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Environmental and lunar cues are predictive of the timing of river entry and spawning-site arrival in lake sturgeon *Acipenser fulvescens*

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The associations were quantified between daily and interannual variation in the timing of a closed population of lake sturgeon *Acipenser fulvescens* migration and arrival at spawning sites with stream environmental and lunar covariates. Spawning data were gathered from 1262 fish in Black Lake, Michigan 2001 to 2008 and by video monitoring 2000 to 2002. Sex-specific variation in responses to external cues was also tested. Results showed that a greater number of individuals initiated migration from lake to riverine habitats at dawn and dusk relative to other times of the day. Current and lagged effects of water temperature and river discharge, and periods in the lunar cycle were important variables in models quantifying movements into the river and timing of adult arrival at spawning sites. Different suites of covariates were predictive of *A. fulverscens* responses during different periods of the spawning season. The timing of initiation of migration and spawning, and the importance of covariates to the timing of these events, did not differ between sexes. Stream flow and temperature covaried with other variables including day length and the lunar cycle. Anthropogenic disruption of relationships among variables may mean that environmental cues may no longer reliably convey information for Acipenseriformes and other migratory fishes.

Key words: Great Lakes; lagged effects; lunar cycle; migration; photoperiod; reproduction.

INTRODUCTION

Initiation of spawning migrations into streams and the timing of reproduction in fishes represent important behavioural decisions that are elicited by external cues such as seasonal photoperiod (Quinn & Adams, 1996; Bizzotto *et al.*, 2009) and other environmental variables (Kamler, 2002). There is strong selection for adults

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to reproduce at times and in locations that are conducive to offspring survival. As such, at the population level, onset of migration including the timing of sequential events such as river entry and spawning are often predictable across years (Hodgson & Quinn, 2002). The timing of reproductive activities for individual fishes can also be repeatable among years (Forsythe, 2010; Forsythe *et al.*, 2012) as seen for other migratory animals (Bety *et al.*, 2004).

Timing reproduction in response to environmental cues also increases the likelihood that offspring with specific developmental requirements are placed in environments suitable for growth and survival (Hendry *et al.*, 1998; Einum & Fleming, 2000). Migrating at favourable times can also reduce mortality *en route* and can conserve energy needed to compete for mates and quality breeding locations that enhance reproductive success (Hinch & Rand, 1998; Crossin *et al.*, 2003; Cooke *et al.*, 2004). Examples of external variables associated with onset of migration and spawning activity include tidal height (Karppinen *et al.*, 2004), river discharge (Keefer *et al.*, 2009), turbidity (Rakowitz *et al.*, 2008), river water temperature (Workman *et al.*, 2002), period of the lunar cycle (Kuparinen *et al.*, 2009) and demographic composition including relative abundance of conspecifics and sex ratio (Couzin *et al.*, 2005; Kiflawi & Mazeroll, 2006).

Migratory behaviours have been well studied in fishes such as salmonids. The behaviours exhibited during different stages of migration such as the onset of river entry, upstream movement and the initiation of reproduction in relation to external cues, however, are not probably concordant among species, or populations within species (Quinn & Adams, 1996; Dahl *et al.*, 2004). Individuals may also exhibit considerable plasticity in reproductive behaviours in response to cues received from external stimuli, including features of the stream environment. Responses to external cues may differ between males and females due to different reproductive strategies utilized (Bateman, 1948; Shuster & Wade, 2003). Additionally, the interval over which individuals integrate information regarding prior environmental conditions (*i.e.* lagged effects) in the formulation of current or future behavioural responses is largely unknown (Sherrill-Mix *et al.*, 2008).

The relative importance of external cues to the initiation of reproductive behaviours may be particularly important for highly fecund species that exhibit broadcast spawning and provide no post-ovulatory parental care for young such as Acipenseriformes (Einum & Fleming, 2000; Hendry & Day, 2005; Jørgensen *et al.*, 2008). High and variable mortality during early life stages is also typical (Kempinger, 1988) and thus, the fitness consequences of responses to exogenous cues for long-lived iteroparous species such as Acipenseridae are also probably high.

The primary objective of this study was to test for associations between external variables and the timing of annual reproductive activities in a closed population of lake sturgeon *Acipenser fulvescens* Rafinesque 1817. Specifically, long-term adult capture and stream data were used to test the hypothesis that stream conditions including water temperature and river discharge and phase of the lunar cycle were predictive of daily migratory movements into the river, and timing of arrival at spawning sites. The same suites of external variables were also predicted to be associated with migratory movements of both sexes, during all periods of the spawning season and among years.

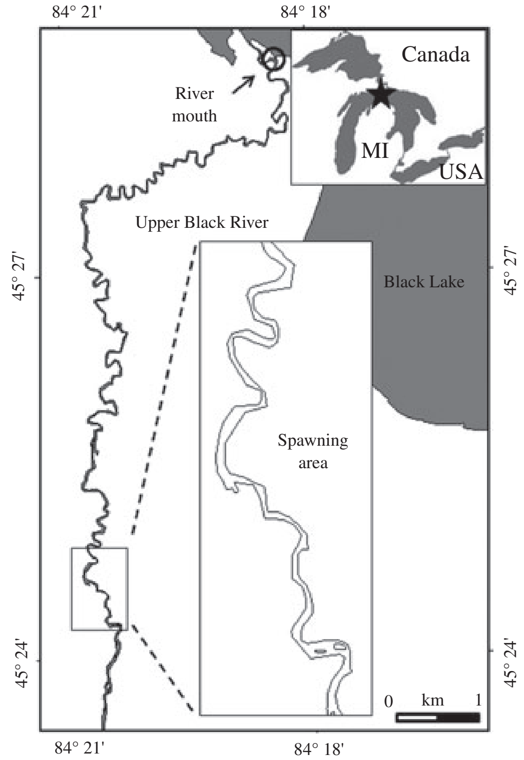

Fig. 1. Map of the Upper Black River, MI, U.S.A. the point of river entry and location of weir (○) and upstream spawning sites used by adult *Acipenser fulvescens*.

MATERIALS AND METHODS

STUDY SITE

Movements of adult *A. fulvescens* into the Upper Black River (UBR), Michigan, U.S.A., were monitored over 3 years (2000–2002) and arrival at upstream spawning areas over 8 consecutive years (2001–2008). The adult *A. fulvescens* population in Black Lake is of moderate size [*i.e.* mean 1085 (883 and 1286 95% c.i.); E. A. Baker, unpubl. data]. The population is closed to immigration by dams. Migration and reproduction occurs in the spring (April to June) and is restricted to an 11 km section of the UBR (Baker & Borgeson, 1999; Smith & Baker, 2005), a fourth-order tributary flowing into Black Lake (Smith & King, 2005). The UBR downstream from Kleber Dam (45° 23′ 30″ N; 84° 20′ 00″ W) to Black Lake is used by *c*. 200 adults each year. Individuals migrating into the river passed a weir where observations were made in shallow (<1·2 m) water. Spawning only occurred within a shallow (<1·5 m) and wadable 1·5 km section of the river (Fig. 1). These characteristics allowed unrestricted access to migrating and spawning adults, resulting in a large proportion of the spawning population observed entering the river and captured as they arrived at spawning areas each year.

OBSERVATIONS OF RIVER ENTRY AND ARRIVAL AT SPAWNING SITES

Movements into the UBR were quantified using a weir and video-surveillance system at the river mouth (Fig. 1). During each of 3 years, the weir was constructed on 22 April

2000, 15 April 2001 and 16 April 2002, a minimum of 3 days before any observations were recorded and presumably before the first fish entered the river, and was removed after a minimum of 5 consecutive days with no observations of upstream movement. The weir consisted of metal fencing arranged in a configuration that guided migrants through a 3 m opening ($<1{\cdot}2$ m water depth) and over a sheet of white painted aluminum placed on the stream bottom. Given the restricted area of fish passage, visibility of fish using the video-surveillance system was believed to be 100%. A video recorder (Sony Digital Handycam, Model DCR-TRV720; www.sony.com) was placed overhead at the weir opening to capture images of passing fish. Halogen lights illuminated the opening at night allowing 24 h of observation daily. Lights were directed downward and illuminated only a few metres of up- and down-stream areas.

Daily monitoring of the spawning areas was initiated when adults were observed entering the river. Individuals were captured as they arrived at upstream sites and while spawning over 8 consecutive years (2001–2008). Long-handled nets (78·7 cm base, 30·5 cm top and 70·5 cm length) were used to capture fish as personnel waded the entire spawning area one or more times each day over the entire spawning period (April to June). All individuals captured were marked internally with PIT tags inserted using a syringe, and a coloured combination of plastic external Floy tags (Floy Tag & Mfg Inc; www.floytag.com) unique to each year, spawning group (*i.e.* early *v.* late) and sex. Sex was determined by pressing on the abdomen to extrude gametes (Bruch *et al.*, 2001). Because adults were readily visible in the UBR, and because the entire spawning area was traversed a minimum of once per day throughout the spawning season, and was extended as necessary, based on fish abundance, the number of individuals captured was thought to reflect the relative abundance on the day of capture, though effort (number of people) each year differed. Surveys were discontinued after no less than 5 days of observations without sighting fish.

EXPLANATORY VARIABLES

Environmental data, including water temperature, river discharge and the lunar phase that have been used as predictor variables in previous studies of migratory fish behaviour (Salinger & Anderson, 2006; Kuparinen *et al.*, 2009) were collected continuously through the migratory and spawning periods each year. River water temperature was recorded hourly using HOBO data loggers (Onset Computer Corp; www.onsetcomp.com) placed at the river mouth and at the spawning sites. No significant difference in river temperatures were observed among stream locations (P. S. Forsythe, unpubl. data), and therefore temperatures as recorded at the river mouth were used for all analyses. Daily discharge data were obtained from the U.S. Geological Survey (USGS) National Streamflow Information Program (http://water.usgs.gov/nsip). Because the USGS gauging station was removed from the UBR in 2000, estimates of daily UBR discharge from 2000 to 2008 were based on predictions from a simple linear regression between historical discharge data collected over 50 years (1950–2000) concurrently from the UBR and from the Pigeon River, a nearby tributary of comparable size (regression, $F_{1,4056} = 9355$, $P < 0{\cdot}001$, $r^2 = 0{\cdot}68$; Forsythe, 2010). Lunar phase data were obtained from the Astronomical Applications Department of the U.S. Naval Observatory (http://aa.usno.navy.mil).

STATISTICAL ANALYSES

Initiation of migration upon entry at the river mouth

The number of adults entering the UBR was determined by hour for each day within a year (2000 to 2002). Hourly counts of adults entering the river were analysed using a general linear mixed model (GLM) with the MIXED procedure in SAS (SAS, 2008*a*). Hour and year were treated as fixed effects and model error was considered to be a first-order auto-regressive process (*i.e.* hourly counts closer in time were assumed more highly correlated than those further apart). *Post-hoc* pair-wise comparisons of least-square means were performed for each hour. Nominal alpha levels were adjusted for multiple comparisons using the Tukey–Kramer method.

Variation in migration and spawning activity within years

The number of individuals captured for the first time at upstream spawning sites was summed for each day within a year (2001–2008). The effect of stream and lunar variables on the total number of daily weir observations of individuals entering the river or captures at the time of arrival at spawning sites was analysed using a generalized linear mixed model (GLMM) implemented using the GLIMMIX procedure in SAS (SAS, 2008*b*). Daily numbers were considered Poisson distributed to account for days having zero observations or captures. Non-independence among daily observations that could affect statistical interpretation of migratory data (Trépanier *et al*., 1996; Erkinaro *et al*., 1999) were also accounted for using a low-rank radial smoothing algorithm applied through the course of the spawning period (Gurrin *et al*., 2005). Smoothing algorithms provide accurate predictions (Pyper & Peterman, 1998) and robust estimates of model β (Wang, 1998; Verbyla *et al*., 1999; Paige *et al*., 2009). Data spanning the period from the first capture to the last capture during a year was used.

Year and day of the year were used as random and fixed explanatory variables for all statistical models, respectively. Treating day of the year as a fixed effect partially accounted for expected intra-annual changes in numbers of new migrants (*i.e.* negative or positive slopes were held constant in the analysis). In a base model, variables quantifying stream conditions on the day of observation at the river mouth or day of capture at spawning areas (*i.e.* no lagged effects) including average daily river-water temperature, average daily river discharge and a variable that defined periods of the lunar cycle [cosine θ (full through to new moon function)] previously shown to be associated with the onset and peak of breeding activity in fishes (Takemura *et al*., 2004) were treated as fixed effects. Here, θ was the angular-transformed lunar cycle day (day divided by $29 \times 2\pi$) and thus times within the lunar month was treated more appropriately as continuous rather than discrete variable (deBruyn & Meeuwig, 2001). Preliminary analyses (Forsythe, 2010) also indicated that river entry and arrival to spawning sites may be a quadratic (*i.e.* curvilinear) function of water temperature. Thus, a quadratic term was added.

Migratory fish species also respond to changes in river conditions during migration and reproduction, *e.g.* increasing or decreasing water temperature (Workman *et al*., 2002). Variables representing both the direction (positive or negative) and magnitude of change of water temperature and river discharge were included in the analysis and were estimated as the difference between mean observations taken 24, 48 or 72 h apart. Lagged environmental variables characterizing river temperature and discharge conditions and periods of the lunar month 24, 48 or 72 h prior to observation or capture were also tested. Unfortunately, while significant colinearity among model variables with the same lag (*i.e.* lagged temperature one day and lagged discharge one day) did not exist ($r < 0{\cdot}3$; Forsythe, 2010), variables such as water temperature with different lags (24, 48 or 72 h prior to observation) were highly correlated and thus evaluated in three separate lagged-effect models. Interactions among fixed effects were not found during preliminary analyses (Forsythe, 2010) and were not re-evaluated in this study to avoid over-parameterization and convergence issues.

Detecting the model of best fit to the data is an important analytical step. The parameter estimation methods (*i.e.* pseudo-likelihoods or an approximation to the joint probability distribution of a collection of random variables) in the GLIMMIX procedure, however, do not currently allow for model selection (*i.e.* stepwise) or quantitative comparisons *e.g.* Akaike information criterion (AIC) or Bayesian information criterion (BIC) (Burnham & Anderson, 2002), particularly when models contain random effects (*i.e.* year and smoothing functions) and when models are not nested (Bolker *et al*., 2009). Thus, while lagged effects may not be consistent across all variables, *e.g.* no immediate change in the response of individuals to temperature while lag effects in river discharge may exist, only full models with the same suite of lagged predictors (no lag, lag of 24, 48 and 72 h) were evaluated. As the dispersion parameter of a model approaches one (computed as the total model deviance model divided by d.f.; referred to as generalized χ^2), however, correlation among observation have been appropriately accounted for, estimates of the S.E. and 95% C.I. for model parameters are probably unbiased and the probability of making type I errors are minimized (SAS, 2008*b*). Here, fully parameterized models were qualitatively ranked based on the dispersion parameter under the assumption that highest ranked model is most appropriate for the data. Sex-specific differences in timing of arrival to spawning sites and associations with fixed effects were tested using two-way interactions *e.g.* sex × discharge. Interactions were retained in the model based on significance ($P < 0{\cdot}05$).

RESULTS

RIVER ENTRY

Observations at the weir located just upstream from the river mouth indicated that 264, 258 and 235 *A. fulvescens* migrated upriver during 2000–2002, respectively. The initial day of river entry (23 April in 2000; 24 April in 2001; 23 April in 2002), and the first peak of migration activity (26 April in 2000; 3 May in 2001; 27 April 2002) was consistent with respect to calendar date, water temperature (9·6° C in 2000; 10·8° C in 2001; 8·9° C in 2002) and river discharge (7·8 $\text{m}^3\ \text{s}^{-1}$ in 2000; 11·8 $\text{m}^3\ \text{s}^{-1}$ in 2001; 9·9 $\text{m}^3\ \text{s}^{-1}$ in 2002) relative to seasonal ranges observed in the UBR (Fig. 2). The onset of river entry for the year was not consistent with the period of the lunar cycle. The part of the moon illuminated was 82% in 2000; 0% in 2001 and 79% in 2002. Migratory movements into the river lasted for a maximum of 36 days across years. An average of eight individuals entered the stream daily at water temperature and river discharge ranging from 8 to 21°C and 5 to 24 $\text{m}^3\ \text{s}^{-1}$. The number of individuals entering the UBR daily varied from 1 to 55 individuals across all years, and no behavioural modification such as rapid back-and-forth movements were observed.

VARIABLES ASSOCIATED WITH RIVER ENTRY

Counts of individuals entering the river differed significantly by hour of the day (GLM; $F_{23,46} = 31{\cdot}3$, $P < 0{\cdot}001$). Significantly greater numbers of individuals entered the UBR in the morning (0600–1100 hours) and the early evening (1700–2200 hours) (GLM, $P < 0{\cdot}05$; Fig. 3), a pattern that was consistent across years (GLM, $F_{2,46} = 1{\cdot}15$; $P > 0{\cdot}05$; Fig. 3). A model that included three-day lagged effects (temperature, discharge and lunar variables) most appropriately estimated parameters and predicted observations of daily migration into the river based on generalized χ^2 information (Table I, Fig. 4 and Table SI in Supporting Information). Within this model, the magnitude and direction of change in river discharge was significantly negatively associated with daily numbers of individuals entering the river (GLMM, $F_{1,86} = 20{\cdot}47$, $P = 0{\cdot}001$) *i.e.* movement was lowest on days when river discharge was increasing rapidly during the previous 72 h. The number of individuals entering the river was also a quadratic, *i.e.* downward curvilinear, function of increasing water temperature (GLMM, $F_{1,86} = 6{\cdot}26$; $P < 0{\cdot}05$). The positive slope, however, was not significantly different from zero, *i.e.* lagged water temperature (GLMM, $F_{1,86} = 1{\cdot}54$, $P > 0{\cdot}05$) indicating that there was no overall relationship with water temperature. The significance and sign of parameter estimates for lagged discharge and change in discharge were similar across models with and without lagged effects (Table I and Table SI in Supporting Information).

SPAWNING SITE ARRIVAL

From 2001 to 2008, a total of 1262 captures of *A. fulvescens* arriving at spawning sites were recorded. The number of individuals captured per season ranged from 104 to 226. More observations of males were made relative to females (360 females;

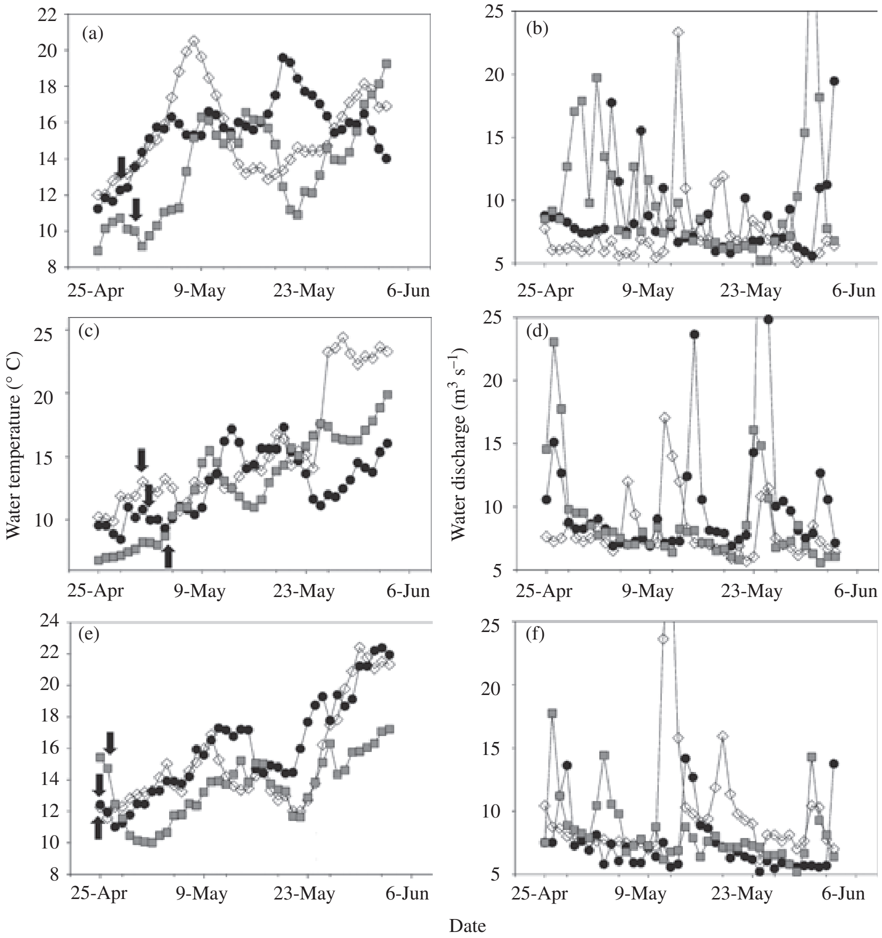

FIG. 2. Measurements of daily (a), (c), (e) water temperature and (b), (d), (f) river discharge of the Upper Black River, Michigan during the spring in (a), (b) 2000 (◇), 2001 (●) and 2002 (▨), (c), (d) 2003 (◇), 2004 (●) and 2005 (▨) and (e), (f) 2006 (◇), 2007 (●) and 2008 (▨). (↓), date of first *Acipenser fulvescens* capture.

902 males). The date of first arrival (20 April to 7 May) and the timing of the first peak of arrival (21 April to 9 May) was variable across years, as were river conditions (river water temperature 8·0 to 14·9° C) and extent of lunar illumination (2–87%) (Fig. 2). River discharge during spawning, however, was generally low (8·1–12·7 m^3 s^{-1}) relative to seasonal ranges. Further, concurrent observations of river entry and arrival to spawning sites during 2001 and 2002 showed that the duration of river residency was longer in 2002 (14 days) when average river discharge was higher (Fig. 2) than in 2001 (4 days).

VARIABLES ASSOCIATED WITH SPAWNING-SITE ARRIVAL

Newly arriving individuals at spawning sites based on PIT-tag number and year-specific Floy tag colour were captured over a period of 19 to 43 days, generally

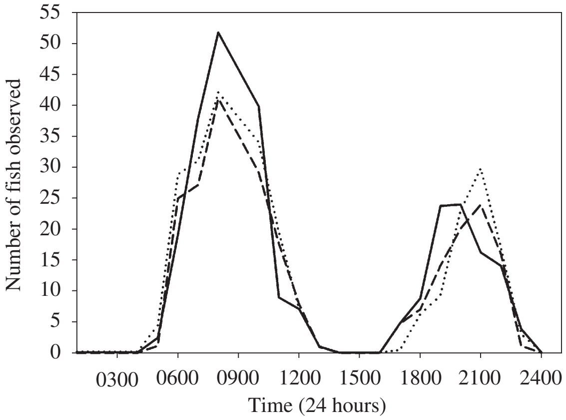

FIG. 3. Mean number of *Acipenser fulvescens* entering the Upper Black River, Michigan, recorded by hour of the day for 24 h over three consecutive years [2000 (——), 2001 (.......) and 2002 (– – –)].

encompassing a full lunar cycle (Fig. 5). Patterns in arrival were characterized by two (*e.g.* 2002, 2003 and 2005), three (*e.g.* 2004 and 2007) or four (*e.g.* 2001, 2006 and 2008) groups (defined by a peak in numbers) of individuals spawning at water temperature ranging from 8 to 19° C and river discharge ranging from 5–9 $m^3 s^{-1}$ (Fig. 5). The model that best fit daily captures of newly arriving individuals at the spawning sites (Table II and Fig. 5) was a model including lagged effects characterizing the stream environment 3 days before capture (Table II). Within this model, the

TABLE I. Parameter estimates (β), lower (L) and upper (U) 95% C.L. for β, F statistics and probabilities of significance for the highest ranked full model based on the dispersion parameter (see generalized χ^2; χ^2 divided by d.f. and Table SI in Supporting Information) describing daily numbers of individual *Acipenser fulvescens* observed entering the mouth of the Upper Black River, Michigan, from 2000 to 2002 as a function of environmental conditions 3 days before observation (*i.e.* abiotic variables lagged 3 days). Day was included to correct for intra-annual trends (*i.e.* slope) in the number of new migrants observed

Model variables	β	95% L.C.L.	95% U.C.L.	F	Probability $> F$	χ^2 divided by d.f.
Daily number of adults observed =						2·26
Day	0·26	−1·57	2·08	0·10	0·758	
Temp	0·15	−0·09	0·39	1·54	0·217	
Temp^2	−0·06	−0·10	−0·01	6·26	0·014	
Tchange	−0·04	−0·16	0·08	0·38	0·541	
Discharge	−0·05	−0·11	0·01	2·65	0·114	
Dchange	−0·12	−0·17	−0·07	20·5	<0·001	
Cosine θ	−1·07	−5·91	3·77	0·24	0·626	

Temp, average daily river water temperature, Temp^2, quadratic effect of daily water temperature; Tchange, magnitude and direction of change in water temperature over 72 h; discharge, average daily river discharge; Dchange, magnitude and direction of change in river discharge over 72 h; cosine θ, cosine transformation of the lunar phase.

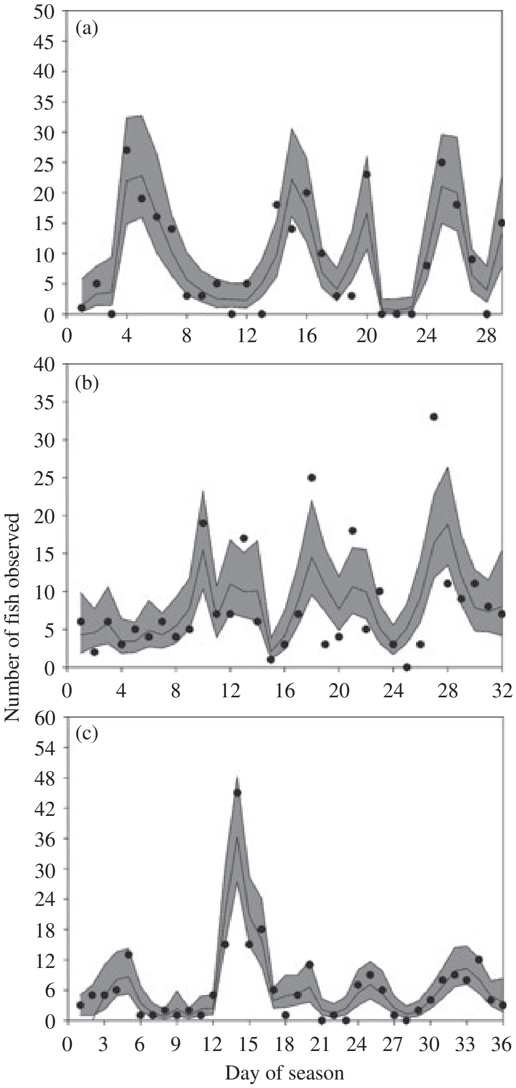

FIG. 4. Observed (●) and predicted (——) number of *Acipenser fulvescens* entering the Upper Black River (UBR), Michigan, daily during (a) 2000, (b) 2001 and (c) 2002. Predictions and 95% C.I. from a linear mixed model with stream and lunar covariates are also provided (▩). No fish were observed entering the UBR before or after the days shown.

number of newly arriving individuals at spawning sites was significantly negatively associated with lagged discharge (GLMM, $F_{1,458} = 12{\cdot}08$, $P < 0{\cdot}001$), the rate and direction of change in water temperature (GLMM, $F_{1,458} = 14{\cdot}01$; $P < 0{\cdot}001$) and cosine (GLMM, $F_{1,458} = 10{\cdot}14$, $P < 0{\cdot}01$) of the lunar angle. The number of new adults arriving at spawning sites was also a quadratic function (*i.e.* increasing curvilinear) of lagged water temperature (Table II) but the overall positive relationship was not significantly different from zero, *i.e.* lagged water temperature (GLMM, $F_{1,458} = 0{\cdot}25$, $P > 0{\cdot}05$).

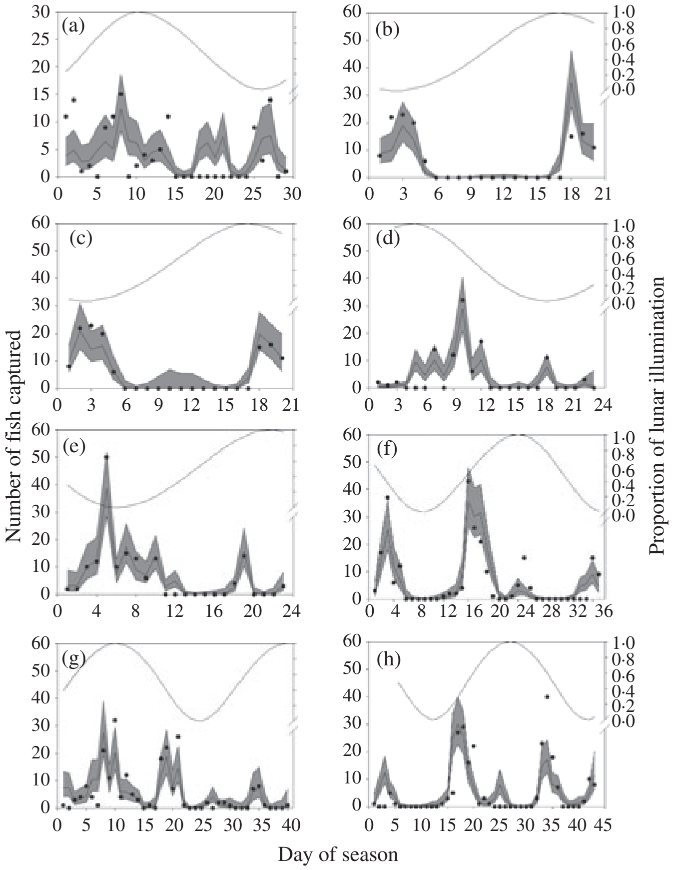

FIG. 5. Observed (●) and predicted (——) number of *Acipenser fulvescens* arriving at spawning sites in the Upper Black River, Michigan, each day during 8 years ((a) 2001, (b) 2002, (c) 2003, (d) 2004, (e) 2005, (f) 2006, (g) 2007 and (h) 2008), and the proportion of the moon that was illuminated each day (——). Predictions and 95% C.I. shown are based on a linear mixed model incorporating both stream and lunar covariates (■). No individuals were captured at spawning sites before or after the days shown.

Analysis indicated higher numbers of adults arriving to spawning sites on days with lower river discharge ($7–15\ m^3\ s^{-1}$), and at times when water temperature was warmer or increasing at a relatively fast rate (positive lagged effect), particularly when the cosine of the lunar angle approached zero or one (at times of full or new moon; Fig. 5). Parameter estimates for all models for the number of newly arriving individuals at spawning sites when expressed as a function of zero, 1 or 2 day lagged variables were consistent with respect to the sign (*i.e.* slope) and thus yielded similar interpretations (Table II and Table SI in Supporting Information). Responses to environmental and lunar covariates did not differ between males and females (*i.e.* no statistical support for sex × environmental or lunar-effect interaction). Rates of arrival of new individuals over the course of the spawning season, however, differed significantly by sex, *i.e.* sex × day interaction (GLMM, $F_{1,12} = 23{\cdot}89$, $P < 0{\cdot}001$), being negative for newly arriving females and positive for newly arriving males. The disparity *i.e.* increasing numbers of males and decreasing numbers of females,

TABLE II. Parameter estimates (β), lower (L) and upper (U) 95% C.L. for β, F statistics and probabilities of significance for the highest ranked full model based on the dispersion parameter (see generalized χ^2; χ^2 divided by d.f. and Table SI in Supporting Information) describing daily numbers of individual *Acipenser fulvescens* captured (= 1·96) at upstream spawning sites in the Upper Black River, Michigan, during 8 years (2001–2008) as a function of variables describing environmental conditions 3 days before capture (*i.e.* abiotic variables lagged 3 days). Day and day × sex interaction terms were included to correct for intra-annual trends (*i.e.* slope) in the number of new male and female migrants arriving upstream

Model variables	β	95% L.C.L.	95% U.C.L.	F	Probability $> F$	χ^2 divided by d.f.
Daily number of adults captured =						1·96
Day	0·15	−3·28	3·58	0·01	0·935	
Sex				19·9	<0·001	
Day × sex female	−0·03	−0·04	−0·02	23·1	<0·001	
Day × sex male	0·03	0·02	0·05	23·1	<0·001	
Temp	0·02	−0·06	0·10	0·25	0·404	
Temp^2	0·04	0·02	0·07	16·1	<0·001	
Tchange	0·13	0·06	0·20	14·1	<0·001	
Discharge	−0·09	−0·14	−0·04	12·1	<0·001	
Dchange	−0·03	−0·07	0·02	1·52	0·465	
Cosine θ	0·28	0·11	0·45	10·1	0·002	

Temp, average daily river water temperature; Temp^2, quadratic effect of daily water temperature; Tchange, magnitude and direction of change in water temperature over 72 h; discharge, average daily river discharge; Dchange, magnitude and direction of change in river discharge over 72 h; Cosine θ, cosine transformation of the lunar phase.

through the spawning period reflected the increasingly male-biased sex ratios of spawning groups arriving later in the season (Table II).

DISCUSSION

During pre-spawning migration, individuals respond to external cues culminating in reproduction (Duriez *et al.*, 2009). The relative importance of external cues often varies from the onset of migration to reproduction, and multiple cues may work in concert to elicit different responses. Data collected for this study suggest that stream temperature and discharge and period of the lunar cycle were significantly associated with *A. fulvescens* behaviour including the initiation of migration, and timing of arrival at spawning sites. The relative importance of cues such as photoperiod, river discharge, water temperature and the lunar cycle, however, vary leading up to and during reproduction.

EFFECTS OF PHOTOPERIOD ON MIGRATORY AND SPAWNING BEHAVIOUR

The onset of entry into the UBR occurred at nearly the same calendar date over a three-year period. Day length mediates the endogenous cycle of oocyte maturation in other migratory fishes (Taranger *et al*., 1998; Lee *et al*., 2002) including Acipenseridae (Doroshov *et al*., 1997; Webb *et al*., 2001) and may explain the interannual consistency in the beginning of upstream movement. Earlier arrival at spawning sites, *e.g.* April 20 in 2006 (Fig. 2), however, was noted suggesting that individuals move into the UBR earlier in years with comparatively higher water temperatures. Thus, although day length may strongly influence timing of river entry, the duration of river occupancy prior to spawning and the timing of spawning activities varied as a function of changing stream conditions, *e.g.* rate of increase in water temperature.

Time of day (*i.e.* dusk and dawn) was also a significant predictor of river entry (Fig. 3). Nocturnal migratory activity has been observed in several species and may be a behavioural response to predator activity or harvest by humans. Migratory movements of some species also have a crepuscular pattern as individuals avoid the physiological stress of moving during cooling evening water temperatures, which can be considerable in shallow northern temperate streams (Binder & McDonald, 2008). These may in part explain the behaviour of UBR *A. fulvescens*. Timing of entry into the UBR could be due to the shallow water depth and to human activity. Given the majority of fish passed the weir during periods of the day when some natural light was present (Fig. 3), and the lack of visual observations of flight behaviour when passing the weir, it was assumed that artificial lighting at the weir did not affect the timing of fish passage.

RIVER CONDITIONS PREDICT TIMING OF MIGRATION AND SPAWNING

Low or receding flow conditions were significantly associated with higher numbers of individuals entering the UBR and arrival time at spawning sites (Tables I and II). The negative effect of higher river discharge on the number of individuals entering the river and arriving at upstream spawning sites may be due to the increased physiological costs imposed by the higher discharge. UBR *A. fulvescens* may also time arrival at spawning sites to coincide with low-flow conditions to increase offspring survival (Auer, 1996*a*, *b*). Low flow conditions may also increase probabilities of egg fertilization and the probability that eggs are deposited within desirable substrata at selected spawning sites (LaHaye *et al*., 1992; Auer, 1996*a*; Paragamian & Wakkinen, 2002).

River discharge may have a greater influence on migratory behavior in smaller and shallower systems like the UBR relative to larger systems. Differences in the response of *A. fulvescens* to river discharge may also reflect species- and location-specific migration strategies such as those found in well-studied salmonids ((Hinch & Rand, 1998). In smaller river systems, the period over which environmental conditions are suitable for reproduction may be shorter than in larger systems. For example, seasonally reduced discharge may reduce stream flow to levels where fishes cannot access spawning sites.

Positive relationships between daily numbers of individuals entering rivers and water temperature are frequently reported in migratory fishes including Acipenseridae (Paragamian *et al*., 2002; Dahl *et al*., 2004). There was no change in the levels of migratory activity in the range of spring temperatures observed on the UBR. One possibility for this difference is that river discharge in the UBR is a much stronger and reliable cue for river entry and any influence of temperature was not detected with only 3 years of data.

The number of new individuals arriving at spawning sites was associated with the rate of increase in water temperature over successive days. Temperature-dependent spawning-site arrival could be the result of an elevated physiological readiness of individuals, facilitating more intense spawning behaviour (Bruch & Binkowski, 2002). Kempinger (1988) and Paragamian & Wakkinen (2002) noted that a decline in water temperature reduced spawning activity and caused individuals to leave spawning sites. Adults may also seek to enhance offspring survival by placing offspring in conditions that are less likely to exceed thermal limit or expose individuals to additional mortality sources before hatch. Consistency in the relationships between the arrival at spawning sites and onset of spawning in the UBR with the incubation requirements of embryos (8–20° C; Dettlaff *et al.*, 1993; Van Eenennaam *et al.*, 2005) supports this latter hypothesis. Further, consistency in the relationship between arrival at spawning sites and temperature over multiple spawning seasons, for groups spawning at different times in the UBR and elsewhere (Scott & Crossman, 1973; LaHaye *et al.*, 1992), and those reported at the onset of spawning and seasonally for populations across the species geographic range (LaHaye *et al.*, 1992; Auer, 1996*b*; Bruch & Binkowski, 2002) are noteworthy.

Interactions between stream covariates were not tested for, although evidence has been reported. For example, Svendsen *et al.* (2004) found that the probability of anadromous female brown trout *Salmo trutta* L. (1758) moving upstream significantly increased with increasing river discharge, but this probability was differentially affected by water temperature. The relative effect of water temperature and discharge, and thus the potential for interaction on inducing upstream movement, also clearly varies among systems (Jonsson *et al.*, 1991; Workman *et al.*, 2002). Because the UBR is small and environmental cues like temperature and discharge vary over a shorter temporal scale, both migratory, arrival to spawning sites and spawning activities are likely to be more detectable responses relative to larger rivers.

EFFECTS OF LUNAR CYCLE PHASE ON MIGRATORY AND SPAWNING BEHAVIOUR

Acipenser fulvescens entered the UBR and arrived to upstream spawning areas during several phases of the lunar cycle (Figs 4 and 5). Spawning activity in the UBR, however, was most strongly associated with times just prior to or approaching a new moon and during or just after full lunar illumination (Table II). These findings are consistent with reports indicating that spawning in both lake and Gulf sturgeon *Acipenser oxyrinchus desotoi* Vladykov 1955 occurred in association with new (Auer & Baker, 2002) and full (Sulak & Clugston, 1998) phases of the lunar cycle. Lunar cues have been suggested to have important ecological implications for many species (Benoit-Bird *et al.*, 2009; Grant *et al.*, 2009). In broadcast spawning fishes, reproductive synchrony tied to reliable cues such as period in the lunar cycle may increase fertilization success dependent on both adult number and sex ratio (Rowe *et al.*, 2004). The duration of incubation for *A. fulvescens* embryos is also predictable given water temperature and maternal effects associated with the time and location of spawning (Duong *et al.*, 2011*a*,*b*). The duration of larval residence in the substratum prior to downstream dispersal also decreases in the UBR with increasing temperatures as the season progresses (Crossman, 2008; Duong *et al.*, 2011*a*). Thus, synchronizing reproduction with the lunar cycle, *i.e.* early spawning adults at colder temperatures and longer incubation and developmental periods (Doung *et al.,* 2011*a*) relative to adults spawning later and in warmer water, may reduce predation pressure on drifting larvae because dispersal of larvae from early and late spawning adults will coincide with periods of lower lunar illumination. Based on this result, lunar-based migration and spawning in migratory fishes may be of greater biological relevance than previously discussed (Kuparinen *et al.*, 2009).

IMPORTANCE OF PRIOR CONDITIONS TO TIMING OF MIGRATION AND SPAWNING

Information regarding environmental conditions experienced during previous periods may provide reliable cues to initiate migration and spawning. Fishes have the ability to retain information associated with prior experiences that have been shown to enhance foraging performance, facilitate anti-predator responses, increase spatial awareness and foster the ability to recognize conspecifics, kin and mates (Brown *et al.*, 2003; Laland *et al.*, 2003). The timing of entry into the UBR and arrival at spawning locations appear to be influenced by environmental conditions experienced over several days in the immediate past. While traditional model comparison was not possible in this study, evidence that a model with three-day lagged stream and lunar variables was a better predictor of daily observations of the number of adults entering the river and numbers arriving at spawning sites than models with zero, one and two-day lagged effects was documented. Thus, consistency in trends in discharge and temperature may be considered more reliable and are acted on with greater predictability than associations based on current effects or lagged effects of shorter duration.

The ability of adults to detect conditions during previous days, *e.g.* lag effects of temperature and discharge, indicated that individuals are situated near the source of such cues, for example, in the immediate vicinity of the river mouth, prior to the onset of migration. Data showing interannual variation in time from initial river entry and arrival at the spawning grounds suggest that adults may also be staging after river entry in locations close to the spawning areas. The importance of lagged effects on numbers arriving at spawning grounds suggests that individuals utilize information gathered over several days to decide when to complete migration and initiate spawning. Staging has been reported for *A. fulvescens* in other systems, *i.e.* staging in deep river pools before spawning (Bruch & Binkowski, 2002), and for other migratory fishes (High *et al.*, 2006; Godinho *et al.*, 2007).

MALE AND FEMALE RESPONSES TO ENVIRONMENTAL AND LUNAR CUES

No evidence of differences in male and female responses to external conditions at the time of spawning was found. This result differed from previous reports of differences between males and females in other species. Paragamian & Kruse (2001) showed that male white sturgeon *Acipenser transmontanus* Richardson 1836 were significantly less likely to respond to changes in water temperature and discharge while moving upstream than females. One possibility for this discrepancy is that sex-based effects in the UBR were small relative to other systems and thus not detectable. It is likely, however, that sex-based responses may not be important to initiation of spawning as observed during other stages during migration. Significant differences for the numbers of males and females arriving at spawning sites over the entire season were observed. This finding is based on the increasingly male-biased sex ratio during later portions of the spawning season based on resampling data not included in this study (Forsythe, 2010).

STUDY IMPLICATIONS

These data have revealed the importance of lagged effects (multi-day trends) including declining flow rates and increasing temperatures on spawning behaviours throughout the spawning season. Human uses that alter natural environmental cues on which organisms rely for processes such as development, reproduction and migration can have large effects at the individual and population level. Knowledge of relationships between individual behaviours and environmental variables is critical to predict how altered environmental conditions will affect survival and population persistence. Poikilothermic species are especially susceptible to environmental stochasticity given their strong dependence on the environment for metabolic functions, reproductive activities and development during early ontogenetic stages. Greater understanding is needed of the effects of environmental variables on behaviours as described in this study to predict whether particular segments of populations that spawn at certain times or locations are more or less likely to be capable of responding to future changes in environmental conditions.

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SUPPORTING INFORMATION

Supporting Information may be found in the online version of this paper:

TABLE SI. Parameter estimates (β), lower and upper 95% C.I. for β, F statistics and probabilities of significance, and generalized χ^2; χ^2 divided by d.f. (*i.e.* dispersion parameter) for alternative full models describing daily numbers of individual *Acipenser fulvescens* observed entering the Upper Black River, Michigan, from 2000 to 2002 and daily numbers of individuals captured at upstream spawning locations from 2001 to 2008 as a function of environmental conditions 0, 1, or 2 days before observation. Day was included to correct for intra-annual trends (*i.e.* slope) in the number of new migrants observed. A day × sex interaction term was included to correct for intra-annual trends (*i.e.* slope) in the number of new male and female migrants captured arriving upstream.

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