



OPEN Changes in lake sturgeon spawning periodicity is associated with prior reproductive effort

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Long-lived iteroparous organisms vary resource expenditures toward migration and reproduction in response to individual physical factors and conspecific interactions, which can affect future reproductive timing and interval. Reproductive actions can lead to trade-offs associated with allocations to current vs. future reproduction, including longer reproductive interval, require additional study. The objective of this study was to evaluate associations between physical stream characteristics, individual behaviors, and breeding demographics and spawning periodicity in lake sturgeon (*Acipenser fulvescens*). We used Radio Frequency Identification tags to monitor spawning migration by male ($N=1931$) and female ($N=683$) adults over seven consecutive years (2016 through 2022) in the Black River, Cheboygan Co., MI. We used ordinal regression models to quantify associations. Male spawning periodicity (1.60 ± 0.63 years; mean \pm SE) decreased with increasing body size and intra-sex interactions and increased with increasing cumulative temperature, discharge, number of inter-sex interactions, and complete river migrations in a season. Female spawning periodicity (3.19 ± 0.05 years, mean \pm SE) decreased with increasing upstream swimming time and inter-sex interactions. Results demonstrated spawning periodicity shortened as male lake sturgeon age, and future breeding opportunities decreased, while female periodicity may be more individualized and is more likely to be affected by resource acquisition.

Keywords Inter-spawning interval, Migrations, Spawning periodicity, Life-history, Reproduction

In fishes, the period between spawning events is associated with resource acquisition, which effects the timing of, and future expenditure of resources toward, reproduction^{1–3}. When resource acquisition after a spawning season is insufficient for immediate production of gametes, fish may delay a spawning season, lengthening spawning periodicity^{4–7}. Skipped or delayed spawning has been documented globally in marine and freshwater fish, is common across iteroparous fishes^{6,7}, and can significantly affect stock recruitment⁸.

Skipped spawning is common in long-lived large-bodied teleosts⁶, particularly when proportional allocations of resources to reproduction relative to somatic growth increases with increasing age^{9,10}. Prior study has consistently shown skipped spawning to be associated with resource availability and acquisition, and to body condition generally during the period between reproductive episodes^{11–13}. Skipped spawning has been linked to low resource levels (e.g., bull trout, *Salvelinus confluentus*¹⁴ and white crappie, *Pomoxis annularis*¹⁵). While there is considerable knowledge that variability in spawning periodicity exists amongst long-lived fish^{16,17}, studies which evaluated members of the family Acipenseridae associated commercial and recreational harvest and inaccessibility of potential spawning habitat with these differences^{18,19}. Comparatively, few studies have examined how individual behavior, body size, and physical stream factors experienced during the reproductive period may result in delayed or variability spawning periodicity across multiple spawning seasons in a long-lived species.

Reproductive behavior differs between males and females²⁰. In general, selection is expected to favor male reproductive behaviors that increase reproductive success through access to mates, whereas females invest more heavily in offspring number and quality²¹. Inter-sex differences in reproductive behavior may result in different energetic costs during the spawning period, including costs incurred due to physical conditions experienced during the reproductive period. As a result, factors which affect current and future reproduction may also differ between males and females, particularly in long-lived species, necessitating sex-specific evaluation. Despite male behaviors expressed during the spawning period, including longer and energetically costly spawning area

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residence relative to females, females require longer spawning periodicity resulting from the larger energetic and nutrient investment required to produce eggs compared to the production of sperm^{6,7}.

Some fish species migrate between lakes and rivers or ocean and rivers for reproduction to enhance opportunities to acquire mates and to access habitats conducive to survival of offspring during early life stages²². Reproductive migrations often are initiated and coincide with physical environmental cues indicating suitable conditions to meet energetic demands of migration, and to increase the likelihood of progeny survival²³. Concordantly, variability of stream conditions could potentially alter the duration and modality of the reproductive period or reproductive behavior of migratory fishes, which may present a tradeoff between current and future reproductive potential. However, the degree to which physical stream conditions and behavior during a single reproductive event can affect future reproductive effort remains unclear.

Physical conditions during the spawning period can be highly variable and have been shown to influence behavior during reproduction. For example, water temperature and discharge are strong predictors of spawning migration in both Atlantic sturgeon (*Acipenser oxyrinchus*) and shortnose sturgeon (*Acipenser brevirostrum*)²⁴. Generally, variable physical conditions are evaluated in the context of a single season of reproduction, however, how stream variation can affect the period between reproductive seasons remains unclear necessitating studies of longer duration.

To evaluate the role of physical conditions experienced during the reproductive period (river discharge and temperature), adult demography (sex ratio and age/size composition of spawners), behavior (migrations in a season, and river residence time), and their association with delayed spawning (defined by longer spawning periodicity) we used long-lived lake sturgeon (*Acipenser fulvescens*). Lake sturgeon is a potamodromous, iteroparous fish species of conservation concern throughout its native range²⁵. Lake sturgeon are a highly fecund, broadcast-spawning species that aggregates in large mixed-sex groups to increase probability of fertilization. Adult behavior during the spawning season is variable for males and females, including variability in river residence time, upstream migration time, number of complete river migrations during a single season²⁶, and spawning periodicity²⁷. Longer residence time can reduce gamete quality of females²⁸ and males²⁶.

The general objective of this study was to determine whether behavioral (river residence time, upstream swimming time, number of annual migrations), demographic (inter- and intra-sex interactions, body size) and physical stream variables (discharge, exceedance flow days, temperature) were associated with variability in spawning periodicity for male and female lake sturgeon, and whether spawning periodicity was consistent across multiple capture events. We based observations on lake sturgeon for which spawning periodicity is known for nearly all adult males and females in the population during multiple spawning seasons. We hypothesized that probability of lengthening period between spawning events was associated with behavior, demographic, and physical conditions during the current reproductive period. We further hypothesized that the length of the period between spawning events would decrease with increasing body size (a surrogate of age)²⁴.

Methods

Study site

This study was conducted during the spring spawning season (mid-April through early-June) in seven consecutive years (2016–2022) in the Upper Black River (UBR), a tributary of Black Lake in Cheboygan County, MI, USA (Fig. 1). Spawning occurs in the UBR over an area limited to 17 km upstream of Black Lake and downstream of Kleber Dam (Fig. 1). A dam impounds the river 8 km downstream of Black Lake²⁹, effectively isolating the population. The Black Lake sturgeon population was estimated to be 1,183 (536 females, and 647 males) individuals in 2022 based on an open population model estimate³⁰. RFID antennae arrays based on radio frequency identification (RFID) technology were deployed throughout the UBR in regions accessible to lake sturgeon during the study. The relatively small size of the UBR allowed daily physical capture of ~70–85% and daily RFID detection of >95% of the known spawning population in specific stream spawning sections, annually²⁶. Because spawning lake sturgeon experience intra- and inter-annual variability in spawning biotic and physical conditions, as nearly all adults are tagged, and because of the long-term and inter-disciplinary breadth of detailed studies on the Black Lake, MI population, this population was well suited to evaluate the relative contributions of factors associated with current and future reproduction.

Animal ethics

Animal handling for the project was conducted under approved Michigan State University IACUC protocol PROTO202000023, and all experiments were performed in accordance with relevant guidelines and regulations. This study was conducted in accordance with ARRIVE guidelines, and did not require euthanasia.

Adult capture and handling

Lake sturgeon were captured using long handled dip nets by personnel wearing scuba suits, masks and snorkels. Fork length (cm, FL), body mass (kg), girth (cm) and sex were recorded for all individuals along with date of capture and river location. As FL, mass, and girth were correlated, fork length was the only body size variable used in analyses. Sex was determined by at least one event in which direct expression of gametes was conducted at the time of physical capture or genetically using PCR and sex-specific primers which amplified the AllWSex2 marker³¹.

RFID data collection

In the UBR, 1,132 adult lake sturgeon (95.7% of the estimated adult population³⁰, unpublished data) have been tagged with a 23 mm (0.6 g) or 32 mm (0.8 g) half-duplex 134.2 kHz tags. Eight RFID antennas were maintained in the UBR including three antennas installed 0.5-km upstream of the mouth of the river at FO5 bridge (Fig. 1), two antennas installed immediately downstream of known spawning areas ~14-km upstream of the mouth of the

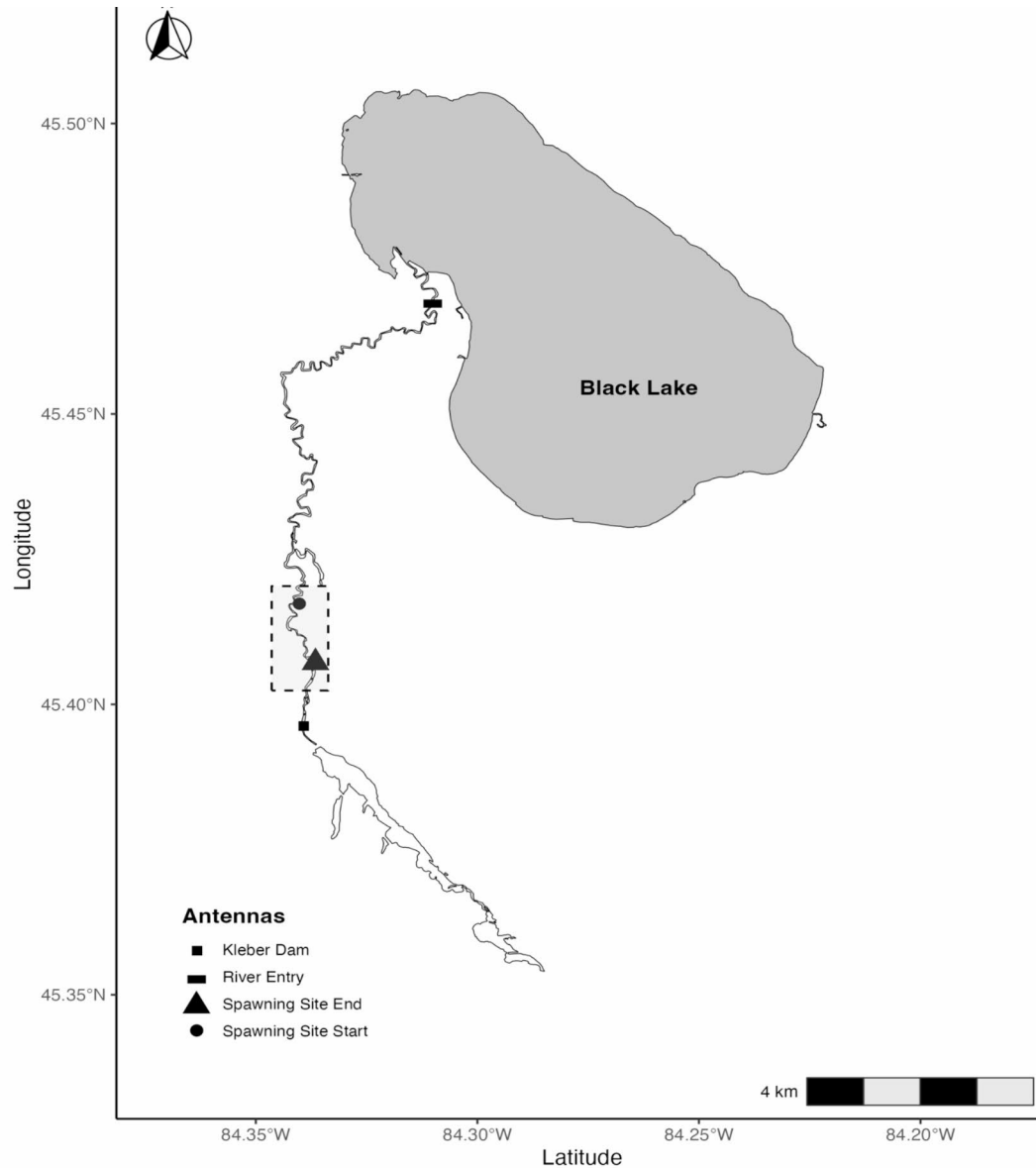


Fig. 1. Map of the Upper Black River and Black Lake in Cheboygan County, MI, USA. Dashed box indicates the known spawning area. Shapes indicate radio frequency identification (RFID) antenna locations including the mouth of the river (Black Rectangle), start of the known spawning area (Black Circle), end of the known spawning area (Black Triangle), and Kleber Dam (Black Square), at the upstream most point accessible for lake sturgeon in the upper Black River. Figure was created using R (4.3.3, www.r-project.org).

UBR (Fig. 1), a single antenna at the upstream most point of the known spawning areas, and 200-m downstream of Kleber Dam, 17-km upstream of the river mouth. Individuals were censored from the dataset under two conditions: (1) if missing RFID detections would not allow for determination of a complete migration into and out of the river and known spawning area in any year of the study period; and (2) if it was determined that they were removed through the system through natural mortality, or harvest. Additionally, spawning periodicity was evaluated only between times during the study period when there was a first and return detection. Detections before and after the study period were not considered.

Behavioral variables calculated from RFID data

Detections from the RFID antennas were used to quantify migratory and spawning behavior, including the number and duration of inter- and intra-sexual interactions, and river residence time of males and females co-occupying the same river reach. All variables have been shown to be associated with individual intra-annual reproductive success²⁶. River residence time (hours), or the cumulative time spent in the river during the spawning season, was calculated as time spent above the river mouth. Upstream migration time (hours) was calculated as the time from river entry to arrival in the spawning area (Fig. 1). The number of intra-annual

migrations was calculated by determining the number of complete up- and down-stream river migrations during the spawning season. To be considered a complete migration, an individual would need to be detected entering and leaving the spawning areas and the river. Male × male and female × female (intra-sex competition) as well as male × female (inter-sex competition) interactions were calculated based on counts of known co-occurrence in the spawning areas. Spawning periodicity interval (the number of years between reproductive events) was calculated as the number of years between RFID river detections, conditional on the individual being detected at both the downstream-most antennae array at the FO5 Bridge and at the downstream end of the spawning area (Fig. 1).

Physical stream data collection

Stream data, including river water temperature (°C) and discharge (m³·sec⁻¹) were collected hourly each year throughout the spring period of river entry, migration, and spawning using an Onset HOBO pressure and temperature logger (Onset Computer Corp, Cape Cod, Massachusetts, USA) deployed in the most upstream segment of the spawning area (Fig. 1). Methods used to calculate hourly discharge are described by the USGS in detail³². We also focused on the effects of periods of unusually high discharge. Data retrieved from the U.S. Geological Survey (USGS) National Streamflow Information Program (<http://water.usgs.gov/nsip>) from 1942 until it was removed from the UBR in 2000 were used to generate a flow duration curve for the UBR that was used to document periods of high exceedance flow during the period of the study. Previous study demonstrated discharge in the UBR was predictable during time after the USGS gauging station was removed³⁵. The flow duration curve estimated the probability that measured flow rate will be equaled or exceeded, as well as categorized 5% exceedance flow values. 5% exceedance flow was selected as it is the largest of the five most common exceedance flow values and represents most extreme flow events. Cumulative thermal units during river residence were quantified by subtracting Kempinger's constant of 5.8 °C from the daily average temperature³⁴ and calculated as the cumulative temperature experienced over each fish summed for all days the fish was detected above the RFID antenna at the mouth of the river³⁵.

Analysis of spawning periodicity

We used RFID detections to determine the number of years between river spawning events (spawning periodicity). Differences in male and female reproductive behavior^{36–38} led to development of separate male and female spawning periodicity models. Variation in periodicity was evaluated using the ordinal logistic regression analysis, which is a type of logistic regression applied to a response variables with a relative ordering. Separate models were fit to male and female fish. We fit the models under a proportional odds assumption meaning that we assumed that the behavioral, demographic, and physical stream covariates had a similar effect on the different spawning periodicity levels (i.e., the logistic model coefficients for the covariates do not depend on the exact spawning periodicity). Assuming Y is the spawning periodicity response variable for a particular sex with exact spawning periodicities denoted by 1, 2, ..., k and X denotes the different behavioral, demographic, and physical stream covariates, the proportional odds ordinal logistic regression model can be specified as.

$$P\left(Y \leq j | X\right) = \frac{\exp\left(\alpha_j - X\beta\right)}{1 + \exp\left(\alpha_j - X\beta\right)} \quad j = 1, 2, \dots, k.$$

where α_j are the unknown intercept parameters that satisfy $\alpha_1 \leq \alpha_2 \leq \dots \leq \alpha_k$ and β is a vector of unknown regression covariates related spawning periodicity to the covariates. The ordinal logistic regression model was fit in R using the `plogit()` function available from the MASS library^{39,40}.

Differences in the number of years until a subsequent spawning event when the first spawning year and associated physical and behavioral conditions was 2016, 2017, 2018, or 2019 (males only) were evaluated using a Chi-square test. Observed values were the number of fish from a given year (t) which returned in subsequent years ($t+1$, $t+2$, $t+n$). The expectation was an approximately equal number of fish returning in $t+1$, $t+2$, ..., $t+n$ from the initial year of spawning from 2016 to 2018. Because female spawning interval can exceed four years, only spawning periods beginning from 2016 to 2018 could be evaluated. Post-hoc evaluation was done using the Bonferroni method for multiple comparisons. To evaluate the difference in spawning behavior, annual demographics, and physical conditions between years because annual capture numbers differed by year, we used a non-parametric Kruskal-Wallis test with a post-hoc Dunn's Test of Multiple Comparisons⁴¹. Differences in physical and behavior variables between sexes were evaluated using non-parametric Mann-Whitney tests. Results of between year differences can be found in Supplemental Materials.

Results

Estimates of spawning adult composition

During the same period, 2,614 lake sturgeon (683 females and 1,931 males) were detected on the passive RFID antennas (Table 1). The number of individual lake sturgeon detected on RFID antennas in a season ranged from 292 to 462. RFID efficiency, or the number of adult lake sturgeon physically captured during the upper Black River annual capture survey which were also detected on RFID antennas, ranged from 94.24% in 2020 to 98.48% in 2016. RFID adult detection totals, annual operational sex ratio, and RFID detection efficiency are presented in Table 1.

Year	RFID Detections			Spawning Period ¹			Occupational Sex Ratio (male:female)	Efficiency RFID Detection Efficiency (%)
	Male	Female	TOTAL	Date of First Detection	Date of Final Detection	Spawning Period Duration (Days)		
2016	220	72	292	16-Apr	9-Jun	54	3.06	98.48
2017	257	92	349	16-Apr	3-Jun	48	2.79	96.64
2018	265	100	365	2-May	6-Jun	35	2.65	96.50
2019	329	96	425	21-Apr	17-Jun	57	3.43	95.56
2020	247	89	336	12-Apr	6-Jun	55	2.78	94.24
2021	333	129	462	9-Apr	8-Jun	60	2.58	95.73
2022	280	105	385	25-Apr	3-Jun	39	2.67	96.87

Table 1. Number of male and female lake sturgeon detected on passively monitored radio frequency identification (RFID) antenna array in the upper Black River, MI from 2016–2022. RFID detection efficiency calculated as the total number of fish which were captured in the physical adult survey but were not detected on RFID antenna (excludes untagged, non-handled fish).

Variability of physical conditions

During the seven-year period of study, the range of dates on which fish were first detected entering the spawning area was between 9 April (2021) and 2 May (2018). The range on which fish were last detected in the spawning area was between 3 June (2022) and 17 June (2019). The shortest and longest spawning period ranged from 35 days (2018) to 60 days (2019), (42 ± 9 mean \pm SE days, Table 1; Fig. 2).

Joint effects of river environment and spawning adult demography and behavior

River temperatures and discharge affected the number and sex ratio of adults concurrently present in spawning areas (Fig. 2), and river residence time, and in turn affects spawning activity as reflected in the number of inter- and intra-sexual interactions (Table 2). Reduced physical stream variability lengthened the spawning run and increased the number of days spawner density was high (Fig. 2). Spawning run modality and spawning season duration was associated with the magnitude, number, and duration of changes in discharge and temperature. Cumulative discharge (Sup. Figure 2), days when river discharge exceeded 5% of all recorded values (Sup. Figure 3), and CTUs (Sup. Figure 4) all varied significantly by year.

Spawning periodicity

Spawning Periodicity was highly variable across years. Average male spawning periodicity was 1.60 ± 0.02 years (mean \pm SE, range 1.00–3.00 years). Average female spawning periodicity during the study period was 3.19 ± 0.05 years (mean \pm SE range 2.00–5.00 years). Associations between physical and behavioral variables and male lake sturgeon spawning periodicity were significant (Table 3). For every additional cubic meter per second of discharge experienced by a male lake sturgeon in a spawning season, the odds of male lake sturgeon experiencing a longer spawning periodicity increased by 1.005 (95% CI: 1.002 to 1.009, Table 3). Similarly, an increase of one critical thermal unit increased the odds of male lake sturgeon experiencing a longer spawning periodicity by 1.005 (95% CI: 1.001–1.008, Table 3). For every additional intra-annual migration run the odds of male lake sturgeon experiencing a longer spawning periodicity increased by 1.402 (95% CI: 1.178–1.671). From a biological perspective, lake sturgeon size and the number of inter-sex and intra-sex interactions were found to have a significant effect on spawning periodicity. Lake sturgeon size and number of intra-sex interactions decreased the odds that fish experienced a longer spawning periodicity. For every additional intra-sex interaction, the odds of male lake sturgeon having a longer spawning periodicity decreased by 0.959 (95% CI: 0.947–0.971). For every 1 cm increase in fork length, the odds of male lake sturgeon having a longer spawning periodicity decreased by 0.978 (95% CI: 0.968–0.988). Conversely, for every additional inter-sex interaction, the odds of male lake sturgeon have a longer spawning periodicity increased by 1.005 (95% CI: 1.000–1.009, Table 3).

The number of fish of returning to the river in subsequent spawning years for males differed by the initial year of spawning ($\chi^2 = 19.887$, $p = 0.0029$) resulting from individual physical conditions experienced. Post-hoc analysis indicated number of returning adults was different for males which spawned in 2018 compared to 2019 ($p = 0.013$). When first spawning occurred in 2018, 52.4% returned in year $t + 1$, 42.1% in year $t + 2$, 5.5% in year $t + 3$. When first spawning occurred in 2019, 34.4% returned in year $t + 1$, 49.4% in year $t + 2$, 16.1% in year $t + 3$ (Fig. 3). Detailed probability of annual male return based on initial year of spawning can be found in supplemental results and Fig. 3. Complete spawning history of male lake sturgeon considered in this study can be found in Supplemental Fig. 9.

Female lake sturgeon spawning periodicity was not associated with variable physical stream conditions, but was influenced during migration to the spawning areas by time swimming upstream, and inter-sex interactions during the spawning period (Table 3). For every additional hour spent swimming upstream, the odds that female experienced a longer spawning periodicity decreased by 0.980 (95% CI: 0.967–0.992). Similarly, for each additional inter-sex interaction the odds that fish experienced a longer spawning periodicity decreased by 0.978 (95% CI: 0.930–0.995) (Table 3).

Female lake sturgeon return probability was evaluated for years 2016–2018, as female spawning periodicity prevents more than four years of evaluation from 2019 through the end of the study period. Of the female lake

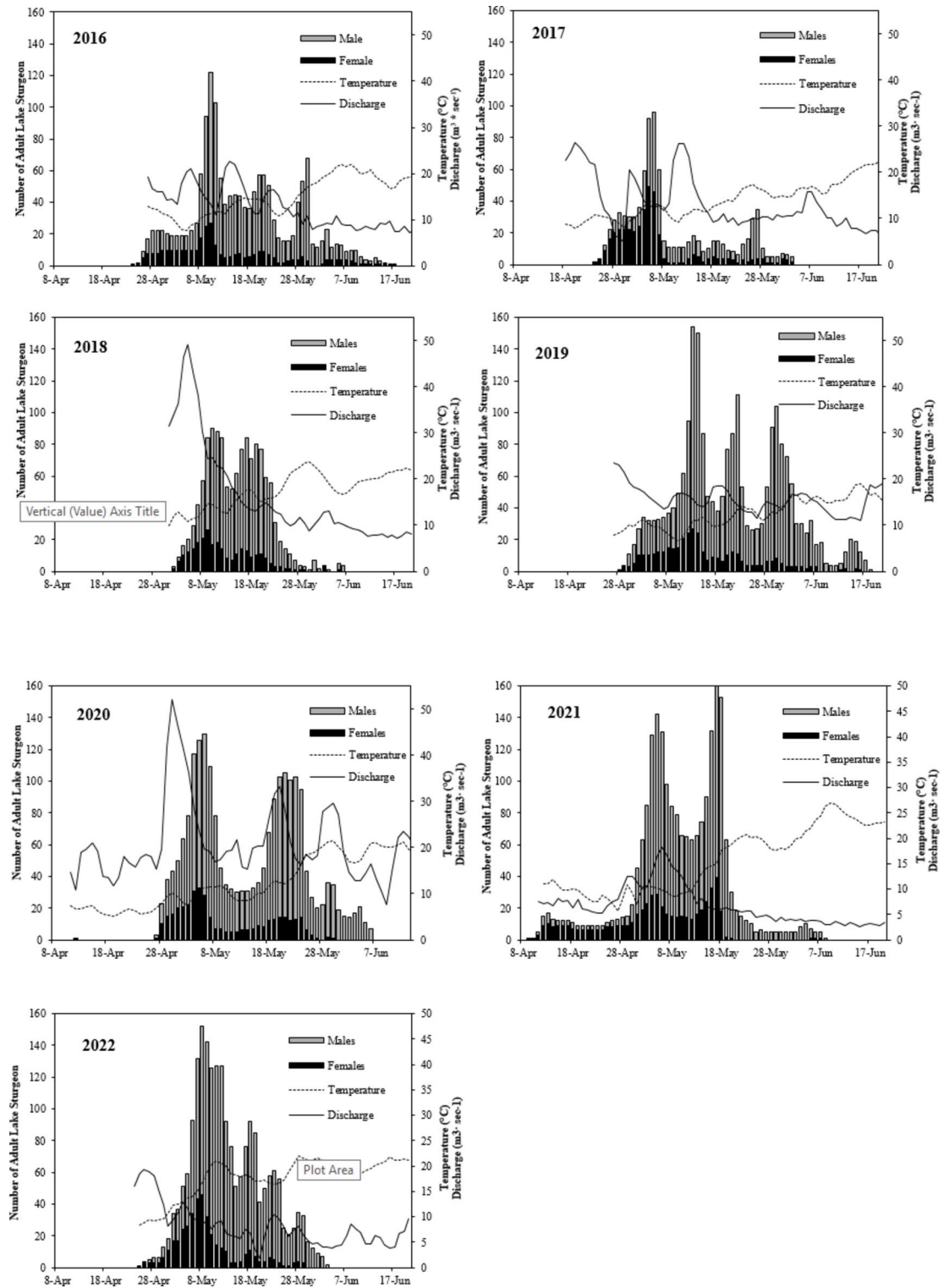


Fig. 2. Male and female lake sturgeon present in the river by day during the 2016–2022 spawning season. The dashed line represents daily average temperature (°C). The solid line represents daily average discharge (m³·sec⁻¹) measured by a HOBO pressure and temperature logger (Onset Computer Corp, Cape Cod, Massachusetts, USA).

sturgeon that spawned in 2016 (*t*), 0.0% returned in 2017 (*t*+1), 11.8% returned in 2018 (*t*+2), 70.6% returned in 2019 (*t*+3), and 17.6% returned in 2020 (*t*+4). Of the females which spawned initially in 2016, none took more than 4 years to return to spawn (Fig. 9). Of the females that initially spawned in 2017, 0.0% returned in year *t*+1, 7.3% in year *t*+2, 58.5% in year *t*+3, 31.7% in year *t*+4 and 2.4% took five or more years to return.

	2016	2017	2018	2019	2020	2021	2022
Males							
Discharge (m ³ ·sec ⁻¹)	47.32 ± 3.71	70.56 ± 4.67	114.24 ± 5.44	107.91 ± 5.43	207.18 ± 9.55	74.51 ± 4.69	61.02 ± 2.45
Exceedance Flow (Number of Days)	1.80 ± 0.16	0.81 ± 0.11	2.95 ± 0.22	2.62 ± 0.12	7.41 ± 0.35	0.85 ± 0.06	0.03 ± 0.02
Temperature (°C)	89.11 ± 5.25	41.95 ± 2.25	56.61 ± 2.54	48.96 ± 2.66	62.98 ± 3.11	49.43 ± 3.06	81.83 ± 3.64
Inter-sex Interactions (Number per Year)	24 ± 1	37 ± 2	25 ± 1	27 ± 1	33 ± 1	41 ± 1	38 ± 2
Intra-sex Interactions (Number per Year)	97 ± 3	120 ± 4	98 ± 3	159 ± 3	134 ± 3	157 ± 3	132 ± 3
Fork Length (cm)	130.16 ± 2.05	134.97 ± 2.45	131.67 ± 2.73	133.02 ± 1.93	131.24 ± 2.88	129.51 ± 0.93	131.73 ± 0.92
Migrations (Number per Year)	1.55 ± 0.07	1.55 ± 0.05	1.28 ± 0.04	2.02 ± 0.05	1.73 ± 0.07	1.36 ± 0.04	1.32 ± 0.04
River Residence Time (Hours)	263.35 ± 13.04	247.29 ± 11.89	172.36 ± 8.43	283.44 ± 10.97	268.67 ± 10.97	273.57 ± 12.21	182.89 ± 7.62
Upstream Swimming Time (Hours)	62.77 ± 4.42	69.07 ± 3.96	40.76 ± 3.27	69.08 ± 3.74	57.69 ± 4.80	68.64 ± 5.35	36.30 ± 2.09
Females							
Discharge (m ³ ·sec ⁻¹)	43.35 ± 5.94	80.15 ± 7.72	119.18 ± 11.38	86.49 ± 11.36	183.20 ± 14.27	69.95 ± 8.77	50.20 ± 4.42
Exceedance Flow (Number of Days)	1.47 ± 0.23	1.32 ± 0.20	3.29 ± 0.34	1.83 ± 0.27	5.87 ± 0.43	0.53 ± 0.10	0.14 ± 0.08
Temperature (°C)	75.08 ± 10.91	39.22 ± 3.36	40.74 ± 4.28	29.68 ± 4.19	37.99 ± 2.64	36.52 ± 3.46	40.62 ± 2.87
Inter-sex Interactions (Number per Year)	97 ± 5	124 ± 5	80 ± 4	111 ± 8	118 ± 4	128 ± 6	112 ± 4
Intra-sex Interactions (Number per Year)	24 ± 2	44 ± 2	24 ± 1	22 ± 2	32 ± 1	37 ± 2	39 ± 2
Fork Length (cm)	153.70 ± 2.95	155.94 ± 2.52	152.41 ± 3.11	153.00 ± 2.07	147.55 ± 2.69	151.37 ± 1.46	154.39 ± 1.55
Migrations (Number per Year)	1.29 ± 0.09	1.34 ± 0.03	1.07 ± 0.03	1.25 ± 0.07	1.22 ± 0.07	1.17 ± 0.05	1.12 ± 0.04
River Residence Time (Hours)	162.14 ± 31.56	181.33 ± 16.17	119.70 ± 11.92	199.32 ± 17.90	181.06 ± 14.69	197.78 ± 19.98	144.37 ± 11.02
Upstream Swimming Time (Hours)	40.86 ± 5.82	54.46 ± 7.10	37.07 ± 5.05	51.68 ± 7.65	38.15 ± 6.85	41.61 ± 4.35	45.75 ± 5.68

Table 2. Average (\pm standard error) discharge (m³·sec⁻¹), exceedance flow (days), cumulative thermal units (°C), inter-sex interactions, intra-sex interactions, fork length (cm), annual migrations (number per year), river residence time (hours), and upstream swimming time (hours) experienced by male (TOP) and female (BOTTOM) adult lake sturgeon by year from 2016–2022.

For females that initially spawned in 2018, 0.0% returned in 2019 ($t+1$), 3.4% returned in 2020 ($t+2$), 51.7% returned in 2021 ($t+3$), and 44.8% returned in 2022 ($t+4$) (Fig. 3).

The probability of returning to the river in subsequent spawning years for females did not differ by the initial year of spawning. Probability of annual female return based on initial year of spawning can be found in supplemental results and Fig. 3. Complete spawning history of female lake sturgeon considered in this study can be found in Supplemental Fig. 10.

Discussion

Across iteroparous species including fishes, there is considerable variability in reproductive behavior among individuals within a year and by the same individual inter-annually^{6,42}. Reproductive behaviors, including migrations from marine or lacustrine habitats to spawning areas in riverine habitats often vary among individuals in response to differences in exposure to spatially or temporally variable physical stream conditions within a spawning season and across years (e.g., temperature and discharge; Fig. 2 in this study)³³. Demographic factors including spawning adult abundance, sex ratios, and size/age structure also affect behavior including river residence time and the number and duration of inter- and intra-sexual encounters^{26,28}. For long-lived iteroparous species such as lake sturgeon, behaviors exhibited by spawning adults in response to sources of stream conditions and demographics during migration and spawning area residency lead to resource investment actions that affect current and future reproductive allocation and success, and cumulative life-time fitness^{6,43}. Trade-offs between current and future resource expenditures to reproduction^{44,45} are important to managers seeking to forecast future changes in population recruitment⁴⁶. Information is increasingly important to reduce population viability risk in the current era of climate variability and change⁴⁷. Consistent with other studies^{16,48}, managers should consider the variability in spawning periodicity due to delayed spawning when estimating stock-recruitment relationships.

This study provided a unique opportunity to characterize migratory and spawning behavior for more than 90% of spawning adults in an isolated lake sturgeon population during seven entire reproductive seasons, demonstrating the value of long-term monitoring of populations of long-lived organisms on an individual basis⁴⁹. River temperature and discharge and RFID monitoring devices concurrently measured physical stream characteristics and current year migratory and spawning behavior, respectively that are associated with resource investments to reproduction. Physical stream features such as temperature and discharge are shown to be important cues that initiate migration³³ or repeated within-year migration²⁶. More generally, these conditions affect onset, duration, interruption, and cessation of spawning activity^{50,51} and spawning periodicity.

Multiple migratory events within a season

River temperatures and discharge affected the number of within year migrations. We documented an increase in spawning periodicity as the number of within year migrations increased, likely because lake sturgeon exhibit poor aerobic swimming ability and incur high energetic costs during spawning migrations^{52,53}. Multiple

Male Lake Sturgeon	Units	Log Odds Ratio	Odds Ratio	Std. Error	t	p	Log Odds Ratio		Odds Ratio	
							CI (2.5%)	CI (97.5%)	CI (2.5%)	CI (97.5%)
Individual Physical Variables										
Cumulative Discharge	m ³ ·sec ⁻¹	0.005	1.005	0.002	2.958	0.003*	0.002	0.009	1.002	1.009
5% Exceedance Flow	Days	-0.057	0.944	0.042	-1.352	0.176	-0.141	0.026	0.869	1.026
Cumulative Temperature Units	°C	0.005	1.005	0.002	2.468	0.014*	0.001	0.008	1.001	1.008
Behavioral Variables										
Complete River Migrations	Number per year	0.338	1.402	0.089	3.787	<0.001*	0.164	0.514	1.178	1.672
Upstream Swimming Time	Hours	-0.002	0.998	0.001	-1.496	0.135	-0.005	0.001	0.995	1.001
River Residence Time	Hours	0.001	1.001	0.001	0.916	0.359	-0.001	0.002	0.999	1.002
Demographic Variables										
Fork Length	cm	-0.022	0.978	0.005	-4.088	<0.001*	-0.033	-0.012	0.968	0.988
Intra-sex Interactions	Number per year	-0.042	0.959	0.006	-6.615	<0.001*	-0.054	-0.029	0.947	0.971
Inter-sex Interactions	Number per year	0.005	1.005	0.002	2.091	0.037*	0.000	0.009	1.000	1.009
Baseline Probability										
Spawning Periodicity 1 Year 2 Years	-	-2.596	-	-	-	-	-	-	-	-
Spawning Periodicity 2 Years 3 Years	-	0.194	-	-	-	-	-	-	-	-
Female Lake Sturgeon		Value	Odds Ratio	Std. Error	t	p	Log Odds Ratio		Odds Ratio	
							CI (2.5%)	CI (97.5%)	CI (2.5%)	CI (97.5%)
Individual Physical Variables										
Cumulative Discharge	m ³ ·sec ⁻¹	0.008	1.008	0.005	1.484	0.138	0.002	0.009	0.997	1.018
5% Exceedance Flow	Days	-0.016	0.984	0.167	-0.098	0.922	-0.141	0.026	0.709	1.369
Cumulative Temperature Units	°C	0.004	1.004	0.007	0.506	0.613	0.001	0.008	0.989	1.019
Behavioral Variables										
Complete River Migrations	Number per year	0.308	1.361	0.402	0.767	0.443	0.164	0.514	0.625	2.996
Upstream Swimming Time	Hours	-0.020	0.980	0.006	-3.206	0.001*	-0.005	0.001	0.967	0.992
River Residence Time	Hours	0.003	1.003	0.003	0.984	0.325	-0.001	0.002	0.998	1.009
Demographic Variables										
Fork Length	cm	-0.035	0.966	0.019	-1.841	0.066	-0.033	-0.012	0.930	1.002
Intra-sex Interactions	Number per year	0.019	1.019	0.022	0.884	0.377	-0.054	-0.029	0.977	1.064
Inter-sex Interactions	Number per year	-0.023	0.978	0.009	-2.531	0.011*	0.000	0.009	0.960	0.995
Baseline Probability										
Spawning Periodicity 2 Years 3 Years	-	-9.424	-	-	-	-	-	-	-	-
Spawning Periodicity 3 Years 4 Years	-	-5.409	-	-	-	-	-	-	-	-

Table 3. Ordinal regression models quantifying associations between spawning periodicity of male (top) and female (bottom) lake sturgeon with individual physical stream, behavioral, and demographic variables in the upper Black River, MI. Significant effects indicated with (*).

spawning migrations within a season are rare, particularly for large-bodied fish like lake sturgeon^{28,54}, and likely result from responses to short-term variation in physical stream conditions⁵⁴. Lake sturgeon can travel long distances to spawn^{55,56}. However, multiple lake sturgeon migrations have only been documented in short rivers and in situations where access to historical spawning areas has been impeded by man-made dams.

It is likely that spawners experienced differences in resource expenditures resulting from variable physical conditions across years. Female residence time was significantly shorter than males in all years. Males with longer river residence times and greater numbers of intra- and inter-sexual interactions during the spawning season (a measure of reproductive effort²⁶) had significantly longer spawning periodicity. Male lake sturgeon increased inter-sex interactions as residence time increased²⁶. Years with longer spawning runs likely result in greater within year reproductive energetic costs are realized in terms of reduction of sperm count and motility²⁶. Female lake sturgeon reproductive success is also associated with male availability (operational sex ratio²⁸).

Spawning behavior and spawning periodicity

Years when river residence time was shortest coincided with the highest next year ($t + 1$) return probability for male lake sturgeon. Conversely, in years when residence time was longer (e.g., 2019), significantly lower one-year return probabilities were observed for male lake sturgeon. Male spawning periodicity increased as inter-sex interactions increased. Data revealed for males increasing inter-sex interactions increased with increasing body size (and therefore age). Differences in the onset and duration of the spawning run were associated with differences in male river residence time, which may result in a trade-off by increasing spawning periodicity. Female

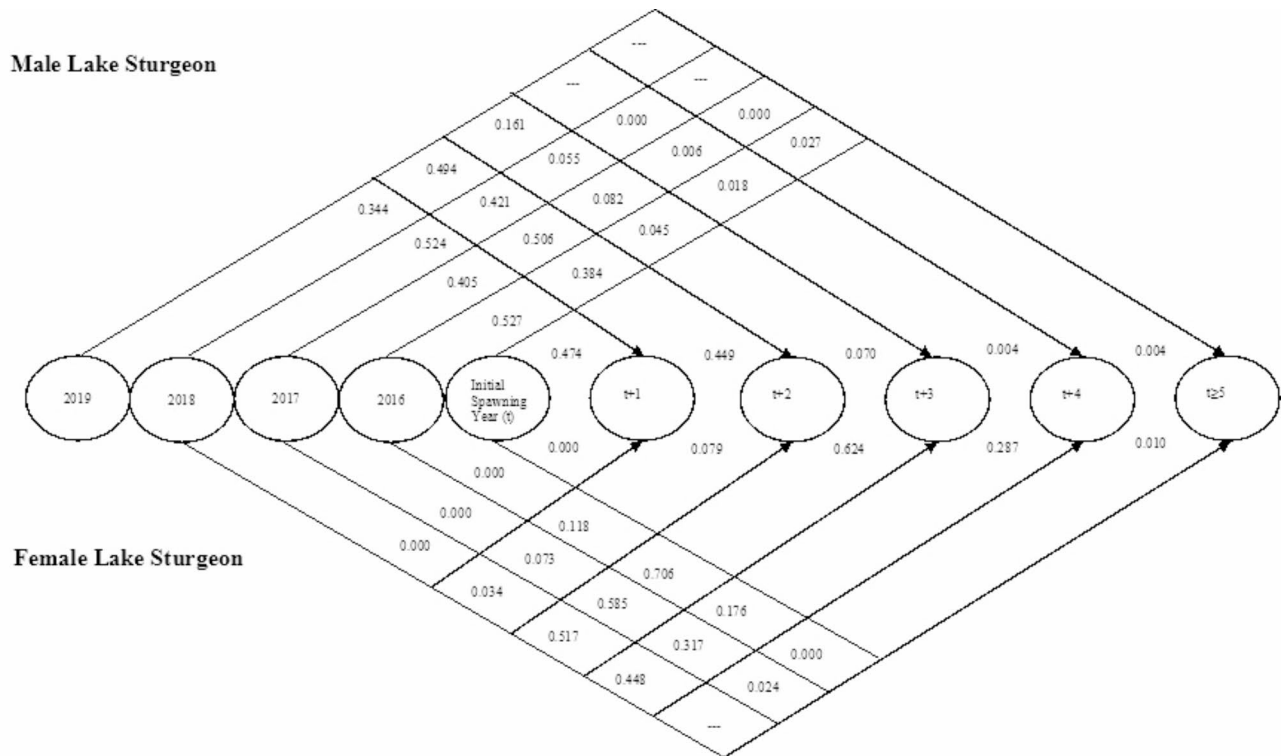


Fig. 3. Probability of return to the river to spawn in years following first observed spawning event in year t for male and female lake sturgeon in the upper Black River, Michigan based on radio frequency identification (RFID) data collected from 2016–2022. Numbers on each axis represent the return year proportion based on each initial year of spawning for males and females. Numbers listed horizontally represent the mean proportional return across the duration of the study period for males and females.

spawning periodicity was significantly longer than in males and was not associated with physical conditions, or inter-sexual interactions. There was no evidence that female spawning periodicity varied between spawning years. In general, females of iteroparous species take longer than males to recover following reproduction^{57–59}. In the case of lake sturgeon, male testosterone levels and gonadosomatic index typically return to pre-breeding levels within a month of the end of the breeding season. This contrasts with females, which maintain low steroid concentrations and GSI through fall of the reproductive year⁶⁰. The length of the inter-breeding period is related to the costs of reproduction and the availability of resources during inter-spawning periods^{61,62}. In general, spawning interval is likely to lengthen early in life, when energetic costs of migration and reproduction are high, and when food availability during non-breeding period is too low for gonad development⁵.

Females have higher energetic demands associated with reproduction, thus breeding period can be affected by physical stream conditions^{13,58}, which may limit the ability of females to acquire resources during the non-breeding period. The lack of associations between female spawning periodicity and the variables evaluated could also be due to the proportionally lower sample size for females relative to males, both in terms of absolute numbers per year and study duration. Most females in this study were captured initially with only one additional capture event during the study period. It is possible that the lack of multiple spawning events resulting from longer inter-spawning periods may have contributed to the lack of significant associations with body size and physical stream conditions. The number of intra-sex interactions and upstream swimming time both reduced the probability of a shorter spawning periodicity which may be related to individual behavior. Notably, decreasing spawning periodicity as a function of increased upstream swimming time may be explained by short-stopping, or decreased swimming effort and resting during migration. Body size (fork length) was not associated with spawning periodicity and may suggest that spawning period is largely individualized by females and is more likely to be affected by resource acquisition.

Male body size and spawning periodicity

We documented negative associations between male current year reproductive expenditures and both spawning periodicity and size (a surrogate of age) males. The reduction of inter-spawning interval in males with increasing

body size could be a response to the reduced number of residual breeding opportunities as an individual ages, and the reduced need for energy allocated to somatic growth^{5,63}. Life history theory predicts that resource expenditures toward current reproduction should increase as an organism ages and residual reproductive value decreases⁶³. Findings that decreasing spawning periodicity was associated with increasing body size is consistent with prior study⁶³, which predicts that spawning periodicity should be longest immediately following first maturity and decrease with increasing age. Other authors have demonstrated⁵⁸ that the period between lake trout (*Salvelinus namaycush*) spawning events decreased as fish aged. Additionally, in cod (*Gadus morhua*) shorter inter-breeding periods were observed as age increased⁶⁴.

While male lake sturgeon spawning periodicity was associated with individually experienced physical conditions within a season, female spawning periodicity was not. It is possible that female spawning periodicity may be explained by factors not evaluated in this study or that more information is needed. Because the period between female spawning events can exceed three years, most females in this study were only captured twice, including the initial time of capture. Future work should evaluate female spawning periodicity with multiple recapture events.

Alternate explanations for associations between body size and spawning periodicity

Delayed breeding (longer spawning periodicity) has also been documented in fish with diminished energy reserves⁶, or as a response to unfavorable physical stream conditions⁷. Black Lake adults reside within a 4100-ha watershed that is much smaller than open-water Great Lakes habitats that the system was once connected to. A closed inland lake system may not provide similar foraging limitations for adults compared to adults in populations with access to the Great Lakes. Additionally, there is high repeatability in adult spawning times³³. Individuals that repeatedly spawn during certain times are more likely to experience conditions that are energetically more demanding and are more likely to exhibit greater spawning periodicity. For example, higher discharge early in the spawning periods annually may differentially predispose early spawning adults to have longer spawning periodicity.

There are inter-annual differences in spawning adult sex ratios each year because of differences in male and female spawning periodicity. Spawning sex ratios dictate that potential number of intra- and inter-sexual encounters and resource expenditures are tied to spawning periodicity. Therefore, the inter-spawning period may oscillate episodically though perhaps predictably as a function of spawning adult sex ratio. Further, river residence time alone may not result in successful reproduction. It is common for some fishes to undertake upstream migration without successfully spawning. In past study, follicular atresia has been noted in lake sturgeon during the breeding period, potentially indicating egg reabsorption²⁸. Notably, in both cases, females successfully produced progeny. In the case of both male and female lake sturgeon, there is a strong relationship between reproductive opportunity (inter-sex interactions) and reproductive success (successful production of progeny in a breeding season^{26,28}).

Conclusions

Actions taken by iteroparous organisms to invest resources in current vs. future reproduction^{9,65} are often cast in terms of reproductive value or expected reproductive contributions of individuals to future population growth⁶⁶, which generally declines with increasing age^{9,67}. Theory predicts that current reproductive effort as a portion of an individuals' total energy budget should increase as residual reproductive value decreases^{9,64,68}. Findings from this study demonstrated that long-lived species such as lake sturgeon are consistent with the predictions of life history theory exhibiting a shorter spawning periodicity as they increase in size (and by extension, age). Additionally, findings from this study demonstrated that breeding periodicity is not fixed, but is influenced by the individual behavior, and the demographics of the breeding population, and physical conditions experienced by organisms during the breeding period.

Annual variability in the onset, degree of asynchrony, and duration of spawning highlights future challenges for managers seeking to forecast lake sturgeon recruitment. Migratory fishes are reliant on external cues which signal the onset of spawning migration^{69,70}. Sturgeon species perceive lagged effects of increasing temperature and decreasing discharge^{24,71} and lunar phase³³ to initiate spawning migration. Generally, migration occurs when stream conditions are likely to be most suitable for offspring survival^{23,72}. As climate change is predicted to increase environmental stochasticity, formerly reliable cues for initiation of spawning migrations and spawning are likely to become less predictive⁷³ of suitable conditions for spawning and for offspring survival during early ontogeny. Ultimately, the mismatch between maternal and offspring experiences may alter offspring behavior and survival, thereby posing a threat to population levels of recruitment⁷⁴.

Data availability

Data are available in project form via GITHUB repository which is available upon reasonable request.

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Author contributions

D.L.L., E.A.B., and K.T.S. conceptualized the study, obtained funds for the project, and organized sample collection, processing and data analysis. K.T.M supervised the study. D.L.L completed the data analysis, figure generation, and developed the first draft of the manuscript. T.O.B. contributed significantly to the data analysis. D.L.L., T.O.B., E.A.B., and K.T.S assisted with additional analysis and manuscript revisions. All authors read and approved the final manuscript.

Declarations

Competing interests

The authors declare no competing interests.

Additional information

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