Individual-based analyses reveal high repeatability in timing and location of reproduction in lake sturgeon (*Acipenser fulvescens*)

Patrick S. Forsythe, James A. Crossman, Nora M. Bello, Edward A. Baker, and Kim T. Scribner

Abstract: Few studies have quantified the repeatability of reproductive decisions by individuals or assessed their relationship with environmental variables over multiple seasons for long-lived iteroparous fish species. Using individual-based data collected for 678 lake sturgeon (*Acipenser fulvescens*) over 8 consecutive years, we evaluated hypotheses regarding spawning periodicity and repeatability of spawning location, spawning time, and environmental cues associated with spawning. At our study site (Upper Black River, northern Michigan, USA), interspawning interval differed between males (2.3 ± 0.08 years) and females (3.7 ± 0.16 years), but was not significantly related to age. Individual spawning behavior was highly repeatable with respect to spawning time (relative day within the spawning season) for both sexes regardless of size or age, but was less repeatable, though still significant, relative to water temperature, river discharge, and lunar phase. Breeding area was also repeatable, with individuals spawning earlier in the season selecting locations further upstream than those spawning later. Repeatability in spawning times and locations suggest that subpopulation differentiation may develop among different spawning groups, even within small and spatially contiguous areas.

Résumé : Peu d'études ont mesuré la répétabilité des décisions de reproduction des individus ou évalué leur relation avec les variables du milieu sur plusieurs saisons chez les poissons itéropares à longue durée de vie. En utilisant des données basées sur l'individu récoltées sur 678 esturgeons jaunes (*Acipenser fulvescens*) pendant 8 années consécutives, nous évaluons certaines hypothèses concernant la périodicité de la fraie, la réutilisation des sites de fraie, le moment de la fraie et les signaux environnementaux associés à la fraie. À notre site d'étude (Upper Black River, nord du Michigan, É.-U.), l'intervalle entre les fraies diffère entre les mâles (2,3 ± 0,08 années) et les femelles (3,7 ± 0,16 années), mais n'est pas significativement relié à l'âge. Le comportement reproducteur individuel est fortement répétable en ce qui a trait au moment de la reproduction (jour relatif durant la saison de reproduction) chez les deux sexes sans égard à la taille ou l'âge, mais il est moins répétable, bien que significatif, en ce qui concerne la température de l'eau, le débit de la rivière et la phase de la lune. Les zones de fraie sont aussi réutilisées, avec les individus qui fraient plus tôt dans la saison choisissant des sites plus en amont que ceux qui fraient plus tard. La répétabilité dans le calendrier de fraie et les sites de reproduction laisse croire qu'il peut se développer une différenciation de sous-populations au sein des groupes de reproducteurs, même dans des zones petites et contigües.

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Introduction

Associations between environmental cues and decisions made by adults with respect to the timing and location of reproduction substantially affect interindividual variation in reproductive success and population levels of recruitment. Environmental conditions experienced by offspring during embryogenesis and early life stages are largely determined based on the timing and stream characteristics associated with location of spawning that are selected by the parents (Kamler 2002). In aquatic habitats, for example, water temperature and stream discharge affect the timing of larval hatch (Pepin et al. 1997), timing of larval dispersal (Duong et al. 2011*a*), offspring phenotype (Mousseau and Fox 1998), and offspring developmental rate and survival (Trippel et al. 1997; Jørgensen et al. 2008). Generally, repeatability in expression of reproductive decisions is adaptive, given that such decisions are based on reliable cues associated with successful reproduction and recruitment (Williams and Nichols 1984).

Many species use cues in their physical environmental to guide choices of when and where to reproduce in temporally and spatially complex aquatic landscapes (Beall and de Gaudemar 1999; Hodgson and Quinn 2002; Dahl et al. 2004). Spawning time and breeding area selection have been attributed to genetic and physiological effects (Jennings et al. 1996; Quinn et al. 2000; Stewart et al. 2002), adult age or size (Trépanier et al. 1996; Stewart et al. 2002), use of alternative reproductive tactics (Morbey 2003), social influences (Brown and Laland 2003), and olfactory cues (Dittman and Quinn 1996). External cues are important because environmental variables that affect spawning site quality are related to offspring survival (Malcolm et al. 2009; Smith and Marsden 2009). Survival during early life stages is in turn often related to recruitment (Bailey and Houde 1989).

Despite the importance of selecting favorable spawning times and locations, comparatively few data are available regarding individual repeatability in the timing and location of reproductive events within a season (Pankhurst and King 2010). Mechanisms controlling gametogenesis are likely acted on by selection, and therefore spawning behavior is an individual- rather than population-level attribute. If individual behaviors are repeatable, and interindividual differences can be predicted based on associations with quantifiable environmental variables, then at the population level, spawning times have should major consequences for interannual variation in recruitment (Wright and Trippel 2009).

Riverine habitats are dynamic in space and time (Fausch et al. 2002). Thus, cues that reflect current conditions may not enable individuals to anticipate the location or timing of future (and preferred) conditions. Long-lived iteroparous species are likely to experience different environmental conditions from year to year over multiple reproductive episodes in an individual's lifetime. Accordingly, plasticity in response to changing environmental conditions is likely and will have fitness consequences (Schlichting and Pigliucci 1998). Even if adults use the same environmental cues (e.g., specific temperatures, flow rates, substrate types, and depth) during each reproductive event, over multiple spawning episodes, the location and time at which these cues are expressed are like to vary greatly. Therefore, variability in environmental characteristics at specific spawning locations during the course of the reproductive season and across years should decrease the degree of repeatability in an individual's selection of spawning locations and in timing of reproduction.

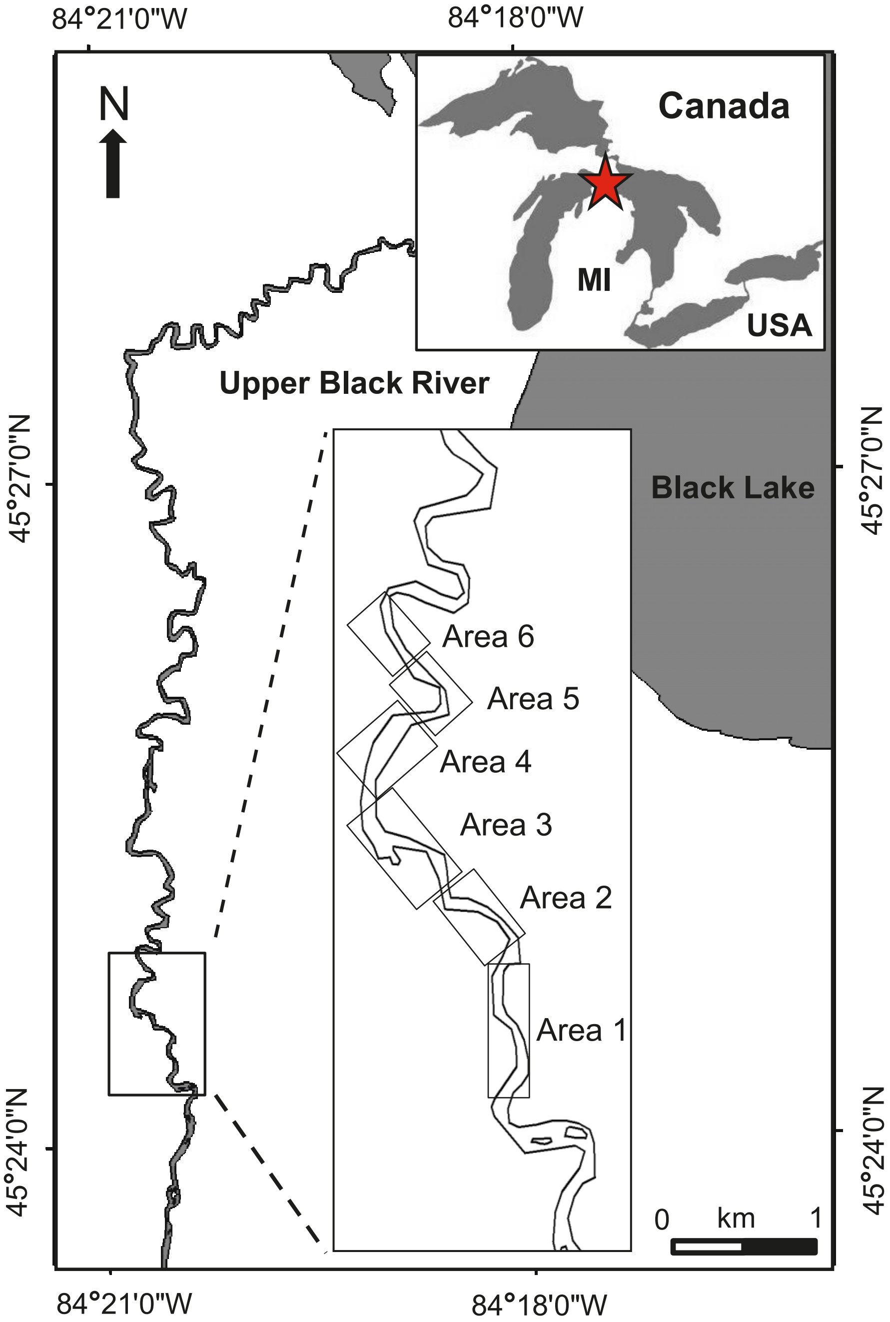
In addition to within-season repeatability, little is known regarding the periodicity or frequency of reproduction (i.e., interannual spawning interval across years) for individuals. The ability to acquire sufficient resources to allocate to reproduction is likely to vary among individuals (van Noordwijk and de Jong 1986). In particular, gametogenesis and reproductive success is generally thought to be limited by resources to a greater degree in females than in males (Stearns 1992). Accordingly, individual-based analysis are predicted to reveal that the time required to acquire sufficient resources between reproductive episodes is likely greater for females than for males.

Several predictions have been made regarding age-specific variation in interspawning interval. Based on well-established relationships among maternal investment in egg size, egg number, body size, and age (Berkeley et al. 2004; Kindsvater et al. 2011), interspawning interval is predicted to be longer for larger (or older) females than smaller (or younger) females. From a life history perspective, the frequency of spawning may be expected to decrease in older females owing to trade-offs between investments in current vs. future reproduction (Stearns 1992). Studies have shown that females with lower expected future reproductive potential (e.g., older females) will devote more resources to produce more and larger offspring (Marshall et al. 2010) and have higher frequency of reproduction (Congdon et al. 2003) than do younger females. For males, reproductive success is highly correlated with mate number (Bateman 1948), which can be increased based on higher reproductive frequency.

Lake sturgeon (*Acipenser fulvescens*) is a useful species for individual-based studies of periodicity and repeatability in spawning time and location. Sturgeon are long-lived and iteroparous (Rochard et al. 1990; Birstein 1993; Peterson et al. 2007), affording opportunities to gather data over multiple reproductive events. Lake sturgeon also exhibit variation in reproductive behavior, distance from spawning areas and habitats occupied during nonspawning times, and use of migratory routes that potentially affect spawning time, physiological condition, and rates of gamete maturation within and among populations. As in other fish species, early life stages of lake sturgeon experience high mortality (Kempinger 1988; Forsythe 2010). Adult behaviors tied to environmental conditions at the time and location of reproduction may thus contribute substantially to rates of mortality during early life stages (Duong et al. 2011*b*) and in turn represent a substantial component of variation in lifetime fitness.

An individual-based analysis was used to quantify the degree of repeatability in spawning time and location for lake sturgeon. Based on mark–recapture data collected over 8 consecutive years, we evaluated several hypotheses concerning individual repeatability in location and timing of reproduction and sex and age differences in repeatability in interspawning interval. First, we evaluated whether adults consistently respond to environmental cues across years and spawn at predictable locations and times. We predicted that analyses would reveal evidence for repeatability across years in repro-

Fig. 1. Location (upper inset) and map of the Upper Black River, Michigan, USA. Lower inset: spawning areas used by adult lake sturgeon. Areas generally represent a single spawning location. Arrows indicate direction of water flow.



ductive behavior including spawning time within a breeding season (e.g., early vs. late), spawning site location within a tributary, or environmental conditions (e.g., water temperature or stream discharge that could serve as cues). Secondly, we predicted that spawning periodicity (i.e., interannual spawning interval across years) would be shorter for males than for females and would decrease as a function of age.

Materials and methods

Study location

Research was conducted over 8 consecutive years (2001–2008) on a lake sturgeon population located in Black Lake, Michigan, USA. The Black Lake system is well suited for conducting ecological long-term research. It is dammed and thus closed to immigration. Lake sturgeon use a single tributary, the Upper Black River (UBR), for reproduction and all spawning occurs within a 1.5 km stretch of the UBR that is approximately 9 km upstream from the lake (45°43′N, 84°15′W; Fig. 1). Upon arrival at the spawning grounds, UBR adults congregate to spawn in groups for one to several days (Forsythe 2010). During the spawning period, individuals are easily observed and readily captured at several accessible and wadable areas (Fig. 1). Individuals can also be visually monitored nearly continuously because of their large size and because of the narrow stream channel (<25 m), shallow water depth (<1.5 m), and relatively low flow volume (daily average 8.3 $m^3{\cdot}s^{-1}$ during the spawning season; Forsythe 2010).

Data collection and preparation

Lake sturgeon were captured at several spawning areas within the 1.5 km stretch of the UBR (Fig. 1) using long-handled landing nets. Personnel searched this entire stretch of the stream by wading at least once daily during the entire spawning season each year. Captured individuals were sexed by examining cloacal morphology (Bruch et al. 2001) or by pressing on the abdomen to expel gametes. Total length (TL, cm), mass (kg), and location (area) of capture were collected at the time of capture. All individuals captured were marked with plastic external Floy tags (Floy Tag & Mfg., Inc.) using a fabric gun, as well as internal PIT (passive ntegrated transponder) tags inserted using a syringe, and identified in subsequent years using a hand-held scanner (Biomark, Inc.). Studies estimate that PIT tag retention in adult lake sturgeon (Donofrio 2007) and other sturgeon species is >95% (Clugston 1996).

Quantitative data were collected continually throughout each spawning season on environmental and biological variables of interest to explain spawning behaviors (Forsythe 2010). Water temperature was recorded hourly using Onset Hobo temperature loggers. Because the United States Geological Survey (USGS) stream flow gauging station on the UBR was removed in 2002, daily river discharge over the duration of the study was estimated using a statistical model ($F_{[1,4056]} = 9355$, $P < 0.0001$, $R^2 = 0.68$) that predicted daily average discharge based on the relationship between long-term historical (1950–2000) discharge of the UBR and discharge of the Pigeon River, a nearby stream of comparable size. Discharge data for the Pigeon and UBR rivers were obtained online from the USGS National Streamflow Information Program (http://water.usgs.gov/nsip). Daily data on the lunar phase in the form of proportion of the moon illuminated were obtained from the Astronomical Applications Department of the US Naval Observatory (http://aa.usno.navy.mil/data/docs/MoonFraction.php).

Data were summarized into the following explanatory variables to be used in statistical models: average daily water temperature, average daily river discharge, 24 h rate of change in average daily water temperature, 24 h rate of change in average daily discharge (i.e., provides both direction and magnitude), 24 h lagged water temperature, 24 h lagged discharge, and the proportion of the moon illuminated each day. Recapture histories of all individual fish were recorded, and summaries of all environmental variables were linked to daily capture data based on calendar day for each year. Because the onset and duration of spawning activity varied across years, spawning time was also quantified using standardized spawning date (SSD), defined as the day of spawning for a given year (y) divided by the total duration of spawning activity (n, in days) observed for that year. The first day of spawning site arrival each year was assigned a value of 1. Thus, SSD placed the time of spawning on the same relative 0 to 1 scale across years.

Statistical analyses

All statistical analyses were conducted using linear mixed models implemented with SAS software (version 9.1, SAS Institute Inc., Cary, North Carolina). A general or generalized implementation of linear mixed models was used to accommodate the normal or non-normal nature of each response variable, respectively. Mixed effects models are appropriate for the data structure because these models can account for repeated, thus correlated, measurements on the same individual across years and thus estimate variance components within and among individuals. These variance component estimates can then be used to compute repeatability.

Spawning periodicity

Spawning periodicity, defined as the interval between observed spawning events across years, was computed as the difference in years between consecutive captures. If an individual was captured in ≥2 years over the period from 2001 to 2008, spawning periodicity was computed as the average interval between successive captures, such that each individual was represented by only one value. Spawning periodicity was then analyzed as a function of the fixed effect of sex, the covariate TL as a measure of body size, and the interaction between sex and body size. Since body size changes little between years for older individuals (Smith and Baker 2005), TL at the first capture was used. Least square means and standard errors (SEs) were used to estimate spawning periodicity for male and female lake sturgeon as a function of body size.

Spawning repeatability

Repeatability was used to evaluate environmental covariates and the degree of consistency in lake sturgeon timing (SSD) and location (area) of spawning. Repeatability estimates are frequently used to describe the extent to which behaviors remain consistent over multiple measurements (e.g., Boake 1989; Farrell et al. 2009). Repeatability (r) can be defined as the ratio of among-individual variance to the total variance for a given trait and was estimated as

$$(1) \qquad \widehat{r} = \frac{\widehat{\sigma}_u^2}{\widehat{\sigma}_u^2 + \widehat{\sigma}_e^2}$$

where $\widehat{r}$ is the estimated repeatability, $\widehat{\sigma}_u^2$ is the estimated variance among individuals, and $\widehat{\sigma}_e^2$ is the estimated variance within individuals (Lessells and Boag 1987). Note that if there was no variation between multiple observations collected on the same individual ($\sigma_e^2 = 0$), then $\widehat{r} = 1$. In contrast, if all individuals had identical mean responses, no variation would be present among individuals ($\sigma_u^2 = 0$), and all variation would be associated with repeated observations collected on the same individual (i.e., $\widehat{r} = 0$).

To compute repeatability, we estimated σ_u^2 and σ_e^2 for dependent environmental variables, timing of reproduction (i.e., calendar day and SSD), and spawning site location. Linear mixed models were fitted separately for females and males, and thus no statistical comparisons between sexes are provided. All variance components were estimated using restricted maximum likelihood in the context of a sex-specific linear model that included an overall intercept. All models included the random effect of individual to account for correlation between repeated observations on the same individual and to estimate the random variation among individuals (i.e., σ_u^2). Sex-specific, among- and within-individual variance estimates, as computed using SAS (version 9.2, SAS Institute Inc., Cary, North Carolina) under the models described, were then used to calculate repeatability as per eq. 1.

We were also interested in changes in repeatability of responses as a function of increasing age. Body length is predictive of age in lake sturgeon despite slow growth rates (Baker and Borgeson 1999; Bruch et al. 2009) and was used as a proxy for age. We used quantiles to define three categories of body length for females and males separately. The definition of categories based on quantiles was intended to yield a similar number of observations per category. Female categories for this analysis included individuals that were (f1) 142–164 cm (28–42 years; $n = 24$), (f2) 166–174 cm (43–48 years; $n = 24$), and (f3) 175–189 cm (49–57 years; $n = 22$) TL, while male categories included individuals that were (m1) 112–140 cm (15–25 years; $n = 77$), (m2) 141–152 cm (26–30 years; $n = 76$), and (m3) 153–179 cm (35–52 years; $n = 79$) TL. Likelihood ratio tests were used to compare fit between models with homogeneous versus heterogeneous residual (within-individual) and random (among-individuals) variance components as a function of body size (i.e., variance components are provided separately for each length category). A p value < 0.05 on a likelihood ratio test is considered evidence for improved model fit with heterogeneous variances, thereby providing significant evidence to support size-based differences in repeatability. For each response of interest, estimates of within- and among-individual variance components were used to calculate sex-specific repeatability for the gth size category (g = f1, f2, f3, m1, m2, m3), as described in the previous paragraph, such that:

$$(2) \qquad \widehat{r}_g = \frac{\widehat{\sigma}^2_{u,g}}{\widehat{\sigma}^2_{u,g} + \widehat{\sigma}^2_{e,g}}$$

where $\widehat{\sigma}^2_u$ is the estimated variance among individuals in length category g, and $\widehat{\sigma}^2_e$ is the estimated variance within individuals in length category g.

Spawning area selection

Temporal patterns in the use of different river areas for spawning were modeled using a generalized linear mixed model (GLIMMIX procedure, SAS version 9.2, SAS Institute Inc., Cary, North Carolina) that used the logit link function to fit the fixed effect of SSD to spawning area of capture (multinomial categorical response; see Agresti 2007). No random factors were included in the model. The response of interest (area of capture) included six categorical levels (stream areas; Fig. 1). Odds ratio estimates resulting from this model are interpreted as the odds of a spawning event occurring in the focal area relative to such odds at a reference area. The spawning area furthest upstream (Area 1; Fig. 1) was used as a reference, based on empirical observations that spawning groups appeared to utilize spawning areas further downstream as the season progressed (Forsythe 2010). An odds ratio of 1 indicates that spawning is equally likely to occur in both the area of observed spawning and reference area for a given SSD. An odds ratio greater (or smaller) than 1 indicate that spawning events are more (or less, respectively) likely to occur in the observed area relative to the reference area. Inference was based on 95% confidence intervals (CIs) on odds ratios and whether these intervals included the null value of 1.

Variation in size of spawning adults arriving through the season

To determine whether body size differed between early and late spawners, a linear mixed model was fitted to the response variable TL (dependent variable) at each capture. This model included the fixed effects of sex, SSD, and their interaction. The random effects of year and individual were also included in the model to account for variation among years and for repeated measurements on each individual across years.

Results

A total of 1260 captures of 678 adult lake sturgeon were made over 8 consecutive spawning seasons (2001–2008). This represented 70% of the estimated 966 adults (916–1044; 95% CI; E.A. Baker, unpublished data) in the population. Most individuals were captured in multiple years. Between 100 and 234 adult lake sturgeon were observed spawning in the UBR each year. Duration of spawning activity (range 19 to 43 days; Fig. 2) varied among years. Moreover, spawning activity was not continuous. Rather, distinct groups of males and females were observed arriving, spawning, and departing from spawning areas (Fig. 2). The number of spawning groups and the duration of intervals between consecutive spawning groups also varied among years.

Spawning periodicity

Of the 678 adults captured between 2001 and 2008, 69 females (26% of total females captured) and 232 males (57% of total males captured) were observed spawning during at least 2 of the 8 years surveyed (Fig. 3). Among recaptured individuals, spawning interval was significantly longer for recaptured females (3.7 ± 0.16 years, estimated least square mean ± SE) compared with recaptured males (2.3 ± 0.08 years) ($F_{[1,299]} = 49.5$, $P < 0.001$). The intervals between spawning observations for an individual ranged from 1 to 7 years for males and from 2 to 7 years for females (Fig. 4). There was no statistical evidence for an overall association between spawning interval and TL ($F_{[1,299]} = 0.04$, $P = 0.84$). Moreover, there was no evidence for an interaction between sex and the covariate body size on interspawning interval, thereby indicating no significant difference between sexes in the rate of change of the response ($F_{[1,299]} = 1.23$, $P = 0.15$).

Repeatability in spawning

Repeatability estimates for spawning time were comparable in magnitude for day of calendar year and SSD (data not shown). Since SSD better facilitates comparisons among years, only results for SSD are provided. Variables with the highest repeatability estimates were comparable for both sexes and included SSD, river area, fraction of lunar illumination, and average river temperature (Table 1). Repeatability of SSD was high for males and females (0.56 and 0.42) despite the large interannual variation in the duration of spawning (Fig. 2). Thus, spawning time (SSD) for individual males and females could be estimated with a high degree of certainty (Fig. 5). Based on a likelihood ratio test, there was no

Fig. 2. Number of male (grey bars) and female (black bars) lake sturgeon captured upon arrival to spawning areas during each year for each day of the season over 8 consecutive years (2001–2008) in the Upper Black River, Michigan. Day 1 is the first day of spawning activity for each year.

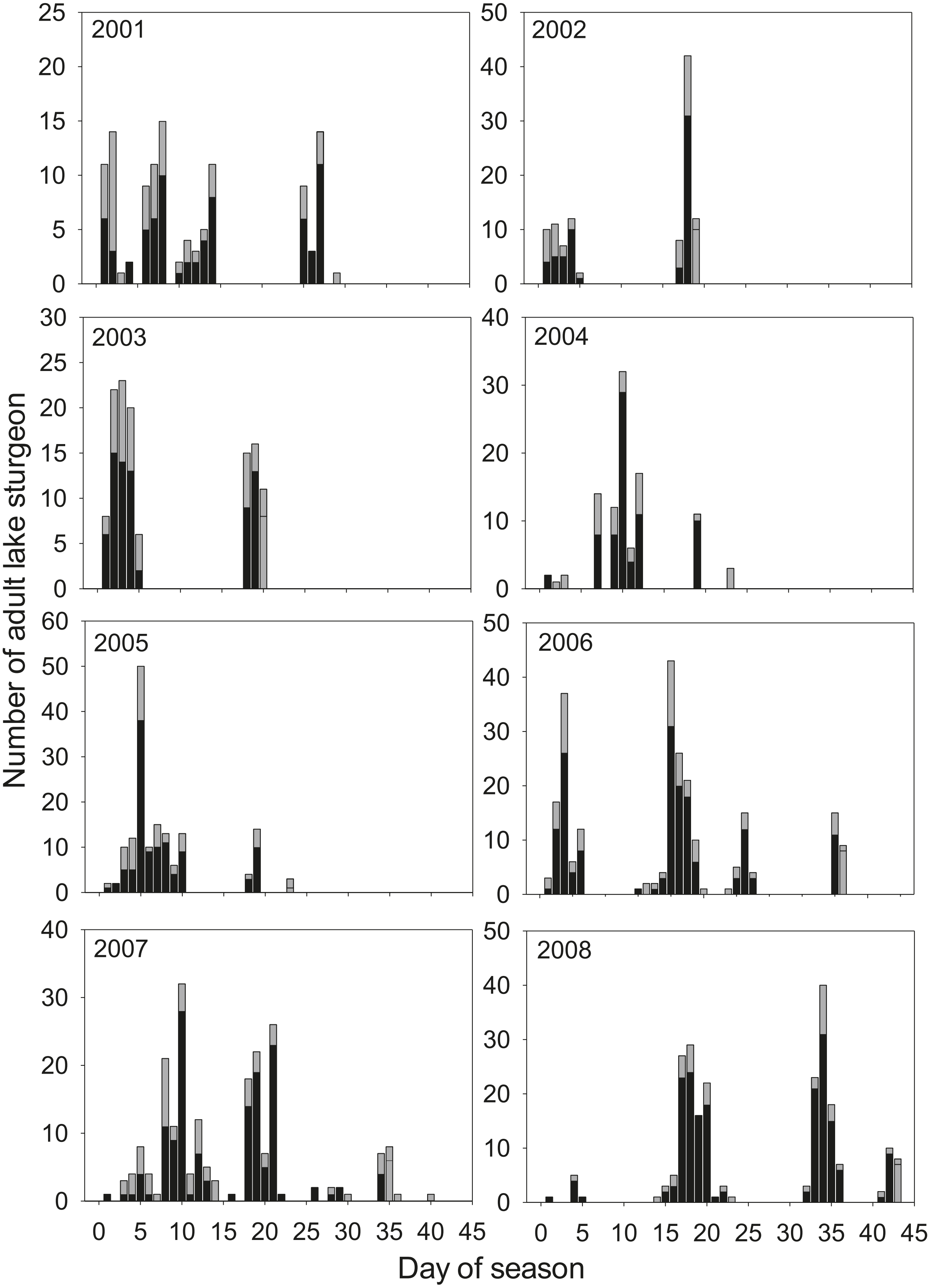
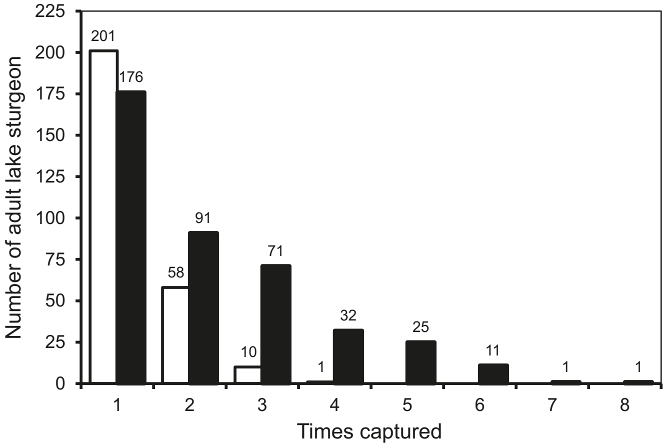


Fig. 3. Frequency distribution of capture and recapture events ($N = 1260$) for male (black bars; $N = 408$ individuals) and female (open bars; $N = 270$ individuals) lake sturgeon collected arriving to spawning locations over 8 consecutive years (2001–2008) in the Upper Black River, Michigan.



evidence for differences in repeatability between sex-specific size categories for most variables. In contrast, for discharge variables, statistical comparison of model fit supported heterogeneity of variances, and thus heterogeneous repeatability, among sex-specific size categories (Table 1).

Repeatability in spawning area selection

A significant association was identified between area of spawning and SSD for both male and female lake sturgeon, indicating that individuals were significantly more likely to spawn in progressively downstream areas as the spawning season progressed. Specifically, the odds of spawning in downstream areas, relative to Area 1, were estimated to increase by an overall factor of 9.7 (Area 3), 40.2 (Area 4), 90.9 (Area 5), and 31.7 (Area 6) for every 0.1 increase in standardized spawning day ($P < 0.001$ for each area; Fig. 6). No evidence for differences was apparent between Areas 1 and 2 ($F_{[1,1247]} = 1.82$; $P = 0.07$). The choice of different areas (1 or 2) as the reference upstream location did not affect these conclusions (data not shown).

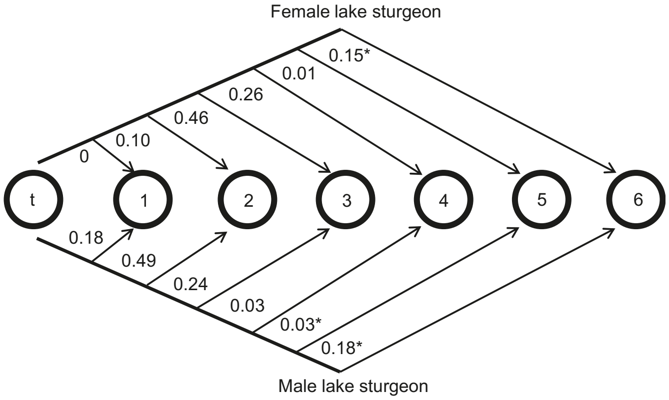
Variation in size of spawning adults arriving through the season

A significant association was also found between TL and SSD ($F_{[1,569]} = 9.02$, $P = 0.0028$), indicating larger (i.e., positive slope; 2.7 ± 1.2 cm (SE) increase per day) and presumably older individuals arriving at spawning areas as the season progressed. The interaction between SSD and sex was nonsignificant ($F_{[1,569]} = 2.84$; $P = 0.092$).

Discussion

Individual-based analyses that included data from a large proportion of the adult lake stugeon population in Black Lake revealed that variation in spawning periodicity (i.e., interannual duration between spawning events) was small, was shorter for males than for females, and was unrelated to age. We also showed that intraannual individual reproductive behaviors, such as relative spawning time within a season (i.e., early vs. late) and locations selected for breeding over 1.5 km (upstream vs. downstream), were consistent from spawn to spawn. Analyses indicated that repeatability of spawning in terms of water temperature, river discharge, and the lunar cycle was comparably lower.

Fig. 4. Estimated probabilities of female (top) and male (bottom) lake sturgeon returning to spawn in the Upper Black River, Michigan, during year $t + x$, given that spawning has occurred in year t. For example, there is an 18% chance that a male spawning in year t will spawn in year $t + 1$. Asterisks indicate upwardly biased probability estimates due to individuals likely missed between captures.



Spawning periodicity

Individual-specific estimates of spawning periodicity are not commonly available for long-lived, iteroparous fish species. Interannual spawning intervals have been reported to vary with environmental cues that influence the physiological condition of individuals and rates of gonad maturation (Doroshov et al. 1997; Taylor 1986). Small variation in estimated spawning periodicity suggests that the frequency of reproduction in this population of lake sturgeon is unaffected by interannual variation in environmental conditions that individuals experience during nonspawning periods. This result may be specific to the Black Lake system (~3500 ha), where year-to-year variation in environmental conditions may be small in comparison with other larger systems (i.e., the Laurentian Great Lakes). However, our estimates of spawning interval for UBR lake sturgeon (2–4 years) are comparable with those reported for other lake sturgeon populations inhabiting more expansive and potentially heterogeneous areas (Roussow 1957; Magnin 1966; Bruch et al. 2009). Our estimates are also consistent with other sturgeon species, including green (*Acipenser medirostris*) (2–4 years; Erickson and Webb 2007), white (*Acipenser transmontanus*) (3–5 years; Paragamian et al. 2005), and Atlantic sturgeon (*Acipenser oxyrinchus*) (3 years; Caron et al. 2002), which have different life histories and utilize large areas of open ocean during nonspawning periods. Thus, estimates of spawning periodicity may be generalizable to other locales and sturgeon species.

Because fecundity generally increases linearly with body mass in fishes (Gross et al. 2002), and energetic allocation to reproduction is substantially greater for larger individuals, we predicted that spawning intervals would increase with increasing age or size. In contrast, we found no evidence for an association between spawning periodicity and individual size.

Table 1. Estimated repeatability (range: 0–1) for standardized spawning day, river area (see Fig. 1), and environmental stream variables in female and male lake sturgeon of the Upper Black River, Michigan.

	Size class (cm)							
	Female				Male			
Variable	Total	142–164	166–174	175–189	Total	112–140	141–152	153–179
Standardized spawning day	0.56	—	—	—	0.42	—	—	—
River area	0.16	—	—	—	0.14	—	—	—
Lunar illumination	0.15	—	—	—	0.04	—	—	—
Lagged water temp.	0.13	—	—	—	0.02	—	—	—
Average water temp.	0.12	—	—	—	0.00	—	—	—
Temp. change	0.00	—	—	—	0.00	—	—	—
Average discharge	—	0.01	0.05	0.01	—	0.02	0.01	0.01
Lagged discharge	—	0.00	0.08	0.00	—	0.00	0.01	0.00
Discharge change	—	0.04	0.00	0.00	—	0.04	0.00	0.00

Note: Variables are rank ordered by the magnitude of repeatability estimates. Repeatability estimates are presented as overall means or on a size- or age-group basis, depending upon statistical evidence of heterogeneous variances for body size as per a likelihood ratio test (see Materials and methods: Spawning repeatability).

Fig. 5. Predicted standardized spawning day (±1 SE) for recaptured (*a*) female ($N = 70$) and (*b*) male ($N = 232$) lake sturgeon captured on more than two occasions during 8 consecutive years (2001–2008). Individuals are presented in rank order by predicted standardized spawning day.

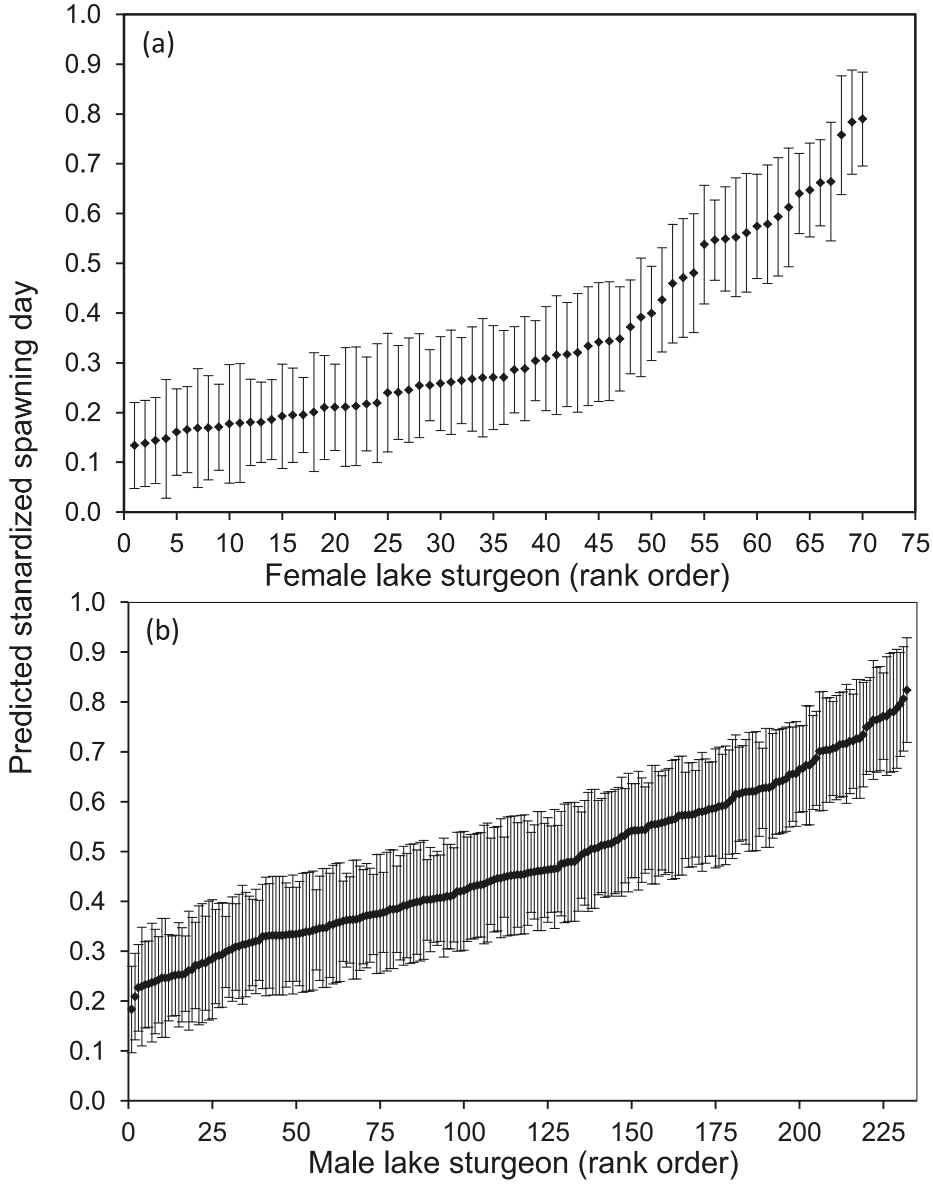
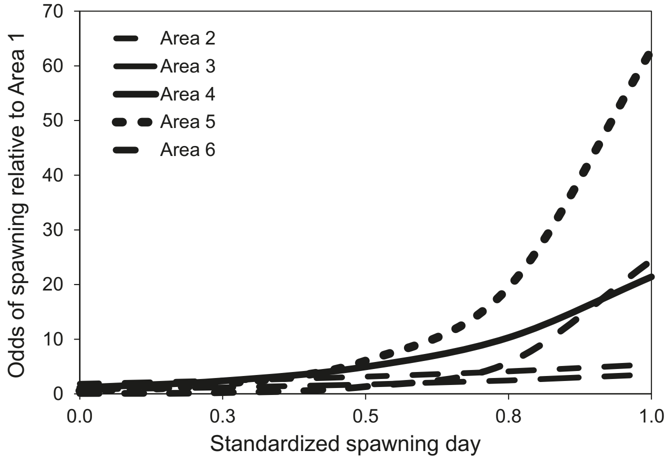


Fig. 6. Estimated odds of lake sturgeon spawning in river Areas 2 to 6 (relative to upstream-most Area 1) in the Upper Black River, Michigan (Area 1) as a function of standardized spawning day.



Given that reproductive frequency (interspawning interval) is tied to lifetime reproductive success in long-lived species (Stearns 1992) and should be under selection, lack of a positive association between interspawning interval and age or size could be due to the fact that the Black Lake lake sturgeon have been harvested extensively and have a young age structure (Baker and Borgeson 1999).

Interspawning interval was significantly shorter for male than for female lake sturgeon. Differences in the reproductive frequency between sexes are likely determined by resource allocation that dictates predictably longer egg than sperm development times (Stearns 1992; Bruch et al. 2001). However, 13% of females were recaptured spawning within 2 years of their previous spawning, suggesting the time required to accumulate and allocate energy to reproduction may not be a constraint on spawning time for at least some individuals in this population. Further information regarding reproductive effort during each year would be needed to evaluate alternative explanations for interindividual variation in female reproductive frequency.

Differences in spawning periodicity between males and females are important in lake sturgeon and other long-lived iteroparous species, particularly in situations of low adult population size and polygamous mating systems (Sugg et al. 1996). Spawning asynchrony between males and females will lower probabilities of encountering and mating with the same or potentially related individuals over multiple reproductive episodes. Shorter interspawning intervals for males result in male-biased operational sex ratios each year (Duong 2010; Forsythe 2010). For broadcast-spawning species, male-biased sex ratios can be important to increase fertilization rates and reproductive success (Emlen and Oring 1977; Levitan and Petersen 1995).

Repeatability of spawning

Spawning time is affected by physiological, environmental, and genetic factors in migratory fish (Rogers et al. 2006; Cushing 1990). In the UBR, lake sturgeon spawn over 23 days per year on average, with peaks of spawning activity occurring in association with phases of the lunar cycle (i.e., full or new moon), increasing water temperature, and declining river discharge (Forsythe 2010). Lunar cycles have been implicated in endocrine activity (Takemura et al. 2004). Spawning during new or crescent phases of the lunar cycle may also facilitate larval dispersal from spawning sites during periods of greater darkness, thereby reducing risk of predation from visual predators. Hernandez-Leon (2008) further suggested that lunar-cued spawning activity that exposes larvae to conditions of reduced visibility (i.e., dark moon phases) or increased probabilities of encountering food at the onset of exogenous feeding (i.e., light moon phases) affects recruitment in other fish species.

Several factors should be considered when interpreting the data. Although observations were made based on captures and recaptures of approximately 70% of the estimated adult population in Black Lake, our measurements of repeatability were dominated by observations from consecutive spawning episodes over a relatively short period of time. Thus, there may be temporal autocorrelation in environmental variables that would not be evident over an individual's lifetime. However, estimates of SE for predicted SSD for individuals captured twice were not different from SE estimated from individuals captured more than two times (data not shown). Our observations were also made from a single population, and our findings may differ in other systems. However, considerable similarities and synchrony in spawning chronology of other Great Lakes tributaries with the UBR can be found (Elliott and Gunderman 2008), and intra-annual variability, as evidenced by multiple spawning groups within year, has been documented (Auer and Baker 2002). Further, our quantitative results at the individual-level support reports of population-level variation documented in earlier studies (Auer 1996; Bruch and Binkowski 2002; Paragamian and Kruse 2001). Whether repeatability would be this stereotyped in larger systems, where the window of opportunity to reproduce for individuals may be considerably larger, remains an important future avenue of research.

Our results, showing the occurrence of multiple and temporally segregated breeding groups and high repeatability of spawning date, also suggest the intriguing possibility that early and late spawning groups of adults may be reproductively isolated by time (Hendry and Day 2005). The tendencies for adults to spawn at specific times as a function of different environmental characteristics can promote divergence in phenotypic, physiological, or life history traits of offspring (Woody et al. 2000; Hendry and Day 2005; Stillwell and Fox 2005). For example, individuals that spawn consistently at the same time within a season may have similar gonad maturation schedules entrained by time-related environmental cues, such as photoperiod. Photoperiod has been shown to be a important cue for lake sturgeon to enter the UBR (Forsythe 2010) and to affect the timing of reproduction for other temperate fishes (Doroshov et al. 1997; Taranger et al. 1998; review by Migaud et al. 2010). These patterns, along with evidence for the covariation of early life traits with environmental conditions (Crossman 2008), suggest that subpopulation differentiation may have developed among different spawning groups. However, high repeatability for spawning time (SSD) and spawning location may also indicate future challenges for numerically depressed iteroparous species. If early and late spawning segments represent reproductively isolated subpopulations, assortative mating as a function of repeatable timing of reproduction will decrease the effective breeding population size (Frankham 1995).

Repeatability in spawning area selection

Spawning site selection can contribute greatly to variation in inter- and intra-annual reproductive success of migratory fish (e.g., Bernier-Bourgault and Magnan 2002). Our observations indicated that the UBR has numerous suitable spawning areas throughout a 1.5 km section. Despite the close proximity of spawning areas in the UBR, adults arriving earlier in the season were more likely to select locations further upstream (Areas 1–3) relative to individuals arriving later (Areas 3–6) . This trend was consistently observed across years despite inter- and intra-annual variation in temperature and stream hydrogeomorphology in the UBR (Forsythe 2010). Similar seasonal patterns have been noted in other migratory fish (e.g., Orians and Wittenberger 1991; Doctor and Quinn 2009). Studies have implicated behavioral traits allowing individuals to select certain environmental features (reviewed in Olson et al. 1978; Kieffer and Colgan 1992), including mate copying, homing, genetics (Hansen and Jonsson 1991), or olfaction (Quinn et al. 1999, 2006), all of which can return individuals consistently to areas differing in intrinsic physical properties within natal streams.

Data showing early and late spawning adults consistently using different spawning areas, despite their proximity, suggest temporal variation in habitat quality within a spawning season. Alternatively, early and late spawning individuals may differ in their responses to environmental cues. This difference in spawning area selection may also reflect differences in the physiological, hormonal condition, or age–size of individuals at the time of arrival to spawning areas (Crossin et al. 2008). Late arriving females, for example, may be in the final stages of gonad maturation and thus spawn in the first suitable (i.e., downstream) location encountered relative to females with the predisposition to arrive early and with more time to select spawning areas. Alternatively, relatively high estimates of repeatability for spawning area (especially for females) may suggest a degree of homing, genetic effects, or selection for hydro- and geomorphological cues that vary consistently across a spawning season and among locations.

Age-specific variation in reproductive behavior

Age- and sex-dependent reproductive behaviors have been reported for many species, including migratory fish (e.g., Dickerson et al. 2002; Paitz et al. 2007; Niemelä et al. 2006). Because lake sturgeon are long-lived and individuals have opportunities to breed multiple times, repeatability could increase as a function of reproductive experience (i.e., learning), (e.g., *Cyanistes caeruleus*; Grieco et al. 2002). Although repeatability associated with some environmental variables (e.g., river discharge) varied among age classes, we found no statistical evidence that repeatability for SSD or for environmental conditions changed over size categories that are generally related to increasing age. Lower repeatability in male spawning time may be a reflection of sex-based alternative reproductive strategies or greater flexibility in reproduction among males (Bateman 1948; Shuster and Wade 2003), whereby males may modify where and when they spawn to increase mate number based on the timing of spawning and locations used by females.

Broader implications

Sturgeons have complex life histories that provide opportunities to document environmental effects on reproductive activities at the individual and population levels over multiple temporal and spatial scales. However, these long-lived fishes are among the least-studied fishes in North America. Most species are also declining world-wide because of anthropogenic influences. These influences modify spawning habitats, which decouple associations between the timing of reproduction and environmental conditions and can be tied to offspring survival (Pörtner and Farrell 2008).

Studies that have attempted to document the degree of spatial and temporal segregation of breeding groups at comparatively small scales have been hampered by a lack of long-term data (Doctor and Quinn 2009). Based on our 8-year time series (Forsythe 2010; Duong 2010; data presented here), we suggest that for lake sturgeon, and potentially populations of other long-lived iteroparous fish species, environmental conditions during spawning events at certain times and locations within a spawning season may be more predictive of recruitment at the population level than population demographic composition (i.e., the number of spawning adults utilizing these locations). High repeatability for spawning time, and findings showing that temperature and discharge are important cues that individuals responded to repeatedly across reproductive episodes (Forsythe 2010), can be used to guide management decisions associated with dam operations and to predict timing and location of spawning in response to natural inter- and intra-annual environmental variation.

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References

Agresti, A. 2007. An introduction to categorical data analysis. John Wiley and Sons, Inc., Hoboken, N.J.

Auer, N.A. 1996. Response of spawning lake sturgeon to change in hydroelectric facility operation. Trans. Am. Fish. Soc. **125**(1): 66–77. doi:10.1577/1548-8659(1996)125<0066:ROSLST>2.3.CO;2.

Auer, N.A., and Baker, E.A. 2002. Duration and drift of larval lake sturgeon in the Sturgeon River, Michigan. J. Appl. Ichthyology, **18**(4–6): 557–564. doi:10.1046/j.1439-0426.2002.00393.x.

Bailey, K.M., and Houde, E.D. 1989. Predation on eggs and larvae of marine fishes and the recruitment problem. Adv. Mar. Biol. **25**: 1–83. doi:10.1016/S0065-2881(08)60187-X.

Baker, E.A., and Borgeson, D.J. 1999. Lake sturgeon abundance and harvest in Black Lake, Michigan, 1975–1999. N. Am. J. Fish. Manage. **19**(4): 1080–1088. doi:10.1577/1548-8675(1999)019<1080:LSAAHI>2.0.CO;2.

Bateman, A.J. 1948. Intra-sexual selection in *Drosophila*. Heredity, **2**(3): 349–368. doi:10.1038/hdy.1948.21. PMID:18103134.

Beall, E., and de Gaudemar, B. 1999. Plasticity of reproductive behaviour in Atlantic salmon *Salmo salar* Salmonidae in relation to environmental factors. Cybium, **23**(1): 9–28.

Berkeley, S.A., Chapman, C., and Sogard, S.M. 2004. Maternal age as a determinant of larval growth and survival in a marine fish, *Sabastes melanops*. Ecology, **85**(5): 1258–1264. doi:10.1890/03-0706.

Bernier-Bourgault, I., and Magnan, P. 2002. Factors affecting redd site selection, hatching, and emergence of brook charr, *Salvelinus fontinalis*, in an artificially enhanced site. Environ. Biol. Fishes, **64**(1–3): 333–341. doi:10.1023/A:1016006303854.

Birstein, V.J. 1993. Sturgeons and paddlefishes: threatened fishes in need of conservation. Conserv. Biol. **7**(4): 773–787. doi:10.1046/j.1523-1739.1993.740773.x.

Boake, C.R.B. 1989. Repeatability — its role in evolutionary studies of mating behavior. Evol. Ecol. **3**(2): 173–182. doi:10.1007/BF02270919.

Brown, C., and Laland, K.N. 2003. Social learning in fishes: a review. Fish Fish. **4**(3): 280–288.

Bruch, R.M., and Binkowski, F. 2002. Spawning behavior of lake sturgeon (*Acipenser fulvescens*). J. Appl. Ichthyology, **18**(4–6): 570–579. doi:10.1046/j.1439-0426.2002.00421.x.

Bruch, R.M., Dick, T., and Choudhury, A. 2001. A field guide for the identification of stages of gonad development in lake sturgeon, *A. fulvescens* Rafinesque, with notes on lake sturgeon reproductive biology and management implications. Publ. Wisc. Dept. Nat. Res. Oshkosh and Sturgeon For Tomorrow. Graphic Comm. Center, Inc., Appleton, Wisc.

Bruch, R.M., Campana, S.E., Davis-Foust, S.L., Hansen, M.J., and Janssen, J. 2009. Lake sturgeon age validation using bomb radiocarbon and known-age fish. Trans. Am. Fish. Soc. **138**(2): 361–372. doi:10.1577/T08-098.1.

Caron, F., Hatin, D., and Fortin, R. 2002. Biological characteristics of adult Atlantic sturgeon (*Acipenser oxyrinchus*) in the St. Lawerence River estuary and the effectiveness of management rules. J. Appl. Ichthyology, **18**(4–6): 580–585. doi:10.1046/j.1439-0426.2002.00416.x.

Carr, J.P., and Kaufman, L. 2009. Estimating the importance of maternal age, size, and spawning experience to recruitment of Atlantic cod *Gadus morhua*. Biol. Conserv. **142**(3): 477–487. doi:10.1016/j.biocon.2008.10.004.

Clugston, J.P. 1996. Retention of T-bar anchor tags and passive integrated transponders by gulf sturgeons. N. Am. J. Fish. Manage. **16**(3): 682–685. doi:10.1577/1548-8675(1996)016<0682:ROTBAT>2.3.CO;2.

Clutton-Brock, T.H. (*Editor*). 1988. Reproductive success: studies of individual variation in contrasting breeding systems. University of Chicago Press, Chicago, Ill.

Congdon, J.D., Nagle, R.D., Kinney, O.M., van Loben Sels, R.C., Quinter, T., and Tinkle, D.W. 2003. Testing hypotheses of aging in long-lived painted turtles (*Chrysemys picta*). Exp. Gerontol. **38**(7): 765–772. doi:10.1016/S0531-5565(03)00106-2. PMID:12855285.

Crossin, G.T., Hinch, S.G., Cooke, S.J., Welch, D.W., Patterson, D. A., Jones, S.R.M., Lotto, A.G., Leggatt, R.A., Mathes, M.T., Shrimpton, J.M., Van der Kraak, G., and Farrell, A.P. 2008. Exposure to high temperature influences the behaviour, physiology, and survival of sockeye salmon during spawning migration. Can. J. Zool. **86**(2): 127–140. doi:10.1139/Z07-122.

Crossman, J.A. 2008. Evaluating collection, rearing and stocking methods for Lake Sturgeon *Acipenser fulvescens* restoration programs in the Great Lakes. Ph.D. dissertation, Department of Fisheries and Wildlife, Michigan State University, East Lansing, Mich., USA.

Cushing, D.H. 1990. Plankton production and year-class strength in fish populations — an update of the match mismatch hypothesis. Adv. Mar. Biol. **26**: 249–293. doi:10.1016/S0065-2881(08)60202-3.

Dahl, J., Dannewitz, J., Karlsson, L., Petersson, E., Lof, A., and Ragnarsson, B. 2004. The timing of spawning migration: implications of environmental variation, life history, and sex. Can. J. Zool. **82**(12): 1864–1870. doi:10.1139/z04-184.

Dickerson, B.R., Quinn, T.P., and Willson, M.F. 2002. Body size, arrival date, and reproductive success of pink salmon, *Oncorhynchus gorbuscha*. Ethol. Ecol. Evol. **14**(1): 29–44. doi:10.1080/08927014.2002.9522759.

Dittman, A.H., and Quinn, T.P. 1996. Homing in pacific salmon: mechanisms and ecological basis. J. Exp. Biol. **199**(1): 83–91. PMID:9317381.

Doctor, K.K., and Quinn, T.P. 2009. Potential for adaptation-by-time in sockeye salmon (*Oncorhynchus nerka*): the interactions of body size and in-stream reproductive life span with date of arrival and breeding location. Can. J. Zool. **87**(8): 708–717. doi:10.1139/Z09-056.

Donofrio, M. 2007. Fishery report: lake sturgeon survey report — Menominee River, Wisc. Retention of T-bar anchor tags and passive integrated transponder tags by lake sturgeon in the Menominee River, WI. Wisconsin Department of Natural Resources, Peshtigo, Wisc. Correspond. Memo. File Ref. 3600.

Doroshov, S.I., Moberg, G.P., and VanEenennaam, J.P. 1997. Observations on the reproductive cycle of cultured white sturgeon, *Acipenser transmontanus*. Environ. Biol. Fishes, **48**(1/2/3/4): 265–278. doi:10.1023/A:1007336802423.

Duong, Y.T. 2010. Effects of spawning behavior and environmental factors on adult reproductive ecology and larval dispersal of Lake Sturgeon (*Acipenser fulvescens*). Ph.D. dissertation, Department of Zoology Michigan State University, East Lansing, Mich., USA.

Duong, Y.T., Scribner, K.T., Crossman, J.A., Forsythe, P.S., Baker, E. A., and Magnan, P. 2011*a*. Environmental and maternal effects on embryonic and larval developmental time until dispersal of lake sturgeon (*Acipenser fulvescens*). Can. J. Fish. Aquat. Sci. **68**(4): 643–654. doi:10.1139/f2011-008.

Duong, Y.T., Scribner, K.T., Crossman, J.A., Forsythe, P.S., Baker, E. A., Kanefsky, J., Homola, J.J., and Davis, C. 2011*b*. Relative larval loss among females during dispersal of lake sturgeon (*Acipenser fulvescens*). Environ. Biol. Fishes, **91**(4): 459–469. doi:10.1007/s10641-011-9804-4.

Elliott, R.F., and Gunderman, B.J. 2008. Assessment of remnant lake sturgeon populations in the Green Bay Basin, 2002–2006. Final Report to the Great Lakes Fishery Trust. Proj. No. 2001.113/2004.610.

Emlen, S.T., and Oring, L.W. 1977. Ecology, sexual selection, and the evolution of mating systems. Science, **197**(4300): 215–223. doi:10.1126/science.327542. PMID:327542.

Erickson, D.L., and Webb, M.A.H. 2007. Spawning periodicity, spawning migration, and size at maturity of green sturgeon, *Acipenser medirostris*, in the Rogue River, Oregon. Environ. Biol. Fishes, **79**(3–4): 255–268. doi:10.1007/s10641-006-9072-x.

Farrell, T.M., May, P.G., and Pilgrim, M.A. 2009. Repeatability of female reproductive traits in pigmy rattlesnakes (*Sistrurus miliarius*). J. Herpetol. **43**(2): 332–335. doi:10.1670/08-191R.1.

Fausch, K.D., Torgersen, C.E., Baxter, C.V., and Li, H.W. 2002. Landscapes to riverscapes: bridging the gap between research and conservation. Bioscience, **52**(6): 483–498. doi:10.1641/0006-3568(2002)052[0483:LTRBTG]2.0.CO;2.

Forsythe, P.S. 2010. Exogenous correlates of migration, spawning, egg deposition and egg mortality in the lake sturgeon (*Acipenser fulvescens*). Ph.D. dissertation, Department of Zoology Michigan State University, East Lansing, Mich.

Frankham, R. 1995. Effective population/size adult population size ratios in wildlife: a review. Genet. Res. **66**(2): 95–107. doi:10.1017/S0016672300034455. PMID:18976539.

Grieco, F., van Noordwijk, A.J., and Visser, M.E. 2002. Evidence for the effect of learning on timing of reproduction in blue tits. Science, **296**(5565): 136–138. doi:10.1126/science.1068287. PMID:11935025.

Gross, M.R., Repka, J., Robertson, C.T., Secor, D.H., and Van Winkle, W. 2002. Sturgeon conservation: insights from elasticity analysis. Am. Fish. Soc. Symp. **28**: 13–30.

Hansen, L.P., and Jonsson, B. 1991. Evidence of a genetic component in the seasonal return pattern of Atlantic salmon, *Salmo salar* L. J. Fish Biol. **38**(2): 251–258. doi:10.1111/j.1095-8649.1991.tb03111.x.

Hendry, A.P., and Day, T. 2005. Population structure attributable to reproductive time: isolation by time and adaptation by time. Mol. Ecol. **14**(4): 901–916. doi:10.1111/j.1365-294X.2005.02480.x. PMID:15773924.

Hernandez-Leon, S. 2008. Natural variability of fisheries and lunar illumination: a hypothesis. Fish Fish. **9**(2): 138–154.

Hirshfield, M.F., and Tinkle, D.W. 1975. Natural selection and the evolution of reproductive effort. Proc. Natl. Acad. Sci. U.S.A. **72**(6): 2227–2231. doi:10.1073/pnas.72.6.2227. PMID:1056027.

Hodgson, S., and Quinn, T.P. 2002. The timing of adult sockeye salmon migration into fresh water: adaptations by populations to prevailing thermal regimes. Can. J. Zool. **80**(3): 542–555. doi:10.1139/z02-030.

Jennings, M.J., Claussen, J.E., and Philipp, D.P. 1996. Evidence for heritable preferences for spawning habitat between two walleye populations. Trans. Am. Fish. Soc. **125**(6): 978–982. doi:10.1577/1548-8659(1996)125<0978:EFHPFS>2.3.CO;2.

Jørgensen, C., Dunlop, E.S., Opdal, A.F., and Fiksen, O. 2008. The evolution of spawning migrations: state dependence and fishing-induced changes. Ecology, **89**(12): 3436–3448. doi:10.1890/07-1469.1. PMID:19137949.

Kamler, E. 2002. Ontogeny of yolk-feeding fish: an ecological perspective. Rev. Fish Biol. Fish. **12**(1): 79–103. doi:10.1023/A:1022603204337.

Kempinger, J.J. 1988. Spawning and early life history of lake sturgeon in the Lake Winnebago system, Wisconsin. Am. Fish. Soc. Symp. **5**: 110–122.

Kieffer, J.D., and Colgan, P.W. 1992. The role of learning in fish behaviour. Rev. Fish Biol. Fish. **2**(2): 125–143. doi:10.1007/BF00042881.

Kindsvater, H.K., Bonsall, M.B., and Alonzo, S.H. 2011. Survival costs of reproduction predict age-dependent variation in maternal investment. J. Evol. Biol. **24**(10): 2230–2240. doi:10.1111/j.1420-9101.2011.02351.x. PMID:21745251.

Lessells, C.M., and Boag, P.T. 1987. Unrepeatable repeatabilities — a common mistake. Auk, **104**(1): 116–121.

Levitan, D.R., and Petersen, C. 1995. Sperm limitation in the sea. Trends Ecol. Evol. **10**(6): 228–231. doi:10.1016/S0169-5347(00)89071-0. PMID:21237018.

Magnin, E. 1966. Quelques données biologiques sur la reproduction des esturgeons *Acipenser fulvescens* Raf. de la Rivière Nottaway, tributaire de la Baie James. Can. J. Zool. **44**(2): 257–263. doi:10.1139/z66-024.

Malcolm, I.A., Soulsby, C., Youngson, A.F., and Tetzlaff, D. 2009. Fine scale variability of hyporheic hydrochemistry in salmon spawning gravels with contrasting groundwater-surface water interactions. Hydrogeol. J. **17**(1): 161–174. doi:10.1007/s10040-008-0339-5.

Marshall, D.J., Heppell, S.S., Munch, S.B., and Warner, R.R. 2010. The relationship between maternal phenotype and offspring quality: Do older mothers really produce the best offspring? Ecology, **91**(10): 2862–2873. doi:10.1890/09-0156.1. PMID:21058547.

Migaud, H., Davie, A., and Taylor, J.F. 2010. Current knowledge on the photoneuroendocrine regulation of reproduction in temperate fish species. J. Fish Biol. **76**(1): 27–68. doi:10.1111/j.1095-8649.2009.02500.x. PMID:20738699.

Morbey, Y.E. 2003. Pair formation, pre-spawning waiting, and protandry in kokanee, *Oncorhynchus nerka*. Behav. Ecol. Sociobiol. **54**(2): 127–135.

Mousseau, T.A., and Fox, C.A. 1998. Maternal effects as adaptations. Oxford University Press, New York.

Niemelä, E., Orell, P., Erkinaro, J., Dempson, J.B., Brørs, S., Svenning, M.A., and Hassinen, E. 2006. Previously spawned Atlantic salmon ascend a large subarctic river earlier than their maiden counterparts. J. Fish Biol. **69**(4): 1151–1163. doi:10.1111/j.1095-8649.2006.01190.x.

Olson, D.E., Shupp, D.H., and Macins, V. 1978. A hypothesis of homing behavior of walleyes as related to observed food patterns of passive and active movement. Am. Fish. Soc. **11**: 52–57. [Special publication.]

Orians, G.H., and Wittenberger, J.F. 1991. Spatial and temporal scales in habitat selection. Am. Nat. **137**(Suppl. 1): S29–S49. doi:10.1086/285138.

Paitz, R.T., Harms, H.K., Bowden, R.M., and Janzen, F.J. 2007. Experience pays: offspring survival increases with female age. Biol. Lett. **3**(1): 44–46. doi:10.1098/rsbl.2006.0573. PMID:17443962.

Pankhurst, N.W., and King, H.R. 2010. Temperature and salmonid reproduction: implications for aquaculture. J. Fish Biol. **76**(1): 69–85. doi:10.1111/j.1095-8649.2009.02484.x. PMID:20738700.

Paragamian, V.L., and Kruse, G.O. 2001. Kootenai River White Sturgeon spawning migration behavior and a predictive model. N. Am. J. Fish. Manage. **21**(1): 10–21. doi:10.1577/1548-8675(2001)021<0010:KRWSSM>2.0.CO;2.

Paragamian, V.L., Beamesderfer, R.C.P., and Ireland, S.C. 2005. Status, population dynamics, and future prospects of the endangered kootenai river white sturgeon population with and without hatchery intervention. Trans. Am. Fish. Soc. **134**(2): 518–532. doi:10.1577/T03-011.1.

Pepin, P., Orr, S.C., and Anderson, J.T. 1997. Time to hatch and larval size in relation to temperature and egg size in Atlantic cod (*Gadus morhua*). Can. J. Fish. Aquat. Sci. **54**(S1): 2–10. doi:10.1139/f96-154.

Peterson, D.L., Vecsei, P., and Jennings, C.A. 2007. Ecology and biology of the lake sturgeon: a synthesis of current knowledge of a threatened North American Acipenseridae. Rev. Fish Biol. Fish. **17**(1): 59–76. doi:10.1007/s11160-006-9018-6.

Pörtner, H.O., and Farrell, A.P. 2008. Physiology and climate change. Science, **322**(5902): 690–692. doi:10.1126/science.1163156. PMID:18974339.

Quinn, T.P., Volk, E.C., and Hendry, A.P. 1999. Natural otolith microstructure patterns reveal precise homing to natal incubation sites by sockeye salmon (*Oncorhynchus nerka*). Can. J. Zool. **77**(5): 766–775. doi:10.1139/z99-028.

Quinn, T.P., Unwin, M.J., and Kinnison, M.T. 2000. Evolution of temporal isolation in the wild: genetic divergence in timing of migration and breeding by introduced chinook salmon populations. Evolution, **54**(4): 1372–1385. PMID:11005303.

Quinn, T.P., Stewart, E.L., and Boatright, C.P. 2006. Experimental evidence of homing to site of incubation by mature sockeye salmon, *Oncorhynchus nerka*. Anim. Behav. **72**(4): 941–949. doi:10.1016/j.anbehav.2006.03.003.

Rochard, E., Castelnaud, G., and Lepage, M. 1990. Sturgeons (Pices, Acipenseridae) — threats and prospects. J. Fish Biol. **37**: 123–132. doi:10.1111/j.1095-8649.1990.tb05028.x.

Rogers, M.W., Allen, M.S., and Porak, W.F. 2006. Separating genetic and environmental influences on temporal spawning distributions of largemouth bass (*Micropterus salmoides*). Can. J. Fish. Aquat. Sci. **63**(11): 2391–2399. doi:10.1139/f06-122.

Roussow, G. 1957. Some considerations concerning sturgeon spawning periodicity. J. Fish. Res. Board Can. **14**(4): 553–572. doi:10.1139/f57-016.

Schlichting, C.D., and Pigliucci, M. 1998. Phenotypic evolution: a reaction-norm perspective. Sinauer Associates, Inc., Sunderland, Mass.

Shuster, S.M., and Wade, M.J. 2003. Mating systems and strategies. Princeton University Press, Princeton, N.J.

Smith, K.M., and Baker, E.A. 2005. Characteristics of spawning lake sturgeon in the Upper Black River, Michigan. N. Am. J. Fish. Manage. **25**(1): 301–307. doi:10.1577/M03-229.1.

Smith, S.J., and Marsden, J.E. 2009. Factors affecting sea lamprey egg survival. N. Am. J. Fish. Manage. **29**(4): 859–868. doi:10.1577/M07-196.1.

Stearns, S.C. 1992. The evolution of life histories. Oxford University Press, Oxford, UK.

Stewart, D.C., Smith, G.W., and Youngson, A.F. 2002. Tributary-specific variation in timing of return of adult Atlantic salmon (*Salmo salar*) to fresh water has a genetic component. Can. J. Fish. Aquat. Sci. **59**(2): 276–281. doi:10.1139/f02-011.

Stillwell, R.C., and Fox, C.W. 2005. Complex patterns of phenotypic plasticity: interactive effects of temperature during rearing and oviposition. Ecology, **86**(4): 924–934. doi:10.1890/04-0547.

Sugg, D.W., Chesser, R.K., Dobson, F.W., and Hoogland, J.L. 1996. Population genetics meets behavioral ecology. Trends Ecol. Evol. **11**(8): 338–342. doi:10.1016/0169-5347(96)20050-3. PMID: 21237872.

Takemura, A., Rahman, S., Makamura, S., Park, Y.J., and Takano, K. 2004. Lunar cycles and reproductive activity in reef fishes with particular attention to rabbitfishes. Fish Fish. **5**: 317–328.

Taranger, G.L., Haux, C., Stefansson, S.O., Bjornsson, B.T., Walther, B.T., and Hansen, T. 1998. Abrupt changes in photoperiod affect age at maturity, timing of ovulation and plasma testosterone and oestradiol-17 beta profiles in Atlantic salmon, *Salmo salar*. Aquaculture, **162**(1–2): 85–98. doi:10.1016/S0044-8486(98)00168-9.

Taylor, M.H. 1986. Environmental and endocrine influences on reproduction of *Fundulus heteroclitus*. Am. Zool. **26**(1): 159–171.

Trépanier, S., Rodriguez, M.A., and Magnan, P. 1996. Spawning migrations in landlocked Atlantic salmon: time series modeling of river discharge and water temperature effects. J. Fish Biol. **48**(5): 925–936. doi:10.1111/j.1095-8649.1996.tb01487.x.

Trippel, E.A., Kjesbu, O.S., and Solemial, P. 1997. Effects of adult age and size structure on reproductive output of marine fishes. *In* Early life history and recruitment in fish populations. *Edited by* R. C. Chambers and E.A. Trippel. Chapman & Hall, London, UK. pp. 31–62.

van Noordwijk, A.J., and de Jong, G. 1986. Acquisition and allocation of resources: their influence on variation in life history tactics. Am. Nat. **128**(1): 137–142. doi:10.1086/284547.

Wilbur, H.M. 1975. The evolutionary and mathematical demography of the turtle *Chrysemys picta*. Ecology, **56**(1): 64–77. doi:10.2307/1935300.

Williams, B.K., and Nichols, J.D. 1984. Optimal timing in biological processes. Am. Nat. **123**(1): 1–19. doi:10.1086/284182.

Woody, C.A., Olsen, J., Reynolds, J., and Bentzen, P. 2000. Temporal variation in phenotypic and genotypic traits in two sockeye salmon populations, Tustumena Lake, Alaska. Trans. Am. Fish. Soc. **129**(4): 1031–1043. doi:10.1577/1548-8659(2000)129<1031:TVIPAG>2.3.CO;2.

Wright, P.J., and Trippel, E.A. 2009. Fishery-induced demographic changes in the timing of spawning: consequences for reproductive success. Fish Fish. **10**: 283–304.