Spawning and Reproductive Biology of the Greater Redhorse, *Moxostoma valenciennesi*, in the Grand River, Ontario

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Reproductive ecology of the Greater Redhorse, *Moxostoma valenciennesi*, was studied in the middle reaches of the Grand River, Ontario, from 1995 to 1998. Upstream migration to a weir with two fishways was observed during early spring. Spawning began in late May, when water temperatures were above 13°C, and lasted for up to 14 days, except in 1998, when spawning began in early May and only lasted five days. Spawning occurred in shallow riffle areas comprised of pebble, gravel and cobble. Videographic observations indicated that males usually remained on or near spawning riffles, while females were either attracted by the presence of, or conspicuous behaviour of males. Rapid bursts of snout and lip vibrations were observed in males for up to 5.7 seconds. Vibrations from one male triggered other males to follow suit. When females were present, male snout vibrations usually preceded spasmodic spawning activity among one or two females and up to seven males. Males rolled over one another and the centrally located female, while dorsal and caudal fins vibrated and broke the water surface for up to 10 seconds. Male and female fish were observed to consume eggs of conspecifics. The youngest fish captured from spawning areas were a five year old male and six year old female. Fecundity ranged from 32 000 to 72 000 eggs per female for seven fish, that were between 558 and 610 mm.

Key Words: Greater Redhorse, *Moxostoma valenciennesi*, life history, behaviour, videography, Ontario.

Greater Redhorse, *Moxostoma valenciennesi* Jordan 1886, are considered generally uncommon or rare with possibly disjunct distributions within their general range (Jenkins and Jenkins 1980; Lee et al. 1980). Many conventional creel studies and stream surveys have likely failed to detect the presence of individual redhorse species due to problems with identification and the typical clumping of these fish into the category of suckers or coarse fish. Greater Redhorse are known to inhabit rivers and lakes within the Great Lakes basin, as well as the Ohio River, the upper Mississippi River, and the north basins of the Red River (Kay et al. 1994). Existing reports of spawning behaviour of Greater Redhorse are anecdotal or emanate from visual observations recorded from the Thousand Islands Region of the St. Lawrence River during the early 1970s (Jenkins and Jenkins 1980).

To date, there are no reported descriptions of Greater Redhorse spawning behaviour in smaller streams and river systems. Scott and Crossman (1973) suggested that Greater Redhorse spawn between May and early July in rapidly flowing streams, although they acknowledged that less is known about this species than any other congener.

Spawning by Greater Redhorse has been reported to occur in streams with moderate to swift current at depths of approximately 0.5–1 m (Jenkins and Jenkins 1980). Those authors reported spawning activity in runs with a bed of sand, gravel, and small rubble; however, egg deposition usually occurred over gravel. Other reports suggested that Greater Redhorse probably spawned in river channels and rapids, where eggs were deposited among boulders in water about 3 m deep (Goodyear et al. 1982), although this report is lacking in any specific accounts. The only report of fecundity and sexual maturity was by Mongeau et al. (1992) from a study in Quebec.

The aim of our study was to elucidate the reproductive biology of the Greater Redhorse in the Grand River, Ontario. Visual observations and videography were used to examine spawning behaviour, migratory tendencies, and habitat use. Fecundity was also calculated.

Study Area

The Grand River is a large tributary of Lake Erie located in southwestern Ontario. A detailed description of the conditions of the middle reaches of the Grand River and the study site are presented in Bunt et al. (1998). Greater Redhorse are becoming regarded for their sporting quality (Jenkins and Burkhead 1993), making them worthy targets for anglers during the spring in the Grand River (Steven Cooke, unpublished data), and likely elsewhere. Greater Redhorse were observed to spawn in a 1 km long study site which extended downstream from the Mannheim Weir (43° 25′ N, 80° 25′ W). Qualitative observations were also made along a 16 km reach downstream of the main study site, to Parkhill Dam in Cambridge.

Methods

Reproduction by Greater Redhorse was studied during the springs of 1995 to 1998. As water temperature increased after breakup, the river was monitored twice daily by observers on the banks to document the initiation and cessation of spawning. Fish were only observed to spawn on riffles in the Grand River, so the majority of the sampling effort was directed to these areas. In 1995 and 1996, visual observations were made from river banks. Observers crouched among riparian vegetation and used polarized glasses during the day and small hand-held lights after dusk. When possible, fish were sexed based on the presence of conspicuous caudal and anal fin tubercles. During our extensive field sampling (1995–1998), we observed very few species with similar morphology or colouration which could be misidentified as Greater Redhorse. River Redhorse, *Moxostoma carinatum*, were never collected or observed and Shorthead Redhorse, *Moxostoma macrolepidotum*, were only collected in very limited numbers in 1995 (Chris Bunt, unpublished data). In 1997 and 1998, underwater videography was used to obtain detailed observations of the Greater Redhorse spawning act. A small black and white pin-hole camera housed in black PVC tubing (6 cm diameter, 120 cm long) was positioned to face downstream in a riffle that was used by actively spawning Greater Redhorse on 30 May 1997. The inconspicuous camera housing was anchored with small rocks and did not affect flow conditions over the riffle. Greater Redhorse returned within minutes of positioning the camera in the riffle and resumed what was later determined to be normal spawning behaviour. Similar observations were collected on 5 May 1998 using a small (8 cm diameter, 20 cm long) colour underwater camera. Field of view for both cameras was determined to be 1.13 m^2. Further qualitative observations were recorded by drifting downstream while Greater Redhorse spawned during 1995, 1996 and 1997.

Midday water temperature (12:00 h) was monitored throughout the reproductive period. Discharge information was remotely collected at a station 6 km downstream from the most upstream end of the study site. No major tributaries enter the Grand River between the study site and the flow gauging station. Data were tested for normality using a Lilliefors test (SYSTAT 1992) and were then examined for homogeneity of variance using an F-test (Sokal and Rohlf 1995). Data were considered normal so a model one fixed-effect, one way ANOVA was used to test the null hypothesis of no difference among temperatures or discharge during spawning among each of the four years. The Tukey-Kraemer HSD test (Day and Quinn 1989) was used to examine differences among means. All means reported are ± 1 SE and tests were determined significant at $\alpha = 0.05$.

Throughout the spring in all years, gill-netting, seining, and angling were carried out in a variety of runs, pools and backwaters within the study area. Spawning colours and tuberculation patterns were carefully documented and during 1997, ovaries were removed from randomly selected ripe females collected within two weeks prior to the initiation of spawning. Eggs were counted using the gravimetric method (McGregor 1922). Scales were removed as described by Meyer (1962), cleaned, pressed between glass slides and aged on a microfiche projector.

We surveyed the riffles where spawning activity was observed during 1997 at 128 locations. A 100 cm^2 quadrat was randomly distributed within riffles where spawning was observed. Depth was measured with a calibrated rod to the nearest cm in the center of the quadrat. Surface and bottom velocities were recorded as 10 s averages using a Sigma PVM velocity meter (± 1 $cm \cdot s^{-1}$). Substrate was described using a modified Wentworth Scale (boulder > 256 mm; cobble 64–256 mm; pebble 16–64 mm; gravel 2–16 mm; sand 0.0625–2 mm; silt < 0.0625 mm) [Cummins 1962] and was grouped into a complex based upon the two dominant substrate types within the quadrat. Embeddedness of substrate was categorized as completely embedded, 3/4 embedded, 1/2 embedded, 1/4 embedded and unembedded (Crouse et al. 1981). The percentage of substrate covered by *Cladophora* spp. was also noted.

Results and Discussion

Morphology

When observed out of water, the sides of female and male Greater Redhorse were yellow-gold, dorsal surfaces were olive coloured and ventral surfaces were white. The dorsal and caudal fins were bright red, becoming orange distally. Spawning male Greater Redhorse developed large white tubercles on the anal fin, up to 5 mm in basal diameter. Both caudal fin lobes had tubercles, which tended to be smaller than those on the anal fin. Some males developed fine tubercles on the lower caudal fin and on the snout. Colouration was relatively consistent, but the degree of tuberculation among males was highly variable. Female Greater Redhorse were nontuberculated and usually larger than males. Males handled during spawning tended to lose their tuberculated scales easily. A lateral stripe was not clearly evident on Greater Redhorse as has been observed for other members of the genus (Bob Jenkins, Roanoke College, personal communication).

Timing and Conditions

Spawning events began when mid-day water temperatures rose above 13°C, at which time river levels had fallen below the spring peak. In 1995, spawning was first observed on 20 May when mid-day water temperature was 13.4°C (Figure 1). In 1996 and 1997, spawning was not observed until 26 May, when water temperatures were 13.3°C and 13.7°C, respectively. Despite spawning beginning at similar temperatures in these two years, the mean tempera-

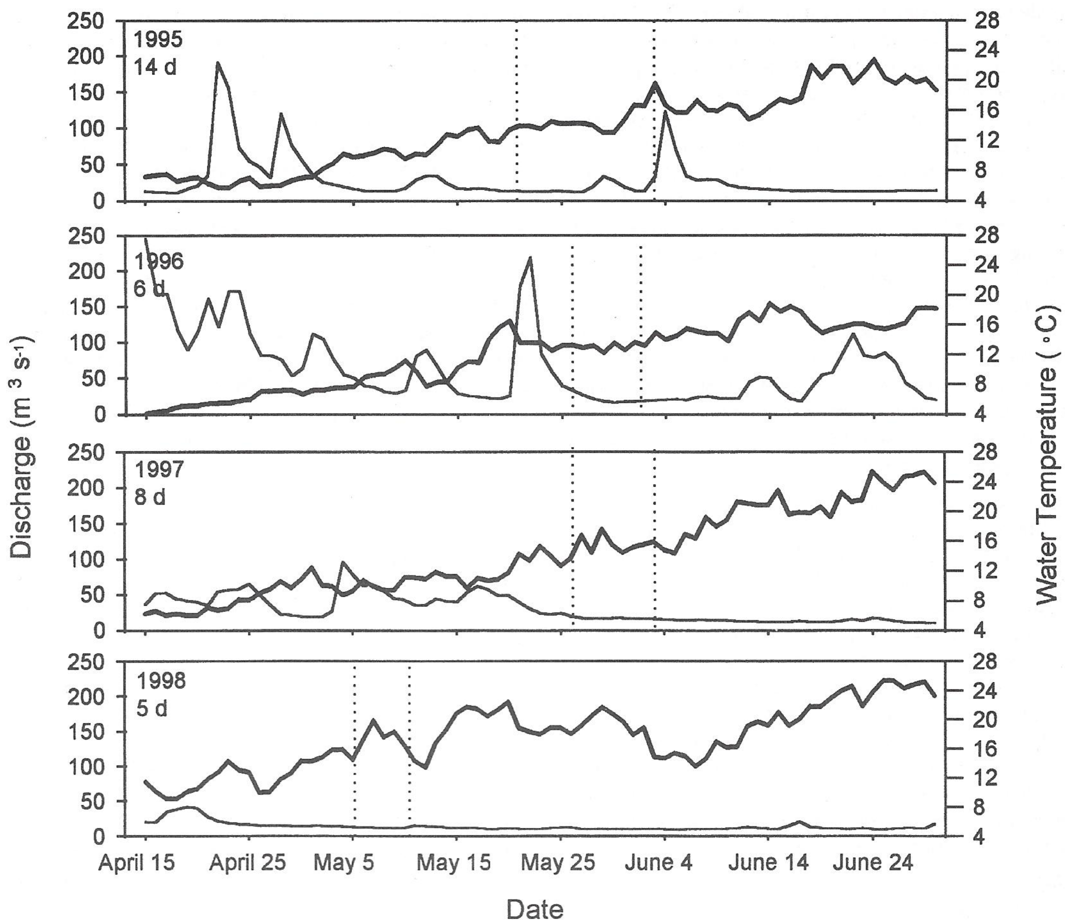

FIGURE 1. Trends in mid-day (12:00 h) water temperature (°C) (thick line) and mean daily discharge (m^3 s^{-1}) (thin line) from 15 April to 30 June, 1995-1998. Periods of Greater Redhorse spawning activity are indicated by the area between the dashed vertical lines for each year. The duration of spawning is indicated in the top left corner of the figures.

tures during the spawning period were significantly higher in 1997 ($p<0.05$). During 1998, spawning began on 5 May, at a temperature of 14.5°C. The mean mid-day water temperature (17.5 ± 0.9°C) for the 1998 spawning period was higher than all other years ($p<0.05$).

Individuals were observed to spawn on riffles for 14 d in 1995, at water temperatures ranging from 13.0 to 19.6°C. Spawning was apparently interrupted when discharge increased from 13.2 to over 33.8 $m^3 \cdot s^{-1}$, although it is also possible that the termination of spawning at this time was simply coincidental. Spawning was observed for only 6 days in 1996 and 8 days in 1997. Prior to the initiation of spawning in 1996 and 1997, discharge was highly variable, although temperatures were within the range observed previously. Mid-day water temperature during spawning ranged from 12.2 to 13.6°C in 1996 and 13.7 to 17.6°C in 1997. In 1998, spawning only lasted for 5 days with mid-day temperatures ranging from 14.5 to 19.9°C during which time discharge conditions were stable (12.6 ± 0.24 $m^3 \cdot s^{-1}$). No significant differences in mean discharge were observed among each of the four years ($p>0.05$).

The environmental cues that regulate the initiation of spawning by *Moxostoma* spp. are largely unknown, but seasonality, temperature, photoperiod, and stream discharge are reported to be contributing factors (Kwak and Skelly 1992). Spawning in the Thousand Islands region of the St. Lawrence River occurred during late June to early July, when water temperatures were 16 to 19°C (Jenkins and Jenkins 1980). Although these dates appear late for catostomid spawning, this reach of the St. Lawrence River warms relatively slowly (Jenkins and Jenkins 1980).

Evidence from the Grand River suggests that Greater Redhorse spawning was triggered by a combination of low, stable discharge following spring freshets and water temperatures above 13°C. By the end of the spawning period, most fish were spent, although one ripe male (553 mm TL) was captured 9 days after the last spawning events were recorded in 1996. In 1995, fish that had not completed spawning before discharges increased, and remained ripe, were not observed to spawn when water levels receded. The exceptionally warm and dry spring in 1998 may have reduced spawning duration. Flows were stable throughout this period suggesting that temperature was the final variable influencing the initiation and duration of spawning.

Individuals most actively spawned during sunny afternoons; however, some activity was recorded when it was overcast and raining. Greater Redhorse also spawned after sunset, sometimes as late as midnight. Jenkins and Jenkins (1980) also observed night spawning by Greater Redhorse.

Migrations and Fishway Use

Mature Greater Redhorse swam upstream during early spring in the Grand River. Upstream movements to the Mannheim Weir were observed each year. However, Greater Redhorse were rarely successful at ascending the Denil fishways at the weir. Between 1995 and 1997, only five Greater Redhorse were collected in fishway traps, and three were caught on the same day (20 May 1995) in the east fishway, at a water velocity of 0.56 m•s^{-1} and a water temperature of 14.1°C. Just prior to initiation of spawning, individuals actively explored the region immediately below the weir before returning to riffle areas located further downstream.

Habitat Use

Between 15 May and 25 May 1997, prior to spawning, Greater Redhorse were captured in runs and pools below spawning riffles. Up to 15 Greater Redhorse were observed in aggregations with Common Carp, *Cyprinus carpio*. Smallmouth Bass, *Micropterus dolomieu*, Golden Redhorse, *Moxostoma erythrurum*, and Northern Pike, *Esox lucius*, were also collected in the prespawn pools occupied by Greater Redhorse. Greater Redhorse were not observed feeding but broke the water surface and porpoised frequently in the downstream pools prior to the initiation of spawning; a behaviour observed during the spawning period by Jenkins and Jenkins (1980).

Spawning occurred along edges and midstream areas of riffles of apparent similar morphometry. Riffle depths ranged from 10 to 63 cm (mean 34.4 ± 1.0 cm), surface and bottom velocities varied and ranged from 3.8 to 116.9 cm•s^{-1} (mean 38.21 ± 2.67 cm•s^{-1}) and 4.1 to 87.1 cm•s^{-1} (mean 29.02 ± 1.86 cm•s^{-1}), respectively. Pebble and cobble (59%), and pebble and gravel (30%) were the most commonly used substrate types. Substrate was relatively unembedded and provided large interstitial spaces for egg deposition. Aquatic vegetation in the Grand River during spawning was mostly composed of sparse *Cladophora* spp. However, Greater Redhorse spawning riffles supported large amounts of *Myriophyllum spicatum* and *Potomogeton pectinatus* by early July. Greater Redhorse were observed to use almost every shallow riffle (ca.<60 cm deep) in a 17 km reach between the Mannheim Weir and the Parkhill Dam.

Other species observed with spawning Greater Redhorse were Common Shiner, *Luxilus cornutus*, Striped Shiner *Luxilus chrysocephalus*, Northern Hog Sucker, *Hypentelium nigricans*, White Sucker, *Catostomus commersoni*, and Iowa Darter, *Etheostoma exile*. Carp spawned at similar times, but were seen only in the deeper (i.e., >60 cm) tails of riffles. Between Greater Redhorse spawning events, Common and Striped shiners were observed to spawn on the same riffles, in areas where Greater Redhorse also spawned.

Behaviour

From shore, Greater Redhorse were observed to spawn in groups with between two and seven males and one or two females. One observer counted an aggregation of over 100 Greater Redhorse on a 45 m^2 riffle at one time. Spawning was most intense during the first three days of the spawning period, when spawning events occurred every 1 to 3 s in a 100 m section, 800 m downstream from the Mannheim Weir. During the latter part of the spawning period, and after dark, spawning was less frequent (e.g., every 1 to 2 min). During 1998, spawning was sustained at a consistent level of high intensity for the entire 5 d that spawning was observed. Although we observed hundreds of spawning events from shore, it was more difficult to accurately identify the number and sex of participants from our low vantage-point. Greater Redhorse in the Grand River were particularly wary, making visual observations from shore somewhat difficult.

Underwater videographic observations yielded detailed images showing that males usually remained stationary on or near spawning areas. When an individual female approached from downstream, two, or more commonly three males, attempted to initiate spawning (Table 1). Male Greater Redhorse rapidly vibrated their rostrums and lips prior to and during spawning; a behaviour that was observed to last for up to 5.7 s. Gentle nudging behaviours were often observed between males when no females were present on the spawning riffle, as also observed by Jenkins and Jenkins (1980). This nudging behaviour may be widespread among suckers (Page and Johnston 1990).

During the spawning act, dorsal and caudal fins vibrated vigorously, and broke the water surface in most instances. Males rolled over one another and the centrally located female, while gametes were released. Similar rolling behaviour was observed for Shorthead Redhorse by Burr and Morris (1977).

TABLE 1. Summary of spawning behaviour based on underwater videographic observations. Camera was deployed for a total of 6.5 h between 15:30 and 18:30 on 30 May 1997 and 16:00 and 20:00 on 5 May 1998.

Date	Spawning Act Participants Male	Spawning Act Participants Female	Duration (s)	Time Between Acts (min:s)	Snout Vibrations Participants	Snout Vibrations Sex
30 May 1997	3	1	3.5	a	1	m
30 May 1997	2	1	4.7	01:55	1	m
30 May 1997	3	1	4.5	04:50	3	m
30 May 1997	3	1	4.1	00:01	3	m
30 May 1997	b	b	2.6	20:00	b	b
30 May 1997	3	1	4.0	18:10	2	m
30 May 1997	3	1	6.0	45:30	2	m
30 May 1997	3	1	8.2	19:40	1	m
30 May 1997	3	1	3.4	16:57	2	m
05 May 1998	3	1	1.9	a	1	m
05 May 1998	3	1	2.6	55:12	3	m
05 May 1998	c	c	3.7	24:15	1	m
05 May 1998	3	1	7.6	37:35	2	m

[a]First event following camera placement
[b]Details obscured
[c]At least one male and female observed

Spawning events usually involved males on either side of a female while a satellite male attempted, sometimes successfully, to displace one or both spawning males. The mean duration of the spawning act was 4.4 ± 0.5 s and the mean time between spawning acts within the camera viewing area was 22.2 ± 5.3 min (Table 1). Spawning act durations reported here are similar to those reported by Jenkins and Jenkins (1980).

Although Greater Redhorse do not construct nests prior to spawning (Jenkins and Jenkins 1980), areas of egg deposition eventually became conspicuous following repeated spawning events. Spawning activity cleared finer substrates, created unembedded areas, and removed patches of *Cladophora* spp. The spawning sites appeared lighter in colour and remained evident for up to two weeks following the cessation of spawning. Greater Redhorse eggs were found in the interstitial spaces of the substrate, to a depth of 25 cm. Kwak and Skelly (1992) were unable to determine if Black Redhorse, *Moxostoma duquesnei*, and Golden Redhorse nests were created prior to spawning, but similar to our findings, they suggested that depressions may be created by agitation during the spawning act.

Between spawning events, males and females moved about the riffle and interacted with other conspecifics clumped in aggregations. In some cases, fish rested motionless and maintained positions using only pectoral fins. Lundberg and Marsh (1976) described two behaviours referred to as "fin-standing" and "fin-appression" which were observed in captive Silver Redhorse, *Moxostoma anisurum* and Northern Hog Sucker. Videographic observations of Greater Redhorse between spawning events indicated that pectoral fins were used in a similar manner. Greater Redhorse exhibited fin-standing while in areas of lower velocity (e.g., margins of the riffle) and fin appression while in faster regions of the riffle. Fish were usually oriented upstream, and movements were usually directed laterally or upstream.

After Greater Redhorse reached the head of spawning riffles, and the end of suitable spawning habitat, they moved into adjacent runs and fell back to the tail of the riffle before resuming upstream spawning movements. Some fish were individually identifiable by distinct markings, torn flesh or the presence of fungal lesions. Although it is unknown whether fish spawned on a multiple of riffles, our evidence suggests that individual fish occupied riffles within one general area until they were spent or until spawning was halted by high discharge or low temperature. The territoriality observed during Golden Redhorse spawning (see Kwak and Skelly 1992) was not observed among Greater Redhorse. No fish defended territories, and even during spawning, no fish appeared to be dominant.

Male and female Greater Redhorse consumed eggs released by other fish and gametes from spawning events in which they participated as observed on video. Diet analysis of Greater Redhorse confirmed that egg-like material (i.e., yolk) was a component of stomach contents collected during spawning and was of sufficient quantity to likely rule out accidental ingestion. Intraspecific egg consumption among *Moxostoma* spp., has not been previously documented. No interspecific egg predation was observed, unlike previous reports (Jenkins and Jenkins 1980).

Fecundity and Maturity

The earliest age of maturity in the Grand River was 5 years for males and 6 years for females. The oldest fish observed spawning were a 13 year-old male and an 11 year-old female. Mongeau et al. (1992) reported that external sexual dimorphism in the Richelieu River, Quebec, was not evident until age 8 and that males and females did not spawn until age 9. Jenkins (1970) suggested that maturity, based upon tuberculation, occured in males between 380 and 540 mm (SL) and males probably matured at ages 5 and 6. In the Grand River, immature individuals were not found in aggregations with mature individuals before or during spawning. It should be noted that the ages presented here are likely conservative, as use of scales may result in underestimates of age.

Calculations of the number of eggs produced by female Greater Redhorse varied between 31 759 and 71 920 (mean ± 1 SE, 39 554.3 ± 5472.5) for seven fish between 558 and 610 mm TL (Age 6–9). These values are within the range reported for similarly sized Greater Redhorse by Mongeau et al. (1992). They reported fecundity ranging from 25 190–51 430 eggs for 10 females. They also reported that gonadosomatic index values continued to increase into mid-June, when water temperatures were greater than 16°C.

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