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Riverine drift communities during larval fish dispersal over multiple recruitment years

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Abstract Predation during the downstream dispersal of larval stages represents a major recruitment bottleneck for fish populations. The co-occurrence of other organisms in river drift may reduce predation, but our knowledge of the factors influencing the composition and abundance of drift communities during post-hatch dispersal of larval fish remain limited. A multi-year (2011–2018) study was conducted to investigate abiotic factors influencing drift communities during larval lake sturgeon (*Acipenser fulvescens*) dispersal in the Upper Black River (Cheboygan, MI, USA). Cumulative water temperature was a strong predictor of drift for larval lake sturgeon, suckers (Catostomidae) and macroinvertebrates, with reduced macroinvertebrate drift during lunar phases with higher lunar illumination. Nights with a new moon had on average, three times the drifting macroinvertebrate biomass as nights during a full moon, with Heptageniidae and Isonychiidae displaying higher abundances during lower light conditions. Favorable conditions for other taxa to reduce larval lake sturgeon predation through predator swamping were common, though variability in timing (overlap between drifting taxa), biomass, and

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abundances likely alters the strength of such effects among years. A better understanding of the conditions influencing drifting communities during larval fish dispersal may assist in predicting larval mortality and year-class strength for managed fish populations.

Keywords Macroinvertebrate · Drift · Lake sturgeon · Predator–prey dynamics · Lotic system · Abiotic factors

Introduction

In lotic systems (e.g., river and streams), aquatic invertebrates drift downstream for a variety of reasons (Hynes, 1970; Waters, 1972). From entering the drift due to high flow conditions (Miller & Judson, 2014), dispersal to new habitats to avoid overcrowding, predator avoidance (Huhta et al., 2000), entering the drift to feed or as part of their life histories, invertebrates regularly become part of the communities that can be found in the water column of flowing waters (Waters 1966; Brittain & Eikeland, 1988). The abundance of drifting macroinvertebrates is mediated by a variety of biotic and abiotic factors (Waters 1972; Wiley & Kohler 1984; Gibbins et al., 2016). Discharge, temporal variation, and photoperiod/illumination all impact the abundance, diversity, and taxonomic composition of drifting invertebrates, whereby different taxa display varied responses to changing conditions (Imbert & Perry, 2000; Fenoglio et al., 2013). In temperate regions, drift communities vary seasonally (generally lower abundances and diversity observed in winter months), and within a day (generally higher abundances and diversity at night), though differences exist among taxa (Waters 1962; Brittain & Eikeland, 1988). While some taxa (e.g., Ephemeroptera and Plecoptera) are found in greater abundance during lower illumination/night conditions (Culp & Scrimgeour 1993), other taxa (e.g., Coleoptera or Diptera: Chironomidae) either have no preference or drift in greater abundance during the day, partially related to their feeding behavior (Wiley & Kohler 1984; Brittain & Eikeland, 1988; Fenoglio et al., 2004; Doretto et al., 2018).

When macroinvertebrates leave their benthic habitats they are highly vulnerable to aquatic predators (Brittain & Eikeland, 1988). A variety of taxa prey on drifting invertebrates, including fish and other invertebrates (e.g., Perlidae and Crustacea) (Brittain & Eikeland, 1988; Bridcut, 2000; Huhta et al., 2000; Waraniak et al., 2019). The preference of many taxa to drift during lower light conditions has been hypothesized as a strategy to avoid visual predators (Allan, 1978; Peckarsky, 1982; Flecker, 1992). Indeed, the feeding efficiency of visual predators (e.g., perch and trout) is markedly reduced during low light conditions (Diehl, 1988; Taylor et al., 2006).

Macroinvertebrates are not the only aquatic organisms to experience high levels of predation while drifting downstream. Early life stages of numerous fish species [e.g., lake sturgeon (Acipenseridae: *Acipenser fulvescens* Rafinesque, 1817) and suckers (Catostomidae)] experience high predation while drifting (Duong et al., 2011; Lechner et al., 2016; Waraniak et al., 2017, 2018). The predation of egg and larval stages represent a major bottleneck for increasing population recruitment (Johnston et al., 1995; Caroffino et al., 2010; Forsythe et al., 2013). Many adfluvial species, including lake sturgeon, exhibit high repeatability in the timing and location of spawning across years (Forsythe et al., 2011, 2012). Due to multiple adult spawning events within a year, larval drift typically occurs during two or more peaks rather than uniformly throughout the season (Auer & Baker, 2002; Smith & King, 2005). Larval lake sturgeon are commonly collected in higher abundances during nocturnal sampling (Kempinger, 1988), though daytime drift does occur in deeper, fast flowing areas (Auer & Baker, 2020). Following egg hatch, larval lake sturgeon remain in substrate interstitial spaces and develop using endogenous yolk reserves. Once these yolk reserves are depleted, larvae (approx. 16–18 mm length) emerge from the substrate and disperse downstream to locate suitable habitat and additional food resources. Larvae experience high predation rates until the development of bony scutes and increased swimming ability provide some protection (Auer & Baker, 2002). Temperature differences coincident with early (colder) and later (warmer) spawning, incubation, and early larval rearing lead to considerable differences in larval body size that can affect predation risk (Angilletta et al., 2004). Variation in the abundance and timing of drift can also have considerable consequences for recruitment due to reduced effectiveness of predator swamping behaviors (i.e., too many prey items for predators to ingest during a short period of time Ims, 1990;

Furey et al., 2016). Similarly, the presence of detritus and other debris in the river can considerably influence the foraging success of drift feeding fish (Neuswanger et al., 2014).

Understanding the factors affecting early life mortality is particularly important for threatened or managed fish populations, where the goal is to increase or maintain population sizes (Peterson et al., 2007; Auer & Baker, 2020). Mortality during larval drift can have lasting impacts on population recruitment, with smaller numbers of drifting larvae leading to reduced mature cohorts (e.g., 3 or 4 years later in walleye populations, Johnston et al., 1995). Many taxa are predators of fish larvae, with lake sturgeon larvae for example being found in the diets of hornyhead chub [*Nocomis biguttatus* (Kirtland, 1840)], rock bass [*Ambloplites rupestris* (Rafinesque, 1817)], and rusty crayfish [*Orconectes rusticus* (Girard, 1852)] (Crossman et al., 2018; Waraniak et al., 2018). While lake sturgeon and other larval fish represent an abundant though ephemeral resource, predators feed on a range of other prey, the presence and relative abundance of which can influence larval mortality rates (Hamilton, 1971; Delm, 1990; Waraniak et al., 2017, 2018).

Well studied in drifting macroinvertebrates and fish communities individually, there has been limited work in understanding how abiotic conditions influence the co-occurrence of different drifting taxa during larval fish dispersal, or the impacts of that co-occurrence. Given the abundance and biomass of other drifting species can affect feeding behavior, mortality rates, and population levels of recruitment in fish (Murdoch, 1969; Reiss et al., 2014; McPhee et al., 2015; Waraniak et al., 2017, 2018; Sánchez-Hernández et al., 2020), a better understanding of the factors underlying this co-occurrence may have implications for understanding and modeling variation in early life mortality (Copp et al., 2005; Carpenter & Mueller, 2008; Rosenfeld et al., 2014; Naman et al., 2016). For other drifting species to substantially contribute to a prey swamping effect beneficial to larval lake sturgeon, there needs to be both the presence of drifting larval sturgeon and high abundance/biomass of alternative prey items. In an experimental study where mayflies (Ephemeroptera: Heptageniidae) and suckers (Catostomidae) were introduced into artificial flumes containing larval lake sturgeon and a common predator [rock bass or hornyhead chub] in various groupings, mayflies were preferred over lake sturgeon with the abundance of alternative prey affecting lake sturgeon predation rates (Waraniak et al., 2017). In field experiments, higher biomass of drifting macroinvertebrates and larval suckers similarly reduced the probability fish predators consumed larval lake sturgeon (Waraniak et al., 2018). Previous studies provide strong support for the presence of other drifting taxa to influence larval lake sturgeon predation, however investigations of co-drifting communities and the abiotic factors which influence them, remain limited, especially over multi-year periods.

The goals of this study were to investigate: (i) how abiotic factors influence drift communities during larval lake sturgeon dispersal, (ii) whether natural larval lake sturgeon drift consistently overlaps with taxa previously shown to reduce lake sturgeon predation, (iii) how common are the conditions which may allow other taxa to contribute to a prey swamping effect during larval dispersal, and (iv) what is the potential magnitude of this effect based on previous lake sturgeon predation studies.

Methods

Sample collection

This study was conducted in the Upper Black River (Cheboygan, Michigan, USA), a fourth order stream which serves as the primary spawning area for a moderately sized isolated population [$N \sim 1189$, Pledger et al., 2013, Michigan Department of Natural Resources unpublished data] of lake sturgeon. Five drift nets (1600 µm net mesh, 1000 µm codpiece, 78 × 55 cm) were established nightly across the channel following lake sturgeon spawning events as described by Auer and Baker (2002) and Crossman et al. (2018). While this mesh size is larger than commonly used for investigations of macroinvertebrate communities, the focus of this study was on macroinvertebrates of relatively similar sizes to that of drifting larval sturgeon (which would be predated upon by similar predators). As such, macroinvertebrate and co-drifting fish abundances may be biased against smaller sized taxa. However, molecular diet analysis of predatory fish gut contents (Waraniak et al., 2019) suggests that smaller taxa (of a size too small to be reliably collected in the drift nets) were not a large component of the diet of predators which feed on lake sturgeon larvae.

Drift nets were set at the same location each year (8 years, 2011–2018), approximately 2 km downstream of the main lake sturgeon spawning area in similar locations as previous studies (Smith and King, 2005; Crossman et al., 2011; Waraniak et al., 2018). Upstream migration of lake sturgeon (from Black Lake) in the Upper Black River is restricted to a 11.5 km section by an upstream dam (operated under ‘run-of-river’ conditions for the period of this study). At the sampling location and throughout this reach, the river is shallow with a depth consistently 1 m or less. To capture as much of the vertical water column as possible, nets rested directly on the substrate (predominantly sand), which was of consistent bathymetry across the sampled section of river. Drift sampling began 15–23 days after initial lake sturgeon spawning events (range: 17 April–9 May) with an average of 30 nights of drift sampling per year (range 23–40). Sampling efforts in each year began several days prior to the expected onset of larval lake sturgeon dispersal (determined by daily observations of spawning behavior and larval hatching estimates, calculated using hourly river cumulative temperature units; Kempinger, 1988), and ended when no lake sturgeon larvae were captured in three consecutive nights of sampling. Each night (240 total), samples were collected hourly from 22:00 until 02:00. Hourly samples from the same night were considered sub-samples and combined for all analyses except for determining the effect of collection hour.

Lake sturgeon larvae were enumerated individually while a subset of each sample (5%, by volume) was preserved in 95% ethanol for enumeration and identification of fish larvae and macroinvertebrates. The subsample was taken by filling a bucket with 5 l of water, mixing, and taking a 250 ml subsample. Abundances of macroinvertebrates and suckers were multiplied by 20 to account for the 5% subsampling. Macroinvertebrates were identified using dichotomous keys to the family level (Merritt et al., 2008). While most crayfish identified were rusty crayfish (*Orconectes rusticus*), crayfish were treated as a single family for analyses.

Macroinvertebrate biomass was estimated using length–weight regressions. Twenty individuals of each macroinvertebrate family were randomly chosen, and total body length was measured using ImageJ software (Schindelin et al., 2015). Total body length was used, along with published weight-length regressions (Benke et al., 1999) to determine individual dry weight biomass. Only families with greater than 20 individuals collected (across all years) were included in biomass calculations (34 of 66 total families). Individual lake sturgeon and sucker larval biomass were estimated by randomly selecting 20 larvae collected during early and late season peaks (typically late May and late June) and determining dry weight (ash free dry mass).

Mean water column velocity (m sec^{-1}) was measured at the mouth of each drift net using a Marsh McBirney Flow-Mate 2000 (Hach, Loveland, CO, USA). Velocity was measured at three points (center, left edge, and right edge of net mouth) at 21:00 each night and averaged to obtain the average velocity through each net (m/sec), which was multiplied by the area of each net (0.429 m^2) to determine the discharge sampled by each net. The discharge sampled by each net ($N=5$) was combined to determine the total discharge sampled (m^{3}sec^{-1}). To facilitate comparisons with other studies and standardize for Catch Per Unit Effort (CPUE Smith and King, 2005; Baxter et al., 2017), abundance and biomass were normalized to be represented as the number per 100 m^3 water volume [abundance per 100 m^3 = (abundance × 100)/(time × area sampled × mean velocity)] (Baxter et al., 2017).

Velocity and depth measurements were taken nightly at one-meter intervals across a transect perpendicular to the river’s width and combined to determine total river discharge. Temperature was measured hourly using in-stream HOBO data loggers (Onset, Bourne, MA, USA). Cumulative Temperature Units (CTU) were determined as described previously (Kempinger, 1988; Smith & King, 2005), starting at initial lake sturgeon spawning. Lunar phase and percent lunar illumination were determined from US Naval Observatory data (www.usno.navy.mil).

Catostomidae species identification

To determine the species of drifting Catostomidae larvae, sequencing of the Cytochrome c oxidase I (COI) gene was performed. Samples were selected proportionally relative to the counts of suckers obtained per evening with 96 samples sequenced per year. Exceptions to this were 2011–2013 where samples were selected from several dates corresponding to 'early' and 'late' peaks in drifting suckers. Following the manufacturer's protocol, the DNeasy Blood and Tissue kit (QIAGEN, Inc., Germantown, MD) was used to extract DNA. A region of the cytochrome c oxidase subunit I (COI) gene commonly used for DNA barcoding in fish was amplified using a mix of the M13 tagged primers VF2-t1, FishF2_t1, FishR2_t1, FR1d_t1 (Ivanova et al., 2007). PCR reactions were carried out as described in Ivanova et al. (2007). The Qiagen QIAquick PCR purification kit (QIAGEN, Inc., Germantown, MD) was used to purify the PCR products, which were quantified using a Nanodrop 1000 spectrophotometer (ThermoFisher Scientific, Waltham MA) and diluted to 10 ng/μl for sequencing.

Sanger sequencing of the PCR products with the M13F(-21) primer was carried out at the Michigan State University Research Technology Support Facility on an ABI 3730xl 96-capillary DNA sequencer (ThermoFisher Scientific, Waltham MA). MEGA version 6 (Tamura et al., 2013) was used to inspect, truncate, and manually align sequences. After removal of primers and low-quality sequences, sequence length over all samples ranged from 385 to 555 bp. The GenBank database was queried with the sequences using BLAST (Altschul et al., 1990), and the species and accession number of top BLAST hit for each sequence were recorded, along with their percent match and E-value.

Statistical analysis

Generalized Additive Models (GAMs) were used to model the effect of abiotic variables on drift concentrations. GAMs were used over other approaches to better model the observed data (e.g., continuous, bimodal distributions), and the expected characteristics of the species sampled (commonly multiple peaks in larval fish drift abundance are observed within a year). For modeling, drift concentrations (abundance per 100 m^3) were log transformed with a small constant (0.001) added to allow for transformation of zero values. Pearson correlation was used to measure correlation between the numeric abiotic factors investigated (water temperature, day of year, river discharge, CTU, lunar illumination (%). Correlations between the categorical moon phase and numeric variables were assessed visually with boxplots. As day of year, and CTU were highly correlated (Pearson's $\geq$ 0.99, Fig. S1), CTU was used in subsequent analysis. Percent lunar illumination and moon phase were highly correlated, so moon phase was used for subsequent analysis. Within each group examined (lake sturgeon, suckers, and macroinvertebrates), moon phase, Cumulative Temperature Units (CTU), river discharge, and water temperature were investigated as fixed effects individually as well as in combination with each other. No interaction terms were included in models due to low sample size.

Models were selected using Akaike Information Criterion (AICc), with AICc weights calculated using the R package bbmle (v. 1.0.22; Pinheiro et al., 2012; Bates et al., 2014; Brooks et al., 2017). Models with a ΔAICc within two of the best model were presented as best-fit models. AICc weights closer to one indicate greater relative support for the model while closer to zero indicate less support. To examine the effect of temporal autocorrelation, Autocorrelation Function (ACF) plots as well as Durbin-Watson tests were conducted in R (v. 3.6.2) using the DHARMa (v. 0.2.6) package (Hartig, 2017). All models included a random effect of year and an AR1 autocorrelation structure accounting for temporal autocorrelation between sampling dates within each year as counts on adjacent days were not likely to be completely independent. GAM modeling was performed and visualized using the itsadug (v 2.3), mgcv (v. 1.8–31), gratia (v. 0.4.1), and mgcViz (v. 0.1.4) packages (Wood, 2011; Pinheiro et al., 2012; Van Rij et al., 2017; Fasiolo et al., 2019; Simpson, 2019). Confidence intervals for GAM models are 95% simultaneous confidence intervals and were calculated using the itsadug package (v. 2.3Marra & Wood 2012; Van Rij et al., 2017). Plots of models with multiple terms are shown as the effect of the plotted term at the mean values for other terms in the model.

The effect of lunar phase (e.g., new moon and first quarter) and collection hour on drift concentration (abundance per 100 m^3 drift) and biomass (g per 100 m^3 drift) were tested with Kruskal–Wallis and Mann–Whitney tests with False Discovery Rate (FDR) correction (Benjamini & Hochberg 1995). Differences in concentration and biomass of the top macroinvertebrate families (> 3% of total macroinvertebrate abundance) among lunar phases were compared with Kruskal–Wallis and Mann–Whitney tests with FDR corrections. Figures were created using a combination of ggplot (v. 3.2.1), phyloseq (v. 1.30), and ggpubr (v. 0.2.4) (McMurdie & Holmes, 2013; Wickham et al., 2016; Kassambara, 2017) packages, with all analyses conducted in R (R Core Team, 2021).

Results

Drift samples were collected on 240 nights over 8 years (2011–2018), with sampling beginning 15–23 days after initial lake sturgeon spawning events (range: 17 April–9 May, Table 1). While the estimated yearly number of drifting macroinvertebrates (based on 5% subsample) ranged between 28,660 and 70,080, the number of lake sturgeon (range 922–46,932), and estimated sucker larvae (5% subsample, range 56,480–414,960) had greater inter- and intra-annual variation, with larval lake sturgeon numbers varying by more than 10 times among years (Fig. 1a–c, Table 1). Macroinvertebrates were generally collected throughout the sampling period (Fig. 1a), while sucker (Fig. 1b) and lake sturgeon (Fig. 1c) larvae were collected in pulsed, discrete events (i.e., a few sampling days where a large proportion of the yearly total was collected, Fig. S2).

Across all samples, total river discharge varied between 3.61 and 10.69 m^3 sec^{-1} with an average of 6.46 m^3 sec^{-1} (SE ± 0.08, Fig. S3), while sampled discharge varied from 0.43 to 3.63 m^3 sec^{-1} (mean = 0.95, SE ± 0.02, Fig. S4). Nightly water temperature (averaged across the nightly sampling period) varied between 12.2 °C and 23.4 °C with a mean of 19.0 °C (SE ± 0.16 Fig. 1d).

Abiotic effects on drifting larval fish

Yearly peak lake sturgeon larval abundance occurred, on average, 212.4 Cumulative Temperature Units (CTU, SE ± 19.0) after initial spawning events (Table 1), with 82% of all observed larvae collected between 150 and 250 CTUs. Peak drift did not consistently occur during a single lunar phase each year but occurred over a range of lunar conditions, from 8% (Waxing Crescent) to 97% (Waning Gibbous) lunar illumination (cloud cover was not considered in measurements of lunar illumination).

Both cumulative temperature from first adult lake sturgeon spawning and water temperature on the night of collection were predictive of the concentrations of drifting fish larvae. Eight samples were removed as outliers before modeling drift concentrations (abundance per 100 m^3 drift) due to the discharge sampled during those nights being more than four standard deviations from the mean (Fig. S4). The best-fit model (GAM, AICc weight = 0.46) for lake sturgeon drift concentrations included CTU (concurvity estimate = 0.46) and water temperature (concurvity = 0.55, Pearson correlation between

Table 1 Drift sampling dates and collection totals

Year	First lake sturgeon spawning	First sampling	Last sampling	CTU range	Highest Larval Sturgeon Drift	CTU of Highest Sturgeon Drift	Sturgeon larvae	Macroinvertebrates	Sucker larvae
2011	4-May	19-May	22-Jun	208.9–829.2	26-May	325.7	9,399	46,240	71,840
2012	17-Apr	9-May	23-Jun	192.1–1049.0	25-May	466	11,037	60,700	329,700
2013	3-May	18-May	24-Jun	231.8–881.2	20-May	264	922	40,860	114,420
2014	8-May	26-May	28-Jun	249.6–909.7	31-May	351.3	15,473	73,920	306,040
2015	3-May	18-May	5-Jul	237.6–1108.2	4-Jun	516.1	1,723	58,040	414,960
2016	3-May	18-May	1-Jul	207.2–1084.5	25-May	323.6	4,053	70,080	242,500
2017	28-Apr	15-May	25-Jun	218.5–985.2	21-May	317.8	19,135	48,620	83,380
2018	9-May	24-May	24-Jun	246.2–885.0	25-May	265.3	46,932	28,660	56,480

CTU range refers to Cumulative Temperature Units (from first lake sturgeon spawning date) from the beginning to the end of drift sampling

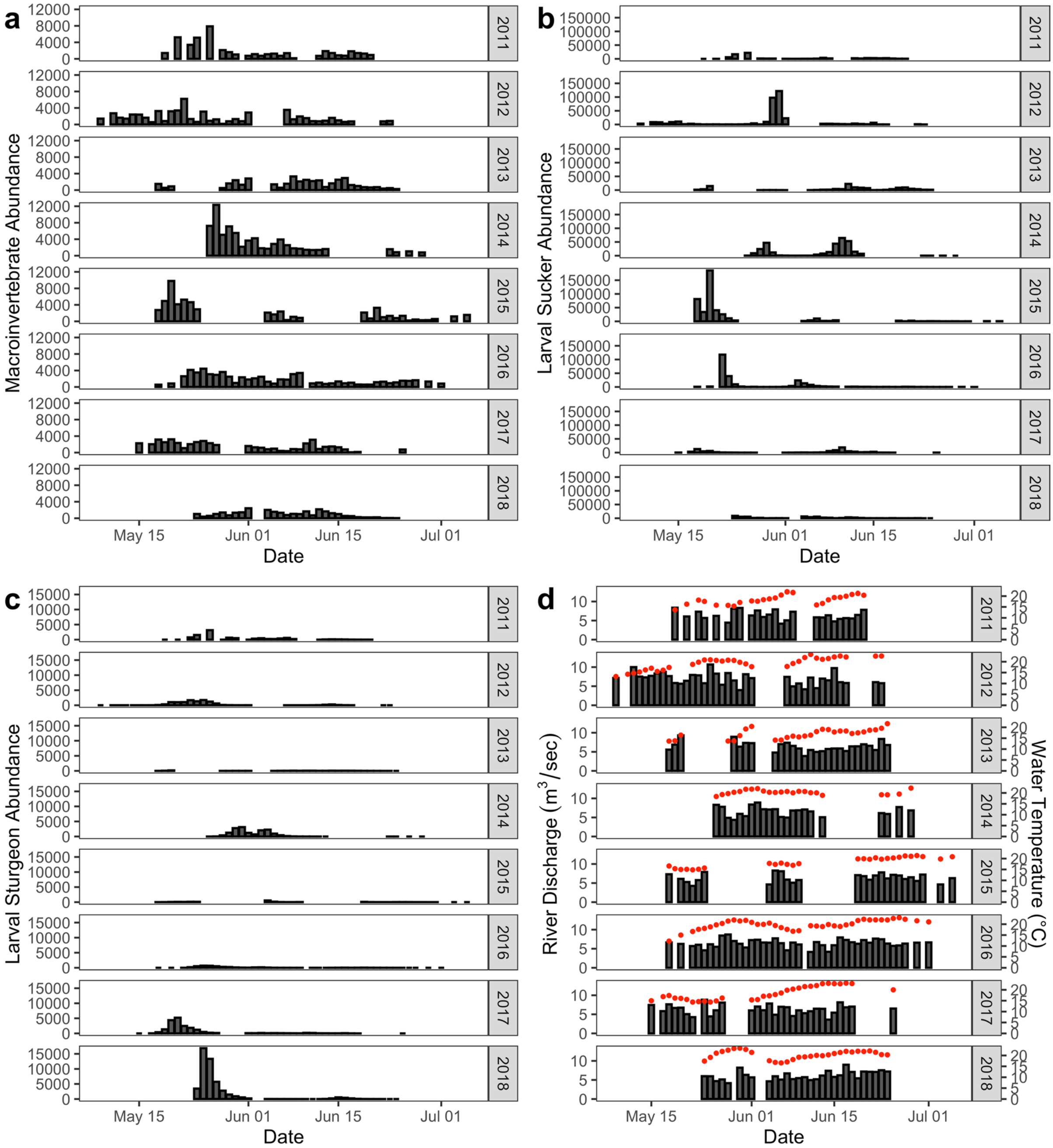


Fig. 1 Drifting fish larvae and macroinvertebrates collected by year. **a** Drifting macroinvertebrates collected by date and year **b** Drifting sucker larvae collected by date and each year. **c** Larval lake sturgeon abundance by date and year **d** River conditions. Bars indicate river discharge (m^3/sec, left axis) for each sampling date across years, points indicate water temperature (right axis). Gaps indicate days where sampling did not occur

CTU and temperature = 0.54), and explained 58% of the variation (R^2-adj) in drifting larval density (Table 2, Table S1). CTU had a larger effect size (F = 31.7, following a bell-shaped distribution with a peak around 200 CTU, Fig. 2a) than water temperature (F = 23.2, higher drifting concentrations above

Table 2 Best-fit models for drifting concentration

Model	AICc Weight	R^2-adj	Term				
			Intercept	Estimate	SE	*t*-value	Pr(> |t|)
				− 1.55	0.31	− 4.95	< 0.001
				Edf	Ref.df	*F*-value	*P*-value
log(Sturgeon concentration) ~ s(CTU) + s(Temperature)	0.46	58.0%	s(CTU)	7.66	8.55	31.66	< 0.001
			s(Temperature)	1.0	1.0	23.16	< 0.001
			Intercept	Estimate	SE	*t*-value	Pr(> |t|)
				− 1.55	0.32	− 4.89	< 0.001
				Edf	Ref.df	*F*-value	*P*-value
log(Sturgeon concentration) ~ s(CTU) + s(Temperature) + s(River Discharge)	0.39	58.1%	s(CTU)	7.71	8.59	31.79	< 0.001
			s(Temperature)	1.0	1.0	23.23	< 0.001
			s(River Discharge)	1.0	1.0	1.35	0.25
			Intercept	Estimate	SE	*t*-value	Pr(> |t|)
				2.35	0.27	8.66	< 0.001
				Edf	Ref.df	*F*-value	*P*-value
log(Sucker concentration) ~ s(CTU) + s(Temperature) + s(River Discharge)	0.72	49.2%	s(CTU)	8.05	8.8	15.6	< 0.001
			s(River Discharge)	1.0	1.0	5.20	0.02
			s(Temperature)	2.38	3.0	3.97	0.01
			Intercept	Estimate	SE	*t*-value	Pr(> |t|)
				2.05	0.23	8.73	< 0.001
log(Macroinvertebrate concentration) ~ Moon Phase + s(CTU) + s(River Discharge) + s(Temperature)	0.84	58.4%	Moon Phase: Full Moon	− 0.001	0.32	< 0.01	0.99
			Moon Phase: Last Quarter	0.28	0.28	1.02	0.31
			Moon Phase: New Moon	0.42	0.29	1.47	0.14
			Moon Phase: Waning Crescent	0.35	0.21	1.72	0.09
			Moon Phase: Waning Gibbous	0.69	0.21	3.30	0.001
			Moon Phase: Waxing Crescent	0.37	0.20	1.84	0.07
			Moon Phase: Waxing Gibbous	−0.24	0.20	− 1.23	0.22
				Edf	Ref.df	*F*-value	*P*-value
			s(CTU)	5.98	7.16	6.54	< 0.001
			s(River Discharge)	2.17	2.77	0.67	0.47
			s(Temperature)	3.08	3.87	4.19	0.004

Concentration is expressed as abundance per 100 m^3 drift. Edf indicates the estimated degrees of freedom, Ref. df indicates the reference degrees of freedom. CTU refers to Cumulative Temperature Units from lake sturgeon spawning. Models include a random effect of year and an AR1 autocorrelation structure of date within each year. S indicates a smoothing term was used. Full lists of GAM models tested can be found in Table S1–S3

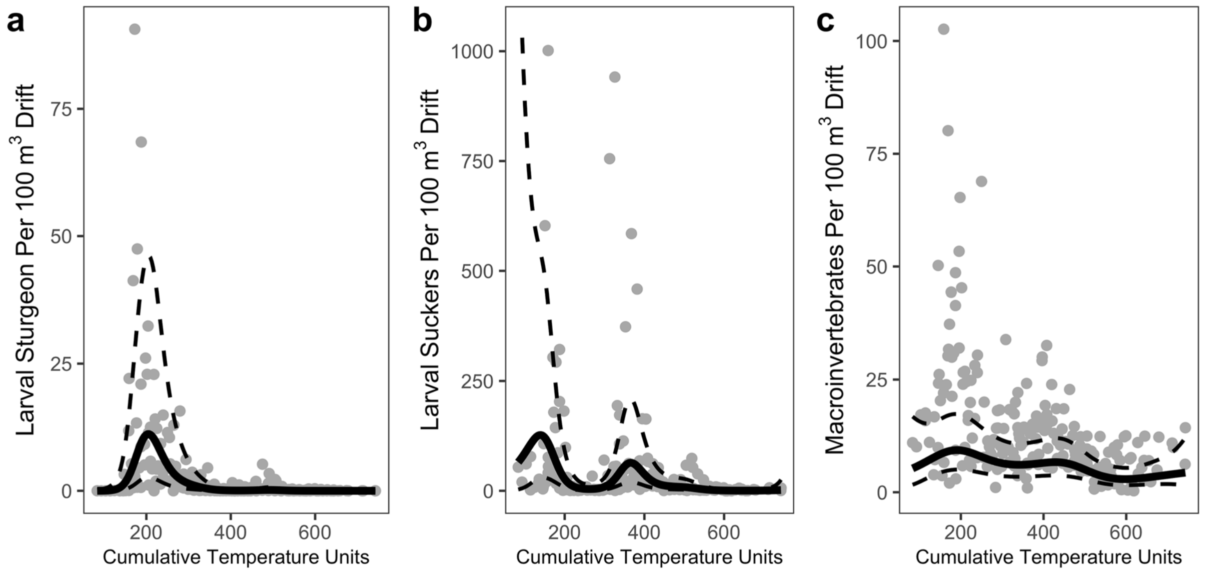


Fig. 2 Best-fit drift models. **a** Larval sturgeon concentration (abundance per 100 m^3) by Cumulative Temperature Units (CTU, GAM). **b** Larval sucker concentration by CTU (GAM). One sucker value (1515 suckers per 100 m^3 at 169 CTU) was omitted from the plot but included in modeling **c** Macroinvertebrate concentration by CTU (GAM). Each plot shows the term with the highest effect size for each model and the other model terms set to their mean values (e.g., macroinvertebrate concentration in c is shown at the mean values for discharge and temperature and moon phase set as waxing gibbous). Models are given in Table 2. Solid lines indicate the modeled value while dashed lines indicate 95% confidence intervals

18 °C, Fig. S5, Fig. S6). The second best-fit model (ΔAICc = 0.3, AICc weight = 0.39), included CTU (F = 31.8, concurvity = 0.51), temperature (F = 23.2, concurvity = 0.56) and river discharge, though discharge did not have a strong effect (F = 1.35, concurvity = 0.24).

The best-fit model for sucker abundance per 100 m^3 (AICc weight = 0.72) included CTU (concurvity = 0.51), water temperature (concurvity = 0.56), and discharge (concurvity = 0.24, Fig. S7, Table S2). CTU had the strongest effect on sucker concentration (F = 15.6), followed by river discharge (F = 5.2) and water temperature (F = 3.97). Most larvae collected around two peaks, one at approximately 150 CTU and a second at 380 CTU (Fig. 2b). Though there was considerable variability in drifting sucker concentrations, higher mean concentrations were observed with increasing temperatures (above 18 °C) and at lower river discharges (below 7 m^3 sec^{-1}, Fig S8).

Abiotic effects on macroinvertebrate concentrations

The best-fit model for macroinvertebrate abundances per 100 m^3 drift included moon phase, CTU (concurvity = 0.52), river discharge (concurvity = 0.25), and water temperature (concurvity = 0.61), Table 2, Table S3). In the best-fit model (AICc weight = 0.83, Fig. S9), CTU had the highest effect size (F = 6.54) followed by water temperature (F = 4.19), while discharge did not have a strong effect (F = 0.67). Macroinvertebrate concentration had a negative relationship with CTU, decreasing from 9.31 macroinvertebrates per 100 m^3 (95% CIs = 5.05–17.15) at 200 CTU to 2.92 at 600 CTU (95% CIs = 1.58–5.39, Fig. 2c). Mean drifting macroinvertebrate concentrations were highest when water temperatures were between 15 and 18 °C (Fig. S10).

To further investigate potential effects of illumination, the effects of categorical proxies for nightly illumination (i.e., moon phase and collection hour) were examined individually on drifting concentrations and biomass. Moon phase (e.g., new moon and waxing gibbous) had a strong effect on both drifting macroinvertebrate concentration (Kruskal–Wallis, $\chi^2 = 39.98$, $P < 0.001$, Fig. S11) and biomass (correlation between concentration and biomass = 0.96, Kruskal–Wallis, $\chi^2 = 49.3$, $P < 0.001$, Fig. 3a).

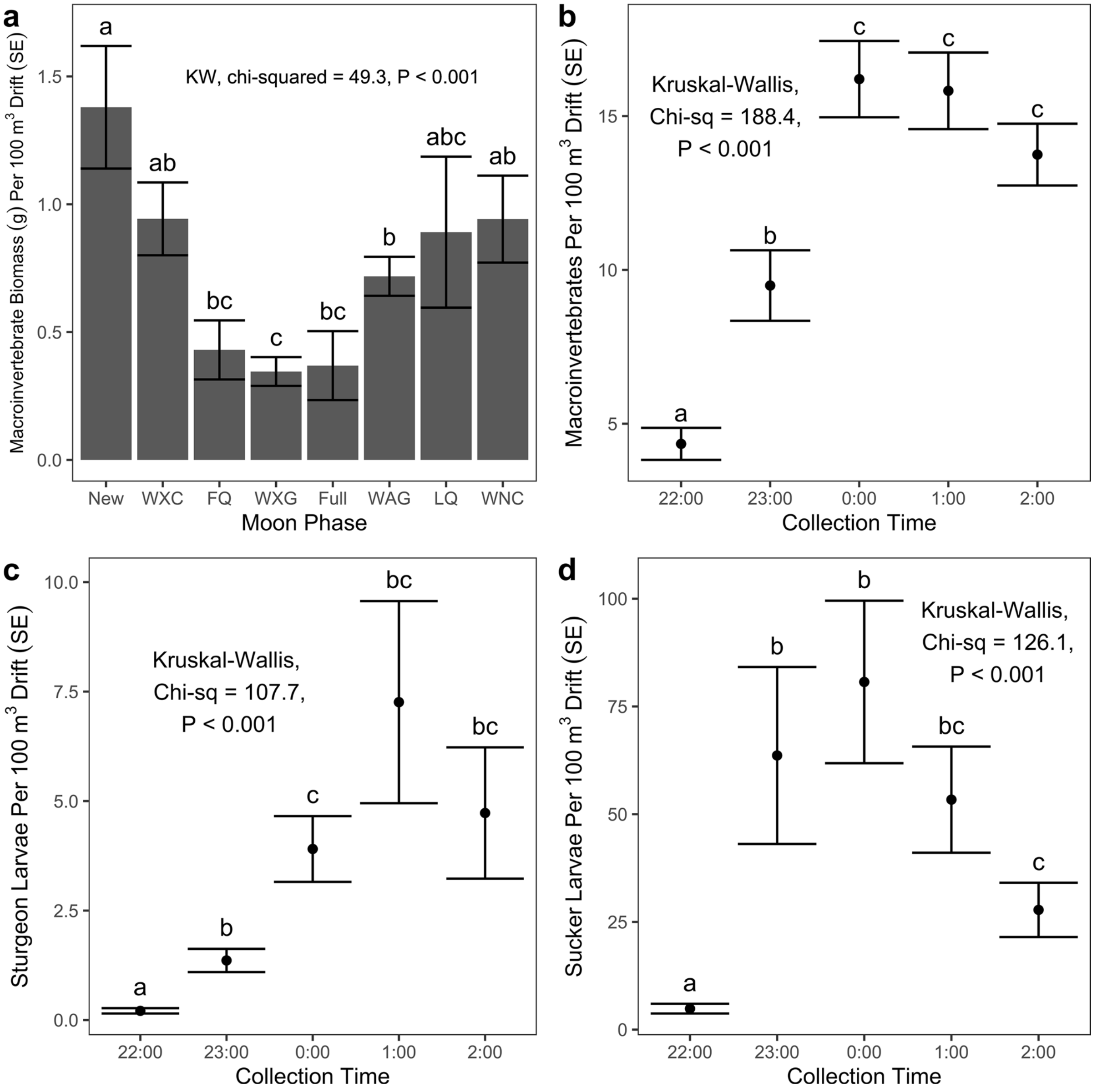


Fig. 3 Effect of lunar phase and collection time on drifting concentrations. **a** Drifting macroinvertebrate biomass by lunar phase. Moon phase abbreviations from left to right are: New Moon (New), Waxing Crescent (WXC), First Quarter (FQ), Waxing Gibbous (WXG), Full Moon (Full), Waning Gibbous (WAG), Last Quarter (LQ), Waning Crescent (WNC). **b** Effects of collection time (hours) on drifting macroinvertebrate concentration. **c** Effects of collection time (hours) on drifting lake sturgeon larval concentration. **d** Effects of collection time (hours) on drifting sucker larval concentration. Error bars are standard error and letters indicate pairwise significance between groups. Overall tests were Kruskal–Wallis tests with Mann–Whitney test (*P*-adj < 0.05) used for pairwise comparisons

Higher abundances and biomass were observed during phases with lower illumination (e.g., new moon and waxing gibbous). Samples collected during a full moon had a mean (± SE) macroinvertebrate biomass of 0.37 g per 100 m^3 (± 0.13), less than 30% of the biomass during a new moon (1.38 g per 100 m^3 ± 0.24, Mann–Whitney, P-adj = 0.025). Drifting sucker concentration did not differ substantially between moon phase (KW, $P = 0.28$). Larval lake sturgeon concentration was statistically different between moon phases (KW, F = 15.2, $P = 0.03$) though there were no significant pairwise comparisons between individual moon phases (MW, P-adj > 0.05, Fig. S12).

While samples collected at each hour of the same night were considered sub-samples and combined for the purpose of all other analyses, there was a strong effect of collection hour on drifting macroinvertebrate concentration (KW, $\chi^2 = 188.4$, $P < 0.001$). Macroinvertebrate samples collected at 0:00 (midnight) had on average three times greater concentrations than those collected at 22:00 (10 pm, Fig. 3b). Similar patterns were observed for both lake sturgeon (Fig. 3c) and sucker larvae (Fig. 3d), with higher concentrations (KW, $\chi^2 > 100$, $P < 0.001$, Mann–Whitney adj-$P < 0.05$) during collection hours after 22:00.

Taxon specific responses to abiotic conditions

Sixty-six macroinvertebrate families were identified with eighteen families (crayfish were treated as a single family for the purpose of comparison) present in more than 10% of all samples. Of the six most abundant taxa, which each comprised greater than 3% of the total macroinvertebrates collected (Isonychiidae, Heptageniidae, crayfish, Leptoceridae, Ephermerillidae, and Hydropsychidae), two responded significantly to lunar phase (KW, adj-$P < 0.05$, Fig. 4a, Fig. S13). Isonychiidae and Heptageniidae (the abundance of which has been shown previously to reduce relative lake sturgeon predation, Waraniak et al., 2018) differed between lunar phases. Isonychiidae concentrations were significantly higher during the new moon (12.52 individuals per 100 $m^3 \pm 3.0$) than the full moon (2.31 ± 0.93, Mann–Whitney, adj-$P < 0.05$), while Heptageniidae concentrations were higher

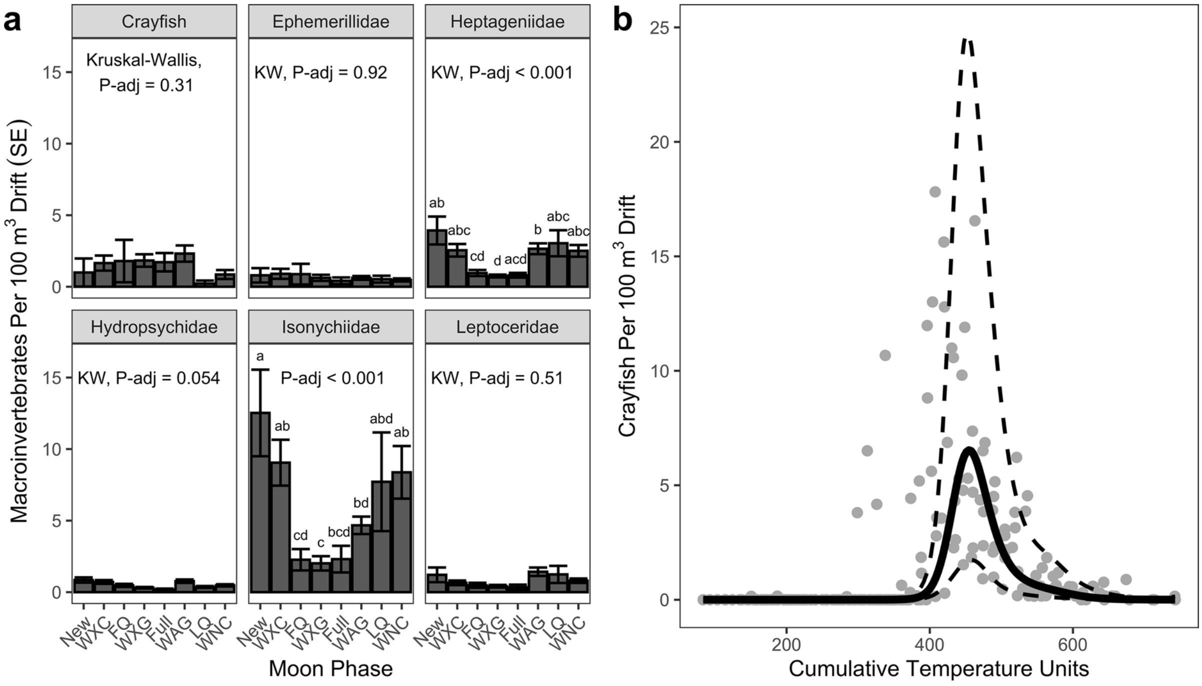


Fig. 4 Macroinvertebrate family specific responses to abiotic factors. **a** Macroinvertebrate concentration by moon phase for six most abundant families. Groups which had a significant overall test (Kruskal–Wallis, FDR correction, P-adj < 0.05) were further tested with Mann–Whitney tests (FDR correction) with pairwise significance denoted by lowercase letters. Moon phase abbreviations from left to right are: New Moon (New), Waxing Crescent (WXC), First Quarter (FQ), Waxing Gibbous (WXG), Full Moon (Full), Waning Gibbous (WAG), Last Quarter (LQ), Waning Crescent (WNC). **b** Crayfish concentration across cumulative temperature units. Solid line indicates mean predicted value from the GAM model and dashed lines indicate 95% CIs

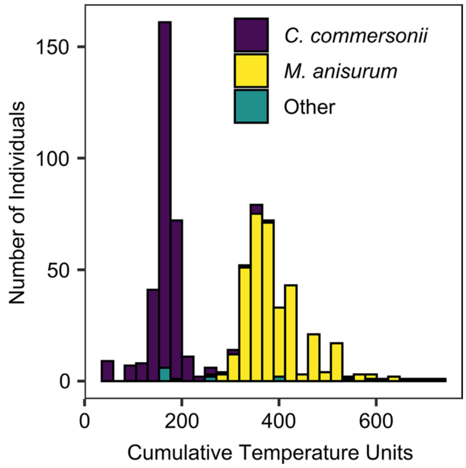


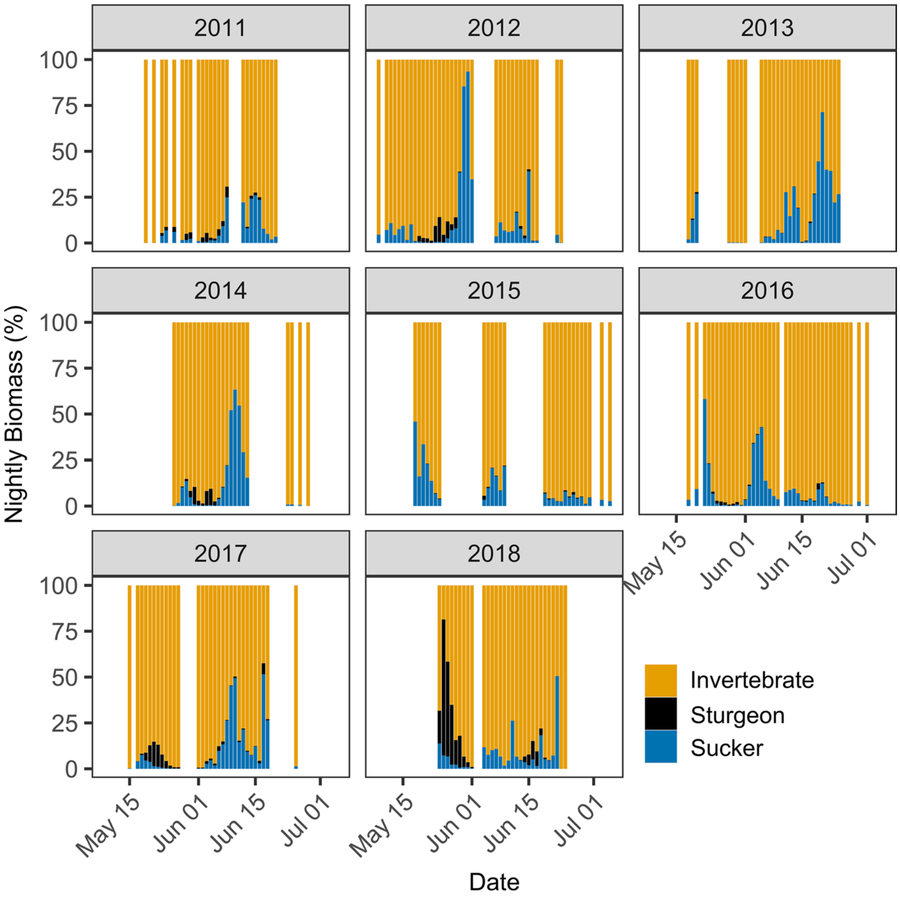
Fig. 5 Identification (based on mitochondrial COI gene) of sucker (Catostomidae) by Cumulative Temperature Units (CTU). *C. commersonii* = white suckers. *M. anisurum* = silver redhorse. All years are combined, number of individuals indicates number sequenced, not total numbers collected

during the new moon phase compared to the waxing gibbous phase (MW, adj-$P < 0.05$).

For the three most abundant macroinvertebrate taxa (Isonychiidae, Heptageniidae, and crayfish), Isonychiidae concentrations decreased over time with higher concentrations in May and early June compared to later dates. In the best-fit GAM models for all three taxa, CTU had the largest effect size. Heptageniidae concentrations showed a similar decrease as Isonychiidae with lower concentrations at higher CTU values (Fig. S14). The highest concentrations of crayfish were observed between June 3rd and June 23rd with 90.6% of all crayfish collected during that 20-day period. Crayfish concentrations displayed a bell-shaped distribution with CTU as the only model term ($F = 65.8$, $P < 0.001$, peaking between 400 and 500 CTU, Fig. 4b).

The individual sucker species which drifted during larval sturgeon dispersal showed highly repeatable and distinct responses to environmental conditions. Across all years, the COI gene of 667 individual

Fig. 6 Proportional contribution of each group to nightly biomass. Each taxonomic group is expressed as the percentage of total biomass within each night. Blank dates within a year indicate days where drift was not sampled



suckers were sequenced and assigned to species with > 99% of samples assigned to either white suckers [*Catostomus commersonii* (Lacépède, 1803)] or silver redhorse [*Moxostoma anisurum* (Rafinesque, 1820)]. White suckers reliably comprised the first peak in larval sucker drift (approx. May 15th–28th, < 250 CTU after lake sturgeon spawning), while silver redhorse larvae were collected exclusively during the second peak (approx. June 1st–20th, > 250 CTU, Fig. 5, Fig. S15).

Drifting community biomass

The relative biomass of larval sucker and macroinvertebrates should be a key determinant of the strength of a potential shielding effect for lake sturgeon larvae. On most nights (228/240, 95%), macroinvertebrate biomass was higher than larval lake sturgeon and sucker biomass combined, though there was considerable variation within and across years. Notably in 2018, larval lake sturgeon biomass exceeded both macroinvertebrate and sucker biomass on several nights (Fig. 6), comprising > 50% of total biomass on May 25th and 26th. Total organismal biomass (macroinvertebrates, larval lake sturgeon, and larval sucker combined) averaged 0.87 g per 100 m^3 and ranged from 0.01 to 6.91 g per 100 m^3. While drifting macroinvertebrate biomass averaged 0.746 g per 100 m^3 (SE ± 0.06, range 0.005–6.78), larval lake sturgeon and sucker biomass was 0.0167 g (SE ± 0.003, 0–0.453), and 0.111 g (SE ± 0.02, 0–2.41) per 100 m^3, respectively. Six families (Isonychiidae, Heptageniidae, crayfish, Gomphidae, Lepidostomatidae, and Ephemerillidae) comprised 82% of the total collected macroinvertebrate biomass. Of the top six families, the biomass of Isonychiidae and Heptageniidae was greater (Kruskal–Wallis, adj-$P < 0.001$) during lunar phases with lower illumination (Fig. S16), while the other four top macroinvertebrate taxa were not different among lunar phases (KW, adj-$P > 0.05$).

Discussion

We examined how abiotic factors influenced the concentration and biomass of drifting organisms during larval lake sturgeon dispersal in the Upper Black River (MI, USA). Though the abiotic factors which influence drifting macroinvertebrates has been studied previously in a variety of river systems (Waters, 1961, 1972; Wiley & Kohler, 1984; Brittain & Eikeland, 1988; Baxter et al., 2017), there have been few studies of macroinvertebrate drift coincident with larval fish dispersal events. Variability in the relative abundances (and biomass) of co-distributed larvae and other drifting taxa, while exposed to the same abiotic conditions, suggest that the relationship between larvae and co-distributed taxa may have future utility in helping to explain inter-year variation in larval fish mortality rates. Larval dispersal in riverine systems represents a major bottleneck in fish recruitment due to high mortality (Schiemer et al., 2002). Greater understanding of how populations interact with other drifting species during dispersal may improve the management of threatened fish populations (Pepin 2009; Caroffino et al., 2010; Duong et al., 2011).

Abiotic influences on drift communities

Abiotic factors such as water temperature, discharge, and season are known to influence macroinvertebrate drift, while responses differ between river type and region (Allan, 1987; Brittain & Eikeland, 1988; Koetsier and Bryan, 1995; Hansen & Closs, 2007; Hay et al., 2008). In this study, water temperature, through real-time and cumulative temperature, had the strongest effect on drift abundance and biomass, likely reflecting a response to a combination of seasonally varying factors. Total macroinvertebrate concentrations and biomass decreased over time, with lower concentrations in June–July than in May.

That cumulative temperature from first lake sturgeon spawning (CTU) was a strong predictor for non-lake sturgeon models (e.g., sucker drift concentrations) does not necessarily indicate that the drift of those groups is dependent on lake sturgeon spawning behavior but rather is likely a consequence of early season conditions and/or a strong metabolic control of behavior (e.g., depletion of yolk reserves as a precursor for entering the drift). Due to limitations with sampling water temperature early in the season (i.e., ice) and variability across years, we used the date of first lake sturgeon spawning to represent a "zero" time point for calculating cumulative temperature. Lake sturgeon spawning behavior is dependent on early season environmental factors (Bruch & Binkowski, 2002; Forsythe et al., 2011, 2012), and likely more reflective of early year abiotic conditions than choosing an arbitrary date across years.

Both macroinvertebrates and sucker larvae drift in considerable abundances during larval lake sturgeon drift events in the Upper Black River. The abundances of drifting larval lake sturgeon, suckers, and macroinvertebrates were affected by similar nightly and seasonal abiotic factors, including cumulative temperature, and collection hour. We observed a strong effect of both lunar phase and collection hour, likely due, at least partially, to an avoidance of light (Waters, 1972; Wiley & Kohler, 1984; Flecker, 1992; Koetsier & Bryan, 1992; Forrester, 1994; Duong et al., 2011). However, within drifting macroinvertebrates, there were taxon-specific differences, likely related to behavioral or phenological differences (Hynes, 1970; Brittain & Eikeland, 1988). For instance, Isonychiidae and Heptageniidae drifted in higher densities during darker moon phases, while other macroinvertebrates (e.g., crayfish, Chironomidae, Ephemerellidae), did not differ among lunar phases. Although macroinvertebrates were only identified at the family level, 100% of Isonychiidae genera recorded in North America (NA) are considered to belong to the collector functional feeding group while 81% of Heptageniidae genera (within NA) are scrapers (Benbow et al., 2019), behaviors which leave them exposed to predators on and among benthic surfaces when feeding.

The larger net sizes than typically used for macroinvertebrate drift sampling (1600 µm mesh, 1000 µm codpiece) may have biased our abundance and biomass estimates against smaller macroinvertebrate taxa compared to other studies using finer net mesh. However, the net size used likely adequately captured macroinvertebrate taxa that were of a similar size to lake sturgeon larvae, and presumably more likely to be an alternative prey target for predators of lake sturgeon larvae than smaller taxa, though additional studies on size-selectivity are needed in the context of lake sturgeon predation. In an earlier study of predatory fish diets using molecular metabarcoding during the drift period in the Upper Black River, Waraniak et al. (2019) found no evidence for the presence of macroinvertebrate DNA in predator guts from taxa not collected in the same nets employed in this study. The major macroinvertebrate families collected in this study were broadly similar to previous investigations of fish diet (Waraniak et al., 2018, 2019) as well as an extensive macroinvertebrate kick-net survey conducted in the same river (Doretto et al., 2022).

Macroinvertebrate drift abundances decreased later in the sampling period (early summer in Michigan, USA) with limited effects of discharge. While discharge is an important abiotic factor influencing drift communities (Brittain & Eikeland, 1988; Koetsier & Bryan, 1992; Gibbins et al., 2016), compared to cumulative temperature, river discharge had a weaker effect on macroinvertebrate drift in this study. This may have been a result of the relatively small amount of variation in measured discharge. Additionally, the inability to place and safely sample drift nets on days with higher discharges (e.g., following large rain events) limited our ability to sample during these conditions.

Macroinvertebrates in the drift declined over the course of the survey period within each year, while lake sturgeon and sucker larvae abundances peaked at discrete times. Larval lake sturgeon collections were consistent with the timing of adult lake sturgeon spawning and temperature dependent larval development described previously (Auer & Baker, 2002; Smith & King, 2005; Duong et al., 2011). Although the timing of sucker drift was consistent across years, there was considerable inter-year variation in both abundances and biomass of drifting larvae. The observed peaks in larval sucker drift resulting from the distinct behavior of two suckers species, white sucker and silver redhorse were consistent with those observed previously in the UBR though Smith and King (2005) reported golden redhorse [*Moxostoma erythrurum* (Rafinesque, 1818)] as the second peak of drifting sucker larvae rather than silver redhorse.

Co-drifting organisms and larval lake sturgeon

A substantial portion of the drifting larval fish and macroinvertebrate biomass was likely consumed and incorporated into the aquatic food web either during drift or after settling in the benthos (Waters, 1966, 1972; Brittain & Eikeland, 1988; Caroffino et al., 2010; Duong et al., 2011; Benbow et al., 2020). The availability of a reliable food source (macroinvertebrates), in generally greater biomass than larval fish, may be a contributing factor in the behavioral preference of predatory fish for macroinvertebrates (e.g., Heptageniidae) over lake sturgeon larvae (Waraniak et al., 2017, 2018).

Due to logistical constraints associated with the multi-year study design, and the difficulty in accurately estimating drifting larval mortality, larval lake sturgeon mortality and predation were not directly measured. However, concurrent experiments conducted in the UBR, (24 May–7 June 2015 & 2016, with identical drift sampling methods) related to predation allow for an estimate to illustrate the potential impacts of co-drifting taxa on lake sturgeon in this river system (Waraniak et al., 2018). With the assumption of similar predation rates as previously observed (Waraniak et al., 2018, a 23% decrease in the probability lake sturgeon DNA is found in the gut of a predator for each 52 g of drifting macroinvertebrates per night), a 20% reduction in macroinvertebrate drift biomass from the mean nightly biomass (96.4 g) increased the probability that larval lake sturgeon DNA is present in an individual fish predator's gut by 8.5%. The onset of larval lake sturgeon drift across years was similar in terms of cumulative temperature from spawning, though lunar phase varied during peak drift events. If larval lake sturgeon drift alongside the mean nightly macroinvertebrate biomass found during a new moon (171.3 g, assuming other conditions remain equal), the probability of a predator's gut containing lake sturgeon would be reduced by over half (56.7%) compared to drifting with the mean nightly macroinvertebrate biomass found during a full moon (43.2 g). Similarly, Waraniak et al. (2018) observed a 28% reduction in predators containing lake sturgeon DNA for each 10% increase in the relative biomass of larval suckers. While not all larval lake sturgeon peak dispersal events observed in this study overlapped with the drift of white sucker or silver redhorse larvae, those that did likely had increased protection from predation compared to drifting during periods without sucker larvae. While the predation comparisons presented above are estimates only and do not directly address larval mortality or other influences on predation rates such as the impact of detritus, this study and previous investigations (Waraniak et al., 2017, 2018) suggest lake sturgeon larvae consistently drift with species that can influence larval predation rates.

Though lunar phase was important to modeling the drifting communities of the Upper Black River, additional sources or modifiers of apparent illumination (e.g., light pollution, and cloud cover) can alter macroinvertebrate and larval fish drift communities' responses. In other river and marine systems, increased light levels reduced drifting macroinvertebrates by approximately 50% (Perkin et al., 2014), and increased predation rates on larval and post-larval fish (Beauchamp et al., 1999; Gadomski & Parsley, 2005; O'Connor et al., 2019; Tabor et al., 2004). With a number of lake sturgeon-bearing streams present in human populated areas, the presence of artificial light may diminish any potential prey swamping effects through the dual effects of reducing alternate prey (i.e., drifting macroinvertebrates) while making larvae themselves more suspectable to predation by visual predators.

The relationship between abiotic factors, drift dynamics, and larval fish survivorship is complex, but additional work could provide insight into previously unexplained variation in mortality rates that would be important for the management of fish populations. In years or rivers with larger cohorts of drifting lake sturgeon (e.g., 2018: 46,932 larvae collected), lake sturgeon may be able to swamp predators solely with their own numbers but in other years with smaller cohorts of larvae (e.g., 2013 & 2015: < 2000 larvae collected), survival may be more dependent on the presence of macroinvertebrates and other fish larvae in the drift. A better understanding of how co-distributed prey species affect drifting fish recruitment may highlight the need for changes in policy related to co-occurring species. For example, modifying current policies related to limiting habitat disturbance (e.g., dredging restrictions around sturgeon spawning periods) to better encompass co-drifting species with slightly different timings may reduce mortality through contributions to prey swamping. Additional work will be needed to combine investigations of co-drifting communities with direct measurements of drifting larval mortality.

Conclusion

Similar abiotic factors influence macroinvertebrate, sucker, and lake sturgeon larval drift, though how these groups respond is organism-specific and has implications for their co-occurrence and relative abundance in the drift during larval lake sturgeon dispersal. The potential for other species to contribute to prey swamping during larval lake sturgeon dispersal was high over our eight-year study period although abiotic conditions and stochastic variability likely causes the strength of these effects to fluctuate. With the assumption that greater co-occurrence leads to a stronger effect, macroinvertebrates likely have a more consistent influence on any potential prey shielding effects (i.e., a reduction in predation due to the presence of other taxa) related to larval lake sturgeon recruitment than sucker larvae in the Upper Black River, due to their consistently greater biomass, lower variation in concentrations during peak lake sturgeon drift, and lower variation across years.

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Data availability The data that supports the conclusions in this paper, along with all code use in analysis is available at: https://github.com/BenbowLab/UBRDrift2020.

Declarations

Conflict of interest The authors have no competing interests to declare.

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