GREAT LAKES FISHERY COMMISSION
Research Completion Report *

ESTIMATING LARVAL POPULATION DENSITIES OF LANDLOCKED SEA LAMPREY

by

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ABSTRACT

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Larval sea lamprey (*Petromyzon marinus* Linnæus) population estimates were derived for five Lake Ontario (Canada) tributaries by electrofishing in eight sites (range 5.85 to 389 m^2) per stream and by surveying the streams as to habitat distributions and surface area (range 2.57 to 26.2 ha; average 11.0 ha). Observed densities were as high as 7.00 larvæ $\cdot$ m^{-2}, but averaged 0.210 ± 0.802 [sε] larvæ $\cdot$ m^{-2}. Direct enumerations, removal method estimates, and Petersen capture-mark-recapture method estimates were compared for suitability under the census protocol. Removal method estimates were preferable because of their consistency, and their accuracy compared to direct enumeration (chemical treatment). Observed densities, fitted to a 5 parameter stochastic model, revealed habitat type and stream area to be useful predictors ($P < 0.0001$, $R^2 \approx 0.66$). Stream-wide population estimates ranged from 5810 larvæ (Bowmanville Creek) to 28000 (Bronte Creek), with an average of 13900. The standard errors of the mean densities and the relative temporal costs of sampling each habitat type were used to suggest an optimum sampling scheme.

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Introduction

Abundance estimates are indispensable to understanding the dynamics of animal populations, but it is rarely practical to count all individuals in a population. Census techniques are employed to estimate population parameters from sample statistics. A diversity of techniques has arisen because species differ in their habits and cannot all be censused in the same way (Blower et al. 1981). This diversity has brought questions of propriety of application and of comparability (Blower et al. 1981).

Post-embryonic larval sea lamprey, *Petromyzon marinus* Linnæus, are phytophagous (Moore and Mallatt 1980) residents of the soft substrate of streams (Applegate 1950, Thomas 1962, Potter 1980). After 2 to 17 or more years as larvæ (Manion and McLain 1971, Potter 1980), they undergo metamorphosis, characterised by profound physiological and behavioural changes (Manion and Stauffer 1970, Youson 1980). After migrating from their natal stream, the juvenile sea lampreys spend 20 months or more in the open water (Applegate 1950, Parker and Lennon 1956, Wigley 1959, Hardisty and Potter 1971b), before they mature, migrate to rivers, breed and, shortly thereafter, die.

Larval distribution in a stream is not uniform (Thomas 1963, Malmqvist 1980). Work by Lee (1989) has demonstrated that larvæ prefer substrates with small (<1.0 mm diameter) particles and high (>0.5 cm·min^{-1}) permeability, at least in graded mixes typically used in the laboratory. Field studies, however, where substrates are decidedly less uniform, are more equivocal (Mallatt 1982). Streams can be partitioned into areas virtually devoid of larvæ, and those of higher density sometimes called "beds" (Baxter 1957,

Thomas 1962). Only in streams, or portions thereof, where mean water velocity is low are larvæ more or less generally distributed (Thomas 1962).

Under simple random sampling designs, highly contagious distributions can be statistically problematic to the estimation of population density (Seber 1973, Wiens 1976). Unless each sample represents a large fraction of the stream, low densities of animals will constitute the largest classes of observations, and higher densities will be increasingly infrequent. The distribution of observed densities, then, will peak at or near zero, and will tail off rapidly with increasing density. An important component of this study was to estimate larval populations by fitting a stochastic model involving the effects of habitat. The distribution of errors from such a model is unlikely to be normal, invalidating the standard significance tests of estimated parameters (Snedecor and Cochran 1980, Draper and Smith 1981). Although techniques do exist for mitigating the damage wrought by non-normal errors (Bartlett 1947, Box and Cox 1964, John and Draper 1980), or for fitting alternative error distributions (Pennington 1983, 1986), it is always preferable also to adopt a sampling strategy such that non-normality is mitigated in the original observations (Atkinson 1973, Draper and Smith 1981). One such approach is to increase the probability of any sample containing animals. To accomplish this, a stream may be subdivided into areas called strata, based upon the relative suitability of each stratum as habitat (Seber 1973, Steel and Torrie 1980, Blower et al. 1981).

The objectives of this study were to evaluate the suitability, precision and accuracy of three census techniques for the estimation of larval abundance, and to derive an estimation protocol for larval populations.

Materials and Methods

The Study Area -- Five tributaries to the north shore of Lake Ontario (Canada), known to contain sea lamprey, were examined: Bowmanville and Soper's creeks (common mouth at 78°43'W 43°54'N), Bronte Creek (79°41'W 43°24'N), Cobourg Brook (78°9'W 43°59'N), and Wilmot's Creek (78°36'W 43°54'N). The total drainage area of each stream is presented in Table 1.

The study area of a stream was defined as the portion treated with lampricide in 1986 by the control agents of the Great Lakes Fishery Commission, excluding the estuary where sampling by electric fishing gear was impractical due to excessive depth.

Habitats and Physical Surveys of the Streams -- In streams colonised by sea lamprey, some areas are clearly unsuitable as habitat. Larvæ will avoid coarse or low permeability substrates when selecting burrowing sites (Thomas 1962, Malmqvist 1980, Lee 1989). Given the profusion of microhabitats, however, measures of particle diameter are not readily adapted to habitat surveys.

Most watercourses may be classified into a succession of habitats known as the riffle/pool sequence. Such a sequence is highly responsive to local gradient conditions, and several schemes have been devised to correlate salmonid numbers with stream habitat classifications (Everest and Chapman 1972, Bisson et al. 1981, Gardiner 1984, Hankin and Reeves 1988). The classifications used in this study, modified from WESLP (1987), are detailed in Table 2.

Table 1. Drainage area of each of the streams (Dave Bell, Lindsay District, Ontario Ministry of Natural Resources, personal communication [save for (a)]).

Stream	County or Region	Drainage Area (10^2 km^2)
Bowmanville Ck	Durham Region	1.1
Bronte Ck	Hamilton-Wentworth Region	2.9[a]
Cobourg Bk	Northumberland County	1.2
Soper's Ck	Durham Region	0.68
Wilmot's Ck	Durham Region	1.1

Notes: a. Alan Murray, Cambridge District, Ontario Ministry of Natural Resources, personal communication.

Table 2. Habitats considered suitable for use by larvæ (after WESLP 1987).

	Run	Flat	Glide	Pool
Depth	Steeply sloping, >0.3 m	Uniform, 0 to 0.5 m, usually <0.3 m	Uniform, 0.1 to 0.3 m.	Steeply sloping, >0.5 m.
Current $(m \cdot s^{-1})$	>1	<0.5	0.5 to 1	<0.5
Flow	turbulent	laminar	laminar	laminar
Substrate	Boulders and coarse sand	Silt or sand/silt	Coarse sand and small rocks	Silt or sand/silt

Thirty to 90% of the total length of each study stream, in 3 to 5 random subsamples, was surveyed as to size and habitat composition. The stream width (± 0.3 m) and per cent occurrence of each of the four suitable habitat types were estimated at a fixed (17 m) interval along the main channel. The sum of the per cent occurrences is always less than or equal to 100 %. The balance, if any, was relegated to an (implicit) unsuitable category. These estimates were then used as the observations in multivariate analysis.

A stream's length tells little about its potential for production of larvæ, since stream width, and hence the area available to larvæ, is not constant throughout the watercourse (Hankin and Reeves 1988). Each stream was longitudinally demarcated into four sections of equal area, termed reaches. These reaches were arbitrarily designated as "Headwaters", "Upstream", "Downstream" and "Mouth". In the absence of longitudinal variation in suitable larval habitat distribution (and assuming no marked concentrations or absences of spawning habitat), each of these reaches would be expected to harbour similar numbers of larvæ.

Experimental Design -- This study is essentially a split-plot design with repeated measures: the five streams are the whole units; nested within these are the reaches (subunits), four per stream. There are thus a total of 20 stream-reach combinations, each of which was randomly assigned two sampling sites of different habitats (Table 2). Each habitat type was represented by a total of two sites within each stream. The distribution of sites within streams is summarised in Table 3.

Table 3. Habitats sampled for larvæ by stream and reach. Two sites were sampled within each habitat type.

Stream	Reach	Habitat Types
Wilmot's Creek	Headwaters	Pool, Flat
	Upstream	Run, Flat
	Downstream	Glide, Run
	Mouth	Pool, Glide
Cobourg Brook	Headwaters	Glide, Run
	Upstream	Pool, Glide
	Downstream	Flat, Pool
	Mouth	Flat, Run
Bowmanville Creek	Headwaters	Glide, Run
	Upstream	Pool, Flat
	Downstream	Glide, Flat
	Mouth	Run, Pool
Bronte Creek	Headwaters	Pool, Flat
	Upstream	Flat, Glide
	Downstream	Pool, Run
	Mouth	Glide, Run
Soper's Creek	Headwaters	Flat, Pool
	Upstream	Run, Glide
	Downstream	Pool, Glide
	Mouth	Run, Flat

Biotic Sampling by Electrofishing -- Survey sites were randomly assigned to a specific habitat, and then to an approximate (random) location within a particular reach. The nearest appropriate site (of the correct type) was sampled, but sometimes a subsection of the total available site was chosen such that, given the current, depth and anticipated larval density, one sampling by electric fishing could be completed in under 1 hour. When such a reduction of a site was necessary, the same subsection of the site was sampled on all subsequent visits. Every effort was made to include in the sampled area as much of the visible diversity of substrate, current, and depth as could be seen in the site as a whole.

The electrofishing unit, of the thyristor-controlled, capacitive discharge type, was powered by a 2-cycle 110 or 220 V gasoline-fueled alternator, producing current at a frequency of 60 Hz. The unit's potential was set to 90 V and the output frequency adjusted so that a current of ½ to 1 A resulted under load. These settings had proven, by trial-and-error, to be effective in capturing larvæ.

Two or more consecutive samplings, without replacement of captured larvæ, were conducted in each site. Effort, expressed as fishing time, was held constant across samplings within a site on any given day. Generally, samping continued until any catch was less than 10% of the previous one, or until no animals were captured (null catch). If the first catch in a site was null, a second was carried out nonetheless.

At the end of each sampling, larvæ were anæsthetised, measured and marked by subcutanæous injection of a fluorescent latex dye (Hanson 1972). Recovering larvæ were placed in a bucket with a screened bottom, positioned in the stream. Any animals which did not show strong and regular movement

of the branchial basket after 30 min, or which failed to burrow within 15 min after release, were removed and treated as mortalities.

Once a site contained marked animals, it was revisited in not less than 6 days (average: 11, maximum: 24) for the recapture effort. At that time, all larvæ, including recaptured animals, were marked anew. Four sites were visited more than twice.

Estimation Methods -- One or more of three models was used to estimate the population at each site: total captures, Zippin's removal method (1956), or Petersen's capture-mark-recapture method. Seber (1973) and Ricker (1975) provide complete discussions of the latter two, including the estimation of variance components.

The simplest method is the total captures wherein all larvæ caught at a site are enumerated.

$$N = [_i\Sigma\ (n_i)], \text{ where}$$

N is the estimated population in the site and n_i is the number of larvæ captured in the ith sampling. The assumptions here are that sampling captures all animals, and that there is no immigration to or emigration from the site during sampling.

The rationale of the reduction/removal methods, of which Zippin's is an example, is that successive samplings, without replacement, will result in declining catches.

$$N = [_i\Sigma\ (n_i)]\ /\ [1-(1-p)^s], \text{ where}$$

p is the estimated probability of capture of any individual, s is the total number of samplings, and the others are as before. The probability of

capture, p, is estimated (iteratively) from the relationship

$$[\textstyle\sum_i (i-1)(n_i)][\textstyle\sum_i (n_i)]^{-1} = [(1-p)(p^{-1})]-[s(1-p)^s(1-(1-p)^s)^{-1}].$$

This is a true single-census method, since an estimate can be had after but one visit to the site. It assumes that the population is closed to immigration and emigration during sampling, that the probability of capture is constant for all individuals still at large, and that this probability does not change across samplings. Note that, as p approaches 1 or as s approaches $+\infty$, Zippin's estimate approaches the total captures.

The Petersen estimate, sometimes called the Lincoln (1930) Index (LeCren 1965), requires two visits to a site. Animals must be captured on each visit, and a portion of those caught in the second sample, preferably a large fraction of the number of marked animals in the population (Chapman 1951, Robson and Regier 1964, 1968), must be marked recaptures from the first sample.

$$N = M/p, \text{ where}$$

N is as before, M is the total number of marked animals at large, and p is the **proportion** of recaptures in the second sample. This model assumes that: the population is closed to immigration and emigration over the entire sampling **interval**; the probability of capture is constant for all animals at large, regardless of whether or not they bear marks; marks are not lost in the interval between samplings; and all recaptures are noted.

Regardless of which method was used, N was divided by the site's area, producing an estimate of larval density, δ. These densities then formed the elements of y, the vector of responses.

Statistical Methods -- Both the estimates of stream width and of habitat occurrence, when fitted to polynomial models, produced residuals with skew-positive distributions due to lower end constraints (i.e. there cannot be less than zero per cent of a habitat type, nor can a stream be infinitely narrow). Response variable transformations were selected to minimise this, using single-parameter maximum likelihood methods (Box and Cox 1964).

These selection methods suggested that observed widths be $\log_e$-transformed. The transformed widths were then fitted to a first or second order model, using downstream distance from the lampricide application point as the independent variable. Similarly, the maximum likelihood estimators suggested that per cent occurrences of each habitat type be square root-transformed. The transformed habitat occurrence values also were fitted to linear or quadratic models using the same independent variable. (Actually, %habitat + 1 was used due to the presence of zeroes in the vector of observations. This permitted searching a broader range of transformations, some of which do not accept zero values.)

The resultant estimated width profile for each stream, combined with known lengths, yielded an area profile, which was then integrated over 10 m intervals, to permit demarcation of the four reaches. Sites were randomly assigned to these reaches with the aid of the random number generator of Lotus 1-2-3 Version 2.01[1].

Larval density estimates were compiled into a vector, y, while the stream, reach, habitat and methods classifications, and their interaction terms were entered as binary ("dummy") variables into the X matrix. Two

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[1] Registered Trademark Lotus Development Corporation.

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approaches to model-building were compared. Least squares regressions were fitted, through a backward elimination procedure (Draper and Smith 1981) using SAS[2] software for the IBM-PC[3], first to the entire response vector, then to a reduced vector including only non-null observations. Coefficients for the "full" and "reduced" model were individually tested for significance by F- or by Student's t-tests; therefore the assumptions of normally distributed residuals, with independent variances, were required (Draper and Smith 1981). A SAS[TM] routine was written to conduct a two-dimensional maximum likelihood search for transformation parameters to enhance normality of the residuals (Box and Cox 1964).

The logit transformation (Berkson 1951, Cox 1970, Snedecor and Cochran 1980) was used to model the log-normal probability of finding larvæ in any given habitat type. Let the (reduced) vector of transformed observations (including only non-null observations) be written as y_r^*. Further, let the predicted value for the density on habitat k from this reduced vector be written as δ_k (i.e. density if larvæ present). If the estimated probability of presence in habitat k is found to be p_k, then the estimated density across habitats of type k (i.e. across those with and without larvæ) can be represented by the product of these:

$$r_k = \delta_k \cdot p_k \text{ where}$$

Γ_k is the predicted density on habitat k.

For each stream, an area profile and four habitat distribution profiles

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[2] Registered Trademark SAS Institute, Cary, N.C.

[3] Registered Trademark International Business Machines.

were available. In general terms, these might be described thusly:

$$A = exp(b_{a0} + b_{a1} D + b_{a11} D^2), \text{ and}$$

$$H_k = (b_{h0} + b_{h1} D + b_{h11} D^2)^2 - 1, \text{ where}$$

A is the estimated area of the stream, the b's are estimated regression coefficients, D is the distance from the uppermost lampricide application point, and H_k is the estimated per cent occurrence of habitat type k. In no case did the sum of the four habitat type estimates exceed 100%. Note that each of these equations results from inverse transformation of its respective postulated model. To calculate the estimated area of any given habitat at any point along the stream, we need the product of these:

$$AH_k = A \cdot H_k, \text{ where}$$

AH_k is the estimated area of habitat type k at a given location on the stream, and the others are as before.

These equations for each of the four habitat types on each stream were used to construct Lotus[TM] worksheets containing a series of vectors of the estimated area of each habitat type in 10 m lengths of stream. The regression coefficients from the density estimation models were then multiplied along these vectors to give predicted larval numbers, also in 10 m stream lengths. These were summed to predict the streamwide contributions to the larval population from each habitat type. Summing across habitat type totals provided streamwide total predicted larval populations.

A detailed consideration of the propagation of error in this scheme was not attempted, but an approximate confidence interval for each of the totals was provided by performing the same series of summations as noted above,

using the lower and upper bounds on the 95% confidence limits for each regression coefficient, in whatever combinations resulted in the widest interval. These intervals, then, carry considerable latitude in interpretation, and can probably be thought of as "worst case" situations. Actual intervals are almost certainly narrower than those calculated here.

Post-Lampricide Treatment Collections -- The Great Lakes Fishery Commission operates a lampricide treatment programme aimed at controlling juvenile sea lamprey numbers in the Great Lakes. Colonised streams are treated at regular intervals with the lampricide TFM (3-trifluouromethyl-4-nitrophenol [Sandoz]). The lampricide is introduced to the streamflow so as to maintain the concentration at or above a level lethal to 99.99% of larvæ ($LC_{99.99}$) when exposed for a period of 12 to 16 hours (Smith et al. 1974).

Typically, after about one hour of exposure to the chemical, larvæ leave the substrate and swim actively. During treatment, collections were made of swimming larvæ in at least one previously surveyed site on each stream. This provided a means whereby the accuracy of electrofishing estimates in that site could be judged.

If significant numbers of larvæ remain burrowed during treatment and die within the substrate, however, population estimates from treatment collections will be consistently low. To gauge the magnitude of this potential bias, known numbers of burrowed larvæ were placed, at least 4 days prior to treatment, in cages in two locations in each of three streams. These were observed during and after passage of the treatment block to determine the proportion of larvæ available to collection during treatment.

Results

Stream Sizes and Habitat Distributions -- Generally, stream width was found to increase significantly in the direction of flow (Figures 1 and 2). The width, area and habitat distribution profiles provided models describing stream characteristics from which to predict total larval populations. Table 4 contains the estimated regression coefficients for these models. Residuals plots from some of the width models suggested the presence of serial correlation among the observed errors. This is likely due to the fact that a watercourse tends to have a definite sequence of habitats sometimes called the riffle/pool sequence. Each habitat has a characteristic relative width, presumably related to depth and volume of flow. The presence of serial correlation does not invalidate any estimates derived from such data, but will usually result in an underestimate of the variability about those estimates. In this sense, the estimated standard errors about the mean widths on all streams are probably optimistic. Fortunately, width measurements were the most accurate of the physical measurements made in this study. Serial correlation was not seen in habitat estimation models, nor in the results of biotic sampling, and, being thus "isolated", it could not propagate throughout the modelling procedures. Only to the production of stream-wide population estimates, which involves a synthesis of all models, could any bias have been transmitted. Leaving this to one side, however, the polynomial models fitted here explained from 30 to 80 % of the observed variation in the independent variables. Graphs of all width profiles are found in Appendix 3. Table 5 details the mean observed width and habitat occurrence values by stream.

10

6

Danforth Rd.

7

Factory

8

Creek

9

HWY 401

Dam

HWY 45

1

2

HWY 2

3

Cobourg
Brook

4

5

Baseline Rd.

HWY 2

N

0   500m

LAKE ONTARIO

84°   80°   76°

46°

Georgian
Bay

Lake
Huron

Cobourg
Brook

Toronto

Lake Ontario

42°

Lake Erie

A Main Branch

B Factory Creek Tributary

C Western Branch of Factory Creek Tributary

Stream Width (m)

Distance Downstream (m) from Lampricide Application
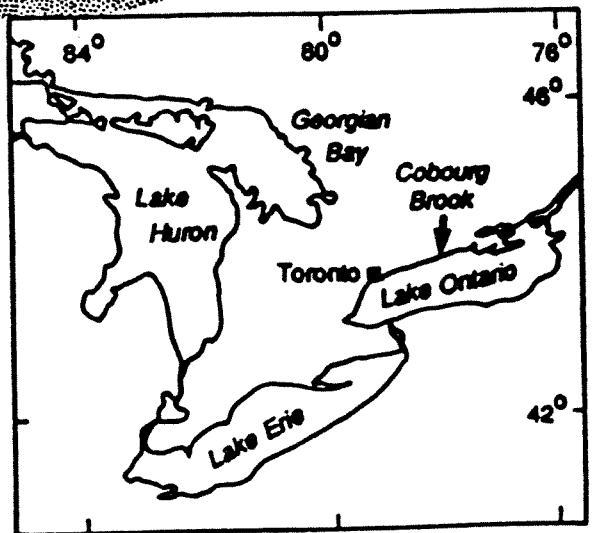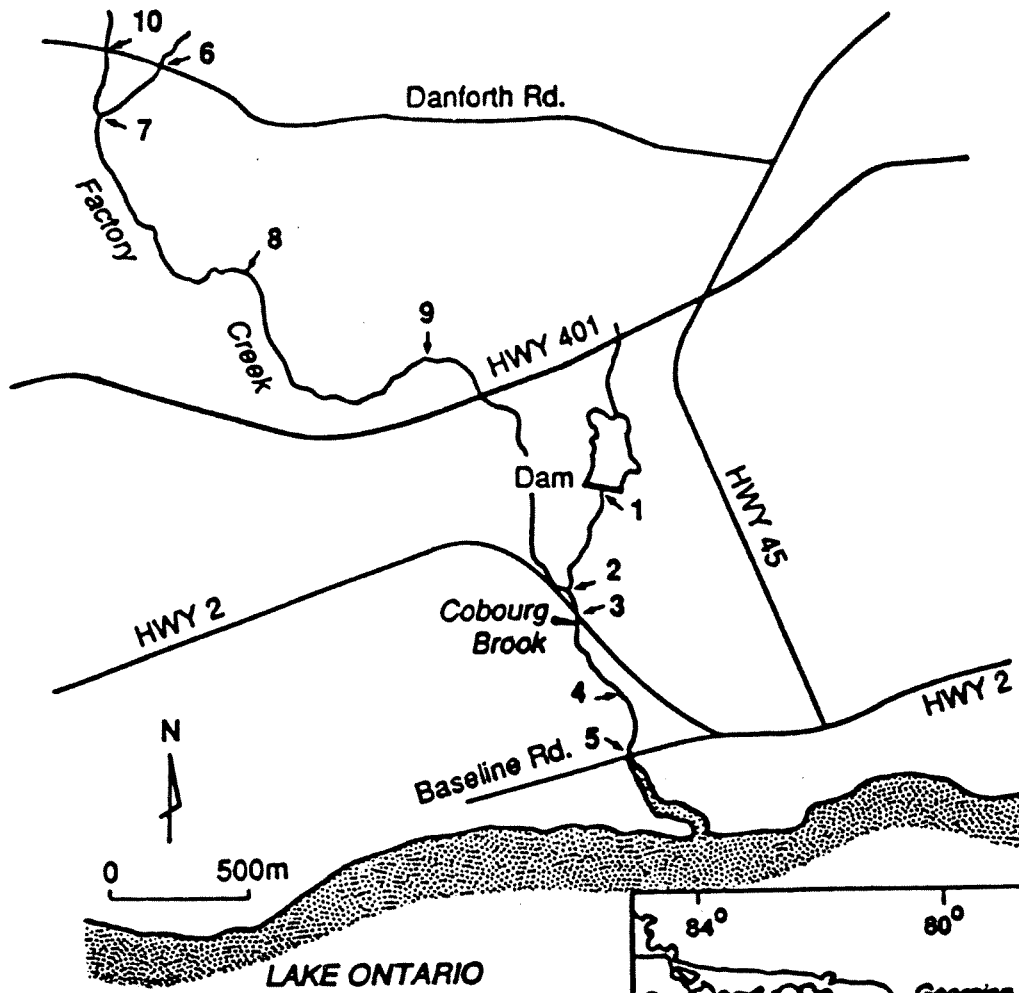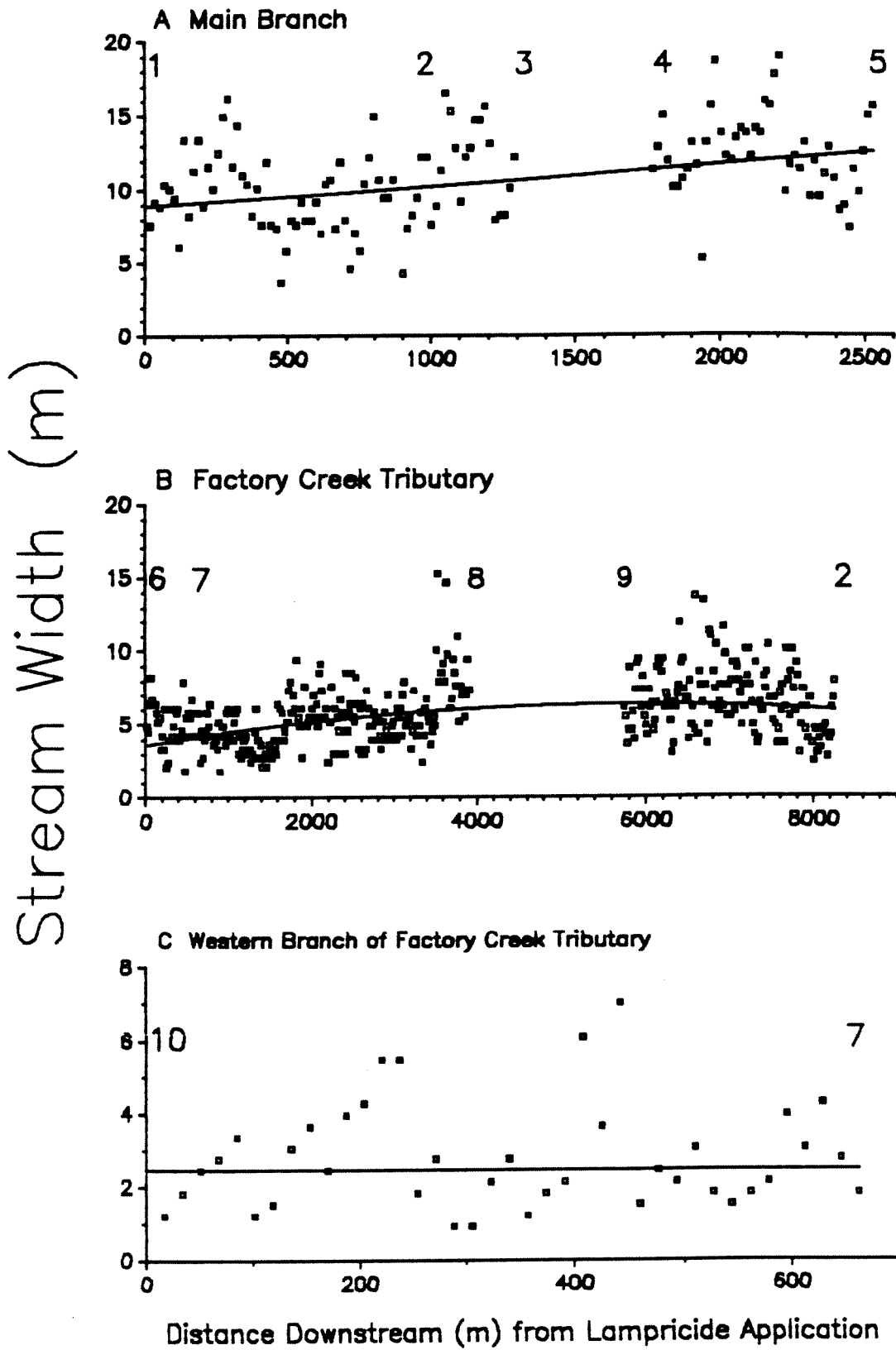
Table 4. Parameter estimates for equations: $Y^* = b_0 + b_1 \cdot D + b_{11} \cdot D^2$, where Y^* is the transformed response, and D is distance (m).

Stream (Branch)	Regression Parameter	Width	Area	Run	Flat	Glide	Pool
Wilmot's (Main) ($n = 208$)	b_0	1.52	4.37	5.01	3.47	4.60	4.76
	b_1	3.17E-5	3.11E-5	-1.18E-4	5.32E-5	3.40E-5	-3.43E-4
	b_{11}	NS	NS	NS	NS	NS	1.75E-8
Orono (Main) ($n = 131$)	b_0	1.16	4.04	4.34	2.72	3.99	4.62
	b_1	2.63E-4	1.92E-4	-7.99E-4	3.93E-3	4.62E-4	8.33E-4
	b_{11}	-1.22E-7	-8.49E-4	NS	-1.36E-6	NS	-6.68E-7
Orono (Eastern) ($n = 23$)	b_0	1.08E-1	3.22	2.65	6.86	1.77	2.66
	b_1	4.32E-4	-1.85E-3	-1.37E-2	9.94E-4	1.93E-2	3.08E-2
	b_{11}	NS	4.48E-6	2.70E-5	NS	-5.23E-5	-8.92E-5
Cobourg (Main) ($n = 121$)	b_0	2.19	5.03	3.37	4.78	3.08	6.71
	b_1	1.34E-4	1.29E-4	1.77E-3	-9.72E-4	3.26E-3	-3.78E-3
	b_{11}	NS	NS	-1.19E-6	NS	-1.62E-6	7.18E-7
Factory (Main) ($n = 380$)	b_0	1.33	4.17	3.01	5.85	3.35	4.89
	b_1	1.81E-4	1.86E-4	-9.05E-5	NS	1.15E-4	NS
	b_{11}	-1.56E-8	-1.62E-8	NS	NS	NS	NS
Factory (Western) ($n = 39$)	b_0	8.98E-1	3.80	3.21	5.70	3.84	4.87
	b_1	NS	NS	NS	NS	NS	NS
	b_{11}	NS	NS	NS	NS	NS	NS
Bowmanville ($n = 111$)	b_0	2.52	5.38	3.14	5.38	3.46	4.57
	b_1	-1.80E-4	-2.00E-4	NS	NS	NS	NS
	b_{11}	NS	NS	NS	NS	NS	NS
Bronte (Main) ($n = 476$)	b_0	1.91	4.75	5.08	3.02	4.75	1.85
	b_1	6.15E-5	6.11E-5	-3.07E-4	3.20E-4	NS	4.14E-4
	b_{11}	-1.60E-9	-1.60E-9	8.10E-9	-1.09E-9	NS	-1.59E-8
Limestone ($n = 94$)	b_0	1.16	4.02	1.52	6.11	3.62	6.45
	b_1	NS	NS	3.57E-3	NS	NS	-1.75E-3
	b_{11}	NS	NS	-1.90E-6	NS	NS	NS
Soper's ($n = 190$)	b_0	1.98	4.81	3.85	4.23	4.25	3.70
	b_1	-6.53E-5	-4.25E-5	-8.93E-4	-1.65E-5	6.46E-5	1.14E-3
	b_{11}	2.08E-8	1.67E-8	1.26E-7	NS	NS	-1.56E-7

Note: NS = not significant at the $\alpha = 0.05$ level.

Table 5a. Mean observed width and habitat values by stream. The 95 % confidence limits are symmetric about their mean on the transformed scale.

Stream	Parameter	Min	Max	Mean	95 % CI
Cobourg	Width (m)	3.6	19.0	10.5	(5.75, 18.7)
(Main)	Run (%)	0	65	7.9	(1.45, 55.9)
(n = 121)	Flat (%)	0	80	11.9	(-0.91, 55.2)
	Glide (%)	0	80	12.1	(0.51, 70.7)
	Pool (%)	0	90	12.1	(2.93, 84.1)
Factory	Width (m)	2.0	15.3	5.5	(2.50, 11.0)
(Main)	Run (%)	0	70	6.0	(-0.05, 38.5)
(n = 380)	Flat (%)	0	100	38.2	(2.69, 94.5)
	Glide (%)	0	100	13.4	(-0.37, 69.4)
	Pool (%)	0	100	23.0	(-0.96, 98.9)
Factory	Width (m)	1.0	7.0	2.5	(0.75, 6.2)
(Western)	Run (%)	0	75	9.8	(0.03, 56.6)
(n = 39)	Flat (%)	3	100	31.5	(3.43, 85.3)
	Glide (%)	0	60	13.7	(-0.96, 61.2)
	Pool (%)	0	75	22.7	(-0.74,104.)
Bowmanville	Width (m)	3.6	22.0	10.5	(5.59, 19.1)
	Run (%)	0	70	8.9	(0.56, 55.7)
(n = 111)	Flat (%)	0	100	28.0	(-0.17, 96.1)
	Glide (%)	0	70	11.0	(-0.26, 59.6)
	Pool (%)	0	90	18.9	(-0.45, 92.2)
Soper's	Width (m)	3.3	20.3	8.1	(4.07, 15.4)
	Run (%)	0	70	8.1	(-0.21, 46.9)
(n = 190)	Flat (%)	0	80	16.5	(-0.24, 55.2)
	Glide (%)	0	90	19.0	(-0.82, 86.9)
	Pool (%)	0	95	22.3	(-0.33,109.)

Table 5b. Mean observed width and habitat values by stream (cont'd). The 95 % confidence limits are symmetric about their mean on the transformed scale.

Stream	Parameter	Min	Max	Mean	95 % CI
Wilmot's	Width (m)	2.6	14.0	6.45	(3.18, 12.3)
(Main)	Run (%)	0	70	13.1	(−0.79, 62.6)
(n = 208)	Flat (%)	0	70	15.4	(−0.84, 58.3)
	Glide (%)	0	100	23.4	(−0.98, 93.8)
	Pool (%)	0	90	13.3	(0.47, 76.0)
Orono	Width (m)	1.6	10.0	3.54	(1.69, 6.65)
(Main)	Run (%)	0	75	10.9	(−0.15, 60.0)
(n = 131)	Flat (%)	0	90	22.4	(−0.54, 80.1)
	Glide (%)	0	85	19.3	(−0.88, 74.3)
	Pool (%)	0	99	18.7	(−0.33, 93.0)
Orono	Width (m)	0.6	2.6	1.3	(0.47, 2.5)
(Eastern)	Run (%)	0	20	0.6	(−0.87, 7.6)
(n = 23)	Flat (%)	0	100	48.8	(3.52,143.)
	Glide (%)	0	45	7.3	(−0.06, 44.2)
	Pool (%)	0	95	15.8	(0.83, 90.2)
Bronte	Width (m)	3.6	41.0	9.7	(4.60, 19.5)
(Main)	Run (%)	0	90	9.8	(1.15, 63.7)
(n = 476)	Flat (%)	0	100	18.8	(−0.94, 73.9)
	Glide (%)	0	90	19.8	(−0.77, 91.3)
	Pool (%)	0	100	12.1	(3.14, 85.2)
Limestone	Width (m)	1.6	7.6	3.2	(1.57, 6.0)
	Run (%)	0	70	6.7	(−0.79, 35.2)
(n = 94)	Flat (%)	5	80	36.3	(8.67, 82.0)
	Glide (%)	0	50	12.1	(−0.96, 48.6)
	Pool (%)	0	70	24.6	(−0.35, 85.8)

a) *Wilmot's Creek* -- The total length of this system is 22.1 km, comprising a total surface area of 12.8 ha. The system is composed of the main branch (84% of the total length and 91% of the area) and an eastern tributary known as Orono Creek (15% of the length and 8.6% of the area). Orono Creek itself has a small, eastern tributary (1.7% of the length and 0.41% of the area). The width of the main branch increases roughly linearly down the watercourse, while that of Orono Creek decreases. The small tributary of Orono Creek is relatively constant in width.

b) *Cobourg Brook* -- The total length of this system is 11.4 km, comprising a total surface area of 7.64 ha. The system (Figure 1) is composed of the main branch (22% of the total length and 35% of the area) and a western tributary known as Factory Creek (72% of the length and 62% of the area). Factory Creek itself has a small, western tributary (5.8% of the length and 2.3% of the area). Migration of spawning adult lampreys is blocked, on the main branch, by a dam some 3.5 m in height, just north of Elgin Street in the Town of Cobourg. The width of the main branch (Figure 2a) increases roughly linearly down the watercourse, while the curve for Factory Creek (Figure 2b) shows some convexity with downstream distance. The small tributary of Factory Creek (Figure 2c) is fairly constant in width. This latter figure (2c) illustrates well the potential problem of serial correlation among the residuals.

c) *Bowmanville Creek* -- This stream has a length of 2.55 km, comprising a surface area of 2.57 ha. Migration of spawning adults is blocked by a dam (Goodyear Dam) some 2 m in height behind the Goodyear Tire and Rubber Company plant in the Town of Bowmanville. The width was found to decrease with downstream distance. It is felt that this pattern of

decreasing width is an artifact of the use of the valley as a cow pasture. Cattle have full access to the upper sections of the stream, resulting in severely pummelled banks and a wider stream profile than otherwise might be expected. About midway along the length of the stream, the cattle are confined to just the northeast bank. Cattle access is completely precluded below Baseline Road in the town of Bowmanville, where the land use becomes mainly light industrial. Agricultural land is again found near the estuary, but the adjoining areas are mainly in orchards.

d) *Bronte Creek* -- The total length of this system is 25.8 km, comprising a total surface area of 26.2 ha. It is composed of the main branch (94% of the total length and 98% of the area) and a tributary known as Limestone Creek (6.2% of the length and 2.0% of the area). Migration of spawning adults, on the main branch, is blocked by a dam some 3 m in height, just west of the settlement of Cedar Springs. There is an impoundment (average width 23 ± 10.1 m [sE]) on the main branch, about 3 km below the lampricide application point. The impoundment was excluded from width calculations. The width of the main branch was found to increase along the watercourse, while that of Limestone Creek is basically constant.

e) *Soper's Creek* -- This stream has a total length of 6.87 km, comprising a surface area of 5.64 ha. There is a marked quadratic increase in width along the length of this watercourse.

Larval Densities and the Estimation Model -- In general, runs and glides were sparsely populated, and were also least likely to contain larvæ. Table 6 summarises larval occurrence by habitat type. The response vectors of observed densities were transformed to approximately normalise the model

Table 6. Summary of observed larval presence by habitat type, and of the estimated log-normal probability of a non-null sample within a habitat.

Habitat Type	Sites Surveyed	Sites w/ Larvæ	Non-Zero Observat'ns	Total Observat'ns	%Prob of presence[a] (95% CL follow)
Run	10	1	2	20	21.7 (3.94, 39.5)
Flat	10	10	28	28	96.9 (92.5 ,101)
Glide	10	2	5	21	38.5 (18.8 , 58.1)
Pool	10	9	18	20	87.2 (76.4 , 98.0)

Note: a. Determined by logit transformation to the log-normal probability.

error term distributions (Box and Cox 1964, Atkinson 1985). For the "reduced model", the maximum likelihood search for transformation parameters yielded the following:

$$\delta_{ri}{}^{*} = [4/(\delta_{ri})]^{\frac{1}{2}}, \text{ and,}$$

for the "full model", the suggested transformation was:

$$\delta_{i}{}^{*} = [-1/(\delta_{i} + 0.4)], \text{ where}$$

$\delta_{i}{}^{*}$ is the transformed larval density at the site $[m^{2} \cdot larva^{-1}]$, δ_{i} is the the i th element of the vector of observed densities at all sites $[larvæ \cdot m^{-2}]$, and δ_{ri} is the i th element of the reduced vector of observed densities at inhabited sites only. In either case, the vector of transformed densities, δ^{*}, was used as the dependent variable for all further analysis. Figure 3 shows the improvement in the residuals frequency distribution due to transformation for the full model. In this figure, the trend lines have been smoothed by a linearly weighted moving average of seven points, which was found by trial to be a useful aid in interpretation:

$$q_{i} = \{[(z_{i-3} + z_{i+3}) + 2(z_{i-2} + z_{i+2}) + 3(z_{i-1} + z_{i+1}) + 4(z_{i})] \div 16\}, \text{ where}$$

q_{i} is the transformed frequency of the i th residuals class,

$$z_{i} = log_{e}(f_{i} + 1), \text{ and}$$

f_{i} is the frequency of the i th residuals class.

Regardless of whether only inhabited sites were included in the model or not, the basic result was the same. Observed densities ($N = 152$) showed the longitudinal distribution of larvæ in streams to be non-random, but each stream has its characteristic pattern. There is otherwise no detectable difference among streams. The majority of this stream dependence is a function of the area available below any given point on the stream. This is

Figure 3. Weighted trend lines comparing Studentised residuals frequency distributions. Lines shown are the weighted moving average of seven points, joined by a smooth curve. See the text for details of the weighting transformation. Upper graph -- residuals from untransformed response. Lower graph -- residuals from transformed response. Ideally, the curves should be Gaussian.

Class midpoints (dimensionless)
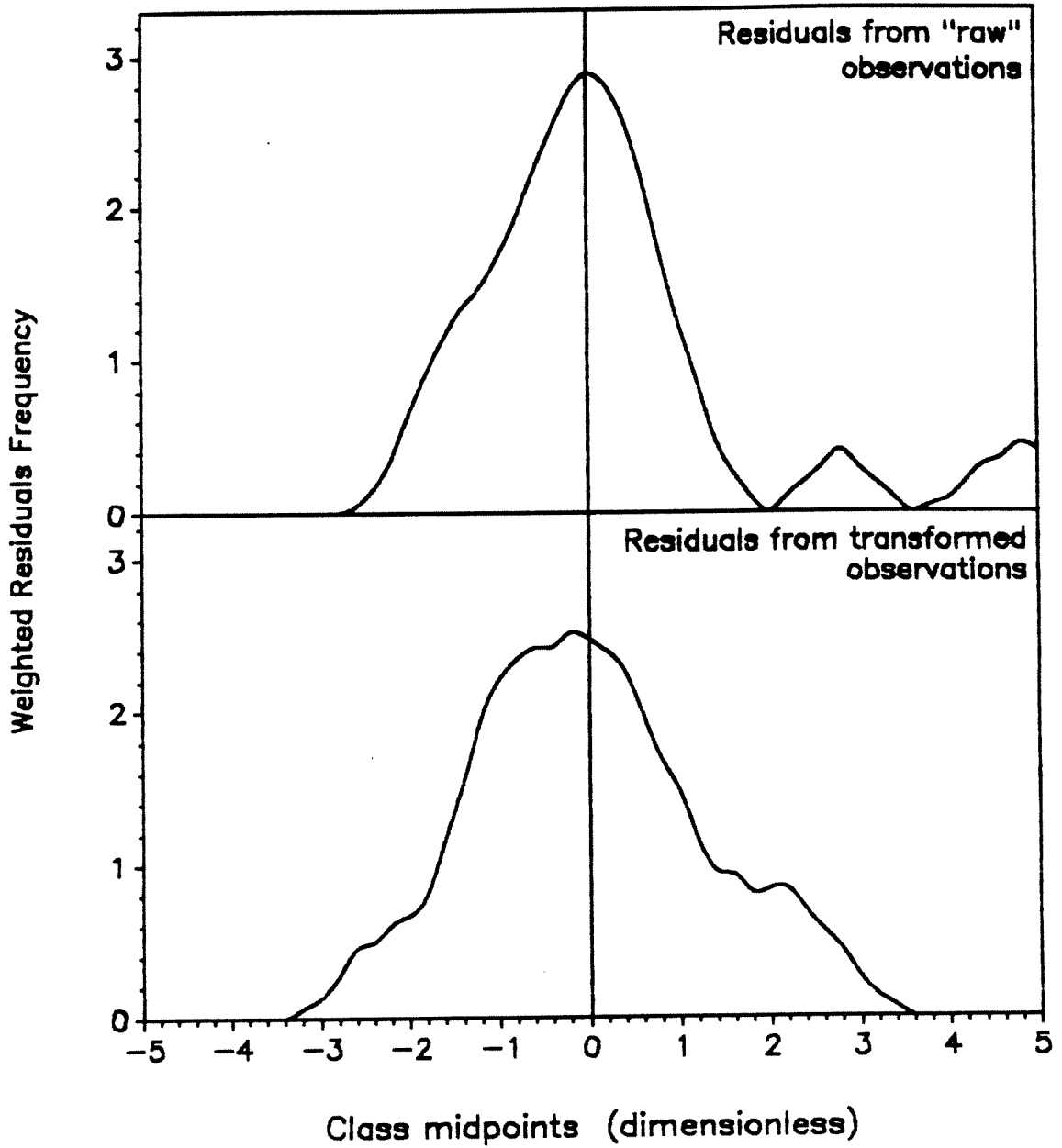
an indication that densities, in general, tend to increase as one moves downstream. Since the goal of this study is to construct a simple, predictive model, it is preferable to employ a model which does not require prior knowledge of the detailed distributional pattern on any one stream. For example, fitting a 13 parameter model, including variables for specific stream-reach interactions, explains 81% of the variability in observed densities. A 5 parameter model, including the area below the reach midpoint as a covariate, explains 66% of the variability in observed densities. Almost two-thirds of the variation, then, can be accounted for with knowledge of only the habitat type and area profiles of a stream.

Regarding habitat use, flats are significantly more densely populated than any other habitat type. Glides and runs were the least populated surveyed habitats, and were not statistically distinguishable. Of the three estimation methods used, Petersen estimates were significantly higher (by as much as an order of magnitude) than total captures or depletion estimates. The latter two did not differ significantly from one another. There was a significant interaction between Petersen estimates and the stream area below the site. That is to say, densities estimated by Petersen's method tend to be significantly higher in the upper sections of streams than in the lower reaches. Predictions and observed densities from the two models for all stream-reach-habitat combinations are shown in Table 7.

The Model Equation -- Larval density estimates were available from both the full and reduced models, permitting comparison of the performance of each relative to the other. The density of larvæ in any site can be predicted

Table 7a. Wilmot's Creek observed and predicted densities (m^{-2}) in relation to habitat type. Sites were visited more than once, and are thus represented by multiple observations. N/A = estimate not attempted or not possible.

Reach	Run TotCap[a]	Depltn[b]	Ptrsn[c]	Flat TotCap	Depltn	Ptrsn	Glide TotCap	Depltn	Ptrsn	Pool TotCap	Depltn	Ptrsn
Headwaters												
Observed	N/A	N/A	N/A	0.74	0.84	4.45	N/A	N/A	N/A	0.20	0.27	N/A
Observed				0.56	0.56					0		
Predict-F[d]	-0.01	-0.01	0.17	0.49	0.49	2.53	-0.01	-0.01	0.17	0.21	0.21	0.76
Predict-R[e]	0.00	0.00	0.00	0.22	0.22	1.22	0.00	0.00	0.00	0.22	0.22	1.22
Upstream												
Observed	0	N/A	N/A	0	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A
Observed	0			0.17	0.17							
Predict-F	0.00	0.00	0.16	0.53	0.53	2.25	0.00	0.00	0.16	0.23	0.23	0.71
Predict-R	0.00	0.00	0.00	0.22	0.22	1.22	0.00	0.00	0.00	0.22	0.22	1.22
Downstream												
Observed	0	N/A	N/A	N/A	N/A	N/A	0	N/A	N/A	N/A	N/A	N/A
Observed	0						0					
Predict-F	0.01	0.01	0.14	0.56	0.56	1.85	0.01	0.01	0.14	0.24	0.24	0.64
Predict-R	0.00	0.00	0.00	0.22	0.22	1.22	0.00	0.00	0.00	0.22	0.22	1.22
Mouth												
Observed	N/A	N/A	N/A	N/A	N/A	N/A	0	N/A	N/A	0.20	0.23	N/A
Observed							0			0		
Predict-F	0.01	0.01	0.12	0.56	0.56	1.49	0.01	0.01	0.12	0.24	0.24	0.55
Predict-R	0.00	0.00	0.01	0.22	0.22	1.22	0.00	0.00	0.01	0.22	0.22	1.22

Notes:
a. TotCap = Total larvæ captured at the site in one visit.
b. Depltn = Zippin's Removal Method Estimate
c. Ptrsn = Petersen's Capture-Mark-Recapture Method Estimate
d. Predict-F = Density Predicted by the "Full" Model (i.e. all sites).
e. Predict-R = Density Predicted by the "Reduced" Model (i.e. only sites with larvæ present).

Table 7b. Cobourg Brook observed and predicted densities (m^{-2}) in relation to habitat type. Sites were visited more than once, and are thus represented by multiple observations. N/A = estimate not attempted or not possible.

Reach	Run TotCap[a]	Depltn[b]	Ptrsn[c]	Flat TotCap	Depltn	Ptrsn	Glide TotCap	Depltn	Ptrsn	Pool TotCap	Depltn	Ptrsn
Headwaters												
Observed	0	N/A	N/A	N/A	N/A	N/A	0	N/A	N/A	N/A	N/A	N/A
Observed	0						0					
Predict-F[d]	0.01	0.01	0.15	0.54	0.54	2.09	0.01	0.01	0.15	0.23	0.23	0.68
Predict-R[e]	0.00	0.00	0.00	0.22	0.22	1.22	0.00	0.00	0.00	0.22	0.22	1.22
Upstream												
Observed	N/A	N/A	N/A	N/A	N/A	N/A	0	N/A	N/A	0.38	0.38	1.54
Observed							0			0.51	0.51	
Predict-F	0.01	0.01	0.14	0.56	0.56	1.85	0.01	0.01	0.14	0.24	0.24	0.64
Predict-R	0.00	0.00	0.00	0.22	0.22	1.22	0.00	0.00	0.00	0.22	0.22	1.22
Downstream												
Observed	N/A	N/A	N/A	0.05	0.05	N/A	N/A	N/A	N/A	0	0.57	0.85
Observed				0.05	0.05					0.42		
Predict-F	0.01	0.01	0.13	0.56	0.56	1.62	0.01	0.01	0.13	0.24	0.24	0.58
Predict-R	0.00	0.00	0.00	0.22	0.22	1.22	0.00	0.00	0.00	0.22	0.22	1.22
Mouth												
Observed	0	N/A	N/A	2.15	2.32	7.00	N/A	N/A	N/A	N/A	N/A	N/A
Observed	0			2.15	2.15							
Predict_F	0.01	0.01	0.11	0.56	0.56	1.42	0.01	0.01	0.11	0.24	0.24	0.54
Predict-R	0.01	0.01	0.01	0.22	0.22	1.22	0.01	0.01	0.01	0.22	0.22	1.22

Notes:
a. TotCap = Total larvæ captured at the site in one visit
b. Depltn = Zippin's Removal Method Estimate
c. Ptrsn = Petersen's Capture-Mark-Recapture Method Estimate
d. Predict-F = Density Predicted by the "Full" Model (i.e. all sites).
e. Predict-R = Density Predicted by the "Reduced" Model (i.e. only sites with larvæ present).

Table 7c. Bowmanville Creek observed and predicted densities (m^{-2}) in relation to habitat type. Sites were visited more than once, and are thus represented by multiple observations. N/A = estimate not attempted or not possible.

Reach	Run TotCap[a]	Depltn[b]	Ptrsn[c]	Flat TotCap	Depltn	Ptrsn	Glide TotCap	Depltn	Ptrsn	Pool TotCap	Depltn	Ptrsn
Headwaters												
Observed	0	N/A	N/A	N/A	N/A	N/A	0.06	0.07	0.07	N/A	N/A	N/A
Observed	0						0.07	0.07				
Predict-F[d]	0.01	0.01	0.12	0.56	0.56	1.55	0.01	0.01	0.12	0.24	0.24	0.57
Predict-R[e]	0.00	0.00	0.00	0.22	0.22	1.22	0.00	0.00	0.00	0.22	0.22	1.22
Upstream												
Observed	N/A	N/A	N/A	0.84	0.88	0.95	N/A	N/A	N/A	0.04	0.04	0.06
Observed				0.53	0.53					0.06	0.06	
Predict-F	0.01	0.01	0.12	0.56	0.56	1.49	0.01	0.01	0.12	0.24	0.24	0.55
Predict-R	0.00	0.00	0.01	0.22	0.22	1.22	0.00	0.00	0.01	0.22	0.22	1.22
Downstream												
Observed	N/A	N/A	N/A	6.15	6.15	6.15	0	N/A	N/A	N/A	N/A	N/A
Observed				2.90	2.90		0					
Predict-F	0.01	0.01	0.11	0.56	0.56	1.42	0.01	0.01	0.11	0.24	0.24	0.54
Predict-R	0.01	0.01	0.01	0.22	0.22	1.22	0.01	0.01	0.01	0.22	0.22	1.22
Mouth												
Observed	0.03	0.03	0.03	N/A	N/A	N/A	N/A	N/A	N/A	0.73	0.79	0.99
Observed	0.03	0.03								0.65	0.65	
Predict-F	0.01	0.01	0.11	0.56	0.56	1.36	0.01	0.01	0.11	0.24	0.24	0.52
Predict-R	0.03	0.03	0.07	0.22	0.22	1.22	0.03	0.03	0.07	0.22	0.22	1.22

Notes:
a. TotCap = Total larvæ captured at the site in one visit
b. Depltn = Zippin's Removal Method Estimate
c. Ptrsn = Petersen's Capture-Mark-Recapture Method Estimate
d. Predict-F = Density Predicted by the "Full" Model (i.e. all sites).
e. Predict-R = Density Predicted by the "Reduced" Model (i.e. only sites with larvæ present).

Table 7d. Bronte Creek observed and predicted densities (m^{-2}) in relation to habitat type. Sites were visited more than once, and are thus represented by multiple observations. N/A = estimate not attempted or not possible.

Reach	Run TotCap[a]	Depltn[b]	Ptrsn[c]	Flat TotCap	Depltn	Ptrsn	Glide TotCap	Depltn	Ptrsn	Pool TotCap	Depltn	Ptrsn
Headwaters												
Observed	N/A	N/A	N/A	0	N/A	4.1	N/A	N/A	N/A	0	N/A	N/A
Observed				0.24	0.35	0.93				0		
Observed				0.38	0.43	0.80						
Observed				0.08	0.10							
Observed				0.10	0.10							
Predict-F[d]	-0.09	-0.09	0.08	0.16	0.16	1.09	-0.09	-0.09	0.08	0.03	0.03	0.44
Predict-R[e]	0.00	0.00	0.00	0.22	0.22	1.22	0.00	0.00	0.00	0.22	0.22	1.22
Upstream												
Observed	N/A	N/A	N/A	0.34	0.49	1.3	0	N/A	N/A	N/A	N/A	N/A
Observed				0.43	0.57	1.3	0					
Observed				0.32	0.87	0.91						
Observed				0.21	0.21							
Predict-F	-0.03	-0.03	0.16	0.36	0.36	2.23	-0.03	-0.03	0.16	0.14	0.14	0.71
Predict-R	0.00	0.00	0.00	0.22	0.22	1.22	0.00	0.00	0.00	0.22	0.22	1.22
Downstream												
Observed	0	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	0.20	0.29	3.56
Observed	0											
Predict-F	-0.00	-0.00	0.17	0.51	0.51	2.44	-0.00	-0.00	0.17	0.22	0.22	0.75
Predict-R	0.00	0.00	0.00	0.22	0.22	1.22	0.00	0.00	0.00	0.22	0.22	1.22
Mouth												
Observed	0	N/A	N/A	N/A	N/A	N/A	0.00	0.00	N/A	N/A	N/A	N/A
Observed	0						0.00	0.00				
Observed							0.00					
Predict-F	0.01	0.01	0.13	0.56	0.56	1.67	0.01	0.01	0.13	0.24	0.24	0.60
Predict-R	0.00	0.00	0.00	0.22	0.22	1.22	0.00	0.00	0.00	0.22	0.22	1.22

Notes:
a. TotCap = Total larvæ captured at the site in one visit
b. Depltn = Zippin's Removal Method Estimate
c. Ptrsn = Petersen's Capture-Mark-Recapture Method Estimate
d. Predict-F = Density Predicted by the "Full" Model (i.e. all sites).
e. Predict-R = Density Predicted by the "Reduced" Model (i.e. only sites with larvæ present).

Table 7e. Soper's Creek observed and predicted densities (m^{-2}) in relation to habitat type. All sites but one were visited more than once, and are thus represented by multiple observations. N/A = estimate not attempted or not possible.

Reach	Run TotCap[a]	Run Depltn[b]	Run Ptrsn[c]	Flat TotCap	Flat Depltn	Flat Ptrsn	Glide TotCap	Glide Depltn	Glide Ptrsn	Pool TotCap	Pool Depltn	Pool Ptrsn
Headwaters												
Observed	N/A	N/A	N/A	0.52	0.52	N/A	N/A	N/A	N/A	0.73	0.77	0.73
Observed				1.12	1.12					0.07	0.07	
Observed										0.07	0.07	
Predict-F[d]	0.01	0.01	0.14	0.55	0.55	1.87	0.01	0.01	0.14	0.24	0.24	0.64
Predict-R[e]	0.00	0.00	0.00	0.22	0.22	1.22	0.00	0.00	0.00	0.22	0.22	1.22
Upstream												
Observed	0	N/A	N/A	N/A	N/A	N/A	0	N/A	N/A	N/A	N/A	N/A
Observed	0						0					
Predict-F	0.01	0.01	0.13	0.56	0.56	1.69	0.01	0.01	0.13	0.24	0.24	0.60
Predict-R	0.00	0.00	0.00	0.22	0.22	1.22	0.00	0.00	0.00	0.22	0.22	1.22
Downstream												
Observed	N/A	N/A	N/A	N/A	N/A	N/A	0	N/A	N/A	0.67	0.67	N/A
Observed							0					
Predict-F	0.01	0.01	0.12	0.56	0.56	1.54	0.01	0.01	0.12	0.24	0.24	0.56
Predict-R	0.00	0.00	0.00	0.22	0.22	1.22	0.00	0.00	0.00	0.22	0.22	1.22
Mouth												
Observed	0	N/A	N/A	0.05	0.05	1.16	N/A	N/A	N/A	N/A	N/A	N/A
Observed	0			1.07	1.12							
Observed				0.63	0.68							
Predict-F	0.01	0.01	0.11	0.56	0.56	1.40	0.01	0.01	0.11	0.24	0.24	0.53
Predict-R	0.01	0.01	0.02	0.22	0.22	1.22	0.01	0.01	0.02	0.22	0.22	1.22

Notes:
a. TotCap = Total larvæ captured at the site in one visit
b. Depltn = Zippin's Removal Method Estimate
c. Ptrsn = Petersen's Capture-Mark-Recapture Method Estimate
d. Predict-F = Density Predicted by the "Full" Model (i.e. all sites).
e. Predict-R = Density Predicted by the "Reduced" Model (i.e. only sites with larvæ present).

from the following equation:

$$\delta = (-1/(b_0 + b_1 \cdot F + b_2 \cdot Pl + b_3 \cdot P + b_4 \cdot R \cdot A \cdot P + b_5 \cdot (R \cdot A)^3)) - 0.4,$$

where the b's are estimated regression coefficients (Table 8), A is the total treated area of the stream (ha), $F = 1$ if the site is a flat-type (Table 2) habitat (0 otherwise), $Pl = 1$ if the site is a pool-type (Table 2) habitat (0 otherwise), $P = 1$ if a Petersen-type estimate is desired, and R is a coded reach value:

$$R = 1.125 - 0.25 \cdot Rn, \text{ where}$$

$Rn = 1$ for the Headwaters Reach, $Rn = 2$ for the Upstream Reach, $Rn = 3$ for the Downstream Reach, and $Rn = 4$ for the Mouth Reach.

Alternatively, the reduced model yielded the following prediction equation:

$$\delta = (p_1 \cdot RG + p_2 \cdot FP) \cdot (4/(b_0 + b_1 \cdot P + b_4 \cdot R \cdot A \cdot RG)), \text{ where}$$

the p's are estimated probabilities, $RG = 1$ if the site is a run-type or glide-type (Table 2) habitat (0 otherwise), $FP = 1$ if the site is a flat-type or pool-type habitat (0 otherwise), and the others are as before. Again, both equations result from the inverse transformation of the fitted models. The coefficients for both models are detailed in Table 8.

Stream-wide Density Estimates -- The five streams of this study range from 2.57 to 26.2 ha (mean 11.0 ha) in area, and have average estimated (full-model) larval populations of 13900 stream^{-1}. The estimated populations and densities, as well as the approximate 95% confidence intervals, for each stream are shown in Table 9.

Table 8. Estimated regression coëfficients, with their standard errors and significance levels, for the larval density estimation model equations (see text).

Coëfficient	Estimate	Standard Error	P-value
Full Model			
b_0	-2.445	$6.844 \cdot 10^{-2}$	0
b_1	1.405	$9.772 \cdot 10^{-2}$	0
b_2	$8.839 \cdot 10^{-1}$	$1.030 \cdot 10^{-1}$	$1.266 \cdot 10^{-14}$
b_3	$4.637 \cdot 10^{-1}$	$1.673 \cdot 10^{-1}$	$6.309 \cdot 10^{-3}$
b_4	$2.888 \cdot 10^{-2}$	$1.445 \cdot 10^{-2}$	$4.741 \cdot 10^{-2}$
b_5	$-6.307 \cdot 10^{-5}$	$1.275 \cdot 10^{-5}$	$2.054 \cdot 10^{-6}$
Reduced Model			
p_1	$3.010 \cdot 10^{-1}$	$9.353 \cdot 10^{-2}$	
p_2	$9.284 \cdot 10^{-1}$	$5.777 \cdot 10^{-2}$	
b_0	4.108	$4.677 \cdot 10^{-1}$	$1.010 \cdot 10^{-4}$
b_1	-2.362	1.077	$3.044 \cdot 10^{-2}$
b_2	7.645	$5.045 \cdot 10^{-1}$	$1.006 \cdot 10^{-4}$

Table 9. Total predicted stream areas and larval populations by stream from each of the model equations detailed in the text. Values in parentheses are approximate 95 % confidence intervals, symmetric on the transformed scale, about the means.

Stream	Area (ha)	Full Model Population (10^3 larvæ)	Reduced Model Population (10^3 larvæ)
Wilmot's	12.82	14.3 (6.89,27.3)	7.97 (3.62, 14.3)
Cobourg	7.643	14.4 (7.88,26.2)	7.59 (4.53, 12.7)
Bowmanville	2.573	5.81 (4.08, 8.21)	2.72 (1.59, 4.90)
Bronte	26.20	28.0 (6.84,50.6)	7.93 (2.18,28.8)
Soper's	5.638	8.77 (4.62,21.7)	2.68 (1.38, 5.42)

Larval Behaviour under Treatment -- Larvæ may respond to the presence of lampricide by leaving the substrate, by burrowing more deeply into the substrate, or by maintaining their location in the substrate. It was not possible from observations of caged larvæ to discriminate reliably between the latter two cases. Most larvæ within cages responded to the presence of lampricide by leaving their burrows, and this was generally coincident with the same response by larvæ at large in the site. A small number (7) of 163 caged larvæ died within the substrate. The estimated probability (normal approximation) of an individual leaving the substrate during treatment was 0.96 (N = 163; r = 156; p_{hat} = μ_{hat} = 0.96; q_{hat} = 0.043; [sd] = $(pq/n)^{\frac{1}{2}}$ = 0.016).

Treatment Collections -- During lampricide treatment, actively swimming larvæ were collected from a total of 10 previously surveyed sites. As well, these sites were repeatedly scoured for exposed, inactive or dead larvæ on the surface of the substrate up to 3 hours after cessation of treatment. In each case, the number of larvæ in the treatment collection from a site was within the fiducial limits of depletion and/or Petersen estimates already conducted there.

Discussion

The results of this study make it possible, given the width and habitat profiles of a stream, to predict larval sea lamprey densities on a streamwide basis. Point estimates of density are still possible if only information on stream width is available (i.e. in the absence of a habitat survey). The major difficulty with the method, however, is the considerable time required to survey a stream as to habitat and size. It is likely that reliable estimates, though, can be generated after a total of about one week of work per stream.

The importance of comprehensive habitat surveys is seen in comparing population estimates for Wilmot's Creek with those for Cobourg Brook (Table 9). Although the former has almost twice the treated area of the latter, the estimated populations are virtually identical. Cobourg Brook has relatively more flat- and pool-type habitats (the more densely populated categories) than does Wilmot's Creek. Similarly, Bronte Creek has more than 10 times the area of Bowmanville Creek, but has less than 5 times the estimated population, again due to differing habitat distribution profiles. Without habitat surveys, the only difference one would discern might be those based solely on stream area.

A "full" model was fitted to the vector of observations including null catches, while a "reduced" model was fitted to the vector of observations including only inhabited sites. For the reduced model, density estimates were then multiplied by the estimated probability of larval presence. Each method has distinct advantages and disadvantages. Neither results in noticeably tighter estimates, though the reduced model predicts substantially lower total populations, and ensures that the predicted density will be

positive. Several pieces of evidence, however, suggest that these reduced model estimates are almost certainly too low. Firstly, concurrent work by others (using a different protocol) on Wilmot's and Bronte creeks produced streamwide population estimates at least an order of magnitude higher than those from the reduced model (Jerry Weise, Department of Fisheries and Oceans, Sea Lamprey Control Centre, Sault Ste Marie, Ontario, personal communication). Secondly, on the day of treatment on Bowmanville Creek, we scoured the stream for dead larvæ, with the aim of recovering marked animals. Our primary efforts were concentrated in areas near sites where we had previously released marked animals. We had released a total of 173 marked larvæ in Bowmanville Creek, and we examined a total of 619 for marks. Ten of those 619 were marked. If we assume the probability of finding a marked animal to be distributed as a Poisson random variable, the total streamwide population is more likely to be the full model estimate than that from the reduced model (Snedecor and Cochran 1980).

$$n = 619; \quad r = 10; \quad p = 173/2718 \text{ (reduced)}; \quad p = 173/5810 \text{ (full)};$$

$$\mu = n \cdot p = 39.4 \text{ (reduced)} = 18.4 \text{ (full)};$$

$$P(r \leq 10) = 2.55 \cdot 10^{-8} \text{ (reduced)} = 2.45 \cdot 10^{-2} \text{ (full)}., \text{ where}$$

n is the number of animals examined for marks, r is the number of successes (marked animals), p is the proportion of marked animals in the population, μ is the expected mean number of successes, and $P(r \leq 10)$ is the probability of finding 10 or fewer marked animals in a sample of this size.

Although eight sites per stream were sampled in this study, it is unclear what the optimum number might be. The question of how sampling effort should be distributed among habitat types within a stream, however,

has been clarified by the efforts of this study. The optimum sampling regime under stratification by habitat categories, as defined here, is a function of the variability in density on each habitat, and the relative cost of sampling each of the habitat types (Snedecor and Cochran 1980). Only temporal costs are considered here, but they will usually represent the largest portion of economic costs. The time required to sample a site is directly related to the total number of samplings required to deplete the subpopulation, and of the density of animals present (handling time). Regardless of density, a minimum of two complete samplings must be conducted at each site. Run-type habitats never required more than two samplings, and also had the lowest average densities. By assigning a nominal cost of 1 to runs, the other surveyed habitats were related to runs in order to estimate their relative cost of sampling. For example, flats on average required 2.6 times the number of samplings as did runs, and had 81 times the density; flats therefore take an average of about $3\frac{1}{2}$ times as long to sample as do runs of an equal size. The cost of sampling flats relative to runs was thus set at 3.5. Estimates of this type do not need to be especially accurate to optimise sampling, but it is best if they are reasonable (Snedecor and Cochran 1980). The assumed costs for all habitat types are detailed in Table 10.

The proportion of samples which should focus on any habitat, h, is given by (Snedecor and Cochran 1980):

$$p_h = e_h \, / \, \Sigma \, e_h, \text{ where}$$

$$e_h = (P_h \cdot S_h) \, / \, (c_h)^{\frac{1}{2}}, \text{ and where}$$

p_h is the proportion of samples from habitat h, e_h is the sampling effort devoted to habitat h, P_h is the proportion of the useful habitat in the stream

Table 10. Comparative temporal costs and standard deviations, by habitat, for allocation of sampling sites. Run-type habitats are assigned a base cost of 1 unit; all others are as compared to runs.

	Run	Flat	Glide	Pool
Average number of samplings per visit	2.00	5.18	2.20	4.40
Samplings cost (1)	1.00	2.59	1.10	2.20
Average density (larvæ / 10 m^2)	$5.12 \cdot 10^{-2}$	4.15	$1.03 \cdot 10^{-1}$	2.13
Density cost (2)	1.00	$8.10 \cdot 10^{1}$	2.01	$4.16 \cdot 10^{1}$
c_h = Assumed cost	1.00	3.50	1.10	2.43
S_h = Standard deviation	$7.33 \cdot 10^{-2}$	$6.75 \cdot 10^{-1}$	$1.50 \cdot 10^{-1}$	$6.56 \cdot 10^{-1}$
$S_h \div (c_h)^{\frac{1}{2}}$	$7.33 \cdot 10^{-2}$	$3.61 \cdot 10^{-1}$	$1.43 \cdot 10^{-1}$	$4.21 \cdot 10^{-1}$

of type h, S_h is the standard deviation of the mean density in habitat h, and c_h is the relative cost of sampling habitat h. This method of allocating samples to the various habitats minimises both the cost of sampling and the standard error about the mean density for that minimum cost (Snedecor and Cochran 1980). For example, Bronte Creek is composed of (average values) 10% run, 19% flat, 20% glide and 12% pool, for a total of 61% usable area. Of this 61%, 0.16 is the proportion run, 0.31 is the proportion flat, 0.33 is the proportion glide, and 0.20 is the proportion pool. These are the P_h values in the above equation. Substitution of these, and the figures from Table 10, reveal that a total sampling effort (Σ e_h) of 0.2549 is required. Thus 5% of the sampled sites should be runs, 44% should be flats, 18% should be glides and 33% should be pools. This is far from the 25% equal allocation used in this study. Implementation of these allocation guidelines on Bronte Creek would reduce the average standard error about the mean across habitat types by 26.9 % over the equal allocation situation (Snedecor and Cochran 1980). Since these values are calculable only after the standard errors and relative costs associated with sampling each of the habitats is known, the results of this study can be used, at least as a first approximation, in the design of future investigations of this sort.

Of the three estimation methods employed, Petersen estimates were significantly higher (by an average of 300 %) and more variable than either total captures or removal estimates. In many cases, it was felt that point estimates of abundance by Petersen's method grossly over-represented the number of animals present in a site, and it seems clear that adherence of the experimental protocol to the assumption of a closed population over the sampling interval was suspect at best. Zippin's method assumes either a

closed population, or that immigration equals emigration during sampling. These are more realistic assumptions, since an estimate is procured in but one visit to the site. Petersen estimates require that an interval elapse between visits, and that the population remain closed over this interval. The alternative assumption that immigration equals emigration is not appropriate in the Petersen case, since, with the Petersen method, immigration of animals to the study area has the effect of "diluting" the number of marked animals in the site, resulting in an overestimate of N. Emigration will affect N only if marked and unmarked animals have different probabilities of emigration. Since it is impractical to block the upper and lower ends of a site over the interval between visits, we should expect, if larvæ move about in the stream, that the Petersen method will consistently overestimate density. This is likely the case in the present study. For studies such as this one, where sampling is done in sites of relatively small area (increasing the chance of immigration or emigration), removal method estimates are more accurate than Petersen estimates.

Treatment collections did little to clarify the question of estimation method accuracy, as the 95% confidence limits for Petersen estimates were always broad enough to include both removal estimates and treatment collection values. On the other hand, removal method confidence limits seldom included Petersen estimates on a given site, but did include treatment collection values. An attempt to estimate the magnitude of immigration to and emigration from a site, using Ricker's two release method (Ricker 1975), yielded widely fluctuating results. At the Bronte Creek upstream flat site, estimates of 20 to 80% replacement were found, roughly at 3 week intervals. This means that from 20 to 80% of animals at the site were not there on the

previous sampling occasion about 3 weeks earlier. Removal method estimates on the same dates, however, were fairly consistent, suggesting that, while animals move substantially within the stream, the density at any one site is fairly stable. This implies, then, that average rates of immigration to and emigration from sites are large, but roughly equal. Therefore, the arrival of numbers of (unmarked) immigrants to the population will consistently result in overestimates of the number of animals present. Regardless, this situation argues for the use of the removal method for density estimates as conducted here.

The significant interaction between Petersen estimates and the stream surface area below a site, and the absence of such an interaction with the removal estimates, means that Petersen estimates are consistently higher in upper stream sections than in lower reaches. Animals, then, must be more mobile in the upper sections of a stream. This may be associated with differences in gradient, since some investigators have reported that larval movement is largely passive (Hardisty and Potter 1971a). The gradient in streams is often greatest in the upper reaches. At the same time, densities in general fall off quite rapidly in the upper sections of the largest streams, suggesting that adult sea lamprey will not necessarily penetrate a stream as far as possible on the upstream migration. Densities in Wilmot's and Bronte creeks are near minimum about 12 km from the estuary. The average width of the lower 12 km of Bronte Creek is about 13 m, while that for Wilmot's Creek is about 8 m. If spawning habitat is assumed not to be limiting, the size of spawning run typical of Bronte Creek is fully accommodated by about 16 ha of stream surface area, while those on Wilmot's Creek cover some 10 ha. In this sense, then, the full model equation breaks down, as a predictive tool,

only in the upper reaches of these two streams, by providing negative density predictions on the untransformed scale (Table 7). The large areas of these streams make the final term in the full model equation larger than the sum of the preceding terms.

Conclusions -- The first requirement in estimating streamwide larval numbers is the production of models of stream size and habitat distributions. The methods used here, although temporally expensive, produced polynomial models capable of explaining from 30 to 80% of the observed variance in these physical parameters.

Secondly, estimates of larval density for each of the habitat types are required. The electrofishing techniques, in conjunction with Zippin's (1956) removal method, produced estimates which were consistent in repeated measures on the same sites, and which proved to be accurate when compared to numbers revealed by chemical treatment.

Standard model-building techniques permitted rejection of several potential predictors as relatively unimportant in this study. Among these were water temperature, season (fall vs spring), reach classifications per se, and total area of the site. The most important predictors were found to be habitat type and stream area below a given site. These variables, given the estimation methods used and interactions terms, explained 66% of the observed variation in larval density. A two-stage model which modelled separately larval density and probability of presence produced excessively small population estimates. Streams greater than 10 ha in treated area tended to have unusually low densities in the upper sections.

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APPENDICES

Appendix 1

Detailed Electrofishing Records

WILMOT'S CREEK

Headwaters-Pool -- Site Area=66.3 m^2

Date	Temp		Total Capture	Mortalities	Depletion Estimate	V(Dpltn)	Petersen Estimate	V(Ptrsn)	Pass No	No
	Air	Water								
10/28/88	8	6	13	13	18	62.7673	N/A	N/A	1	2
									2	2
									3	4
									4	2
									5	1
									6	2
									7	0
11/12/88	9	6	0	0	N/A	N/A	N/A	N/A	1	0
									2	0

Headwaters-Flat -- Site Area=10.8 m^2

Date	Temp		Total Capture	Mortalities	Depletion Estimate	V(Dpltn)	Petersen Estimate	V(Ptrsn)	Pass No	No
	Air	Water								
10/29/88	10	6	8	0	9	3.94644	N/A	N/A	1	4
									2	1
									3	3
									4	0
11/12/88	9	6	6	0	6	N/A	48	1715.74	1	6
									2	0
									3	0

Upstream-Run -- Site Area=29.7 m^2

Date	Temp		Total Capture	Mortalities	Depletion Estimate	V(Dpltn)	Petersen Estimate	V(Ptrsn)	Pass No	No
	Air	Water								
10/29/88	10	6	0	0	N/A	N/A	N/A	N/A	1	0
									2	0
11/11/88	8	6	0	0	N/A	N/A	N/A	N/A	1	0
									2	0

Upstream-Flat -- Site Area=17.7 m^2

Date	Temp		Total Capture	Mortalities	Depletion Estimate	V(Dpltn)	Petersen Estimate	V(Ptrsn)	Pass No	No
	Air	Water								
10/29/88	11	6	0	0	N/A	N/A	N/A	N/A	1	0
									2	0
11/11/88	11	6	3	3	3	N/A	N/A	N/A	1	3
									2	0

WILMOT'S CREEK

Downstream-Glide -- Site Area=62.4 m^2

Date	Temp		Total Capture	Mortalities	Depletion Estimate	V(Dpltn)	Petersen Estimate	V(Ptrsn)	Pass No	No
	Air	Water								
10/29/88	12	6	0	0	N/A	N/A	N/A	N/A	1	0
									2	0
11/11/88	11	6	0	0	N/A	N/A	N/A	N/A	1	0
									2	0

Downstream-Run -- Site Area=49.9 m^2

Date	Air	Water	Total Capture	Mortalities	Depletion Estimate	V(Dpltn)	Petersen Estimate	V(Ptrsn)	Pass No	No
10/29/88	12	6	0	0	N/A	N/A	N/A	N/A	1	0
									2	0
11/11/88	11	6	0	0	N/A	N/A	N/A	N/A	1	0
									2	0

Mouth-Glide -- Site Area=389 m^2

Date	Air	Water	Total Capture	Mortalities	Depletion Estimate	V(Dpltn)	Petersen Estimate	V(Ptrsn)	Pass No	No
10/30/88	9	6	0	0	N/A	N/A	N/A	N/A	1	0
									2	0
11/12/88	7	6	0	0	N/A	N/A	N/A	N/A	1	0
									2	0

Mouth-Pool -- Site Area=30.7 m^2

Date	Air	Water	Total Capture	Mortalities	Depletion Estimate	V(Dpltn)	Petersen Estimate	V(Ptrsn)	Pass No	No
10/30/88	6	6	6	0	7	8.71730	N/A	N/A	1	3
									2	1
									3	1
									4	1
11/12/88	8	6	0	0	N/A	N/A	N/A	N/A	1	0
									2	0

COBOURG BROOK

Headwaters-Glide -- Site Area=29.0 m^2

Date	Temp		Total Capture	Mortalities	Depletion Estimate	V(Dpltn)	Petersen Estimate	V(Ptrsn)	Pass No	No
	Air	Water								
04/23/89	14	9	0	0	N/A	N/A	N/A	N/A	1	0
									2	0
05/18/89	25	9	0	0	N/A	N/A	N/A	N/A	1	0
									2	0

Headwaters-Run -- Site Area=24.2 m^2

Date	Temp		Total Capture	Mortalities	Depletion Estimate	V(Dpltn)	Petersen Estimate	V(Ptrsn)	Pass No	No
	Air	Water								
04/23/89	14	9	0	0	N/A	N/A	N/A	N/A	1	0
									2	0
05/18/89	25	9	0	0	N/A	N/A	N/A	N/A	1	0
									2	0

Upstream-Pool -- Site Area=7.80 m^2

Date	Temp		Total Capture	Mortalities	Depletion Estimate	V(Dpltn)	Petersen Estimate	V(Ptrsn)	Pass No	No
	Air	Water								
04/24/89	14	5	3	0	3	N/A	N/A	N/A	1	3
									2	0
05/18/89	27	11	4	0	4	N/A	12	78.5454	1	4
									2	0

Upstream-Glide -- Site Area=50.2 m^2

Date	Temp		Total Capture	Mortalities	Depletion Estimate	V(Dpltn)	Petersen Estimate	V(Ptrsn)	Pass No	No
	Air	Water								
04/24/89	10	5	0	0	N/A	N/A	N/A	N/A	1	0
									2	0
05/18/89	26	10	0	0	N/A	N/A	N/A	N/A	1	0
									2	0

COBOURG BROOK

Downstream-Flat -- Site Area=22.1 m^2

Date	Temp		Total Capture	Mortalities	Depletion Estimate	V(Dpltn)	Petersen Estimate	V(Ptrsn)	Pass No	No
	Air	Water								
04/23/89	12	7	1	1	1	N/A	N/A	N/A	1	1
									2	0
05/17/89	27	11	1	1	1	N/A	N/A	N/A	1	1
									2	0

Downstream-Pool -- Site Area=7.06 m^2

Date	Air	Water	Total Capture	Mortalities	Depletion Estimate	V(Dpltn)	Petersen Estimate	V(Ptrsn)	Pass No	No
04/23/89	10	4	0	0	N/A	N/A	N/A	N/A	1	0
									2	0
05/17/89	27	10	3	0	4	6.12264	N/A	N/A	1	1
									2	2
									3	0

Mouth-Flat -- Site Area=6.04 m^2

Date	Air	Water	Total Capture	Mortalities	Depletion Estimate	V(Dpltn)	Petersen Estimate	V(Ptrsn)	Pass No	No
04/23/89	16	8	13	0	14	1.20869	N/A	N/A	1	4
									2	7
									3	1
									4	1
									5	0
05/17/89	27	10	13	0	13	0.14798	42.25	219.075	1	10
									2	3
									3	0

Mouth-Run -- Site Area=28.4 m^2

Date	Air	Water	Total Capture	Mortalities	Depletion Estimate	V(Dpltn)	Petersen Estimate	V(Ptrsn)	Pass No	No
04/23/89	16	8	0	0	N/A	N/A	N/A	N/A	1	0
									2	0
05/17/89	27	11	0	0	N/A	N/A	N/A	N/A	1	0
									2	0

BOWMANVILLE CREEK

Headwaters-Glide -- Site Area=53.9 m^2

Date	Temp Air	Water	Total Capture	Mortalities	Depletion Estimate	V(Dpltn)	Petersen Estimate	V(Ptrsn)	Pass No	No
11/25/88	9	5	3	0	4	4.35865	N/A	N/A	1	1
									2	1
									3	1
									4	0
12/03/88	8	4	4	0	4	N/A	4	0	1	4
									2	0

Headwaters-Run -- Site Area=48.3 m^2

Date	Temp Air	Water	Total Capture	Mortalities	Depletion Estimate	V(Dpltn)	Petersen Estimate	V(Ptrsn)	Pass No	No
12/03/88	7	4	0	0	N/A	N/A	N/A	N/A	1	0
									2	0
12/09/88	-4	2	0	0	N/A	N/A	N/A	N/A	1	0
									2	0

Upstream-Pool -- Site Area=69.5 m^2

Date	Temp Air	Water	Total Capture	Mortalities	Depletion Estimate	V(Dpltn)	Petersen Estimate	V(Ptrsn)	Pass No	No
12/03/88	7	4	3	0	3	N/A	N/A	N/A	1	3
									2	0
12/09/88	-4	2	4	0	4	0.05966	4	0	1	3
									2	1
									3	0

Upstream-Flat -- Site Area=26.2 m^2

Date	Temp Air	Water	Total Capture	Mortalities	Depletion Estimate	V(Dpltn)	Petersen Estimate	V(Ptrsn)	Pass No	No
12/02/88	2	4	22	1	23	2.20517	N/A	N/A	1	15
									2	5
									3	2
12/09/88	-3	2	14	0	14	0.09840	24.5	3.19281	1	11
									2	1
									3	2
									4	0

BOWMANVILLE CREEK

Downstream-Glide -- Site Area=39.6 m^2

Date	Temp		Total Capture	Mortalities	Depletion Estimate	V(Dpltn)	Petersen Estimate	V(Ptrsn)	Pass No	No
	Air	Water								
12/02/88	2	4	0	0	N/A	N/A	N/A	N/A	1	0
									2	0
12/09/88	-4	2	0	0	N/A	N/A	N/A	N/A	1	0
									2	0

Downstream-Flat -- Site Area=5.85 m^2

Date	Temp		Total Capture	Mortalities	Depletion Estimate	V(Dpltn)	Petersen Estimate	V(Ptrsn)	Pass No	No
	Air	Water								
11/25/88	8	5	36	4	36	0.45416	N/A	N/A	1	26
									2	6
									3	3
									4	1
12/03/88	6	4	17	1	17	0.57848	36.27	5.63569	1	10
									2	5
									3	2
									4	0

Mouth-Run -- Site Area=33.4 m^2

Date	Temp		Total Capture	Mortalities	Depletion Estimate	V(Dpltn)	Petersen Estimate	V(Ptrsn)	Pass No	No
	Air	Water								
11/25/88	8	5	1	0	1	N/A	N/A	N/A	1	1
									2	0
12/03/88	6	4	1	1	1	N/A	1	N/A	1	1
									2	0

Mouth-Pool -- Site Area=49.4 m^2

Date	Temp		Total Capture	Mortalities	Depletion Estimate	V(Dpltn)	Petersen Estimate	V(Ptrsn)	Pass No	No
	Air	Water								
11/26/88	7	5	36	1	39	8.67741	N/A	N/A	1	16
									2	6
									3	9
									4	5
									5	0
12/03/88	-3	4	32	0	32	0.01078	48.7	10.1500	1	27
									2	3
									3	1
									4	1
									5	0

BRONTE CREEK

Headwaters-Pool -- Site Area=180 m^2

Date	Temp		Total Capture	Mortalities	Depletion Estimate	V(Dpltn)	Petersen Estimate	V(Ptrsn)	Pass No	No
	Air	Water								
09/09/88	21	12	0	0	N/A	N/A	N/A	N/A	1	0
									2	0
10/11/88	12	9	0	0	N/A	N/A	N/A	N/A	1	0
									2	0

Headwaters-Flat -- Site Area=145 m^2

Date	Air	Water	Total Capture	Mortalities	Depletion Estimate	V(Dpltn)	Petersen Estimate	V(Ptrsn)	Pass No	No
09/19/88	12	12	0	0	N/A	N/A	N/A	N/A	1	0
									2	0
09/29/88	21	11	34	2	50	250.966	N/A	N/A	1	7
									2	12
									3	6
									4	7
									5	2
10/06/88	9	9	55	6	62	33.9101	586.7	92340.7	1	41
									2	14
11/22/88	4	5	12	0	14	8.38667	133.7	976.045	1	5
									2	4
									3	2
									4	1
11/29/88	5	5	14	14	15	1.15306	116.2	342.249	1	7
									2	5
									3	2
									4	0

BRONTE CREEK

Upstream–Flat -- Site Area=205 m^2

Date	Temp		Total	Mortalities	Depletion	V(Dpltn)	Petersen	V(Ptrsn)	Pass	No
	Air	Water	Capture		Estimate		Estimate		No	
09/16/88	18	15	70	4	100	387.507	N/A	N/A	1	13
									2	27
									3	17
									4	6
									5	7
09/25/88	21	14	88	0	116	248.795	264	1468.87	1	30
									2	30
									3	20
									4	8
11/15/88	8	7	66	0	179	18199.2	264	567.865	1	4
									2	24
									3	22
									4	12
									5	4
11/24/88	6	5	43	43	45	4.16942	186.7	82.5482	1	20
									2	10
									3	10
									4	2
									5	1

Upstream–Glide -- Site Area=55.2 m^2

Date	Air	Water	Total Capture	Mortalities	Depletion Estimate	V(Dpltn)	Petersen Estimate	V(Ptrsn)	Pass No	No
09/16/88	21	12	0	0	N/A	N/A	N/A	N/A	1	0
									2	0
10/11/88	13	10	0	0	N/A	N/A	N/A	N/A	1	0
									2	0

BRONTE CREEK

Downstream-Pool -- Site Area=126 m^2

Date	Temp		Total Capture	Mortalities	Depletion Estimate	V(Dpltn)	Petersen Estimate	V(Ptrsn)	Pass No	No
	Air	Water								
09/27/88	21	13	19	1	4E+3	4E+11	N/A	N/A	1	3
									2	4
									3	2
									4	8
									5	2
10/13/88	10	9	25	2	37	184.534	450	173920.	1	7
									2	6
									3	5
									4	5
									5	2

Downstream-Run -- Site Area=103 m^2

Date	Air	Water	Total Capture	Mortalities	Depletion Estimate	V(Dpltn)	Petersen Estimate	V(Ptrsn)	Pass No	No
09/27/88	19	10	0	0	N/A	N/A	N/A	N/A	1	0
									2	0
10/13/88	8	9	0	0	N/A	N/A	N/A	N/A	1	0
									2	0

Mouth-Run -- Site Area=118 m^2

Date	Air	Water	Total Capture	Mortalities	Depletion Estimate	V(Dpltn)	Petersen Estimate	V(Ptrsn)	Pass No	No
10/14/88	12	10	0	0	N/A	N/A	N/A	N/A	1	0
									2	0
12/01/88	6	5	0	0	N/A	N/A	N/A	N/A	1	0
									2	0

Mouth-Glide -- Site Area=356 m^2

Date	Air	Water	Total Capture	Mortalities	Depletion Estimate	V(Dpltn)	Petersen Estimate	V(Ptrsn)	Pass No	No
09/23/88	28	13	1	0	1	N/A	N/A	N/A	1	1
									2	0
10/04/88	14	10	1	0	N/A	N/A	N/A	N/A	1	0
									2	1
10/14/88	14	10	1	0	1	N/A	N/A	N/A	1	1
									2	0

SOPER'S CREEK

Headwaters-Flat -- Site Area=13.4 m^2

Date	Temp Air	Water	Total Capture	Mortalities	Depletion Estimate	V(Dpltn)	Petersen Estimate	V(Ptrsn)	Pass No	No
12/10/88	-7	1	7	2	7	0.09963	N/A	N/A	1	5
									2	1
									3	1
									4	0
04/11/89	5	3	16	0	16	0.58584	N/A	N/A	1	7
									2	5
									3	2
									4	1
									5	1
									6	0
04/19/89	7	5	7	0	7	N/A	16	0	1	7
									2	0

Headwaters-Pool -- Site Area=28.6 m^2

Date	Temp Air	Water	Total Capture	Mortalities	Depletion Estimate	V(Dpltn)	Petersen Estimate	V(Ptrsn)	Pass No	No
12/10/88	-7	1	21	0	22	0.88568	N/A	N/A	1	14
									2	7
									3	0
04/11/89	4	3	2	0	2	N/A	21	0	1	2
									2	0
04/19/89	7	5	2	0	2	N/A	N/A	N/A	1	2
									2	0

Upstream-Run -- Site Area=45.5 m^2

Date	Temp Air	Water	Total Capture	Mortalities	Depletion Estimate	V(Dpltn)	Petersen Estimate	V(Ptrsn)	Pass No	No
04/12/89	6	3	0	0	N/A	N/A	N/A	N/A	1	0
									2	0
04/18/89	6	7	0	0	N/A	N/A	N/A	N/A	1	0
									2	0

SOPER'S CREEK

Upstream-Glide -- Site Area=33.2 m^2

Date	Temp		Total	Mortalities	Depletion	V(Dpltn)	Petersen	V(Ptrsn)	Pass	No
	Air	Water	Capture		Estimate		Estimate		No	
04/12/89	6	3	0	0	N/A	N/A	N/A	N/A	1	0
									2	0
04/18/89	6	7	0	0	N/A	N/A	N/A	N/A	1	0
									2	0

Downstream-Glide -- Site Area=51.1 m^2

Date	Air	Water	Capture	Mort	Depletion	V(Dpltn)	Petersen	V(Ptrsn)	Pass	No
04/12/89	4	3	0	0	N/A	N/A	N/A	N/A	1	0
									2	0
04/18/89	5	7	0	0	N/A	N/A	N/A	N/A	1	0
									2	0

Downstream-Pool -- Site Area=7.43 m^2

Date	Air	Water	Capture	Mort	Depletion	V(Dpltn)	Petersen	V(Ptrsn)	Pass	No
04/24/89	16	5	5	0	5	1.36153	N/A	N/A	1	2
									2	2
									3	1
									4	0

Mouth-Run -- Site Area=11.9 m^2

Date	Air	Water	Capture	Mort	Depletion	V(Dpltn)	Petersen	V(Ptrsn)	Pass	No
04/12/89	4	3	0	0	N/A	N/A	N/A	N/A	1	0
									2	0
04/18/89	5	7	0	0	N/A	N/A	N/A	N/A	1	0
									2	0

SOPER'S CREEK

Mouth-Flat -- Site Area=20.6 m^2

Date	Temp		Total Capture	Mortalities	Depletion Estimate	V(Dpltn)	Petersen Estimate	V(Ptrsn)	Pass No	No
	Air	Water								
12/10/88	-7	1	1	1	1	N/A	N/A	N/A	1	1
									2	0
04/12/89	2	3	22	4	23	1.57461	N/A	N/A	1	10
									2	3
									3	6
									4	2
									5	1
									6	0
04/18/89	5	7	13	1	14	2.32599	29.25	23.6604	1	7
									2	6
									3	0

Appendix 2

Electrofishing Field Record Sheets

Watercourse:_____   Date:_____

Reach: Hdwtrs Upstrm Dnstrm Mouth   Ambient T:_____ °C

Habitat Type: Run Flat Glide Pool Area:_____m^2 Water T:_____ °C

Marked Side: L R Colour:_____ Probe Voltage:_____V Frequency:_____Hz

No. of incidental mortalities (all passes):_____   Current:_____Amps

Collecting Conditions:_____

_____

Comments:_____

_____

_____

_____

_____

Recaptures: Mark:_____ Total:_____ Mark:_____ Total:_____ Total:_____

Total non-target ammocoetes (all passes):_____ Total No passes (k):_____

Total *Petromyzon marinus* ammocoetes (all passes) (T):_____Record No:_____

Pass No (i):_____   Page _____ of _____   Record No:_____

mm	Tally	mm	Tally	mm	Tally	mm	Tally
15		59		103		147	
16		60		104		148	
17		61		105		149	
18		62		106		150	
19		63		107		151	
20		64		108		152	
21		65		109		153	
22		66		110		154	
23		67		111		155	
24		68		112		156	
25		69		113		157	
26		70		114		158	
27		71		115		159	
28		72		116		160	
29		73		117		161	
30		74		118		162	
31		75		119		163	
32		76		120		164	
33		77		121		165	
34		78		122		166	
35		79		123		167	
36		80		124		168	
37		81		125		169	
38		82		126		170	
39		83		127		171	
40		84		128		172	
41		85		129		173	
42		86		130		174	
43		87		131		175	
44		88		132		176	
45		89		133		177	
46		90		134		178	
47		91		135		179	
48		92		136		180	
49		93		137		181	
50		94		138		182	
51		95		139		183	
52		96		140		184	
53		97		141		185	
54		98		142		186	
55		99		143		187	
56		100		144		188	
57		101		145		189	
58		102		146		190	

Non-target Ammocoete Tally:_____ Total Non-target Ammocoetes:_____
Recaptures: Mark:_____ Tally:_____ Mark:_____ Tally:_____ Total:_____
Comments (this pass):_____

Total *P. marinus* ammocoetes (this pass) $(y(i))$:_____

Appendix 3

Scatter Plots and Regression Lines
for all Stream Width Models
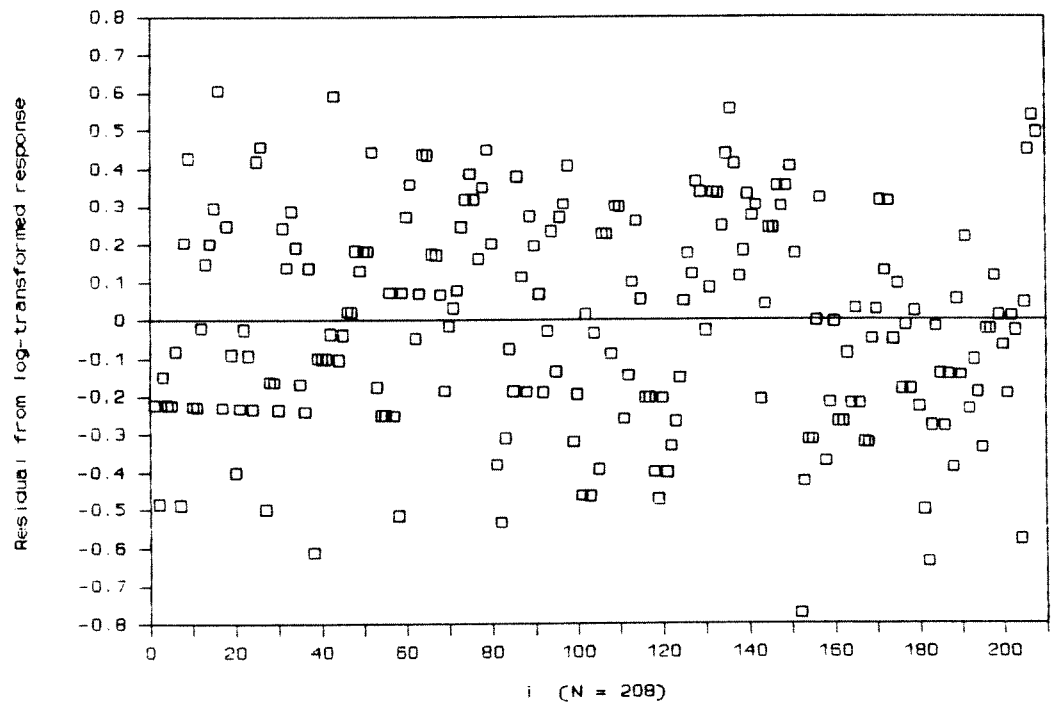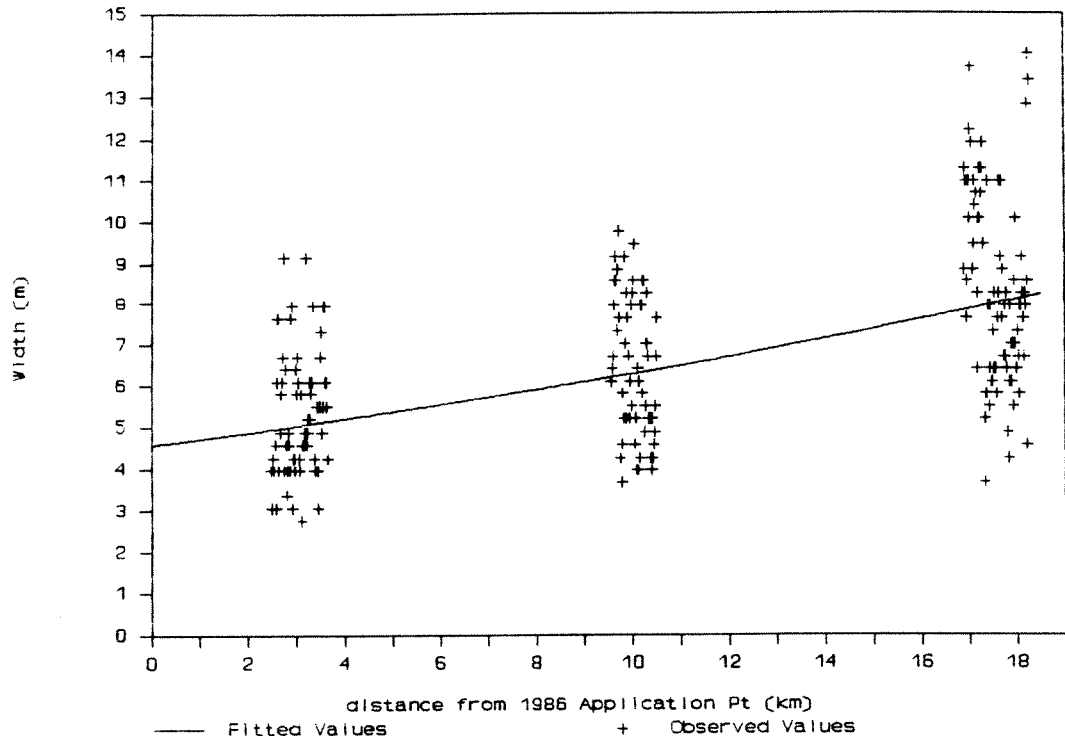
Figure A3 - 1a. Width profile of Wilmot's Creek (upper panel) and its residual plot (lower panel).
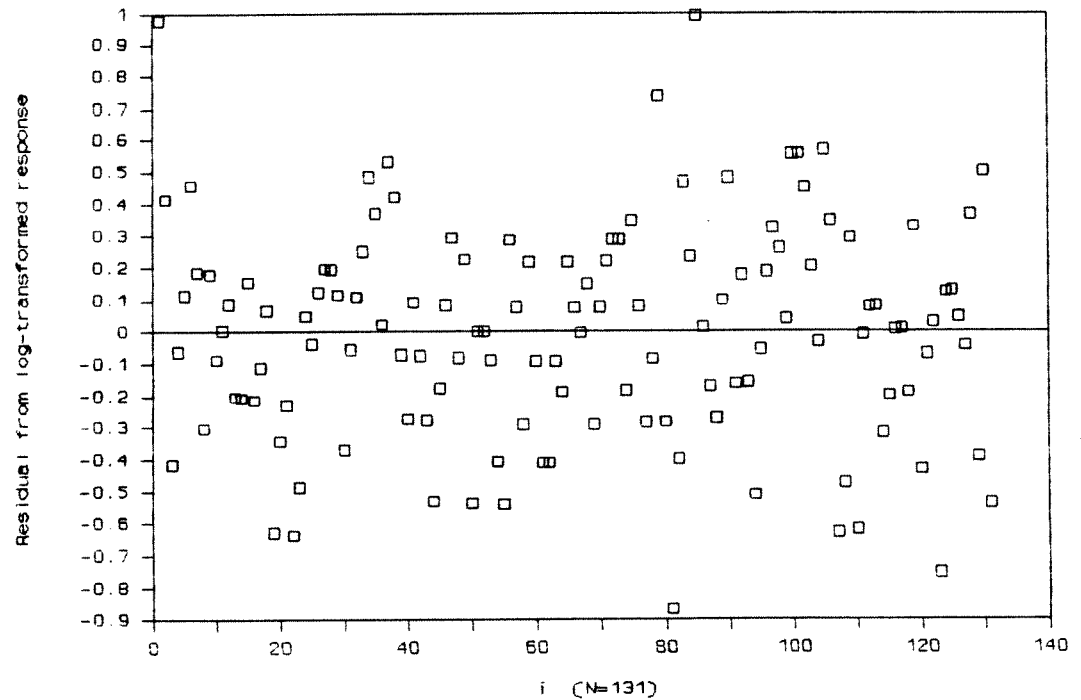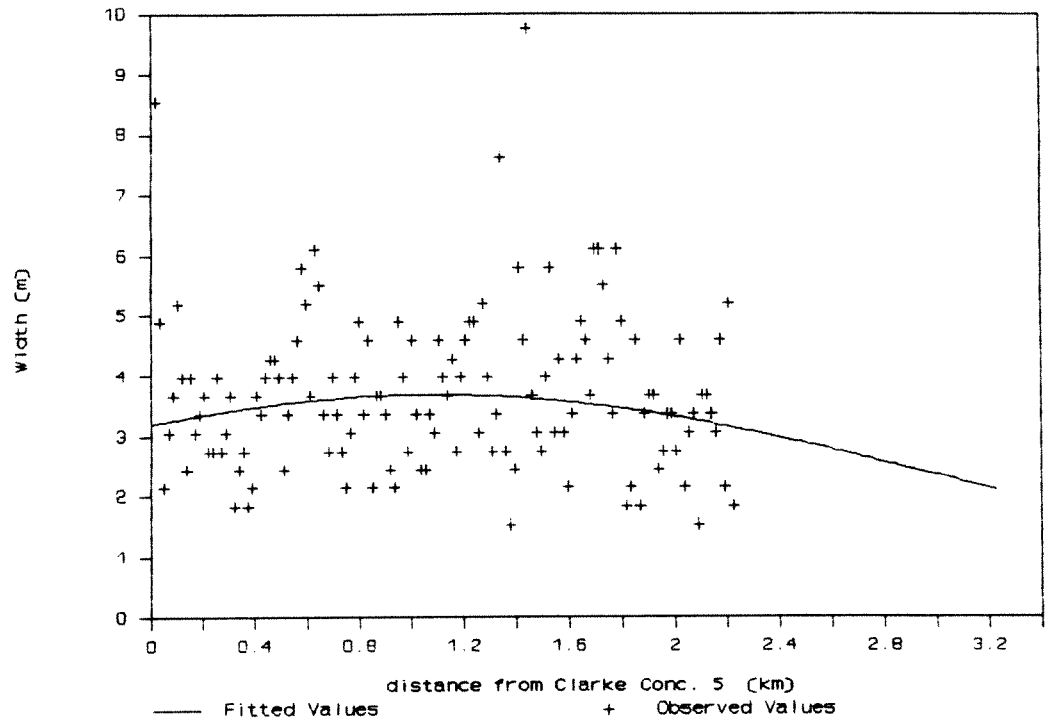
Figure A3 - 1b. Width profile of Orono Creek (upper panel) and its residual scatter plot (lower panel). This stream is a tributary of Wilmot's Creek (Fig. A3 - 1a).
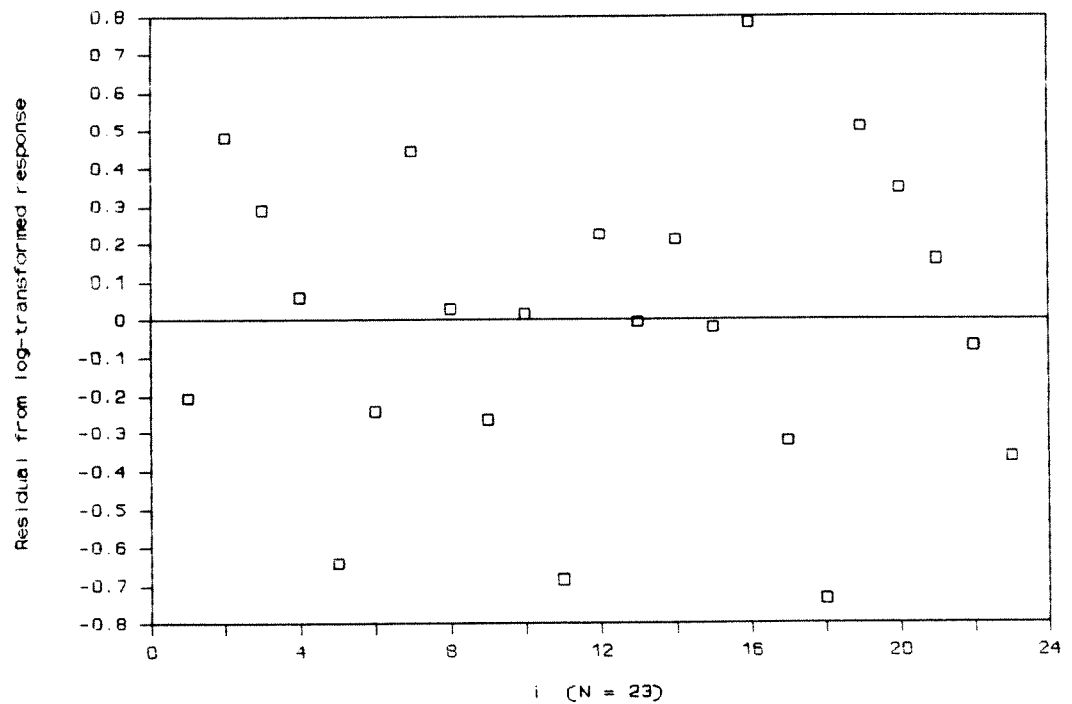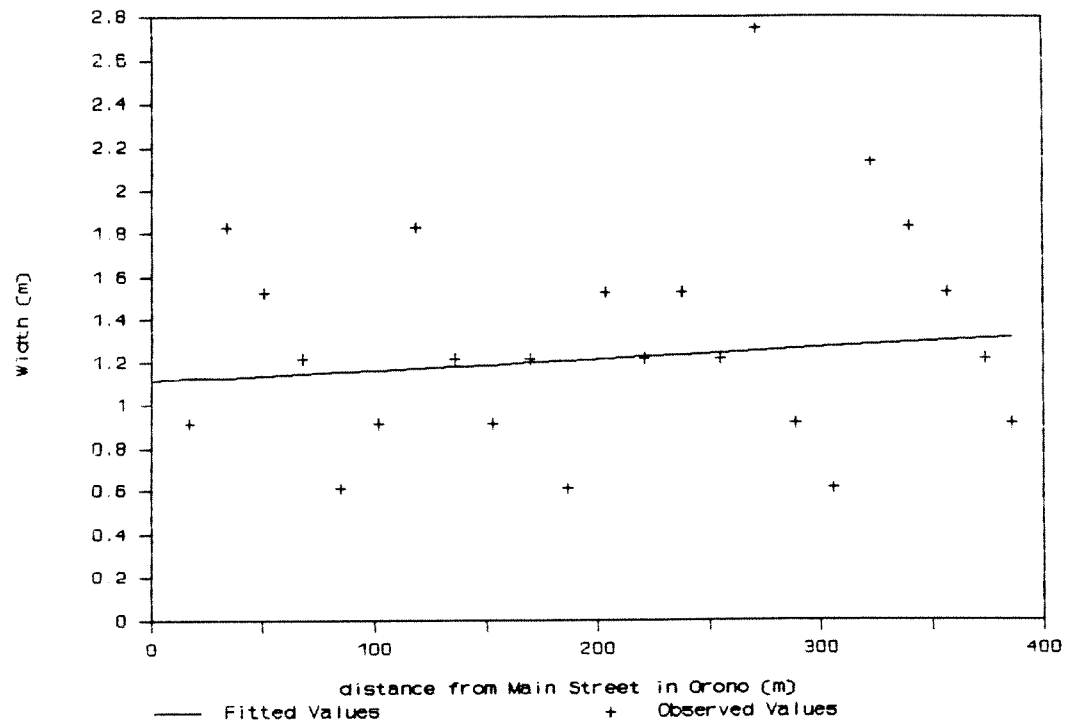
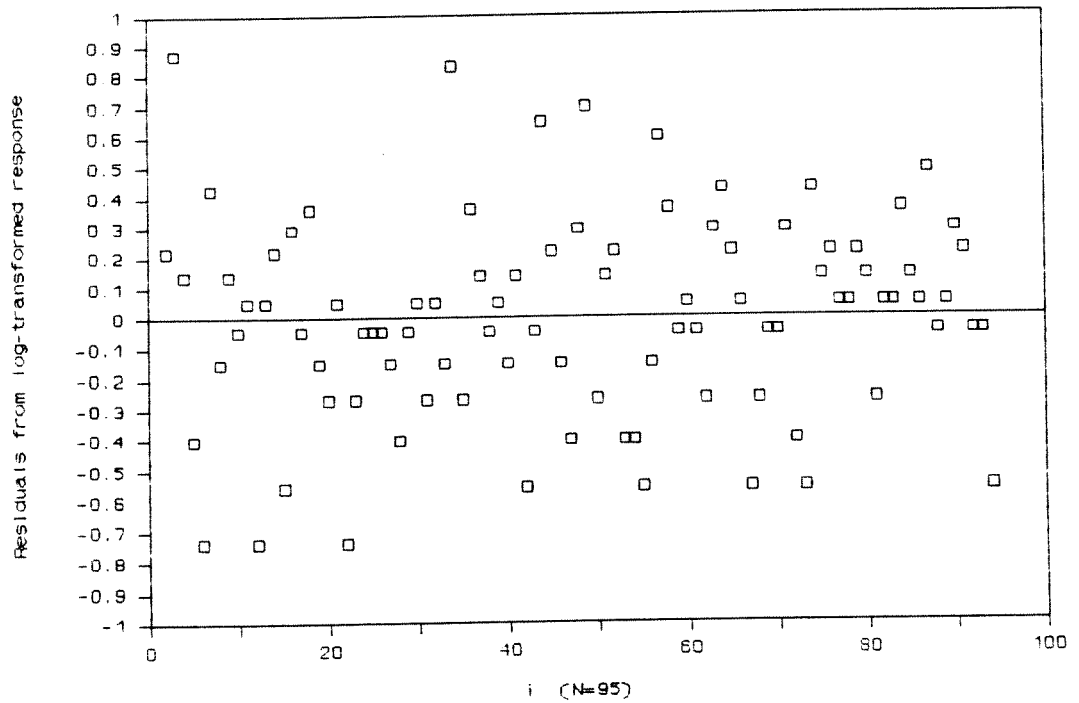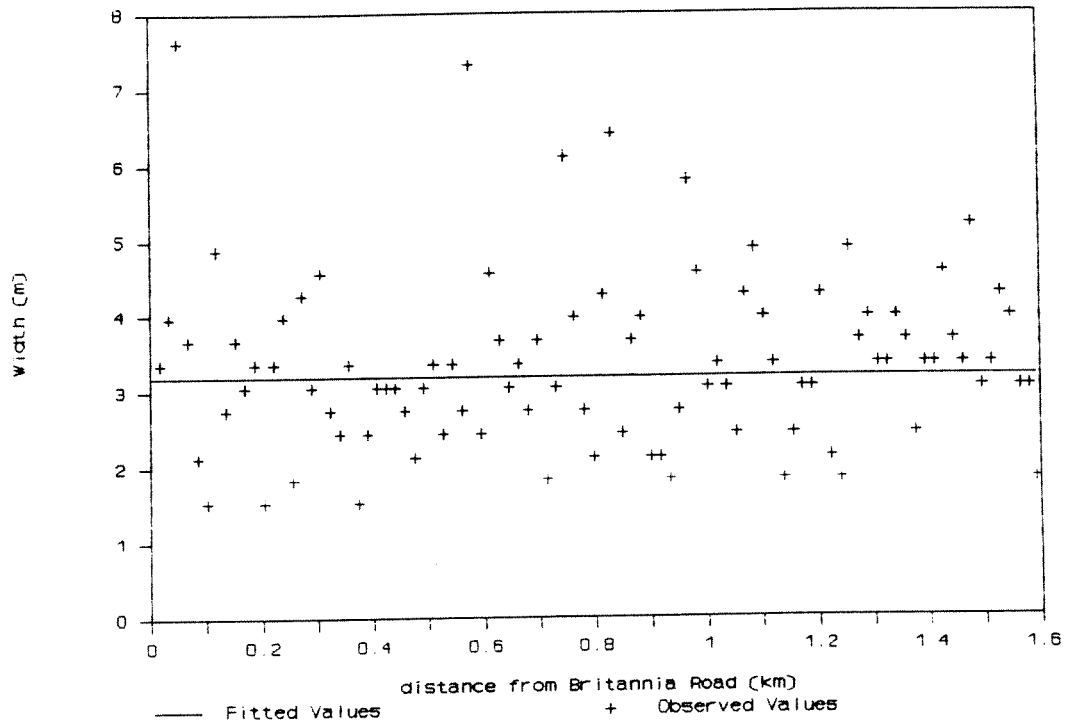**Figure A3 - 1c.** Width profile of eastern branch of Orono Creek (upper panel) and its residuals plot (lower panel). This stream is a tributary of Orono Creek (Fig. A3 - 1b).
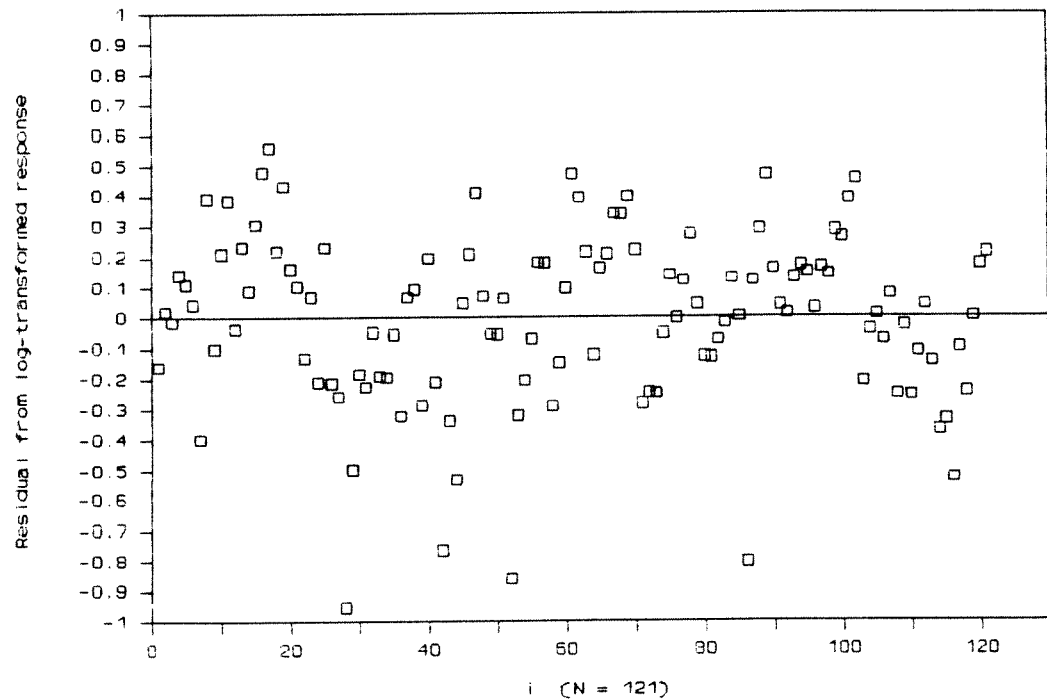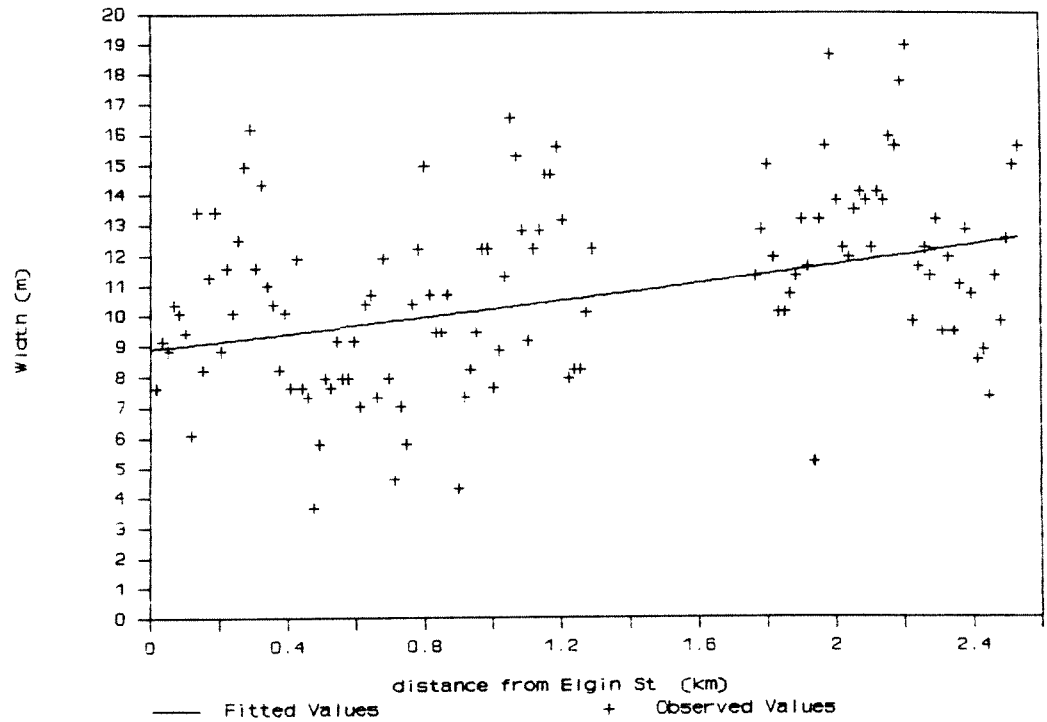
Figure A3 - 2a. Width profile for Cobourg Brook, main channel (upper panel), and its residuals plot (lower panel).
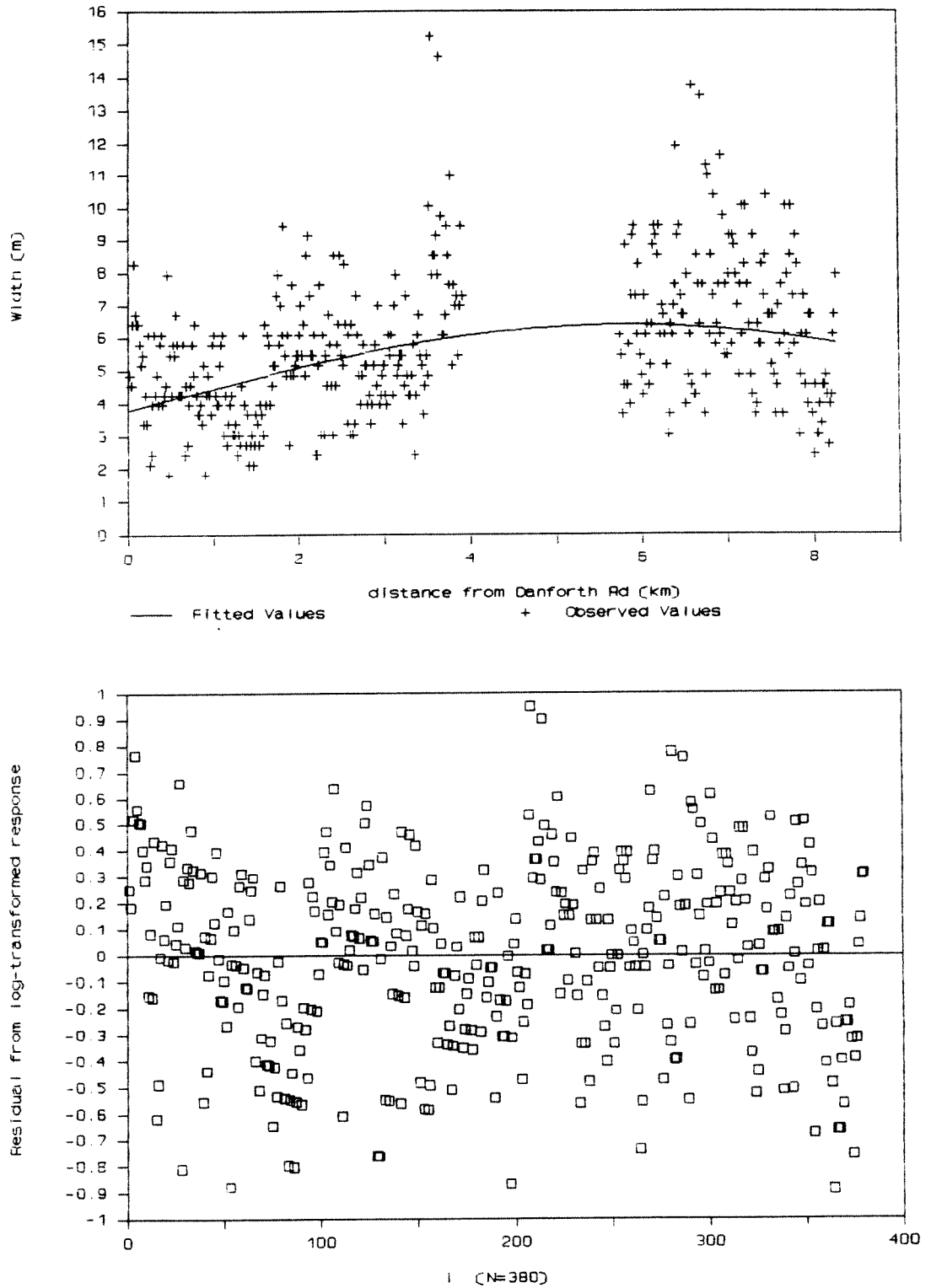
Figure A3 - 2b. Factory Creek width profile (upper panel) and its residuals plot (lower panel). This watercourse is the primary tributary of Cobourg Brook (Fig. A3 - 2a).
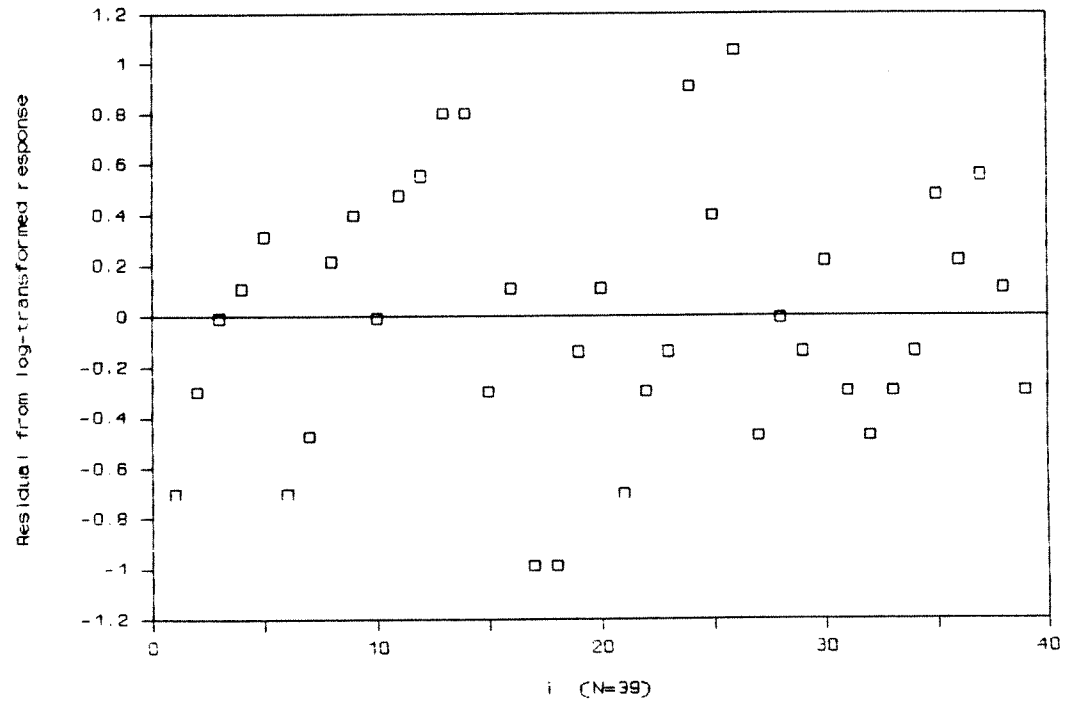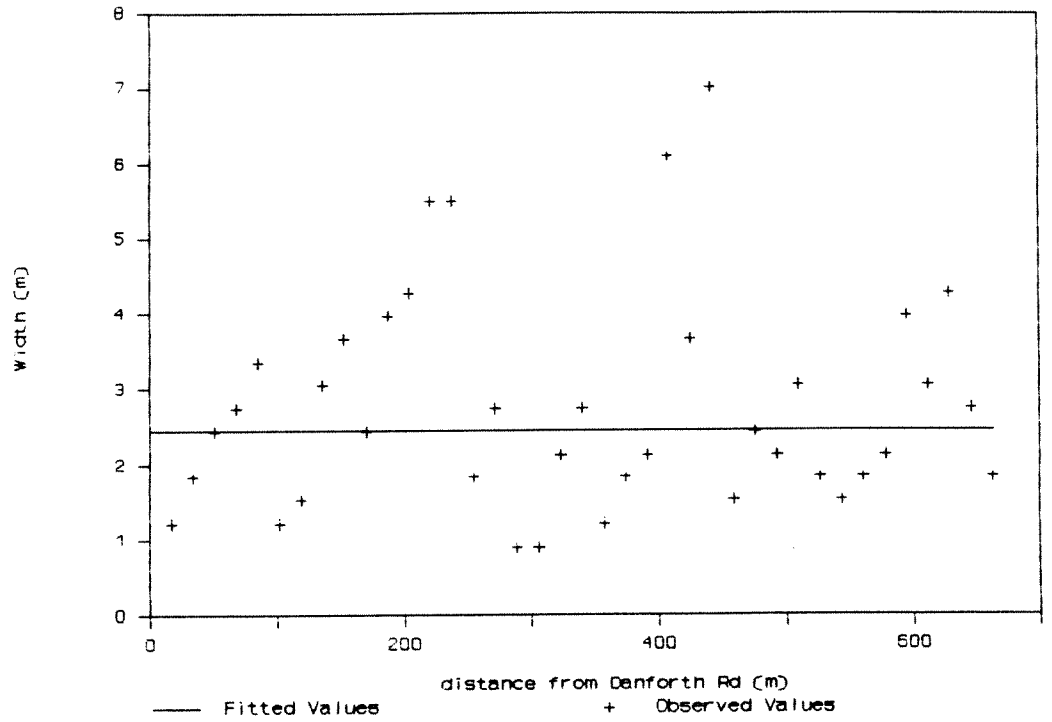
Figure A3 - 2c. Western branch of Factory Creek width profile (upper panel) and its residuals plot (lower panel). This stream is a tributary of Factory Creek (Fig A3 - 2b).
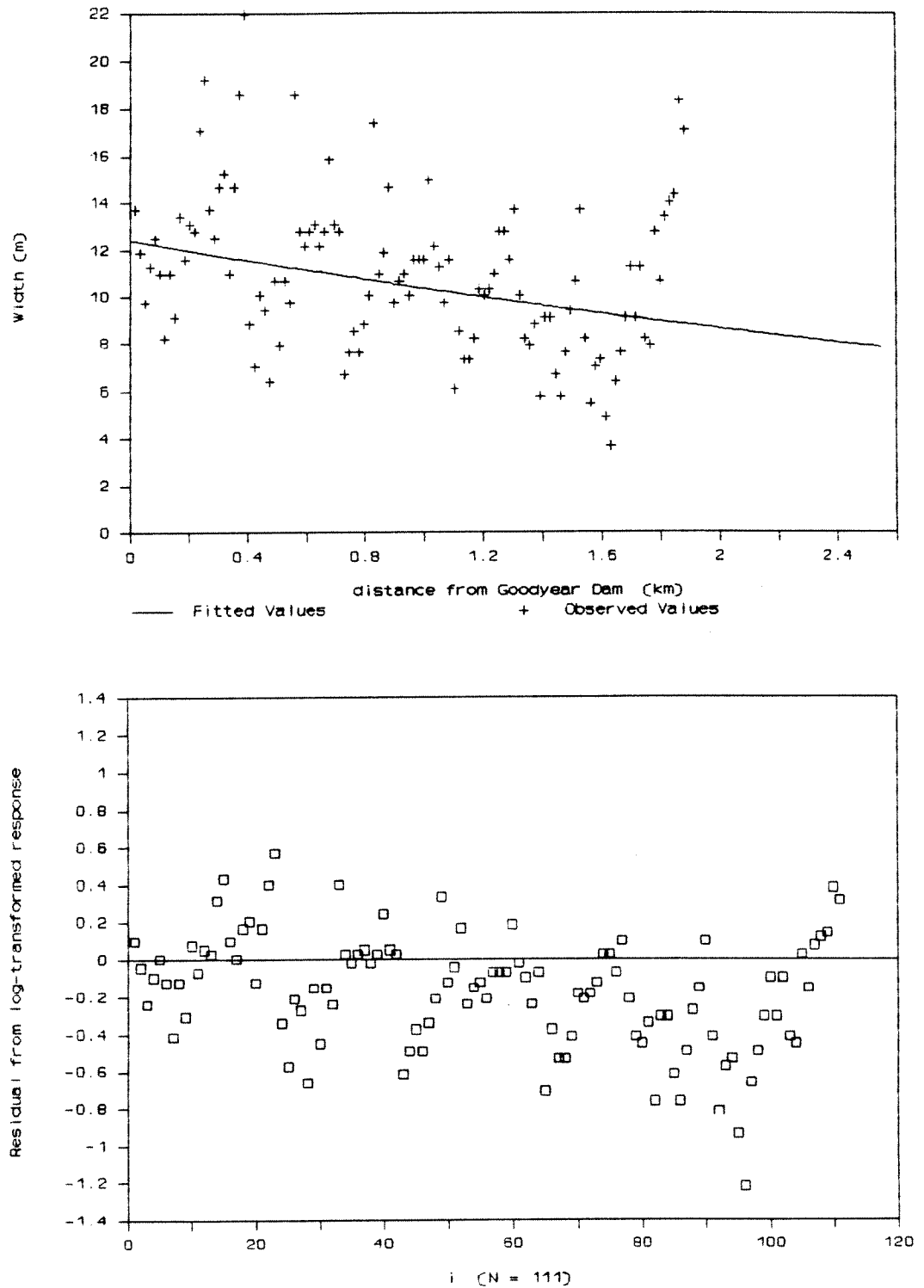
Figure A3 - 3. Width profile for Bowmanville Creek (upper panel) and its residuals plot (lower panel). The upper half of the stream is in pasture, where cattle severely pummel the banks. This results in a wide channel in the upper stream sections.
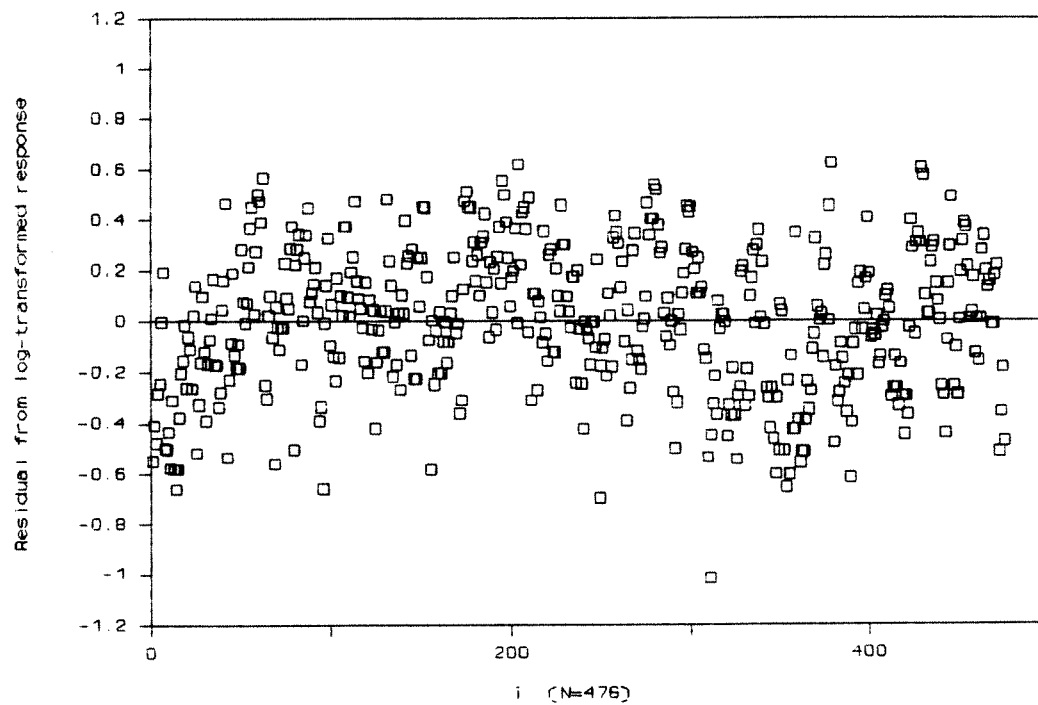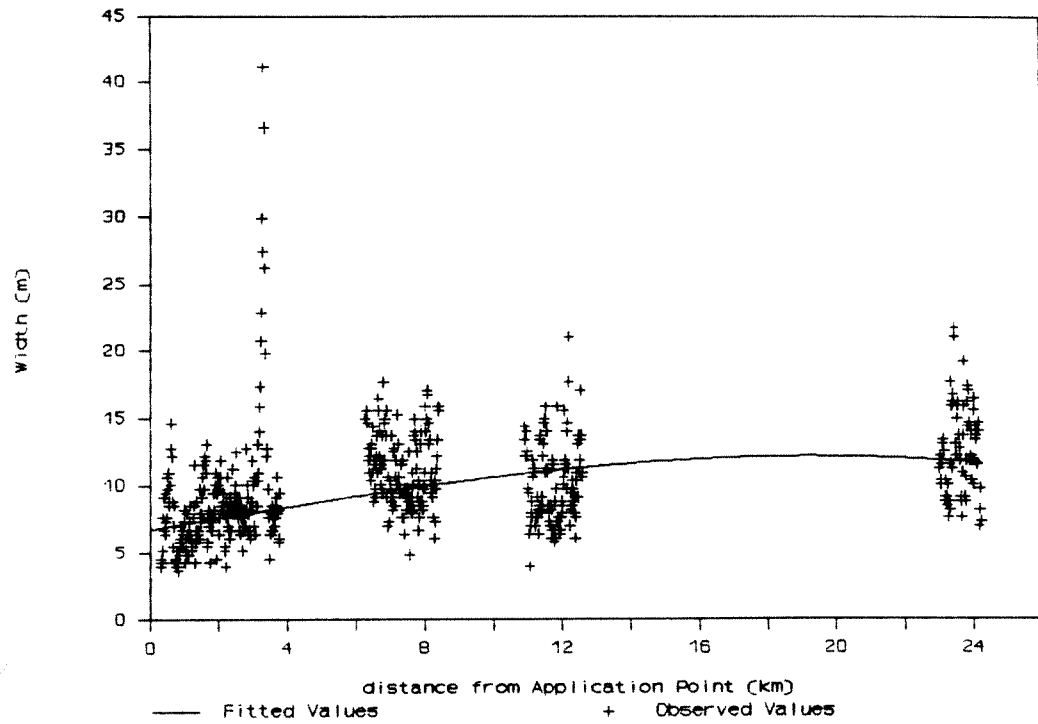
Figure A3 - 4a. Width profile of Bronte Creek (upper panel) and its residuals plot (lower panel). An impoundment (not used in fitting the curve) about 3 km from the lampricide application point is seen as a sharp "spike".

Figure A3 - 4b. Width profile of Limestone Creek (upper panel) and its residuals plot (lower panel). This stream is a tributary of Bronte Creek (Fig. A3 - 4a).
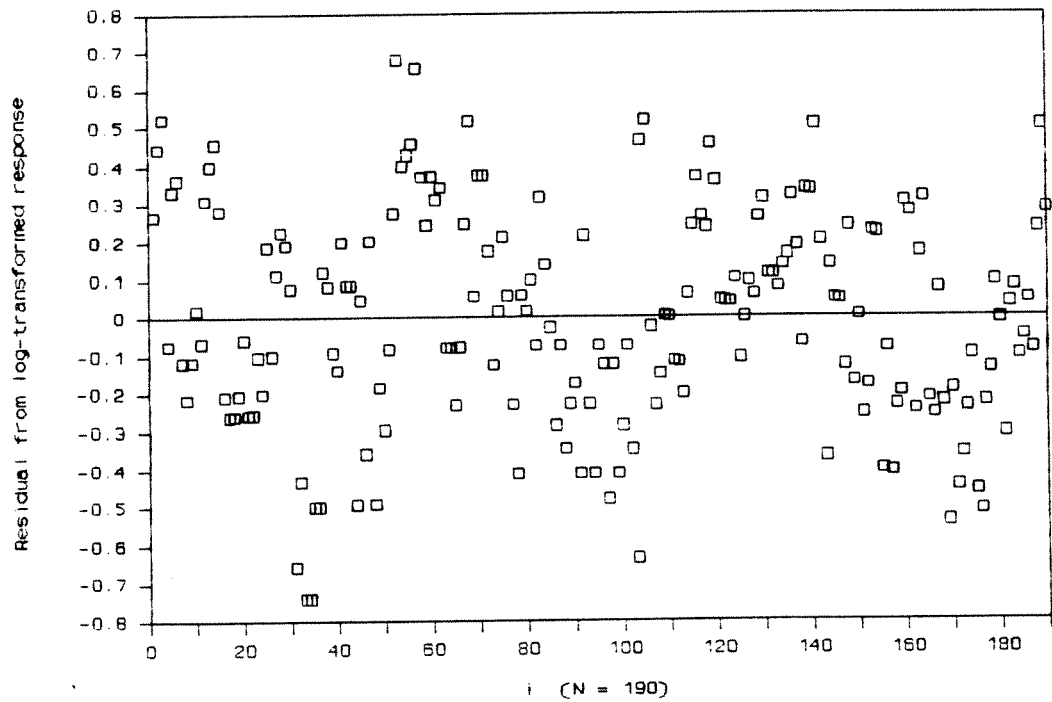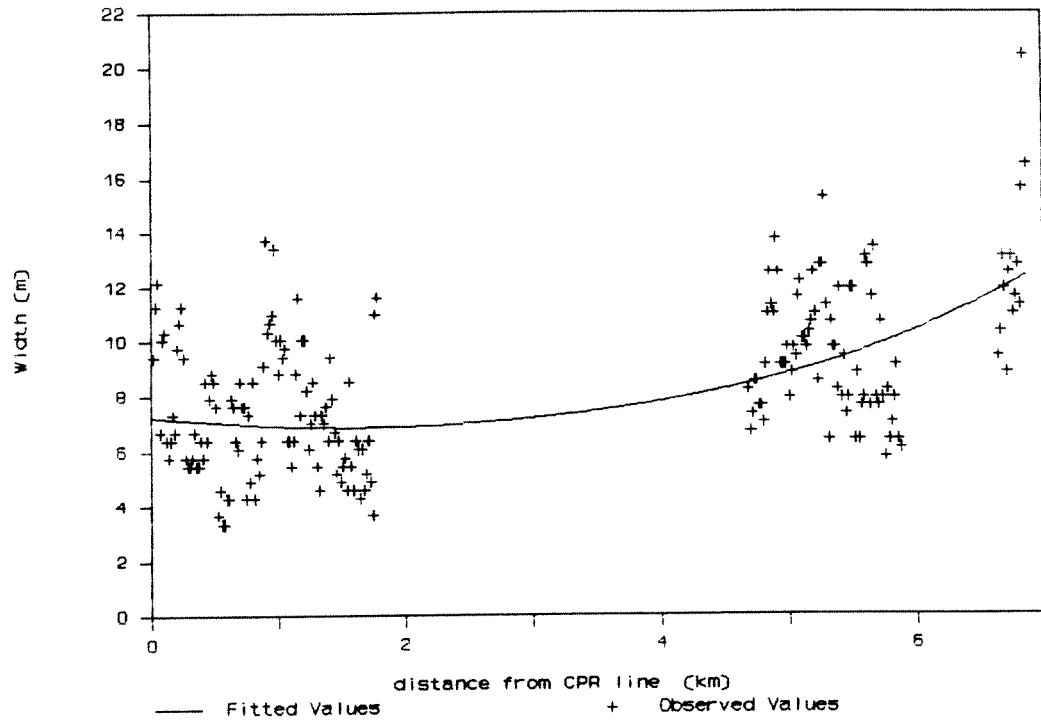
Figure A3 - 5. Width profile of Soper's Creek (upper panel) and its residuals plot (lower panel).