Environ Biol Fish
DOI 10.1007/s10641-011-9804-4

Relative larval loss among females during dispersal of Lake Sturgeon (*Acipenser fulvescens*)

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Received: 14 March 2010 / Accepted: 23 March 2011

Abstract Mortality that occurs during larval dispersal as a consequence of environmental, maternal, and genetic effects and their interactions can affect annual recruitment in fish populations. We studied larval lake sturgeon (*Acipenser fulvescens*) drift for two consecutive nights to examine whether larvae from different females exposed to the same environmental conditions during dispersal differed in relative levels of mortality. We estimated proportional contributions of females to larval collections and relative larval loss among females as larvae dispersed downstream between two sampling sites based on genetically determined parentage. Larval collections were composed of unequal proportions of offspring from different females that spawned at upstream and downstream locations (~0.8 km apart). Hourly dispersal patterns of larvae produced from females spawning at both locations were similar, with the largest number of larvae observed during 22:00–23:00 h. Estimated relative larval loss did not differ significantly among females as larvae were sampled at two sites approximately 0.15 and 1.5 km from the last section downstream of spawning locations. High inter- and intra-female variation in larval contributions and relative larval loss between nights may be a common feature of lake sturgeon and other migratory fish species, and likely is a source of inter-annual and intra-annual variation in fish recruitment.

Keywords Larval dispersal · Mortality · Maternal effects · Lake sturgeon

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Published online: 07 April 2011

Introduction

Mortality during early life stages is a major factor affecting recruitment in fish populations (review in Pepin 2009). Quantifying mortality rates of fish at early life stages is important to understand fish population dynamics (Keesing and Halford 1992; Pepin 2009). During the larval stage, high mortality occurs at critical periods, for example, when larvae switch from endogenous feeding (yolk absorption) to exogenous feeding (Kamler 1992; Fuiman and Higgs 1997), and when individuals disperse from spawning locations to nursing grounds (Bartsch et al. 1989; Kamler 1992; Fuiman and Higgs 1997). In many fish species, these two events occur at or near the same time, as larvae often begin feeding prior to or during dispersal [e.g., lake sturgeon *Acipenser fulvescens* (Auer and Baker 2002)]. Therefore, larvae become most susceptible to mortality during the initial period of dispersal when larvae emerge and disperse from the spawning ground (Einum and Fleming 2000).

Exogenous and endogenous factors can contribute to larval mortality during dispersal (Kamler 1992; Cowen and Sponaugle 2009). Major exogenous sources include biotic (e.g., predation, food availability) and abiotic factors (e.g., extreme temperatures, stream flow) (Mion et al. 1998; Kamler 1992; Cowen and Sponaugle 2009). Endogenous factors such as egg size, egg energy content (yolk size), larval size, etc., involve female phenotypes as maternal effects (e.g., size, age) (Hutchings 1991; Keckeis et al. 2000; Kamler 2005). Spawning time and location, which are also classified as maternal effects (Mousseau and Fox 1998) also determines the environmental conditions that developing eggs and larvae are exposed to after egg deposition (Trippel et al. 1997; Hendry and Day 2005; Jorgensen et al. 2008). Therefore, maternal effects can influence probabilities of survival at embryonic, larval and juvenile stages (Kamler 1992; Chambers 1997). Previous studies have emphasized that exogenous factors are dominant sources of larval mortality (Kamler 1992). Recently, increasing emphasis has been placed on the importance of larval behavior and genetic and maternal effects, which can lead to different probabilities of individual survival even when exposed to similar environmental conditions (Heath and Gallego 1997; Bolnick et al. 2003; Leis 2006; Fiksen et al. 2007; Clobert et al. 2009). When larvae are exposed to a common environment, if maternal effects are weak, and differences in probability of individual survival are small compared to strong effects of external environmental factors, the relative rates of offspring mortality among females would be expected to be similar. The opposite prediction would lead to greater inter-family variation compared to intra-family variation, which are two important components of selection, associated with larval survival. We tested these predictions using a well-studied population of lake sturgeon (*Acipenser fulvescens*).

Lake sturgeon are characterized by a long life span, delayed maturity, iteroparity and high fecundity but low annual recruitment due to high mortality during early life stages (Peterson et al. 2007; Forsythe 2010). Lake sturgeon do not provide post-ovulatory parental care for eggs or larvae (Bruch and Binkowski 2002). Deposited eggs adhere to stream substrates and hatch following 5 to 11 days of incubation depending on water temperature (Auer and Baker 2002; Smith and King 2005). Newly-hatched larvae remain in the stream substrates until yolk-sac reserves are depleted. Larvae are negatively phototactic and disperse downstream at night (Auer and Baker 2002; Kynard and Parker 2005; Smith and King 2005). This nocturnal behavior is considered to be an adaptive means of predator avoidance (Auer and Baker 2002), and has been observed in other sturgeon species (Kynard and Parker 2005) and other fishes (Crisp and Hurley 1991; Bradford and Taylor 1997). Previous studies have investigated spatial and temporal patterns in abundance of dispersing lake sturgeon larvae in relation to environmental conditions (e.g., water temperature and water flow), revealing that dispersing larvae were distributed in a non-uniform manner across the width of stream and position in the water column, and over different hours of the night (Auer and Baker 2002; Smith and King 2005). Little information is available about the contributions of different females to dispersing larvae each night. Neither are quantitative estimates available regarding relative larval loss among females during the larval dispersal period for many fish species including lake sturgeon.

The objectives of this study were to (i) quantify proportional contributions of different females to dispersing larvae collected during two consecutive nights; (ii) characterize hourly dispersal patterns of larvae from females spawning at different locations; and (iii) quantify relative larval loss among females and among female groups spawning at different

locations. Data pertaining to inter-family variation in contributions to larval dispersal and the relative roles of maternal and stream environmental effects on larval survivorship during dispersal can lead to greater understanding of inter-annual and intra-annual variation in fish recruitment.

Methods

Study site

A well-studied population of lake sturgeon located in Black Lake, northern Michigan was used for this study. In this system, the Upper Black River (UBR) is the largest tributary to Black Lake and the sole location used for spawning (Fig. 1). The Black Lake population is isolated by dams blocking immigration and emigration from other populations (Smith and King 2005). Adults spawn over ~1 km-section of the UBR, classified for the purposes of this study into two areas referred to as upstream (site B) and downstream (site C), which are utilized consistently by spawning females in all years (Forsythe 2010).

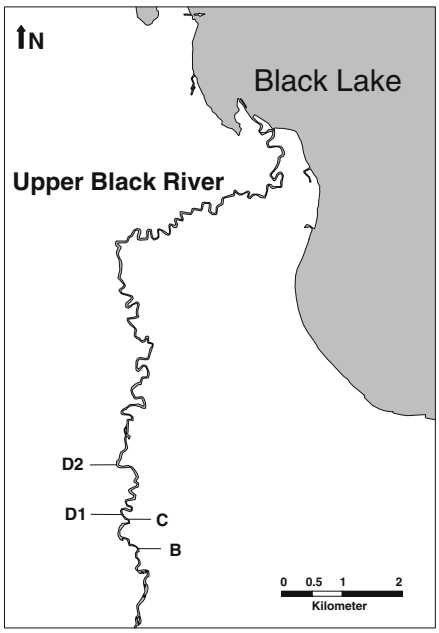

Fig. 1 The study site in the Upper Black River, Michigan, USA (latitude 45°43′N, longitude 84°15′W), showing upstream and downstream adult spawning locations (B and C, respectively); and upstream and downstream larval collection sites (D1 and D2, respectively)

Mean river width and water depth at sites B and C were 21 m and 0.46 m (range 0.0–0.96 m), and 12 m and 0.7 m (range 0.05–1.31 m), respectively. The small size and shallow depth of the river at spawning locations provided unrestricted access to the vast majority of spawning adults. In addition, we were able to observe where and when spawning was occurring as well as occupancy time at the spawning sites.

Sampling design, sample collection and measurement of environmental factors

Lake sturgeon adults were sampled daily as they arrived at spawning locations during the 2006 spawning season that occurred from April 20 to May 26. We walked the entire spawning area one or more times per day using long-handled dip nets to capture spawning adults. Each adult was tagged with an internal PIT (Passive Integrated Transponder) tag and with a large colored floy tag. Unique combinations of floy tag location (right vs. left side of dorsal fin) and tag color allowed us to identify gender and time of initial capture (i.e. early in spawning run) of individuals by sight after initial tagging so that location and spawning activity could be easily observed. Biological information including sex, capture date and location was recorded for all individuals at first capture. A dorsal fin clip (~1 cm^2) was taken from each individual for genetic analysis.

Larvae were sampled at 2 sites located 0.15 (D1) and 1.5 (D2) km downstream from the most downstream zone where adults spawned (Fig. 1). Larval sampling was conducted during two nights, May 28 and 29, 2006. At each site, five D-frame larval nets were placed across the river channel (description in Smith and King 2005) and were checked hourly from 22:00 to 02:00 h. Mean water depth at sites D1 and D2 was 0.56 m and 0.71 m respectively and larval drift nets were completely submerged during sampling. Based on discharge data the larval drift nets sampled from 8.9–11.6% of the total river volume at the sampling sites. Captured larvae were kept separate by hour of capture and site and were reared in a streamside hatchery until they were large enough (for 3 months) for fin clips to be taken. Mortalities during the rearing period were recorded and kept (in ethanol) separate by hour and site. Then, 30% of all the fish (both fin clips and hatchery mortalities) were sub-sampled randomly by hour and sampling site for genetic analysis. We

genotyped 831 larvae including 283 and 145 larvae collected at sites D1 and D2 on May 28, and 271 and 132 larvae at sites D1 and D2 on May 29, respectively.

We measured water temperature and water velocity every day of the spawning season through the larval sampling period. Water temperature was recorded hourly using HOBO data loggers (Oneset Computer Corp.) at three locations: the upstream spawning location, upstream of, and downstream of larval collection sites. Three water velocity readings (left, center, right) were taken in front of the drift net openings (0.6 m of the stream depth measured downward from the surface) with a Marsh-McBirney Flo-Mate 2000 (Marsh-McBirney Inc., Fredrick, MD, USA). Measurements of water velocity were also recorded from the entire cross-sectional area of the channel at 1 m intervals across a standardized transect. In this study, we reported water temperature and water velocity in two days of larval sampling. Average (±SD) temperatures and velocity among locations measured on May 28 and 29 were 20.33±0.69°C and 20.72±0.05°C; and 0.36±0.11 ms^{-1} and 0.47±0.12 ms^{-1}, respectively.

Genetic analysis

DNA was extracted from larval tissue samples using the QIAGEN DNeasy(R) kit (QIA 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 as described in the above references. All PCR reactions were conducted using a Robocyler 96 thermal cycler (Stratagene). PCR products were run on 6% denaturing polyacrylamide gels and visualized using a Hitachi FMBIO II scanner. Allele sizes were scored independently by two experienced personnel. Genotyping errors were checked by blindly re-genotyping a random subset of 10% of all samples.

Parentage analysis

The number of candidate parents affects the success rate of and confidence in parentage assignment (Marshall et al. 1998). We used a subset of all captured spawning adults for parentage analysis based on empirical estimates of the cumulative temperature units from the period from egg deposition to larval dispersal in the same Black Lake population (Smith and King 2005; Duong et al. 2011), and estimated spawning date (based on date of capture) of females. Using these criteria larvae collected on May 28–29 were expected to be offspring of adults captured from May 1 to May 15 (35 females and 91 males, Fig. 2). The offspring of these adults were predicted to disperse on average 17 days following the female spawning date under mean water temperature (from May 1, the first day of spawning by these adults, to May 29, the last day of collecting larvae) of 14.7±2.4°C. Meanwhile, offspring of females spawning earlier (from April 20–24) were predicted to disperse approximately 19 days post-spawning, and offspring of females spawning later (May-25–26) predictably dispersed 13 days post-spawning. Thus, although dispersal duration of larvae produced by the same female can last for 11 days (Duong et al. 2011), at the time we sampled, larvae from early spawning females had already dispersed and larvae from late spawning adults had not hatched or dispersed yet.

Two software programs, the Parentage Allocation of Singles on Open Systems (PASOS), version 1.0 (Duchesne et al. 2005) and CERVUS 3.0 (Kalinowski et al. 2007) were used for parentage analysis. Parental assignments for individual larvae from the two programs were compared and jointly used for further analysis.

We used two functions in PASOS including the allocation function for assigning offspring to collected adults and estimating missing parents that were not collected, and the simulation function for estimating the probability that any assignment is correct (correctness probability). Simulations to determine accuracy (correctness) of parentage assignments were conducted over 5 iterations using 1000 simulated offspring. Using CERVUS, we first simulated 10 000 offspring to determine the likelihood of assignment and confidence levels of parental assignment based on population estimates of allele frequencies (N=126 spawning adults), captured adult proportions estimated from PASOS, and the empirical estimate of genotyping errors (0.67%). From the assignment output, a "true parent pair" of an offspring was chosen from the most

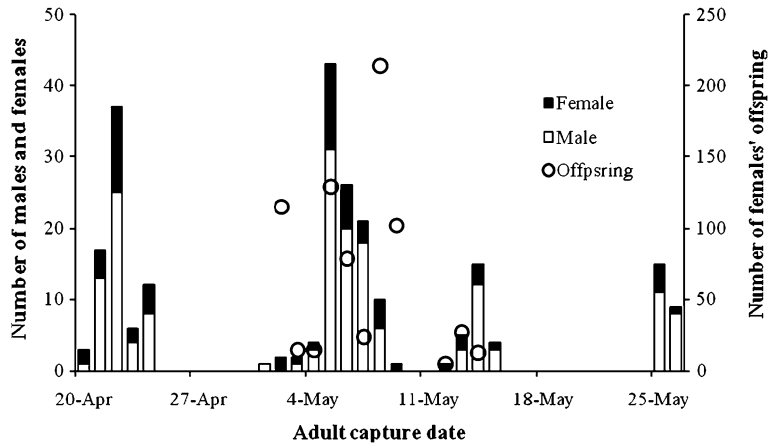

Fig. 2 Numbers of adults captured each day of the 2006 spawning season and total number of offspring collected on two nights (May 28 and 29) that were assigned to captured females using genetically determined parentage

likely candidate parents. We then compared the concordance of parental assignment outputs from the two programs. Inconsistent assignments of offspring to two collected parents between the two programs were evaluated based on biological information (e.g. proximity of captured time and location of both parents).

Data analysis

We first tested the hypothesis that females contributed the same proportion of larvae to collections at both sampling sites (upstream D1 and downstream D2) during each of 2 nights (May 28 and 29). Proportional contributions of larvae from each female were estimated as the ratio of the number of offspring per female to the total number of offspring collected at each larval sampling site each night (hereafter called standardized offspring). We used a general linear mixed model approach to quantify differences in standardized offspring among females as a fixed effect at two larval sampling sites and at two nights. Because sites and nights of sampling were not independent, they were treated as random effects (Burnham and Anderson 2002; Bolker et al. 2009). We used likelihood ratio tests to determine significance of random effects and Wald tests for fixed effects.

A mixed model was also used to compare proportions of larvae from the upstream and downstream spawning locations, which contributed to the total number of larvae collected at sites D1 and D2. In this model, spawning location was treated as a fixed effect and female as a random effect.

Hourly dispersal patterns of larvae from females spawning at upstream (site B) and downstream (site C) across five consecutive hours of sampling at site D1 during each of two nights were also characterized. We used nonparametric Mann-Whitney Wilcoxon tests to compare the number and proportion of larvae collected by hours from two female groups spawning at upstream and downstream sites.

We then estimated and compared the relative loss of larvae among females between upstream and downstream collection sites. Relative loss by a female was defined as the ratio of the number of larvae that were collected at the downstream site and assigned to each female to the total number of the same female's offspring collected at both upstream and downstream sites (D1 and D2, respectively). Differences in relative loss among females were tested using a general linear mixed model including the fixed effect of female and the random effect of sampling dates. Similarly, relative loss for female groups spawning at upstream and downstream locations was also compared with a mixed model including spawning locations as a fixed effect and females as random effects.

Results

Parentage assignment

Based on program PASOS, 741 larvae (89% of the total number of larvae genotyped) were assigned to two collected parents with allocation correctness estimated to be 0.82±0.01. Male and female adults

captured were estimated (by the program) to represent 89.3 and 91.8%, respectively, of the total number of adults estimated to have contributed to the larvae sampled. The assignment rate obtained from CERVUS was 91.8%. Comparing parental assignment outputs from the two programs revealed that 72.4% (602 larvae) of all sampled larvae were concordantly assigned to the same two collected parents. Based on biological information regarding timing of spawning observed for putative male-female pairs to evaluate discordance in assignment of the two programs, we finally selected 738 larvae for further analysis. We compared results of the analysis from only concordant assignments (N=602) and from the larger set of 738 selected larvae. Results from the two analyses did not differ and the results presented below are based on the analysis of the 738 selected larvae.

Hourly pattern of larval dispersal

The number of larvae collected revealed an hourly pattern of larval dispersal from each spawning area. Hourly patterns were consistent across the 2 nights and between female spawning locations (Fig. 3). Based on stream velocity (0.36 and 0.47 ms^{-1} on May 28 and 29, respectively), the time necessary to disperse passively from the upstream spawning location (site B) to the upstream larval collection site (D1) was about 35–45 min. Genetic data revealed that when checking nets hourly, larvae from both spawning sites were present in the upstream larval collection. We observed an approximately one hour lag between the peaks of larvae captured at upstream and downstream locations. The highest number of larvae from both spawning sites was observed from 22:00–23:00 h at site D1 and 23:00–24:00 h at site D2. The ranked number and proportion of larvae collected by hour at both larval collection sites were not significantly different between the two groups of females that spawned at locations B (upstream) and C (downstream) (Wilcoxon tests, p>0.5 for all tests).

Proportional contributions of females to larval collections at two sampling sites and nights

The number of larvae captured during 2 nights and assigned to a female varied from 1 to 140 individuals (mean = 21, median = 11, mode = 5). Standardized offspring also varied significantly among females ($F_{34,\ 104}$=32.0, p<0.001). Four females consistently had higher standardized offspring at both sampling locations and dates (Fig. 4). Random effects of sampling night and sampling site were not significant (LRT≈0, df=1, p=0.99). Therefore, the rank order of standardized offspring among females was consistent between two nights and also between the two larval sampling sites.

The number of larvae produced by females from the upstream location B comprised a higher proportion of larvae captured relative to larvae from females spawning at the downstream spawning location C ($F_{1,\ 137}$=14.4, p<0.01). However, in terms of larval proportion (standardized offspring) contributed by each female, standardized offspring per female spawning at location B was not significantly higher than that of females spawning at location C ($F_{1,\ 104}$=1.90, P=0.17). There was a large variation in standardized offspring among females within each spawning location.

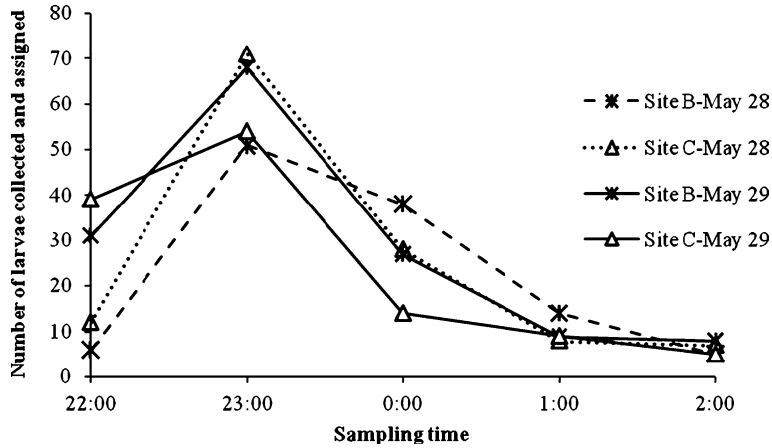

Fig. 3 Hourly pattern of larval dispersal based on collections at sampling site D1 on 2 nights (May 28 and 29). Larval numbers are cumulative totals over all females spawning at upstream (Site B) and downstream (Site C) locations (Fig. 1)

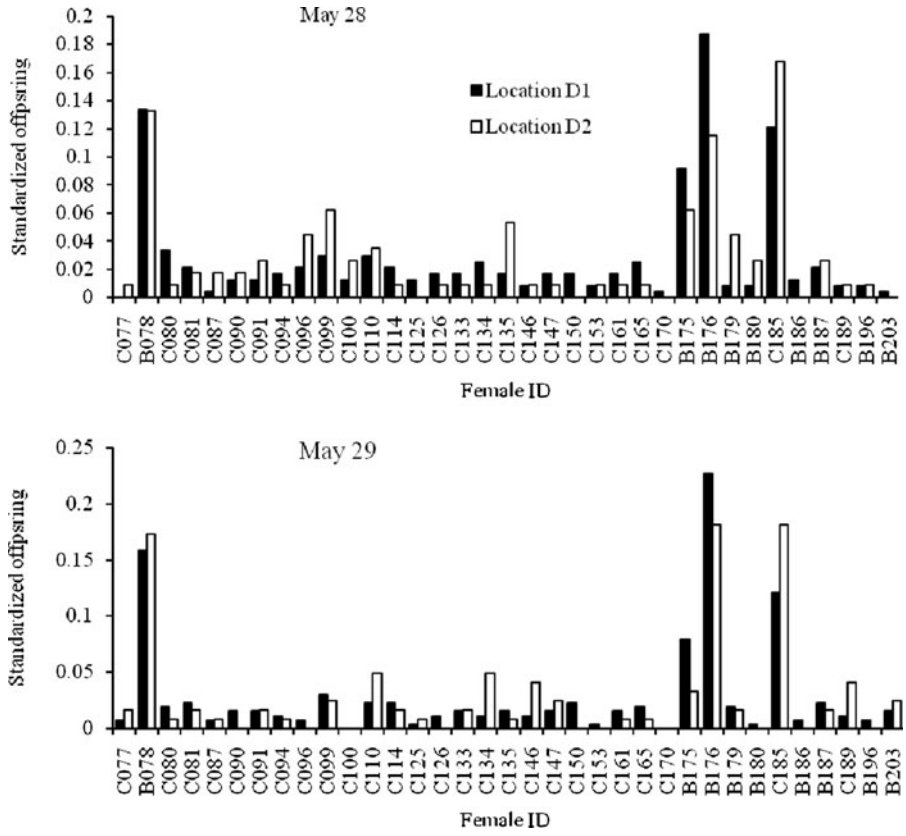

Fig. 4 Standardized offspring produced by each female estimated based on collections at two larval sampling sites on two consecutive sampling nights. Female IDs include reference to spawning locations (B vs. C) and are presented in order of spawning date (May 1–15, Fig. 2)

Relative larval loss

Differences in the number of offspring between upstream and downstream larval sampling sites provided a measure of relative larval loss among females between the sampling sites. Relative larval loss was not significantly different among females ($F_{34,\ 34}$=1.36, p=0.19). This result indicates that females with higher numbers of offspring lost proportionally more offspring than did females contributing comparatively fewer offspring, when larvae from all females dispersed through a common environment from site D1 to site D2. However, large variation in relative larval loss within female (the same female between nights) and among females was observed (Fig. 5). Partitioning components of variance in relative larval loss revealed that a small proportion (3%) of total variance was attributed to random effects of sampling nights (across females), and a larger proportion (97%) was attributed to variance in relative

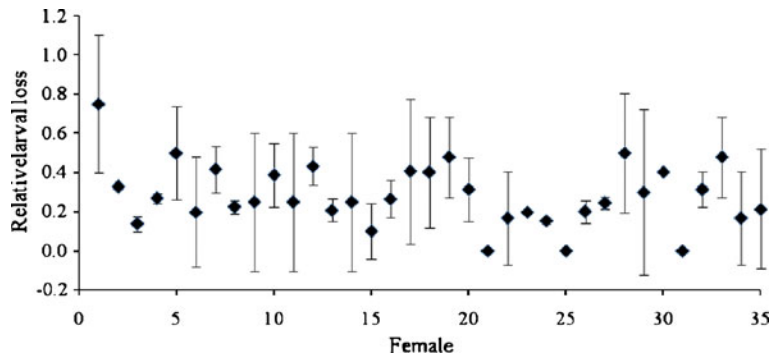

Fig. 5 Relative larval loss among females (bars represent 1SD between two nights). The order of females was as the same as Fig. 4

loss of the same female in two nights (residual error). When females were grouped by spawning site, estimated relative larval loss from females spawning at the upstream location (0.25±0.20) was not significantly different from females spawning at the downstream location (0.29±0.22) ($F_{1, 34}$=0.55, p=0.46). The non-significance in relative loss of females from two spawning locations was likely attributed to the large degree of variation among females within each spawning location.

Discussion

Differences in trait expression among individual larvae, which affect survival, can occur as a result of maternal and genetic effects, even when individuals are exposed to the same environmental conditions (Heath and Gallego 1997; Bolnick et al. 2003; Leis 2006; Fiksen et al. 2007; Clobert et al. 2009). Further, inter- and intra-family variation in phenotypes at larval stages can affect traits and survival at later life stages, providing the opportunity for the evolution of maternal traits and behavior (e.g., spawning time) in natural populations (Einum and Fleming 2000). One important question is whether larvae produced by different females are differentially susceptible to mortality when exposed to a common environment, for example, when larvae disperse from spawning grounds to areas utilized during subsequent early life stages. Such a question cannot be addressed without genetic data or other measures establishing pedigree relationships and estimates of reproductive success and survival. Variation in relative larval mortality among females would imply that maternal effects and individual variability outweigh the effects of stream environmental factors.

Using genetically determined parentage, we quantified the intra- and inter-female variability of larval loss during dispersal through a common natural stream environment over a distance of 1.5 km during two consecutive nights. A considerable portion of mortality during early life stages occurs at emergence and during the initial period of dispersal (Einum and Fleming 2000). Therefore, the time and distance over which we examined larval loss was predicted to be an important period when larvae experienced high mortality. Results showed that lake sturgeon females differed in both absolute numbers and relative proportions of offspring contributed to larval collections each night. However, no significant difference in relative larvae loss among females or between groups of females spawning at upstream and downstream locations was detected. This result indicates stronger effects of exogenous factors (e.g., predation, food availability, temperature, water flow, etc.,) than endogenous factors (e.g., maternal effects and larval behavior) on mortality of larvae from all females and spawning locations. However, variation in relative larval loss between the two sampling nights for each female (within female) was as high as variation among females (Fig. 5). Such large intra-female variation can mask the significant effects of inter-female variability in larval loss. On the other hand, daily mortality at larval stages can vary greatly, and is a common phenomenon across species (e.g., walleye *Stizostedion vitreum* (Mion et al. 1998); Pepin 2009). Accordingly, the large degree of intra-and inter-female variation in larval loss observed in lake sturgeon may be a normal feature in stream environments.

Estimates of larval loss between two sampling sites can likely be attributed to natural mortality (e.g., due to starvation or predation), differences in capture efficiencies at the two larval sampling sites or differences in movement behavior among larvae. We believe the latter two hypotheses are unlikely. First, if we assumed that all larvae had an equal probability of capture, differences in capture efficiencies between sampling sites would not bias estimates of relative larval loss among females. Second, it is possible that downstream movement may not be consistent among larvae (Siegel et al. 2003; Leis 2006; Shanks 2009). For example, some larvae could settle in substrates between the two sampling sites or slow their movement. However, based on our observation of stream conditions over the stream area surveyed and consistent patterns of larval dispersal by hour each night (Fig. 3), variation in larval movement behavior was likely minor and did not contribute to differences in relative larval loss among females. In sum, the lack of differences in relative larval loss among females was likely due to similar susceptibility to natural mortality during the two nights.

The main sources of natural mortality during the initial period of larval dispersal can be predation, starvation, and physical injure due to water velocity (Kamler 1992; Mion et al. 1998; Cowen and

Sponaugle 2009). Water velocity (Mion et al. 1998) and other exogenous abiotic factors such as oxygen concentration and temperature (Kamler 2005) are unlikely to cause larval loss in this study because the stream conditions were characterized by intermediate levels of water velocities (0.36–0.47 ms^{-1}) and stable temperatures (20–21°C) during the two nights. Predation is one of the most significant causes of larvae mortality during dispersal for numerous fish species (Paradis et al. 1996; Cowen and Sponaugle 2009). Predators of lake sturgeon larvae in the Upper Black River included crayfish (*Orconectes rusticus*) and rock bass (*Ambloplites rupestris*) (Crossman 2008; Forsythe 2010). Larvae are not able to escape predators during dispersal until the juvenile stages (Auer and Baker 2002). Therefore, the effects of predation on larval mortality are expected to be random among females. Starvation can cause substantial mortality of larvae in several fish species [e.g., trout *Salmo trutta* (Elliott 1986); plaice *Pleuronectes platessa* (Fox et al. 2007)]. In lake sturgeon, larvae emerge from the substrate and disperse after depleting yolk-sac reserves (Auer and Baker 2002; Kynard and Parker 2005; Smith and King 2005). Accordingly, starvation likely results in mortality during the initial period of larval dispersal. Given starvation mortality may be related to egg size and egg energy content (Keckeis et al. 2000), which are components of maternal effects (Mousseau and Fox 1998; Kamler 2005), larger inter-female variation compared to intra-female variation in relative larval loss would be expected if starvation or decreased energy levels due to food limitation was a main source of mortality. However, our study showed that intra- and inter-female variation were approximately equal, suggesting predation mortality was dominant over starvation mortality.

Biologists have examined whether larvae dispersing in groups consisted of offspring from different families, in order to understand schooling behavior of fish during dispersal (Avise et al. 2002). We found that collections of dispersing lake sturgeon larvae each night were comprised of offspring from the majority of females sampled in spawning locations. However, proportional contributions from different females varied greatly (Fig. 4). Different proportional contributions of females to larval drift could be explained due to variability in female fecundity (Bruch et al. 2006), hatching rate (Nichols et al. 2003; Crossman 2008), and survival from egg deposition to larval dispersal (Caroffino et al. 2010). These factors could result in different reproductive success of individual females. Although this study was not designed to disentangle the causes of differences in proportional contribution of females to larval collections, a large range in the numbers of offspring captured and the consistent magnitude of differences in standardized offspring among females between two sampling nights is indicative of high variation in reproductive success among females.

Our study also revealed similar hourly dispersal patterns of larvae produced from females spawning at upstream and downstream locations in two nights, with the peak of larval drift occurring between 22:00 and 23:00 h. Under average water velocities of 0.36–0.47 ms^{-1}, similar patterns of dispersal across hours (nets were checked hourly) observed in larvae from two spawning locations implies that movements of larvae downstream over the distance investigated were likely passive. These patterns were observed consistently for 2 consecutive nights in this study and also in other studies conducted in different years (e.g., from 2000–2003, Smith and King 2005).

The short sampling period might have limited our ability to detect differences in relative larval loss among females. We did not collect larvae produced from females representing the entire spawning period. Given that daily mortality of larvae within and among families is highly variable (Mion et al. 1998; Pepin 2009), many days of sampling may reduce intra-family variation and thus allow detection of inter-family variation in larval loss. In addition, because larvae produced from the same spawning event may disperse over many days (Smith and King 2005; Duong et al. 2011), proportional contributions of larvae from females and relative loss interpreted based on two sampling nights and a short distance may not reflect differences in numbers of offspring produced by females and relative larval loss among females over the entire period of larval dispersal.

Further studies that use genetic markers to quantify relative larval loss by families could profitably explore the effects of timing, duration and distance of dispersal on larval loss. Severe environmental conditions such as high river discharge, high predation pressure, extreme temperatures, and other exogenous factors may accentuate differences in rates of mortality among families.

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