Environmental and maternal effects on embryonic and larval developmental time until dispersal of lake sturgeon (*Acipenser fulvescens*)

Thuy Yen Duong, Kim T. Scribner, James A. Crossman, Patrick S. Forsythe, and Edward A. Baker

Abstract: For migratory fish like lake sturgeon (*Acipenser fulvescens*), the period from egg deposition through embryonic and larval development until dispersal (ELDTUD) contributes substantially to variation in survival at the individual level and to population levels of recruitment. Using genetically determined parentage, we examined the relative importance of environmental variables in a stream environment (e.g., temperature and discharge) and maternal effects (including individual female body size, spawning time, and location) to ELDTUD on an individual basis. Adult lake sturgeon ($n = 208$) spawning in the Upper Black River (Michigan, USA), and larvae ($n = 1444$) dispersing downstream were captured during the 2007 spawning season. We used generalized mixed models and multimodel inference based on Kullback–Leibler information-theoretic criteria to demonstrate that environmental variables and the maternal effects of individual female and spawning time were both important predictors of ELDTUD. Decreasing ELDTUD during the season resulted from linearly increasing temperature and nonlinearly decreasing river discharge. Spawning time and individual female explained a large proportion of variation in ELDTUD. The individual-based approach used in this study provided precise estimates of ELDTUD and also facilitated the partitioning of variation in ELDTUD of larvae produced by the same female and among females spawning at different times and different environmental conditions.

Résumé : Chez les poissons migrateurs comme l'esturgeon jaune (*Acipenser fulvescens*), la période qui commence à la ponte des œufs, comprend les développements embryonnaire et larvaire et s'étend jusqu'à la dispersion (ELDTUD) contribue considérablement à la variation de la survie pendant toute la vie au niveau individuel et au recrutement au niveau de la population. Nous examinons l'importance relative des variables environnementales des cours d'eau (par ex., température et débit) et des effets maternels, en particulier la taille corporelle, le moment de la fraie et la position dans le milieu, sur l'ELDTUD chez des individus dont l'ascendance a été déterminée par des méthodes génétiques. Pendant la saison de reproduction de 2007, nous avons capturé des esturgeons jaunes adultes ($n = 208$) frayant dans l'Upper Black River (Michigan, É.-U.), ainsi que des larves ($n = 1444$) qui se dispersaient vers l'aval. Des modèles mixtes généralisés et l'inférence multimodèle basée sur les critères de Kullback–Leibler fondés sur la théorie de l'information nous ont permis de démontrer que tant les variables du milieu que les effets maternels reliés à la femelle et le moment de la fraie sont de bonnes variables prédictives d'ELDTUD. La diminution de l'ELDTUD au cours de la saison s'explique par un accroissement linéaire de la température et d'une réduction non linéaire du débit de la rivière. Le moment de la fraie et les femelles individuelles expliquent une forte proportion de la variation de l'ELDTUD. L'approche basée sur l'individu utilisée dans notre étude fournit des estimations précises de l'ELDTUD et facilite la répartition de la variation de l'ELDTUD entre les larves produites par une même femelle et entre les femelles frayant à divers moments et dans des conditions différentes du milieu.

[Traduit par la Rédaction]

Received 21 January 2010. Accepted 23 November 2010. Published at www.nrcresearchpress.com/cjfas on 12 April 2011.
J21624

Paper handled by Associate Editor Pierre Magnan.

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Introduction

Estimating the timing of development and of transitions between ontogenic events during early life stages and determining the relative importance of factors effecting developmental time under natural conditions are important subjects in fish biology. Embryonic and larval developmental time until dispersal (ELDTUD) is a critical period that exposes larvae to high risks of mortality due to biotic (e.g., predation and competition; Garvey et al. 1994; Paradis et al. 1996), and abiotic factors (e.g., temperature, oxygen; Chandler and Bjornn 1988; Einum and Fleming 2000). ELDTUD may vary as a function of environmental factors (e.g., temperature, stream discharge, etc.) and maternal effects (e.g., egg size) (Gillooly et al. 2002; Kamler 2002; O'Connor et al. 2007). Environmental conditions during embryonic and larval development are typically selected by parents (Trippel et al. 1997; Kamler 2002; Jørgensen et al. 2008). Therefore, maternal effects, which occur when female phenotype or environments experienced at the time and location of spawning influence offspring phenotypic traits (Mousseau and Fox 1998), and together with environmental variables associated with spawning time and spawning location can collectively contribute to embryonic and larval developmental time (Einum and Fleming 2000; Kamler 2002) and dispersal (e.g., in aquatic invertebrates, Reitzel et al. 2004; in fish, Edwards et al. 2007).

Water temperature and stream discharge are two environmental factors that play an important role in the timing of larval hatch and dispersal (Heggberget 1988; Pepin et al. 1997; Tetzlaff et al. 2005) and thus ELDTUD. Metabolic rate increases with temperature (Gillooly et al. 2001), which decreases the time required for incubation and yolk absorption. Temperature-dependent developmental time has been reported in a variety of taxa including insects (Pritchard et al. 1996; Johnson et al. 2007; Arbab et al. 2008), fish and invertebrates (Gillooly et al. 2002; O'Connor et al. 2007), and amphibians (Gillooly et al. 2002). River discharge indirectly influences developmental time via oxygen supply (Kamler 2002), and directly affects dispersal time by changing drifting and swimming speeds of larvae (Elliott 1987; Fausch et al. 2001; Siegel et al. 2003).

ELDTUD may also vary owing to maternal effects including spawning time and location, and effects associated with female body size or age. Spawning at specific times and locations has been shown to dictate conditions for offspring development and survival (Trippel et al. 1997; Jørgensen et al. 2008). Empirical and modeling studies have shown that adult spawning time and location also affect timing of larval emergence and dispersal (Einum and Fleming 2000; Reitzel et al. 2004; Edwards et al. 2007). Maternal effects on egg size, where larger females usually produce larger eggs, have been observed in fish (Chambers and Leggett 1996; Heath et al. 1999; Heins et al. 2004). Larger eggs may require longer time for embryonic development (Pepin et al. 1997; Gillooly and Dodson 2000). In addition, for many species, genetic differences among adult groups spawning at different times (isolation by time) may contribute to variation in phenotypic traits of offspring (review in Hendry and Day 2005).

Studies that simultaneously evaluate environmental and maternal effects may better explain variation in ELDTUD than studies that focus on effects of one set of variables alone. There is a lack of research that simultaneously quantifies effects of environmental factors and maternal effects on ELDTUD at the individual-level under natural conditions. Reasons for the lack of data include difficulties in identifying genealogical relationships between adults and larvae, and the need to collect a large number of parents and offspring from natural populations. The problem can be overcome using genetic makers to genetically determine parentage (Garant and Kruuk 2005; Pemberton 2008) of a population reproducing in natural and accessible habitats.

In this study, we used genetically determined parentage to examine effects of environmental factors and maternal effects on ELDTUD in a threatened fish species, the lake sturgeon (*Acipenser fulvescens*). Lake sturgeon exhibit an aggregate mating behavior where eggs and sperm are released by spawning adults over rock and gravel without nest preparation or parental care (Bruch and Binkowski 2002). Because of the species mating behavior and exposure of eggs and post-hatch larvae to environmental conditions, larval lake sturgeon experience extremely high mortality early in life (Kempinger 1988; Forsythe 2010). Therefore, selection of spawning times and locations, which determines environmental conditions that affect eggs and larvae (Mousseau and Fox 1998), by adult lake sturgeon could play important roles in offspring survival and ELDTUD. Newly-hatched larvae generally remain in the stream substrate until yolk-sac reserves are depleted, and then individuals disperse downstream in the current at night (Auer and Baker 2002; Kynard and Parker 2005; Smith and King 2005). However, factors underlying variation in ELDTUD at the individual level are still unknown.

Similar to heritable spawning time observed in many salmonid species (Siitonen and Gall 1989; Gall and Neira 2004) repeatability of spawning time among adult groups in iteroparous species may have a genetic basis. Repeatability has been used as a measure of trait heritability (Boake 1989). Data collected on spawning lake sturgeon in the Black River, Michigan (USA) over 8 years (2001–2008) revealed that repeatability of spawning time for females and males who have been captured more than two occasions was high (0.56 and 0.42, respectively, Forsythe 2010). We also observed that early-spawning lake sturgeon females produced offspring that had longer incubation times, larger body size, and larger yolk-sac reserves at hatch compared with offspring of late-spawning females (Crossman 2008), which might lead to longer period from egg deposition to dispersal (ELDTUD). If groups of lake sturgeon spawning at different times are genetically differentiated and if spawning time affects ELDTUD, genetic factors could contribute to differences in ELDTUD.

The main objective of this study was to evaluate the relative importance of environmental factors (water temperature and discharge) and maternal effects (individual female as a random effect, body size, spawning time and location) and their interactions to ELDTUD of lake sturgeon under natural conditions. We also tested whether different adult groups whose offspring differed in ELDTUD were genetically differentiated. Additionally, we quantified the degree of temperature-dependence (cumulative thermal units or CTU) for ELDTUD to evaluate the practicality of this single variable as a predictor of the timing of larval dispersal for lake sturgeon.

Materials and methods

Study site

Our study was conducted in Upper Black River (UBR), the largest tributary to Black Lake, Michigan, USA (latitude 45° 43′N, longitude 84°15′W; Fig. 1*a*). The lake sturgeon population in Black Lake is isolated from other populations in adjacent lakes by dams blocking immigration and emigration from Lake Huron (Smith and King 2005). Adults spawn over a 1.5 km-section of UBR. This section can be divided into six locations of spawning activity that were used across years (Fig. 1*b*). Shallow spawning areas (~1 m deep) and low turbidity allowed most adults to be observed and captured (Crossman 2008; Forsythe 2010) and larvae dispersing from all spawning areas to be collected (Smith and King 2005).

Sample collection

Sampling for adults was conducted daily in 2007 by wading through the entire length of the stream encompassing all spawning sites one or more times per day during the entire spawning season. We captured spawning adults (143 males and 63 females) using long-handled nets. The sex of the adults was determined by extruding gametes, and all individuals were measured for mass (kg) and fork length (cm). We also recorded date and location of capture, which were assumed to be the date and location of spawning based on our observation that lake sturgeon females spent only a few days on the spawning grounds (Forsythe 2010). A dorsal fin clip (~1 cm^2) was taken for genetic analysis.

Larval sampling was conducted at night, when the vast majority of larvae dispersed (Auer and Baker 2002). The larval sampling site was about 2 km downstream from the spawning areas (Fig. 1*a*). Five D-frame larval nets were evenly spaced across the river channel (description in Smith and King 2005) and were checked hourly from 2100–0200 h. Net locations remained consistent throughout the sampling period. Sampling began 10 d after the first spawning event was observed, and continued until there were two consecutive nights with no larvae captured. Larvae were transferred to a stream-side hatchery and were reared in different tanks by sampling night (n = 31) until individuals were large enough for dorsal fin clips to be collected nonlethally. Mortality during the rearing period was recorded, and dead larvae were preserved in 95% ethanol by sampling night. In total, 1444 tissue samples from dead and surviving larvae were available for genetic analysis. Based on the estimates of stream velocity and the proportions of total stream width sampled, juveniles collected were estimated to represent approximately 13% of total larval production (Smith and King 2005).

Environmental data

Water temperature and river discharge data were collected continuously throughout the season. Water temperatures were recorded hourly using HOBO® data loggers (Onset Computer Corp.) placed at spawning areas (Fig. 1*b*). UBR discharge was predicted based on current discharge data obtained from the United States Geological Survey (USGS) gauging station on the Pigeon River, a nearby tributary of Mullet Lake, Michigan. Using UBR and Pigeon River discharge data during April–June for 50 years (1950–2000, USGS National Streamflow Information Program), we found that daily discharge of the UBR could be predicted as a linear function of daily discharge from the Pigeon River (r^2 = 0.68, $F_{[1,4056]}$ = 9355, $P < 0.001$). We used this relationship to estimate UBR daily discharge during 2007 because there were no discharge data from the UBR that year.

Genetic analysis

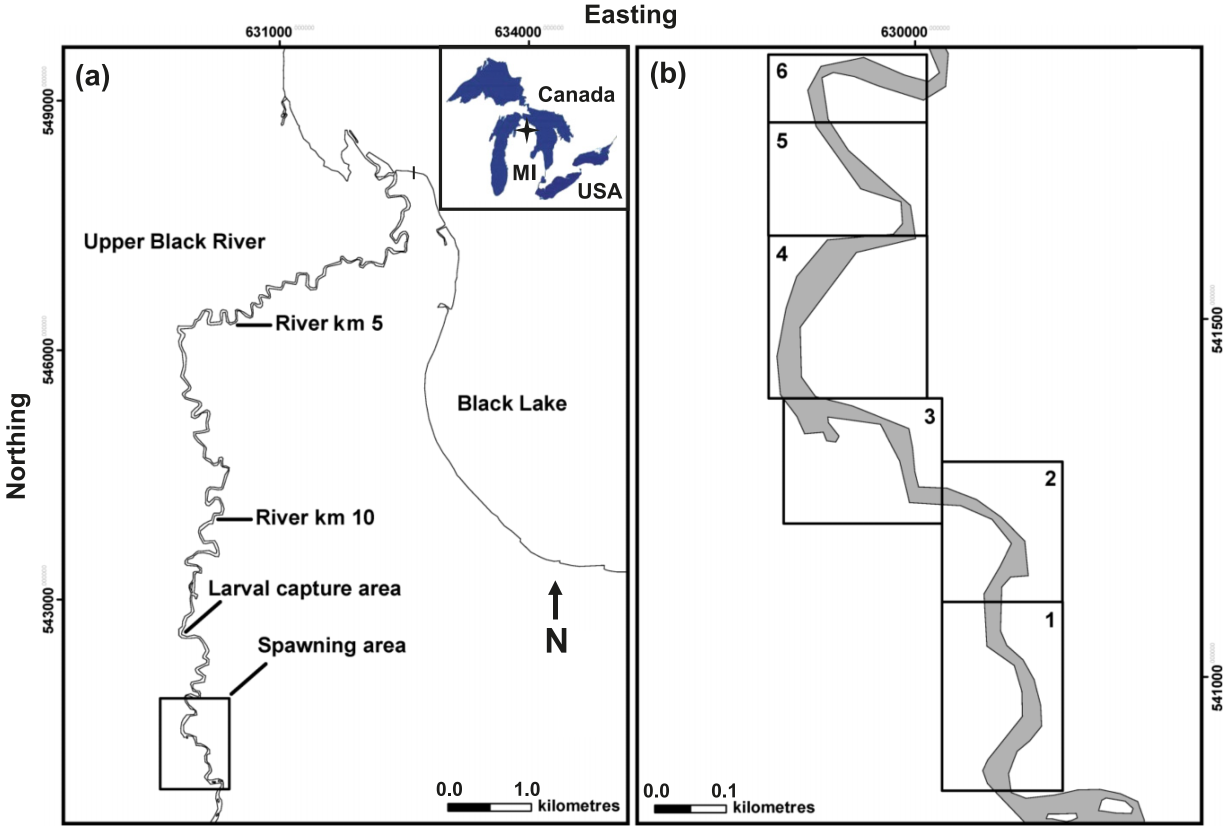
DNA was extracted from fin clips using the QIAGEN DNeasy$^{(R)}$ kit (QIAGEN, Inc.). DNA concentration was measured using a Nanodrop 1000 spectrophotometer (Thermo Fisher Scientific, Inc.). All samples were genotyped at 12 tetra-nucleotide microsatellite loci including *Spl 120* (McQuown et al. 2000); *AfuG 68B* (McQuown et al. 2002); *Aox 27* (King et al. 2001); *AfuG 68*, *AfuG 9*; *AfuG 63*, *AfuG 74*, *AfuG 112*, *AfuG 56*, *AfuG 160*, *AfuG 195*, and *AfuG 204* (Welsh et al. 2003). Using polymerase chain reaction (PCR), 100 ng DNA was amplified in 25 μL reaction mixtures containing 2.5 μL of 10X PCR buffer (1 mol·L^{-1} tris-HCl, 1.5 mol·L^{-1} MgCl$_2$, 1 mol·L^{-1} KCl, 1 g·L^{-1} gelatin, 1 mL·L^{-1} NP-40, and 1 mL·L^{-1} triton X); additions of 1 mmol·L^{-1} MgCl$_2$ (1.5 mmol·L^{-1} MgCl$_2$ for *AfuG 9*) for all reactions, but no additional MgCl$_2$ for *AfuG 63*, *Aox 27*, and *AfuG 74*; 0.8 mmol·L^{-1} deoxy-nucleotide-triphosphate (dNTP); 10 pmol fluorescently labeled forward and unlabeled reverse primers and 0.5 U of *Taq* polymerase.

All PCR reactions were conducted using a Robocyler 96 thermal cycler (Stratogene). The PCR conditions were 94 °C for 2 min, followed by 30 cycles of 1 min for primer-specific annealing temperatures (48 °C for *AfuG 9*, *AfuG 63*, and *AfuG* 112; 50 °C for *AfuG 74*; 53 °C for *Aox 27*; 56 °C for *AfuG 68* and *AfuG 68B*; 58 °C for *AfuG 56*, *AfuG 160*, and *AfuG 195*; and 62 °C for *Spl 120* and *AfuG 204*), 72 °C for 1 min, and the final extension for 2.5 min at 72 °C. PCR products were run on 6% denaturing polyacrylamide gels and visualized using a Hitachi FMBIO II scanner. Allele sizes were determined independently by two experienced personnel, based on commercially available standards (MapMarker^{TM}, Bioventures Inc.) and samples of known genotype. Errors in genotyping were empirically checked by blindly regenotyping a random 10% of all samples. Reported genotyping error is the ratio between observed number of allelic-errors and total number of alleles compared (Bonin et al. 2004).

Parentage analysis

There are numerous programs that utilize multilocus genetic data to estimate parentage (e.g., CERVUS, Kalinowski et al. 2007; PASOS, Duchesne et al. 2005; COLONY, Jones and Wang 2010), and the efficacy of use of different programs or combinations of programs has been widely debated (Christie 2010; Jones et al. 2010; Walling et al. 2010). Use of multiple programs that are based on different statistical properties to determine parentage has been advocated (Lee 2008; Jones et al. 2010). We used complimentary aspects of two programs, the Parentage Allocation of Singles on Open Systems (PASOS) program, version 1.0 (Duchesne et al. 2005) and CERVUS version 3.0 (Kalinowski et al. 2007) to conduct parentage analysis. Output of putative parent–offspring allocations from the two programs were jointly used to in-

Fig. 1. Study site on the Upper Black River, Michigan (MI), USA, showing positions of adult spawning areas and larval collection sites (*a*), and an enlarged view of the six spawning areas (*b*).



crease the proportion of offspring allocated to parents and allocation accuracy. We used PASOS to estimate the proportion of adults captured and parentage allocation correctness. PASOS can detect missing parents when they have not been collected, based on multilocus genotypes of both parents and offspring. We set the maximum number offset tolerance (MOT), the maximum number of offsets between a parental and an offspring allele that PASOS accepts as possibly due to a scoring error (Duchesne et al. 2005), of 1 and the error model (0, 0.01, 0.98, 0.01, 0) for simulations in PASOS. We conducted simulations over five iterations of 1000 pseudo-offspring to estimate the allocation correctness. Under the restricted MOT (MOT of 1 is more restricted than MOT of 2), we used the allocation function in PASOS to assign each offspring to two collected parents and estimate the proportion of adults captured from the natural population. The proportion of captured adults was used to parameterize analysis in CERVUS program.

CERVUS is the most commonly used categorical parentage technique (Christie 2010; Jones et al. 2010) and assigns progeny to a particular nonexcluded parent based on likelihood scores (LOD scores obtained by taking the natural log of the ratio of likelihoods) derived from the genotypes of all offspring and parents sampled (Marshall et al. 1998; Jones and Ardren 2003; Kalinowski et al. 2007). Simulations conducted within CERVUS to determine power and likelihood of assignment were based on empirical estimates of population allele frequency, the proportion of adults captured (PASOS output) and an empirical estimate of genotyping error (1.04%). Most likely candidate parent pairs of offspring from the assignment output were accepted as "true parent pairs" based on the criteria of ≥65% trio confidence with zero or 1 mismatch between parents and offspring genotypes. Assignment outputs from the two programs based on criteria above were then compared. Each male parent-female parent-offspring triplet that was inconsistent between the two programs was evaluated based on biological information (e.g., proximity of captured time and captured location of both parents).

Genetic differences and relatedness among spawning groups

Repeatability in spawning time and spawning location for individual lake sturgeon males and females that have been captured 2 or more times (Forsythe 2010) suggests the possibility of genetic differentiation among spawning groups within the UBR population, which may contribute to differences in ELDTUD. Owing to higher repeatability in individual spawning time than in spawning location (0.56 and 0.42 vs. 0.16 and 0.04 for females and males, respectively, Forsythe 2010), we predicted that genetic differences could be detectable among members of different adult groups spawning at different times but not among groups spawning at different locations. We first estimated genetic differentiation (F_{ST}) among the three temporal spawning groups (early, middle, and late) and among six spatial spawning groups of adults using the method of Weir and Cockerham (1984) implemented in the program FSTAT 2.9.3 (Goudet 2001 (updated from Goudet 1995)). If adult groups could be genetically differentiated, we then compared distributions and mean of inter-individual relatedness (r_{xy}) within and between genetically different groups. When a population is structured by groups of adult spawning at different times, nonrandom mating by spawning time (temporal assortative mating (Fox 2003; Devaux and Lande 2008)) can increase genetic relatedness among individuals within groups. Other authors have specifically suggested that r_{xy} is an appropriate means to quantify the degree of genetic differences between members of different groups within a population (Hendry and Day 2005). We used moment-based estimators for pair-wise relatedness, r_{xy} (Queller and Goodnight 1989) based on 12 microsatellite-locus genotypes obtained using the KIN-GROUP version 2 program (Konovalov et al. 2004). Nonparametric Kolmogorov–Smirnov tests were used to compare distributions of r_{xy} among adult groups. A permutation approach was used to test for difference in mean relatedness within and among spawning groups using a SAS-based program as in Ratnayeke et al. (2002). We also report allelic diversity, heterozygosity, probabilities of false parental exclusion, and tests (with Bonferroni correction) for deviations from Hardy–Weinberg equilibrium using CERVUS.

Statistical analysis

We defined the embryonic and larval developmental time until dispersal (ELDTUD) as the number of days elapsed between the day of female capture and the day of offspring capture as the larvae dispersed downstream from the spawning site (Fig. 1*a*). Accordingly, ELDTUD included periods of incubation, yolk absorption in the stream substrate, and migration over a distance of 2 km.

We calculated cumulative thermal units (CTU) and examined the importance of factors affecting ELDTUD. CTU (degree-day, °C) was calculated using the method of Kempinger (1988). CTU for each larva was estimated as the sum of daily temperature (adjusted by subtracting a constant 5.8 °C) during the period from egg deposition until dispersal.

We used analysis of variance (ANOVA) and pair-wise *t* tests with unequal variance to test CTU differences among offspring produced by females that spawned at different times (“early”, “middle”, and “late”). Females were grouped into three categories based on observed discontinuities in spawning dates among adult groups. Difference in CTU among larval groups would indicate other factors beside temperature affecting ELDTUD (Kamler 2002).

We used generalized linear and nonlinear mixed effect models to simultaneously examine environmental factors and maternal effects affecting ELDTUD. Environmental factors include mean daily water temperature and mean daily river discharge that larvae experienced during the period from egg deposition until capture. We defined maternal effects to include female spawning date (day of year), spawning location ($n = 6$, Fig. 1*b*) and body size (i.e., fork length) and the random effect of females. Females were treated as a random effect to account for nonindependence among offspring of the same female.

We initially fit data to the full model including fixed effects of water temperature (Tem_j), river discharge (Dis_l), spawning day of year (Date_m), spawning location (Loc_n), fork length (Len_o), and possible two-way interactions of fixed effects and random effect of females (Fem_u) using generalized linear mixed effect models. Two-way interactions of fixed effects were examined based on biological relevance as recommended by Burnham and Anderson (2002). Accordingly, the effect of female body size on ELDTUD would not be expected to vary as a function of the time or location of spawning. Therefore, we excluded interactions with female body size from the initial full model. We also tested for multicollinearity among independent variables of the model by examining the variance inflation factor (VIF) from the linear model with all fixed effects without interactions and the Pearson correlation of variable pairs (Graham 2003). There was evidence of multicollinearity between water temperature and day of year (VIF of temperature and day of year was 10.3 and 7.8, respectively; Pearson correlation, $r = 0.91$, $n = 1154$, $P < 0.001$). To isolate confounded effects of these two explanatory variables, we first assumed one variable was more explanatory of observed variance. We then replaced the less important variable by its residuals from the regression against the more important variable (Graham 1997, 2003; review in Heikkinen et al. 2006). We reasoned that day of year representing the conditions including temperature at spawning would be a more important explanatory variable than mean water temperature. The unique contribution of day of year was disassociated from the shared effects of temperature by adding temperature residuals (T.res_j) from regression of water temperature (dependent variable) against day of year (independent variable) in the full model. We evaluated normality of the data by examining residual plots of response and predicted variables. Based on the plot showing the nonlinear relationship between ELDTUD and river discharge, the quadratic term of river discharge was treated as a fixed effect and was also added to the model:

$$\text{[1]}\quad \begin{aligned} \text{ELDTUD} = {} & \mu + \text{T.res}_J + \text{Dis}_l + \text{Dis}_l^2 + \text{Date}_m \\ & + \text{Loc}_n + \text{Len}_o + \text{Dis} \times \text{Date}_{lm} + \text{Dis} \\ & \times \text{Loc}_{\text{ln}} + \text{Date} \times \text{Loc}_{mn} + \text{Fem}_u \\ & + \varepsilon_{ijlmnou} \end{aligned}$$

where μ is the overall mean, (×) represents the interaction of two variables; and $\varepsilon_{ijlmnou}$ is the residual error for each larva. In the above model, the random effect of females (Fem_u) was assumed to be normally distributed.

Model selection for the best model from a set of all possible combinations of environmental factors and maternal effects in eq. 1 was based on Akaike Information Criterion (AIC) (Burnham and Anderson 2002). The inclusion of females as a random effect in the full model was examined first, followed by selecting fixed effects of interactions and main effects (Ngo and Brand 1997). The random effect was included if the AIC difference (ΔAIC) of the full model without and with random effect of females was greater than 4, indicating the model without random effect was less supported by the data (Burnham and Anderson 2002). We used restricted maximum likelihood (REML) to fit models differing by the presence of the random effect and maximum likelihood (ML) for competing models differing in fixed effects (Pinheiro and Bates 2000). The relative importance of environmental factors or maternal effects in ELDTUD was assessed based on ΔAIC [Δ_i = (AIC of the *i*th model) – (smallest AIC)] and Akaike weights ($w_i = \exp(-\Delta_i/2)$). Variables with higher sum w_i (importance weight) from all models containing the variables in question are more important

(Burnham and Anderson 2002). We also used a confidence set for Kullback–Leibler best models (Burnham and Anderson 2002) to provide the best explanation of variation in ELDTUD. The 95% confidence set represents the subset of models with the sum of $w_i \geq 0.95$. All statistical analyses were conducted using R (R Development Core Team 2009).

Results

Adult capture, larval collection, and parentage analysis

The 2007 spawning season extended from 23 April to 1 June. Timing of spawning activity was multimodal with three distinct peaks in spawning (Fig. 2*a*). More individuals were observed spawning at the beginning ("early" adults, $n = 108$ individuals) and middle of May ("middle" adults, $n = 74$) as opposed to later in May ("late" adults, $n = 24$). Larvae dispersed in two peaks 15–20 d following adult spawning (Fig. 2*b*). Water temperatures increased throughout the spawning season, from 10.6 °C to 22 °C. River discharge (range 5.71–9.61 $m^3 \cdot s^{-1}$) was higher and more variable during adult spawning than during the larval dispersal period.

Estimates of allele diversity (range from 2 to 11, average 5.3 alleles per locus) and expected heterozygosity (0.59) of lake sturgeon adults were moderate. Genotype frequencies from 11 of 12 loci conformed to Hardy–Weinberg expectations for all adults sampled. Mean polymorphic information content and nonexclusion probability for parental pairs over all 12 loci were 0.53 and 0.00006, respectively.

Of the total number of captured adults (143 males and 63 females) PASOS estimated that 89.2% of females and 87.2% of males contributed to the larvae collected. The assignment rate of offspring to two collected parents was 74.7% (1079 parents–offspring allocations) and mean allocation correctness (±SD) was estimated to be 79.1 ± 0.6%. The assignment rate from CERVUS was 85.5% (1234 allocations). Comparison of parent–offspring triplets assigned from the two programs revealed assignment consistency to be 78.6%. Exclusion of larvae with allocation discrepancies between the two programs did not affect results (data not shown). Each parent–offspring triplet in PASOS parental allocations was also one of the most likely triplets with positive LOD scores found in CERVUS. Based on concordant assignments from both programs, 1154 offspring (79.9% of larvae collected) were assigned to collected parents including 137 male parents (94.5% of males captured) and 58 female parents (92.1% of females captured). The average number of offspring collected per male was 8.4 ± 6.5 and per female was 19.9 ± 14.3.

Embryonic and larval developmental time until dispersal

ELDTUD varied from 4–36 days (mean ± SD = 20.3 ± 5.7, $n = 1154$). ELDTUD of larvae from the same female parent (the time period from the first to the last offspring collected) was 11.6 ± 4.0 d ($n = 58$ female parents). ELDTUD was significantly different among larvae whose female parents spawned during different segments (early, middle, or late) of the breeding season ($F_{[2,96.3]} = 655$, $P < 0.001$) (Table 1). Cumulative thermal units (CTU) averaged 201 ± 53 degree-days and also differed among larval groups (Table 1).

Certain combinations of both environmental variables and maternal effects better explained variability in ELDTUD than did variables within only one or the other of the variable categories (Table 2). ELDTUD was best explained by model 8 ($w_i = 0.66$; Table 2) including the random effect of females and fixed effects of temperature residuals, river discharge, quadratic effect of discharge, spawning date, spawning location, and the discharge and spawning date interaction. Fixed effects in the model explained most of variation in ELDTUD (88.0%). Of the remaining variation unexplained by the fixed effects, the random effect representing differences among females (variance 8.77, CI = 6.05–12.71) accounted for 94.5% (CI = 92.8%–95.8%), which is much greater than differences within females (i.e., residual variance) in average ELDTUD.

Based on Kullback–Leibler criteria, river discharge and spawning date associated with temperature were equally important predictors of ELDTUD. Importance weights for all of these factors (sum of w_i for models containing these factors) were close to 1 (Table 2). ELDTUD was nonlinearly related to river discharge. Coefficient estimates of the linear term (slope ± SE = –143 ± 3.0) and quadratic term (slope ± SE = 2.58 ± 0.16) of river discharge in the final model (Table 3) indicate the nonlinear decrease in ELDTUD with increasing river discharge. Larvae produced by females spawning early in the season when water temperature was comparatively low (14–15 °C) dispersed after longer periods of time compared with larvae produced by females spawning later in the year (slope ± SE = –6.40 ± 0.12, $t_{[1,56]} = -51.9$, $P < 0.001$). However, the magnitude of effects of spawning date and river discharge on ELDTUD depended on the interaction between these variables (Table 3). Spawning date effects on ELDTUD included the effect of water temperature (Pearson correlation, $r = 0.91$, $n = 1154$, $P < 0.001$). Spawning date alone explained 55.8% of the variation in ELDTUD, compared with 20.9% variation explained by water temperature (based on coefficient of determination, r^2, from linear models of ELDTUD with each predictor of spawning date and temperature, respectively). Nevertheless, temperature residuals increased model fit. The full model with temperature residuals had an AIC score lower compared with the same model without temperature residuals (ΔAIC = 6), indicating the importance of temperature when its effect was disassociated from the shared effect of spawning date on ELDTUD.

Spawning location and female body size were less important predictors of ELDTUD (importance weights were 0.30 and 0.15, respectively; Table 2). When the fixed effect of spawning date and random effect of females were included in the model to account for variation in ELDTUD of larvae from different families, the effects of spawning location and female body size on ELDTUD no longer improved model predicting (comparing AIC values of models 9 and 10, Table 2).

The confidence set for Kullback–Leibler best models included models 8, 7, and 5 (sum $w_i = 0.95$). These nested models supported the hypothesis that a combination of environmental factors and maternal effects best explained variation in ELDTUD. There was no evidence ($w_i \sim 0$) supporting the hypotheses that either environmental factors or reproductive variables alone provided the best prediction of ELDTUD of lake sturgeon.

Genetic differences and relatedness among spawning groups

Genetic differences (F_{ST}) were not significant among females and adult groups spawning at different locations

Fig. 2. (*a*) Number of adults captured and (*b*) number of larvae collected and those assigned to early, middle, or late female groups, together with mean daily water temperature and river discharge during the periods from egg deposition through embryonic and larval development until dispersal (ELDTUD).

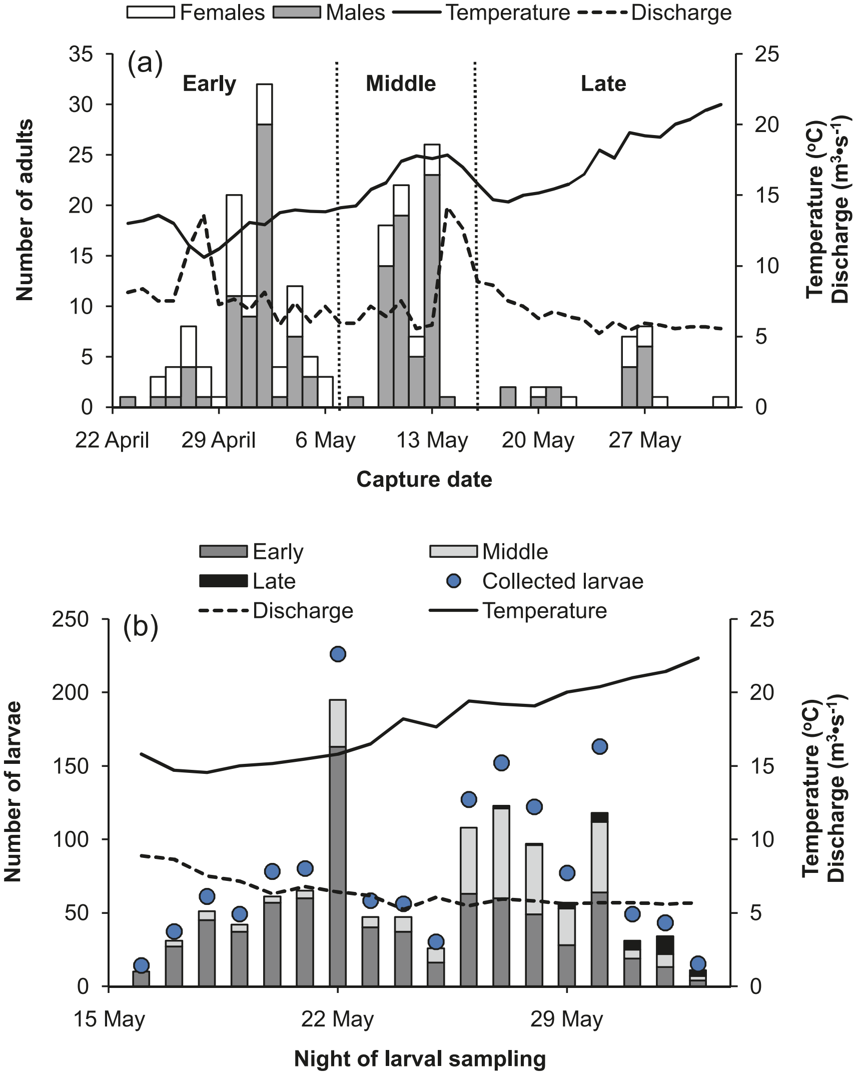


Table 1. Mean (±1 SD) temperature at spawning and daily temperature over the embryonic and larval developmental time until dispersal (ELDTUD) and cumulative thermal units (CTU) of three larval groups illustrated in Fig. 3.

Larval group (female spawning date)	No. of observations	Spawning temperature (°C)	Mean daily temperature (°C)	ELDTUD (days)	CTU (degree-days)
Early (25 April – 6 May)	792	12.9±1.0	15.4±0.5	22.7±4.6	219±48
Middle (10–13 May)	329	16.9±0.8	16.6±0.3	15.4±3.4	168±41
Late (20–27 May)	33	15.9±1.3	18.3±0.7	9.2±2.7	114±33

Note: ELTUD, egg deposition through embryonic and larval development until dispersal. All variables differed significantly among periods ($P < 0.001$).

(95% confidence interval of overall F_{ST} (bootstrapping over loci) for only females ranged from 0.000 to 0.016, and for all adults from 0.000 to 0.002). Genetic differences were observed among adult groups (males and females) spawning at different times but not among different spawning groups of females. Pairwise F_{ST} between early and middle adults groups (0.007) was significant ($\alpha = 0.05$, after standard Bonferroni corrections, P-value adjusted = 0.016). However, no genetic differences were observed between early–late (F_{ST} = 0.002) and middle–late (F_{ST} = 0.006) adult groups (P = 0.17 and 0.20, respectively). Mean interindividual relatedness (r_{xy}) among adults of the middle spawning group (mean ± SD; 0.034 ± 0.213) was significantly higher than r_{xy} among members of the early spawning group (–0.015 ± 0.223) and late spawning group (–0.017 ± 0.209). Distributions of cumulative expected frequencies of r_{xy} values were significantly different between middle adult group compared with early and late groups (differences in distribution, Kolmogorov–Smirnov tests, 9.8% and 12.1%, respectively, $P < 0.001$). No differences in mean (P = 0.45) and distribution (P = 0.81) of

Table 2. Model structure describing embryonic and larval developmental time until dispersal (ELDTUD) and model selection criteria based on Akaike Information Criterion (AIC), AIC difference (ΔAIC), and Akaike weight (w_i).

No.	ELDTUD Model	k	AIC	ΔAIC	w_i
	Including environmental and maternal effects				
1	T.res$_j$ + Dis$_l$ + Dis$^2{}_l$ + Date$_m$ + Loc$_n$ + Len$_o$ + Dis×Date$_{lm}$ + Dis×Loc$_{ln}$ + Date×Loc$_{mn}$ + Fem$_u$	24	2868	27	0.00
2	T.res$_j$ + Dis$_l$ + Dis$^2{}_l$ + Date$_m$ + Loc$_n$ + Len$_o$ + Dis×Date$_{lm}$ + Dis×Loc$_{ln}$ + Date×Loc$_{mn}$	23	4678	1837	0.00
3	T.res$_j$ + Dis$_l$ + Date$_m$ + Loc$_n$ + Len$_o$ + Dis×Date$_{lm}$ + Dis×Loc$_{ln}$ + Date×Loc$_{mn}$ + Fem$_u$	23	361	220	0.00
4	T.res$_j$ + Dis$_l$ + Dis$^2{}_l$ + Date$_m$ + Loc$_n$ + Len$_o$ + Dis×Date$_{lm}$ + Date×Loc$_{mn}$ + Fem$_u$	19	2848	7	0.02
5	T.res$_j$ + Dis$_l$ + Dis$^2{}_l$ + Date$_m$ + Loc$_n$ + Len$_o$ + Dis×Date$_{lm}$ + Fem$_u$	14	2844	3	0.15
6	T.res$_j$ + Dis$_l$ + Dis$^2{}_l$ + Date$_m$ + Loc$_n$ + Len$_o$ + Fem$_u$	13	3980	1139	0.00
7	T.res$_j$ + Dis$_l$ + Dis$^2{}_l$ + Date$_m$ + Loc$_n$ + Dis×Date$_{lm}$ + Fem$_u$	13	2844	3	0.15
8	T.res$_j$ + Dis$_l$ + Dis$^2{}_l$ + Date$_m$ + Dis×Date$_{lm}$ + Fem$_u$	8	2841	0	0.66
9	Dis$_l$ + Dis$^2{}_l$ + Date$_m$ + Dis×Date$_{lm}$ + Fem$_u$	7	2847	6	0.03
	Including only maternal effects				
10	Date$_m$ + Loc$_n$ + Len$_o$ + Date×Loc$_{mn}$ + Fem$_u$	15	6249	3408	0.00
11	Date$_m$ + Fem$_u$	4	6232	3391	0.00
	Including only environmental variables				
12	Tem$_j$ + Dis$_l$ + Dis$^2{}_l$ + Tem×Dis$_{jl}$	6	6310	3469	0.00
13	Tem$_j$ + Dis$_l$ + Tem×Dis$_{jl}$	5	6309	3468	0.00

Note: ELTUD, egg deposition through embryonic and larval development until dispersal. Models include different combinations of fixed effects of temperature residuals (T.res$_j$, from temperature [Tem$_j$] regression against spawning day of year [Date$_m$]), river discharge (Dis$_l$), location (Loc$_n$), Fork length (Len$_o$), and interactions of discharge – day of year (Dis×Date$_{lm}$), discharge–location (Dis×Loc$_{ln}$), and day of year – location (Date×Loc$_{mn}$), and random effect of females (Fem$_u$); k, total number of parameters including intercept and error terms. Models 1 and 2 were fit by restricted maximum likelihood (REML) for testing the importance of random effect.

Table 3. Coefficient estimates of fixed effects in the best model (model 8 in Table 2) representing relationships between model parameters and embryonic and larval developmental time until dispersal (ELDTUD).

Parameters	Coefficient estimate	SE	denDF	t value	P value
Intercept	1072	18.60	1092	57.60	<0.001
Temperature residual	–0.43	0.16	1092	–2.62	<0.010
Discharge	–143	3.00	1092	–48.10	<0.001
Discharge^2	2.58	0.16	1092	16.06	<0.001
Spawning date	–6.40	0.12	56	–51.87	<0.001
Discharge×spawning date	0.72	0.02	1092	44.08	<0.001

Note: ELTUD, egg deposition through embryonic and larval development until dispersal. SE, standard error; denDF, denominator degrees of freedom. The numerator degrees of freedom for all parameters are equal to 1.

r_{xy} were observed between early and late groups. Mean r_{xy} estimated within and between groups of adults were also not significantly different ($P = 0.08$).

Discussion

The individual-based approach used in the present study revealed that environmental and maternal factors were relatively important to ELDTUD, and that variation in ELDTUD was lower among larvae produced by the same female relative to those produced by different females. Similarly, variation in ELDTUD was lower among larvae produced by females spawning within the same group relative to those produced by females that spawned at different times (early, middle, or late) of the spawning season.

Nongenetic components of maternal effects (e.g., spawning time and spawning location) confounded by environmental factors affected ELDTUD. Using statistical approaches to account for correlations among variables and multimodel inference based on Kullback–Leibler information (Burnham and Anderson 2002; Johnson and Omland 2004), we disassociated confounding effects due to collinearity among predictor variables. Maternal effects (individual female as a random effect and spawning date) and environmental factors (water temperature and discharge) were in the confidence set for Kullback–Leibler best models, indicating that these variables were of comparable importance to ELDTUD of larval lake sturgeon.

Temperatures during spawning and embryonic and larval development can affect offspring traits, including body size (Fox and Czesak 2000) and developmental time (Gillooly and Dodson 2000; Stillwell and Fox 2005). Although temperature impacts larval developmental time in many species (e.g., Gillooly et al. 2001; O'Connor et al. 2007), interindividual variation in developmental time may be substantial. In our study, mean daily temperature only explained 20.9% of variation in ELDTUD of larval lake sturgeon. The degree of temperature-dependency of ELDTUD could differ during the three consecutive developmental periods represented by this composite variable including (*i*) embryonic development, (*ii*) yolk sac absorption, and (*iii*) emergence and dispersal from spawning areas. The first two periods are likely more dependent on water temperature (i.e., Wang et al. 1985; Pepin et al. 1997; Kamler 2002). The third period may depend more on other environmental factors (e.g., river discharge, food, and predators), larval age or size (Elliott 1987; Day and Rowe 2002), larval behavior (Shanks 2009), lunar cycle effects on larval concealment (Hernandez-Leon 2008), and female spawning behavior (Copp et al. 2002; Hogan and Mora 2005; Shanks 2009).

Another environmental factor, river discharge, has been shown to affect the timing of larval emergence (Fausch et al. 2001) and movements (Elliott 1987; Siegel et al. 2003), and therefore was predicted to affect ELDTUD. Fausch et al. (2001) found that emergence of rainbow trout (*Oncorhynchus mykiss*) fry occurred during the period of high water velocity. After emergence, larvae can be dislodged from substrate by strong currents (salmonids, Elliott 1987; pallid sturgeon *Scaphirhynchus albus*, Kynard et al. 2007). However, for some species such as reef fishes, larvae can actively adjust their swimming speed. At high river discharge, larvae swim more slowly (Hogan and Mora 2005). Similarly, lake sturgeon larvae might exhibit considerable behavioral plasticity by remaining in substrates longer during times of high river discharge.

The effect of female spawning date on ELDTUD could be due to differences in environmental conditions (e.g., water temperature and discharge) at spawning and also to differences among adult groups. In many fish species, adult groups spawning early or late in the season might differ in maternal effects (Chambers 1997; Einum and Fleming 2000). This is also the case for lake sturgeon, evidenced by highly significant differences in ELDTUD among the three larval groups (Fig. 3) and greater among-female than within female variation in ELDTUD (Fig. 4). Adult groups that spawned at different times exhibited the low levels of genetic differentiation, providing a certain degree of support for the hypothesis that maternal effects on ELDTUD could be due in part to genetic factors. Higher F_{ST} among temporal spawning groups than spatial spawning groups is consistent with stronger effects of spawning time compared with spawning location on ELDTUD, which provides further evidence of a genetic component that may partly contribute to differences in ELDTUD. However, given the low intergroup variance in frequency of alleles at the microsatellite loci used, gene flow among members of different spawning groups is likely. Further investigation of the concordance among measures of intergroup variance in additive and neutral genetic traits is warranted.

The importance of spawning date in determining larval developmental and dispersal time observed in lake sturgeon was also reported in marine fish and invertebrates (Reitzel et al. 2004). Edwards et al. (2007) used 2-dimensional dispersal kernels to examine factors affecting larval dispersal, and found that spawning time and location might be more important than larval behavior in determining larval dispersal time. In our study, the effect of spawning location on larval dispersal time was less important than spawning date. The relatively small spawning areas of the lake sturgeon population covering 1.5 km of UBR may explain comparatively minor effects of spawning locations on ELDTUD.

Incorporating both ecological and genetic data in this study provided a useful tool to explore degrees of, and factors contributing to interindividual variation in ELDTUD of lake sturgeon. Individual-level measurement of ELDTUD based on the knowledge of parentage was more informative compared with population-based observations. For example, our results of CTU influences on ELDTUD were different from those reported by Smith and King (2005) for the same lake sturgeon population. Smith and King (2005) calculated CTU based on observations from the day of adult spawning to the day of peak larval drift. They reported that CTU for two or three larval groups from each spawning season from the years 2000 through 2002 ranged from 136.2–181.2. In their study, CTU and time to dispersal of the early larval group were lower than for the late larval group in the same year, which is opposite of our findings. Water temperature is generally colder early in the spawning season. Consequently, the time from egg deposition to dispersal of larvae would be expected to be longer, owing to temperature-dependent development (O'Connor et al. 2007). Importantly, population-based approaches could not detect important relationships between developmental time at early life stages and spawning

Fig. 3. Embryonic and larval developmental time until dispersal (ELDTUD) of three groups of larvae whose maternal parents spawned during "early" (open circle), "middle" (open diamond), or "late" (open triangle) periods of the spawning season. Where symbols appear darker, this is because more than one offspring was characterized by the same ELDTUD and female spawning date.

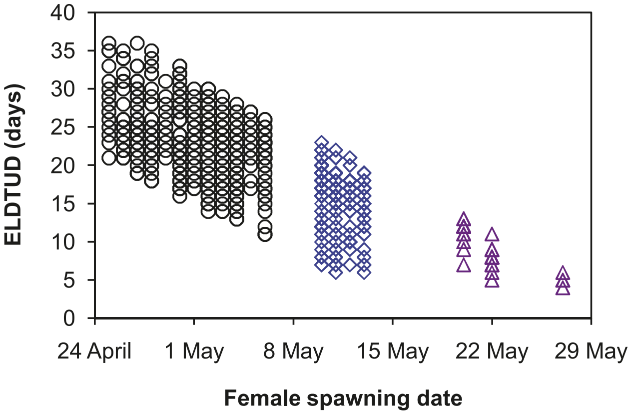
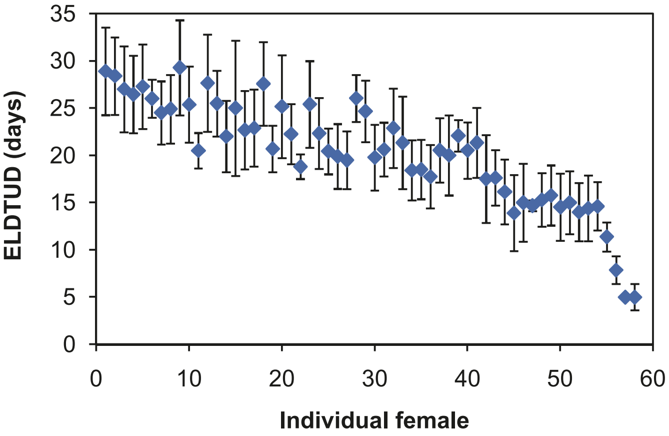


Fig. 4. Mean and standard deviation of embryonic and larval developmental time until dispersal (ELDTUD) among siblings from the same female parent. Individual females were ordered left to right by spawning date.



behavior of individual female parents. Population-based estimates of CTU might introduce considerable bias in estimating ELDTUD in the absence of genetic data that conclusively ties larvae to a specific date and location of a spawning event.

Several factors should be considered when interpreting the data. First, the characterizations of spawning time and spawning locations were based on the time and location of adult capture. This assumption could lead to decreased precision in calculating ELDTUD. However, daily surveys of the spawning sites suggest that few females spent more than 2 or 3 days in the spawning areas (Forsythe 2010), indicating minor effects on ELDTUD given the duration of spawning activity. Second, data were collected from a single year, while interannual variation in environmental conditions can be large and different groups of adults spawn in different years (Forsythe 2010). Based on Akaike weights of the best model set, we believe that the relative importance of the variables in our model will not vary substantially, although ELDTUD observed as a function of these variables may vary depending on interannual variation in environmental conditions realized each spawning season. Finally, the dispersing larvae were collected within 2 km of the spawning area, and numbers captured during this critical life stage may not reflect the numbers of larvae that disperse over different ELDTUD periods and survive.

Future research into the costs of timing of dispersal is necessary, and can be accommodated using the genetic methodologies employed in this study. Rates of mortality may vary as a function of larval body size, whereby selection acts to select individuals that disperse at different times and concomitantly at different sizes (Sogard 1997). Predation acting on different size classes of juveniles is likely a significant source of mortality (e.g., Mittelbach and Persson 1998). Spatially complex rearing habitats are expected to contribute to variation in larval growth and dispersal time. Costs of dispersal are expected to be high, and can increase if larvae disperse at certain times or developmental stages in response to stream conditions. Further analyses are warranted to address the costs of dispersal time in terms of probability of mortality during this period.

Our findings have important implications for early life history studies and for species of conservation concern. CTU and timing of adult spawning events should be simultaneously taken into account when predicting larval ELDTUD. Individual-based estimates revealed different levels of variation in ELDTUD within and between female families and among female groups. Such variation likely provides conditions for natural selection to act, and may be of importance for retention of levels of viability at the population level. Effects of environmental factors did not outweigh maternal effects including spawning time on ELDTUD. Accordingly, we suggest that the maternal effects may counter the effects of the environmental variables on development, performance, and survival of larval lake sturgeon as well as other fish species.

Acknowledgements

Funding for this study was provided by the Great Lakes Fishery Trust, the Michigan Department of Natural Resources, and the Michigan Agricultural Experiment Station at Michigan State University. C. Davis, A. Ohm, and R. VanHorn assisted with collection of larvae in the field. J. Bence, D. Hayes, and G. Mittlebach provided constructive comments and discussion pertaining to earlier drafts of the paper. Comments from anonymous reviewers helped improve the manuscript. Duong Thuy Yen would like to thank the Vietnamese government's "Project 322" for financial support and the opportunity to pursue her Ph.D. studies at Michigan State University, USA.

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