Technical Report No. 32

The Freshwater Mussels of the Lower Missisquoi River: Current Status and the Potential for a Refugium from Zebra Mussel Impacts

Lake Champlain Basin Program

By
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PUBLICATION SERIES

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1. *A Research and Monitoring Agenda for Lake Champlain.* Proceedings of a Workshop, December 17-19, 1991, Burlington, VT. Lake Champlain Research Consortium. May, 1992.

2. *Design and Initial Implementation of a Comprehensive Agricultural Monitoring and Evaluation Network for the Lake Champlain Basin.* NY-VT Strategic Core Group. February, 1993.

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   (C) *GIS Data Inventory for the Lake Champlain Basin Program.* Vermont Center for Geographic Information, Inc. March, 1993.

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   Lake Champlain Sediment Toxics Assessment Program. An Assessment of Sediment - Associated Contaminants in Lake Champlain - Phase 1. Executive Summary. Alan McIntosh, Editor, UVM School of Natural Resources. February 1994.

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   (B) Lake Champlain Nonpoint Source Pollution Assessment. Appendices A-J. Lenore Budd, Associates in Rural Development Inc. and Donald Meals, UVM School of Natural Resources. February 1994.

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(A) *Dynamic Mass Balance Model of Internal Phosphorus Loading in St. Albans Bay, Lake Champlain.* Eric Smeltzer, Neil Kamman, Karen Hyde and John C. Drake. March 1994.

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(C) *Report on Institutional Arrangements for Watershed Management of the Lake Champlain Basin. Appendices.* Yellow Wood Associates, Inc. January 1995.

12. (A) *Preliminary Economic Analysis of the Draft Plan for the Lake Champlain Basin Program. Executive Summary.* Holmes & Associates and Anthony Artuso. March 1995

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23. (A) *Lake Champlain Sediment Toxics Assessment Program. An Assessment of Sediment - Associated Contaminants in Lake Champlain - Phase 11. Executive Summary.* Alan McIntosh, Mary Watzin and Erik Brown, UVM School of Natural Resources. October 1997

(B) Lake Champlain Sediment Toxics Assessment Program. An Assessment of Sediment - Associated Contaminants in Lake Champlain - Phase 11. Alan McIntosh, Mary Watzin and Erik Brown, UVM School of Natural Resources. October 1997

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31. Estimation of Lake Champlain Basinwide Nonpoint Source Phosphorus Export, William Hegman, Associates in Rural Development, Inc., Deane Wang and Catherine Borer, UVM Water Resources & Lake Study Center, September 1999.

32. *The Freshwater Mussels of the Lower Missisquoi Rivers: Current Status and the Potential for a Refugium from Zebra Mussel Impacts.* Paul Marangelo, VT Agency of Natural Resources, Dept of Environmental Conservation. August 1999.

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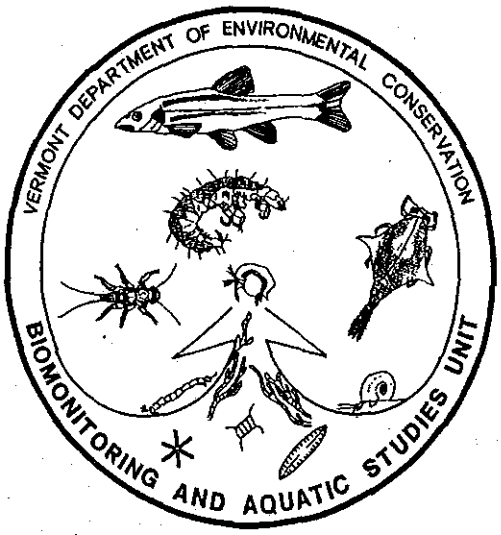
The Freshwater Mussels of the Lower Missisquoi River: Current Status and the Potential for a Refugium from Zebra Mussel Impacts



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INTRODUCTION

The Missisquoi River in northwest Vermont (Fig. 1a) contains one of the most diverse assemblages of freshwater mussels (family Unionidae) in the Lake Champlain Basin, with historical records of 12 species (Fichtel and Smith 1995; Smith 1985; Table 1). The lower portion of the Missisquoi River mainstem, from the delta at Lake Champlain to the principle fall line at Highgate Falls (Fig. 1b), was intensively surveyed in 1998 to assess the abundance, density, and distribution of a targeted set of seven regionally rare mussel species known from the river: *Ligumia recta* (black sandshell), *Anodontoides ferussacianus* (cylindrical papers hell), *Lampsilis ovata*[1] (pocketbook), *Lasmigona costata* (fluted shell), *Leptodea fragilis* (fragile papershell), *Potamilus alatus* (pink heelsplitter), and *Pyganodon grandis* (giant floater).

The latter four species are historically known to occur in delta areas in Lake Champlain (Fiske and Levy 1995), from which they are rapidly disappearing due to overgrowth by the invasive zebra mussel (*Dreissena polymorpha*). An additional target species has also been recently observed in a *Dreissena* - infested part of Lake Champlain (*A. ferussacianus* in the Lamotte Passage off of Isle Lamotte, personal observation). Hence the present study will assess the potential for the river to serve as a refugium for these species from zebra mussel impacts, as habitat conditions and/or physiochemical variables may preclude intensive zebra mussel colonization in the Missisquoi River.

The study reach (Fig. 1) consists of 26.1 km (thalweg length) of large river, mostly low-gradient habitats. The channel is 100 - 130 m wide, and depths at low flow range up to 6 m, with maximum channel depths in the most common habitat (slow run) ranging from 2 - 4 m. The study area is bisected by a low-head dam at Swanton (15.5 km upstream of Lake Champlain), which lies just upstream of a small falls. Above the dam, the river consists mostly of slow-run habitats. A complex of islands and slightly higher gradient creates the most heterogeneous habitat in the study area just downstream of the Highgate gorge. Below the dam, the river descends to lake level within 5 km (depending on lake level). The last 10.5 km of river passes through river delta habitats in the Missisquoi National Wildlife Refuge with no gradient. The Missisquoi diverges into four main channels just before it empties into Lake Champlain.

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[1]This nomenclature is consistent with Fichtel and Smith (1995). Future work to resolve taxonomic uncertainty on this species in the Champlain Basin may prove it to be *L. cardium* instead of *L. ovata*

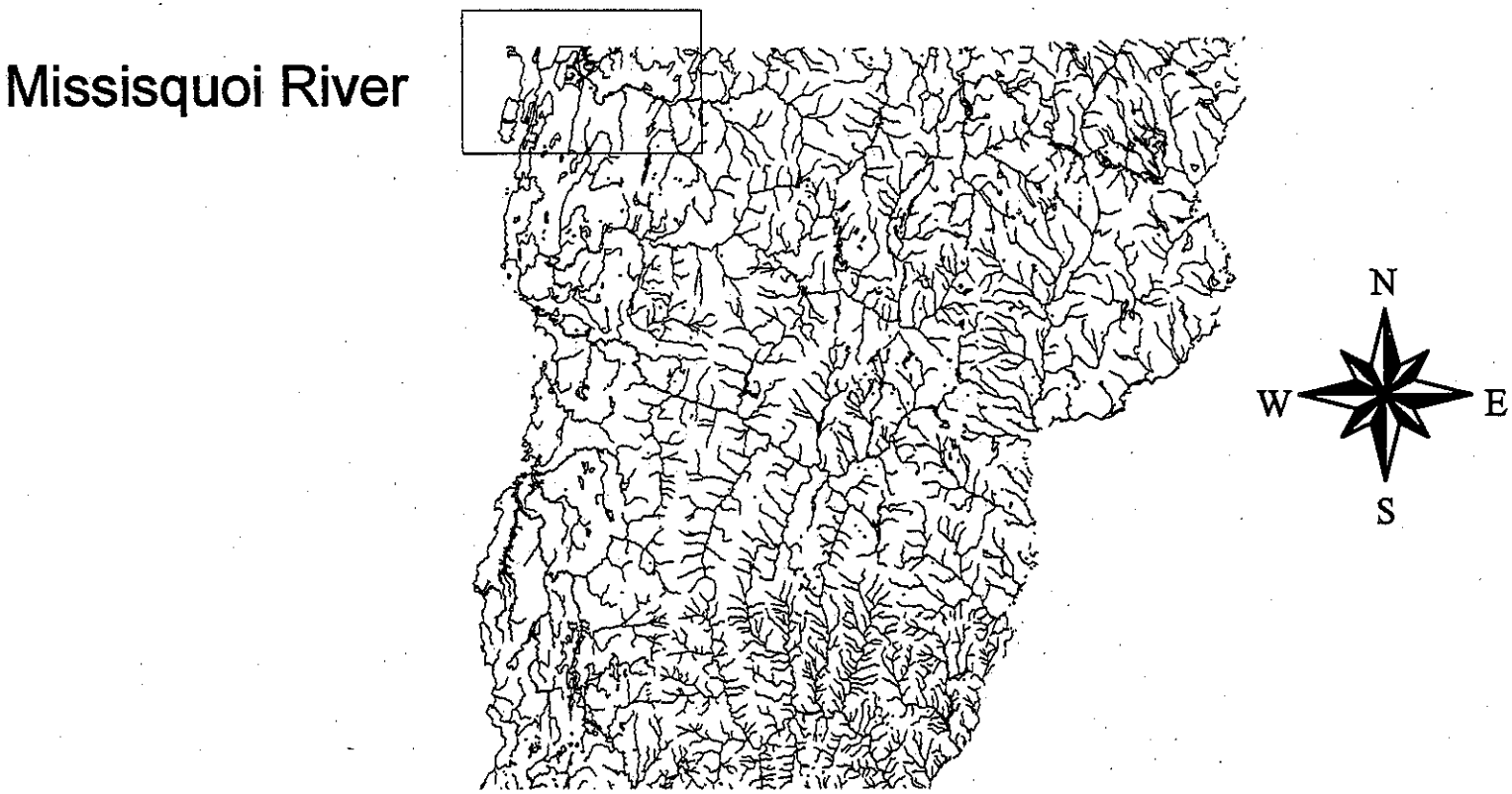

Figure 1a: Location of the Missisquoi River in Vermont

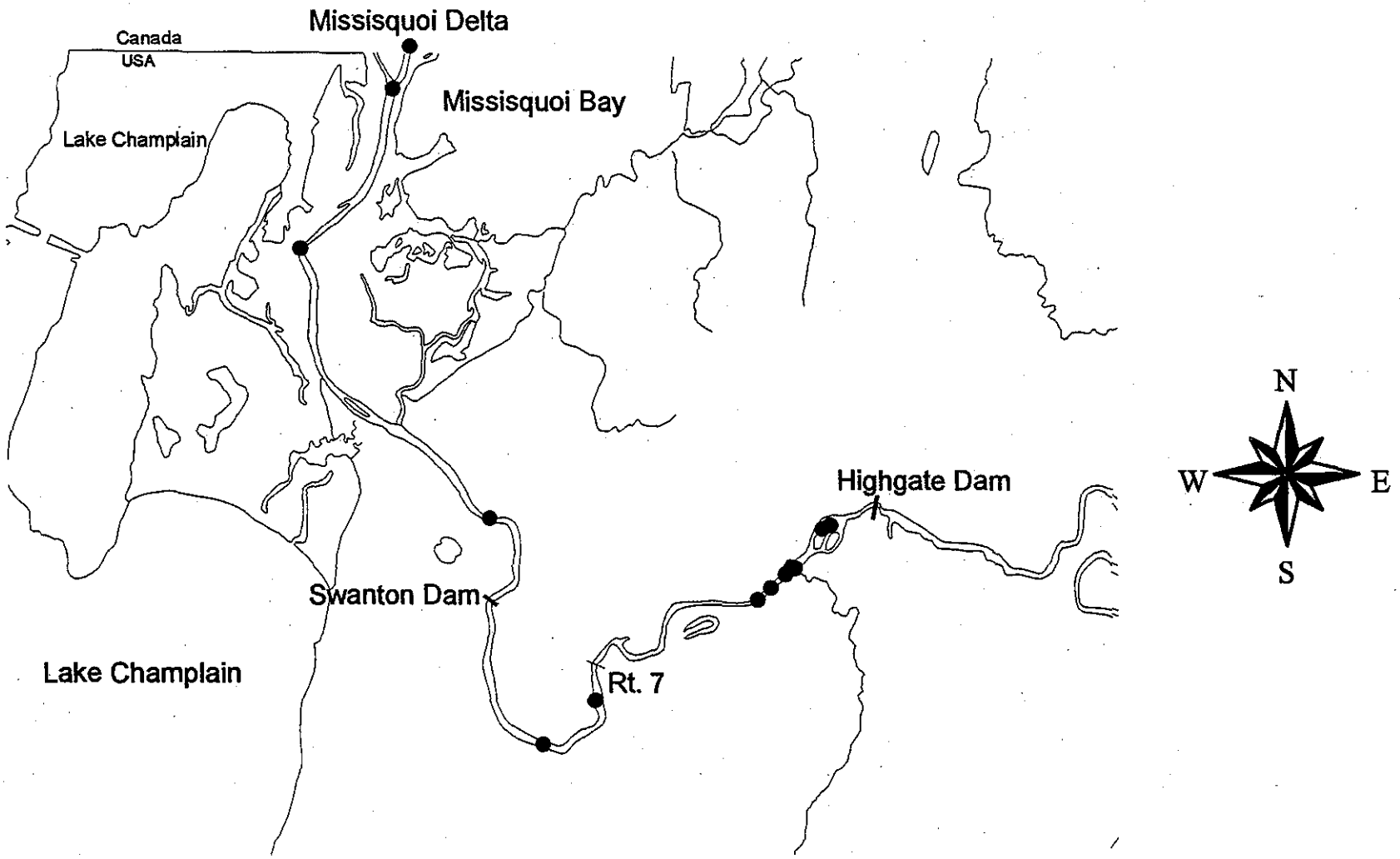

Figure 1b: Missisquoi River Study Area. Bullets mark the locations of quantitative survey sites. Channel distance from the Missisquoi Delta to Highgate Falls is 26km.

Table 1: List of Freshwater Mussel Species known from the lower Missisquoi River^ (Fichtel and Smith 1995). Target species in bold.

Alasmidonta undulata (triangle floater)
***Anodontoides ferussacianus* (cylindrical papershell)**
Elliptio complanata (eastern elliptio)
***Lampsilis ovata* (pocketbook)**
Lampsilis radiata (eastern lamp mussel)
Lasmigona costata* (fluted shell)
***Leptodea fragilis* (fragile papershell)**
***Ligumia recta* (black sandshell)**
***Potamilus alatus* (pink heelsplitter)**
***Pyganodon grandis* (giant floater)**
Pyganodon cataracta (eastern floater)
Strophitus undulatus (squawfoot)

* no published records, recent records (1997) of spent shells from Madeleine Lyttle, USFWS.
^ an additional species (*Lasmigona compressa*) has been recorded in upper areas of the watershed.

METHODS

A two-tiered, stratified sampling approach was used (modeled after Smith *et al.* 1996, with modifications), consisting of a qualitative phase followed by a quantitative phase.

First, a total of 44 sites (Table 2; Figs 2a - c) were qualitatively surveyed by snorkel (20 sites) and SCUBA (24 sites) to assess species distribution, species-habitat relationships, and relative abundances of target species. Sites were chosen by a subjective assessment of mussel habitat potential (based on a surface assessment of water velocity and probable substrate composition) and approximated an even spatial coverage in the study area. Every macro-habitat encountered (e.g. slow run, pool, dam backwaters, eddy, etc.) was sampled at least once.

At each site, two individuals scanned substrate for the presence of mussels for at least 20 minutes. An additional 10 - 40 minutes was spent at a site if more than 10 target species specimens were detected. Catch per unit effort (CPUE) figures for each species found were calculated from total elapsed search time at each site. Habitat

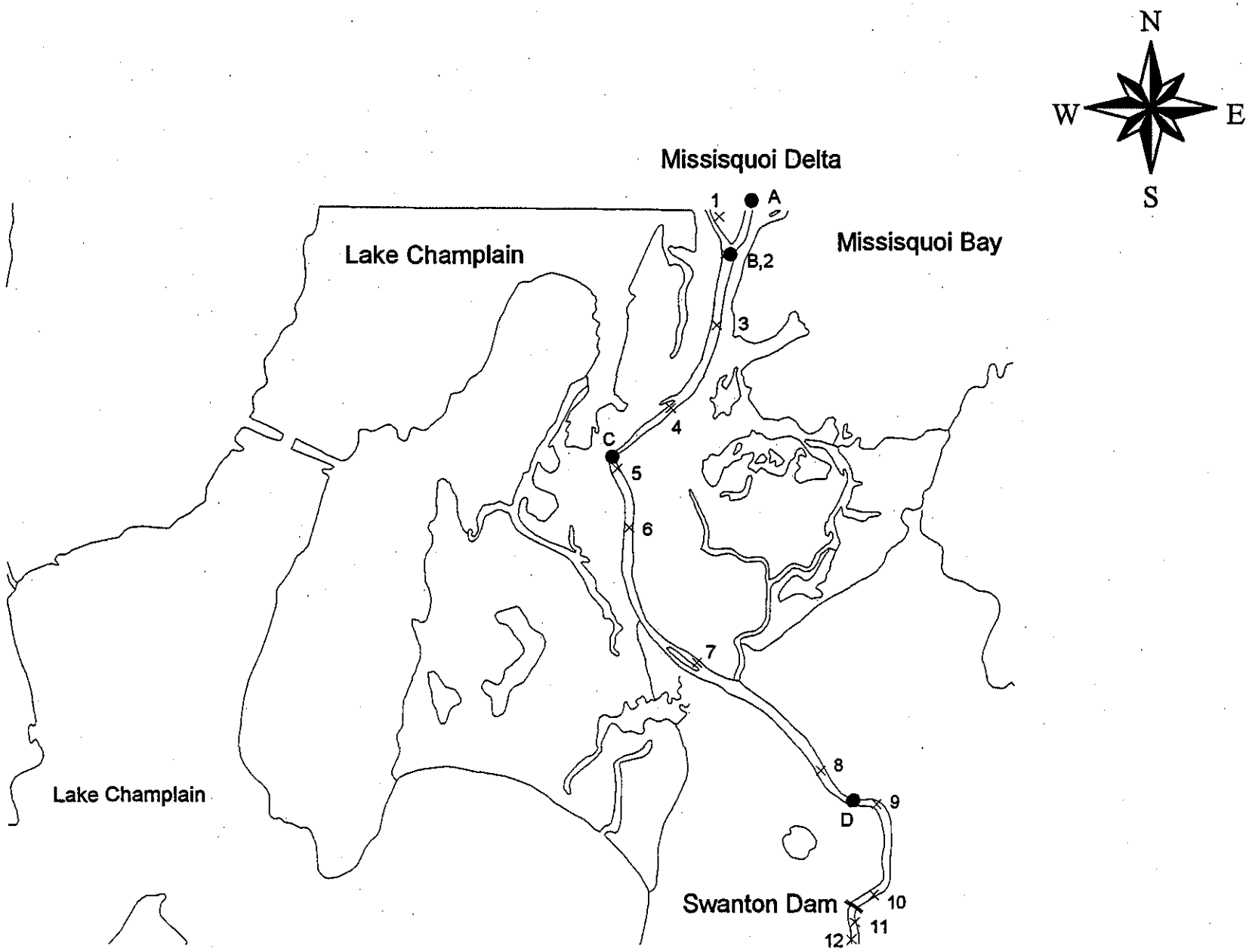

Figure 2a: Survey sites in the lower study area. Qualitative sites, denoted by "x", and site numbers correspond to Table 2. Quantitative sites denoted by bullets. Site letters correpond to Table 4. Channel distance between Lake Champlain and Swanton Dam = 15.5 km.

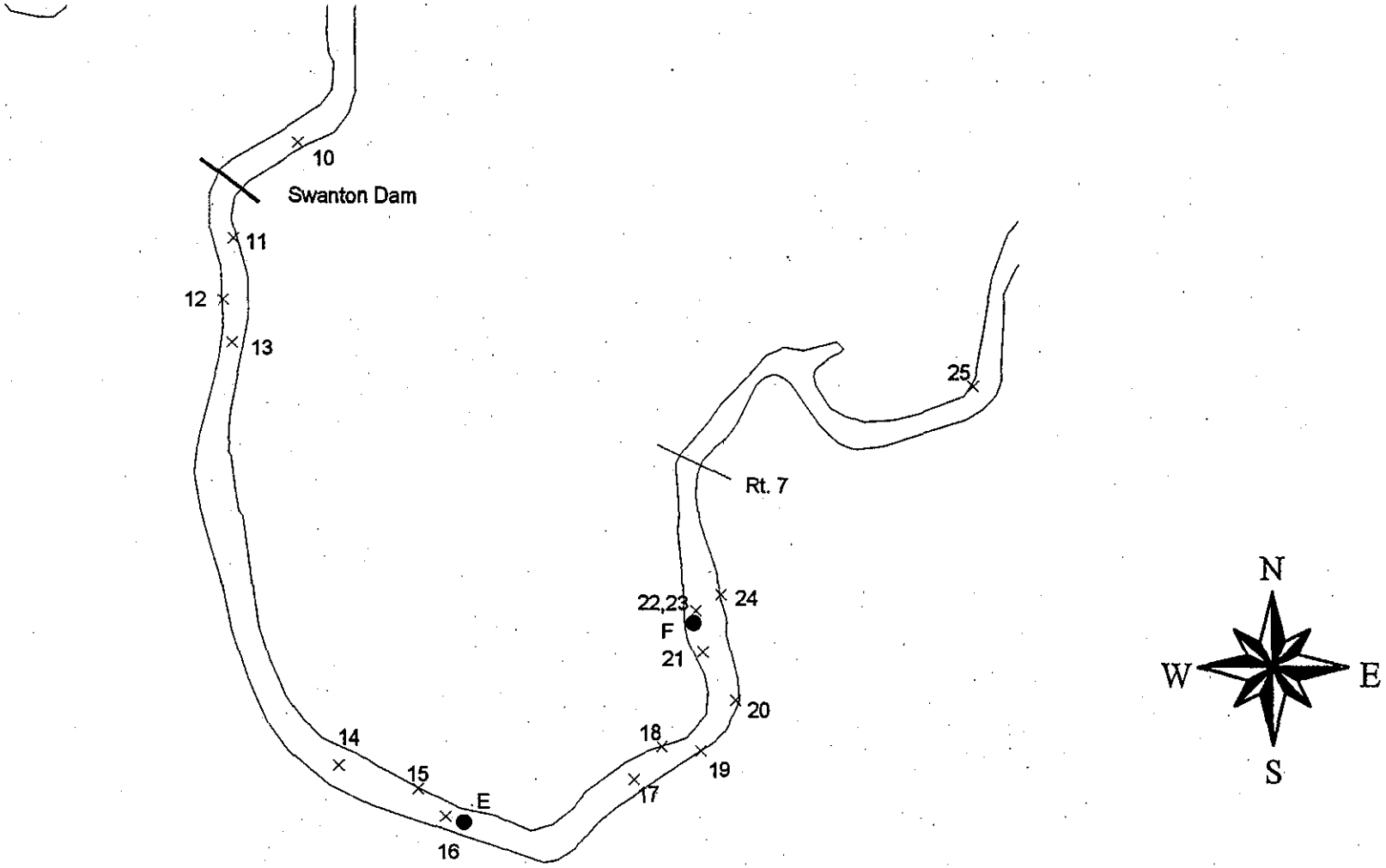

Figure 2b: Survey sites near Swanton Dam. Qualitative survey sites are marked "x". Site numbers refer to Table 2. Quantitative sites marked with bullets. Site letters refer to Table 4. Distance between Swanton Dam and Rt. 7 = 5.4 km

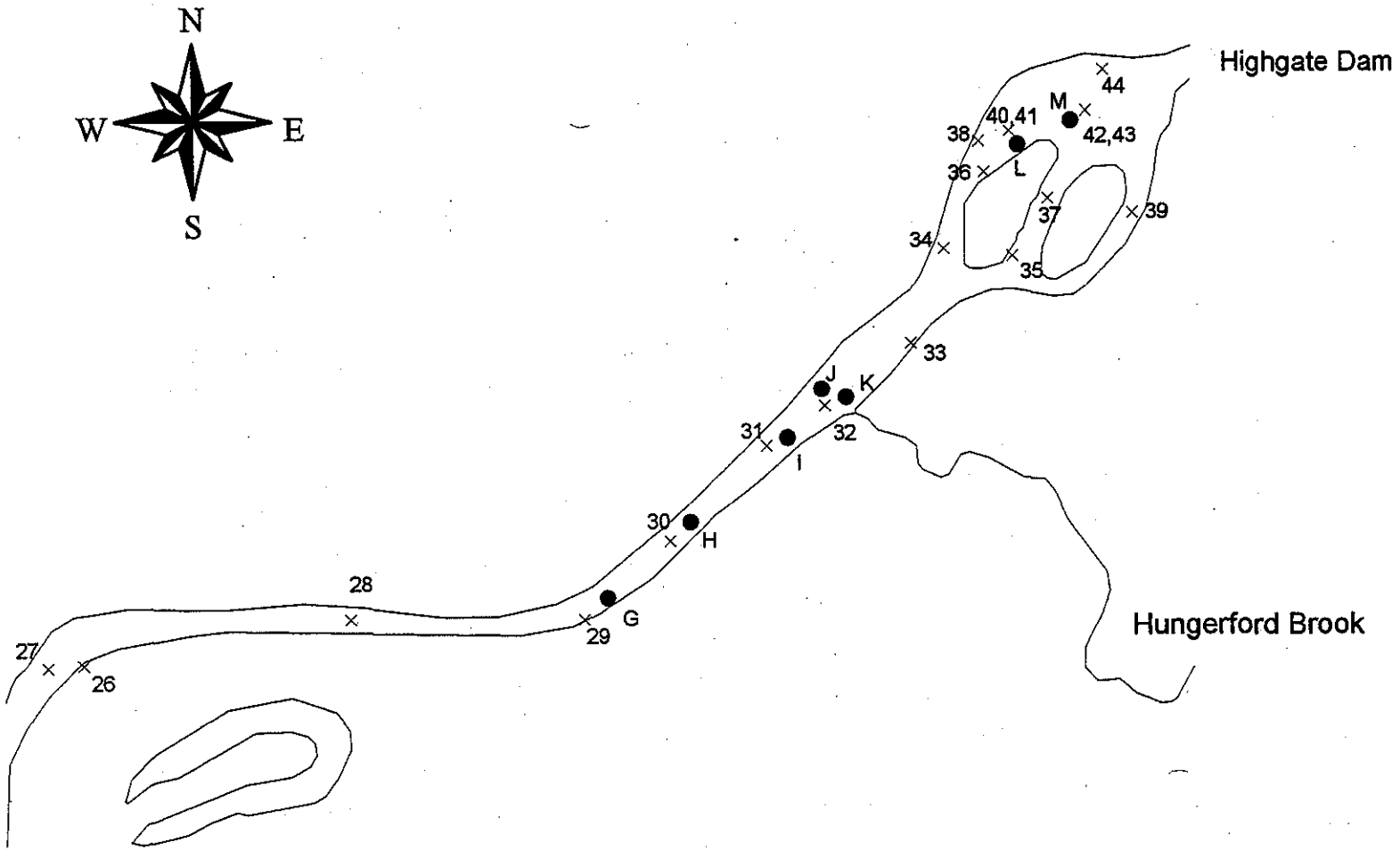

Figure 2c: Survey sites in the upper study area. Qualitative sites marked with "x". Numbers correspond to Table 2. Bullets denote quantitative sites. Letters correspond to Table 4. Distance between sites 44 and 27 = 3.6 km.

characteristics (substrate type, gradient/velocity) and habitat-species relationships were noted at each site. To supplement CPUE data, at three sites, a 15 or 30 m transect line was deployed through a productive area, and all mussels within 1m of the line were identified and counted to give a rough density estimate.

Based on CPUE and line-transect data, the river was then stratified into density (high/low) and velocity-based habitat (run/pool/riverbank) strata (Table 3). Strata were partitioned via a flexible criterion of 10 target animals CPUE, subjectively modified by perceived sampling efficiency at a given site[2] and richness of target species (sites with lower densities of target species were upgraded in the strata scheme if they appeared to support a large number of target species), and by a visual evaluation of habitat based on substrate and velocity. Sites in the most productive strata received priority for quantitative sampling, and site locations within a strata were selected to reflect inter-strata variation. This strategy was modified in the study area below Swanton Dam, where sampling hazards (large numbers of underwater snags) and low abundances (relative to the stratification threshold) of target species not found in the upper study area were encountered (see Table 2). Here, quantitative site selection criteria were the presence of target animals and scarcity of underwater snags, with preference being given to sites that had higher densities of target species.

Thirteen sites were sampled quantitatively. Most of this effort (8 of 13 sites; Fig. 2 a-c) was expended in high-density/slow-run strata between Highgate Dam and Swanton. Upper area site locations were non-randomly chosen to sufficiently describe the heterogeneity of slow run/high density strata suggested by the CPUE data.

Between Swanton Dam and Lake Champlain, the abundance of underwater snags at most river bank locations (Strata 3; particularly in the delta areas in the lower portions of the study area) limited quantitative sampling to the few areas that could be safely surveyed with SCUBA equipment. CPUE figures and habitats/substrates were more homogeneous in this region in terms of target species and species/habitat relationships, so less quantitative effort was needed to adequately describe the populations of target species in this strata.

An unusually wet summer and frequent high water constricted the sampling time available. Thus little sampling effort was expended in low- density strata (Strata 2: zero sites; Strata 4: one site).

Overall, 11 quantitative sites were sampled via SCUBA and two were sampled via snorkeling. A grid, consisting 60 to 230 regularly-spaced 0.25m^2 quadrats, was

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[2] Qualitative sampling efficiency for target species was hindered at some sites (e.g. Site 32) by having to "process" large numbers of non-target animals (most notably *Elliptio complanata*). Hence CPUE figures for these sites were biased downwards. Conversely, efficiencies and CPUE figures were enhanced by low densities of this species (e.g; Site 20).

Table 2: Qualitative survey sites in the Missisquoi Study area. Corresponding quantitative sites are listed in parentheses after qualitative site number. Numbers represent CPUE data. Site numbers/letters correspond to Figs. 2 a - c. CPUE was estimated for some non-target species as follows: ABUN: >60 CPUE; COM: 15 - 60 CPUE; UNC: 3 - 14 CPUE; RARE: < 2 CPUE. s = spent shell only. SCB = SCUBA; SNR = Snorkeling.

site	*LO*	*LC*	*AE*	*LRe*	*PG*	*LF*	*PA*	*EC*	*LRa*	*AU*	*PC*	*SU*	method	CPUE*
1					2.4	14.4		ABUN	COM				SCB	16.8
2(B)					7.7	3.4		COM	COM				SCB	11.1
3					1.5	1.5		COM	COM				SCB	3
4					2.4	8		ABUN	COM				SCB	3.2
5								COM	COM				SCB	0
6								UNC	UNC				SCB	0
7								UNC	UNC				SCB	0
8	1.1					s		ABUN	COM				SCB	1.1
9	3.7		s	s		s		COM	COM				SCB	3.7
10	1.1							COM	COM	s			SCB	1.1
11			2					ABUN	COM				SNR	2
12			6					ABUN	COM				SNR	6
13	1.7		0.6					UNC	UNC				SCB	3.4
14	2							COM	COM				SNR	2
15								ABUN	UNC				SNR	0
16(E)	12		5.5	s	s			ABUN	ABUN	s			SCB	18.5
17	4.5	s		s				ABUN	ABUN				SCB	4.5
18			4.6					ABUN	COM				SNR	4.6
19								ABUN	UNC				SNR	0
20	9.7		3.2					ABUN	COM				SNR	14.6
21	11.4	s	2.4					ABUN	COM				SNR	13.8
22(F)	7.5	s		s				ABUN	ABUN				SCB	7.5
23(F)	9.7	s		s				COM	COM				SNR	9.7
24	1							ABUN	COM				SNR	1
25								UNC	UNC				SNR	0
26	5.1		0.8					UNC	UNC				SCB	6.4
27	3		1.5					UNC	UNC				SNR	4.5
28	22.3	s	3.4	s				ABUN	COM			s	SCB	25.7
29								ABUN	COM				SNR	0
30(H)	14		4.1	0.8				COM	COM				SCB	18.9
31(I)	26		2.2					COM	COM				SCB	28.2
32(K,J)	9	s		s	s			ABUN	COM	0.5			SNR	9
33	1.7		1.7					ABUN	ABUN				SNR	3.4
34	2.7		2.7					ABUN	COM				SCB	5.3
35	1.7							UNC	UNC				SNR	1.7
36	7.8							COM	COM			1.1	SCB	7.8
37	7.5		2.9					COM	UNC			s	SCB	10.7
38								ABUN	UNC				SNR	0
39			3								9		SNR	3
40(L)	25.1		4.4					COM	COM				SNR	29.4
41(L)	19.6		19.6	1.3				COM	COM		1.3	1.3	SCB	40.4
42(M)	15.6							UNC	UNC				SNR	15.6
43	26.7		3.2					COM	COM				SCB	30
44	1		3					UNC	UNC		1	3	SCB	4

* Catch Per Unit Effort of target species.

Species key: *LO = Lampsilis ovata; LC = Lasmigona costata; LRe = Ligumia recta; PG = Pyganodon grandis; LF = Leptodea fragilis; PA = Potamilus alatus; EC = Elliptio complanata; Lra = Lampsilis radiata; AU = Alasmodonta undulata; PC = Pyganodon cataracta; SU = Strophitus undulatus*

Table 3: Stratification summary for quantitative sampling

strata	target sp. density	habitat	# Sites	strata locations
1	high	run/slow run; stable gravel/cobble substrate	8	Channel bottoms mostly above Swanton Dam.
2	low	run/slow run; sandy/silty unstable (unconsolidated) substrates	0	Channel bottom habitats mostly above Swanton Dam.
3	high	pool/riverbanks; silt/clay substrate with macrophytes	4	Riverbanks, mostly in river delta habitats below Swanton Dam.
4	low	pool/riverbanks; silt/clay substrate with macrophytes	1	River banks in gradient habitats mostly above Swanton Dam; Swanton Dam backwaters; Channel bottoms in the river delta area below Swanton Dam.

systematically sampled within each targeted site. Marked, weighted ropes stretched parallel to the direction of flow between weighted buoys, were used to reference the placement of quadrats for SCUBA sampling, and rebar stakes were used to delineate cross river transects of quadrats in shallow snorkel sampling areas. Quadrats were spaced apart so that between 3 - 5% of the grid deployment area would be sampled. Low-visibility conditions necessitated the close spacing of quadrats for logistical purposes at SCUBA sites. Points of delineation to define specific quantitative sampling areas were chosen randomly within a site that was pre-defined via the objectives described earlier in the treatment the stratification protocol.

Mussels from each quadrat sampled were picked by hand and immediately replaced in the substrate. Also, dominant substrate type, water depth, and presence/absence and percent cover of macrophytes were recorded. Specimens of target species were measured lengthwise with rulers to the nearest mm (+/- 3 mm). To estimate the endobenthic fraction of mussels at a given site, every other quadrat was excavated to a depth of 10 cm following the removal of visible mussels, and the excavated material was sieved underwater through 1/4 in. hardware cloth and examined for mussels. Excavating and sieving clay substrate in riverbank habitats below (Sites A - D; Site G) proved too time consuming for limited-air SCUBA sampling efforts. Instead, the clay substrate was manually probed for mussels, a technique which was able to detect juvenile mussels as small as 10 mm in length.

The mean number of endobenthic mussels/excavated quadrat was calculated for each species at each site. These figures were used to adjust the mean densities of epibenthic specimens to provide an estimate of the combined mean density of endo and epibenthic mussels.

Adaptive Cluster Sampling (ACS; Thompson 1992) was used for selected rare target species (ACS target species)[3] at most sites. ACS is designed to increase sampling efficiency when specimens are rare and patchily distributed (Thompson 1992). This technique entails the sampling of adjacent quadrats to any quadrat where an ACS target species is detected. The process of sampling adjacent quadrats proceeds until no ACS targets are detected in any of the outer quadrats (or edge units) of a quadrat cluster. This results in clusters (or networks) of quadrats where quadrats containing ACS target species are nested within quadrats devoid of ACS target species. A modified Thompson-Horvitz density and variance estimator (Thompson 1992) was calculated via a program specifically written for this purpose (Smith 1995). ACS sampling was not employed at three SCUBA sites (Table 4) where high densities of *Ellipto complanata* substantially hindered sampling efficiency.

For this survey, the sampling of an ACS network was triggered whenever an ACS target species was observed in the initial quadrat either on the surface or in excavated material. The subsequent quadrats sampled in the ACS network around the initial quadrat were not excavated.

ACS target species were chosen for each site via the criterion of not being more abundant than $0.5/m^2$ collectively (David Smith, USGS, personal communication). This criterion is necessary to ensure that ACS quadrat clusters would not become prohibitively large and time consuming. Non-target species (*E. complanata, L. radiata, P. cataracta, S. undulatus*, and *A. undulata*) were not sampled with ACS, regardless of density. Study area target species were identified as ACS target species for a specific site as long as they met the density criteria. CPUE and/or line transect data from the qualitative surveys were used to infer densities to evaluate against this criteria.

Six physiochemical variables crucial to evaluating unionid and zebra mussel habitat (Temperature, conductivity, DO, alkalinity, calcium, pH) were measured at four sites in the study area (two sites above and two sites below Swanton Dam) at a variety of times and flow levels. Samples for DO measurements were obtained before dawn once during low-flow conditions, to establish a lower bound of DO levels.

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[3]Different sets of species were sampled with ACS at different sites. The term "ACS target species" is not to be confused with the set of seven target species that are the focus of this survey.

Table 4: Quantitative methodology used at each site. Densities were calculated by taking the mean of all quadrats at a site when ACS was not used.

Site	ACS	Excavations	Remarks
A	Y	N	clay substrate: problematic excavation
B	Y	N	clay substrate: problematic excavation
C	N	N	clay substrate: problematic excavation. *Elliptio complanata* too abundant to use ACS.
D	Y	N	clay substrate: problematic excavation
E	Y	Y	
F	Y	Y	
G	N	N	clay substrate: problematic excavation. *Elliptio complanata* too abundant to use ACS.
H	Y	Y	
I	Y	Y	
J	Y	Y	No ACS targets found. *Lampsilis ovata* too abundant to be targeted for ACS.
K	Y	Y	*Lampsilis ovata* too abundant to be targeted for ACS.
L	Y	Y	*Lampsilis ovata* too abundant to be targeted for ACS.
M	Y	Y	

RESULTS

Patterns of target species distribution observed in qualitative surveys (Table 2) can be used to partition the river into two distinct reaches - above and below the Swanton Dam. Three target species (*Leptodea fragilis*, *Pyganodon grandis*, and *Potamilus alatus*) were primarily found below the dam, and four (*Lampsilis ovata*, *Anodontoides ferussacianus*, *Ligumia recta*, and *Lasmigona costata* - shells only) were found mostly above the dam. The fauna of these two areas overlapped (Site D, Table 5; Sites 9 and 10, Table 2) in a reach between lake level (5 km downstream of the Swanton Dam) and the Swanton Dam, though all target species were either very rare or observed only as spent shells in this area.

CPUE sampling detected three major species-habitat relationships (Table 6). Habitat association #1 is found in channel areas from the downstream side of the pool at Highgate Dam to 5 km downstream of the Swanton Dam, excluding areas of the large pool just below the Highgate Dam and the backwaters behind the Swanton Dam. This association (Strata 1) was the most heavily sampled in the quantitative surveys (8 sites; Table 5). Target species (primarily *L. ovata* and *A. ferussacianus*) were most abundant at the sites proximate to the complex of islands downstream of Highgate Dam (Fig. 3). Site L, specifically, was the most exceptional.[4] Here, *L. ovata* was too abundant to sample via ACS, but *L. ovata* mean density was 1.2/m^2 (Fig. 3; Table 5). Moreover, this site had relatively high species richness (seven species). Also, a live specimen of *L. recta* was found here during the qualitative surveys (Site 41), and for *A. ferussacianus*, the ACS (Horvitz - Thompson) density estimator was two times larger than the next largest site. Overall, mean densities of target species at quantitative sites sampled in Strata 1 ranged from 0.28 - 1.9. Eleven species were observed in these sites, three of which were live specimens of target species (Table 5).

Target species appear to become less abundant in the mainstem channel between the old railroad bridge near Rt. 7 and Swanton Dam (Fig. 4; Table 5). The sites that were sampled quantitatively (Site E) and qualitatively (Sites 11 - 19) in this area indicate that most of the target species exist in the deeper water (8 -12 feet) near the south bank of the river in a small band where the substrate grades from gravel to cobble/boulder/bedrock.

Little quantitative sampling effort was expended in habitat association #2 (Strata 4), as it hosted only one target species (*A. ferussacianus*). The one site that was sampled quantitatively (Site G) was a productive example of this association, with a mean density of over 140 unionids/ m^2, most of which were *E. complanata*. This habitat has a large

[4]It should be noted that the hydrodynamics of this site may be changing. Water flow is all but cut off from this area by an upstream gravel bar during low flow. Further deposition on this bar may reduce flow at the site, possibly altering the mussel habitat.

Table 5: Quantitative sampling results. At sampling sites where Adaptive Cluster Sampling (ACS; Thompson 1992) was used, figures represent the Horvitz-Thompson ACS density estimator (/m^2) for species targeted for ACS sampling. Mean densities/m^2 (adjusted for endobenthic specimens found in excavations, where applicable) are listed in parentheses following the ACS estimator. At non-ACS sites, adjusted mean densities are listed singularly. Target species listed in bold.

SPECIES	A	B	C	D	E	F	G	H	I	J	K	L	M
Anodontoides ferussacianus				S	1.08(0.44)	0.04(0)^	0.64	0.68(0.16)	0.20(0.05)		0.16(0.	2.2	0.72(0.25)
Lampsilis ovata				s	1.24(0.21)	0.68(0.28		0.68(0.24)	2.20(1.20)	1.44	0.88	1.2	2.20(0.20)
Lasmigona costata						S		s		s	S		
Leptodea fragilis	0.8(0.2)	0.96(0.34)	0.52	0.25(0.06)									
Ligumia recta				s	s	0.04(.01)		L			s	L	
Potamilus alatus	0.08(0)^	0.36(0.10)		s									
Pyganodon grandis	0.41(0.12)	0.80(0.10)	1.00	0.25(0.06)				s					
Alasmidonta undulata						S					L		
Elliptio complanata	17.72	7.16	86.40	52.64	1.98	3.40	139.60	0.20	2.00	2.16	30.00	2.2	2.76
Lampsilis radiata	3.20	2.68	21.20	16.04	0.16	0.12	7.60	0.08	1.80	1.28	2.40	1.2	0.84
Pyganodon cataracta			0.52	0.12			<0.05					L	
Strophitus undulatus												0.4	
Strata #	3	3	3	3	1	1	4	1	1	1	1	1	1
quadrats sampled*	n = 125	n = 184	n = 64	n = 80	n = 96	n = 228	n = 90	n = 144	n = 80	n = 98	n =	n =	n = 80
ACS sampling	Y	Y	N	Y	Y	Y	N	Y	Y	Y	Y	Y	Y
excavations	N	N	N	N	Y	Y	N	Y	Y	Y	Y	Y	Y

s =old spent shells. S= recent spent shells. L = present in qualitative surveys but not found in quadrat sampling

* not accounting for quadrats sampled beyond the initial grid quadrat in ACS networks.

^no specimens found in any of the initial quadrats sampled, but specimen(s) found in subsequent ACS network quadrats whose sampling was triggered by the observation of a different ACS target species in an initial quadrat. Thus the mean density/m^2 is zero while the Horvitz-Thompson estimator is > zero.

distribution in the study area, existing on most riverbanks in silt/clay substrate (excluding inside banks of riverbends, where few animals are found), though many such habitats are not as productive as Site G.

Habitat association #3 (Strata 3) was extensively distributed in the lower study area in river delta habitats. Qualitative surveys suggest that densities of target species (*L. fragilis* in particular) might be greater in riverbank habitats close to the lake, as targets were observed at Sites 1- 4 but not at Sites 5 - 7 (Table 2). Much of the riverbank

Table 6: Major species-habitat associations in the Missisquoi study area. Relationships are cross-referenced with sampling strata from Table 3. Target species are in bold.

Habitat association	General Characteristics	Species
1) run/slow run channel bottom communities: Strata 1 and 2	Slow run/run habitat, Substrate ranges from sand to medium gravel.	***Lampsilis ovata*** ***Anodontoides ferussacianus*** ***Ligumia recta*** ***Lasmigona costata**** ***Pyganodon grandis**** *Elliptio complanata* *Lampsilis radiata* *Strophitus undulatus* *Pyganodon cataracta* *Alasmidonta undulata*
2) Riverbank communities (above Swanton Dam) Strata 3 & 4	Pool conditions on riverbanks. Unionids most abundant on outside banks of bends. Substrate mostly silt and clay with some macrohphytes present.	***Anodontoides ferussacianus*** *Elliptio complanata* *Lampsilis radiata* *Pyganodon cataracta*
3) Riverbank communities (below Swanton Dam) Strata 3 and 4	Riverbanks in delta areas. Numerous snags and macrophytes in some areas. Substrate is silt and clay. Low water visibility under best conditions.	***Leptodea fragilis*** ***Potamilus alatus*** ***Pyganodon grandis*** *Pyganodon cataracta* *Elliptio complanata* *Lampsilis radiata*

* Spent shells only, no live animals.

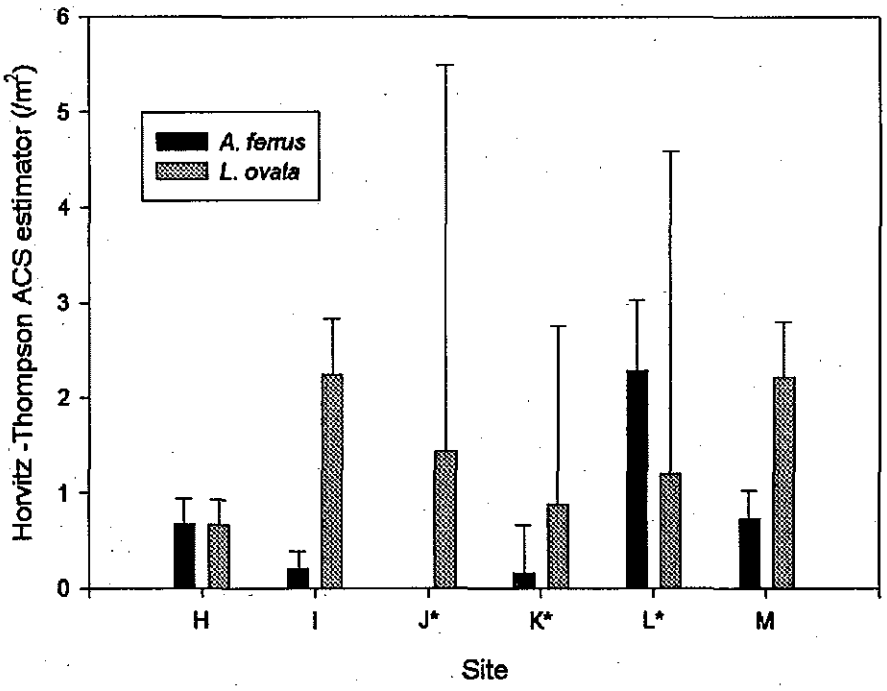


Figure 3: Densities of target species for quantitative sites above Rt. 7. Site letters correspond to Table 4 and Fig. 2c. An asterisk marks sites where *L. ovata* densities were measured with simple random sampling adjusted for the endobenthic animals found in excavations. All other densities were estimated via the Horvitz - Thompson estimator from ACS.

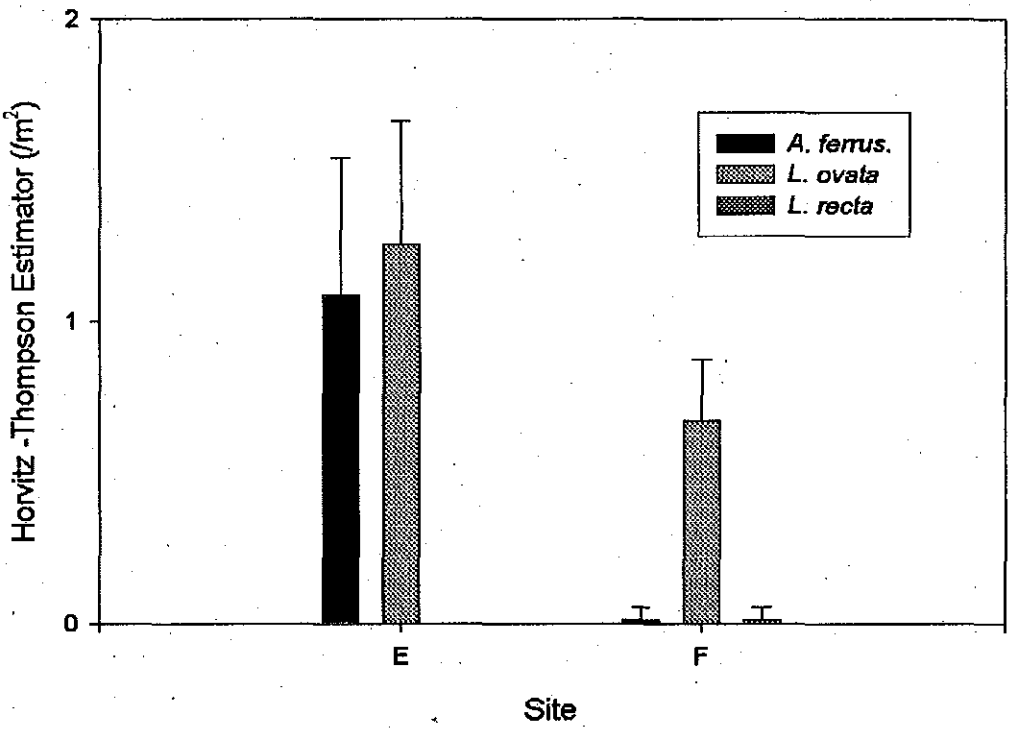


Figure 4: ACS density estimator figures for target species at sites in the vicinity of Rt. 7 upstream of the Swanton Dam. Letters correspond to Table 4 and Fig. 2b. Note that *L. recta* and *A. ferussacianus*were detected only as single specimens at Site F.

habitat in this area is characterized by a profusion of underwater snags. These areas are difficult (and hazardous) to effectively sample via SCUBA or snorkeling, although we did manage to include one such site (Site 1) in this survey. Combined densities of target species at sites sampled in this strata ranged from 0.12 - 1.52, and live specimens of six species were observed, three of which were target species(Table 5).

Much of the lower Missisquoi supported either no mussels at all or sparse numbers of non-target species (*L. radiata and E. complanata*): backwater habitats behind the Swanton Dam (excluding riverbank areas; Strata 4), channel bottom habitats in the river delta area (Strata 4), and areas consisting of loose, unconsolidated sand that are patchily distributed in slow-run areas (Strata 2). It is difficult to estimate the proportion of the channel bottom habitats in slow - run areas that falls into this latter category, given its patchy distribution and inability to be discerned from surface characteristics. However, SCUBA dives conducted during CPUE sampling between Sites 27 and 32 suggest that it comprises approximately 30 - 50% of the channel bottom in slow-run areas.

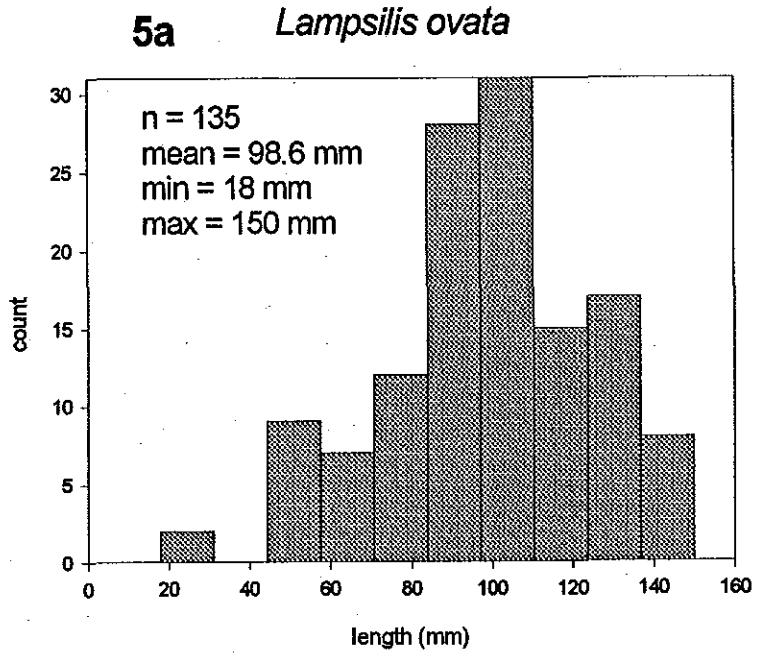
Target Species Distribution

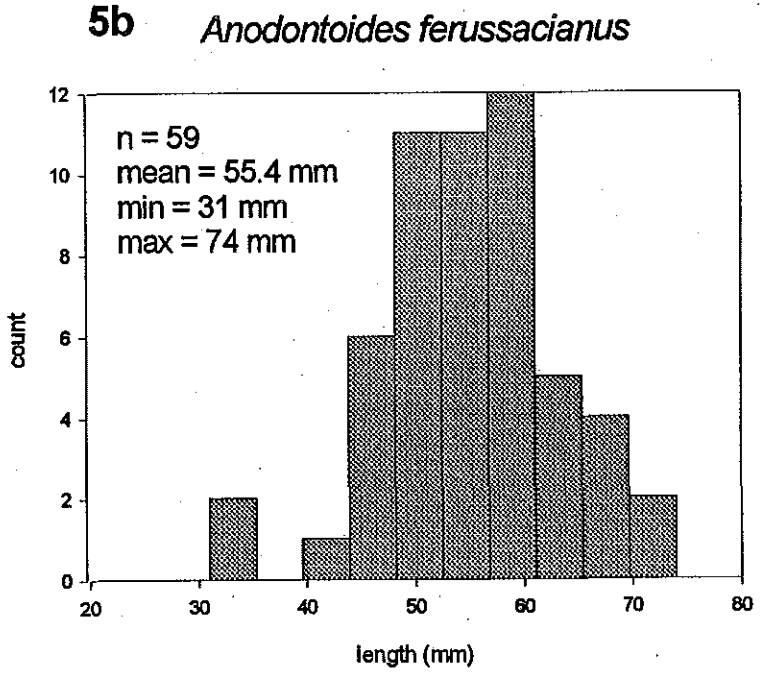
Individual target species had characteristic distributions in the study area as follows:

Lampsilis ovata (pocketbook)

Distribution: Found in slow run/channel bottom habitats above lake level. This was the most abundant target species found at quantitative sampling sites. Sites downstream from the complex of islands near the Highgate Dam (Fig 2c) yielded the highest densities. Also, this species exhibited an exceptionally patchy distribution at Site M in the pool downstream of Highgate Dam, as indicated by the unusually large discrepancy between ACS estimator and simple random sampling density figures in Table 5. Lower densities are found throughout the study area above the river delta area, from riverbend pools (Site 27) to below the Swanton Dam (Sites 8 - 10). Pocketbooks are found in a variety of substrate types, but seem to be most abundant in mixes of gravel/sand. The most abundant target species in the study area, maximum densities have been estimated above $2/m^2$ (Table 5) by ACS sampling.

A few small specimens of this species were sampled in the upper study area (Fig. 5a), and a considerable number of apparently gravid females were observed displaying mantle flaps early in the field season (June and early July). These observations indicate that at least some reproduction and recruitment is occurring in the population. Size distribution approximates normality with a slight positive skew (Fig. 5a), which suggests that the population of this species has had consistent recruitment lately, considering that growth rates (annual increases in length) are likely larger in younger animals than in fully mature specimens.





Figures 5 a & b: Size-frequency histograms for the two most abundant target species at sites above the Swanton Dam (Sites E - M) found in quantitative surveys.

Anodontoides ferussacianus (cylindrical papershell)

Distribution: Found in a variety of habitats above lake level. This species is found in riverbank habitats in low densities mixed among large numbers of *E. complanata* and *L. radiata* (e. g. Site G, Table 5), and appears to be most abundant where these species are most numerous. It also occurs in association with *L. ovata, E. complanata,* and *L. radiata* in channel bottom run - slow run habitats with mixed sand/gravel substrate, being most abundant at Site M (Fig. 3; Table 5). In terms of overall numbers, *A. ferussacianus* may approach *L. ovata* despite its lower densities, considering that it is found in more habitat associations (Table 6) than *L. ovata* and that the riverbank habitat in which it occurs is spatially extensive. No small juvenile animals were found (Fig. 5b), suggesting that either the population has not seen recent recruitment or that juveniles are difficult to find. Shorter life spans associated with small, thin shelled species such as *A. ferussacianus* suggests the latter, as highly sporadic recruitment would likely result in rapid population declines.

Ligumia recta (black sandshell)

Distribution: Shells of this species have been found throughout run/slow run habitats above lake level (upstream of Site D). Only three live specimens (all mature females > 130 mm) have been detected by this survey, although 15 spent shells have been found. Shells were most abundant near the north bank of the channel near the island immediately downstream of the Rt. 7 bridge crossing in 4 - 8 feet of water (low flow; a live specimen was found here at Site F). Shells have also been found in deep slow-run areas (Sites 9,16,17, and 28). Shell sizes ranged between 120 - 155mm.

Lasmigona costata (fluted shell)

Distribution: No live specimens of this species were found, although 16 spent shells were collected. Shells were most abundant in gravel shoal areas of the river (Sites 22,23, and 32), with some being found in deeper channel habitats. All shells were found between the confluence of Hungerford Brook with the mainstem and the backwaters of the Swanton Dam. Also, some appeared fairly recent (crudely estimated at 5 -10 years old via deterioration of the nacre and periostracum), though none were fresh-dead. The status of this species in the Missisquoi is puzzling, as shells have been found in the river since 1997 (Madeleine Lyttle, USFWS, unpublished data), but live specimens have yet to be observed.

Pyganodon grandis (giant floater)

Distribution: Primarily in riverbank habitats in river delta areas, although two shells were found upstream of the Swanton dam in gravel substrate in run/slow run habitats. This species was most abundant at Site C (Fig. 6), which was situated on the outside bank of a riverbend (Fig. 2a). *P. grandis* exhibited evidence of recent recruitment (Fig. 7b), as a small number of

juveniles (10 - 20 mm in length) were observed. The absence of intermediate size classes for this species suggests that recruitment is highly variable, with periods of high recruitment interspersed with periods of low recruitment or total recruitment failure.

Leptodea fragilis (fragile papershell)

Distribution: Primarily in riverbank habitats in river delta areas. It is also found in lesser abundances up to the Swanton Dam above lake level. *L. fragilis* is the most abundant target species in the lake level/delta habitats in the river (Fig. 6; Table 5). It is found in association with other unionids in the lower study area in riverbank habitats, residing in soft silt/clay substrate, often near or among macrophytes. Local densities among shoreline snags are likely greater than those detected by the quantitative surveys: the highest CPUE for this species was found in such an area at Site 1 (Table 2). No specimens were found smaller than 65 mm (Fig.7a), suggesting that successful recruitment has not occurred in this species recently, or that juveniles are cryptic - very difficult to find and/or located in different areas than adults.

Potamilus alatus (pink heelsplitter)

Distribution: This species is found in association with *L. fragilis* and *P. grandis* in riverbank habitats in the river delta area. It was not detected at all in qualitative surveys, probably because of its relative scarcity (Fig. 6; Table 5). Only the two sites closest to lake Champlain yielded live specimens (Sites A and B). Two spent shells were found at a third site (Site D). This species appears to exist primarily in areas close to the lake with populations consisting of scattered individuals. Only seven live mature specimens (90 - 160 mm in length) were found, too few to infer the age structure of the population.

Water Chemistry

Results of physiochemical sampling is presented in Table 7. Chemical variables measured in the Missisquoi suggests that the river is relatively calcium poor (13.5 - 15.6 mg/l; Table 7) and of low alkalinity. pH levels were correspondingly low, between 7.1 and 7.6. Alkalinity ranged between 30 and 50.9 mg $CaCO_3$/l, with three aberrant readings of 113 - 125 mg/l recorded on September 16. Dissolved oxygen (DO) levels ranged from 6.7 - 7.95 mg/l (81 - 96% saturation) during an early morning low flow period, during which the maximum temperature of 25° C was recorded, and 7.5 - 8.1 mg/l (81 -91% saturation) during a high flow event.

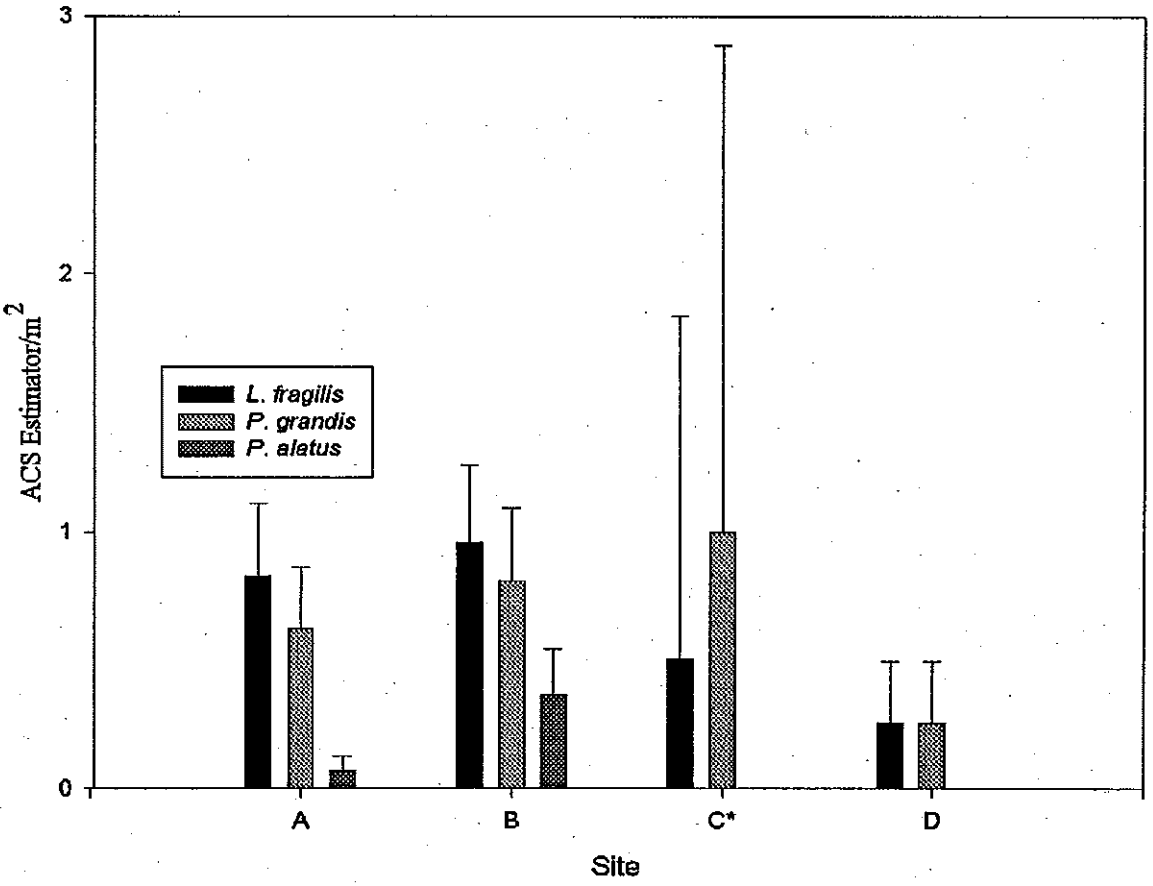
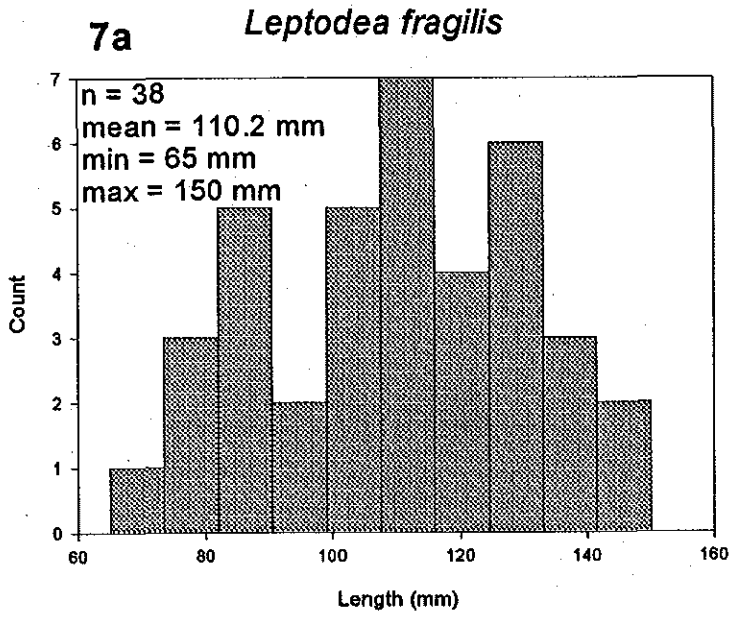
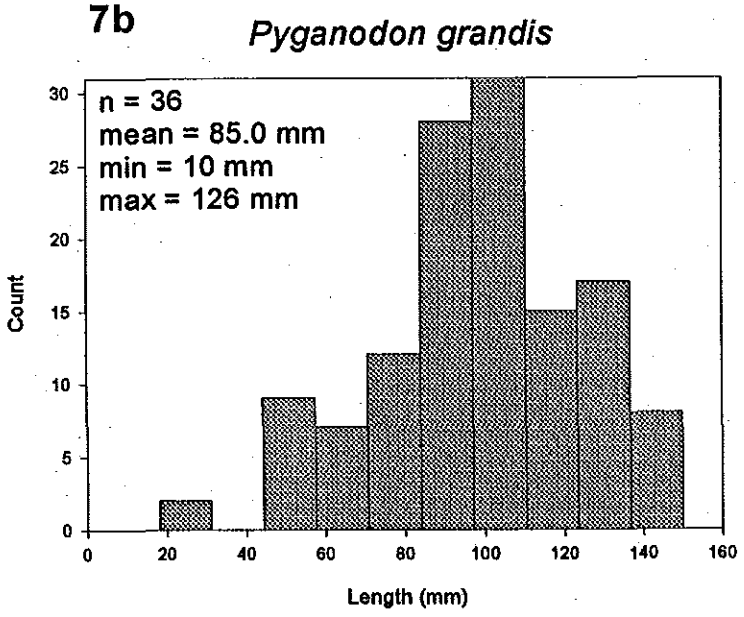


Fig. 6. Horvitz - Thompson ACS density estimators for target species at all quantitative sites below Swanton Dam. Sites A, B, and C are in river delta habitats. Asterisk at site C denotes that densities are derived from simple random sampling instead of ACS sampling. Letters correspond to Table 4 and Fig. 2a.





Figures 7a & b: Size-frequency histograms for the two most abundant target species at sites A - D (below Swantron Dam) found in quantitative surveys.

Table 7: Water chemistry variables in the study area. ("Lower" site is near Site C; "Rt. 7" is at the Rt. 7 overpass; "Dam" is just below the Swanton Dam; and "Upper" is adjacent to Site 26.) DO readings taken before sunrise.

SITE	Date	TEMP	pH	COND (umhos/cm)	ALK (mg/l)	DO (mg/l); % saturation	CA (mg/l)	discharge*	exceedance prcnt.^
Lower	7-24	23			38.5			500	3
	8-6	25	7.21		44.8	7.95(96%)		120	1
	8-12	23	7.49		46.8			630	3
	8-13	21	7.49		40	7.5(84%)		700	3
	9-9	19	7.56	146			15.6	360	2
	9-16	18	7.12	37.3	115		12.2	330	2
Dam	8-6	25	7.42		43.2	7.2(87%)		120	1
	8-13	21	7.28		32.3	8.1(91%)		700	3
	9-9	19	7.66	147			16	360	2
	9-16	17	7.38	138	43.6		15.3	330	2
Rt. 7	7-24	23			36.1			500	3
	8-6	25	7.28		43.9	7.5(91%)		120	1
	8-12	23	7.63		50.9			630	3
	8-13	20.5	7.42		30	7.9(81%)		700	3
	9-9	19	7.5	131			14.5	360	2
	9-16	17	7.54	43.4	125		13.8	330	2
Upper	8-6	25	7.1		43.8	6.7(81%)		120	1
	8-13	21	7.15		29.2	8.1(91%)		700	3
	9-9	19	7.33	127			13.5	360	2
	9-16	18	7.39	38.8	113		12.3	330	2

* provisional USGS flow data in cfs at East Berkshire, VT gauge site.

^ flow exceedance percentile based monthly mean data for water years 1915 - 1923; 1929 - 1997:

1 = 1% - 25%; 2 = 26% - 50%; 3 = 51% - 75%; 4 = 76% - 100%

DISCUSSION

Results from this survey indicate that at least five of the seven target species have considerable populations in the study area. Four of these species (*L. ovata, A. ferussacianus, L. fragilis,* and *P. grandis*) are abundant enough to reasonably assume that their populations are reproductively viable. Moreover, size frequency data suggest that reproduction is occurring in at least two species (*L. ovata* and *P. grandis*).

Historical records suggest that both *Lasmigona costata* and *Ligumia recta* have always been rare in the Champlain basin, and the results from this study confirm the present scarcity of these animals in the Missisquoi. While the failure to detect live specimens of *L. costata* is puzzling, conclusions of extirpation are premature. Spent shells were of comparable abundance (16) to those of *L. recta* (15). Some of the shells that were detected were recent enough to conclude that live fluted shells were present in the Missisquoi in the recent past. It is possible that this species still exists in the river at densities below detection thresholds. This is the first published record of *L. costata* from the Missisquoi, as shells were not found in the river until 1997 (Madeleine Lyttle, USFWS, unpublished data).

Fichtel and Smith (1995) describe *L. recta* as never being common in the Champlain Basin. Given that only three live specimens were found despite a considerable amount of underwater search time spent during qualitative sampling (28 person-hours), the scarcity of this species may raise questions as to its reproductive viability in the Missisquoi River. However, *L. recta* may have been persisting in the Champlain Basin over the past few decades despite low densities, considering that historical records are so sparse. Records of *L. recta* in the Missisquoi are scarce, consisting of observations of spent valves by Smith (1985) in the late '70's (Mark Ferguson, personal communication) and of a live specimen in 1997 (Madeleine Lyttle, unpublished data). Populations of both these rare species may be biologically valuable in an evolutionary sense insofar that they represent genetic stock that exists at the edge of their respective ranges.

Potamilus alatus is the least abundant target species of the three that are found in the river delta area. Only seven mature specimens were found during this survey at two sites (Sites A and B). Two spent shells were found at Site D. Though it is difficult to determine whether the riverine populations of this species are self-sustaining or not, it appears that a small population exists in riverbank habitats in the delta area.

It is tempting to use the habitat data gathered in the quantitative surveys to create generalizations about species habitat preferences. However, previous attempts to predict unionid densities from quantified habitat variables such as water depth, substrate granulometry, substrate roughness, etc. (Strayer and Ralley 1993) have been unsuccessful. Strayer and Ralley (1993) suggested that the most important factor in explaining unionid variation is water velocity, with largest densities found at intermediate velocities. Moreover, there is some indication that for at least some systems, substrate stability during high discharge events may be an important factor in explaining mussel abundance (Strayer 1998).

Observations from the Missisquoi River suggests that water velocity explains density patterns for some of the target species: for example, *L. ovata* seems to be most abundant where velocities appear to be greatest (though for *E. complanata,* densities seem to be highest at low-velocity sites along riverbanks). Velocities (exclusive of the falls below the Swanton Dam) were greatest in the areas around Sites 40, 41 (L), and 31. In the lower study area, this relationship does not apply since the target species found in these areas are adapted to lentic habitats.

Refugium Potential from Zebra Mussel Impacts

The Missisquoi River clearly harbors one of the most exceptional freshwater mussel communities in the Champlain Basin for the four most abundant target species. In this sense, both sections of the study area (below and above the Swanton Dam) may be considered crucial habitat for the persistence of these species in the Champlain Basin. Moreover, the river represents crucial habitat for the less abundant target species (*L. recta*, *L. costata*, and *P. alatus*), as there are only a few other rivers in the basin where these species are known to exist (e.g. Poultney River).

The section of the river above Swanton Dam (especially above Rt. 7) contains areas where the abundance of target animals and overall unionid diversity are outstanding in the Champlain Basin. Moreover, one of the most abundant target species in this section (*L. ovata)* is also known from Lake Champlain, where they will likely disappear due to zebra mussel impacts. Moreover, the Missisquoi is the only known viable population of *A. ferussacianus* in Vermont, further enhancing the importance of the river to Vermont's mussel fauna. Also, the river delta habitats below Swanton Dam may be a suitable refugium for the three target species being impacted by zebra mussels in Lake Champlain (*Pyganodon grandis*, *Leptodea fragilis*, and *Potamilus alatus*). For at least two of these species (*L. fragilis* and *P. grandis*), populations subjectively appear large enough to be viable independent of lake populations.

Given that zebra mussels will likely be introduced into the river by recreational boats moving either upriver from Lake Champlain or over land via public access sites, mussels in the Missisquoi will be insulated from the effects of zebra mussel invasion to the extent that the river is either unable to become colonized by zebra mussels or unable to support high-density zebra mussel populations. There are two main considerations in evaluating the susceptibility of the Missisquoi to such colonization: 1) Are key water chemistry variables sufficient to support dense zebra mussel populations in the river? 2) Are fluvial habitat characteristics in the study area amenable to zebra mussel colonization?

Of all the water chemistry variables measured in the Missisquoi (Table 7), calcium is the most definitive indicator of the river's susceptibility to invasion. Hinks and Mackie (1997) reported that the minimum calcium levels needed to support the growth of *Dreissena* veligers is 20 mg/l, and Mellina and Rasmussen (1994) reported that zebra mussels do not develop dense populations below 21 mg Ca^{2+}/l. In Europe, Ramacharan *et al.* (1992)

indicated that zebra mussels were absent from all lakes with concentrations below 28.3 mg Ca^{2+}/l. Calcuim levels (Table 7) in the Missisquoi are clearly lower than the thresholds reported by these authors. Moreover, cumulative results from water quality sampling at the Swanton Dam between 1992 and 1996 reports a mean calcium concentration of 9.2 mg/l, with a range between 5.4 and 15.3 (Vermont DEC 1998). Thus even if zebra mussels are transported up river by boat or overland via public access, and manage to establish breeding populations in the river, low calcium will likely inhibit the development of dense populations of zebra mussels.

pH levels appear to be slightly better for zebra mussels in the Misissquoi River. pH values ranged from 7.1 - 7.7 in 1998, while in 1998, *Dreissena* pH thresholds have been reported as follows: 7.4 for growth (Neary and Leach 1991), 7.4 for veliger development and 6.5 for adult growth (McMahon 1996), and 7.3 for existence in European Lakes (Ramcharan *et al.* 1992).

Even if zebra mussels manage to colonize and produce large numbers of veliger larvae in the Missisquoi despite the low calcium levels, it still appears improbable that they will be able to substantially impact Missisquoi unionids on account of the unsuitability of *Dreissena*'s life cycle to fluvial habitats: The dispersal dynamics of the free-swimming veliger stage of the zebra mussel's life-cycle limits the range of its natural dispersal potential to areas accessible to veliger propagules that drift in the direction of prevailing water currents. In rivers, these areas are primarily limited to reaches downstream of spawning zebra mussels. The duration of this life cycle stage (5 days - 7 weeks; Ackerman, *et al.* 1994) makes the development of large self-sustaining populations in river habitats unlikely, in the sense that the veliger progeny of colonizing zebra mussels will be flushed far downstream, and thus will not be able to sustain and replace the original colonizing population. On account of this life history characteristic, large scale invasions seem unlikely to be initiated from limited and widely dispersed introductions into a river.

In systems with sufficient calcium, other studies have noted that a necessary condition for zebra mussels to colonize rivers and streams is the presence of large spawning populations in upstream lakes (Horvath *et al.* 1997). Moreover, the severity of river colonization from these sources rapidly diminishes immediately downstream from the source population in an infested lake or impoundment (Marangelo 1997; Horvath *et al.* 1997; Hunter and Janech 1997).

Thus if zebra mussels pose any threat to the Missisquoi River, it comes from the possibility that the impoundment behind the Highgate Dam becomes infested with zebra mussels and that the invading population is able to overcome low calcium levels and successfully reproduce on a large scale in the backwaters behind the dam[5]. Under this scenario, unionid impacts from fluvial colonization patterns observed by Marangelo (1997)

[5] The Swanton Dam and its backwaters appears too low/small to provide sufficient semi-lentic habitats needed to facilitate large scale zebra mussel colonization.

and Hunter and Janech (1997) suggests that impacts on unionids will be limited to the area immediately downstream of the dam itself, which excludes the lower portion of the study area harboring rare species. Though intense zebra mussel colonization has been observed in large rivers (Stoeckel *et al.* 1997; Ricciardi *et al.* 1996; Tucker 1994; Strayer and Smith, 1998) it should be noted that veliger dispersal dynamics in the systems treated by these authors (Illinois River, St. Lawrence River, Mississippi River, and Hudson River, respectively) are likely to differ from the Missisquoi on account of the effects of factors that are absent from the Missisquoi River: semi-lentic pools created by locks and other navigational channel alterations (Mississippi, St. Lawrence), active transport of large numbers of adult zebra mussels by commercial barge/ship traffic (Mississippi, St. Lawrence, Illinois, Hudson), the movement of large numbers of zebra mussel veligers downstream out of an upstream source (Lake Michigan into the Illinois River) and/or upstream freshwater tidal surges (Hudson River).

However, zebra mussels may still pose a threat to unionids, even if they are unable to attain high population densities in the Missisquoi. Little is known about the long-term effects of chronic low-level zebra mussel fouling of unionids (Marangelo 1997). In this sense, even a marginally successful invasion of the Missisquoi might pose a long-term threats to unionids if low-level fouling proves to be deleterious to native mussel populations. Thus it would be prudent to take measures to minimize the potential for zebra mussels to be transported into the Missisquoi, such as targeting likely dispersal vectors (the movement of *Dreissena*-contaminated recreational boats) with mitigative strategies such as anti-dispersal boater advisories. There are presently five public boat access sites in the Missisquoi between Highgate and Lake Champlain (two above three below the Swanton Dam), but only the one at the Missisquoi National Wildlife Refuge is developed, easily accessible, and receives intensive use. At present there is no heavily used boat access above the Swanton Dam, and zebra mussels are unlikely to be introduced into the river in this area.

It seems likely that the habitat characteristics of the lower Missisquoi will offer unionids a large degree of protection against severe zebra mussel invasion. This characteristic makes it a secure refugium for the regionally rare mussel species that occur in the river.

Also, the lower Missisquoi should be considered a desirable recipient site for efforts to transplant lake-dwelling specimens of targeted mussel species that are likely to succumb to zebra mussel impacts. Such relocations should focus on placing animals in habitats where conspecifics are most abundant.[6] This recommendation for relocation is made on the assumption that issues pertaining to the effects mixing of genetic stock of lake and river

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[6]It might be argued that habitats close to Lake Champlain are not desirable relocation sites, as they might be susceptible to some upstream veliger intrusion into the Missisquoi from the lake during periods when the lake level and river discharge are low. However, this is likely to be minimal on account of suppressive effects of low calcium on zebra mussels in Missisquoi Bay (14.2 mg/l; Eliopoulos and Stengel 1998), even though some localized reproduction appears to be occurring in the northeast region of Lake Champlain that has calcium levels below published reproductive thresholds (Eliopoulos and Stengel 1998; see earlier discussion on calcium and *Dreissena* growth/reproduction).

unionid populations and possibly transferring animals between river basins (i.e., from the Winooski delta to the Missisquoi River) are resolved to the satisfaction of all parties involved. Treatment of this issue is beyond the scope of this report.

Recommendations for Population Monitoring

Data collected from this study provides a substantial baseline from which unionid populations in the Missisquoi can be monitored. However there are some difficulties that arise when developing recommendations for an efficient yet effective sampling regime for population monitoring. Foremost among these is the lack of information pertaining to the natural temporal variability of unionid populations. The most critical parameter in determining the power of a proposed monitoring program to detect significant changes in a population is an *a priori* measure of the temporal variance in mean counts that occurs at a given site over a number of sampling episodes (Gibbs 1995; Gibbs 1998). Without this information, it is difficult to statistically distinguish between variation from repeated sampling at the same location and actual population trends.

Considering this caveat, a recommendation for a monitoring program sampling regime is given here based on power calculations from MONITOR4 (Gibbs 1995), which is software that estimates the power of population monitoring sampling regimes to detect animal abundance trends by generating multiple simulated sets (500 replications in this case) of count data based on a user defined sampling program and sample counts drawn at random from distributions defined by the user (Gibbs 1995). For these simulations (Figs. 7 A - D), a crucial part of the user-defined sampling program is the temporal sampling variance which was arbitrarily set at 0.5 of the mean density at a given site. Also, the level of significance for trend detection was set at $\alpha = 0.2$ (set to minimize the probability of generating a false negative result, which is generally appropriate when evaluating population trends in rare animals of conservation interest). Simulations were run for a period of 15 years with sampling intervals of once every 2, 3, 4, and 5 years for animals at densities that correspond to the simple random sampling densities of *Lampsilis ovata* (adjusted for endobenthic animals, Table 5) and *Leptodea fragilis*. Population simulations were run at two and three sites for each species (a total of 4 - 6 sites in the study area).

Given the importance of the temporal variance coefficient (CV) in the power calculations, space needs to be devoted discussing the rationale behind its estimated value for mussels. The CV is a measure of both the inherent variability of the sampling method at the same site over time and of the natural variation in populations (Gibbs *et al.* 1998). For unionids, there is little information pertaining to the latter type of variation, so a caveat associated with the results of the proposed monitoring regime is that any trends detected may be a result of "natural" population variation.

Given that the initial counts used in the MONITOR4 population simulations were from sites (Sites A, B, C, I, L, and K) with means of a set of at least 80 subsamples (number of quadrats/site), it is assumed that the variance that would result from the differential placement of quadrats within a site over successive sampling occasions would not be especially large, considering that unionids are not especially motile. Smaller sampling regimes (less quadrats/site) would certainly increase this variance and increase the CV, reducing the power of the monitoring program.

Gibbs *et al.* (1998) provides a table of CV's for a wide variety of animals and herbaceous plants culled from the literature. This table suggests that there is an inverse relationship between motility and the magnitude of the CV. All the animal species on this list (birds, bats, frogs, snakes, caddisflies, spiders, etc.) are considerably more motile than mussels and have mean CV's that range from 0.3 to 1.3 of mean counts (except for large mammals, which have a mean CV of 0.14). Conversely, non-motile annual herbaceous plants have mean CV's of about 0.22. Mussels are generally relatively stationary and long-lived compared to many of these organisms, attributes that likely minimize the components of the CV attributable to sampling methodology and "natural" population variation. These characteristics imply that the actual CV for mussels would be on the lowest end of the range of CV's in Gibbs *et al. 's* (1998) table. Thus the CV estimate used in this study (0.5 of mean density) is a conservative one the sense that it probably an overestimate of the actual temporal variance, thus minimizing the possibility that the power calculations generated by MONITOR4 are overestimated[7].

Simulation results suggest that re-sampling two sites did not provide enough power to adequately detect positive or negative population trends of less than 10% for either species (Figs. 8c; 8d) at any of the simulated sampling intervals when compared to a power threshold of 0.85. The power to detect positive and negative trends increased when three sites were re-sampled (Figs. 8a, 8b). Power estimates approached 0.85 for sampling intervals of 2 and 3 years for detecting increasing and decreasing trends of 10%, although stochastic re-sampling effects may have resulted in the lower power for the three year re-sampling trends evident in Fig. 8a. Thus for *L. ovata* and L. *fragilis*, three sites each would need to be re-sampled every two or three years to provide data likely to detect significant trends of at least 10% over a fifteen year period.

Note that power to detect trends will decrease with decreasing abundance of target animals. For the Missisquoi, only *P. grandis* is of comparable abundance to *L. ovata* and *L. fragilis* to be monitored with sufficient probability of detecting population trends, given the simulation environment input into MONITOR4. For the other less abundant target species, populations changes can most effectively be evaluated within a context of observed trends of other mussel taxa in the river, changes in water quality variables, or changes/alterations in habitat.

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[7]Overestimating the actual CV results in underestimating trend detection power and vice versa.

Also, continued monitoring of Missisquoi target species can address several interesting questions: the degree of variability of species with exceedingly low population densities such as *L. recta*; can a species persist in a river despite a population trajectory that might have temporarily carried it below the detection threshold for an intensive unionid survey (*L. costata*); are river populations of species that have substantial population segments in Lake Champlain population sinks, or are they self-sustaining (if the latter, *L. fragilis*, *P. grandis*, and *P. alatus* should persist in the Missisquoi despite *Dreissena*-induced extirpation of conspecifics in Lake Champlain)? Also, with repeated sampling, information can be gathered on the "natural" variation of populations of target species, data that can be used to refine the sampling design of population monitoring efforts in the Missisquoi as well as provide data that may be of use for other unionid monitoring efforts.

In the area above Swanton Dam, Sites L, I, and J would be appropriate Long Term Monitoring (LTM) sites. Site L exhibited the largest abundance of target animals, and a live specimen of *L. recta* was found in this area at Site 41. Site J probably has the highest density of *L. ovata* of any site in the study area when quadrat mean densities (exclusive of ACS densities) are compared (*L. ovata* was too abundant to be sampled via ACS at this site).

In the lower study area, Sites A, B, and C (see appendix maps) are the suggested LTM sites. Two of these (A and B) host all three target species in the river delta habitats. Excavations are unnecessary in these areas, as the substrate is soft enough to detect small animals by feel with bare fingers. ACS sampling should be avoided, as *E. complanata* is too abundant at Site C to employ this method. Conversely, ACS could be used in the upper study area as long as the target species do not get too abundant to use this method (collectively > $0.5/m^2$).

During re-sampling, care should be taken to deploy quadrats in the same area on a consistent basis for each site visit (see site maps in appendix), as densities vary within each of these sites in accordance with substrate. In future sampling, quadrats should continue to be excavated at sites above the Swanton Dam, and target animals should continue to be measured to ensure data comparability.

Eighty quadrats should be sampled at each site (except at Site C, where the abundance of *Elliptios* will impede efficiency - 64 were sampled in 1998), which was the lowest maximum that could be sampled at the suggested monitoring sites in a given day in this survey. Hence the field commitment for this suggested sampling regime is 6 days of sampling every 2 - 3 years.

Fig. 8a

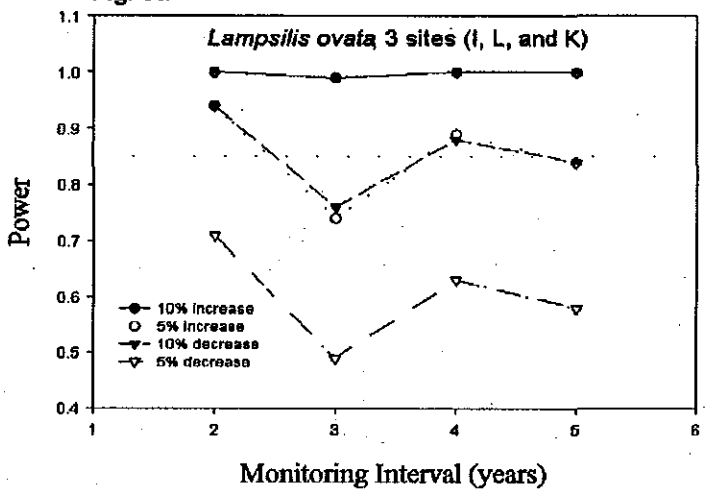
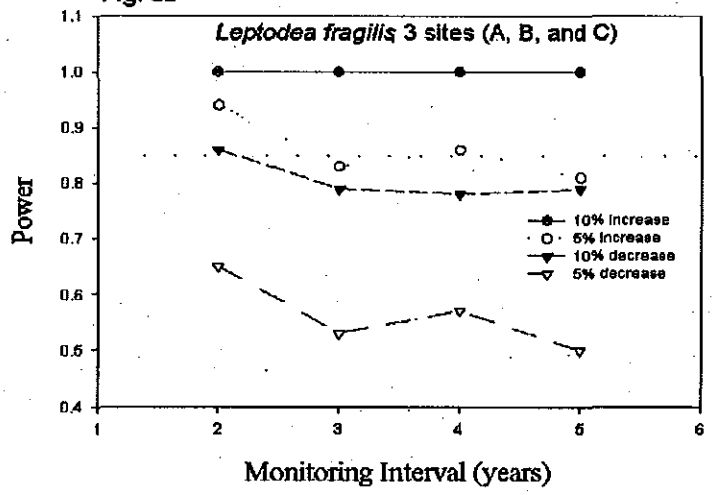


Fig. 8b



Figures 8 a - d: Power to detect 10% and 5% annual population changes over 15 years for two target species using 500 simulations with MONITOR4 (Gibbs 1995) software. Initial plot counts = mean simple random sampling density (adjusted for endobenthic animals), a = 0.2, assumed temporal population variance = 0.5 of mean density for repeated samplings made at the same sites over time; trends per site weighted equally. Dotted line represents suggested power threshold of 0.85.

Fig. 8c

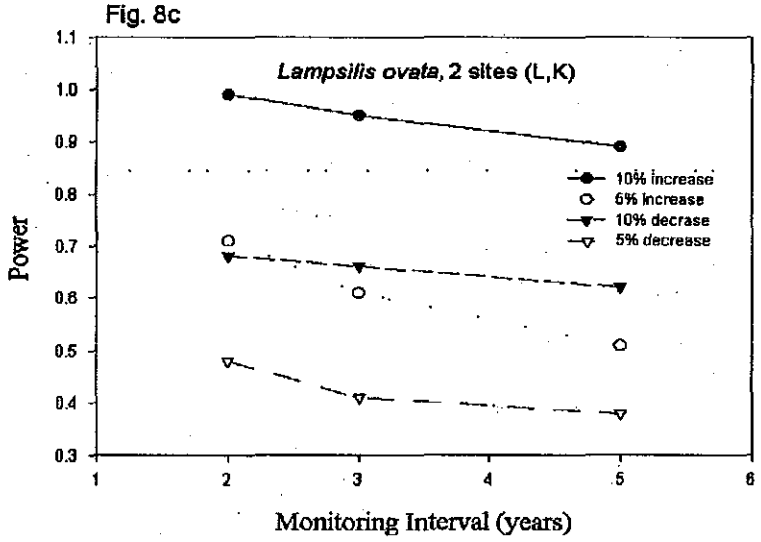
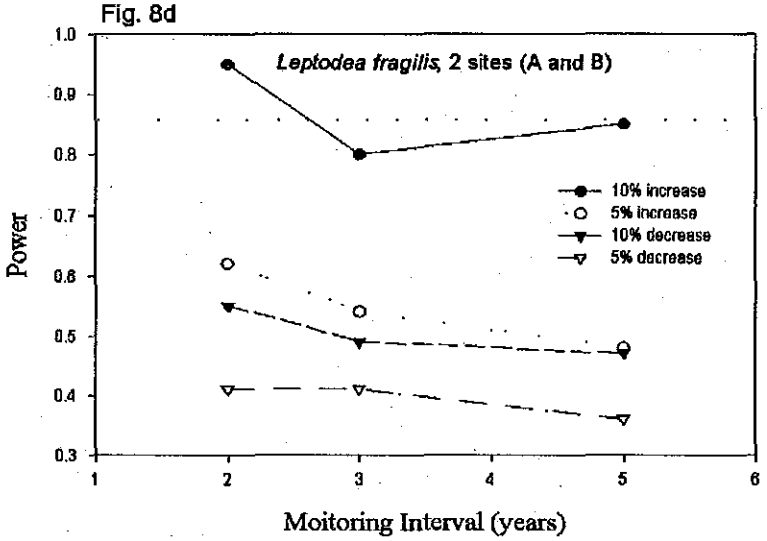

Lampsilis ovata, 2 sites (L,K)
10% increase
6% increase
10% decrase
5% decrease
Power
Monitoring Interval (years)

Fig. 8d


Leptodea fragilis, 2 sites (A and B)
10% increase
5% increase
10% decrease
5% decrease
Power
Moitoring Interval (years)

Literature Cited

Ackerman, J. D, Sim, B., Nichols, S. J., Claudi, R. 1994. A review of the early life history of zebra mussels (*Dreissena polymorpha)*: comparisons with marine bivalves. *Canadian Journal of Zoology,* 72: 1169-1179

Fichtel, C. and Smith, D. 1995. The freshwater mussels of Vermont. Nongame & Natural heritage Program, Vermont Fish and Wildlife Department, Technical report 18. 54 pp.

Gibbs, J. P. 1995. MONITOR Users Manual. Via USGS/NBS Biological Monitoring Website.

Gibbs, J. P., S. Droege, and P. Eagle. 1998. Monitoring populations of plants and animals. *BioScience* 48(11): 935-940.

Hincks, S. S. and Mackie, G. L. 1997. Effects of pH, calcium, alkalinity, hardness, and chlorophyll on the survival, growth, and reproductive success of zebra mussel (*Dreissena polymorpha*) in Ontario Lakes. *Canadian Journal of Fisheries and Aquatic Sciences* (54): 2049-2057

Horvath, G., Lamberti, G., Lodge, D., and Perry, W. 1996. Zebra mussel dispersal in lake-stream systems: source-sink dynamics? *Journal of the North American Benthological Society,* 15(4):564-575

Hunter, R. D. and Janech, M. 1997. Zebra Mussels in a small river: impact on unionids. in Zebra Mussels and Aquatic Nuisance Species, Proceedings of the Sixth International Zebra Mussel and Other Aquatic Nuisance Species Conference , March 1996. D'Itri, F. *ed.* Ann Arbor Press, Chelsa, MI

Marangelo, P. 1997. The zebra mussel (*Dreissena polymorpha,* Pallas) invasion of two rivers in southeast Michigan: Interactions with unionid bivalves and patterns of riverine dispersal and colonization. MS Thesis, University of Michigan, 72 pp.

McMahon, R. F. 1996. The physiological ecology of the zebra mussel. *Dreissena polymorpha,* in North America and Europe. *American Zoologist* 36:339-363

Mellina, E. and Rasmussen, J. B. 1994. Patterns in the distribution and abundance of Zebra Mussel (*Dreissena polymorpha*) in rivers and lakes in relation to substrate and other physiochemical factors. *Canadian Journal of Fisheries and Aquatic Sciences* 51: 1024-1036

Neary, B. P. & Leach, J. H. 1991. Mapping the potential spread of the zebra mussel (*Dreissena polymorpha*) in Ontario. *Canadian Journal of Fisheries and Aquatic Sciences* 49:406-415

Ramcharan, C. W., Padilla, D. K., and Dodson, S. I. 1992. Models to predict potential occurrence and density of the zebra mussel , *Dreissena polymorpha. Canadian Journal of Fisheries and Aquatic Sciences* (49):2611-2620

Ricciardi, A., Whoriskey, F. G., & Rasmussen, J. B. 1996. Impact of the *Dreissena* invasion on native unionid bivalves in the upper St. Lawrence River. *Canadian Journal of Fisheries and Aquatic Sciences*, 54(3) 512-519

Smith, D. R., Villella, R. F., Lemarie, D. P., & Weller, D. A. 1996. Cacapon River Mussel Survey. Poster from "The Conservation and Management of Freshwater Mussels II", St. Loius, MO, October 1995. Displayed at http:/www/lsc/nbs.gov/ael/POSTERS/cacapon/crmsfram.htm

Smith, D. R. 1995. Adaptive Sampling Computation Program. Unpublished. USGS, Aquatic Ecology Laboratory, Leetown, WV.

Smith, D. G. 1985. A study of the distribution of freshwater mussels (Mollusca: Pelecypoda: Unionida) of the Lake Champlain Drainage in Northwestern New England. *The American Midland Naturalist* (114):19-29

Eliopoulos and Stengel 1998. Lake Champlain 1997 Zebra Mussel Monitoring Program. Final Report. Vermont Department of Environmental Conservation

Stoeckel, J., Schneider, D., Soeken, L., Blodgett, D., and Sparks, R. 1997. Larval dynamics of a riverine metapopulation: implications for zebra mussel recruitment, dispersal, and control in a large river system. *Journal of the North American Benthological Society,* 16(3):586-601

Strayer, D. and Ralley, J. 1993. Microhabitat use by an assemblage of stream-dwelling unionaceans (Bivalvia), including two rare species of *Alasmidonta. Journal of the North American Benthological Society,* 12(3):247-258

Strayer D. 1998. The use of flow refugium by unionids. Abstract from the New York Natural History Conference, Albany, NY. October 1998.

Strayer, D. and Smith, L. 1996. Relationships between zebra mussels (*Dreissena polymorpha*) and unionid clams during the early stages of zebra mussel invasion of the Hudson River. *Freshwater Biology* 36: 771-779

Thompson, S. K. 1992. Sampling. Wiley, New York.

Tucker, J. K. 1994. Colonization of unionid bivalves by the zebra mussel, *Dreissena polymorpha*, in pool 26 of the Mississippi River. *Journal of Freshwater Ecology.* 9: 129-134

Vermont Department of Environmental Conservation, 1998. Long term water quality and biological monitoring project for Lake Champlain, cumulative report for project years 1992-1996. Lake Champlain Basin Program, Technical Report No. 26. 34 pp.

Mellina, E. and Rasmussen, J. B. 1994. Patterns in the distribution and abundance of Zebra Mussel (*Dreissena polymorpha*) in rivers and lakes in relation to substrate and other physiochemical factors. *Canadian Journal of Fisheries and Aquatic Sciences* 51: 1024-1036

Neary, B. P. & Leach, J. H. 1991. Mapping the potential spread of the zebra mussel (*Dreissena polymorpha*) in Ontario. *Canadian Journal of Fisheries and Aquatic Sciences* 49:406-415

Ramcharan, C. W., Padilla, D. K., and Dodson, S. I. 1992. Models to predict potential occurrence and density of the zebra mussel , *Dreissena polymorpha. Canadian Journal of Fisheries and Aquatic Sciences* (49):2611-2620

Ricciardi, A., Whoriskey, F. G., & Rasmussen, J. B. 1996. Impact of the *Dreissena* invasion on native unionid bivalves in the upper St. Lawrence River. *Canadian Journal of Fisheries and Aquatic Sciences,* 54(3) 512-519

Smith, D. R., Villella, R. F., Lemarie, D. P., & Weller, D. A. 1996. Cacapon River Mussel Survey. Poster from "The Conservation and Management of Freshwater Mussels II", St. Loius, MO, October 1995. Displayed at http:/www/lsc/nbs.gov/ael/POSTERS/cacapon/crmsfram.htm

Smith, D. R. 1995. Adaptive Sampling Computation Program. Unpublished. USGS, Aquatic Ecology Laboratory, Leetown, WV.

Smith, D. G. 1985. A study of the distribution of freshwater mussels (Mollusca: Pelecypoda: Unionida) of the Lake Champlain Drainage in Northwestern New England. *The American Midland Naturalist* (114):19-29

Eliopoulos and Stengel 1998. Lake Champlain 1997 Zebra Mussel Monitoring Program. Final Report. Vermont Department of Environmental Conservation

Stoeckel, J., Schneider, D., Soeken, L., Blodgett, D., and Sparks, R. 1997. Larval dynamics of a riverine metapopulation: implications for zebra mussel recruitment, dispersal, and control in a large river system. *Journal of the North American Benthological Society,* 16(3):586-601

Strayer, D. and Ralley, J. 1993. Microhabitat use by an assemblage of stream-dwelling unionaceans (Bivalvia), including two rare species of *Alasmidonta. Journal of the North American Benthological Society,* 12(3):247-258

Strayer D. 1998. The use of flow refugium by unionids. Abstract from the New York Natural History Conference, Albany, NY. October 1998.

Strayer, D. and Smith, L. 1996. Relationships between zebra mussels (*Dreissena polymorpha*) and unionid clams during the early stages of zebra mussel invasion of the Hudson River. *Freshwater Biology* 36: 771-779

Thompson, S. K. 1992. Sampling. Wiley, New York.

Tucker, J. K. 1994. Colonization of unionid bivalves by the zebra mussel, *Dreissena polymorpha*, in pool 26 of the Mississippi River. *Journal of Freshwater Ecology.* 9: 129-134

Vermont Department of Environmental Conservation, 1998. Long term water quality and biological monitoring project for Lake Champlain, cumulative report for project years 1992-1996. Lake Champlain Basin Program, Technical Report No. 26. 34 pp.