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RESEARCH ARTICLE

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Short-term effects on Unionid mussel density and distribution before and after low-head dam removal in northern New York

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Abstract

Unionid mussel populations have declined in many environments, particularly those that were altered by human activities such as dam construction and removal. The Fort Covington Dam blocked the Salmon River in northern New York upriver of its confluence with a smaller tributary, the Little Salmon River. This dam was removed in 2009. My study compared the mean ranked density of mussels in both rivers for the pre-removal period (2005–2008) to the post-removal period (2009–2012) with special attention to *Lampsilis cariosa* and *Margaritifera margaritifera*. Systematic sampling was used at six riffles and double sampling at four glides divided between the Salmon and Little Salmon rivers from 2005 through 2012. The Little Salmon River served as a control. Mean ranked adult mussel density was not significantly different between the two rivers in the pre-removal period but was significantly greater in the Little Salmon River after dam removal. Living mussels of 13 species were collected dominated by *Elliptio complanata*. Dam removal did not affect sediment sorting, porosity, water chemistry, or mussel species distribution. Rapid dewatering of the reservoir led to stranding and death of mussels in the reservoir and in the adjacent ponds. Increased water velocity, exacerbated by rain, mobilized sediment that buried a potentially large mussel bed downstream of the dam where *Lampsilis cardium* and *L. cariosa* were abundant, which showed little recovery by 2013.

KEYWORDS
dam removal, mortality, mussel density, sediment, water chemistry

1 | INTRODUCTION

Dams have altered the natural cycle of water flow, sediment transport, and water temperature regimes in many streams in the United States (Ligon et al., 1995; Olden & Naiman, 2010; Poff & Hart, 2002; Vaughn & Taylor, 1999) and globally (Luiyong et al., 2019). Dam removal has been emphasized as a tool to restore rivers to a more natural assemblage of aquatic communities and as a practical approach to dam management (Orr et al., 2006) but mussel community recovery may not resemble the pre-dam condition (Doyle et al., 2005). Research on the effect of dams on macroinvertebrates tends to emphasize taxa that are regionally important, which might result in some ecologically important taxa being understudied (Wang et al., 2019). Changes in land use and instream morphometry due to dams were frequently deleterious to the stream as well as costly in lost property (Schroeder & Savonen, 1997); however, dams have also slowed the reproductive success of Sea Lamprey in Lake Ontario tributaries, range expansion of introduced species, such as Carp (*Cyprinus carpio*) and Round Goby (*Neogobius melanostomus*), and the introduction of disease vectors (Christie, 1974; Hurst et al., 2012). The presence of dams was one cause of mussel loss in the Ohio River, in the Blackstone River (Rhode Island), and in the Fox River (Illinois) where impounded sites had lower species richness and mussel abundance (Raithel & Hartenstine, 2006; Tiemann et al., 2007; Watters & Flaute, 2010). Run-of-river dams generally have a limited impoundment area and do not have the cold-water releases of larger dams

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(Layzer et al., 1993) that would affect downriver mussels and fish. Run-of-river dams restrict fish movement, which can lead to the elimination of fish species that are necessary as hosts for mussel glochidia (Hornbach, 2001). Breached dams (those that have been opened but not removed) may reduce fish species richness (Helms et al., 2011), which could reduce successful mussel reproduction by elimination of glochidial hosts. Published dam removal studies have revealed a complex response by the mussel community to dam removal where mussel density decreased (Gangloff et al., 2011; Sethi et al., 2004), remained unchanged (Heise et al., 2013), or increased (Tiemann et al., 2016).

The Salmon and Little Salmon rivers in northern New York were fragmented by dams that have the potential to disrupt mussel reproduction by blocking fish movement and by altering the natural movement of sediment. The objective of this study was to describe the mussel community of the rivers before and after the removal of the Fort Covington Dam with particular attention to *Lampsilis cariosa* and *Margaritifera margaritifera*. The New York Natural Heritage Program (2017) lists *L. cariosa* as vulnerable (S3) and *M. margaritifera* as imperiled in New York (S2). NatureServe (2018) considers *L. cariosa* as possibly vulnerable globally (G3G4) and the IUCN considers *M. margaritifera* as endangered in Europe (Moorkens et al., 2018).

2 | METHODS

2.1 | Study area

The Salmon and Little Salmon rivers flow northward for 85 km from the northwest part of the Adirondack Park, NY, through Quebec, Canada, and drain into the St. Lawrence River. The Salmon and Little Salmon rivers arise at elevations of 548 m and 427 m, drain about 718 km^2 (NWQMC, 2019), and have a steep gradient (approximately 11 m/rkm) until reaching the last 10 km of river where the gradient declines to 0.6–1.0 m/rkm. The first riffle on the Salmon River was the site of the Fort Covington Dam (Figure 1), an abandoned run-of-river dam first built as a wood-crib dam in the late 1800's and replaced with a concrete gravity dam in 1913. The dam created a reservoir extending approximately 1600 m upriver (near transect 7) with a flat channel bed, a bankfull depth of 1.2 m (surface area of 4–6 ha), and a distinct thalweg at the outside of bends. Two ponds were created by the damming of the river. The east pond was fed by a small stream and was <1 m in depth and the west pond was fed by surface runoff and was about 2.5 m in depth at the downriver end. There were five additional dams on the Salmon River and two on the Little Salmon River, one of which was non-functional.

The Salmon and Little Salmon rivers were fourth-order and cut through a glacial moraine deposit of fine to coarse sand on the north side of Malone, New York. This sand has been deposited in the rivers and remains the dominant physical feature of glide substrate, while cobble is dominant in the riffles. Water discharge was flashy in both rivers and responded rapidly to precipitation. Mean daily river flow in the Salmon River (hereafter SR) can reach 93 m^3 s^{-1} (USGS gage 04270000 at Chasm Falls, approximately 32 km upriver of study area) and 39 m^3 s^{-1} in the Little Salmon River (hereafter LSR) (USGS gage 04270200 at Bombay, approximately 13 km upriver of the study area). The study area extended from the confluence of the SR and LSR near Lewis Marine 7.5 km upriver to transect 9 in the SR, and 3.5 km upriver to transect 15 in the LSR (Figure 1).

In this study, the SR was considered as the experimental river and the LSR as a control under the assumption that adult mussel densities would not be significantly different between the two rivers in the pre-dam removal period and that dam removal would not affect adult mussel density in the LSR. This assumption was based on similarities before dam removal in land use, response to precipitation, mussel density, and mussel distribution.

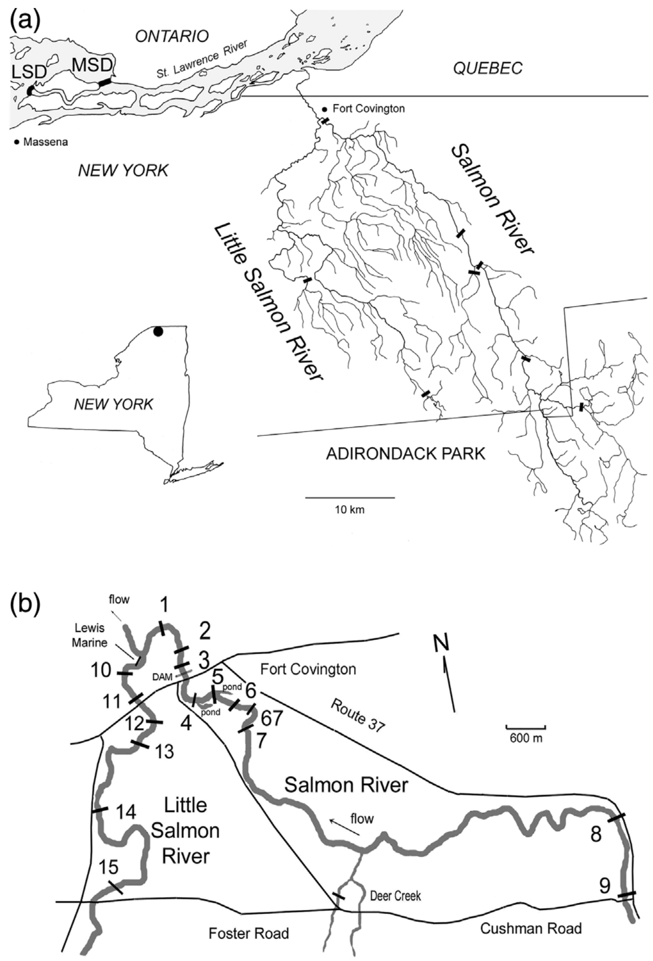

FIGURE 1 Location map of the Salmon and Little Salmon rivers, Franklin County, New York (a). The Fort Covington Dam was the most downstream dam in the Salmon River; the other boxes represent dams upriver from the study area. The black boxes in the St. Lawrence River are the Long Sault Dam (LSD, left) and Robert Moses-Saunders Power Dam (MSD, right) and (b), location of transects used in the dam removal assessment. Transect 67 was a riffle that was exposed after dam breaching. Two ponds, formed by the impoundment (transects 4 and 5), were drained with the removal of the dam. The reservoir extended from transects 3–7.

Agriculture was the primary land use (75%) estimated within 300 m of the river centers determined from 1994 orthophotos (NYSGIS, 1994). Housing development (15%) and forest (10%) accounted for the remainder. The rivers generally had a wooded buffer along the banks except for the portion that runs through the village of Fort Covington, where the river edge was bordered by grass.

2.2 | Mussel sampling

Mussel sampling began as an undirected series of observations in 2002 as part of an assessment for removing the Fort Covington Dam that focused on fish, macroinvertebrates (primarily insects), aquatic plants, sediment, and water chemistry. The expectation was that the dam would be removed at the end of the pre-removal assessment in 2005 but the dam was not removed until 2009: a formal mussel sampling program began in 2005. The dam removal assessment design included 15 transects, 9 in the SR and 6 in the LSR, divided between riffles (transects 3, 7, 9, 13, 15) and glides (transects 1, 2, 4–6, 8, 10–12, 14). Ten transects located in wadeable portions of the rivers were surveyed for mussels in each year. Systematic sampling with three random starts was used at a single transect in each riffle (3, 7, 9, Deer Creek, 13 and 15), and double sampling (Strayer & Smith, 2003) in each glide transect (6, 8, Lewis Marine, and 12; Figure 1) from 2005 through 2012. Transects ranged in width from 70 m at transect 7 to 2 m at Lewis Marine with individual quadrats spaced from 6-m apart at transect 7 to contiguous at Lewis Marine. A maximum of 40 quadrats of 0.25 m^2 was sampled with each random start. Each quadrat was designated by placing a 1 m^2 PVC grid (subdivided into four) on the river bottom; each 0.25-m^2 quadrat was searched with visual and tactile methods and 20% of glide quadrats were excavated to a depth of 20 cm to account for juvenile mussels (Smith et al., 1999). The sediment was washed through a 6-mm screen. Only the glide areas were excavated as the riffle sediment was too compact for mussels to burrow into. This method would underestimate the number of juveniles in the riffles. Estimates of maturation of all northeastern mussel species is not known but maturation of *Elliptio complanata* has been reported to be between 30 and 50 mm and *Pyganodon grandis* at 45 mm (McMahon, 1991). Juvenile mussels of all species for living and empty shells were considered to have a maximum shell length (SL) of 40 mm (Watters, 1993–1994). This might underestimate the numbers of some species and overestimate the numbers of other species. Living mussels were identified, measured with dial calipers for SL, shell height (SH), and shell width (SW), and returned to their original location; empty shells were identified, measured, and retained. The mussels that were identified as *Lampsilis ovata* in reports of this dam removal (Cooper, 2011, 2013; Cooper et al., 2004) are apparently *Lampsilis cardium* according to a consensus arrived at in 2017 (D. Mayer, New York State Museum, personal communication) in the belief that *L. ovata* does not occur in the St. Lawrence River drainage. The identification of *L. cardium* has not been verified by other means.

Sampling was done at low flow to avoid turbidity. Transects were arranged perpendicularly to the river flow except for that in Deer Creek, where the transect was parallel to the river flow due to the small width of the creek (10 m), and the transect at Lewis Marine, which was on the more shallow north shore as the south shore was used for boat docks. Population size estimates for adult mussels were made by multiplying the average count per systematic sample by the number of possible samples in each transect (Strayer & Smith, 2003). Adult mussel density was determined by dividing the population size by the transect area. A ratio estimator was used to compare the number of visible mussels to the number of buried mussels to account for excavation in glides. Population size and density estimates were made only for transects and not extrapolated to the study area because the habitat characteristics beyond transects were not determined in detail. Two ponds created by damming of the river were not sampled for mussels until the dam was removed in 2009.

2.3 | Water chemistry

Water temperature in each year was recorded at 1-h intervals using Onset (Hobo water temperature Pro V2) thermographs at transects 3, 6, 7, 9, 13, 15, and Lewis Marine. Thermographs were deployed at ice-out in late April to early May and removed in late October or early November. Onset level loggers (Hobo U20 water level logger) recorded water-level changes and water temperature at 1-h intervals at transects 3, 6, and Lewis Marine. A separate level logger at Lewis Marine was used to determine barometric pressure to correct the measured values of water level and to record air temperature. Monthly grab samples were used to estimate dissolved oxygen (Hach sension6), pH (Oakton ecotestr pH 2), total dissolved solids (Oakton TDSTestr3), alkalinity (Lamotte titrator), nitrogen ammonia, total chlorine, nitrate, sulfate, and turbidity (Hach DR/870 colorimeter) at transects 3, 7, 9, Lewis Marine, 13, 15, and Deer Creek. Flow velocity measurements were made with a Price-type mini-current meter at transects 3, 6, 7, 8, 9, 13, 15, and Deer Creek. The bucket wheel was set at 40% of water depth (measured from the river bottom) and recorded for 30 s. These monthly samples were taken on the same day and at a similar time relative to each transect.

2.4 | Sediment

Three grab samples, taken with a 15 × 15 cm ponar dredge (0.02 m^2), were composited from each of three areas (east bank, center, and west bank, $N = 9$) of each glide transect to determine grain size. Samples were stored at 3.8°C until analyzed. Grain size was characterized into only three size categories in 2002 (sand, silt, and clay; Cooper et al., 2004) so archived samples were re-screened in 2010: dry material was screened through five mesh sizes (6, 1, 0.5, 0.125, and 0.062 mm). Silt (0.0039–0.031 mm) and clay (0.002 mm) proportions were determined by the dispersal method (Folk, 1980) and all fractions reported as the percent dry weight of the original sample. The same procedure for determining grain size was used in 2010 and 2012. Sorting was determined by the inclusive graphic standard deviation method of Folk (1980), which relates the cumulative percent by weight of sediment fractions to phi values at four percentages (84%, 16%, 95%, and 5%):

$$\frac{\Phi 84 - \Phi 16}{4} + \frac{\Phi 95 - \Phi 5}{6.6}$$

The solution of this equation results in an estimate of the average particle size encompassing 95% of the size distribution. Porosity was determined by dividing bulk density (sediment dry weight divided by volume) by 2.65, the density of quartz, which was the predominant mineral. Pebble counts were made in the riffles in 2012 at a minimum of 100 locations using the zig-zag method (Bevenger & King, 1995). Estimates of embeddedness (Barbour et al., 1999) were made at five locations in the center of each riffle transect in 2004, 2010, and 2012.

2.5 | Statistics

The SR was considered as the experimental river and the LSR as a control under the assumption that adult mussel densities would not be significantly different between the two rivers in the pre-dam removal period and that dam removal would not affect adult mussel density in the LSR. Statistical comparisons were made using non-parametric tests in the General Linear Model of SAS (Version 8; $\alpha = 0.05$) as not all data distributions were normal. Mean ranks of density for living adult mussels were compared by period (pre-dam removal, 2005–2008; post-dam removal, 2009–2012) and within periods for rivers and transects using the Kruskal–Wallis chi-square approximation and the Tukey comparison. Mean ranks of density for living juvenile mussels were compared at Lewis Marine and transect 12 for pre-removal and post-removal periods to estimate any effect due to increased excavation effort after dam removal. Mean water temperature was compared at transects 6 and 3 with the Kruskal–Wallis test to determine any effect of the dam on water temperature for the periods 6 May to 15 July 2008 (pre-dam removal) and 6 May to 15 July 2009 (includes dam breach on 23 June 2009). Water temperature records after 15 July were not used due to confounding effects of sand displacing the water around the sensors at both transects after dam removal. Sediment sorting and porosity values were compared for 3 years (2002, 2010, 2012) and by transect subdivision (east, center, west when facing north) with the Kruskal–Wallis chi-square approximation and the Tukey comparison. The cumulative distribution (number of mussels collected in each transect relative to distance across the river) of living adult mussels across riffles and glides (except Deer Creek and Lewis Marine) was compared using the Kolmogorov–Smirnov test in pre-removal and post-removal periods.

2.6 | Community indices

Several indices were calculated for adult mussels in each river for the pre-dam removal period and post-dam removal period: Shannon evenness, Smith–Wilson evenness, Shannon-Weiner diversity, and Simpson diversity, to determine if there was a difference attributable to dam removal. The latter three were described in Smith and Wilson (1996).

3 | RESULTS

Mean ranks of density of adult mussels were not significantly different between the two rivers (all transects combined within each river) in the pre-dam removal period but mean ranks of density increased significantly in the LSR after dam removal (Table 1). There were no significant differences in mean ranks of density within rivers for the pre-removal and post-removal period. Significant differences were found at transect 6, 12, and 15 (Table 1). Adult mussel mean density at transect 6 (former reservoir) decreased six-fold after dam removal, increased four-fold at transect 12, and increased three-fold at transect 15 (Figure 2). At transect 6, the number of adult mussels collected declined from a mean annual collection of 34 mussels in pre-dam removal years to a mean of 3.2 mussels in post-dam removal years. Adult mussels collected at transect 12 increased from a pre-dam removal mean of 6.2 year^{-1} to a post-dam removal mean of 38 year^{-1} while transect 15 increased from a pre-dam removal annual mean of 7.2 year^{-1} to 25.7 year^{-1} for post-dam removal years.

Transect 13 showed the most variation in adult mussel collection declining from 45 mussels collected in 2005 to a mean of 12 mussels for 2006–2008 and a mean of 10 mussels for 2009–2012. The greater numbers of adult mussels collected in 2005 led to a SE of 0.443, the greatest SE of any transect in any year and this resulted in the statistical comparison being not significant. Transect 8 was the most consistent in adult mussels collected with a mean of 43.2 year^{-1} in pre-dam removal and a mean of 65.7 year^{-1} in post-dam removal. The resulting statistical comparison for pre-dam and post-dam removal was not significant.

Excavation accounted for 4.5% of adult mussels collected in glides and the ratio estimator determined for these samples was 1.01, which would suggest that the estimated number of adult mussels collected would not be substantially increased using increased excavation (Strayer & Smith, 2003). There was a significant increase in the number of adult mussels collected at transect 12 in the post-dam removal period with increased excavation effort. Excavation accounted for 80% of the living juvenile mussels collected (ratio estimator = 5.9) at a minimum size of 6 mm. There was no significant difference in the number of juvenile mussels collected in pre- and post-dam removal periods at transect 12 or Lewis Marine (Table 1).

The cumulative distribution of mussels (all years combined) was significantly different between glide transects and riffle transects (Kolmogorov–Smirnov $D = 0.98$, maximum difference = 44.5, $\alpha = 0.01$). The distribution within glides or riffles was not significantly different when comparing pre-dam removal to post-dam removal years (glides: $K\text{-}S = 0.05$, $D = 0.10$, $P = 0.99$; riffles: $K\text{-}S = 0.08$, $D = 0.17$, $P = 0.79$). Most (87%) living mussels in glide transects were

TABLE 1 Statistical comparisons of mean ranks of mussel densities by river, transect, and period (pre-removal and post-removal).

Adult mussels				
Comparison		$F_{(df)}$	p	**Mean ranked density**
Pre-dam removal SR versus LSR	River	$1.26_{(1,38)}$	0.27	Ns
Post-dam removal SR versus LSR	River	$5.92_{(1,38)}$	**0.02**	Greater in LSR
SR pre-removal versus post-removal	Period	$1.13_{(1,46)}$	0.29	Ns
LSR pre-removal versus post-removal	Period	$3.73_{(1,30)}$	0.06	Ns
SR transects pre- versus post-removal	9	$0.5_{(1,6)}$	0.51	Ns
	8	$2.54_{(1,6)}$	0.16	Ns
	DC	$0.18_{(1,6)}$	0.69	Ns
	7	$0.3_{(1,6)}$	0.60	Ns
	6	$19.2_{(1,6)}$	**0.005**	Pre-removal greater
	3	$0.08_{(1,6)}$	0.79	Ns
LSR transects pre- versus post-removal	15	$20.21_{(1,6)}$	**0.004**	Post-removal greater
	13	$0_{(1,6)}$	1.0	Mean ranks were equal
	12	$19.2_{(1,6)}$	**0.005**	Post-removal greater
	LM	$0_{(1,6)}$	1.0	Mean ranks were equal
Juvenile mussels				
Transects with altered excavation effort	12	$2.54_{(1,6)}$	0.16	Ns
	LM	$1.43_{(1,6)}$	0.28	Ns

Note: Significant comparisons are in bold.
Abbreviations: DC, Deer Creek; LM, Lewis Marine; LSR, Little Salmon River; SR, Salmon River.

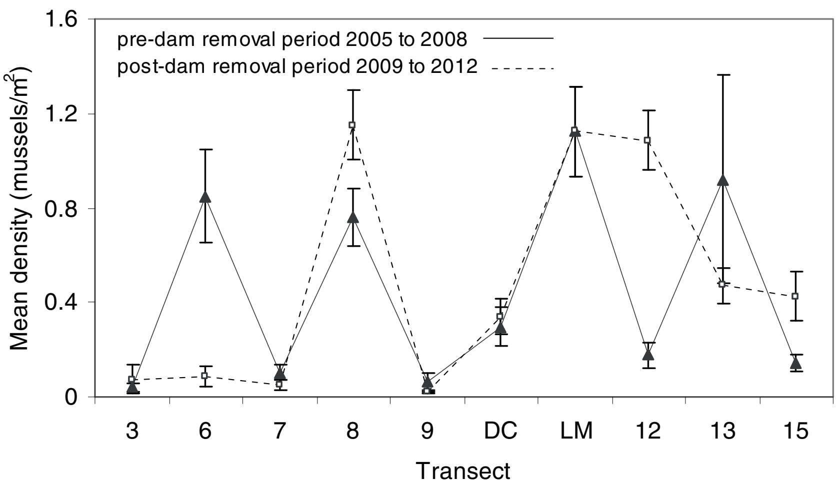

FIGURE 2 Mean adult mussel density (±1 SE) by transect in pre-dam removal period (solid line, 2005–2008) and post-dam removal (dashed line, 2009–2012). DC, Deer Creek; LM, Lewis Marine.

collected in 40% of the available habitat area at the river edges leaving about 60% of the habitat in the glide center unoccupied (Figure 3). For example, only 11% of the 138 mussels collected at transect 6 were found in the center of the river (center defined as 13%–86% of the distance across the river) and no mussels were found in the center after dam removal. Similarly, mussel abundance at transect 8 was greater on the cobble-dominated east side (81%) with the remainder on the west side and none in the river center.

Living adult mussels of 13 species were collected in transects, dominated by *E. complanata*, which was collected from all transects (Table 2). Living *L. cardium* was more abundant at transect 12 (43% of *L. cardium* collected) and Lewis Marine (36% of *L. cardium* collected), and *L. cariosa* was most abundant in Deer Creek (58% of *L. cariosa* collected). One living *M. margaritifera* was collected near transect 9 in 2012 along with two recently dead shells showing evidence of predation (Cooper, 2011). Living *P. grandis* was collected at Lewis Marine and transect 12, which represented the first documentation of this species in the study area.

Density of *L. cardium* ranked third out of the 13 species collected (Table 2). Mean density (all years combined) of *L. cariosa* in Deer Creek and Lewis Marine (0.01 m^{-2}) was an order of magnitude greater than *L. cariosa* at other transects, and mean density of *L. cardium* (0.06 m^{-2}) at Lewis Marine was also an order of magnitude greater than *L. cardium* at other transects.

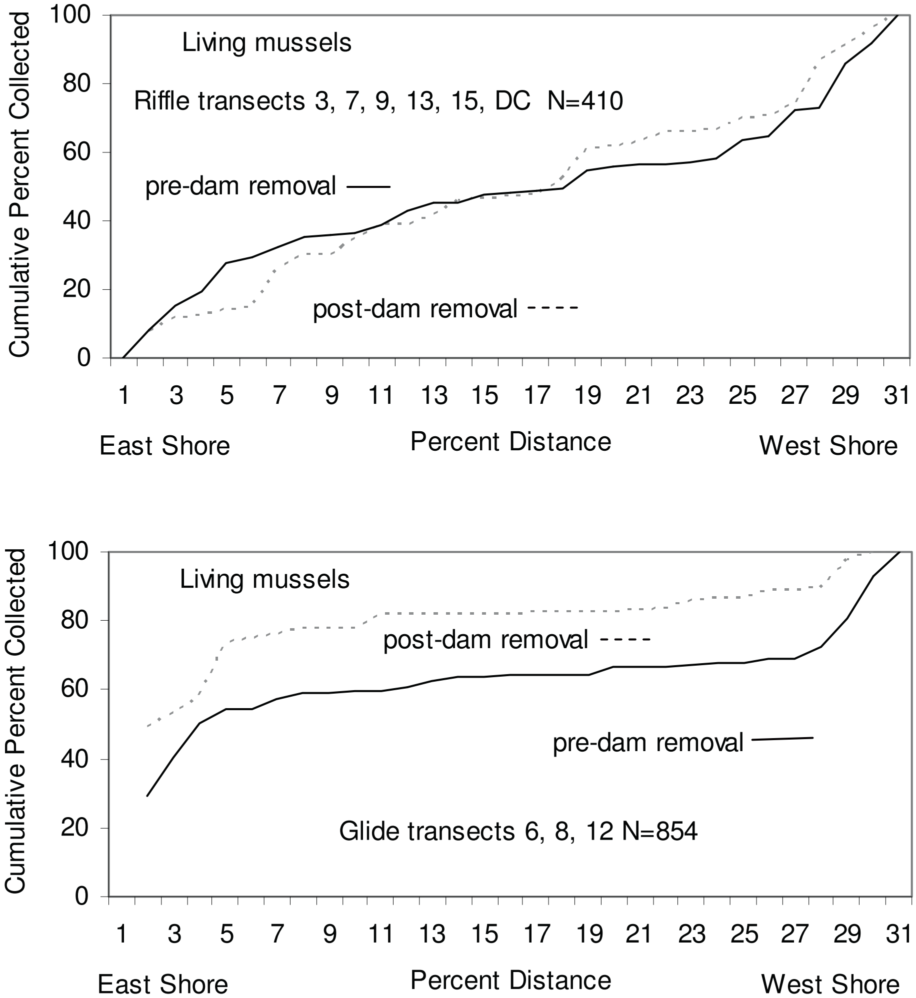

FIGURE 3 Cumulative percent distribution of living adult mussels in glide and riffle transects, excluding 129 mussels from Lewis Marine, from 2005 through 2012. Percent distance refers to the distance across the river starting from the east shore.

TABLE 2 Species of living adult mussels collected from transects (2005 through 2012), and population estimates with 95% confidence intervals.

Species	Adult living	Percent of living	Mean Density (N m^{-2})	Estimated Population size	Population, 95% CI
Elliptio complanata	1079	88.4	0.401	3237	1778–5890
Lampsilis radiata	52	4.3	0.042	156	72–337
Strophitus undulatus	36	2.9	0.014	108	43–268
Lampsilis cardium	11	0.9	0.018	33	16–70
Pyganodon cataracta	11	0.9	0.010	33	14–80
Lampsilis cariosa	9	0.7	0.005	27	13–56
Lasmigona compressa	7	0.6	0.010	21	8–57
Lasmigona costata	6	0.5	0.002	18	8–41
Alasmidonta marginata	5	0.4	0.002	15	7–33
Pyganodon grandis	2	0.2	0.001	6	3–12
Anodontoides ferussacianus	1	0.1	<0.001	3	2–4
Margaritifera margaritifera	1	0.1	<0.001	3	1–7
Alasmidonta undulata	1	0.1			
Total	1221				

Note: Mean density was based on a cumulative transect area of 10,464 m^2. One living *A. undulata* was collected in a benthic sample but the density and population size were not estimated.

The greatest apparent abundance of *L. cardium* and *L. cariosa* was in three adjacent middens near transect 1 where they accounted for 28% of the empty shells collected. Collections made in these middens in 2008 contained four living *L. cardium* as well as four additional species represented by empty shells (*Lasmigona costata*, *Lampsilis radiata*, *Elliptio complanata*, and *Strophitus undulatus*) and may have been part of a large mussel bed (425 articulated empty shells recovered) that was buried under 2.2 m of sand by 2011. Density estimates of mussel species in these middens were not made since the dimensions of the mussel beds could not be determined and there is some evidence that mussel selection by muskrats does not always reflect the density of species in a mussel bed (Watters, 1993–1994). Shell material in the middens might not represent a long-term accumulation as calcium levels in the rivers were low and shells could be dissolved rapidly (Strayer & Malcom, 2007). A small cluster of living mussels, including *L. cardium*, was observed on the east river bank in 2012 where scouring of sediment had revealed part of the original shoreline.

TABLE 3 Index values for the pre-dam removal and post-dam removal periods.

	Index	
River	**Pre-removal**	**Post-removal**
Shannon–Weiner diversity		
Salmon	0.324	0.285
Little Salmon	1.091	0.699
Simpson diversity		
Salmon	0.881	0.899
Little Salmon	0.528	0.697
Smith–Wilson evenness		
Salmon	0.0017	0.0086
Little Salmon	0.0108	0.0004
Shannon evenness		
Salmon	0.167	0.146
Little Salmon	0.496	0.335

Note: Shannon–Weiner diversity index ranges from 0 with no upper limit; Simpson diversity index ranges from 0 to 1 with greater values indicating less diversity; Smith–Wilson evenness ranges from 0 to 1 with evenness increasing to a maximum at 1; and Shannon evenness ranges from 0 to 1.

Distribution of *Alasmidonta undulata*, *Anodontoides ferusscianus*, and *L. costata* was more widespread if empty shells were considered: empty *A. undulata* occurred at transects 7, 8, and 13 but only at transect 8 as living; empty *A. ferusscianus* occurred at transects Deer Creek, 12, 13, and 15 but only at transect 8 as living; and living *L. costata* was collected at transects 12, 13, and 15 but also as empty shells in the lower Salmon River near transect 1. Distribution of other species was similar between living and empty shells.

The Shannon–Weiner diversity and Simpson diversity indices showed a decline in both rivers after dam removal (a greater value indicates lower diversity for the Simpson index). Evenness indices had conflicting results for the SR (Smith–Wilson index increased, Shannon index decreased) and both indices indicated a decrease in evenness for the LSR (Table 3). The number of species declined by one in both rivers from pre-dam removal to post-dam removal. Abundance decreased by 14% in SR, primarily from a decrease in *E. complanata* at transect 6 and abundance of *E. complanata* nearly doubled in LSR due to increased excavation effort at transect 12.

Seven species of living juvenile mussels were collected from 2005 to 2012 (mean SL = 20 mm; Table 4). *E. complanata* was most abundant with *L. radiata* second. The remaining five species (*L. cardium*, *L. cariosa*, *Lasmigona compressa*, *P. grandis*, and *S. undulatus*) accounted for less than 6% of the total. Juvenile mussels were collected from eight transects but not in Deer Creek or transects 6 and 7 during mussel sampling. Lewis Marine and transect 12 accounted for 48% and 46% of the total living juvenile mussels collected. A total of 91 dead stranded juvenile *E. complanata* mussels (mean SL = 33.9 mm) and 3 dead stranded juvenile *S. undulatus* mussels (mean SL = 31.9 mm) were collected in 2009 at transects 6 and 7 after dam removal.

3.1 | Sediment

Sediments were moderately to poorly-sorted in both rivers and had relatively high porosity. The center of the SR was significantly more sorted than the east side but not the west side ($F_{2,51} = 3.79$;

TABLE 4 Mean density (N m^{-2}) of living juvenile mussels collected from 2006 through 2012 by species and transect.

	Glide transects				Riffle transects					Mean	
Species	**LM**	**6**	**8**	**12**	**7**	**9**	**13**	**Total**	**%**	**Density**	**SL**
Elliptio complanata	86	1	1	82			1	171	89.5	1.8	6–39
Lampsilis radiata	4	2		3	1			10	5.2	0.224	9–40
Lampsilis cardium	1	1		1				3	2.2	0.118	12–28
Lampsilis cariosa	1			1		1		3	1.6	0.114	14–32
Lasmigona compressa	2							2	1.0	0.6	17–19
Strophitus undulatus						1		1	0.5	0.015	39
Pyganodon grandis	1							1	0.5	0.03	21
Total	95	4	1	87	1	2	1	191			

Note: No juvenile mussels were collected in 2005. Mean density was based on cumulative transect area where juvenile mussels occurred.
Abbreviations: LM, Lewis Marine; SL, range in shell length (mm).

$p = 0.03$) and there was no significant difference by year. Sorting in the LSR was similar to that in the SR but with no significant differences by location ($F_{2,33} = 0.92$; $p = 0.41$) or by year ($F_{2,33} = 2.34$; $p = 0.12$). Porosity in the SR was significantly greater in the center than in the east or west sides ($F_{2,51} = 17.6$; $p > 0.0001$) as was porosity in the center of the LSR ($F_{2,33} = 7.9$; $p = 0.002$). There were no significant differences in sorting or porosity in either river when comparing means by year.

Very fine to medium sand (0.062–0.5 mm) was the dominant sediment fraction at glide transects before and after dam removal with the exception of dissimilar sediments exposed in the former reservoir after dam removal: layered clay and peat-like material, which were scoured away after 2010. The rapid dewatering of the SR reservoir mobilized the sediment and reduced the water depth at transect 3 from 3 to 0.5 m and to less than 0.1 m at transects 1 and 2. Erosion of sand increased the length of the riffle at transect 7 downriver by 55 m and increased the length of the riffle at transect 3 by 107 m in an upriver direction. Both riffles remained at these dimensions in 2012. The riffle transects were primarily cobble, ranging from 43% cobble at transect 9 to 83% cobble at transect 13. A riffle (designated as 67) within the former reservoir was uncovered after the dam was removed. Pebble counts in this riffle showed that it was composed primarily of cobble (68%) similar to the other riffles. Embeddedness estimates at transect 7 decreased from 40% in 2004 to 20% in 2012 and increased at transect 3 from 20% in 2004 to 60% in 2010 followed by a decrease to 40% in 2012. Embeddedness remained similar at the other riffles (20%–40%) during the study. Sand deposition downriver of the former dam decreased the average water depth by 80%–86% after dam removal in 2009. The deposition of sand downriver reached beyond the confluence of the SR and LSR by May, 2010, and formed a bar adjacent to the mouth of the LSR. This bar was partially removed by flooding in October 2010, reformed by November 2010, but was reduced in length by flooding in March and April 2012. Scouring of shoreline sediments at transects 4–67 shifted the wetted area of the shoreline westward in 2012 and increased the maximum width of these transects by 2–4 m.

3.2 | Water chemistry

Water temperature was not affected by the presence or absence of the dam. Mean water temperature between transects 6 and 3 was not significantly different in 2008 (Kruskal–Wallis = 0.15, $p = 0.70$) or in 2009 for 6 May to 15 July (Kruskal–Wallis = 0.0006, $p = 0.98$). Dissolved oxygen saturation ranged from 76% to 114% from 2008 through 2012 between transects 3 and 7 with no change attributable to the dam. Sulfate, nitrate, and ammonia levels were similar to what would be expected in unpolluted freshwater (Lind, 1979; Table 5) and concentrations did not differ significantly between upriver and downriver of the dam (sulfate, $F_{1,30} = 0.48$, $p = 0.49$; nitrate, $F_{1,29} = 0.61$, $p = 0.44$; ammonia, $F_{1,29} = 0.15$, $p = 0.70$). Alkalinity was greatest in Deer Creek and may have been influenced by groundwater seeps. Several seeps in both rivers had alkalinity ranging from 188 to 288 mg/L and water temperature in the seeps was generally 10°C colder than the river. Calcium concentration was low and was consistent with the metamorphic rock of surface layers of the Adirondack Mountains.

Water level in the SR and LSR followed a seasonal trend, higher in spring from snowmelt, lower in summer but with short-term increases from rain and an increase in fall. The seasonal trend was disrupted by extreme flooding in October 2010, from 7.6 cm of rain over 3 days and in March and April 2012, from ice jams caused by unseasonable warm weather (NOAA, 2012). The apparent decline in water level after 15 July 2009 (Figure 4) was partly due to deposition of sand displacing water around the level logger after the dam was breached. A complete description of the sand deposition was given in Cooper (2011).

Mean bottom water velocity in the center of the reservoir (transect 6) was 0.06 ms^{-1} (SE = 0.01, $N = 3$) in 2008 and increased significantly to 0.43 ms^{-1} ($F_{1,4} = 13.5$, $p = 0.02$, $N = 6$) 2 months after the dam was breached. Bottom water velocity at transects 3 and 7 also increased by 30%–40% after the dam was removed but these values were not statistically significant ($p > 0.05$) when comparing 2008 to 2010 or 2012. Measurements were made at discharge rates of 0.74–

TABLE 5 Mean water chemistry values for 2005 through 2012 (my study) and 1955, 1960, 1961, 1970–1972, 1997–1998, 2005, and 2010 from National Water Quality Monitoring Council (2019) for both rivers combined.

	pH	Alkalinity (mg/L $CaCO_3$)	Total chlorine (mg/L)	Sulfate (mg/L)	Nitrate (NO_3-N, mg/L)	Nitrogen, ammonia (NH_3-N, mg/L)	Calcium ($CaCO_3$, mg/L)	Turbidity (FAU)
2005–2012								
Mean	7.7	87	1.9	4.5	0.49	0.04	NM	6.2
(SE)	0.07	5.1	0.02	1.2	0.04	0.005		0.5
N	129	206	109	109	109	103		111
1955–2010								
Mean	7.4	50.8	7.3	8.3	0.16	0.03	17.2	4.5
(SE)	0.07	1.5	0.4	0.5	0.02	0.004	1.6	0.6
N	57	57	33	57	34	28	41	33

Note: Calcium concentration was not determined in my study. Turbidity in the lower panel is in NTU.

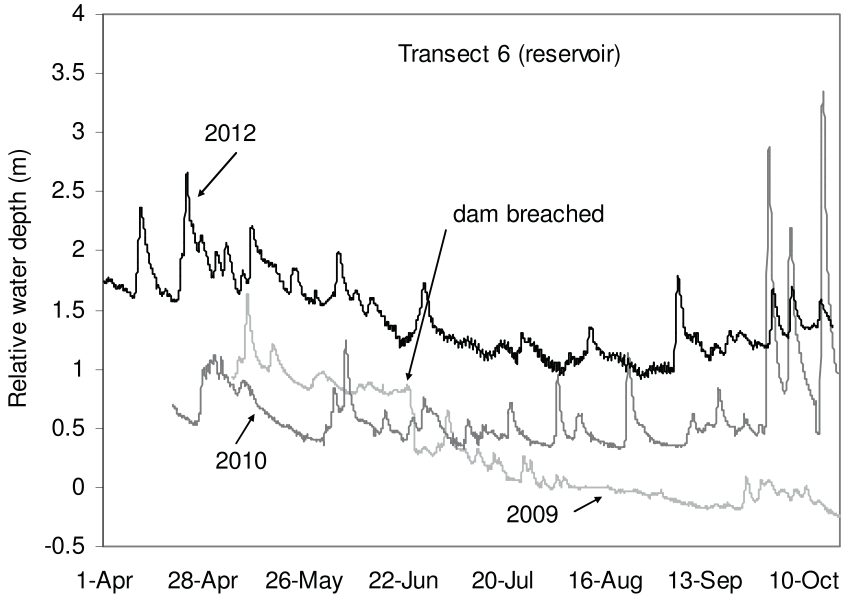

FIGURE 4 Relative water level at transect 6 (mid-reservoir) for 2009, 2010, and 2012. The dam was breached in June, 2009. The declining water level after 15 July 2009, is partly due to sand displacing water around the level logger.

0.82 $m^3\ s^{-1}$. Measurements next to most mussels in cobble-dominated areas were not possible as the physical size of the meter was larger than the space between cobbles so the velocity reported is only an approximation of velocity experienced by mussels.

4 | DISCUSSION

Downriver movement of sediment would be of critical importance in assessing the risks of dam removal. Several studies have documented alterations of the habitat due to deposition of sediments (Burroughs et al., 2010; Shuman, 1995; Stanley et al., 2002) where the erosion of upriver sediments led to an increased gradient and water velocity in the former impoundments and formation of new channels with steeper banks. The design plan for the Fort Covington dam removal included an estimate of 764 m^3 of sediment trapped behind the dam, which was not considered to pose a problem, particularly if draining of the reservoir was done slowly in August at lowest flow to allow shoreline sediment to be stabilized with vegetative cover (J. MacBroom; Milone and MacBroom Inc, personal communication). This recommendation was not followed. The reservoir was drained quickly (25 h) and the increased water velocity (exacerbated by 2.5 cm of rain, NOAA, 2012) resulted in erosion of up to 4 m of the river banks throughout the reservoir that deposited more than 40,000 m^3 of sediment in the lower river over the following 5 months (Cooper, 2011).

Rapid dewatering in Wisconsin (36 h) led to high mussel mortality with declines in mussel density and increased sedimentation in the lower river (Sethi et al., 2004) contrasted with gradual dewatering (2–3 weeks) of a North Carolina reservoir where mussel mortality was low and there was no detectable change in mussel density, species richness, or substrate composition (Heise et al., 2013). Gradual dewatering in the St. Regis River (NY) allowed for effective mussel relocation with low mortality (Jock, 2017).

Three conceptual models have been proposed for the transport of sediments (reviewed in Lisle et al., 1997) where the sediment can (1) move as a discrete mass with little change in shape, (2) move as a diffuse stream of particles over time, and (3) remain in place with only a small proportion moving downriver. The sand that passed through the former reservoir of the SR was most similar to conceptual model 1; the leading edge of the sand was apparent from July to November 2009 (Figure 5). The movement of the sand was similar to that described by Simons and Simons (1991; cited in Doyle et al., 2000) after the removal of the Newaygo Dam on the Muskegon River, Michigan, where sediment moved as a wave at about 1.6 km/year. The average rate observed in the SR was equivalent to 2.3 km/year (Cooper, 2011).

The assumption that dam removal would not affect the LSR was incorrect. Deposition of sediment after dam removal formed a bar across the mouth of the LSR, which reduced the water velocity in the LSR, and facilitated the accumulation of silt and algae at Lewis Marine and transect 12. The decline in bottom visibility necessitated an increase in excavation effort to find mussels but resulted in a statistical difference only for adult mussels at transect 12. The accumulation of silt and algae prompted a response from Eastern Sand Darter *Ammocrypta pellucida*, which moved from Lewis Marine and transect 12 to a clean sand bar in the main channel of the SR, and Brook Silverside *Labidesthes sicculus*, which moved farther up the LSR to avoid the accumulated silt and algae (Cooper, 2013).

The presence of the dam did not alter the distribution of mussel species or the species composition of potential fish hosts as the same fish species were found above and below the dam (Cooper, 2013). Six of the more abundant mussel species were collected above and below the dam. Only two species of mussels (including empty shells) were collected in a single river: *M. margaritifera* only in the SR and *A. marginata* only in the LSR. Formation of the reservoir may have artificially increased the reservoir mussel population by providing more stable sediment with lower water velocity and reducing the effects of ice-scouring.

FIGURE 5 Sand wave from erosion moving downstream in the former reservoir in July, 2009. The leading edge of the sand was 30 cm in height. [Color figure can be viewed at wileyonlinelibrary.com]

Habitat stability is a primary factor in determining mussel occurrence and is particularly important under high flow conditions (Allen & Vaughn, 2010; Haag, 2012). Low habitat stability was found to be limiting to mussels (Clarke, 1981; Haag, 2012; Strayer, 1999). It would follow that those transects in the SR–LSR that had persistent mussel populations over the 8 years of this study would have more stable sediments brought about by a combination of lower gradient and physical structure (cobble) that afforded a refuge from greater water velocity and ice-scouring. High flows (>28.3 $m^3 s^{-1}$) occurred in 6 of the 8 years of this study. Two riffle transects (13 and 15) and two glide transects (8 and 12) had greater mussel density than the other transects in pre-dam and post-dam periods. The increase in mean ranks of density at transects 13 and 15 might be due to increased river flow in 2010 (56 $m^3 s^{-1}$) and 2011 (46 $m^3 s^{-1}$) that moved mussels from upriver into the transect area. Transects 8 and 12 had cobble substrate (TR8, east bank; TR12, west bank) with rooted vegetation. The other glide transects in both rivers had primarily coarse sand substrate with no cobble or rooted vegetation and greater water velocity in the river center, which would suggest that this substrate was relatively unstable. These characteristics resulted in 60% of the available glide habitats being unoccupied by mussels. The relationship of physical variables of a river to mussel bed persistence are not well defined and may be different during high flow compared to low flow when most mussel surveys are conducted (Gangloff & Feminella, 2007). Persistence of mussel beds is well-documented but might not be attributable solely to flow refugia (Sansom et al., 2018).

E. complanata dominated the unionid community in the SR–LSR, as in other tributaries of the St. Lawrence River valley (Harper et al., 2015; Jock, 2017), and was the most common unionid mussel in the Northeast United States (Raithel & Hartenstine, 2006; Sabine et al., 2004; Strayer & Ralley, 1993). Fifteen mussel species are known from tributaries of the St. Lawrence River (Harper et al., 2015; Metcalfe-Smith et al., 2005; Strayer & Jirka, 1997). Two species not found in the SR–LSR were *Potamilus alatus* and *Leptodea fragilis* but have been reported from the St. Regis and Grasse rivers (Harper et al., 2015).

M. margaritifera is circumboreal in distribution, generally in low-productivity water with low calcium concentration and low alkalinity (<10 mg/L as Ca, <45 mg/L as CO_3; Harman & Forney, 1970; Ortmann, 1919; Strayer, 1993). *M. margaritifera* was abundant in third to fifth order-rivers flowing out of the Adirondacks and in central NY streams flowing through the Tug Hill Uplands (Clarke & Berg, 1959; Erickson & Fetterman, 1996). The occurrence of *M. margaritifera* in the lower SR was likely the result of high river flow transporting the mussels downriver as it was collected only once and at the farthest upriver part of the study area. Potential glochidial hosts of *M. margaritifera* (salmon, trout) were rare in the study area: one Brown Trout *Salmo trutta* was collected in 2008. Brook Trout *Salvelinus fontinalis* are the predominant salmonid in the headwaters but were never collected in the lower rivers. Atlantic salmon *Salmo salar* were determined to be extinct in the SR–LSR by the early 1900s (Greeley & Greene, 1930). *M. margaritifera* was not collected in the lower St. Regis River but was present in the headwaters of the Grasse River (Erickson & Fetterman, 1996; Jock, 2017). Both are tributaries of the St. Lawrence River.

5 | CONCLUSION

The Fort Covington Dam did not have a measurable effect on water chemistry due to the short residence time (2 h) of water in the reservoir (volume of reservoir divided by mean annual discharge). A similar lack of effect was found with the removal of the Manatawny Creek Dam (Pennsylvania) due to the short residence time of water in that reservoir (about 1.5 h; Velinsky et al., 2006). Removal of the Fort Covington Dam did not affect sediment sorting or porosity or mussel species distribution but rapid dewatering of the reservoir led to stranding and death of mussels in the former reservoir and in the adjacent ponds. Increased water velocity, exacerbated by rain, mobilized sediment that buried a potentially large mussel bed downriver of the dam where *L. cardium* and *L. cariosa* were abundant. Deposition of sediment formed a sandbar across the mouth of the LSR, which increased turbidity in the post-dam period at two transects and resulted in the abandonment of the lower LSR by two fish species.

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CONFLICT OF INTEREST STATEMENT

The author declares no conflicts of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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