ARTICLE

Biology of lake sturgeon (*Acipenser fulvescens*) spawning below a dam on the Richelieu River, Quebec: behaviour, egg deposition, and endocrinology

J.D. Thiem, D. Hatin, P. Dumont, G. Van Der Kraak, and S.J. Cooke

Abstract: Knowledge of the reproductive biology of wild sturgeon populations is critical to ensure the survival of this unique group of animals. We combined gill-netting surveys, nonlethal blood sampling, radiotelemetry, and egg collection to examine the reproductive biology of lake sturgeon (*Acipenser fulvescens* Rafinesque, 1817) at a suspected spawning ground below a dam on the Richelieu River, Quebec. Lake sturgeon were present at the beginning of sampling in early May, and spawning took place from 26 May to 5 June when water temperature averaged 13.4 ± 0.1 °C (range 11.5–15.5 °C). Daily spawning population estimates ranged from 285 to 1282 individuals and the sex ratio of spawners was estimated at 2.1 males per female. The presence of radio-tagged individuals on the spawning grounds peaked from 20 to 28 May, corresponding with known spawning bouts. Residence time of spawners on the spawning ground ranged from 1 to 27 days (median = 5 days) and there were no differences in residence time between sexes. Nonlethal blood sampling enabled the quantification of steroid levels to determine the spawning population sex ratio, and steroid levels were highest before spawning was known to occur and decreased concurrently with, and after, known spawning events.

Key words: lake sturgeon, *Acipenser fulvescens*, reproductive biology, spawning, telemetry, reproductive steroids.

Résumé : La connaissance de la biologie de la reproduction des populations sauvages d'esturgeons est essentielle pour assurer la survie de ce groupe d'animaux unique. Nous avons combiné des levés au filet maillant, le prélèvement non létal d'échantillons de sang, la radiotélémétrie et la collecte d'œufs afin d'étudier la biologie de la reproduction de l'esturgeon jaune (*Acipenser fulvescens* Rafinesque, 1817) dans un lieu de frai présumé en aval d'un barrage sur la rivière Richelieu (Québec). Des esturgeons jaunes étaient présents au début de la campagne d'échantillonnage au début de mai, et le frai a eu lieu du 26 mai au 5 juin, alors que la température de l'eau moyenne était de 13,4 ± 0,1 °C (dans une fourchette de 11,5 à 15,5 °C). Les estimations de la population en frai quotidienne allaient de 285 à 1282 individus et le rapport des sexes des individus en frai était de 2,1 mâles par femelle. Le nombre d'individus dotés de radio-émetteurs dans le lieu de frai a atteint un maximum du 20 au 28 mai, correspondant à des évènements de frai reconnus. Le temps de séjour des individus en frai dans le lieu de frai allait de 1 à 27 jours (médiane = 5 jours), les deux sexes ne présentant aucune différence à ce chapitre. Le prélèvement non létal de sang a permis de quantifier les concentrations de stéroïdes afin de déterminer le rapport des sexes dans la population en frai; ces concentrations étaient les plus élevées avant le début reconnu du frai et ont ensuite diminué durant et après les évènements de frai reconnus. [Traduit par la Rédaction]

Mots-clés : esturgeon jaune, *Acipenser fulvescens*, biologie de la reproduction, frai, télémétrie, stéroïdes sexuels.

Introduction

Sturgeons represent one of the most threatened fish in the world, with 18 of the 27 recognised species of Acipenseriformes listed as endangered or critically endangered (IUCN 2010). Because of their life-history characteristics including slow growth and late age at maturity, sturgeon are particularly sensitive to low levels of exploitation and habitat degradation (Rochard et al. 1990; Bemis and Kynard 1997). Given the propensity of all species to spawn in freshwater rivers, river fragmentation resulting in the loss of critical spawning habitat places limits on the recovery of many populations already decimated through overharvest (Rochard et al. 1990). Knowledge of the reproductive biology of wild populations of sturgeon is therefore critical to ensure the perpetuation of this unique group of animals (Haxton 2006).

Lake sturgeon (*Acipenser fulvescens* Rafinesque, 1817) are the most widely distributed of the five species of sturgeon (genus *Acipenser* L., 1758) occurring in North America (Peterson et al. 2007). Similar to most sturgeons, lake sturgeon have undergone severe population declines across their range (Scott and Crossman 1973; Peterson et al. 2007). In Canada, the Committee on the Status of Endangered Wildlife (COSEWIC) has listed lake sturgeon populations as being of special concern, threatened, or endangered, depending on the population status in designable units (COSEWIC 2002). Lake sturgeon are potamodromous and generally undertake spawning migrations over a distance of 10s to 100s of kilometres (Auer 1996a). Typically, the construction of dams on large rivers is considered a threatening process for sturgeon, as barriers limit access to historic upstream spawning and nursery areas and isolate populations (Jager et al. 2001), although lake sturgeon will spawn below dams where suitable habitat exists (e.g., LaHaye et al. 1992; Auer 1996b; Bruch and Binkowski 2002; Haxton 2006). The creation of artificial spawning grounds or expansion of existing spawning grounds holds promise for the recovery of the species where suitable spawning grounds are not naturally available (LaHaye et al. 1992; Johnson et al. 2006; Dumont et al. 2011).

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To date, there have been several studies of lake sturgeon reproductive biology in riverine systems (e.g., LaHaye et al. 1992; Bruch and Binkowski 2002; Dumont et al. 2011). Lake sturgeon typically migrate to spawning grounds in May and June, soon after ice-off (Scott and Crossman 1973). As spawning is periodical (every 2 years for males and 3–5 years for females; Bruch and Binkowski 2002), migrations are not undertaken by all individuals each year (Rusak and Mosindy 1997). Spawning grounds are generally located near rapids, in shallow water with moderate to high water velocities (0.25–0.85 m depth and 0.4–1.39 m·s⁻¹ in the L'Assomption River, Quebec, Canada) over coarse gravel or cobble substrate (LaHaye et al. 1992; Auer 1996b). Spawning has been observed over a wide range of water temperatures (8.8–21.1 °C), although generally occurs at water temperatures of 11.5–16 °C (Bruch and Binkowski 2002). Males typically arrive first at spawning grounds and actively search for ovulating females, with spawning activity mainly occurring for 2–4 days at each site (Bruch and Binkowski 2002). Prespawn males are frequently differentiated by the expulsion of gametes; however, as this is rarely observed in females, prespawn peaks and postspawn declines in steroids from nonlethal blood samples can be used to differentiate among sexes (McKinley et al. 1998). Females are typically serviced by multiple males and eggs are broadcast over preferred substrate (Bruch and Binkowski 2002). The demersal, adhesive eggs attach to substrate and hatch after 5–8 days (Scott and Crossman 1973). Several studies have independently monitored egg deposition, behaviour (e.g., arrival at spawning grounds, residency, spawning behaviours, postspawning behaviour), and endocrine status. Combining these approaches to collectively define lake sturgeon reproductive biology enables the use of multiple lines of evidence to identify and characterise critical spawning habitat and assess key spawning population characteristics. For example, relying solely on fish behaviour and presence–absence of mature adults fails to provide direct evidence of spawning without information on gamete deposition and (or) the reproductive state of sturgeon. The identification and protection of essential habitats represents a crucial step in the effective management and recovery of lake sturgeon populations.

The objective of this study was to characterise the reproductive biology of lake sturgeon downstream of the St. Ours dam on the Richelieu River in Quebec, Canada. Specifically, we were interested in determining the location of the spawning ground and quantifying key habitats, as well as determining the timing of spawning, and the abundance, composition, and residency of spawners. This study site that is downstream from a dam equipped with a fishway, which is known to pass lake sturgeon to access upstream spawning habitat (Thiem et al. 2011), enabled a further goal which was to determine if lake sturgeon are able to find and use suitable spawning sites downstream of the dam.

Materials and methods

Study site
This study was conducted on the Richelieu River, immediately downstream of the St. Ours dam in southwestern Quebec, Canada (45°51′48″N, 73°08′60″W; Fig. 1). The Richelieu River originates in Vermont and New York, USA, and after exiting Lake Champlain, empties into the St. Lawrence River near the town of Sorel, Quebec, Canada. The river is 124 km long and its mean annual discharge is 362 m³·s⁻¹. The St. Ours dam is located 18 km upstream of the confluence between the Richelieu and the St. Lawrence rivers and comprises a 180 m wide, 3.4 m high structure divided into a series of five submersible gates (each 30 m wide and a fishway) that are typically open for a short period (2–4 weeks) during the spring flood and then closed from the 3rd week of May onwards. A vertical slot fishway provides access to an additional ~50 km of unimpounded river upstream of the dam and a large set of rapids offering suitable spawning habitat. This study was conducted in an unusually high discharge year in comparison

with the historical mean daily discharge (Fig. 2a), resulting in open dam gates for almost the entire duration of the study to prevent upstream flooding and causing the fishway to be inoperable for most of the study period.

### Capture, tagging, and tracking
Lake sturgeon were captured between 4 May and 3 June 2011 downstream of the St. Ours dam in the Richelieu River using monofilament gill nets (three 10 m long panels with stretched mesh 20.3, 25.4, and 30.5 cm). Gill nets were set for 24 h, perpendicular to the shore and downstream of the dam and locks, in a deep hole located away from the main river current with low water velocity (Fig. 1). This site was chosen based on extensive gill-netting surveys conducted during the same period in 2010 for the collection of adults for a separate study (Thiem et al. 2011), with sampling at other nearby locations resulting in low or zero catch rates. The same capture method is used by government agencies during the spring period for routine lake sturgeon monitoring and the fish are robust to the stress associated with capture (Baker et al. 2008).

Following capture, sturgeon were immediately transferred to a holding tank and measured (total length (TL), mm) and weighed (kg). All sturgeon were tagged with a uniquely coded PIT tag (23 mm × 3.85 mm HDX; Texas Instruments, Dallas, Texas, USA). Each fish was placed ventral side up in a v-shaped cradle, and following a small incision (<5 mm), a PIT tag was inserted approximately 10 cm anterior of the vent and slightly off centre of the ventral midline using a 6-gauge plunger (Baras et al. 1999) and surgical wounds were sealed with cyanoacrylate. No anaesthetics or sutures were used and the entire handling process took <1 min, with care taken to minimize air exposure.

Radiotelemetry was used to monitor lake sturgeon movement onto and away from the spawning grounds. A subset of all captured sturgeon (n = 51) and representing approximate length (1287 ± 18 mm TL, range 955–1620 mm) and masses (13.6 ± 0.7 kg, range 5.1–29.9 kg) of the total catch were fitted with coded external radio tags (149 MHz, 30 mm × 8 mm, 8 g mass in air, burst rate 2 s, 90 day battery life; Sigma Eight Inc., Newmarket, Ontario, Canada) at the base of the dorsal fin (Hatin 1999; Hatin et al. 2002). All individuals were tagged between 6 and 18 May 2011, which encompassed the period prior to detection of any spawning events, and were released immediately following tagging near the point of capture (Fig. 1), with release locations alternating between both river banks each day. Sturgeon were tracked between 7 May and 30 June 2011 using four fixed radiotelemetry receivers (SRX 600; Lotek Inc., Newmarket, Ontario, Canada) combined with three- or five-element yagi antennas. A total of 15 antennas were installed to determine residence time of radio-tagged lake sturgeon on and around the spawning grounds and monitor movements in close proximity (~50 m) of the dam, as well as radio-tagged sturgeon attraction to and entrance into the nearby fishway and potential upstream passage through the fishway. Five antennas monitored each of the five dam gates, three antennas monitored attraction to and entrance into the fishway, two antennas faced upstream of the dam to monitor possible upstream passage, and two antennas monitored approximately 200 m of shoreline on the east and west riverbank. Three antennas were positioned on the west bank of the river approximately 200 m downstream of the dam facing into the river channel to monitor the suspected spawning site based on previous identification of suitable lake sturgeon spawning substrate in this location (Dumont et al. 1997).

To determine the sex ratio of the spawning population of lake sturgeon, we obtained blood samples from the caudal vasculature of all captured sturgeon using 3 mL Vacutainers (Becton Dickinson, Mississauga, Ontario, Canada) and 3.8 cm long, 21 gauge needles. Blood vials were immediately placed into a water–ice slurry for <1 h prior to centrifuging at 10 000g (Compact II Centrifuge;

Fig. 1. Location of the St. Ours dam on the Richelieu River, Quebec, showing egg collection stations (*sn*), gill-net locations, and the location of the radiotelemetry monitoring station used to determine residence of radio-tagged lake sturgeon (*Acipenser fulvescens*). Approximate detection ranges of antennas are indicated by ellipses. Note additional telemetry stations monitored for movement in and around the dam and fishway, although did not detect any upstream passage and minimal activity near the dam and are not represented here.
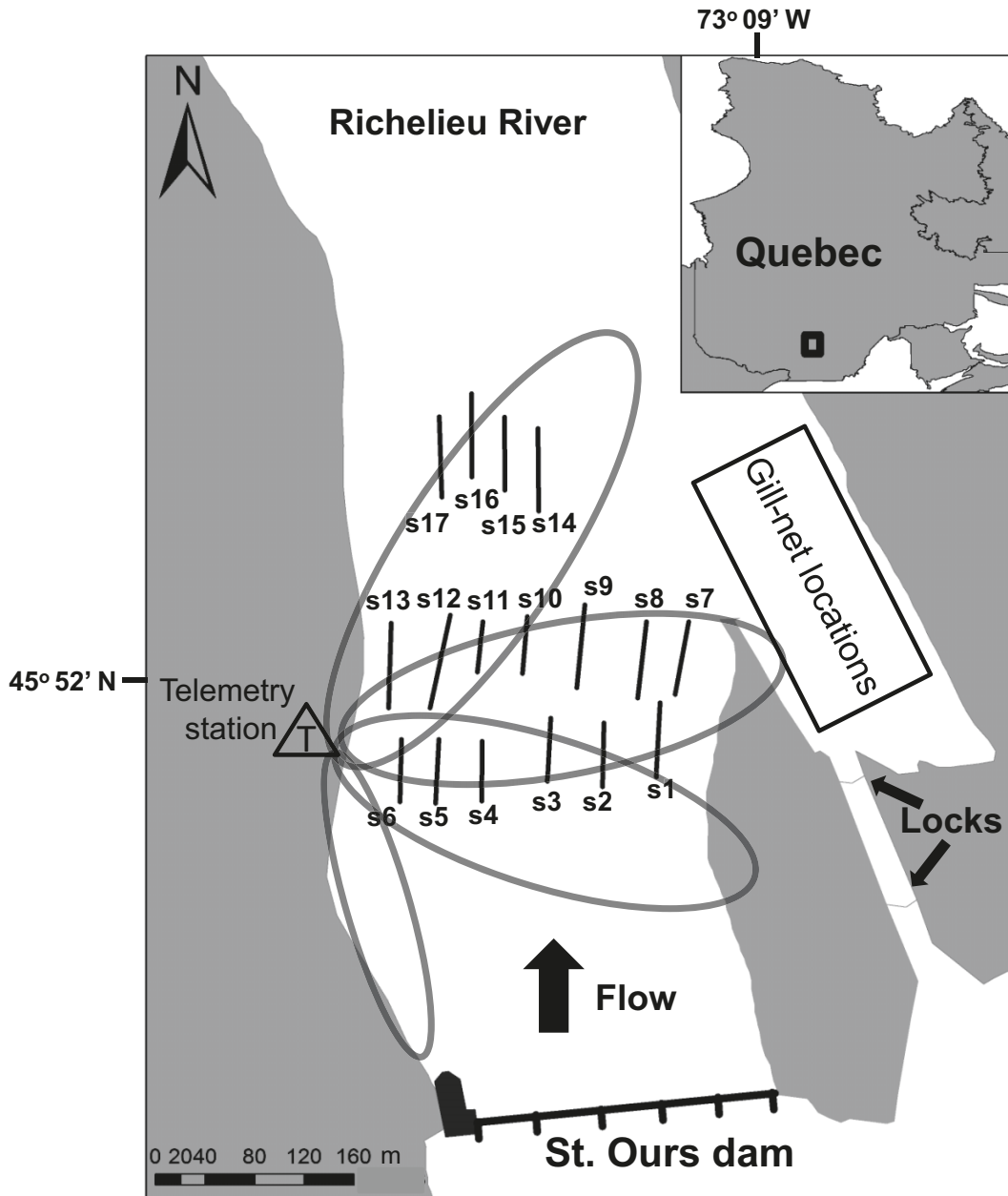
Clay Adams). Plasma was aliquoted into vials and frozen in liquid nitrogen prior to transferring samples to a −80 °C freezer. The plasma content of the circulating steroids 17β-estradiol, 11-ketotestosterone and testosterone were determined for a subset of individuals (*n* = 152) to determine sex ratios of the spawning population and to examine temporal trends in steroid levels in response to spawning events. The samples used were representative of the size range of individuals captured in the study, encompassed the entire capture period, and included 48 radio-tagged individuals. Steroid levels were determined by radioimmunoassay following the methods described by Van Der Kraak et al. (1984, 1990) and Wade and Van Der Kraak (1991). The lowest quantifiable concentrations were 0.1 ng·mL⁻¹ of plasma for 17β-estradiol, 1.25 ng·mL⁻¹ for testosterone, and 5 ng·mL⁻¹ for 11-ketotestosterone. The difference in the detection limits for the three steroids reflects

the manner in which the samples were diluted for analysis. Sex was assigned to individuals based on the expulsion of gametes at the time of capture (*n* = 52, comprising 51 ♂ and 1 ♀) or based on the solved classification functions provided by Webb et al. (2002) for white sturgeon (*Acipenser transmontanus* Richardson, 1836) and previously applied to lake sturgeon (Craig et al. 2009; Shaw et al. 2012):

$$-1.6727 + 2.3678(\log_{10}T) - 3.5783(\log_{10}E2)$$

for females and

$$-5.2972 + 5.2524(\log_{10}T) - 7.5539(\log_{10}E2)$$

Fig. 2. (*a*) Water temperature (°C) (thick solid black line) and daily discharge (m³·s⁻¹) (thin solid grey line) in the Richelieu River, Quebec, for the study period, as well as historical daily discharge (m³·s⁻¹) (dotted line) over the period of record (1937–2011), and (*b*) catch per unit effort (CPUE) of lake sturgeon (*Acipenser fulvescens*) (□, number of sturgeon·net night⁻¹) and of lake sturgeon eggs (■, number of eggs·egg mat night⁻¹ × 10). Grey shading indicates estimated spawning. Asterisks refer to periods where no netting for lake sturgeon was undertaken and does not represent zero CPUE. Zero CPUE of lake sturgeon eggs occurred on 17–20 May, 24–25 May, 27 May, 9 June, and 13 June 2011.
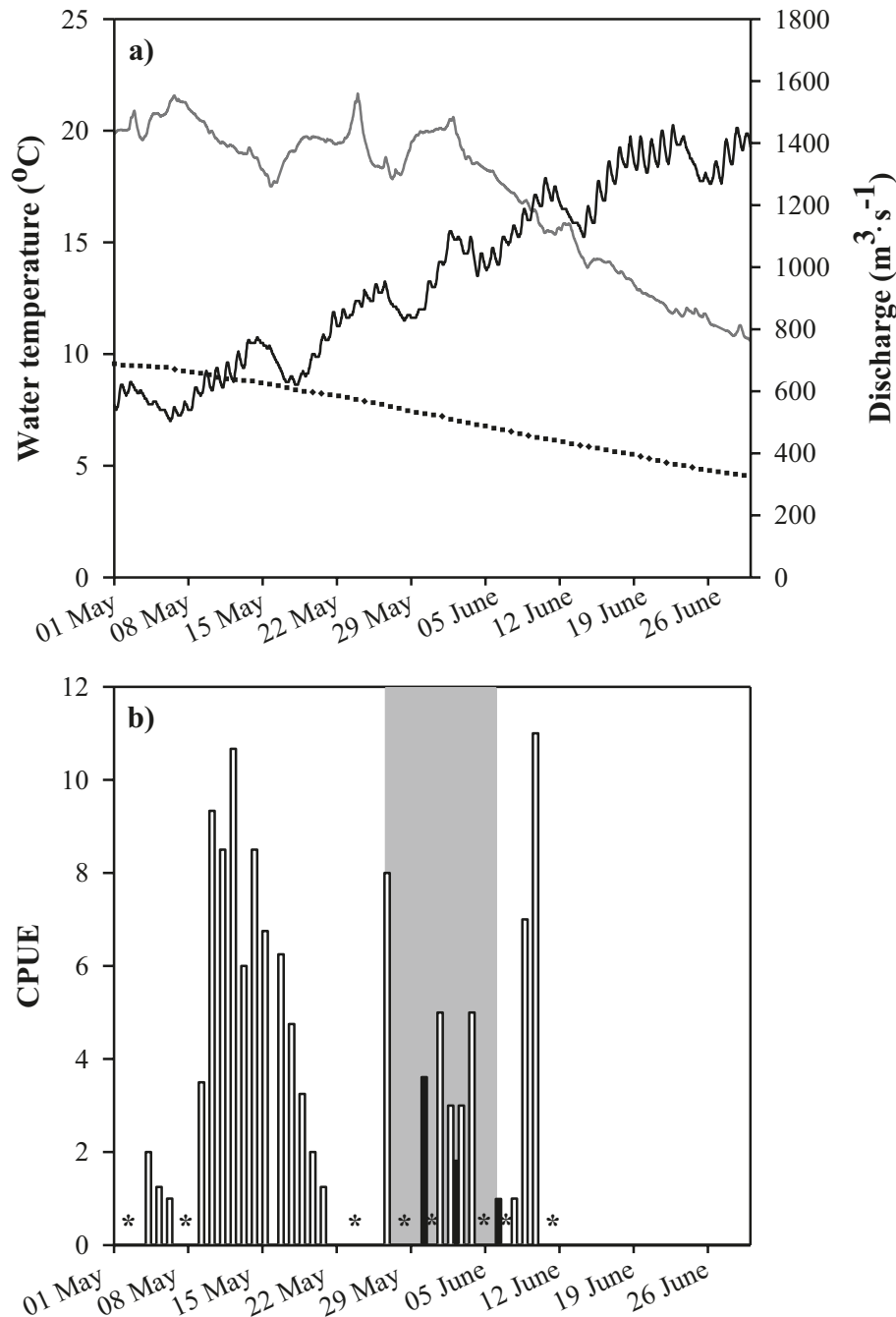
for males, with paired values of 17β-estradiol (E2) and testosterone (T) from individuals substituted and the highest value of the two equations used to predict sex. Four known males were misclassified as females by this method; however, as the sex of >92% of known individuals was correctly identified by this method, it was deemed appropriate. Steroid levels were plotted separately for males and females to determine if steroid levels exhibited temporal trends. Prespawning, spawning, and postspawning periods were defined by the back-calculation of the embryonic age of eggs (Table 1) and retrospectively assigned to individual samples based

on the timing of adult capture coinciding with these periods. Steroid levels were not determined more than once for any individual, and do not provide direct evidence of spawning, as we were unable to validate that spawning was undertaken by the individuals for which steroid levels were measured.

Egg collection

The location and timing of lake sturgeon spawning was studied using 68 artificial egg collection mats deployed in a grid sampling design. The design comprised 17 rows with four mats in each row

Table 1. Embryonic stage and age of lake sturgeon (*Acipenser fulvescens*) eggs collected at a spawning site on the Richelieu River, Quebec.

Capture date	Water temperature (°C; mean ± SE)	Number of viable eggs (total *n*)	CPUE (eggs·mat⁻¹·day⁻¹)	Embryonic stage		Embryonic age (h)	
				Mean ± SE	Range	Mean ± SE	Range
30 May*	12.19±0.05	46 (57)	0.36	14±2.28	6–19	42.09±1.79	18.70–65.55
30 May†	11.84±0.03	30 (34)	—	14±2.15	7–19	42.62±2.28	21.06–67.76
2 June	14.21±0.11	35 (37)	0.18	18±3.05	2–31	69.77±9.12	11.46–162.84
6 June	14.38±0.05	25 (27)	0.10	24±2.31	1–30	93.66±6.76	10.38–145.68

Note: CPUE is catch per unit of effort. Embryonic age of lake sturgeon is calculated from the equation in Wang et al. 1985, using water temperature values from this study.
*Corresponding values are calculated based on egg mats deployed from 25 to 30 May.
†Corresponding values are calculated based on egg mats deployed from 27 to 30 May.

Fig. 3. Length frequency distribution of lake sturgeon (*Acipenser fulvescens*) captured downstream of the St. Ours dam on the Richelieu River, Quebec, for (*a*) the total number of number captured (*n* = 306) and (*b*) males (open bars, *n* = 103) and females (solid bars, *n* = 49), where sex was determined via concentrations of circulating plasma steroids.
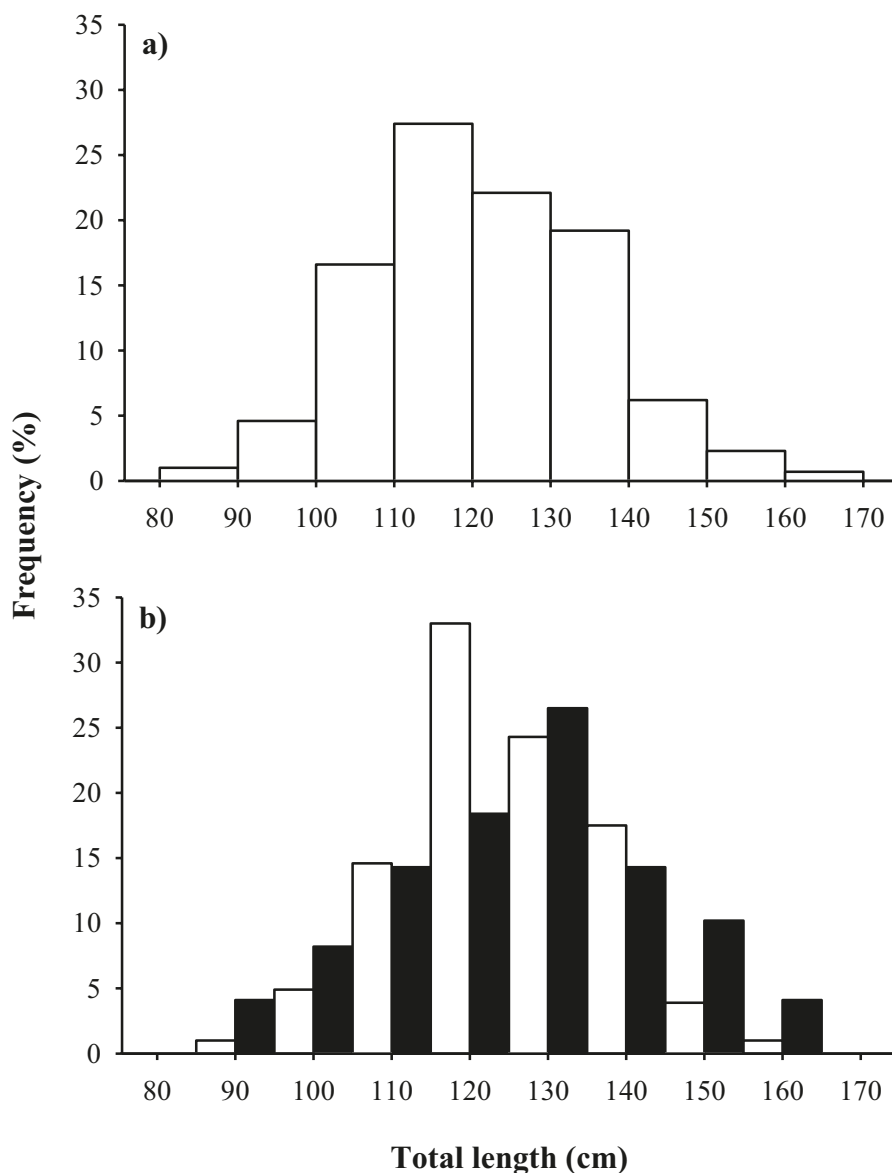
deployed and anchored in the area presenting suitable substrate and water velocity conditions for lake sturgeon reproduction between 12 May and 13 June 2011 (Fig. 1). Egg mats were checked every 2–6 days (median = 4 days), which is shorter than the expected incubation period (e.g., ~9 days from fertilisation to complete hatching at 15 °C; Wang et al. 1985) at the water temperatures observed in this study. Egg collection mats were modified from McCabe and Beckman (1990) and comprised carpets of latex-coated synthetic animal hair wrapped around a concrete block. Location, depth, and bottom water velocity (Gurley Price water velocity meter; Gurley Precision Instruments, Troy, New York, USA) were determined at each mat lift. The mean of each of these variables over the study period was used to describe the physical location and habitat for each egg collection mat. Dominant sub-

strate was obtained for the location of each egg collection mat by first digitising an existing habitat classification map of the study site consisting of 158 substrate point locations (Dumont et al. 1997) in ArcMap (ESRI, Redlands, California, USA). Universal Kriging (Oliver and Webster 1990) was subsequently conducted on the digitised data using the Geostatistical Analyst tool in ArcMap to interpolate dominant substrate at each egg mat location. Hourly water temperature was recorded in the river at the benthos for the duration of the study (DS1921Z iButton; Maxim Integrated Products, San Jose, California, USA) and 15 min discharge data were obtained from a nearby gauging station (station 02OJ007; available from http://www.wateroffice.ec.gc.ca/index_e.html, accessed 7 September 2011).

Each egg collection mat was inspected to find the adhesive sturgeon eggs prior to cleaning with a high pressure hose and redeployment at the same location. Eggs were identified to species (other species eggs collected included American shad (*Alosa sapidissima* (Wilson, 1811)) (n = 7 eggs at 7 locations), mooneye (*Hiodon tergisus* Lesueur, 1818) (n = 12 eggs at 11 locations), and species of common suckers (genus *Catostomus* Lesueur, 1817) (n = 55 eggs at 27 locations)), counted, and preserved in 5% formaldehyde for later embryonic staging in the laboratory. Embryonic stage of each lake sturgeon egg was determined according to Dettlaff et al. (1981). The approximate time of fertilisation of lake sturgeon eggs was calculated using the exponential equation provided by Wang et al. (1985) for lake sturgeon:
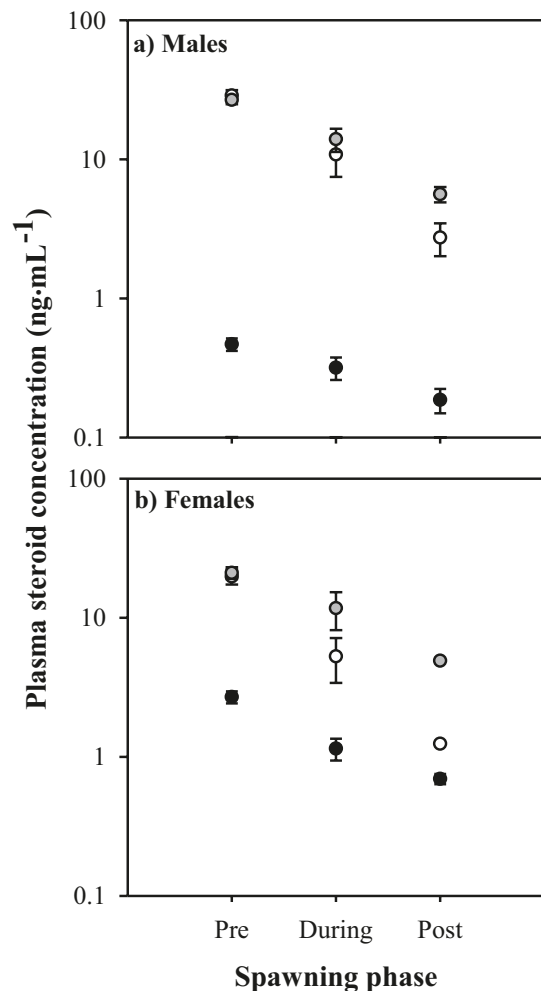
$$Y = ae^{bT}$$

where Y refers to Y hours after fertilisation, T refers to temperature, and a and b refer to the coefficient and slope combinations, respectively, provided by the authors (see Table 2 of Wang et al. 1985) for embryonic developmental stages 14, 22, 29, 35, 36, 40, and 44 (as per Dettlaff et al. 1981). Time of fertilisation was interpolated for each embryonic stage identified in the laboratory using the new equation resulting from the original solved equation of Wang et al. (1985), which included mean hourly water temperature for the duration of each egg mat soak time at the study site (Table 1).

Data analysis

Estimates of the spawning population abundance were determined using the Seber–Jolly method to account for multiple census dates and an open population (i.e., immigration–emigration). Estimates were obtained for different census dates using the package FSA version 0.3-4 (Ogle 2013) in R version 2.14.2 (R Development Core Team 2012). Estimates were deemed reliable on census dates when the total number of recaptures equalled or exceeded three, or the total number of individuals released on a census date and recaptured at a later date equalled or exceeded three (Ricker 1975), resulting in six daily estimates from 23 sampling occasions. On one of these included census dates, the standard error of the estimate was not calculated because of zero recaptures on that date, although abundance was estimated as eight individuals tagged on that date were recaptured at a later date. Analysis of covariance (ANCOVA) was used to determine if (log-transformed) egg abundance (i.e., the total number of eggs collected at a site) covaried with water velocity and differed among substrate types while controlling for water velocity. Post hoc tests were performed using a Bonferroni correction (Field 2009). Telemetry data were filtered to remove the first 24 h of data for each individual to allow for the resumption of normal behaviour following handling. Data were also filtered by fish ID and corresponding frequency channel to remove any erroneous records and data were only retained if there was at least one positive detection within 15 min of another (effectively three full scan cycles) to eliminate the possibility of false detections. As 98% of detections from radio-

Fig. 4. Circulating plasma steroid levels 17β-estradiol (solid), testosterone (open), and 11-ketotestosterone (shaded) for (*a*) male and (*b*) female lake sturgeon (*Acipenser fulvescens*). Prespawning, spawning, and postspawning periods were defined by the back-calculation of the embryonic age of eggs (see Table 1) and retrospectively assigned to individual samples based on the timing of adult capture coinciding with these periods. Data are represented as mean ± SE. Note the log *y*-axis scales.

tagged individuals were from antennas monitoring the spawning site and no evidence of upstream passage or fishway entry was observed, analysis of radiotelemetry data focussed entirely on presence in and around the spawning site using pooled data from four antennas connected to a single receiver (Fig. 1) where detection range of pooled antennas encompassed the entire spawning ground. A residency index was calculated for each individual as the number of days present at the site divided by the number of days monitored (O'Toole et al. 2011). An independent samples Student's *t* test was used to compare differences in residence time between sexes. Where appropriate, data were first tested for the assumptions of normality and homogeneity of variance following the methods outlined by Grafen and Hails (2002) and were transformed and re-evaluated if they did not meet these assumptions. Additionally, the assumption of homogeneity of regression slopes was tested according to the methods outlined by Field (2009) for the ANCOVA. All statistical analyses were deemed significant at $P < 0.05$ and conducted using SPSS version 18 (SPSS Inc., Chicago, Illinois, USA). All data are presented as mean ± SE unless otherwise stated.

Fig. 5. Location of lake sturgeon (*Acipenser fulvescens*) egg collection stations, with circles indicating the total number of viable eggs collected at each location and shading indicating dominant substrate.
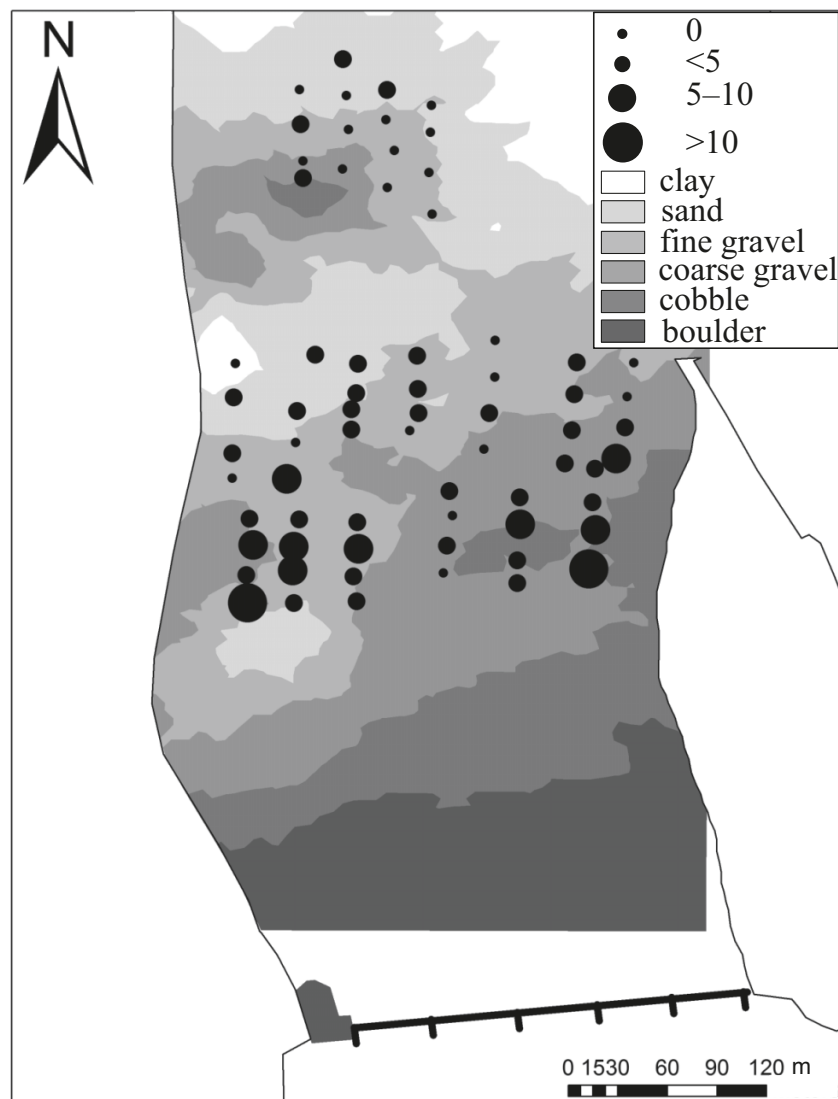

Results

We captured 334 lake sturgeon from 4 May and 3 June 2011 (n = 306 individuals, 1213 ± 8 mm TL (range 862–1653 mm), 10.9 ± 0.3 kg (range 2.6–30.0 kg); Fig. 3*a*), including 28 recaptures resulting in daily spawning population estimates (SE) of 349 (not available), 704 (582), 1202 (1087), 746 (658), 361 (384), and 285 (332) individuals corresponding to 10, 11, 12, 13, 16, and 17 May 2011, respectively. The subset of individuals (n = 152) used in the analysis of circulating steroid levels indicated the sex ratio of the spawning population was 2.1:1 male to female lake sturgeon, respectively. Mean length and mass were, respectively, 1308 ± 24 mm (range 954–1653 mm) and 14.8 ± 0.9 kg (range 4.0–30.0 kg) for females and 1203 ± 12 mm (range 888–1538 mm) and 10.2 ± 0.4 kg (range 3.5–22.2 kg) for males (Fig. 3*b*). Females were characterised by higher levels of 17β-estradiol (2.20 ± 0.22 ng·mL^{-1} plasma for females and 0.40 ± 0.03 ng·mL^{-1} plasma for males). Differences were largely absent between females and males in terms of testosterone levels (15.2 ± 2.1 ng·mL^{-1} plasma for females and 21.1 ± 2.2 ng·mL^{-1} plasma for males) or 11-ketotestosterone levels (17.7 ± 1.8 ng·mL^{-1} plasma for females and 21.0 ± 1.5 ng·mL^{-1} plasma for males). Levels of all three steroids decreased for both sexes over time when data were separated into pre-spawning, during, and post-spawning periods based on embryonic age (Fig. 4). These data suggest that steroid levels are highest before spawning was known to occur, decrease concurrently with known spawning events, and further drop after spawning was finished.

At the beginning of the gill-netting operation on 3 May 2011, lake sturgeon were already present in low abundance downstream of the dam, but CPUE peaked rapidly and was highest on the 12 May 2011 (Fig. 2*b*). During the spawning period, a total of 155 lake sturgeon eggs (136 viable eggs and 19 nonviable eggs) were collected at 46 egg mat stations. Spawning was first detected on 30 May, and subsequently on 2 and 6 June. Relative abundance of eggs was highest on 30 May (0.36 eggs·mat^{-1}·day^{-1}; Table 1, Fig. 2*b*) and declined by 2 June (0.18 eggs·mat^{-1}·day^{-1}) and 6 June (0.10 eggs·mat^{-1}·day^{-1}). The embryonic stage of eggs ranged from 6 to 19 on 30 May, from 2 to 31 on 2 June, and from 1 to 30 on 6 June (Table 1). Back-calculation of embryonic age indicated that fertilisation occurred 19–68 h prior to collection on 30 May, 11–163 h prior to collection on 2 June, and 10–146 h prior to 6 June (Table 1), indicating spawning events took place between 26 May and 5 June 2011 when water temperature averaged 13.4 ± 0.1 °C (range 11.5–15.5 °C).

Fig. 6. Frequency of (*a*) bottom water velocities (m·s⁻¹) and (*b*) dominant substrate types from locations where lake sturgeon (*Acipenser fulvescens*) eggs were collected.
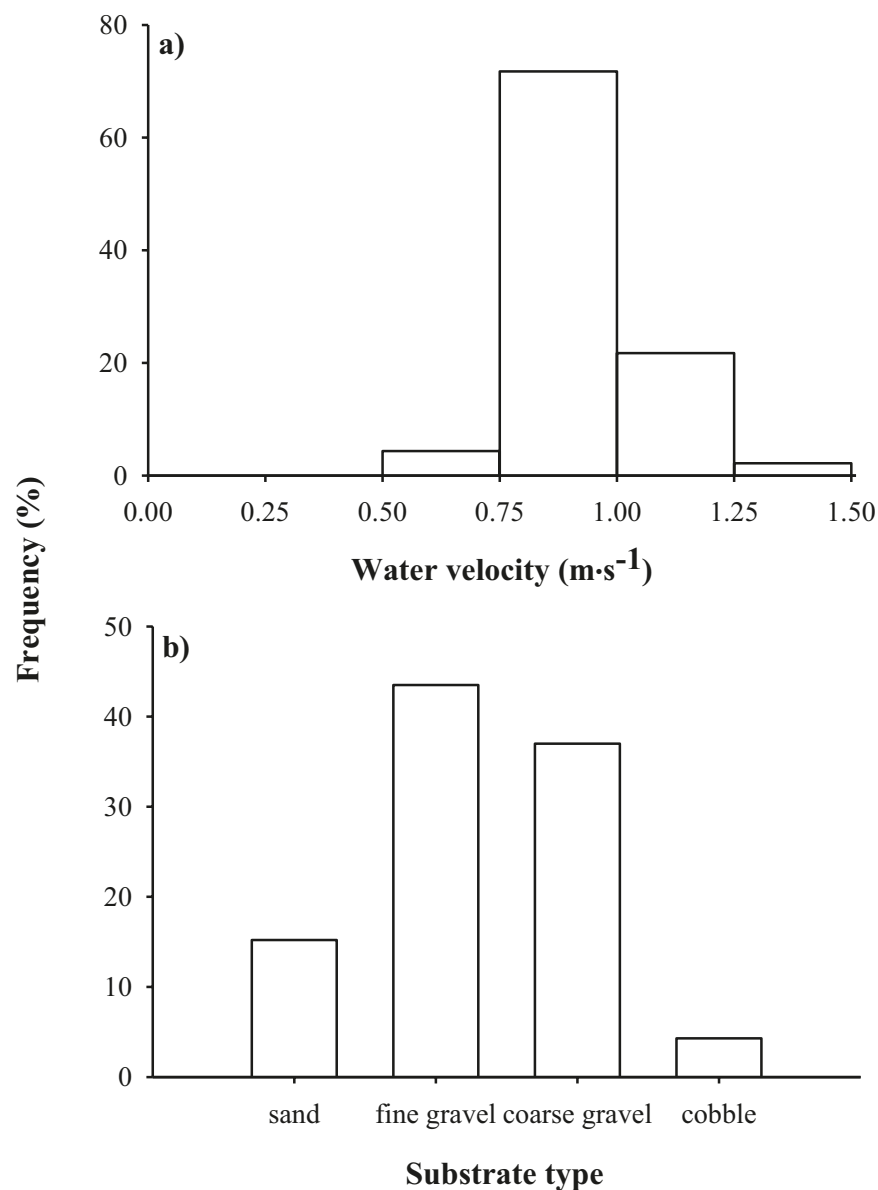

Abundance of viable lake sturgeon eggs ranged from 1 to 14 among stations, with viable eggs not collected from 23 sampling locations, or 34% of the 68 locations sampled (Fig. 5). Viable eggs were collected from water depths of 6.05 ± 0.14 m (range 4.24–7.78 m) and water velocities of 0.93 ± 0.02 m·s⁻¹ (range 0.52–1.27 m·s⁻¹). Lake sturgeon eggs were found mainly at near substrate water velocities from 0.76 to 1.00 m·s⁻¹ (Fig. 6*a*) and dominated by fine and coarse gravel substrates (80%; Fig. 6*b*). Abundance of lake sturgeon eggs at sampling locations was significantly related to the covariate water velocity ($F_{[1,64]}$ = 4.852, P = 0.031) and was also significantly different among substrate types after controlling for the effect of water velocity ($F_{[2,64]}$ = 3.484, P = 0.037). Post hoc comparisons identified significantly higher abundances of lake sturgeon eggs at locations comprising coarse gravel compared with sand, with no significant differences at locations comprising fine gravel with either sand or coarse gravel substrates.

Of the 51 sturgeon equipped with radio tags, 32 were confirmed as male, 18 as female, and the sex of one individual was unknown. Eight individuals (representing 15.7% of the tagged samples, 5 ♂

and 3 ♀) were never relocated on the fixed radiotelemetry station. Of the remaining 43 individuals (27 ♂, 15 ♀, and 1 unknown sex) that were relocated, none were documented approaching or entering the fishway and subsequently no upstream passage past the dam via the fishway was documented. Ten individuals (5 ♂, 4 ♀, and 1 unknown sex) were recorded approaching the dam on a combined total of 13 occasions, and although passage over the flooded dam gates was possible during all occasions, no upstream passage was observed. Presence at the spawning site ranged from 1 to 27 days (median = 5 days) (Fig. 7). There were no differences in the residency index (proportion of days present to days tagged) when comparing between males (median 0.11, range 0.02–0.43) and females (median 0.09, range 0.04–0.23) over the study period (log-transformed, independent samples Student's t test: $t_{[40]}$ = 0.490, P = 0.627). Residency at the spawning ground peaked from 20 to 28 May, with 22%–42% of radio-tagged individuals present during this period (Fig. 8), coinciding with immediate prespawning and early spawning events, water temperatures of 9.9–13.2 °C and river discharges of 1284–1560 m³·s⁻¹.

Fig. 7. Frequency of the number of days radio-tagged lake sturgeon (*Acipenser fulvescens*) were detected in proximity to a spawning site on the Richelieu River, Quebec. Note that data from individuals never detected (*n* = 8) are not included.
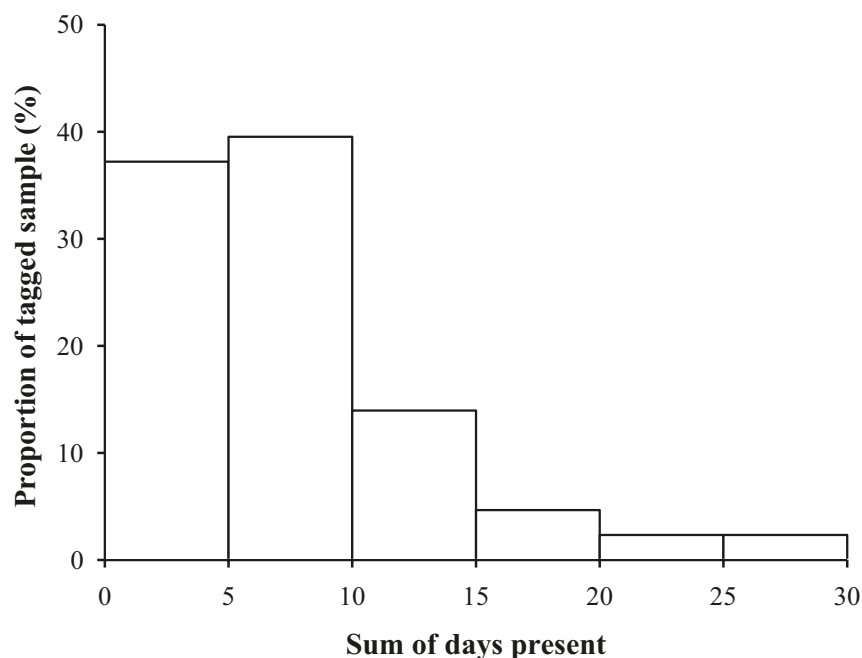
Discussion

Lake sturgeon spawned in late May and early June in the Richelieu River downstream of the St. Ours dam, and at water temperatures consistent with previous studies of this species that promotes optimal survival of eggs and larvae (Wang et al. 1985; LaHaye et al. 1992; Bruch and Binkowski 2002; Caswell et al. 2004; Dumont et al. 2011). The technique developed by Wang et al. (1985) for estimating the duration of early embryonic development in controlled conditions provided a useful method for estimating the actual timing of spawning in the current study, although field application of the technique necessitates the over simplification of variable water temperatures. Survival of eggs to larvae was not quantified in the current study, and year-class strength in this region is predominantly a function of June water temperatures and discharge (Nilo et al. 1997; Dumont et al. 2011).

Lake sturgeon likely form a homogeneous phenotypic and genotypic stock in a section of the St. Lawrence River spanning over 350 km, from Beauharnois Dam at the head of Lac Saint-Louis to the brackish waters downstream of Quebec City including the lower reaches of its tributaries (Fortin et al. 1993; Guénette et al. 1993). After a long period of decline, evidence of a spawning area used by lake sturgeon, which was disused for a long period or previously did not exist (P. Dumont, unpublished data), is promising (Mailhot et al. 2011). The capture of large numbers of running ripe adults over a 3-year period (2010–2012; Thiem et al. 2011; J.D. Thiem, unpublished data) during the expected spawning window for the species, and of a size range typical for that observed on other spawning grounds (e.g., Des Prairies River; Dumont et al. 2011), indicates that use of this spawning site is not an anomaly. The first indication of lake sturgeon spawning activity downstream of the St. Ours dam occurred on 1 June 2005 when ~100 sturgeon eggs were observed in a stomach contents of an American shad captured downstream of the fishway entrance (P. Bilodeau and H. Massé, MRNF, unpublished data).

Using multiple lines of evidence, we confirmed the location of a lake sturgeon spawning ground in the current study. The location of the spawning ground, directly below a dam, is not surprising given that numerous lake sturgeon spawning grounds are located immediately downstream of impassable obstacles, and these ob-stacles frequently provide the necessary habitat requirements conducive to spawning and egg survival including coarse substrate and (or) high water velocities (LaHaye et al. 1992; Auer 1996b; Bruch and Binkowski 2002; Haxton 2006; Dumont et al. 2011). Although the barrier in the current study is fitted with a fishway used by lake sturgeon (see Thiem et al. 2011), no observations were made of passage past the dam during the study period or through the fishway by any of the radio-tagged individuals in this study. Suitable sturgeon spawning habitat exists ~50 km upstream of the dam at another set of rapids, and presumably the mature individuals known to use the fishway during spawning periods access these grounds (Dumont et al. 1997). It should be noted that the current study was conducted during atypical high flood conditions for the site, and during this study the fishway was largely inoperable.

Analysis of plasma levels of circulating steroids provided an appropriate method for sexing lake sturgeon in the current study. Although other nondestructive methods exist for sexing and (or) staging adult sturgeon including ultrasound (Colombo et al. 2004), endoscopes (Kynard and Kieffer 2002), and observation of the urogenital opening (Vecsei et al. 2003), the lack of universal acceptance of a single method is indicative that each method is not without its shortcomings. One possible limitation of the current study, and most others involving the sampling of wild fish, is that the stress associated with capture and sampling may affect circulating steroid levels (reviewed in Fuzzen et al. 2011). However, based on known sex of individuals in the current study (predominantly males), the equations provided by Webb et al. (2002) for white sturgeon resulted in >92% accuracy for differentiation of sex of lake sturgeon. This result is largely similar to the findings of Webb et al. (2002) where the technique resulted in the correct sex classification 79% of the time for males and 85% of the time for females. Although both vitellogenin (Vtg) protein, a female-specific egg-yolk precursor, and calcium (Ca^{2+}) have also been used to differentiate sex in sturgeons (e.g., Webb et al. 2002; Craig et al. 2009), ratios of testosterone and estradiol are reliable predictors of sex (Ceapa et al. 2002).

Circulating steroids followed a temporal trend of decreasing levels over time for both males and females in the current study,

Fig. 8. Presence of individual radio-tagged lake sturgeon (*Acipenser fulvescens*) (M, male; F, female; Uk, unknown sex) presence at a spawning ground (○), with tagging dates (♦) and tag loss (▼) also indicated. Grey shading denotes the estimated spawning period based on back-calculated embryonic age (see Table 1). Note that individuals radio-tagged but never redetected (*n* = 8) are excluded.
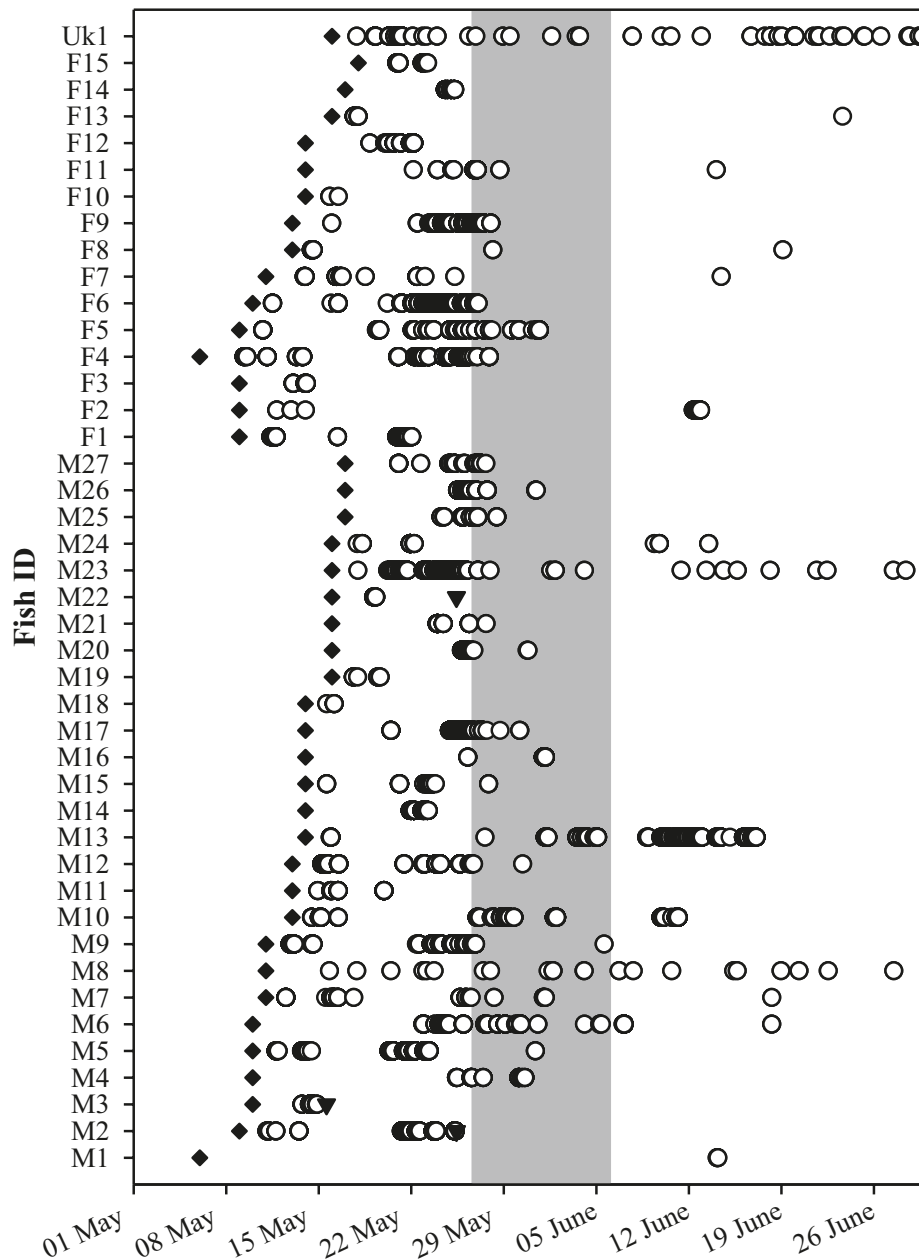
based on the collection of fertilised eggs on the spawning mats and back-calculated egg fertilisation times. Although sample sizes were small for during and, particularly, postspawn categories, depressed levels of steroids either upon final maturation or after reproduction were expected based on previous study of lake sturgeon (McKinley et al. 1998) and other sturgeon species (Barannikova et al. 2004). In a study of lake sturgeon steroids spanning May–October, McKinley et al. (1998) observed a significant decrease in testosterone and 11-ketotestosterone (although not estradiol) in males and a significant decrease in all three steroids in females, corresponding to immediate pre- and post-spawning periods confirmed by gonadosomatic indices. The temporal trends identified in this study do not provide direct evidence of spawning, as we were unable to validate that spawning occurred for the individuals for which steroid levels were measured. However, the results do follow the temporal trend that we expected if some or all of

these individuals undertook spawning. In the absence of fertilised eggs, this information would have provided an additional line of evidence to indicate the possibility of spawning.

Male and female lake sturgeon present at the site when netting began in early May did not demonstrate any differences in residency at the spawning ground and were present for a median period of 5 days (maximum 27 days) following telemetry tagging. This result suggests that the daily abundance estimates for the site likely underestimated the total number of sturgeon in the area during the study period given individuals tagged at the start of sampling were unlikely to be present at the end of the study. While initiation of migration can occur as early as ice-off, or prior to this, arrival at spawning grounds does not typically occur until 2 weeks prior to the first spawning event and is primarily modulated by water temperature, discharge, and the lunar cycle (Bruch and Binkowski 2002; Forsythe et al. 2012*b*). Sturgeon were present

from at least the beginning of May (22 days prior to spawning) until the end of June in the current study, although spawning was only detected over a 10 day period. This spawning duration is in the range identified by Bruch and Binkowski (2002) from data collected over a 16 year period (range 2–14 days). Dumont et al. (2011) also identified spawning occurred over a 9–19 day range in the Des Prairies River from 5 years of monitoring, although spawning peaked for 2–6 days. The breeding strategy of lake sturgeon maximises genetic diversity through polygamy, and the opportunities for males to breed multiple times within a single season can maximise opportunities that otherwise do not occur every season, as interspawning intervals are typically 2 years for males and 4 years for females (Bruch and Binkowski 2002; Forsythe et al. 2012a). This difference in the length of the gonad maturation cycle and the fact that males mature at an earlier age than females (age of sexual maturation is 18–20 years for males and 26 years for females; Scott and Crossman 1973) explain why, in this study and many others (Bruch and Binkowski 2002; Dumont et al. 2011), the number of males present on the spawning grounds generally exceeds the number of females.

Lake sturgeon exhibited a preference to spawning over coarser substrates in the current study, once water velocity was controlled for. Despite evidence that successful spawning does not always transfer to successful recruitment, as sturgeon are known to repeatedly spawn in unsuitable habitat (Paragamian 2012), the results of the current study indicate that suitable spawning habitat is both available and being utilised at this site. Coarser substrates than those currently sampled do exist at this site, although safety issues precluded sampling for eggs closer to the dam where larger substrate sizes and higher water velocities than those sampled predominate. This could potentially explain the low abundance of eggs collected in the current study compared with the relatively large numbers of mature adults that were present. Alternatively, adult spawning effort could be highly localised, and the surface area of egg collection stations represents a small proportion of the available river at this site and may not be indicative of reproductive intensity (Paragamian 2012). Furthermore, actual locations of spawning bouts can shift from year to year depending on river height and discharge (Dumont et al. 2011).

Restoring connectivity of riverine systems that have been fragmented by dams is often viewed as a critical step towards rebuilding sturgeon populations and preventing extinction (Auer 1996a). The current study and numerous others have identified that lake sturgeon will spawn below water control structures if suitable habitat exists (e.g., LaHaye et al. 1992). However, as spawning does not always transfer to successful recruitment (e.g., Paragamian 2012), this result should be viewed with caution and is not universally transferable. Dam construction often results in the loss of large spawning areas by blocking upstream fish passage and altering spawning ground characteristics in the lower and upper reaches of these new barriers (Haxton and Findlay 2008). In the lower St. Lawrence River, considering the location of the major spawning grounds in the upstream portion of the system, the downstream larval drift to the lower reaches and the size distribution observed among subadults and adults in the river, which suggests a downstream–upstream colonization from juvenile to adult stages, Mailhot et al. (2011) considered that preventing additional fragmentation of this 350 km stretch of fluvial habitat is an important protective measure to prevent permanent disruption of the life cycle of the lake sturgeon population. The current study also highlights the challenges of studying passage without also knowing about presence of spawning sites downstream (see Pelicice and Agostinho 2008).

Acknowledgements

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