

Spawning success and early life history of longnose suckers in Great Lakes tributaries

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Abstract – Fish eggs and larvae are often subject to very high mortality, and variation in early life survival can be important for population dynamics. Although longnose suckers (*Catostomus catostomus*) are widespread in northern North America, little is known about their early life history. We examined fecundity and early larval survivorship during sucker spawning events in three small Lake Michigan tributaries. Although egg deposition varied 25% among spawning events, estimated larval export to the lake varied over 25,000-fold from around 1000 to 26 million. Based on variation in environmental conditions across years, it appears that spring flow and temperature may be important determinants of egg survival to larval outmigration. Larval age data suggest that most individuals that survived to outmigration hatched during a 2-day period despite adult spawning across at least 10 days. Most larvae spent <2 weeks in the stream and emigrated around the time of transition from endogenous to exogenous feeding before substantial growth occurred. In two of three cases, larvae drifted exclusively at night; however, high drift rates occurred during both day and night in the case where larvae were very abundant, suggesting density-dependent drift behaviour. Our results indicate that survival in tributary streams from egg deposition to larval export is highly variable in longnose suckers. These large differences in early life survival may translate into variability in recruitment, thereby influencing population structure and dynamics.

Key words: *Catostomus catostomus*; early life history; migration; *Catostomus commersonii*; fecundity; larvae; drift

Introduction

Suckers (Catostomidae) are major components of aquatic faunas across North America (Cooke et al. 2005). Sucker populations serve an important food web role as prey for a wide variety of animals, including bald eagles (*Haliaeetus leucocephalus*) (Hoff et al. 2004), otters (*Lontra canadensis*) (Wengeler et al. 2010) and valuable game fish such as wall-eye (*Sander vitreus*) and northern pike (*Esox lucius*) (Beaudoin et al. 1999; Bertolo & Magnan 2005). Additionally, many suckers are efficient benthic invertivores and can exert top-down control on invertebrate populations (Hayes et al. 1992). In an ecosystem context, suckers serve an important role as vectors of nutrients and energy during their spawning migrations, thereby supporting the productivity of their spawning grounds (Childress et al. 2014). Despite this range of ecological roles in freshwater ecosystems, the controls on sucker population

dynamics remain poorly understood for most species (Cooke et al. 2005).

Longnose suckers (*Catostomus catostomus*) are distributed throughout northern North America and into north-eastern Asia (Scott & Crossman 1973). In spite of this broad distribution, most details of their ecology are poorly documented. Longnose suckers are long-lived with low adult mortality rates (Bailey 1969), and early life history could be an important driver of their recruitment and population dynamics (Vélez-Espino et al. 2006). However, typical rates of spawning success and larval survival have not been quantified.

Fish eggs and larvae are particularly sensitive to abiotic conditions (Mion et al. 1998) and vulnerable to predation (Almany & Webster 2005), which can lead to high mortality rates (Dahlberg 1979). Interannual variability in success during the egg and larval stages can determine year-class strength (Houde 1989; Bailey et al. 2012), so assessing variability in

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early mortality is important for understanding the drivers of recruitment and population dynamics (Chambers & Trippel 1997). In the case of longnose suckers, mortality of eggs and larvae can provide a major source of nutrients and energy to stream organisms when adults migrate into streams to spawn (Childress & McIntyre 2015). Thus, determining egg and larval mortality is important for understanding both sucker population dynamics and the magnitude of the nutrient subsidies they deliver.

In this study, we analyse the fecundity and early life history of longnose suckers in small tributaries of northern Lake Michigan. We present data on the size and phenology of adult spawning migrations, the relationship between female size and fecundity, larval residence time and growth in the stream, diel and seasonal larval drift patterns and rates of survival between egg deposition and larval outmigration. Our observations are derived from intensive field work in three streams and years, which together capture substantial environmental variation to offer insight into abiotic influences on larval production of longnose suckers.

Methods

We studied the early life history of longnose suckers in three tributaries of north-western Lake Michigan: Wilsey Bay Creek (45.7035 N, 86.9335 W) in 2009, Hibbard Creek (44.9877 N, 87.1760 W) in 2012, and Lily Bay Creek (44.8476 N, 87.2684 W) in 2013. All three are low-gradient, second-order streams with sand and silt substrates in pools between riffles with gravel and cobble substrates. The riparian vegetation at each site includes a mix of grasses, cedars and alders. Discharge is strongly seasonal, rising as the snow pack melts and falling throughout the late spring and summer (Fig. 1). The Great Lakes lie near the southern edge of the longnose sucker distribution and the northern edge of the distribution of white suckers (*Catostomus commersonii*) (Scott & Crossman 1973), and all three study streams receive migrations of ~10,000 suckers in April–May, including both longnose and white. Hibbard and Lily Bay Creeks are dominated by longnose suckers, while Wilsey Bay Creek has equal numbers of the two species. Temperature was logged every 5 min near each stream mouth during the study period using a HOBO® UA-002 Pendant (www.onsetcomp.com).

To determine the timing, number, size and sex of spawning suckers, trap nets were deployed during the migration. In Wilsey Bay and Lily Bay Creeks, two nets spanning the entire stream were deployed back-to-back: one faced downstream and caught fish migrating upstream, and the other faced upstream and caught fish leaving the stream. The net wings forced

all fish moving upstream or downstream into the nets. Nets were installed just after the initiation of the migration, and all incoming fish were marked with a dorsal fin clip to enable identification of fish that entered the stream prior to net installation. The number of incoming fish marked plus outgoing unmarked fish provides a robust minimum estimate of the population size of spawners.

In Hibbard Creek, a single trap net spanning 80% of the stream width was deployed facing upstream with gaps along each stream bank. Although the net captured mostly outgoing fish, fish could swim around and then into the net, and some incoming fish were captured. Captured incoming fish were marked with a dorsal fin clip, and population size was estimated using recapture rates of marked fish using the Lincoln–Petersen method with Chapman corrections (Chapman 1951). All incoming captures were treated as a single marking event, and all outgoing captures were treated as the sampling event. Because every fish was subject to capture at the sampling point both when entering and when leaving, this approach meets the assumption of a closed population as long as capture probabilities of marked and unmarked fish were equal during outmigration. Double captures of incoming fish were identifiable from the combination of prespawning phenotype and a mark ($N = 21$), and double captures of outmigrating fish were minimised by transporting fish 100 m downstream, below a riffle. Because >99% of emigrating fish in Lily Bay Creek and Wilsey Bay Creek had the postspawning phenotype and most emigrants with a prespawning phenotype were seriously injured, spawning phenotype is a reliable indicator of movement direction. Our Lincoln–Petersen approach does not explicitly account for mortality; however, assuming that mortality rates for marked and unmarked fish are equal, any mortality on the spawning grounds would decrease the precision of our population estimate without any directional bias. The resulting population estimate for Hibbard Creek 2012 has a confidence interval that overlaps the number of fish captured in 2013, when a complete census of spawners was conducted but larval production was not measured. In all three streams, fish were released daily; incoming fish were released in the first pool upstream of the nets, and outgoing fish were released below the first riffle downstream of the nets. Species and sex were determined for all individuals, and total length was measured on a large subset ($N = 11,359$ of 28,868 fish). Wet mass was measured for a smaller subset of individuals ($N = 507$).

To estimate fecundity and total egg deposition, ovaries were analysed from 41 females collected in Hibbard Creek and Lily Bay Creek. Ovaries were obtained by dissecting newly arrived females after obtaining mass and total length measurements.

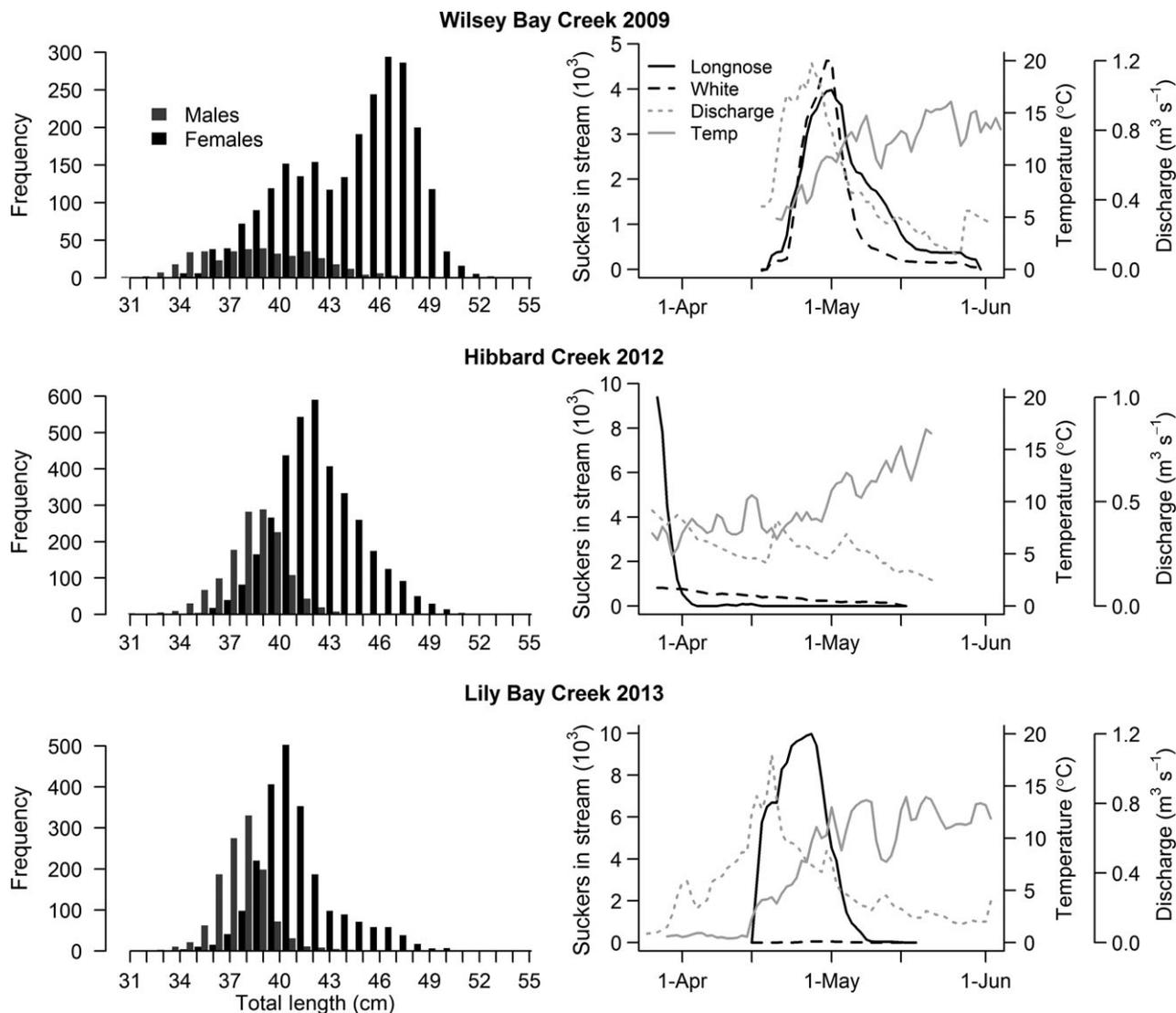


Fig. 1. Length–frequency distributions of spawning longnose suckers and the number of spawning adult suckers in the stream over the course of the sampling season along with mean daily temperature.

Extracted ovaries were weighed immediately and then stored frozen. Ovaries were gravimetrically subsampled ($N = 5$ per ovary; 1.0 ± 0.2 g), and eggs were counted to determine the mean mass per egg (Bagenal & Braum 1978). Total fecundity was estimated by dividing total ovary mass by mean egg mass. We found that ovaries lost 3% of their mass to sublimation while frozen, so fecundity estimates were corrected accordingly. To estimate population-level egg deposition, we used a power-function relationship between fecundity and total length to predict fecundity for every female. Fish without size measurements were assigned the average fecundity of conspecifics from the same stream and year. A similar approach was used to estimate white sucker fecundity and egg deposition in Wilsey Bay Creek in 2009 (H. Wang and P. McIntyre, unpublished data). Based on the observation that large numbers of females began emigrating the day after spawning was first observed,

the timing of egg deposition was estimated by assuming that females deposited their eggs the day prior to emigration. Although it has previously been suggested that some females migrate without spawning (Harris 1962), <1% of females were observed leaving the stream with a prespawning phenotype and most of these had serious injuries. Thus, we assumed that all migrating females deposited their eggs.

Egg density on the stream bottom was measured using daily benthic samples in the most downstream riffle in Lily Bay Creek from May 5 to 22, 2013. A Hess sampler (856 cm^2 area, $500 \mu\text{m}$ mesh) was placed at random within a 30-m sampling reach such that specific locations were not resampled. The substrate and water column were vigorously mixed to a depth of 5 cm for 30 s. Two samples were taken each day and were preserved in 70% ethanol. Eggs were counted in the laboratory under a dissecting microscope with $12\times$ magnification.

To estimate total larval export, the rate of larval drift was measured daily throughout the emigration period using drift nets (363 μm mesh, 45.7 \times 30.5 cm opening). In 2013, when the drifting season was much longer than in other years, sampling was less frequent in the late season when fewer larvae were drifting. To account for variation in larval drift by time of day, we conducted intensive diel sampling at each site for 1–2 days near the peak of emigration. This enabled extrapolation of each daily sample to estimate total daily export. Previous studies (Geen et al. 1966; Clifford 1972) and our own pilot sampling suggested that larvae would not drift during the day, so sampling was conducted for 12 h overnight (20:00–08:00) in 2009. Full 24-h sampling was conducted in 2012 and 2013. The timing of daily samples was targeted to overlap with high drift periods and maximise catch probability, which reduces uncertainty in total drift estimates. Because diel patterns varied among years, sampling times also varied; samples were collected between 22:00 and 1:00 in 2009 and 2012 and between 10:00 to 12:00 in 2013. At least two samples were collected on each day. Larvae were identified as *Catostomus* (following Auer 1982), but no morphological characteristics differentiate young white and longnose sucker larvae (Snyder et al. 2004), so we assume that both species were represented in the drift in proportion to the fecundity of each population.

Daily samples were used to estimate total daily larval export by extrapolating catches to the whole stream and whole day. Length of drift net sets varied among sampling years due to the effects of larval densities on clogging of nets. In 2009 and 2012, nets were set for 15 min, but set times were shortened to 2 min in response to high densities of larvae in 2013. The volume of water sampled by the drift nets was calculated by measuring flow rate at the centre of the net and multiplying by the sample duration and net dimensions. In each year, daily water level measurements taken at a single site within 100 m of larval sampling were used to estimate daily discharge from a power–function relationship between water level and measured discharge ($N = 7\text{--}12$ observations per stream; all $R^2 > 0.95$). Stream discharge was measured using a Marsh–McBirney Flo-Mate™ 2000 (Hach Company, Frederick, MD, USA) at water levels spanning the observed range during larval sampling. Daily larval export was estimated using the following model:

$$\text{Daily Export} = L_s \frac{Q_{\text{tot}}}{Q_s} \times \frac{D_{\text{tot}}}{D_h}$$

Where L_s is the number of larvae per sample, Q_{tot} is the total stream discharge during the sample, Q_s is the discharge sampled, D_{tot} is the total larvae caught during the diel sampling, and D_h is the number of larvae caught at the time of the sample during the diel sampling.

The ratio of stream discharge to volume sampled extrapolates the sample to the stream scale. The ratio of whole day export to export at the sample time, which was based on the diel sampling for each site, extrapolates the single-time sample to the whole day. We analysed the model with a Bayesian approach using Markov chain Monte Carlo (MCMC) methods in JAGS (Plummer 2003) called from R 3.1.0 (R Core Development Team 2014) using the package `r2jags` (Su & Yajima 2009). The Bayesian approach enables accounting for both normally and log-normally distributed errors. Noninformative priors were used for all parameters, and posterior distributions were estimated by taking every 3rd sample from 10,000 iterations of three MCMC chains after a ‘burn-in’ of 10,000 iterations. Convergence was checked by visual examination of mixing of the three chains and using the R-hat statistics, which were all < 1.1 (Gelman & Hill 2007). Each site/year was analysed separately due to qualitative differences in diel and seasonal drift patterns, which suggests that these differ by site and/or year. Larval counts over the course of the diel sampling were modelled as a Poisson distribution with hour as a factor; likewise, the multiple samples from each day through the season were modelled as a Poisson distribution using day as a factor. Stream discharge was estimated as a linear regression between log-transformed water level and log-transformed discharge. Uncertainty estimated from multiple daily samples, multiple samples during each diel period, total export through the net during diel sampling and the fit of the discharge regression is incorporated in the larval export estimates. Because the volume sampled was measured only once per sample, uncertainty of sample volume was not accounted for. Extrapolation of daily samples to whole day estimates relies on two primary assumptions: first, the number of larvae captured is directly proportional to the volume of water sampled; second, the diel sampling is representative of the diel drift patterns for that year and site. In 2013, larval export was estimated on days without direct measurement (14 of 53 days) using linear interpolation.

Larval hatch dates and age at emigration were measured for larvae in Lily Bay Creek in 2013. Because few white suckers spawned in Lily Bay Creek, and our larval export estimate was larger than the number of white sucker eggs deposited, we had high confidence that catostomid larvae were longnose suckers. Larval age was estimated by counting daily growth rings in otoliths from 30 individuals chosen at random from samples representing the full range of capture dates. Otoliths were removed from ethanol-preserved larvae and mounted on glass slides with clear Crystalbond™ adhesive (Secor et al. 1992). The small size of the otoliths made daily rings

visible without sectioning or polishing. Lapillar and sagittal otoliths have both been demonstrated to form daily rings in catostomids beginning on the hatch day (Hoff et al. 1997). Sagittal otoliths were slightly larger than lapillae; however, their morphology changed at around 20 days of age, and the development of rostra obscured daily rings. Thus, lapillar otoliths were used to estimate age. All otoliths were aged by two researchers, and the average of the age estimates was used for analysis. Age estimates were used to back calculate the date of hatching by subtracting age from the capture date.

Size was measured for larvae captured over the range of emigration dates in 2009 ($N = 580$ of 580 captured) and 2013 ($N = 159$ of 49,455 captured). Total length was measured under a microscope (10× magnification) using an ocular micrometre (2009) or digital photographs and IMAGEJ software (2013) (Schneider et al. 2012). All larvae used in size measurements were captured in drift samples with the exception of larvae from Lily Bay Creek on 11 July 2013. On that date, no larvae were captured in drift samples, so a dip net was used to sample larvae from the nearest pool upstream for size measurements.

Results

Total numbers of migrating suckers were broadly similar among all three spawning events, but the ratio of white to longnose spawners varied (Table 1). In Wilsey Bay Creek, 8587 suckers were captured, of which 44% were longnose; Lily Bay Creek had >99% longnose and 11,432 adult suckers were captured. Thirty to fifty per cent of marked fish were recaptured emigrating from the stream, and thus, the adult population estimates are conservatively estimated. All fish were assumed to have spawned regardless of recapture. Because the trap net did not span the entire stream in Hibbard Creek, estimates of the adult spawning population in Hibbard Creek rely on Lincoln–Petersen estimates from mark–recapture data. In Hibbard Creek, 20% of 397 marked longnose suckers were recaptured, and 14% of 146 marked white suckers were recaptured. The total population

was estimated to be 92% longnose with 12,305 (95% CI: 10,370–15,525) longnose and 1028 (759–1790) white suckers. Female longnose suckers were consistently larger than males (Fig. 1), and Wilsey Bay Creek had larger average body size for both sexes than the other two sites. Additionally, fish migrating into Wilsey Bay Creek showed a bimodal size distribution for both males and females, while the other two populations were unimodal. Sex ratios were all biased towards females (Wilsey Bay Creek: 86% female; Hibbard Creek: 68%; Lily Bay Creek: 69%).

Longnose sucker fecundity averaged 31,197 (SD = 10,213) eggs and was positively related to female total length (TL; cm) ($R^2 = 0.76$, $P > 0.001$; Fig. 2; Fecundity = $0.016 * TL^{3.799}$). White sucker fecundity averaged 40,947 per female and was also correlated with length ($R^2 = 0.63$, $P < 0.001$; Fecundity = $7.210 * TL^{2.204}$). Total estimated egg deposition was similar among spawning events with 180×10^6 in Wilsey Bay Creek in 2009, 236×10^6 in Hibbard

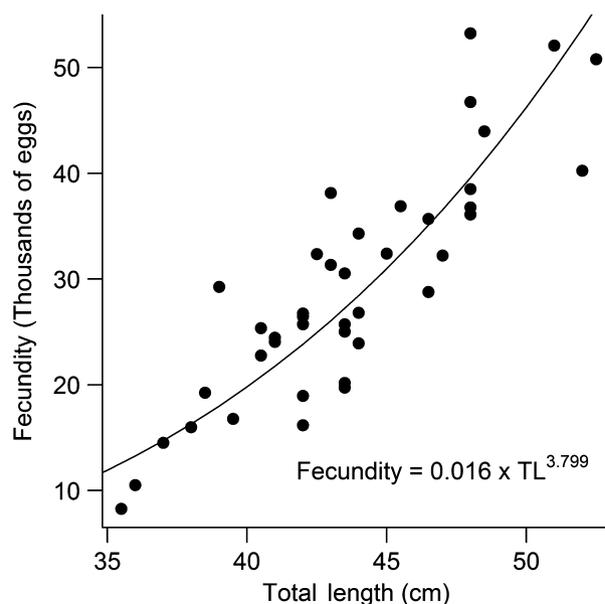


Fig. 2. Total length and fecundity of longnose suckers from Lily Bay Creek and Hibbard Creek ($R^2 = 0.76$, $P < 0.001$).

Table 1. Spawning populations and reproductive success of suckers. Parentheses contain 95% confidence intervals or credible intervals for the larval estimates.

	Wilsey Bay Creek	Hibbard Creek	Lily Bay Creek
Year	2009	2012	2013
Spawning longnose suckers	4211	12,305 (10,370–15,526)	11,352
Spawning white suckers	5376	1028 (759–1790)	80
Total eggs deposited (10^6)	245 (222–271)	225 (174–310)	200 (185–217)
Larval export (10^3)	179 (113–294)	0.954 (0.406–2.27)	26.2×10^3 (22.9–30.4 $\times 10^3$)
Survival to larval outmigration (%)	0.07 (0.04–0.1)	0.0004 (0.0001–0.001)	13.3 (10.5–16.7)

Creek in 2012 and 205×10^6 in Lily Bay Creek in 2013 (see Table 1 for confidence intervals).

Diel larval sampling showed nocturnal peaks in larval drift for all three spawning events, although the timing of the peak differed among streams (Fig. 3). Drift was observed exclusively during the night in 2012, whereas most of the larvae drifted during the daytime in 2013 when densities were much higher (Fig. 3). Although larvae were captured in all diel samples in 2013, there was a distinct diel pattern with fewer larvae drifting at dawn and dusk.

Despite similar numbers of eggs deposited in each spawning event, estimated annual larval export varied 27,000-fold (Table 1). Larval export was highest in Lily Bay Creek in 2013, and large numbers of larvae were drifting when our sampling began, such that total export was likely underestimated. Maximum observed

larval densities in the three streams mirrored the differences in population estimates ranging from 0.31 larvae m^{-3} at Hibbard Creek to 757 larvae m^{-3} at Lily Bay Creek, and Wilsey Creek had a maximum density of 3.8 larvae m^{-3} . At all three sites, a large majority of larvae emigrated during a much narrower time window than the period of adult spawning. More than 90% of all larvae emigrated over 8-day periods in 2009 and 2012, and 77% of larvae emigrated in the first 8 days of sampling in 2013 despite the fact that emigrating larvae were observed for 50 days.

Back calculation of hatch dates showed that emigrating larvae all hatched within a 6-day window in Lily Bay Creek in 2013, despite the fact that these 30 larvae were collected over a 52-day period. In fact, 83% of aged larvae hatched on two consecutive days (Fig. 4). Larval age estimates were precise overall

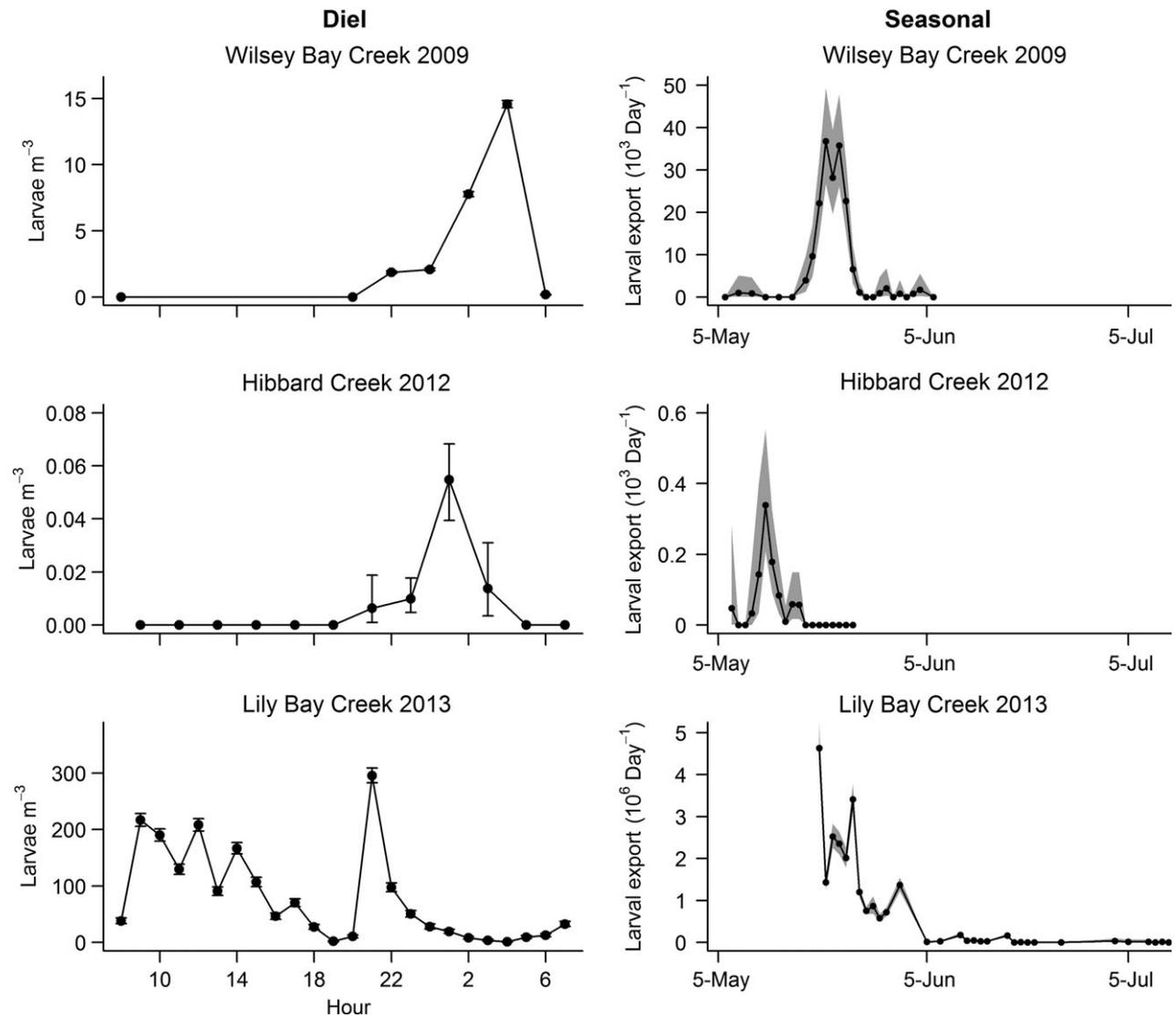


Fig. 3. Diel and seasonal dynamics of larval sucker export. Diel figures represent larval densities in samples across a single day. Seasonal figures show daily estimates of total larval export across the drift season. Note the difference in scales for y-axes over orders of magnitude. Error bars and grey shading represent 95% credible intervals; for daily estimates, this integrates uncertainty from diel sampling, discharge estimates and replicate samples.

with an average coefficient of variation of 3% between readers, but precision declined with larval age. Average difference in age estimates between readers were grouped in 10-day age increments and differed by 0.33 days in larvae younger than 15 days old (i.e. 2% deviation) and <2 days in larvae <45 days old (5% deviation), but agreement decreased to an average difference of 4.2 days in larvae >45 days old (10% deviation). Although precision was lower for older larvae, nine of 10 back-calculated hatch dates for larvae >45 days old overlapped with hatch dates of younger larvae.

Average egg incubation time in Lily Bay Creek in 2013, estimated as the difference between peak egg deposition and peak hatching, was 12 days (Fig. 4). Egg density on the benthos decreased dramatically with most of the decrease occurring prior to hatch dates inferred from larval ages. Most larvae emigrated 9–14 days after hatching, but a small subset remained in the stream as postlarvae for over 50 days. After most individuals had emigrated, larvae were present only in the slow-moving, deep pool just upstream of the mouth; no larvae were observed upstream in reaches with faster flowing water.

Most sucker larvae did not achieve substantial growth prior to emigrating from their natal stream. For instance, in Wilsey Bay Creek in 2009, larvae drifting out of the stream were roughly the same size throughout the short emigration period. The same was true for the majority of larvae leaving Lily Bay Creek in 2013, but a small subset of individuals residing in the stream for >50 days tripled in length before departing (Fig. 5). Across the spectrum of larval growth observed, dry mass (mg) was strongly related to total length (mm) ($R^2 = 0.98$, $P < 0.001$, Fig. 5).

Discussion

Our results demonstrate high variability in larval export among sucker spawning events of similar size. Because similar numbers of eggs were deposited in each case, these fluctuations in larval production appear to be driven by variation in stream conditions,

which influence early life mortality. As a result, survival from egg deposition to larval emigration from streams may act as a recruitment bottleneck even though longnose suckers spend only a few weeks in their natal habitat.

Longnose sucker larval production varied by over four orders of magnitude among spawning events with similar reproductive effort. Such variation suggests that environmental conditions during early ontogeny could strongly influence early survival. Differences in the sampling regime for adult suckers among streams adds to the uncertainty in the spawning population estimates, egg deposition and survival; however, larval production varied 27,000-fold, which exceeds the uncertainty in spawning abundance by at least four orders of magnitude. Abiotic conditions such as temperature and flow during the egg incubation and larval periods frequently influence larval survival in fishes (Mion et al. 1998). In other catostomids, larval success increases with stream discharge (Johnston et al. 1995; Bednarski et al. 2008). Our observational approach prevents direct tests of particular factors, but the spring of 2013 had high, sustained flows and gradual warming during the spawning period. In contrast, 2012 had lower flows and variable temperatures, which resulted in egg deposition low in the watershed and cold temperatures during incubation. Incubation time is negatively related to temperature in suckers, and cold temperatures that extend the incubation period often increase egg mortality (Hamel et al. 1997). Conditions in 2009 were intermediate; flows were moderate and temperature increased gradually. Lack of repeated sampling in multiple years at a single site precludes definitive assessment of controls on larval success, but our observations provide clear evidence of the enormous scope for interannual variation in outcomes.

Anecdotally, we observed Lily Bay Creek daily in 2012 and looked specifically for larvae in backwaters yet found none, whereas thousands of larvae were very conspicuous during similar observations in

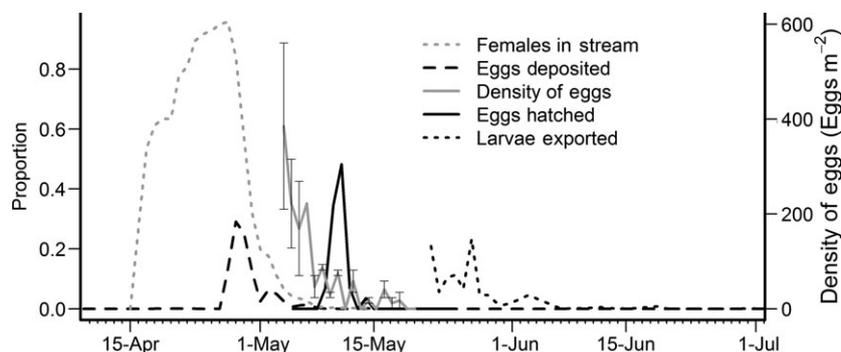


Fig. 4. Timing of adult migration, egg deposition, hatching and larval export of longnose suckers in Lily Bay Creek in 2013.

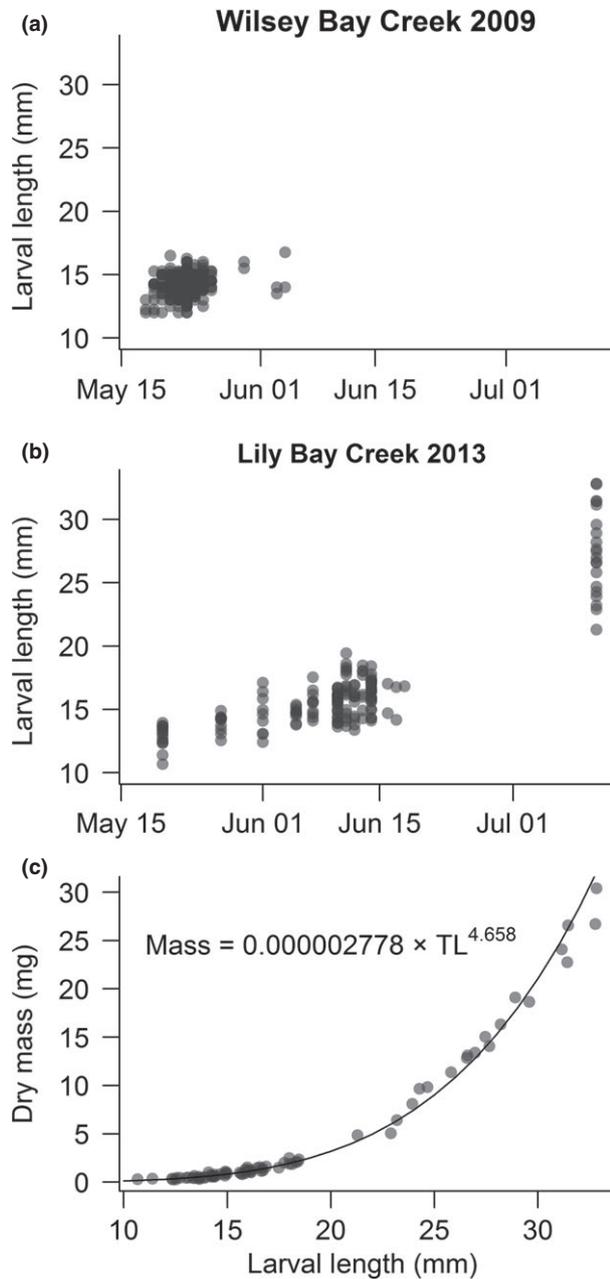


Fig. 5. (a) Sizes of emigrating larvae in Wilsey Bay Creek in 2009. (b) Sizes of larvae from Lily Bay Creek in 2013. Larvae were all captured during emigration except those from 11 July, which were captured with a dip net. (c) Length versus dry mass of young longnose suckers from Lily Bay Creek 2013. Darker grey indicates overlapping points.

2013. Further, the very low larval production in Hibbard Creek (~1000) could not sustain a spawning population of over 10,000 adults, given further mortality during the juvenile and adult stages. Interannual variation in larval production is consistent with the general idea that spring flow conditions are important for early survival of catostomids (Johnston et al. 1995; Bednarski et al. 2008; Scopettone & Rissler

2012) and suggests that abiotic conditions may contribute to recruitment variation in longnose suckers.

The substantial larval drift during daylight hours in 2013 differs from previous reports of sucker drift behaviour. All previous studies have found a peak in larval drift during the night and very little drift during daylight (Geen et al. 1966; Clifford 1972; Walton 1980; Modde & Muirhead 1994; Johnston et al. 1995; Johnston 1997; D'Amours et al. 2001; White & Harvey 2003). Based on these studies and our observation of no daytime drift in Hibbard Creek when larval densities were relatively low, we assumed zero daytime drift in Wilsey Bay Creek. This assumption creates a conservative estimate of larval export if, in fact, there was daytime drift. In contrast to previous studies, when larval densities were high in Lily Bay Creek, far more drift occurred during the day than at night. Catostomid larvae typically seek flow refuge in backwaters during the day (Ellsworth et al. 2010), and it is possible that daytime drift was spurred by high densities of larvae overwhelming the available refuge habitat. However, there were clear diel dynamics with drift minima at dawn and dusk, suggesting that larvae were able to remove themselves from the drift. Larval fish are reported to drift during the day in large, turbid rivers (Reeves & Galat 2010), but our study streams were small and clear with total suspended solids $<1 \text{ mg}\cdot\text{l}^{-1}$ during emigration.

Predation risk is one possible explanation for the interannual variability in diel drift patterns as well as the low drift rates at dawn and dusk in 2013. We observed predation on both eggs and larvae during spawning migrations. Individual rainbow trout (*Oncorhynchus mykiss*) consumed hundreds of eggs. Brook sticklebacks (*Culaea inconstans*) and predaceous diving beetle (Dytiscidae) larvae were observed feeding on sucker larvae. Shiners (*Notropis* spp.), rock bass (*Ambloplites rupestris*) and bullheads (*Ameiurus* spp.) appeared in the streams around the time of larval outmigration, and predatory odonates and juvenile northern pike (*E. lucius*) were also present. Larval drift densities were much higher in Lily Bay Creek in 2013 (often $>100 \text{ m}^{-3}$) than densities observed in previous studies (usually $\sim 1 \text{ m}^{-3}$) or at our other study sites, and high larval densities may reduce predation risk during the day by overwhelming predators (Wrona & Dixon 1991), making diurnal drift a viable strategy. In addition, fish may be particularly vulnerable to predation at dawn and dusk because visual adaptation to light transitions is slow (Munz & McFarland 1973), and the diel dynamics that we observed in 2013 may reflect avoidance of crepuscular predators such as northern pike or trout (Reebs 2002). Further examination of these hypothe-

ses is necessary to determine the drivers of the observed variation in larval drift behaviour.

Estimating larval fish production typically requires substantial extrapolation of samples across both space and time (Mion et al. 1998; Pritt et al. 2014). The observed variation in diel drift patterns across streams highlights the importance of documenting the diel patterns for each site and year. Sampling of diel drift patterns multiple times throughout the season would further improve the accuracy of larval production estimates by accounting for within season variation. Additionally, such sampling would help determine whether drift behaviour is density dependent.

The life history results from this study agree well with the limited information available for longnose suckers and with the characteristics of catostomids more generally. Our estimates of a 12-day egg incubation period agree with laboratory studies documenting incubation times between 8 and 14 days depending on temperature (Walton 1980). Additionally, many larval catostomids emigrate from spawning streams quickly after absorption of the yolk sack, returning to larger downstream habitats around the time of transition from endogenous to exogenous feeding (Cooperman & Markle 2003; Ellsworth et al. 2010). In this study, most larvae achieved little growth in the stream because they emigrated shortly after the transition to exogenous feeding.

Our observed female-biased sex ratios are consistent with previous reports that females experience lower mortality than males (Bailey 1969). Larger female size probably reflects delayed maturity in females relative to males to maximise reproductive output (Grabowski et al. 2012; E. Childress, unpublished data). Although it is plausible that a shortage of males could contribute to low fertilisation efficiency and thus high egg mortality, the sex ratio of longnose suckers was comparable (68% and 69%) between the two cases with the highest (Lily Bay Creek in 2013) and lowest (Hibbard Creek in 2012) larval production.

In the Great Lakes region, white and longnose suckers often spawn in the same tributaries during April and May (Klingler et al. 2003; Burtner et al. 2011). In Wilsey Bay Creek, the number of longnose suckers was slightly less than the number of spawning white suckers, and the lack of differentiating characteristics between the species' larvae (Snyder et al. 2004) introduced uncertainty about whether emigrating larvae were white or longnose suckers. Even if all larvae in Wilsey Bay Creek were longnose suckers, survivorship to larval outmigration would still have been $\leq 0.2\%$. In both Hibbard Creek and Lily Bay Creek, longnose far outnumbered white suckers, and the number of outmigrating larvae in Lily Bay Creek in 2013 was much larger than the

total number of white sucker eggs deposited. When both white and longnose suckers were present, the larval estimates provide an upper bound for longnose larval production, but even this upper bound is four orders of magnitude lower than longnose larval production in Lily Bay Creek. Thus, although there is uncertainty in larval identification, the conclusion that there is large variation in longnose sucker larval production is robust.

Spawning adults that were not recaptured emigrating from the streams when nets were deployed to catch all migrating fish represent a combination of upstream mortality and small numbers of fish remaining in the stream when the nets were removed. Sucker mortality is caused by a combination of human take, nonhuman predation and spawning stress. Although nets were removed only when very few fish were being captured, some individuals were present in the stream, which reduced recapture rates. Lower recapture rates increase uncertainty in the population estimates, but the uncertainty in the spawning population size is dwarfed by the variation in larval production.

The phenology of spawning was not markedly different between white and longnose suckers in our study streams, but there was large interannual variation in spawning dates. Peak spawning densities were approximately 1 month earlier in 2012 relative to 2009 and 2013, revealing substantial flexibility in spawning phenology. The difference in timing suggests that temperature or discharge acts as a spawning cue rather than photoperiod. In 2013, spawning adults were present in the stream 11 days before spawning was observed, and spawning began as temperatures reached 10 °C. After egg deposition, eggs disappeared rapidly from the benthos through mortality and hatching. However, most of this decrease occurred prior to the estimated hatch dates, indicating that egg mortality is likely to be a large component of the overall mortality. Although large quantities of eggs were deposited over a 10-day period, otolith analysis indicated that most larvae hatched on two consecutive days. The short hatching period suggests that successfully hatched eggs were only deposited on a few days, or that warming stream temperatures give rise to greater synchrony in egg hatching than in spawning.

Variability in sucker larval export may influence both stream and lake food webs. Sucker eggs are large contributions of nutrients and energy to stream ecosystems (Childress & McIntyre 2015). Although larvae that survive and emigrate from the stream are not utilised by stream biota, $<20\%$ of eggs survived to outmigration even in the highest survival case. Thus, a large majority of eggs or hatchling larvae serve as inputs to the stream food web. Addition-

ally, exported larvae become available to lake predators. Suckers fall prey to a variety of fish species, including walleye and northern pike, and large influx of larvae from successful spawning events is likely to be a boon for these predators (Beaudoin et al. 1999; Bertolo & Magnan 2005). The resulting variation in prey availability for lacustrine piscivores could be particularly important if spring weather conditions create coherent regionwide swings in larval production of one or more sucker species. Because these suckers are abundant and vulnerable to predation, examining how the high variability in larval production influences food web is ripe for further exploration.

High fluctuation in fish recruitment is typical for Great Lakes fishes and for long-lived, highly fecund fishes in general (Fogarty et al. 1991; Winemiller & Rose 1993; Ludsin et al. 2014). For example, walleye exhibit highly variable larval survivorship driven by river discharge, which determines juvenile and adult year-class strength (Mion et al. 1998). Similarly, recruitment of yellow perch fluctuates due to abiotic (i.e. temperature and wind) and biotic (i.e. predation and food availability) conditions during the larval and juvenile stages (Weber et al. 2011; Kaemingk et al. 2014). The variability in survivorship during these early life stages often determines year-class strength (Houde 1989). Interestingly, adult length–frequency distributions were bimodal in Wilsey Bay Creek and other nearby rivers in 2008 and 2009 for both longnose and white suckers (P. McIntyre, unpublished data). This suggests that the populations were primarily composed of a few very successful year classes because length at age tends to be unimodal within year classes of reproductive-age suckers (Bailey 1969). Predation and food availability may contribute to variability in year-class strength, and research on longnose suckers is lacking in these areas; however, the 26,000-fold variation in larval export likely contributes to variation in year-class strength.

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