, 2014). Substrata in aquatic environments are crucial habitats that larval fish species use for cover. The amount and distribution of habitat used for cover can increase predation risk for larval fishes (*e.g*., substratum type; Gadomski & Parsley, 2005; McAdam, 2011; Smith *et al*., 2012).

How biotic and abiotic factors modify predation rates during the early life stages is particularly important for species of conservation concern that are affected by low recruitment, including lake sturgeon *Acipenser fulvescens* Rafinesque 1817. Many *A. fulvescens* populations have been reduced or extirpated by overfishing and loss of suitable spawning habitat in rivers (Auer, 1996; Bruch *et al*., 2016). Stocking programmes have been instituted to sustain populations with low natural recruitment in the Laurentian Great Lakes region (Baker & Borgeson, 1999; Bruch *et al*., 2016; Peterson *et al*., 2007). The high mortality rates experienced by egg and larval stages have been identified as likely bottlenecks to successful recruitment for *A. fulvescens* populations (Caroffino *et al*., 2010a; Forsythe, 2010). The drifting larval stage in particular appears to be a likely stage where mortality can have a strong influence on recruitment, as drifting larvae can be abundant in some systems where few age 0 juveniles have been observed (Caroffino *et al*., 2010a; Smith & King, 2005b). The period when larval *A. fulvescens* begin feeding exogenously and drift downstream from spawning grounds leaves them particularly vulnerable to predation (Auer & Baker, 2002; Crossman, 2008; Duong *et al*., 2011). Predation of larval *A. fulvescens* and other *Acipenser* spp. L. 1758 species has been difficult to detect and quantify reliably in field surveys using morphological diet analysis methods (Caroffino *et al*., 2010b; Parsley *et al*., 2002). The magnitude and sources of predation on larval *A. fulvescens* are necessary to consider when attempting population recovery of *A. fulvescens*, as even small increases in survival could significantly improve recruitment (Pine *et al*., 2001).

This study used *A. fulvescens* specific DNA barcoding primers to detect the remains of larval *A. fulvescens* in the diets of piscivorous fish in the upper Black River (UBR) in the northern lower peninsula of Michigan, U.S.A. Data collected during field surveys was used to build statistical models that included biotic and abiotic variables as parameters associated with the probability that a predator had consumed larval *A. fulvescens*. The objectives of this study were to quantify prevalence of *A. fulvescens* in predator diets and to assess how the composition of predator and prey communities, habitat and environmental conditions affected the probability of *A. fulvescens* predation.

2 | MATERIALS AND METHODS

2.1 | Study area and sample collection

This study was conducted in the upper Black River, Cheboygan County, MI (Figure 1), the largest tributary of Black Lake, a 4,100 ha inland lake in the northern lower peninsula of Michigan. A population size of *c*. 1200 adult *A. fulvescens* has been estimated for Black Lake (Pledger *et al*., 2013). The UBR serves as the sole spawning area for

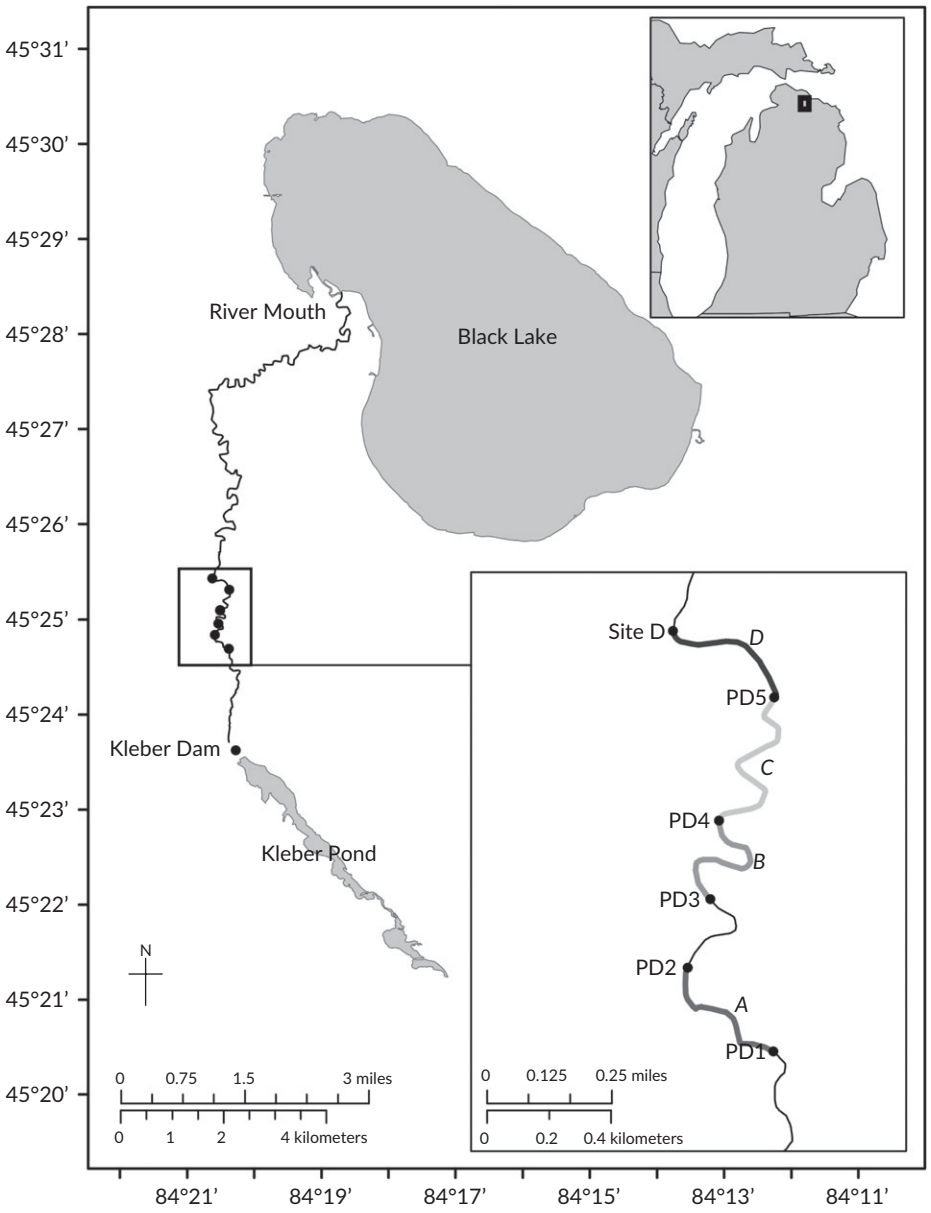

FIGURE 1 Map of the *Acipenser fulvescens* study site in the upper Black River, Cheboygan County, Michigan, U.S.A. Drift sampling was conducted at gravel (PD1, PD3) and sand (PD4, PD5) sites with associated electrofishing transects (gravel, A and B; sand, C and D)

the Black Lake *A. fulvescens* population and is restricted to a 1.5 km stretch of river *c.* 9 km upstream of the river mouth (Figure 1). Access further upstream is impeded by Kleber Dam, 11 km from the river mouth. Sampling for larval *A. fulvescens* was conducted during 2015 and 2016 at sites directly downstream of each of the spawning sites (Figure 1; gravel sites PD1 and PD3) and two other sites further downstream (Figure 1; sand sites PD4 and PD5). Sites had a mean (±S.D.) sampling depth of 0.87 m (±0.23 m) and a mean river width of 23.96 m (±2.67 m). Drift samples were collected for 5 days during the *A. fulvescens* drift period in 2015 (24 May, 4–7 June) and 12 days in 2016 (24–27 May, 29 May–1 June, 3–7 June). High water conditions prevented sampling during parts of the larval *A. fulvescens* drift period in 2015, which is why sampling occurred on fewer days during that year. The abundance of larval *A. fulvescens* drifting downstream each night was quantified using D-frame drift nets (Auer & Baker, 2002). Five D-frame drift nets with 1,600 μm mesh and detachable cod ends were set in a line perpendicular to the flow roughly equal distances apart near the thalweg of the river. Nets were set at one sampling site per night beginning at 2100 hours. Total river discharge ($m^3\ s^{-1}$) and the discharge entering nets were measured using a Marsh McBirney Flo-Mate 2000 (Hach Company; www.hach.com) to estimate the proportion of the river discharge being sampled. Net contents were collected and sorted hourly beginning at 2200 hours and concluding at 0200 hours. Larval *A. fulvescens* were counted on site and returned to the river. A 5% sub-sample of the cod end contents was collected for each hour and preserved in 95% ethanol. Each sub-sample was examined under a dissecting microscope and all larval catostomids [white sucker *Catostomus commersonii* (Lacépède 1803) and silver redhorse *Moxostoma anisurum* (Rafinesque 1820)] and aquatic macroinvertebrates were counted and identified to the family

level to estimate the abundance of each family. Average dry biomass of individuals from each family were measured and used to estimate the total biomass of invertebrates and larval fishes present in the drift (Table S1 in Supporting information; R. M. Walquist & K. T. Scribner, 2015, unpublished data).

Electrofishing surveys were conducted the days following larval drift sampling to collect diet samples of potential predators (n = 1,140 samples from 27 predator species; Table 1). A barge electrofishing unit with a three-person crew sampled a 0.5 km stream segment immediately downstream of the drift sampling sites from the previous night to capture predator fish that were present with drifting *A. fulvescens* larvae. Electrofisher settings were set to 400 V at 4 A. Two crew members carried anodes and netted fish while a third crew member pulled the barge and transferred fish to a live well. Total length (L_T) and species of all fish captured during the survey were recorded. A maximum of 10 fish per species day^{-1} were randomly selected with special attention paid to capturing the L_T range present and were sacrificed for gut-content analysis with an overdose of MS-222 (0.4 mg ml^{-1}). Sacrificed predators were individually stored in Whirl-Paks (Nasco; www.enasco.com) and placed in a − 20°C freezer. Each predator was dissected, the entire GI tract was removed and contents were carefully extracted to minimize the amount of predator tissue in the sample. During dissection, *A. fulvescens* larvae remains that could be morphologically identified were recorded. Diet samples were preserved in 95% ethanol and stored at −20°C prior to DNA extraction.

2.2 | DNA extraction and amplification

Diet samples were coarsely homogenized manually in 1.5 ml micro-centrifuge tubes with forceps, sterile toothpicks and vortexed to homogenize large pieces of tissue and ensure representative subsampling. Approximately 50–100 mg of tissue dissected from predator GI tracts was used in each DNA extraction (this was often the entire sample, otherwise a sub-sample was taken) and washed with sterile water to remove excess ethanol through two rounds of suspension in sterile water and centrifugation at 6000*g* for 5 min. Extraction negative controls (n = 12) using 200 μl of distilled water instead of tissue from GI tracts were created during several rounds of extractions to identify possible contamination of samples during the extraction process. A modified version of the QIAamp Stool Mini Kit (QIAGEN; www.qiagen) protocol was used. The first modification extended lysis

TABLE 1 Sample sizes for each predator species sampled during each year and total number of predator diet samples that tested positive for *Acipenser fulvescens* DNA

Predator species	Predator size range (mm)	Sample size 2015	Sample size 2016	Total sample size	Total positive for sturgeon DNA
Ambloplites rupestris	36–302	28	52	80	0
Ameiurus natalis	178–193	0	2	2	0
Ameiurus nebulosus	240	1	0	1	0
Catostomus commersonii	67–230	4	18	22	0
Chrosomus eos	39–60	0	3	3	0
Cottus bairdii	63	0	1	1	0
Culaea inconstans	43–48	0	4	4	1
Etheostoma caeruleum[a]	32–69	43	129	172	7
Etheostoma exile	54	0	1	1	0
Etheostoma nigrum[a]	46–69	2	20	22	1
Lepomis gibbosus	68–180	10	1	11	0
Lepomis macrochirus	50	0	1	1	0
Lota lota[a]	160–306	6	16	22	1
Luxilus cornutus[a]	29–147	35	81	116	8
Micropterus dolomieu[a]	59–500	17	30	47	1
Moxostoma anisurum	60	0	1	1	0
Nocomis biguttatus[a]	40–152	105	114	219	14
Notemigonus crysoleucas	75	0	1	1	1
Notropis heterodon	31–40	3	3	6	1
Notropis heterolepis	41–57	0	3	3	1
Perca flavescens[a]	59–148	23	73	96	11
Percina caprodes[a]	52–115	19	38	57	12
Percina maculata[a]	53–82	8	16	24	1
Pomoxis annularis	77	0	1	1	0
Rhinichthys atratulus	45–53	4	0	4	1
Semotilus atromaculatus[a]	39–139	33	74	107	7
Umbra limi[a]	50–99	12	105	117	5
Total		353	788	1,141	73

[a] Predator species included in the predator-species parameter used in the regression analysis.

in InhibitEx Buffer from the QIAmp Stool Mini Kit to 30 min at 72°C. Another modification to the QIAGEN protocol added a 10 min bead-beating step using 0.70 mm garnet beads (MOBIO; www.mobio.com) to further homogenize samples after lysis buffer and proteinase K were added to the sample. After elution, DNA concentration was quantified and presence of possible inhibitor proteins was examined with an ND-1000 nanodrop spectrophotometer (NanoDrop Technologies Inc.; www.thermofisher.com). If a high concentration of contaminants (260/280 < 1.7) remained in the sample, a salt precipitation using cold 100% ethanol and 0.15 M sodium acetate was used to clean samples. All samples were diluted using sterile water to a standard concentration of 20 ng μl^{-1} of DNA.

Two *Acipenser* spp. specific primer sets were used to test for the presence of *A. fulvescens* DNA in the diet samples, *Af-COI1* and *Af-COI2* (Waraniak *et al*., 2017). PCR conditions for both primer pairs included 20 ng of template DNA, 0.5 μM for each forward and reverse primer, 200 μM deoxynucleotide triphosphate (dNTP), 1X reaction buffer and 5 U of Taq DNA polymerase (Invitrogen; www.invitrogen.com) and deionized water for a reaction volume of 25 µl. Amplification conditions included an initial denaturation step of 94°C for 3 min; followed by 35 cycles of 94°C (45 s), 56°C (30 s) and 72°C (30 s). Final extension lasted 5 min at 72°C. Ten microlitre of PCR products were visualized on 2% agarose gels stained with ethidium bromide. Successful amplification of a sequence of the appropriate size indicated the presence of *A. fulvescens* remains in diet samples. A positive control of *A. fulvescens* genomic DNA and a negative control of PCR reaction mixtures without template DNA were included for each round of PCR. Eight microlitre of 100 bp ladders (Invitrogen) were run on each gel to approximate the size of PCR products and ensure positive results were the expected size of the target region (*Af-COI1*, 138 bp; *Af-COI2*, 151 bp). An image of each agarose gel was captured under UV light and the image was used to score samples as positive or negative for the presence *A. fulvescens* DNA. Primer pair *Af-COI1*- was used as the primary primer pair tested on all samples and was able to detect concentrations of *A. fulvescens* DNA as low as 0.032 pg μl^{-1} (Waraniak *et al*., 2017). Primer pair *Af-COI2* was used to confirm positive results from primer pair *Af-COI1*. Only samples that were amplified by both primers were considered positive for *A. fulvescens* DNA.

General universal primers were used to verify that there was amplifiable DNA in a sub-set of the samples. In a sub-set of 367 samples, including the extraction negative controls, were amplified with *18 s* V9 ribosomal (r)RNA universal eukaryotic primers (Stoeck *et al*., 2010) and sequenced. These data were used in a separate study to quantify proportional contributions of potential prey species to predator diets and details of the sequencing and taxonomic identification of sequences can be found in Waraniak (2017). Sequences for teleost fishes were identified to the family level and samples that contained sequences identified as Acipenseridae were compared with samples that were marked as positive for *A. fulvescens* DNA by the *Af-COI1* and *AF-COI2* primer pairs.

2.3 | Statistical analysis

2.3.1 | Model description

Data of the presence or absence of *A. fulvescens* DNA in a predator-diet sample was analysed using binomial logistic regression. The regression models tested how the probability that a predator consumed a larval *A. fulvescens* was affected by biotic and abiotic variables. The full model included 15 explanatory variables that broadly encompassed three categories: availability of prey, predator type and abiotic factors associated with visibility and cover.

Variables corresponding to the availability of prey included nightly total biomass estimates for larval *A. fulvescens*, larval catostomids and aquatic macro-invertebrates. Dry mass estimates of individual larval fish and common families of macroinvertebrates (Table S1 in Supporting information; R. M. Walquist & K. T. Scribner, 2015, unpublished data) were applied to count data from the 5% drift sub-samples to get an estimate for catch biomass. The catch biomass was extrapolated to the entire river by multiplying the catch biomass by the inverse of the proportion of discharge that was sampled by the drift nets: *i.e.*, $B_{river} = (B_{catch}\, Q_{river})\, Q_{net}^{-1}$, where B_{River} is the estimated total biomass of a prey type in the drift over the course of one night of the drift survey, B_{Catch} is the dry mass of the catch of a prey type for one night, Q_{river} is the discharge of the river and Q_{net} is the discharge sampled by the net. The sum of biomasses from all macro-invertebrate families was used for a more general invertebrate biomass term. Estimated nightly proportions of the drift biomass made up by larval *A. fulvescens* and larval catostomids were also included in the model. Only two proportions could be included so as not to violate independence assumptions.

Variables associated with the predator included the predator species and L_T of the fish from which a diet sample was collected. Samples from predator species in the data set that had never consumed an *A. fulvescens* larva or had fewer than 10 total samples were removed from further analysis to improve the stability of the predator species term in regression models. This resulted in the predator species variable having 11 well-represented levels (species) and the model selection procedure being based on a sample size of $n = 999$. Abiotic variables included the predominant substratum type (sand or gravel) in the river transect from which a predator was collected, the percentage of the moon that was illuminated (US Naval Observatory, 2016), the average nightly percentage of cloudy skies during drift surveys (NOAA, 2017), river discharge and year in which the sample was collected.

Additionally, three temporal autocorrelation terms were included to account for similarities in prey biomass and environmental conditions across consecutive days, generated by an eigenfunction-based filtering method (Peres-Neto 2006). A temporal association matrix was constructed using the drift-survey sampling dates. Because sampling occurred at regular intervals, the association between consecutive sampling days was set to one and non-consecutive days were set to 0. The temporal autocorrelation terms are the principal coordinates of the eigen analysis of this temporal association matrix. The eigenvectors are synthetically generated expected patterns of autocorrelation based on the temporal structure of the sampling events and can be combined to create a complex function representing the unknown structure of autocorrelation in the data. In this case, the eigenvectors have associations with the 4 day sampling periods, with expectations that the likelihood of predation would be more similar within periods compared with other periods. The second, third and fourth eigenvectors, associated with the sampling periods from 4–8 June 2015,

24–28 May 2016 and 30 May–2 June 2016 respectively, were significantly correlated with the presence of *A. fulvescens* DNA in a diet sample (data not shown), so those three variables were included in the full model.

2.3.2 | Model selection

Models were fitted using the glm function in R 3.2.2 (www.r-project.org). All possible combinations of variables included in the model were fit and AIC values and weights were calculated for each version of the model using functions from the MuMIn library (Bartón, 2017). The relative importance of each variable was calculated by dividing the sum of the weights from the 38 models with ΔAICc < 2, that included a variable by the weights of all 38 models with ΔAICc < 2 (Bartón, 2017).

2.3.3 | Analysis of variable effects

Further exploration of important variables was carried out with the model averaged values across the 38 models with ΔAICc < 2. Differences between different levels in categorical variables and the effects of continuous variables were analysed using the odds-ratio values (O_R). Wald's χ^2 tests were used to further test for differences between levels of categorical variables. The effects of selected continuous variables were visualized using the average model generated from the models with ΔAICc < 2. Predicted probabilities of larval *A. fulvescens* predation were calculated with the plogis function in R. The values of one predictor variable would vary at a time across the range of values seen in the data set for that variable, with all other variables being held constant at their mean value in the actual data set.

The effects of different predator species were tested against each other with the average odds ratios from the 38 best-fit models that included predator species as an explanatory variable. Differences between species were then analysed with Wald's tests (the aod package in R), contrasting one species against all others included in the model. For each species, a contrast was set up with the species of interest having a contrast coefficient of −1 while the other 10 species in the model were assigned contrast coefficients of 0.1. Significance was adjusted using a Holm-Bonferroni correction for multiple comparisons.

3 | RESULTS

3.1 | Field and molecular data analysis

A total of 73 predator diet samples tested positive for *A. fulvescens* DNA using both the *Af-COI1* and *Af-COI2* primer pairs out of 1,140 total samples (6.49%). The *Af-COI1* pair of primers identified 77 positive samples and four of these samples were not amplified by the *Af-COI2* pair of primers. All four of the samples were marked as questionable during analysis of the *Af-COI1* gels, either due to the presence of a smear rather than a distinct band or to imperfections in the agarose gel that made interpretation difficult. Only one larval *A. fulvescens* was morphologically identified in all of the diet samples (0.09%), identified from a smallmouth bass *Micropterus dolomieu* Lacépède 1802 sampled in 2015. The *18s* V9 universal metabarcoding primers amplified DNA from 355 of the 367 samples collected during 2015 (96.7%), indicating large numbers of false negatives due to PCR inhibition is unlikely. Additionally, DNA was amplified from one of the 12 extraction negative controls and none of the recovered sequences from that sample were identified as *A. fulvescens*. All samples that included sequences identified as *A. fulvescens* also had sturgeon-specific amplification PCR products for both *Af-COI1* and *Af-COI2* primer pairs.

Predator communities varied between the 2 years and between sand and gravel habitats. The number of predators from each species and year from which diet samples were taken, as well as the number of predators of each species that tested positive for *A. fulvescens* DNA (Table 1). Sixteen predator species tested positive for *A. fulvescens* DNA, but only 11 of these species had sufficient sample sizes to be included in the final model parameter for predator species.

Estimated dry biomass and relative proportions of the three co-distributed prey types varied over the course of the study (Figure 2). Larval *A. fulvescens* nightly biomass varied from 2 to 243 g with a mean of 65 g and median of 6 g. Larval *C. commersonii* nightly biomass varied from 7 to 2,596 g with a mean of 477 g and median of 215 g. Aquatic macro-invertebrate nightly biomass varied from 47 to 579 g with a mean of 314 g and median of 337 g. Larval *A. fulvescens* made up between 0.2 and 32.7% of the nightly biomass (mean = 9.1%) and larval *C. commersonii* made up between 2.2 and 89.5% of the nightly biomass (mean = 40.9%).

Lunar illumination ranged from full moon (100%) to new moon (0%) conditions (mean = 42.6%). Likewise, cloud cover ranged from completely cloudy skies (100%) to clear skies (0%; mean = 47.0%). River discharge varied from 4.93 to 7.90 $m^3\ s^{-1}$ (mean = 6.52 $m^3\ s^{-1}$).

3.2 | Model selection and variable importance

There were 38 well-performing models with ΔAICc < 2 (Table 2). Across these models, the most important variables are temporal autocorrelation term E_4, the proportions of drift biomass made up by larval *A. fulvescens* and larval catostomids, the biomasses of larval *A. fulvescens* and aquatic macro-invertebrates and lunar illumination (Table 3; relative importance > 0.6). The other temporal autocorrelation terms, predator species, year, biomass of larval *C. commersonii* and cloud cover were relatively unimportant (relative importance < 0.4). The L_T of predators was not included as a variable in any of the 38 best-fit models (relative importance = 0).

3.3 | Analysis of variable effects

The model averaging indicated a strong positive relationship between the probability that a predator would have consumed a larval *A. fulvescens* with the biomass of larval *A. fulvescens* present in the drift the night before (Figure 3(a); binomial logistic regression model average, O_R = 1.025). The O_R indicates that for each additional 24.3 g of *A. fulvescens* biomass present in the drift (10% of the observed range, *c.* 2,800 individual larvae), there was an estimated 82% increase incidences of larval *A. fulvescens* predation. There was a slightly less strong but still significant negative relationship between the probability of larval *A. fulvescens* predation and the biomass of invertebrates (Figure 3(a); binomial logistic regression model average, O_R = 0.995), corresponding to a 23% decrease in *A. fulvescens* predation for each additional 52 g of aquatic invertebrates present in the drift (10% of

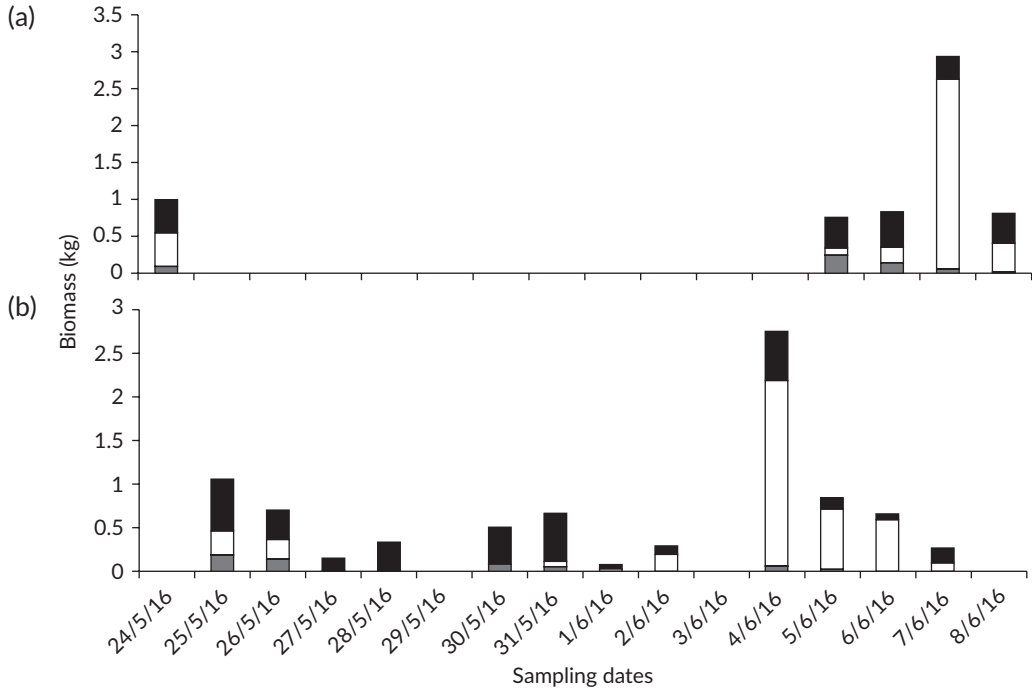

FIGURE 2 Estimated biomass from drift surveys for each of the three types of co-distributed prey (■, aquatic macro-invertebrates; □, larval catostomids; ■, larval *Acipenser fulvescens*) for each night included in the study in (a) 2015 and (b) 2016

the observed range; *c.* 29,000 mayfly larvae, family Heptageniidae, the most abundant insect family). There was also a weak slightly positive relationship with the biomass of larval *C. commersonii* (Figure 3(a); binomial logistic regression model average, O_R = 1.001), showing a 16% increase in the probability of larval *A. fulvescens* predation for each 258 g of larval catostomids present in the drift (10% of the observed range, *c.* 216,000 individual larvae).

The proportional biomass of the drift made up by larval catostomids had a moderately strong negative effect on the probability that a predator had consumed *A. fulvescens* larvae (Figure 3(b); binomial logistic regression model average, O_R = 0.968). This corresponded to a 28% reduction in *A. fulvescens* predation for each 10% of drift biomass made up by larval catostomids. The proportion of the drift biomass made up by larval *A. fulvescens* had a large negative effect on the probability of *A. fulvescens* predation (binomial logistic regression model average, O_R = 0.827), however, this effect was strongly dependent on whether or not the biomass of *A. fulvescens* was included in the model. The actual biomass (B_{LS}) and proportional biomass (B_{PLS}) of larval *A. fulvescens* were correlated (Pearson's correlation, R^2 = 0.805; P < 0.001). Because of this, those two parameters explain much of the same variation, so the behaviour of one parameter could be highly dependent on the presence of the other. The effect of B_{LS} was relatively consistent across models. However, the coefficient of B_{PLS} was dependent on the presence of B_{LS} in the model. In models without B_{LS}, the coefficient of B_{PLS} was either weakly negative or weakly positive on the probability of *A. fulvescens* predation.

Lunar illumination had a moderately strong positive effect on the probability of *A. fulvescens* predation on average for all well-performing models (Figure 3(c); binomial logistic regression model average, O_R = 1.495). For each 10% of the moon that was illuminated, there was an estimated 4% increase in the probability a predator had consumed *A. fulvescens* larvae. Substratum type was a relatively unimportant variable, but did appear in several of the best-fit models (binomial logistic regression model average, O_R = 0.507). The models compared the probability of predation of larval *A. fulvescens* in sand-dominated habitats with gravel dominated habitats, suggesting that larval *A. fulvescens* were less vulnerable in sand substrata habitats, but this difference was not consistent between the two substratum types. Discharge and cloud cover were also relatively unimportant factors. In the best-performing models that the discharge parameter was included, increasing discharge has a moderate negative effect on the probability of *A. fulvescens* predation (binomial logistic regression model average, O_R = 0.469) and increasing cloud cover also decreased the probability of *A. fulvescens* predation (binomial logistic regression model average, O_R = 0.606).

Predator species had relatively low variable importance in the analysis of all the best-fit models, but some predators appeared to have more of an effect than others. In order to test the effects of different predator species, a model was fitted with the predator species parameter as the only explanatory variable. In Wald's test, contrasts between one species and the average of the other 10 species included in the model, logperch *Percina caprodes* (Rafinesque 1818) were the only species that was significantly more likely to consume larval *A. fulvescens* (Wald's test, χ^2 = 19.8, d.f. = 1, P < 0.001) and *Perca flavescens* were nearly significantly more likely to consume larval *A. fulvescens* than the other species after Holm-Bonferroni correction (Table 4; Wald's test, χ^2 = 6.9, d.f. = 1, P < 0.01).

4 | DISCUSSION

The molecular methods used in this study were more successful in identifying predators that had consumed larval *A. fulvescens* (73 out of

TABLE 2 The variables included in each of the 38 models with lowest AICc scores assessing the presence or absence of *Acipenser fulvescens* DNA in a predator-diet sample

Variables included in model	d.f.	ΔAICc	wAICc
$B_I + B_{LS} + B_C + BB_{PLS} + P_C + C_C + E_4$	8	1.65	0.022
$B_I + B_{LS} + B_C + B_{PLS} + P_C + E_2 + E_4$	9	1.22	0.027
$B_I + B_{LS} + B_C + B_{PLS} + P_C + E_4$	7	1.44	0.024
$B_I + B_{LS} + B_C + B_{PLS} + P_C + L + C_C + E_4$	9	1.83	0.020
$B_I + B_{LS} + B_C + B_{PLS} + P_C + L + E_4$	8	0.64	0.036
$B_I + B_{LS} + B_C + B_{PLS} + P_C + L + S_{PP} + E_4$	18	1.21	0.027
$B_I + B_{LS} + B_C + B_{PLS} + P_C + L + Q + E_4$	9	1.82	0.020
$B_I + B_{LS} + B_C + B_{PLS} + P_C + L + S_{ub} + C_C + E_4$	5	1.85	0.020
$B_I + B_{LS} + B_C + B_{PLS} + P_C + L + S_{ub} + E_2 + E_4$	10	1.98	0.018
$B_I + B_{LS} + B_C + B_{PLS} + P_C + L + S_{ub} + E_4$	**9**	**0.00**	**0.050**
$B_I + B_{LS} + B_C + B_{PLS} + P_C + L + S_{ub} + S_{PP} + E_4$	19	1.25	0.027
$B_I + B_{LS} + B_C + B_{PLS} + P_C + S_{PP} + E_2 + E_3 + E_4$	9	1.42	0.024
$B_I + B_{LS} + B_C + B_{PLS} + P_C + Q + E_2 + E_3 + E_4$	10	1.49	0.024
$B_I + B_{LS} + B_C + B_{PLS} + P_C + S_{ub} + E_2 + E_3 + E_4$	10	1.59	0.022
$B_I + B_{LS} + B_C + B_{PLS} + P_C + S_{ub} + S_{PP} + E_2 + E_3 + E_4$	18	1.01	0.030
$B_I + B_{LS} + B_{PLS} + P_C + C_C + E_2 + E_3 + E_4$	9	1.69	0.021
$B_I + B_{LS} + B_{PLS} + P_C + E_2 + E_3 + E_4$	8	0.37	0.041
$B_I + B_{LS} + B_{PLS} + P_C + L + C_C + E_4$	8	0.80	0.033
$B_I + B_{LS} + B_{PLS} + P_C + L + E_4$	7	0.23	0.044
$B_I + B_{LS} + B_{PLS} + P_C + L + S_{PP} + E_4$	17	1.20	0.027
$B_I + B_{LS} + B_{PLS} + P_C + L + Q + E_4$	8	1.95	0.019
$B_I + B_{LS} + B_{PLS} + P_C + L + S_{ub} + E_4$	8	1.17	0.028
$B_I + B_{LS} + B_{PLS} + P_C + Q + E_2 + E_3 + E_4$	19	1.42	0.024
$B_{LS} + L + S_{PP} + E_4$	14	1.89	0.019
$B_{LS} + L + S_{ub} + S_{PP} + Q + E_2 + E_3 + E_4$	18	1.36	0.025
$B_{LS} + P_C + L + S_{ub} + S_{PP} + Q + E_2 + E_3 + E_4$	19	1.92	0.019
$B_{LS} + P_C + L + S_{ub} + Q + E_2 + E_3 + E_4$	9	1.15	0.028
$B_{LS} + B_{PLS} + P_C + E_2 + E_3 + E_4$	7	1.82	0.020
$L + S_{ub} + E_2 + E_3 + E_4$	8	1.28	0.026
$L + S_{ub} + S_{PP} + E_4$	14	1.65	0.022
$L + S_{ub} + Q + E_4$	10	1.85	0.020
$B_{PLS} + L + E_4$	4	1.59	0.023
$B_{PLS} + L + S_{PP} + E_3 + E_4$	15	1.55	0.023
$B_{PLS} + L + S_{PP} + E_4$	14	1.11	0.029
$B_{PLS} + L + Y + E_4$	5	1.08	0.029
$B_{PLS} + P_C + L + E_4$	5	1.18	0.028
$B_{PLS} + P_C + L + S_{PP} + E_4$	15	1.29	0.026
$B_{PLS} + P_C + L + S_{PP} + Y + E_4$	15	0.74	0.034

Note. The model with lowest AICc score is in bold. ΔAICc from the model with the lowest AICc score; wAICc, the model weights; B_C: biomass of larval catostomids; B_I: biomass of invertebrates; B_{LS}: biomass of larval *Acipenser fulvescens*; B_{PLS}: proportion of biomass made up by larval *A. fulvescens*; C_C: cloud cover; L: percentage of moon illuminated; P_C: proportion of biomass made up by larval catostomids; Q: river discharge; S_{pp}: predator species; S_{ub}: substrate type; Y: Year. E_2; E_3; and E_4 are temporal autocorrelation terms.

1,140 predators tested) than traditional morphological diet analysis (1 out of 1,140 predators tested), indicating that predation is more common than previous studies have been able to detect (Caroffino *et al*., 2010b; Parsley *et al*., 2002). Furthermore, with intensive sampling over 2 years, this study was able to highlight possible biotic and abiotic factors that affect predation of larval *A. fulvescens* migrating out of their natal stream. Previous studies of predation that have examined this stage of *A. fulvescens* development have relied on artificial experimental setups or recorded too few observations of predation to quantify effectively (Caroffino *et al*., 2010b; Gadomski & Parsley, 2005; Parsley *et al*., 2002). While the effects of co-distributed species (Frank & Leggett, 1983; Pepin & Shears, 1995) and abiotic factors (Gadomski & Parsley, 2005) on levels of predation of larval fishes have been hypothesized or examined in controlled experiments, there have been few studies evaluating these factors in natural systems. Using a large data set collected from drift and electrofishing field surveys; this study is one of the first using molecular methods to examine how multiple abiotic and biotic factors affect predation of a drifting larval fish.

TABLE 3 Average log odds ratio (O_R) across 38 models with ΔAICc < 2, 95% C.I. of model averaged O_R, and relative importance for each variable

	O_R		
Variable	**Mean**	**±95% C.I.**	**Relative importance**
E_4 – Temporal autocorrelation	1.381×10^{10}	$1.07–1.78 \times 10^{20}$	1.00
Proportion of biomass made up by larval *Acipenser fulvescens* (%)	0.827	0.663–1.032	0.84
Biomass of larval *Acipenser fulvescens* (g)	1.025	1.001–1.050	0.77
Proportion of biomass made up by larval catostomids (%)	0.968	0.933–1.005	0.75
Lunar illumination (%)	1.004	0.936–1.077	0.72
Biomass of invertebrates (g)	0.995	0.989–1.000	0.63
E_3 – Temporal autocorrelation	3.550×10^{-12}	$0.000–4.953 \times 10^{10}$	0.36
Biomass of larval catostomids (g)	1.001	1.000–1.001	0.36
E_2 – Temporal autocorrelation	1.231×10^{-13}	$0.000–6.972 \times 10^{14}$	0.35
Predator species (compared with *Percina maculata*)			0.33
Lota lota	0.913	0.051–16.210	
Umbra limi	0.908	0.098–8.446	
Luxilus cornutus	1.412	0.163–12.259	
Semotilus atromaculata	1.358	0.153–12.078	
Nocomis biguttatus	1.319	0.161–10.792	
Etheostoma nigrum	1.522	0.084–27.574	
Percina caprodes	5.877	0.696–49.579	
Etheostoma caeruleum	0.899	0.103–7.831	
Micropterus dolomieu	0.480	0.028–8.292	
Perca flavescens	2.399	0.284–20.286	
Substratum type (compared with gravel)			
Sand	0.507	0.005–50.897	0.30
River discharge (m^3 s^{-1})	0.469	0.127–1.737	0.20
Cloud cover (%)	0.606	0.212–1.732	0.12
Year (compared with 2015)			
2016	1.590	0.885–2.857	0.06

Note. Continuous variables have units in parentheses following variable description. Odds ratios for categorical variables can only be interpreted compared with a standard category (this standard category is included in parentheses after name of categorical factor). Relative importance is calculated by dividing AIC weights of all models that include the variable as a parameter by the AIC weights of all models in the 38 models with ΔAICc < 2. Importance values of at least 0.4 are required to be considered important.

Synchronized initiation of drifting behaviours is a common occurrence among many species with drifting larvae (Brown & Armstrong, 1985; Carter *et al*., 1986; Gale & Mohr, 1978). This behaviour may be advantageous to the drifting larvae due to predator swamping, where the predator community is overwhelmed with large numbers of prey, reducing overall predation mortality of prey (Frank & Leggett, 1983). The results of this study appear to support predator swamping as a mechanism reducing predation of larval *A. fulvescens*. Factors related to the biomass of alternative prey were present in 29 out of the 38 best-performing models and all of the factors related to alternative prey abundance were included in the AICc selected model. The biomass of invertebrates and the proportion of larval catostomid biomass in the drift both had consistent negative effects on the probability predators had consumed larval *A. fulvescens* and were both relatively

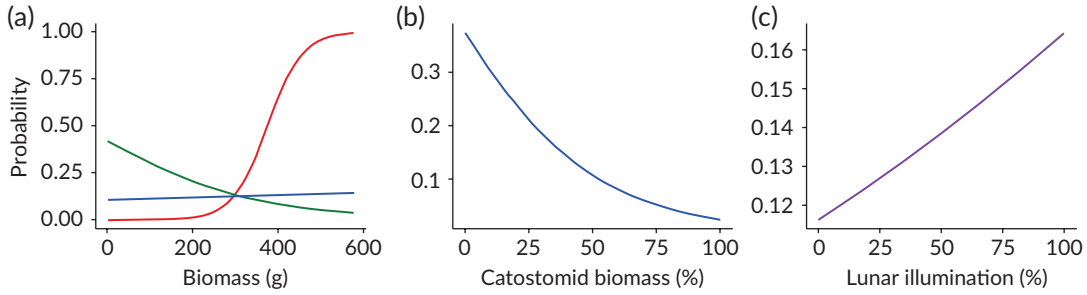

FIGURE 3 Predicted probabilities of predation of larval *Acipenser fulvescens* by a generic predator fish based on a model constructed by model averages of the 38 best performing models. Graphs show relationships between the probability that a predator diet sample contained lake sturgeon DNA and (a) the biomass of larval *Acipenser fulvescens* (——), aquatic macroinvertebrates (——), and larval catostomids (——), (b) the proportion of drift biomass made up by larval catostomids and (c) the proportion of the moon illuminated

TABLE 4 Results of Wald's χ^2-test contrasts for each predator species compared to the other predator species that were included in the full model. Each chi-squared test had d.f. = 1

Predator species	Diet samples containing *Acipenser fulvescens* DNA (%)	Wald's χ^2	*P*
Percina maculata	4.2	2.9000	>0.05
Lota lota	4.5	0.0007	>0.05
Umbra limi	4.3	0.0064	>0.05
Luxilus cornutus	6.9	1.2000	>0.05
Semotilus atromaculatus	6.5	0.8700	>0.05
Nocomis biguttatus	6.4	1.1000	>0.05
Etheostoma nigrum	4.5	0.0007	>0.05
Percina caprodes	21.1	19.8000	<0.001[a]
Etheostoma caeruleum	4.1	0.0430	>0.05
Micropterus dolomieu	2.1	0.6400	>0.05
Perca flavescens	11.5	6.9000	<0.01[b]

[a] Statistical significance after Holm-Bonferroni adjustment.
[b] Near statistical significance after Holm-Bonferroni adjustment.

important factors (Table 3). Synchronized emergence as a predator swamping strategy is most often considered in the context of one species (Ims, 1990), however, predator swamping with multiple co-distributed species may be more important for species that are relatively rare (Frank & Leggett, 1983). In both years of this study, the drifting biomass of larval *A. fulvescens* peaked at approximately the same time as larval catostomids, but the peak biomass for larval catostomids was an order of magnitude larger than the peak biomass for larval *A. fulvescens* (Figure 2). Additionally, the peaks of proportional biomass of larval *A. fulvescens* coincided with the overall biomass peak of larval catostomids, offering a possible explanation as to why the proportional biomass of catostomids had a negative relationship with the likelihood of larval *A. fulvescens* while the actual biomass of catostomid larvae had a weak positive relationship. The catostomids relative biomass peaked when *A. fulvescens* biomass was lower and resulted in lower likelihood of *A. fulvescens* predation, suggesting the relative proportions of larval catostomids were important in influencing likelihood of predation, not the actual abundance. *Acipenser fulvescens* larval production in the UBR is highly variable from year to year (Smith & King, 2005a) and there may be few years in which the *A. fulvescens* larval density alone is able to swamp predators. In most years, survival of larval *A. fulvescens* may more heavily depend on the abundance of co-distributed larval fishes and aquatic macroinvertebrates.

Some abiotic factors that affect the visibility of predators have also been shown to affect the predation of larval fishes. While turbidity was not directly measured, it is known to co-vary with discharge (Mather & Johnson, 2014), which was a moderately important parameter in the logistic regression models. Turbidity has been shown to lower predation of larval *P. flavescens* in Lake Erie (Carreon-Martinez *et al*., 2014) and predation of *A. transmontanus* larvae by slimy sculpin *Cottus cognatus* Richardson 1837 in experimental settings (Gadomski & Parsley, 2005). Visual predators including darters (Becker *et al*., 2016), other percids (Carreon-Martinez *et al*., 2014; Chiu & Abrahams, 2010), centrarchids (Ferrari *et al*., 2014; Johnson & Hines, 1999) and piscivorous cyprinids (Bonner & Wilde, 2002; Dodrill *et al*., 2016) all consumed fewer prey in turbid conditions. Likewise, moonlight is known to have important effects on predator–prey dynamics in terrestrial systems (Prugh & Golden, 2014). Results of this study revealed that percentage of lunar illumination was one of the most important factors influencing predation of larval *A. fulvescens* in the UBR (Table 3). *Acipenser fulvescens* spawning and, concordantly, larval drift is known to coincide with lunar phase (Forsythe *et al*., 2012). Therefore, models that include lunar illumination, but do not include the *A. fulvescens* biomass variable, may overestimate the importance of lunar illumination. However, few of the best-performing models included the lunar illumination term without the term for *A. fulvescens* biomass, so overestimation of the importance of lunar illumination is likely to be minor because any variation explained by increased *A. fulvescens* presence during periods of high illumination would have been accounted for in the biomass variable (Table 2). The effects of moonlight on predatory fish have not been rigorously tested, but many studies have demonstrated that predatory fish are highly sensitive to light levels, with many species exhibiting crepuscular foraging behaviours (Gadomski & Parsley, 2005; Huusko *et al*., 1996; Peterson & Gadomski, 1994) including some of the species in the UBR (Keast & Welsh, 1968). Low light levels, as would be expected during new moon phases, would reduce reaction distances of predatory fish and make foraging less efficient for nocturnal visual predators (Beauchamp *et al*., 1999). Additionally, there is circumstantial evidence that changing moon phases alter foraging behaviour in predatory fishes (Horky *et al*., 2006, Whitty *et al*., 2009).

There was little evidence that predator species was an important predictor of larval *A. fulvescens* predation, indicating few species were consuming larval *A. fulvescens* at higher rates than others and no species was specialized for predation on *A. fulvescens* larvae. Two species of percids included in this study were more likely to consume larval *A. fulvescens* than other species. 21.1% of *P. caprodes* and 11.5% of *P. flavescens* consumed larval *A. fulvescens* in significantly higher frequencies than other species (Table 4). *Percina caprodes* are benthic predators (Leino & Mensinger, 2017) and could have a higher encounter rate with benthic-drifting *A. fulvescens* larvae compared with other potential predators. The high predation rate of larval sturgeon by *P. caprodes* is additionally concerning because the invasive round goby *Neogobius melanostomus* (Pallas 1814) occupies a similar niche (Leino & Mensinger, 2017). While *N. melanostomus* have not been detected in the UBR, they have spread to other *A. fulvescens* breeding grounds in the Laurentian Great Lakes region (Nichols *et al*., 2003). Most of the *P. flavescens* sampled were juveniles age 1 year with L_T *c.* 80–100 mm, a size at which they feed primarily on larval and age 0 juveniles of other fish species, making larval *A. fulvescens* a targeted prey item (Parke *et al*., 2009). While percids were the most likely to consume larval *A. fulvescens*, predatory cyprinids accounted for the most incidences of *A. fulvescens* predation (33 out of the 73 diet samples positive for *A. fulvescens* DNA), mainly due to the larger proportion of the fish community made up by cyprinids in the UBR. Apart from the two percid species highlighted above, most of the predators preyed on larval *A. fulvescens* at similar rates. Most of the incidences of predators consuming larval *A. fulvescens* came from the most numerically abundant fish species.

While most of the predators in this study that did have *A. fulvescens* DNA in their stomach could have reasonably consumed larval *A. fulvescens*, there were a few small-bodied predators that would appear to be gape-limited [*e.g.*, *Notropis* spp. Rafinesque 1818, brook stickleback *Culaea inconstans* (Kirtland 1840) and small rainbow darter *Etheostoma caeruleum* Storer 1845]. All small-bodied predators were captured in the gravel sections of the study area, which were located directly downstream of the main *A. fulvescens* spawning sites. The molecular assay is not able to discriminate between *A. fulvescens* DNA from larvae, eggs, or yolk-sac fry. Positive results of these small-bodied fishes could have resulted from direct predation of *A. fulvescens* life stages other than larvae, which were available throughout the study period. Alternatively, some positive results could have been caused by secondary predation of predaceous or detritivorous invertebrates that were feeding on the remains of *A. fulvescens* eggs or larvae (Sheppard *et al*., 2005).

There is also the concern that environmental (e)DNA from *A. fulvescens* could have entered into the predator GI tracts and caused false positives, but this is unlikely. The amount of eDNA depends on the abundance, biomass and distance from the source of the genetic material (Jane *et al*., 2015; Jerde *et al*., 2011). The patterns of positive results from predator diet samples do not match what would be expected if eDNA accounted for most of the *A. fulvescens* DNA in predator GI tracts. The main source of *A. fulvescens* eDNA in the UBR would come from spawning adults, but periods of high abundance of spawning adults did not coincide with high numbers of predator diet samples that tested positive for *A. fulvescens* DNA, based on concurrent adult surveys. Furthermore, the river distance of the study area is much farther than the distance eDNA can travel in a river the size of the UBR (Jane *et al*., 2015). With congregations of adult *A. fulvescens* in the main spawning areas, more predator diet samples collected from the nearby gravel sections would test positive with the genetic assay due to eDNA than predators further downstream in the sand sections. However, the diet samples of predators from the sand section were actually more likely to test positive for *A. fulvescens* DNA and the probability of a positive result was positively correlated with the biomass of larval *A. fulvescens* present in the drift the night before, providing further evidence that predation was the most likely source of *A. fulvescens* DNA in predator GI tracts, not contamination due to eDNA.

This study took advantage of the regular, predictable periodicity of drifting behaviour in larval sturgeon to semi-quantitatively assess levels of predation. Because larval drift occurred at approximately the same time each sampling day and predators were always collected the same amount of time after larval *A. fulvescens* were available, day-to-day results should be comparable. Quantifying interspecific variability in detection of DNA due to differences in gut evacuation rates could further improve estimates of predation rate, especially if assessing predation of multiple prey species (Brandl *et al*., 2016; Corse *et al*., 2014). Other semi-quantitative methods can be applied to measuring the contributions of certain prey items to predator diets. Genetic markers used for population genetics studies (*e.g.* microsatellites, single nucleotide polymorphisms; SNP) could be used on diet samples to estimate the number of individual prey items of a certain species consumed by a predator (Carreon-Martinez *et al*., 2014). Additionally, a meta-barcoding approach can provide estimates of relative contributions to predator diets across a diverse array of prey taxa (Albaina *et al*., 2016; Corse *et al*., 2017; Elbrecht & Leese, 2015; Waraniak, 2017).

The results of this study would be applicable to streams with similar fish and invertebrate communities and environmental conditions. This study was based on data collected from a single river system during 2 years that were qualitatively similar in terms of overall biomass of prey. Different river systems and even different years within the UBR may be characterized by environmental conditions and biotic communities outside the parameter space of the variables included in the model described in this study. For example, both years included in this study saw relatively similar peaks in biomass of drifting larval sturgeon (2015, 243 g; 2016, 189 g). However, there are records in the UBR historical data set with peaks nearly an order of magnitude higher than the upper end of the range of biomasses of larval *A. fulvescens* represented in this study (Duong *et al*., 2013). Predators may switch to more actively targeting larval *A. fulvescens* if they are present at high abundances (Siddon & Witman, 2004; Sundell *et al*., 2003). Likewise, sampling during high discharge events in 2015 was not possible (hence the lower sample size) and high flow rates could have reduced larval *A. fulvescens* predation if predators were more likely to seek cover from the high flows than forage for prey (Kemp *et al*., 2006). How predators affect larval *A. fulvescens* mortality in larger river systems, such as the St. Clair River, are likely to be quite different, as larger rivers have less variable flow rates and different predator communities (Nichols *et al*., 2003). Additionally, using D-frame drift nets for sampling targeted benthic drifting taxa, potentially biasing biomass estimates by under-representing surface-drifting taxa.

This study demonstrated that emerging molecular diet analysis techniques can semi-quantitatively evaluate predation and are likely to be more useful and accurate than morphological identification methods to evaluate how biotic communities and environmental conditions affect predation on vulnerable life-history stages of a species of conservation concern. This study gives evidence that co-distributed larval fish and aquatic macro-invertebrate communities improve survival of larval *A. fulvescens*. In a system with many visual predators like the UBR, turbidity, moonlight and other factors affecting visibility also appear to play important roles in the mortality of larval *A. fulvescens*. In order to ensure successful natural recruitment of *A. fulvescens* populations, factors such as these should be taken into consideration. How the predator community is managed (*e.g.*, stocking large piscivorous species), habitat restoration that may not directly benefit *A. fulvescens*, but increases abundance of co-distributed prey and restoring connectivity to increase populations of the prey community could all be possible management actions with the potential to reduce predation pressure on larval *A. fulvescens*.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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