GREAT LAKES FISHERY COMMISSION
Research Completion Report *

A STUDY OF THE FEASIBILITY OF DEVELOPING A HABITAT SUITABILITY INDEX FOR SEA LAMPREY HABITAT IN STREAMS OF THE GREAT LAKES

by

Joseph F. Koonce

Department of Biology
Case Western Reserve University
Cleveland, OH 44106

June 6, 1990

* Project completion reports of Commission-sponsored general research are made available to the Commission's cooperators in the interests of rapid dissemination of information which may be useful in Great Lakes fishery management, research or administration. The reader should be aware that project completion reports have <u>not</u> been through a peer review process and that sponsorship of the project by the Commission does not necessarily imply that the findings or conclusions contained in the report are endorsed by the Commission.

INTRODUCTION

The goal of this project was to explore the feasibility of developing a habitat suitability index for estimating ammocoete habitat in streams of the Great Lakes basin. Representation of ammocoete habitat is a central issue in the development of strategies for Integrated Management of Sea Lamprey. This importance arises from the need for quantitative estimates of ammocoete abundance in streams and of subsequent production of transformers. Quantification of ammocoetes, however, begins with density data, and the area of habitat occupied by sea lamprey ammocoetes is required to complete the calculation. At the present time, ammocoete surveys are not designed to estimate overall abundance of larval lamprey in a stream nor is there any explicit accounting of stream area available for ammocoetes. Preliminary work on a stream inventory data base for the Lake Ontario version of the IMSL Decision Support System[1] produced tentative estimates of the area and quality of ammocoete habitat for the 49 known lamprey producing streams tributary to Lake Ontario. Improvement of the reliability of these tentative estimates requires a more rigorous evaluation of factors that determine ammocoete habitat suitability.

The objective of this proposed research was to explore one possible approach to improving quantification of ammocoete habitat in the streams of the Great Lakes Basin. That approach was a modification of the Instream Flow Incremental Methodology and Physical Habitat Simulation techniques developed by the U.S. Fish and Wildlife Service[2]. The attractiveness of this approach was that it relied on hydrologic principles and preference characteristics of individual species to predict habitat suitability. The method requires field studies and habitat mapping for maximum reliability, but can be used to derive estimates of suitable habitat from general hydraulic measures for individual streams and detailed "calibration" studies of a few streams. The objective, therefore, was both to explore the feasibility of this methodology and, thereby, to bridge the gap of estimates of ammocoete habitat until more complete studies are implemented.

The approach to this problem consisted of four primary tasks. The first task was to develop an overview of data and modeling requirements for an application of the IFIM/PHABSIM methodology to ammocoete habitat in the Great Lakes. Second was the development of a model with which to predict a habitat suitability index for ammocoetes from basic hydrologic parameters of streams. The third task involved testing of the model for Lake Ontario. Finally, the fourth task was an evaluation of the habitat suitability index.

ACCOMPLISHMENTS

These tasks were all accomplished with the completion of an M.S. Thesis by Ms. Paola Ferreri (Appendix I). Her work represents a documentation of ammocoete habitat analysis using the IFIM/PHABSIM methodology. She clearly shows the feasibility of developing estimates of habitat availability with readily accessible information from the control agents. Her representation of habitat suitability, however, encountered two problems. First, lack of better characterization of ammocoete habitat preference and allocation of spawning sea lamprey to streams severely limited her predictions of ammocoete abundance. These deficiencies should receive attention in subsequent work. She presents an analysis of additional observations that would improve the reliability of estimates. Second, preliminary comparisons of observed and predicted abundance of ammocoetes in four Ontario streams indicate that ammocoete habitat may not be the most critical factor limiting abundance. Nevertheless, the use of habitat to rank expected abundance of ammocoetes by stream is an effective way of developing a null model with which to isolate other possible factors. This finding deserves additional inquiry. Based on Ferreri's feasibility study and its implications, therefore, I would like to offer the following recommendations for further work.

RECOMMENDATIONS

1. Quantification of ammocoete habitat is essential for better understanding of the variability of transformer production among streams and for better rationalization of decisions concerning treatment priorities of streams. Preliminary attempts to construct a stream inventory database for Lake Ontario relied only on total area of a stream as a measure of ammocoete habitat. Based on the results of this feasibility study, I would recommend that more explicit representation of ammocoete habitat in the stream inventory

database must go forward. This revision should start with Lake Ontario, but completion of a basin-wide stream inventory database should be a high priority.

2. In order to facilitate subsequent analysis of ammocoete abundance and distribution, revision of ammocoete habitat estimates should follow a two-tiered strategy. First, a basic characterization of each stream should be obtained from existing data from the control agents' files. Critical data required are stream width, average depth, average velocity, and bed slope at several locations along a stream. General observations of substrate type would also be helpful. Measurements of these hydraulic characteristics could be added to future stream surveys during treatment studies to improve the estimates. Second, the Great Lakes Fishery Commission ideally should strive to develop more a comprehensive Geographical Information Systems for the streams of the Great Lakes Basin. Depending upon resources, the indirect mapping method of Ferreri could be replaced with direct observation of substrate distribution within each stream.

3. This feasibility study coupled with the results of preliminary workshops and the results of the work of Kelso, Young, and Houston indicate that the data in the files of the control agents is a valuable resource. The IMSL Workshop on Ammocoete Dynamics (February 15-16, 1989) revealed unexpected trends in both treatment collections of

ammocoetes and ammocoete survey data sets. In recent work to extend IMSL to Lake Superior, Gavin Christie has implemented a procedure to use treatment history with stream habitat characteristics to produce expected trends in ammocoete densities and parasitic phase abundance. I recommend, therefore, that these initiative be combined as soon as possible. Better characterization of ammocoete habitat with these data and model predictions is necessary for more complete analysis of sources of variability in observed patterns of variation of ammocoete abundance.

4. Both the U.S. and Canadian control agents are reviewing ammocoete monitoring and assessment activities. Within the context of IMSL, I recommend that routine assessment of stream habitat be included in future monitoring activity. This assessment should have two goals. First, improvements of estimates of ammocoete habitat will require more information of stream hydraulic characteristics and/or substrate maps. Second, ammocoete densities and distributions must be tested against expected values, which will be based on current models and understanding of ammocoete and spawner preferences. Preparation for these monitoring initiatives will involve coordination, and a working meeting should be convened by the IMSL Specialist to consider habitat characterization as well as other standardization issues.

5. Two critical areas of scientific uncertainty emerged from the feasibility study. Preferences of ammocoetes for burrowing substrate are not well known. Estimates of these preferences are necessary for calculation of amount of ammocoete habitat in a stream. Utilization of ammocoete habitat, however, is a function of spawner preferences, which are also poorly understood. Some evidence exists that spawners distribute among streams according to flow rates, but it is not clear what factors influence the upstream distribution of spawners in each stream. Assumptions about both ammocoete and spawner preferences influence predictions of habitat utilization. I recommend, therefore, that further research on these topics be considered a priority by the Great Lakes Fishery Commission.

REFERENCES

1. Koonce, J. F. and Ana Locci-Hernandez. 1989. A decision support system for the integrated management of sea lamprey. Great Lakes Fish. Comm. Spec. Publ., 89-1. 73 pp.

2. Bovee, K. D. 1982. A guide to stream habitat analysis using the Instream Flow Incremental Methodology. Instream Flow Information Paper 12. U. S. Dept. Interior, Fish and Wildlife Service, Office of Biological Services. FWS/OBS-82/26. 248 pp.

APPENDIX I

DEVELOPMENT OF HABITAT SUITABILITY INDICES FOR SEA LAMPREY (PETROMYZON MARINUS) AMMOCOETES IN STREAMS TRIBUTARY TO LAKE ONTARIO

by

CECILIA PAOLA FERRERI

Submitted in partial fulfillment of the requirements for
the Degree of Master of Science

Thesis Advisor: Dr. Joseph F. Koonce

Department of Biology
CASE WESTERN RESERVE UNIVERSITY
August 1990

DEVELOPMENT OF HABITAT SUITABILITY INDICES FOR SEA LAMPREY (PETROMYZON MARINUS) AMMOCOETES IN STREAMS TRIBUTARY TO LAKE ONTARIO

Abstract

by

CECILIA PAOLA FERRERI

Problems in estimating transformer abundance has made understanding the variability of sea lamprey (Petromyzon marinus) transformer production potential among streams difficult. The objective of this study is to establish the feasibility of including biological information in a measure of suitable habitat and using this measure to rank streams in terms of transformer production potential. Using the ammocoete density in a stream as a surrogate measure, transformer production potential is proportional to the amount of suitable burrowing habitat available in the stream. The Habitat Suitability Index (HSI) developed in this study integrates the physical characteristics of the stream with biological information about sea lamprey substrate preference into one measure to allow comparison among streams. Because the ammocoetes tend to migrate in the

downstream direction only, the relative position of spawning and ammocoete habitat along the length of the stream must be included in any measure of habitat suitability. As a result, detailed habitat maps are required. To allow full implementation of HSI development, more information is needed about spawner distribution within the streams, sea lamprey substrate preference, and the physical characteristics of the streams.

ACKNOWLEDGEMENTS

I would like to thank my advisor Dr. Joseph F. Koonce for his invaluable guidance, insightful advice, and everlasting patience throughout the course of my graduate program and preparation of this manuscript.

I would also like to extend my gratitude to the following persons and institutions that aided me during the course of my degree program:

1. Gavin J. Christie for all his help in coordinating activities and exchanging information with the Sea Lamprey Control Center in Sault Ste. Marie, Ontario.

2. Jerry G. Weise who shared his invaluable data to make the completion of this study possible.

3. Tim Adams and Ana Locci for all of their encouragement and helpful suggestions throughout the preparation of this manuscript.

4. The Great Lakes Fishery Commission and the Case Western Reserve University Department of Biology for providing financial support for this study.

My most special thanks goes to my mother and my brothers, Neil and Nicholas, who provided all the love and encouragement which made it possible for me to complete my degree program.

Table of Contents

Table of Figures

Table of Tables

INTRODUCTION

General Background

The Sea Lamprey (Petromyzon marinus) is a vertebrate predator native to the North Atlantic Ocean that has adapted very well to life in the fresh waters of the Great Lakes. The invasion of the Great Lakes by sea lamprey began in Lake Ontario where the first authenticated record of the presence of sea lamprey was taken in 1835. The completion of the Welland Canal in 1829 connecting Lake Ontario with Lake Erie provided access for sea lamprey to the upper Great Lakes around the natural barrier posed by Niagara Falls. The appearance of sea lamprey in Lake Erie in 1921 is usually attributed to the deepening and modification of the Welland Canal which took place in 1919 (Pearce et al. 1980). The colonization of the upper Great Lakes took place slightly later; sea lamprey were found in Lake Michigan in 1936, Lake Huron in 1937, and in Lake Superior, the uppermost lake, in 1938 (Smith and Tibbles 1980).

The absence of any natural predators combined with the presence of ample food and suitable habitat allowed the sea lamprey population to grow at an explosive rate. In Lake Ontario, overharvest by commercial fishing coupled with increased predation by sea lamprey caused the extinction of native lake trout and burbot by 1950 and the collapse of the whitefish population in 1960 (Pearce et al. 1980). In Lakes Michigan and Huron, lake trout virtually disappeared by the mid-1950s (Smith and Tibbles 1980). The negative impact of the sea lamprey on the Great Lakes fisheries was of great concern to both the United States and Canada. After many unsuccessful attempts made between the American and Canadian governments during the period from 1893 to 1952 to establish a joint fisheries commission or uniform regulations, both nations finally ratified a treaty that created the Great Lakes Fishery Commission (GLFC) in 1955. The GLFC was to be responsible for the rehabilitation of the fisheries and the eradication of sea lamprey from the Great Lakes (Fetterolf 1980).

The complex life cycle of the sea lamprey helps to explain the detrimental effect of sea lamprey on the Great Lakes fisheries (Fig. 1). During the spring, the adults enter the streams to spawn in gravel beds and die shortly after the spawning process is completed. Applegate (1950) observed that when young-of-the-year ammocoetes emerge from the nests in the stream, they swim with the current until reaching sluggish waters which guides them to optimal burrowing habitat. The ammocoetes will reside in their ill-defined crescent shaped burrows along the stream bottom for at least three to four years, and in some cases up to twenty years, until transformation to the adult form occurs. During this time, the ammocoetes use a filtering mechanism to feed on aquatic micro-organisms that are abundant on the thin surface layer of debris on the stream bottom.

After reaching a size greater than 125 mm, the process of transformation from the larval form to the adult form is triggered by cues not yet well understood. Transformation usually takes place between mid-July and mid-October with the newly transformed lamprey leaving the stream as soon as the process is completed. The new adult sea lamprey will reside in the open waters of the lake for the next twelve to eighteen months before returning to the streams to spawn. While in the lake, the adult sea lamprey will preferentially attack and feed on the body fluids of the largest prey item available by attaching itself to the prey with its suctorial mouth. Since this feeding process usually causes the death of the prey, the sea lamprey can be very detrimental to fish stocks during this free swimming, feeding phase of its life (Johnson 1987).

The life history study completed by Applegate (1950) indicated that the sea lamprey was most vulnerable during the life stages that occurred in the streams (spawning and ammocoete). The first attempts at sea lamprey control were

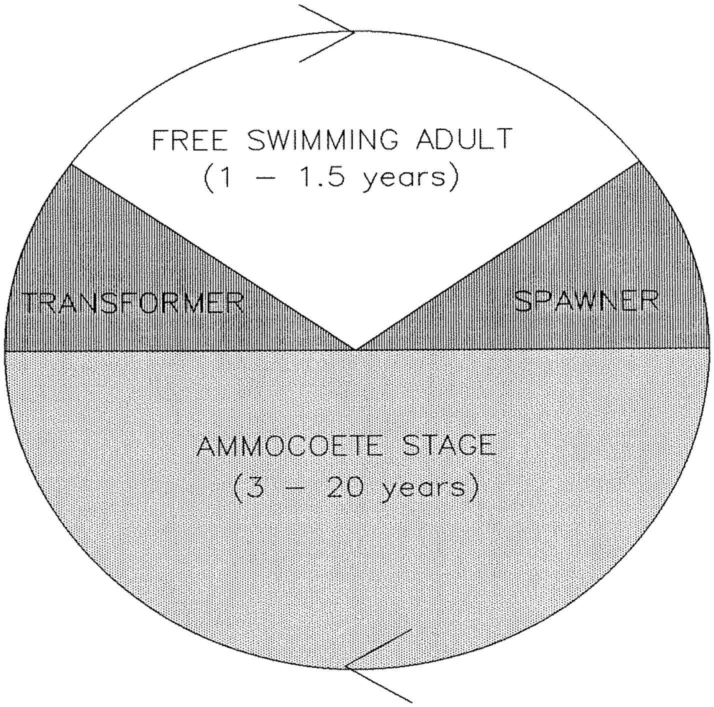

Figure 1: The life cycle of the sea lamprey.

made before the GLFC was established and focused on the spawning phase animals. Mechanical barriers were placed directly below optimal spawning habitat in 21 American and Canadian tributaries to the upper Great Lakes in 1950-51. In 1952, it was established that electromechanical barriers were more effective in blocking spawning runs, and by 1960, 162 of these barriers were installed in the American and Canadian tributaries of Lakes Superior and Michigan.

With the formation of the GLFC, the emphasis of control efforts switched from the spawning phase to the ammocoete phase which is a relatively sedentary population. Also, the effects of control are immediate because several generations of sea lamprey ammocoetes in the stream can be removed before transformation to the adult phase can occur. In contrast, the effects of controlling spawning phase animals are delayed since the several generations of sea lamprey ammocoetes already present in the stream can transform normally. The disadvantage of switching to control of the ammocoete phase is that ammocoetes tend to be dispersed over large areas in the streams. As a result, a toxic chemical was sought that would be selective for sea lamprey ammocoetes and could be distributed over large areas of the streams. The chemical 3-trifluoromethyl-4-nitrophenol (TFM) demonstrated the desired qualities and was chosen for use in the field. In 1958, the GLFC launched a chemical control program in an effort to fulfill its responsibility of eradicating sea lamprey from the Great Lakes.

The routine chemical treatment of streams began in 1958 with Lake Superior for two reasons: native fish stocks that could be used for the rehabilitation of the Great Lakes needed protection and stopping the rapid increase in sea lamprey numbers seemed possible. The chemical control program was expanded to Lake Michigan and the Canadian waters of Lake Huron in 1960. The control program in Lake Huron was interrupted in 1962 due to budget considerations, but was reinstated for the entire lake in 1966 (Smith and Tibbles 1980). In 1971, the control program was expanded to include Lake Ontario because prior attempts to develop a salmonid fishery indicated that sea lamprey induced mortality would prevent the development of an acceptable fishery (Pearce et al. 1980).

The success of the chemical control program depends greatly on an understanding of the streams' transformer production potential. As a result, there has been a great deal of interest in explaining the distribution of sea lamprey ammocoetes within a given stream and between different streams. The River Continuum Concept (Vannote et al. 1980) suggests that the distribution of riverine communities is dependent on the gradient of physical factors such as current velocity, stream gradient, and substrate particle size present in the stream. Many studies (Applegate 1950; Malmqvist 1980; Manion and McLain 1971; Potter et al. 1986; Johnson 1987) have documented the importance of substrate type, as defined by particle size, to ammocoete distribution. Statistical analyses (Robert Young, personal communication) suggest that the occurrence of sea lamprey ammocoetes in the streams of the Great Lakes can be explained by the presence of suitable burrowing habitat and that between stream differences in ammocoete abundance can be explained by differences in available suitable substrate. Young's study also indicates that there is much uncertainty in understanding the variability of ammocoete abundance among streams. An important issue in improving this knowledge is the lack of biologically sensitive measures of habitat availability in streams.

Study Approach

The objective of the present study is to establish the feasibility of quantifying the biological availability of suitable habitat within a stream that would lead to a better measure of transformer production potential. To approach this objective, I chose to develop a Habitat Suitability Index (HSI) for sea lamprey in Lake Ontario streams. HSI is a measure of the suitability of the available habitat in a stream for a particular species. Traditionally, this approach has been used to characterize the suitability of lakes and streams for species residing in the water column (Bovee 1982, Orth and Maughan 1982, Binns and Eisermann 1979). This study is different in the sense that it attempts to establish a HSI for a species that burrows in the sediments of streams. As a result, the key habitat variable used for the development of a HSI for sea lamprey is substrate type, defined by grain size, as opposed to the more traditional variables of depth, velocity, and cover.

Developing HSI for sea lamprey requires the combination of physical and biological aspects (Fig. 2). The physical aspect derives from the stream via a habitat map. A map consists of the area by substrate type for each segment along the length of the stream. The biological aspect deals with habitat utilization which is dependent on the animal's preference for certain substrate types and on the substrate types actually available in a given stream.

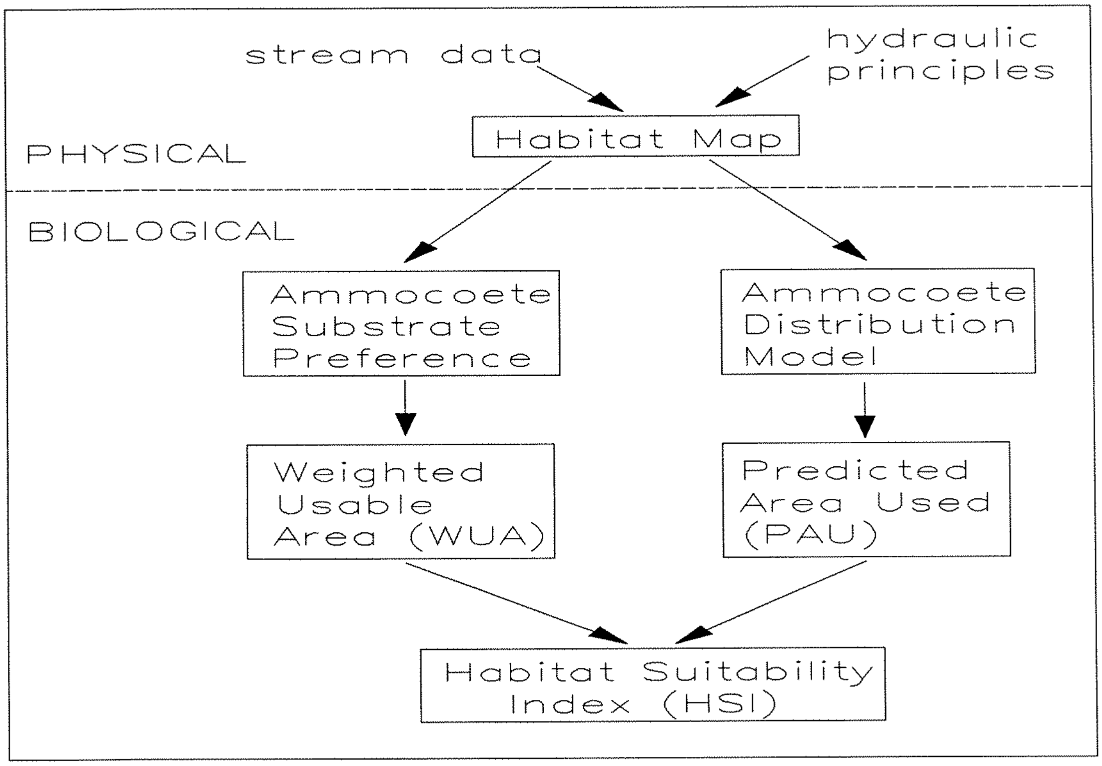

Figure 2: A summary of the key factors to be synthesized into a Habitat Suitability Index.

The process described above was applied to four streams tributary to the Canadian side of Lake Ontario: Salem Creek, Wilmot Creek, Bronte Creek, and Oshawa Creek (Fig. 3). I constructed habitat maps using stream data and hydraulic principles to predict the substrate composition of stream segments and predicted habitat utilization using a distribution simulation that accounts for habitat availability and ammocoete substrate preference.

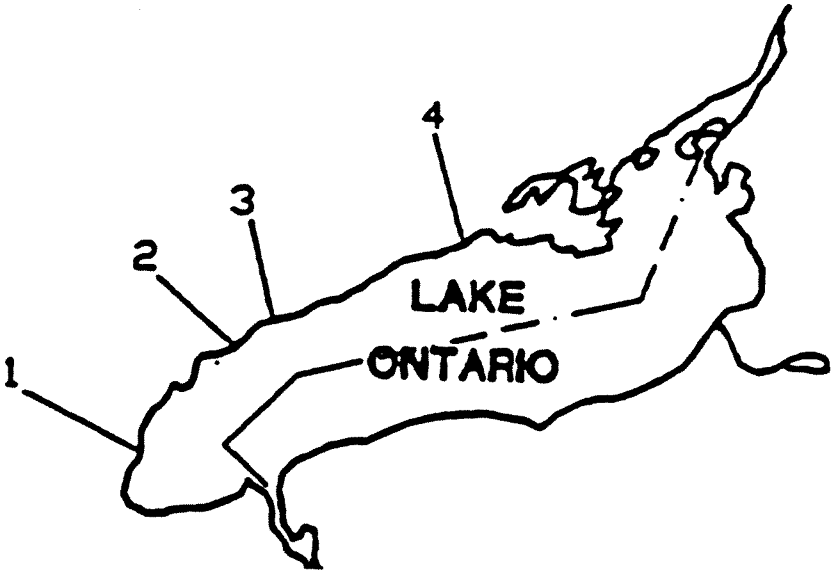

Figure 3: The relative position of the four study streams along the shore of Lake Ontario. 1) Bronte Creek; 2) Oshawa Creek; 3) Wilmot Creek; 4) Salem Creek.

METHODS

Categorization of Ammocoetes and Stream Habitat

To facilitate the calculation sequences in the models, ammocoetes are grouped into three size categories: 1) Small (less than 80 mm) 2) Medium (between 80 and 125 mm), and 3) Large (greater than 125 mm that have not begun to transform). The models also group stream habitat into different substrate type categories according to particle diameter (Table 1).

Table 1: Substrate Categories (Richards 1982)

Substrate Category	Maximum (mm)	Minimum (mm)
Cobble	200	64
Coarse Gravel	64	16
Medium Gravel	16	8
Fine Gravel	8	2
Coarse Sand	2	.5
Medium Sand	.5	.25
Fine Sand	.25	.06
Coarse Silt	.06	.016
Medium Silt	.016	.008
Fine Silt	.008	.002
Clay	.002	.0001

Sea Lamprey Substrate Preference

The biological aspect of HSI development depends on the sea lamprey preference for certain substrate types. The preference describes the probability that a lamprey of a given size and life stage will colonize a particular substrate in any stream segment. Preference criteria can be displayed graphically using a univariate curve that describes the usable range and the optimum range of substrate type for each ammocoete size category. The optimum range has a value of 1 while the usable range has a value between 0 and 1 (Bovee 1986). Although there is much anecdotal information about preference in the literature, there are no actual empirical observations of preference.

Studies (Johnson 1987) have noted that ammocoetes segregate by size into areas of slightly different substrate types indicating that preferences varies with size. Manion and McLain (1971) found ammocoetes to be most plentiful in areas of silt and sand mixture where 90% of the grains were less than 0.5 mm. Other studies (Johnson 1987, Applegate 1950) describe preferred ammocoete habitat as a sand-silt mixture. Thus, a young-of-the-year ammocoete that is about 20 mm in size will prefer a grain size in the medium silt range while an older ammocoete, around 100 mm in size, will prefer a grain size in the fine sand range (see Table 1).

These studies also indicate that ammocoetes can be found in areas with slightly larger grain size than the preferred, but are rarely found in grain sizes smaller than the preferred. Other studies (Johnson 1987) indicate that transformers, individuals undergoing metamorphosis, can be found in sand and even in gravel at times. The adults returning to spawn, on the other hand, prefer substrate dominated by gravel between 9 and 51 mm. in diameter (Manion and Hanson 1980).

A general functional form often used to generate preference curves is:

$$f(x) = \left[\frac{b-x}{b-a}\right]^{c} \cdot e^{(c/d)\cdot\left[1-\left(\frac{b-x}{b-a}\right)^{d}\right]} \qquad (1)$$

where a is the value of x where $f(x)$ equals 1, b is the value of x where $f(x)$ equals 0, c is the shape parameter for the part of the curve to the right of a, and d is the shape parameter for the part of the curve to the left of a (Bovee 1986). The shape of this function seems very applicable to sea lamprey since it indicates that once the substrate size is very near to the preferred grain size, the ammocoete preference rises very quickly reaching the most preferred grain size and then drops off more slowly indicating that the animal will colonize areas of larger grain sizes when the preferred grain size is not available. I constructed preference curves using equation 1 and adjusting the constants until the proper range of grain sizes, as indicated by the studies cited earlier, was included for each lamprey life stage. Equation 1 was evaluated at the midpoint of each substrate category to determine the preference for that category (Table 2). Each life stage has a slightly different preference curve although some, especially the three ammocoete size categories, have overlapping areas. The constants used to construct the preference curves are in Table 3.

Table 2: Sea Lamprey Substrate Preference

Substrate Type	Small	Medium	Large	Trans former	Spawner
Cobble	0	0	0	0	0
Coarse Gravel	0	0	0	0	0.18
Medium Gravel	0	0	0	0	0.86
Fine Gravel	0	0	0	0.07	0.85
Coarse Sand	0	0.06	0.07	0.53	0
Medium Sand	0.06	0.42	0.45	0.92	0
Fine Sand	0.49	0.76	0.82	0.96	0
Coarse Silt	0.88	0.99	0.87	0	0
Medium Silt	0.98	0.20	0.06	0	0
Fine Silt	0.89	0	0	0	0
Clay	0	0	0	0	0

Table 3: Constants Used to Construct Sea Lamprey Substrate Preference Curves

Constant	Small	Medium	Large	Trans former	Spawner
a	0.008	0.03	0.06	0.2	7
b	0.5	1	1	4	64
c	2	2	2	2	2
d	600	300	100	150	60

Stream Channel Model

The physical aspect of HSI development requires habitat maps which are not always available. As a result, the purpose of the stream channel model is to calculate the proportion of stream segment area in each substrate category. The data requirements of the model are the mean annual discharge of the stream, and the width and mean depth at random points along the stream. The discharge data for three of the Canadian streams considered in this study is found in Water Survey of Canada. The discharge for Salem was estimated from discharge calculations made at the time of treatment. The width at random points and the length between those survey points along the four streams comes from special population studies done by Jerry Weise (personal communication). An average width to depth ratio is calculated from cross-sections determined by treatment crews calculating the concentration of TFM needed to treat the stream and used to estimate the average depth at the points for which width is known. This cross-section data can be found in the respective treatment books at the Sea Lamprey Control Center (Sault Ste. Marie, Ont.).

The stream channel model yields the proportion of the stream segment in each of the substrate type categories. Multiplying the proportion by the total segment area gives the actual area of substrate type by segment. Another form of this output is the weighted usable area (WUA) for ammocoetes that is available in the stream. WUA is a concept adapted from the Instream Flow Incremental Methodology (Bovee 1982). This view of available area takes into account the animal's preference for certain physical conditions and weights the area accordingly. For example, a small ammocoete can utilize both medium silt and fine sand, but it prefers medium silt (preference = 0.98) twice as much as fine sand (preference = 0.49). If two sets of one hundred animals sample equal areas of medium silt and fine sand, 98 of them will stay in the medium silt whereas only 49 will stay in the fine sand. Since the fine sand represents marginal habitat, 52 ammocoetes will migrate further in search of more suitable habitat. Hence, WUA allows for a more biological basis for comparison of streams than the unweighted areas.

In the model, the WUA is calculated by segment and by ammocoete size group since substrate preferences change with size. The WUA in segment i for size group j is:

(2) $$WUA_{ij} = \sum_{k} C_{jk} \cdot A_i$$

where C_{jk} is the preference for substrate k by sea lamprey of size group j, and A_i is the area of segment i. The total WUA in a stream for a given size group is simply the sum of the WUAs for that size group over all stream segments. The calculation of the actual substrate area and the WUA is contingent on a description of the substrate composition of the segment.

According to Odgaard (1984), the distribution of the armor layer grain size is best described by a normal curve with a coefficient of variation of 0.57. Armoring is a process that brings the bed into equilibrium so that there is no net sediment deposition or erosion. Assuming that all rivers are working towards equilibrium, I chose the normal distribution to describe the grain size distribution in the four test streams. The value of the Z variable at the eighty-fourth percentile is 1, and the equation for the mean of the distribution is:

(3) $$\mu = k / 1.57$$

where k is the particle diameter at the eighty-fourth percentile. The approximation to the cumulative normal curve (Hastings 1955) uses the mean particle size to calculate the percentage of the total area found between the substrate type endpoints illustrated in Table 1.

Determining μ requires the particle diameter at the eighty-fourth percentile. The method used to predict this particle size depends on the determination of the shear velocity, a measure of the shear stress at the bed with units of velocity (meters per second) (Blatt et al. 1980). I used a computer program, the stream channel model, to calculate the shear velocity and the consequent substrate distribution in a stream segment.

The total area of the segment is the segment length times the segment width. The cross-sectional area of the channel at this point is the product of the width and the mean depth. The mean velocity in the channel segment is:

$$U = \frac{Q_a}{A_{cs}} \tag{4}$$

where Q_a is the mean annual discharge of the given stream and A_{cs} is the cross-sectional area of the particular segment.

This approach assumes a logarithmic velocity profile so that a graph of the natural log of the depth versus the velocity at that depth is a straight line. Calculated shear velocity is a function of two points (velocity, depth pairs) on the line: the surface velocity with the mean depth, and the mean velocity with its corresponding depth. The mean velocity in the water column is 0.8 times the surface velocity (Hamilton and Bergersen 1984), thus the surface velocity at the point of interest is the mean velocity times a factor of 1.2. The depth of the mean velocity is 0.4 times the total depth (Blatt et al. 1980). Completing these calculations provides all of the information needed to calculate the shear velocity as:

$$U_* = \frac{\kappa \cdot (U_1 - U_2)}{\ln\left(\frac{y_1}{y_2}\right)} \tag{5}$$

where κ is von Karman's constant and has a value of 0.4, U_1 is the velocity at depth y_1 (in this case, the surface velocity at the mean depth), and U_2 is the velocity at depth y_2 (in this case, the mean velocity at its corresponding depth).

Knowing the shear velocity, the height above the bed at which velocity equals zero is:

$$y_0 = y_1 - e^{\left(\frac{\kappa \cdot U_1}{U_*}\right)} \tag{6}$$

Finally, I calculated the grain size at the eighty-fourth percentile using the standard empirical approach:

(7) $$\frac{U}{U_*} = a + \frac{1}{\kappa}\ln\left(\frac{y}{k}\right)$$

where a is a coefficient that varies with the type of roughness (assuming a value of 5 here), and k is the sediment diameter of the eighty-fourth percentile. When $U = 0$ then $y = y_0$, the grain size, k in meters, is:

(8) $$k = 7 \cdot y_0$$

where the constant 7 results from the combination of the constants a and κ.

Habitat Utilization Model for Ammocoetes

The biological aspect of the HSI development requires a description of ammocoete habitat utilization within a stream. The purpose of the habitat utilization model is to explore the regulation of ammocoete distribution into available suitable habitat. The model requires habitat maps and an expected annual abundance of young-of-the-year ammocoetes as input. To allow comparison with the stream channel model, this model uses the same segmentation scheme. The habitat utilization model yields the number of ammocoetes in the three size categories in each substrate type per segment.

The model uses an annual time step to calculate habitat utilization as a function of density of ammocoetes in the different substrate categories. Transformation, mortality, and growth affect the ammocoete density within a given substrate type while migration affects the spatial distribution of ammocoetes throughout the stream. The parameters that I used in the simulation are density dependent and are calculated for each segment, substrate type, and age group.

I assumed transformers leave the system once metamorphosis is completed reducing the in-situ density of ammocoetes. Several studies have noted that the probability of transformation increases with size above 125 mm (Johnson 1987). A sigmoidal function describes the relationship between length and the probability of transformation in segment i, substrate j, for age k:

(9)
$$p(t)_{ijk} = m_1 \cdot \frac{x^2}{x^2 + \alpha^2}$$

where m_1 is the maximum probability of transformation, x is the difference between the average size of the animals in question and 125 mm, and α is a constant specifying the size difference at which the transformation rate is one-half of the maximum. The total number of transformers produced by the stream in a given year is:

(10)
$$T = \sum_i \sum_j \sum_k N_{ijk} \cdot p(t)_{ijk}$$

where N_{ijk} is the number of ammocoetes in segment i, substrate j, of age k.

Many studies indicate a direct proportionality between density and natural mortality (Johnson 1987). To model this relationship, I assumed that natural mortality is a sigmoidal function of density:

(11) $$p(z)_{ijk} = z_{\max} + z_{\min} \cdot \left(\frac{N_{ijk}^2}{N_{ijk}^2 + \gamma^2} \right)$$

where $z_{\max}$ is the maximum natural mortality rate, $z_{\min}$ is the minimum natural mortality rate, and γ specifies the location of the inflection point.

Treatment mortality is age rather than density dependent (Johnson 1987). As a result, the number of ammocoetes that survive in a given substrate type is:

(12) $$N_{ijk} = N_{ijk} \cdot e^{-z_n - z_t}$$

where z_n is the natural mortality, and z_t is the age specific treatment mortality.

Growth of ammocoetes is inversely related to density, that is when densities are high, growth rates are lower (Johnson 1987). The average size of ammocoetes in segment i, substrate j, of age k is determined using the growth rate and the maximum length attainable. I assumed the growth rate of ammocoetes in segment i, substrate j, of age k to have the functional form:

(13)
$$b_{ijk} = m_2 \cdot \left(1 - \frac{N_{ijk}}{N_{ijk} + \omega} \right)$$

where m_2 is the maximum growth rate, and ω specifies the density at which growth rate is one-half the maximum. The maximum length attainable by ammocoetes in segment i, substrate j, of age k has the same functional form as growth rate. In this case, m_2 is the maximum length attainable. The average length in mm of the ammocoetes in segment i, substrate j, of age k at the next time is :

(14)
$$\overline{x}_{ijk_{(t+1)}} = y_{ijk} + \left(b_{ijk} \cdot \overline{x}_{ijk_t} \right)$$

where y_{ijk} is the maximum length attainable, and b_{ijk} is the growth rate.

Finally, migration allows the redistribution of ammocoetes throughout the stream once transformation, mortality, and growth have taken place. Observations suggest that the probability of migration increases with increased densities (Johnson 1987). Again, I assume a sigmoidal function to describe the effects of density on the probability of migration:

(15) $$p(m)_{ijk} = m_{\max} + m_{\min} \cdot \left(\frac{N_{ijk}^2}{N_{ijk}^2 + \delta^2} \right)$$

where $m_{\min}$ is the minimum migration probability, $m_{\max}$ is the maximum migration probability, and δ specifies the location of the inflection point. Thus, the number of ammocoetes of age k migrating from segment i, substrate j is:

(16) $$M_{ijk} = N_{ijk} \cdot p(m)_{ijk}$$

where $p(m)_{ijk}$ is the probability of migration.

The migrant ammocoetes choose the type of substrate they will colonize according to the preferences listed in Table 3. Ammocoete migration proceeds downstream from the segment of origination. If a segment does not contain suitable substrate, the ammocoetes will try the following segments until suitable substrate is reached and can be colonized.

The total abundance of ammocoetes in the stream is affected by the number of young-of-the-year ammocoetes is which held constant throughout the simulation, that is every year has the same total hatch. The total number of spawners that could be expected to enter the stream was determined using Heinrich's approximation of 46 spawners per cfs (John Heinrich, personal communication). It was assumed that 100,000 hatchlings was a reasonable number for Salem Creek. The ratio between the total number of expected spawners and the assumed hatch was determined and used to calculate the expected hatch in the other streams once the expected number of spawners had been calculated. This approach to estimating hatch allowed for hatch size to be a function of stream discharge which is believed to be one the primary factors influencing the spawner's choice of streams. The hatch used in the streams is: Salem Creek = 100,000; Oshawa Creek = 1,076,067; Wilmot Creek = 1,115,955; and Bronte Creek = 1,971,243.

I explored the consequences of two assumptions about spawning distribution. One is that spawners allocate themselves uniformly throughout the stream, resulting in the uniform distribution of the hatch throughout the stream. The second assumption is that spawners will distribute themselves throughout the stream in proportion to the available spawning habitat. This assumption results in the non-uniform distribution of young-of-the-year through the stream. The hatch is added to the emigrant pool of the given stream segment and will find suitable habitat when all of the ammocoetes within the segment are re-distributed into different substrate types depending on preferences. Thus, the number of ammocoetes in segment i, substrate j, of age k is:

$$N_{ijk} = N_{ijk} \cdot (1 - p(m)_{ijk}) - T_{ijk} + YOY_{ij} \tag{17}$$

where $p(m)_{ijk}$ is the probability of migration (Eq. 15), T_{ijk} is the number of transformers, and YOY_{ij} is the number of young-of-the-year allocated to substrate i in segment j.

I calculated PAU by combining WUA with the abundance by size group per segment (Eq. 17). The density in segment i of ammocoetes in size group j is:

(18) $$D_{(i,j)} = \frac{N_{(i,j)}}{A_{(i,j)}}$$

where $N_{(i,j)}$ is the number of ammocoetes of size j in segment i, and $A_{(i,j)}$ is the WUA for size group j in segment i. The maximum density per size group over the entire stream is determined and the PAU is calculate by size group as:

(19) $$PAU_j = \frac{N_{(i,j)}}{D_{\max}}$$

Since $N_{(i,j)}$ has units of individuals and $D_{\max}$ has units of individuals per square meter, PAU has units of area (meters squared) and describes the the available area actually used by ammocoetes in the stream.

Synthesis of HSI

Since the four streams used in this study vary greatly in length (Salem Creek = 2.8 km, Wilmot Creek = 11 km, Bronte Creek = 27 km, and Oshawa Creek = 18.5 km) and consequently in total area, I chose to standardize PAU for easier comparison of lamprey habitat by relativizing the PAU to the total WUA available in the stream for ammocoetes of size group j. Thus, the HSI by size groups is:

(20) $$HSI_j = \frac{\sum_i PAU_{ij}}{\sum_i WUA_{ij}}$$

The HSI is a unitless measure that can be used to compare the relative productivity of different streams. The actual ammocoete abundance in a particular stream can be calculated by multiplying a known average density by the PAU.

RESULTS

I constructed habitat maps for the four streams of interest using the stream channel model. Although these streams have been visually mapped (Jerry Weise personal communication), it was important to determine if this modelling approach could be used to develop habitat maps for streams that do not have them. The coarse maps were calibrated against the visual observations to improve the accuracy of the PAU prediction. The longitudinal distribution of gravel, sand, and silt in terms of percent area was determined and averaged over the entire stream to allow comparison with the averaged visual observations (Table 4). After slight calibration, the stream channel model adequately predicts the overall percent of gravel, sand, and silt in the four test streams.

Table 1: Comparison of Observed and Predicted Averaged Percent Substrate Type in the Four Test Streams

Stream	Gravel		Sand		Silt	
	Obs	Pred	Obs	Pred	Obs	Pred
Bronte	14.6	19.6	1.9	4.4	5.6	5.3
Oshawa	18.1	23.4	18.6	13.6	18.8	13.9
Salem	15.9	14.0	10.5	14.2	57.7	56.6
Wilmot	44.3	33.6	6.1	9.0	24.7	26.3

The habitat maps depict the change in substrate composition in terms of spawning (gravel) and ammocoete (sand-silt) area along the length of the stream. Salem Creek (Fig. 4) is unique because the ammocoete available habitat far outweighs the spawning habitat area. It also has most of its spawning habitat in the upstream reach of the study area. Oshawa Creek (Fig. 5) is similar in that the major portion of its spawning habitat is upstream relative to the ammocoete habitat. In contrast, Wilmot Creek (Fig. 6) and Bronte Creek (Fig. 7) have the major portion of spawning habitat towards the middle of the stream. Bronte Creek has much less ammocoete habitat relative to spawning habitat than the other streams.

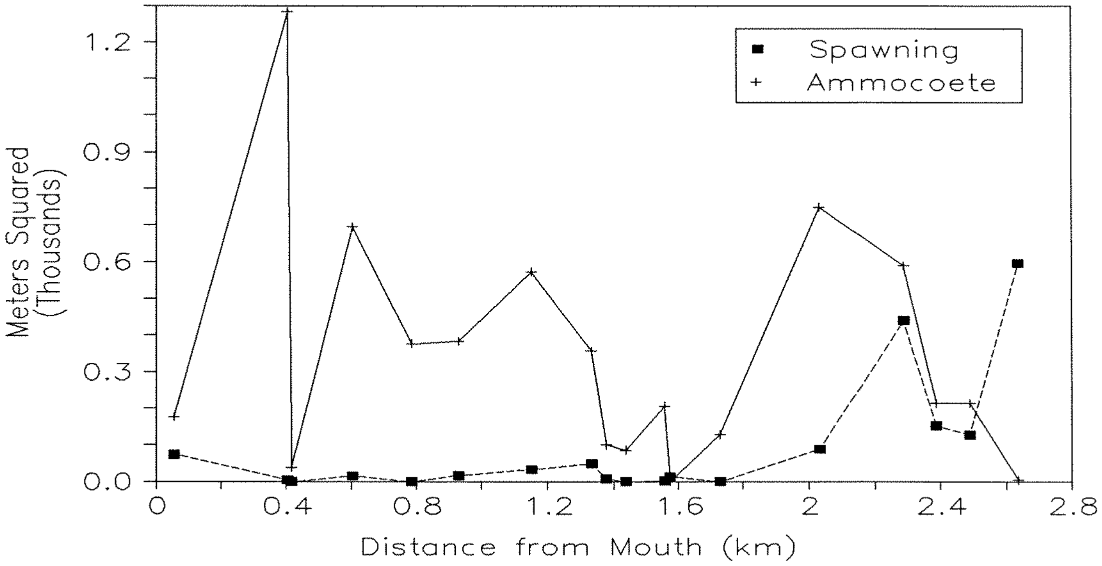

Figure 4: Substrate distribution along Salem Creek for ammocoete and spawning phase sea lamprey.

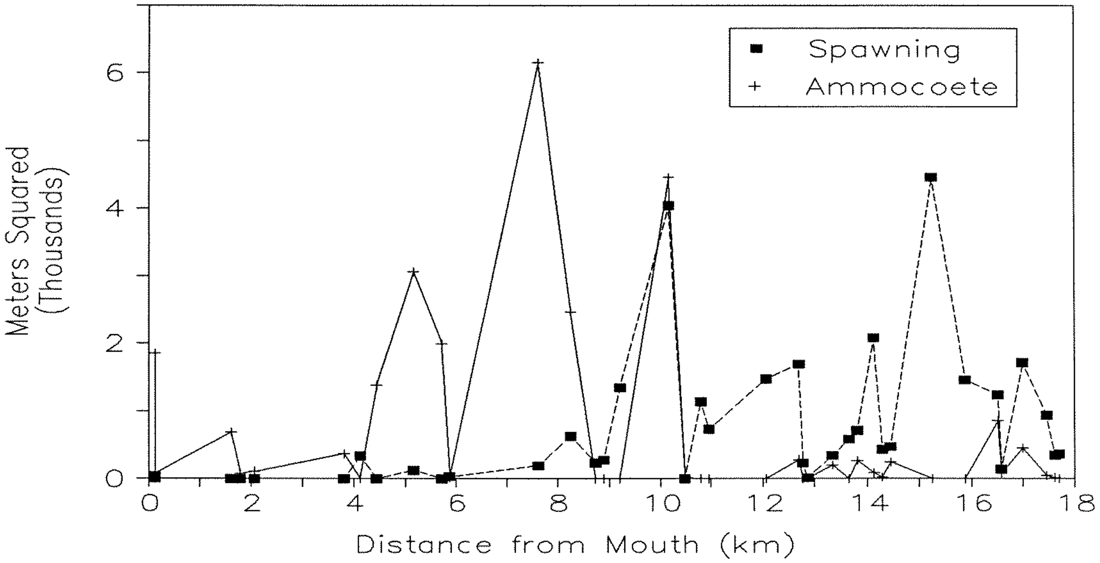

Figure 5: Substrate distribution along Oshawa Creek for ammocoete and spawning phase sea lamprey.

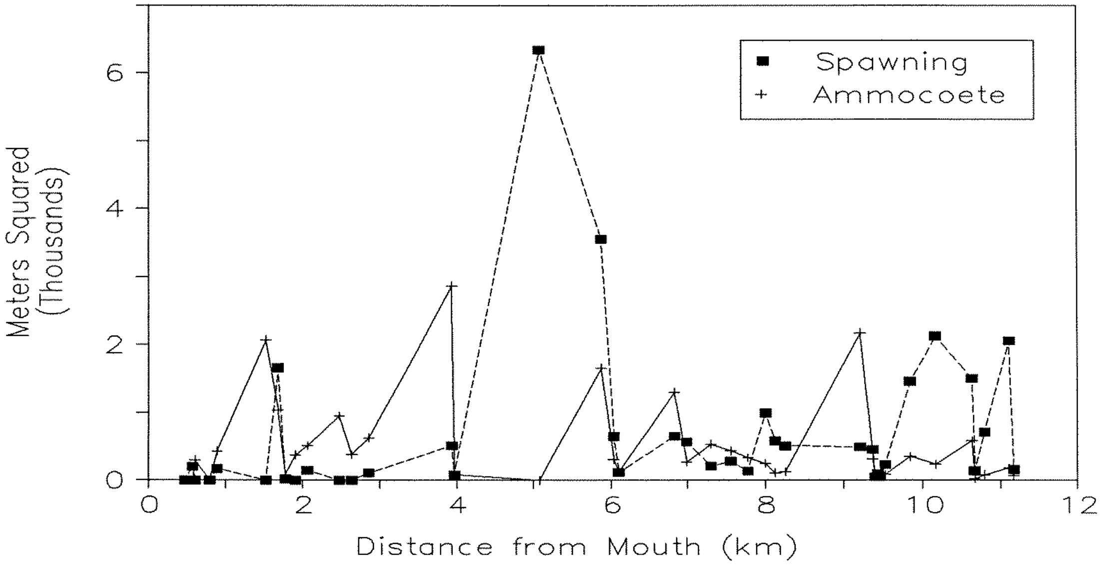

Figure 6: Substrate distribution along Wilmot Creek for ammocoete and spawning phase sea lamprey.

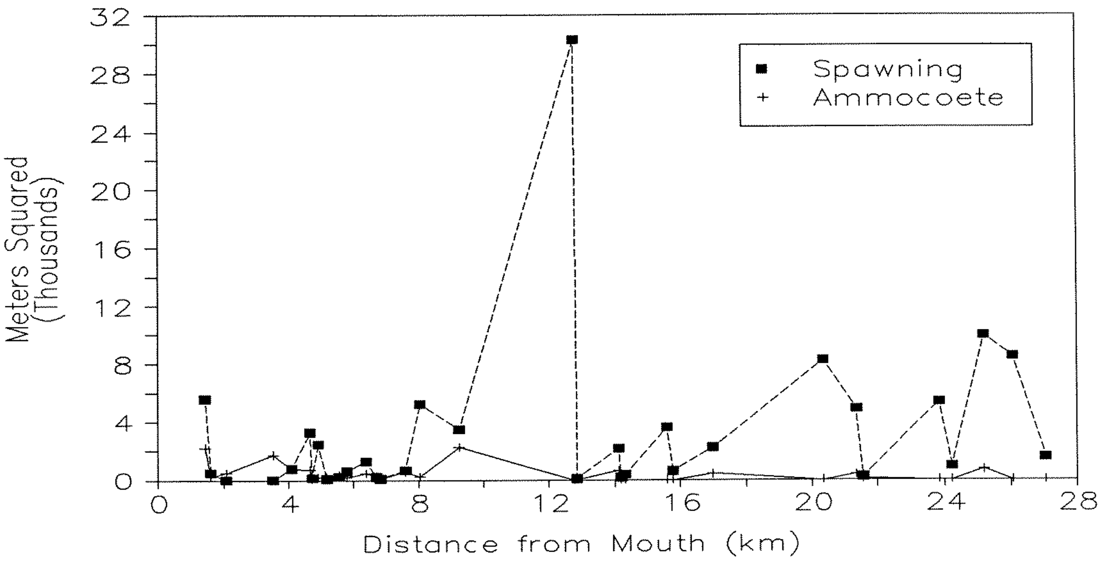

Figure 7: Substrate distribution along Bronte Creek for ammocoete and spawning phase sea lamprey.

Comparing WUA for each life stage in the streams allows for the differences between streams in terms of usable habitat to be seen more clearly. The study sections of the four streams are very different in total length and area; Salem Creek is 2,800 meters long, Wilmot Creek is 11,271 meters long, Oshawa Creek is 18,415 meters long, and Bronte Creek is 27,051 meters long. I chose to relativize the WUA values to the spawning WUA to allow comparison of suitable habitat area available for each sea lamprey life stage (Fig. 8).

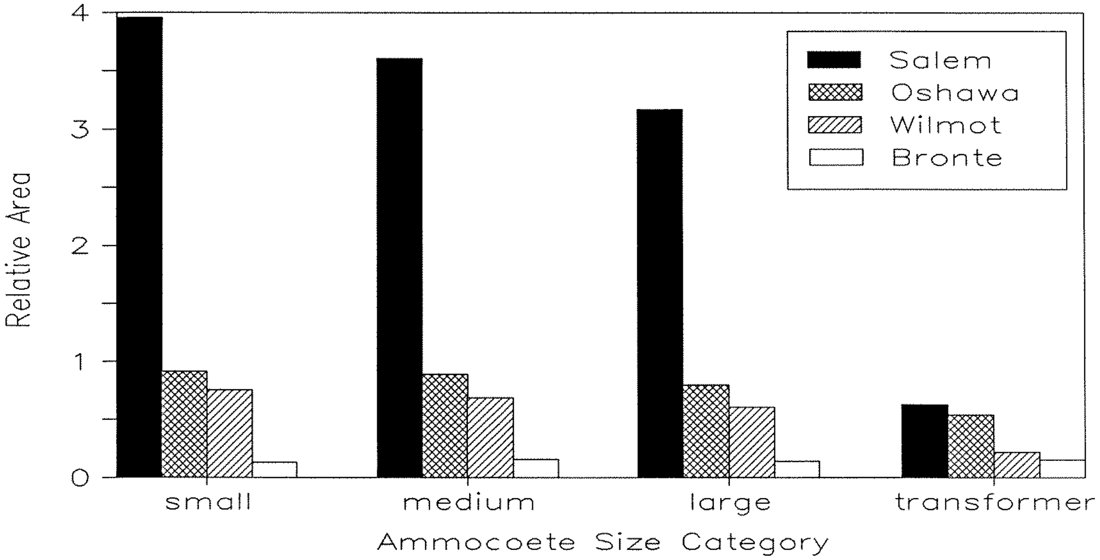

Figure 8: Comparison of the WUA available in each stream for the three ammocoete size categories. Each stream is standardized to its WUA for spawners.

Clearly, Salem Creek has much more suitable habitat for ammocoetes than for spawners. Oshawa Creek is much more evenly distributed in terms of available habitat for the three ammocoete size categories and for spawners. Wilmot and Bronte Creeks, on the other hand, have very little ammocoete habitat relative to the spawning available habitat. None of the streams show a lot of area for transformers relative to spawners. This may be due to transformer preference for transient types of habitat.

I used the ammocoete habitat utilization simulation to determine how ammocoetes distributed themselves into the usable area depicted in the habitat maps. The simulation was run once under the assumption of uniform hatch distribution and once under the assumption of non-uniform hatch distribution. Using the predicted area (PAU) as calculated for each ammocoete size category and weighted against the corresponding total WUA, I compared the four streams in terms of efficiency of use of available habitat by each ammocoete size category (Fig. 9) and found that it is difficult to make a generalization about the stream when the information is depicted in this manner.

I next compiled the size category information into one habitat suitability index by averaging the indices for the different ammocoete size categories (Fig. 10). It is interesting to note that under different assumptions of hatch distribution, the HSI for the streams change slightly. This change may be due to the relative positioning of spawning and ammocoete habitat along the length of the stream because the HSI is based on a measure of the efficiency with which available suitable habitat is used (PAU). Under the assumption of uniform hatch distribution, the HSI for Salem Creek and Oshawa Creek decreases while it increases in Bronte Creek and Wilmot Creek. Bronte and Wilmot have the main portion of spawning habitat in the middle of the stream while having ammocoete habitat both upstream and downstream. Since ammocoete migration occurs primarily downstream, the

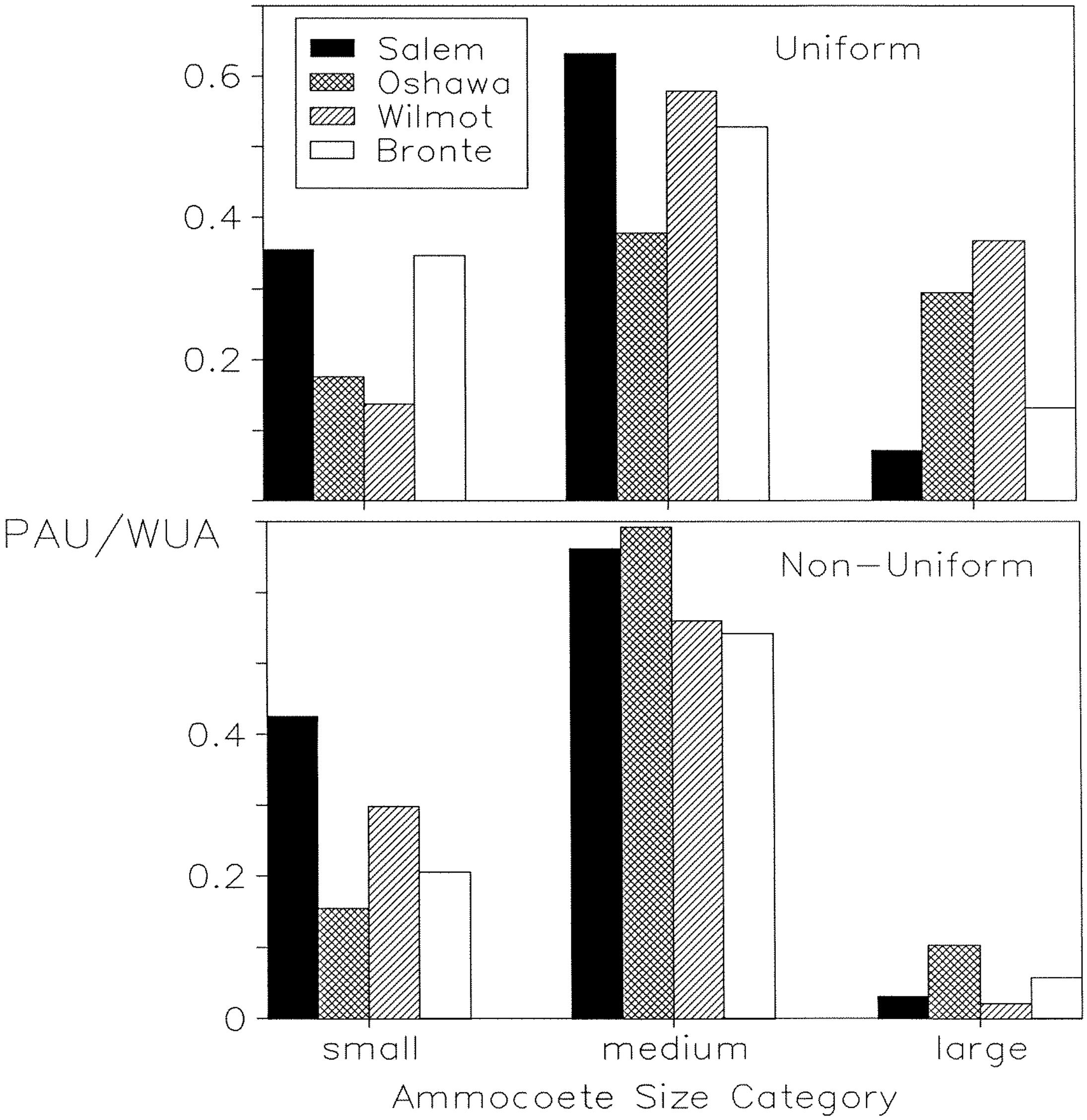

Figure 9: Comparison of the PAU/WUA for the different ammocoete size categories in the four study streams. The top panel shows the result of uniform hatch distribution and the bottom panel shows the result of non-uniform hatch distribution.

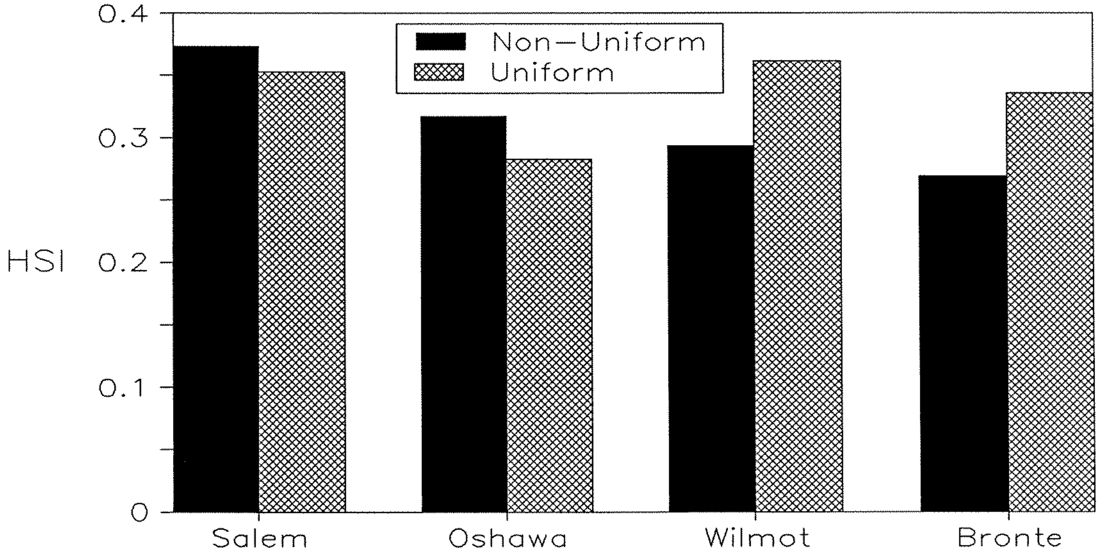

Figure 10: The average habitat suitability index for the four study streams under the assumption of uniform and non-uniform hatch distribution.

upstream portions of ammocoete habitat are not efficiently used under the assumption of non-uniform hatch distribution since most of the hatch is allocated to the middle reaches of the streams. Uniform hatch distribution allows for a larger number of hatch to be distributed to the upstream reaches enhancing the efficiency of habitat use in the streams and raising the average HSI. On the other hand, Salem and Oshawa have most of their spawning habitat upstream from the ammocoete habitat. Distributing the hatch according to spawning available habitat allows for all of the ammocoete habitat downstream to be used efficiently. Under the assumption of uniform hatch distribution, efficiency of habitat use is reduced since not all the habitat is open to colonization by ammocoetes thereby reducing the HSI for the streams.

DISCUSSION

Understanding the variability of transformer production potential among streams is critical to the success of the sea lamprey control program in the Great Lakes. The objective of this study is to establish the feasibility of including biological information in a measure of suitable habitat and using this measure to rank streams in terms of transformer production potential. An understanding of the regulation of ammocoete densities in the streams is needed to understand this production potential.

The regulation of ammocoete density in streams is complicated by the chemical treatment cycle since the treatment is the main source of mortality. If the effects of the treatment were eliminated, I would expect that the ammocoete population would reach a steady state that is regulated by the carrying capacity of the stream for sea lamprey ammocoetes. The distribution of ammocoetes throughout the stream is clumped due to the patchy distribution of suitable burrowing habitat within the stream. Sampling design leads to density of ammocoetes being measured as a mean density over the entire stream. Since the individuals live in a clumped situation, this average density is not the true density felt by the individuals. Using the averaged density leads to misconceptions when trying to determine the density dependent population regulators such as growth, mortality, and migration.

The transformer production potential is the product of the rate of transformation and the density of pre-transformation ammocoetes. Because transformation rates are difficult to estimate, other population states can be used as surrogates for production potential. Two examples of these states are the number of ammocoetes that are longer than 125 mm, and the total abundance of ammocoetes in the stream. The abundance of ammocoetes in the stream is related to the carrying capacity of the stream. This study assumes that carrying capacity is determined by the amount of suitable burrowing habitat available in the stream for ammocoetes. This idea is similar to that used in Instream Incremental Flow Methodology (IFIM). The IFIM was developed as tool for mitigation of water flow in regulated streams. Assuming that the abundance of a certain fish species is limited by the carrying capacity of the stream as defined by the presence of suitable habitat, the methodology calculates the weighted usable area (WUA) at different discharges to determine which discharge maximizes the available habitat and, therefore, the carrying capacity for a certain species. In this case, the WUA, which takes into account the preference of the species for certain habitat characteristics, is used directly as a habitat suitability index.

Because the biology of the sea lamprey ammocoete is different than that of other fish, it is necessary to go one step beyond the WUA in this study. The ammocoetes remain relatively sedentary throughout their time in the stream with brief periods of active migration downstream in search of more suitable habitat. Since the ammocoetes are not as mobile as other fish and tend to migrate in the downstream direction only, the position of spawning habitat relative to ammocoete habitat becomes a critical issue. Only the portions of the stream below spawning habitat are available for ammocoete colonization. Simple summaries of WUA omit important information about the distribution of substrate along the length of the stream. As a result, PAU, a measure of area that takes into account the sea lamprey life cycle and how each phase utilizes the available habitat, offers a higher resolution over WUA for comparison of streams in terms of carrying capacity. The PAU is actually a measure of the stream's production potential since multiplying it by an expected density would yield an expected population estimate.

The HSI, PAU relativized to WUA, is a relative measure that allows comparison between streams. Expectations of relative ammocoete abundance of the four streams can be made using the HSI. Under the assumption of non-uniform spawner distribution, the streams' HSI indicate that Salem will have the highest average density, followed by Oshawa and Wilmot, with Bronte having the lowest. In contrast, under the assumption of uniform spawner distribution, the HSIs indicate that Wilmot is the highest, followed by Salem and Bronte, with Oshawa being the lowest (Fig. 10). The change in the pattern of stream HSI under the different assumptions of hatch distribution illustrates that it is critical to include the relative positions of spawning habitat and ammocoete habitat along the length of the stream in the measure of production potential if spawners are found to distribute themselves non-uniformly throughout the stream. Leaving this element out of the analysis will inflate the predicted measure for streams that have ammocoete habitat throughout the stream while their spawning habitat is concentrated towards the middle of the stream. The change in HSI pattern also indicates that more information is needed in terms of spawner distribution throughout the length of the stream.

Another way in which the streams can be ranked is in terms of absolute abundance. The total abundance of ammocoetes in the stream is determined using the ammocoete habitat utilization simulation. The streams rank as follows: Bronte (299,458), Oshawa (243,773), Wilmot (235,327), and finally Salem (49,883).

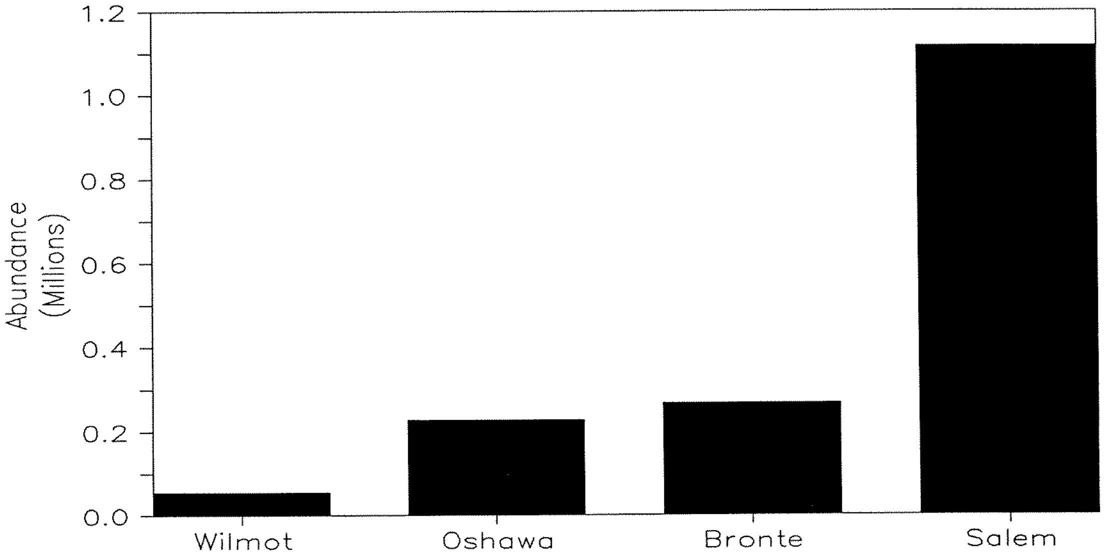

Figure 11: Preliminary population estimates made during special population studies (Jerry Weise, personal communication).

Interestingly, preliminary population studies indicate that Salem Creek has a much higher abundance of ammocoetes than I expected (Fig. 11). Although the HSI, under assumptions of non-uniform hatch distribution, indicates Salem to have the highest average density, it does not indicate the magnitude seen in the abundance measures. If these preliminary findings are correct, more information is required to further refine the HSI. Clearly, more concrete information about ammocoete substrate preference is needed; the preferences may be much more specific than I have suggested and/or the size categories I have used may be too broad. Perhaps the hatch is more successful in Salem than in the other streams. The positioning of the ammocoete habitat relative to the spawning habitat may be more conducive to ammocoete survival than I have indicated, or all of the available habitat for spawners is prime habitat. Other factors such as temperature or conductivity may also need to be included to further refine the HSI.

On the other hand, the dramatic differences in abundances (Fig. 11) may be due to observational error. Efficiency in sampling varies with stream size, making large streams more difficult to sample than smaller streams. Also, since the ammocoetes exhibit clumped spatial patterns, a random design on a very large system may not include enough of the optimal habitat patches to give an accurate description of the average density in the stream. Since the streams seem to be chemically similar (Jerry Weise, personal communication), I feel that perhaps there is some sampling artifact affecting the observed abundances.

In conclusion, I have shown the feasibility of establishing habitat suitability indices for sea lamprey ammocoetes in streams using a biologically sensitive approach. Developing a HSI for sea lamprey in streams is beneficial in several ways. First, the approach, as it is now set up, is easy to use. Second, it requires a minimum of additional data collection for the indirect method of substrate mapping. Finally, and most importantly, it improves the estimates of production potential. Using PAU rather than total stream area to determine density in the stream provides a better approximation to the real density in the patches of suitable substrate which is the density actually felt by the individuals. Therefore, it is more directly associated with density dependent factors such as mortality and growth.

To allow full implementation of HSI development several information gaps need to be filled. First, sea lamprey substrate preferences need to be defined more precisely. Second, more information is needed about spawners and their distribution along the stream. Finally, more physical information about the streams is needed to extend this method basin wide. Detailed, field measured habitat maps would be the best for use in developing HSI at a given point in time. On the other hand, habitat maps can be constructed using information that can easily be collected during routine population surveys. These critical measures are: stream width, average depth, average velocity, and bed slope. Since population surveys are conducted at several points along the streams, this information can be collected at each survey point to provide an indirect way to map the available substrate along the length of the stream. Since the habitat maps can be expected to change with time, the indirect approach to mapping may be more useful since it allows for basic hydraulic relationships to be determined and these will be useful for very long periods of time.

REFERENCES

Applegate, V. C. 1950. Natural history of the sea lamprey (Petromyzon marinus) in Michigan. U.S. Fish and Wildlife Service, Special Scientific Report. Fisheries 55: 237 pp.

Binns, N. A., and F. M. Eiserman. 1979. Quantification of Fluvial Trout Habitat in Wyoming. Trans. Amer. Fish. Soc. 108:215-228.

Blatt, Middleton, and Murray. 1980. Origin of Sedimentary Rocks. Prentice Hall, Inc., Englewood Cliffs. New Jersey.

Bovee, K. D. 1982. A guide to stream habitat analysis using the Instream Flow Incremental Methodology. Instream Flow Information Paper 12. U.S.D.I. Fish and Wildlife Service, Office of Biological Services. FWS/OBS-82/26 248 pp.

Bovee, K. D. 1986. Development and evaluation of habitat suitability criteria for use in the Instream Flow Incremental Methodology. Instream Flow Information Paper 21. U.S. Fish and Wildlife Service. Biol. Rep. 86(7). 235pp.

Hamilton, K., and E. P. Bergersen. 1984. Methods to estimate aquatic habitat variables. Colorado Cooperative Fishery Research Unit. Technical Paper. 350 pp.

Hastings, C. 1955. Approximations for the Digital Computer. Princeton, N.J., Princeton University Press.

Johnson, B. G. H. (ed.). 1987. Evaluation of sea lamprey populations in the Great Lakes: Background papers and Proceedings of the August 1985 Workshop. Great Lakes Fishery Commission, Special Publication 87-2.

Malmqvist, B. 1980. Habitat selection of larval brook lampreys (Lampetra planeri, Bloch) in a south Swedish stream. Oecologia. 45:35-38.

Manion, P. J., and L. H. Hanson. 1980. Spawning behavior and fecundity of lampreys from the upper three Great Lakes. Can. J. Fish. Aquat. Sci. 37:1635-1640.

Manion, P. J., and A. L. McLain. 1971. Biology of larval sea lampreys Petromyzon marinus of the 1960 year class, isolated in the Big Garlic River, Michigan, 1960-65. Great Lakes Fish. Comm. Tech. Rep. 16:35 pp.

Odgaard, A. J. 1984. Grain-size distribution of river-bed armor layers. J. Hydraulic Engineering. 110:1479-84.

Orth, D. J., and O. E. Maughan. 1982. Evaluation of the Incremental Methodology for Recommending Instream Flows for Fishes. Trans. Amer. Fish. Soc. 111:413-445.

Pearce, W. A., R. A. Braem, S. M. Dustin, and J. J. Tibbles. 1980. Sea lamprey (Petromyzon marinus) in the Lower Great Lakes. Can. J. Fish. Aquat. Sci. 37:1802-1810.

Potter, I. C., R. W. Hilliard, J. S. Bradley, and R. J. McKay. 1986. The influence of environmental variables on the density of larval lampreys in different seasons. Oecologia. 70:433-440.

Richards, K. 1982. Rivers: Form and Processes in Alluvial Channels. Methven, New York.

Smith B. R., and J. J. Tibbles. 1980. Sea lamprey (Petromyzon marinus) in Lakes Huron, Michigan, and Superior: history of invasion and control, 1936-78. Can. J. Fish. Aquat. Sci. 37:1780-1801.

Vannote, R. L., G. W. Minshall, K. W. Cummins, J. R. Sedell, and C. E. Cushing. 1980. The river continuum concept. Can. J. Fish. Aquat. Sci. 37:130-137.

Water Survey of Canada. 1987. Surface Water Data: Ontario. Inland Waters Directorate. Ottawa.

APPENDIX 1

Stream Channel Model Variable Documentation

Legend:
* = value updated in model
! = value read in as data by model
u = unitless

Table 1-A: Variables in Stream Channel Model

Variable	Description	Value	Units
a1-a6	Constants in normal distribution approximation.	!	u
area(i,j)	Actual area of substrate type by stream segment.	!	m^2
d16	Diameter of grain size at sixteenth percentile.	*	mm.
depth	Mean depth of stream segment.	!	m
dmvel	Depth of mean velocity.	*	m
ends(i)	Substrate type endpoints as seen in Table 1.	!	mm.
k	von Karman's constant.	0.4	u
meanvel	Mean velocity in stream segment.	*	m/s
perc(i)	Percent of area in segment i of a certain substrate type.	*	u
prefer(i,j)	Sea lamprey preference for a particular substrate type by size category.	!	u

Table 1-A: (continued)

qmean	Mean annual discharge for the stream (Salem = 0.1078; Oshawa = 1.16; Wilmot = 1.203; Bronte = 2.125)	!	cms
s	Standard deviation.	1	u
segarea	Total stream segment area.	*	m^2
seglength	Length of stream segment.	!	m
shearvel	Shear velocity.	*	m/s
surfvel	Surface velocity in stream segment.	*	m/s
t	Adjustment factor in shear velocity calculation.	*	u
u	Mean grain size in stream segment.	*	mm.
wide	Width of stream segment.	!	m
wua(i,j)	Weighted usable area in a particular segment by size category.	!	m^2
xsarea	Cross-sectional area of stream segment.	*	m^2
y0	Depth at which velocity = 0.	*	m

Stream Channel Model Listing

This program determines the substrate composition in a channel section using a logarithmic velocity profile and assuming that substrate is normally distributed.

```
'Open input and output files

  INPUT "Stream Two Letter Code"; x$

  OPEN "b:" + x$ + "chdata.prn" FOR INPUT AS #1
  OPEN "b:" + x$ + "prsubs.prn" FOR OUTPUT AS #2
  OPEN "b:" + x$ + "acarea.prn" FOR OUTPUT AS #3
  OPEN "b:" + x$ + "wuarea.prn" FOR OUTPUT AS #4

'Declare arrays

  DIM ends(23), prefer(11, 5)
  DIM perc(40, 11), wua(40, 5), area(40, 11)

'Read endpoints of substrate categories

  FOR i = 1 TO 23
      READ ends(i)
  NEXT i

  DATA 200, 64, 64, 16, 16, 8, 8, 2, 2, .5, .5, .25, .25,
       .06, .06, .016, .016, .008, .008, .002, .002,
       .0001, .0001

'Read ammocoete substrate preference

  FOR i = 1 TO 11                'substrate category
      FOR j = 1 TO 5             'size category
          READ prefer(i, j)
      NEXT j
  NEXT i

  DATA    0,      0,      0,      0,      0
  DATA    0,      0,      0,      0,    .18
  DATA    0,      0,      0,      0,    .86
  DATA    0,      0,      0,    .07,    .85
  DATA    0,    .06,    .07,    .53,      0
  DATA  .06,    .41,    .45,    .92,      0
  DATA  .49,    .76,    .82,    .96,      0
  DATA  .88,    .99,    .88,      0,      0
  DATA  .98,    .19,    .06,      0,      0
  DATA  .89,      0,      0,      0,      0
  DATA    0,      0,      0,      0,      0
```

```
'Declare constants

  k = .4      'von Karman's constant
  t = .69    'adjustment factor shear velocity
calculation

  a1 = 7.052307839999999D-02      'constants for normal
  a2 = .0422820123#                distribution approx
  a3 = .0092705272#
  a4 = .0001520143#
  a5 = .0002765672#
  a6 = .0000430638#

'Input stream data

  INPUT #1, a, b, c, d
  qmean = a

'Calculation section

  WHILE NOT EOF(1)

      z = z + 1
      t = t / .992

      INPUT #1, a, seglen, wide, depth

      segarea = wide * seglen   'determine segment area
      xsarea = wide * depth     'determine velocity
      meanvel = qmean / xsarea

    'Determine shear velocity

      surfvel = meanvel * 1.2
      dmvel = depth * .4

      shearvel = t * (k * (surfvel - meanvel)) /
                       (LOG(depth) - LOG(dmvel))

    'Determine mean particle size

      y0 = depth / (EXP(k * surfvel / shearvel))
      d16 = (7 * y0) * 1000

      u = d16 / 1.57
      s = u * .57

    'Determine particle size distribution

      totalpercent = 0
      j = 0

      FOR i = 1 TO 21 STEP 2
```

```
      j = j + 1
      hi = ends(i)
      lo = ends(i + 1)

      zhi = (hi - u) / s
      zlo = (lo - u) / s

      xhi = SQR(zhi ^ 2 / 2)
      xlo = SQR(zlo ^ 2 / 2)
      pzhi = 1 - (1 / ((1 + a1 * xhi + a2 * xhi^2 +
            a3 * xhi^3 + a4 * xhi^4 + a5 * xhi^5 +
            a6 * xhi^6) ^ 16))
      pzlo = 1 - (1 / ((1 + a1 * xlo + a2 * xlo^2 +
            a3 * xlo^3 + a4 * xlo^4 + a5 * xlo^5 +
            a6 * xlo^6) ^ 16))

      IF zhi < 0 THEN
          apzhi = .5 - pzhi / 2
      ELSE apzhi = .5 + pzhi / 2
      END IF

      IF zlo < 0 THEN
          apzlo = .5 - pzlo / 2
      ELSE apzlo = .5 + pzlo / 2
      END IF

    'Determine percentage of substrate type
      IF j = 11 THEN
          totp = apzhi
      ELSE totp = (apzhi - apzlo)
      END IF

      perc(z, j) = totp
      totalpercent = totalpercent + perc(z, j)
  NEXT i

'Adjust silt-clay distribution
  rat2 = 0
  rat3 = 0
  rat4 = 0
  rat5 = 0
  rat6 = 0
  rat7 = 0
  rat8 = 0
  rat9 = 0
  rat10 = 0
```

```
totg = perc(z, 2) + perc(z, 3) + perc(z, 4)
tots = perc(z, 5) + perc(z, 6) + perc(z, 7)
totl = perc(z, 8) + perc(z, 9) + perc(z, 10)

IF totg > 0 THEN
    rat2 = perc(z, 2) / totg
    rat3 = perc(z, 3) / totg
    rat4 = perc(z, 4) / totg
END IF
IF tots > 0 THEN
    rat5 = perc(z, 5) / tots
    rat6 = perc(z, 6) / tots
    rat7 = perc(z, 7) / tots
END IF
IF totl > 0 THEN
    rat8 = perc(z, 8) / totl
    rat9 = perc(z, 9) / totl
    rat10 = perc(z, 10) / totl
END IF
IF x$ = "br" THEN
    SELECT CASE z
        CASE 1, 2, 5, 10 TO 15, 17, 19 TO 26,
             28 TO 30, 33
            totg = totg / 5
        CASE 18
            totg = totg / 2
    END SELECT

    SELECT CASE z
        CASE 17, 31
            totl = totl + .4 * tots
    END SELECT

    tots = tots * .1

END IF
IF x$ = "os" THEN
    SELECT CASE z
        CASE 1, 2
            totl = totl + .9 * tots
        CASE 17
            totl = totl + tots * .6
        CASE 8 TO 10, 12, 13, 27, 30, 33, 34, 35
            totl = totl + tots * .4
    END SELECT
```

```
    SELECT CASE z
        CASE 1 TO 21, 23, 24, 26, 27, 30 TO 34, 38
            tots = tots * .1
        CASE 29, 35 TO 37
            tots = tots * .5
    END SELECT
END IF

IF x$ = "sa" THEN
    SELECT CASE z
        CASE 1, 8
            totl = totl + tots * .5
            tots = tots * .5
        CASE 2 TO 4
            totl = totl + tots * .9
            tots = tots * .1
        CASE 5 TO 7, 9 TO 11
            totl = totl + tots * .7
            tots = tots * .1
        CASE 13
            totl = totl + tots * .3
            tots = tots * .7
        CASE 14 TO 17
            totl = totl + tots * .95
            tots = tots * .05
        CASE ELSE
            tots = tots * .1
    END SELECT
END IF

IF x$ = "wi" THEN
    SELECT CASE z
        CASE 12 TO 14, 20
            totg = totg / 4
    END SELECT

    SELECT CASE z
        CASE 3
            totl = totl + tots * .9
        CASE 5, 6, 9 TO 15, 17 TO 27
            totl = totl + tots * .4
        CASE 7, 28 TO 40
            totl = totl + tots * .75
    END SELECT

    SELECT CASE z
        CASE 1 TO 7, 9 TO 22, 24 TO 40
            tots = tots * .1
        CASE 23
```

```
                tots = tots * .6
        END SELECT
    END IF

    perc(z, 2) = totg * rat2
    perc(z, 3) = totg * rat3
    perc(z, 4) = totg * rat4
    perc(z, 5) = tots * rat5
    perc(z, 6) = tots * rat6
    perc(z, 7) = tots * rat7
    perc(z, 8) = totl * rat8
    perc(z, 9) = totl * rat9
    perc(z, 10) = totl * rat10

 'Determine weighted usable area
    FOR j = 1 TO 11        'substrate category

        area(z, j) = perc(z, j) * segarea
        IF (area(z, j) < (.02 * segarea))
          THEN area(z, j) = 0

        FOR i = 1 TO 5     'size category
            wua(z, i) = wua(z, i) + (area(z, j) *
                            prefer(j, i))
        NEXT i

    NEXT j

  'Print screen and file information
    PRINT z,
    PRINT USING "##.##    "; perc(z, 1) * 100; totg *
100;
                tots * 100; totl * 100; perc(z, 11) *
100

    FOR i = 1 TO 11
        PRINT #2, USING "###.##,"; perc(z, i) * 100;
        PRINT #3, USING "#####.##,"; area(z, i);
    NEXT i
    PRINT #2, USING "###.##"; totalpercent * 100
    PRINT #3, USING "#####.##"; segarea

    FOR i = 1 TO 5
        PRINT #4, USING "#####.##,"; wua(z, i);
    NEXT i
    PRINT #4, USING "#####.##"; segarea
  WEND
  CLOSE
  END
```

APPENDIX 2

Ammocoete Habitat Utilization Simulation Variable Documentation

Legend:
* = value updated in model
! = value read in as data by model
u = unitless

Table 2-A: General Variables

Variable	Description	Value	Units
age0len	Length at age 0	20	mm
ammden	Ammocoete density in a particular substrate within a segment	*	ind/m^2
avgabund(k)	Average abundance of age group within particular substrate in a segment	*	u
avgsize(k)	Average size of age group within particular substrate in segment	*	mm
ca(i,j)	Substrate area by segment	!	m^2
cel	Stream segment counter	counter	u
cpref	Preference for a stream segment	*	u
hatch	Number of hatchlings for the year (age 0): Salem = 100,000; Oshawa = 1,076,067; Wilmot = 1,115,955; Bronte = 1,971,243	!	u
hdp(i)	Hatch distribution rule	*	u
i	Segment index	counter	u
initnum	Initial number of ammocoetes in the stream. (initialization)	15000	u

Table 2-A: (continued)

isize	Size category (< 80mm, 80 < size >125mm, >125mm)	*	mm
j	Substrate index	counter	u
k	Age index	counter	u
l(k)	Length at age	!	mm
newtotal	Total number of ammocoetes in a segment after migration and hatch are added	*	u
nsize	Counter	*	u
pref(sz,j)	Substrate preference by size	!	u
treat	Decision to treat in a given year (1 = treat, 0 = no treatment)	*	u
tspa	Total spawning area in stream	*	m^2
xbar	Mean length of ammocoetes age k	*	mm

Table 2-B: Growth Variables

Variable	Description	Value	Units
krho	Constant in equation determining substrate specific slope accounting for density effects	100	ind/m^2
kwk	Constant in equation determining substrate specific y-int accounting for density effects	100	ind/m^2
rho	Substrate specific slope on growth vs density curve	*	u
rhomax	Maximum slope of the growth vs time curve	0.55	u
wk	Substrate specific y-intercept on growth vs density curve	*	mm
wkmax	Maximum y-intercept on a growth vs time curve	74	mm

Table 2-C: Mortality Variables

Variable	Description	Value	Units
kzm	Constant in equation determining substrate specific natural mortality accounting for density	100	ind/m^2
zm	Natural mortality particular to density within given substrate	*	1/yr
zmmax	Maximum natural mortality	0.4	1/yr
zmmin	Minimum natural mortality	0.2	1/yr
ztm(k)	Maximum treatment mortality by age	*	1/yr
ztmax(k)	Maximum treatment mortality by age	!	1/yr

Table 2-D: Transformation Variables

Variable	Description	Value	Units
avgtrans	Average number of transformers per segment	*	u
kpt	Constant in determining probability of transformation as a function of size	25	mm
mintransize	Minimum size required for transformation	125	mm
ptmax	Maximum probability of transformation	1	u
ptrans	Probability of transformation as a function of size	*	u
ptrans(i)	Distribution probability of transformers into segment i	!	u
sizdif	Difference between mintransize and size of ammocoetes	*	mm
trans(i)	Number of transformers in segment i	*	u
ttrans	Total number of transformers in stream	*	u

Table 2-E: Migration Variables

Variable	Description	Value	Units
cpm(k)	Minimum migration probability by age	!	u
kpm(k)	Constant in migration function accounting for density by age	!	ind/m^2
m(i,k)	Migrant ammocoetes by segment and age	*	u
mx(i,k)	Mean size of corresponding migrant ammocoetes	*	mm
nm(i,j,k)	Non-migrant ammocoetes by segment, substrate, age	*	u
nmx(i,j,k)	Mean size of corresponding non-migrant ammocoetes	*	mm
nummig	Intermediate variable used to sum the number migrating over substrate types.	*	u
pmax(k)	Maximum migration probability by age	!	u
pmd	Probability of downstream migration	0.2	u
pmig	Probability of migration due to density effects	*	u
pmn	Exponent in migration function	3	u
pmu	Probability of upstream migration	0.05	u

Ammocoete Habitat Utilization Model Listing

```
'Dimension Arrays
DIM nm(40, 6, 6), m(40, 6), nmx(40, 6, 6), mx(40, 6)
DIM trans(40), ptrans(40), hdp(40)
DIM avgabund(6), ztm(6)
DIM cpm(6), pmax(6), kpm(6)
DIM tmp(40, 12), pref(2, 6), ca(40, 6), cpreff(40,3)
DIM nul80(40), nubet(40), nug125(40), cpref(40, 6, 3)

INPUT "Stream Two Letter Code"; x$
OPEN "b:" + x$ + "acarea.prn" FOR INPUT AS #1
OPEN "b:" + x$ + "abundc.prn" FOR OUTPUT AS #2
OPEN "b:" + x$ + "prduse.prn" FOR OUTPUT AS #3

'FOR i = 1 TO 4
'  OPEN "a:testa" + RIGHT$(STR$(i), 1) + ".dat" FOR
OUTPUT
         AS #i
'NEXT i

'Initial Data
'        Stream Cell Characteristics
        'Substrate areas by cell (CA(i,j))
        cel = 0
        WHILE NOT EOF(1)
            cel = cel + 1
            FOR i = 1 TO 12
                INPUT #1, tmp(cel, i)
            NEXT i

            tspa = tspa + (tmp(cel, 2) + tmp(cel, 3) +
                   tmp(cel, 4) + (tmp(cel, 5) / 2))

        WEND

        'calculate hatch distribution probabilty
        FOR i = 1 TO cel
            hdp(i) = (tmp(i, 2) + tmp(i, 3) + tmp(i, 4)
                     + (tmp(i, 5) / 2)) / tspa
            ca(i, 1) = tmp(i, 5)
            ca(i, 2) = tmp(i, 6)
            ca(i, 3) = tmp(i, 7)
            ca(i, 4) = tmp(i, 8)
            ca(i, 5) = tmp(i, 9)
            ca(i, 6) = tmp(i, 10)
            PRINT hdp(i)
```

```
            thdp = thdp + hdp(i)
        NEXT i
        PRINT thdp

'       Transformer habitat probabilities by stream cell
   'Distribution probability--->ptrans(i)
'       Hatch distribution rule--->hdp(i)
       'Spawner dynamics (hatch)

       SELECT CASE x$
           CASE "sa"
               hatch = 100000!
           CASE "os"
               hatch = 1076067
           CASE "wi"
               hatch = 1115955
           CASE "br"
               hatch = 1971243
       END SELECT
       PRINT hatch
        'std = 20000
        FOR i = 1 TO 40
            ptrans(i) = .05
        NEXT i
'       Parameters

  'Substrate preference (pref(sz,j))
        FOR sz = 0 TO 2 'size category
            FOR j = 1 TO 6'substrate
                READ pref(sz, j)
            NEXT j
        NEXT sz
        'Preference data
        DATA   0, .06, .49, .88, .98, .89
        DATA .06, .41, .76, .99, .19, 0
        DATA .07, .45, .82, .88, .06, 0

  'cell preference index
      FOR i = 1 TO cel
          FOR sz = 0 TO 2
              totpref = 0
              FOR j = 1 TO 6
                  totpref = totpref - pref(sz, j)
                            * (ca(i, j) > 0)
              NEXT j
              cpreff = 0
              FOR j = 1 TO 6
```

```
                cpref(i, j, sz) = -(pref(sz, j) /
                                (totpref + .000001))
                                  * (ca(i, j) > 0)
                cpreff(i, sz) = cpreff(i, sz) -
                           (cpref(i, j, sz) > 0)
            NEXT j
        NEXT sz
    NEXT i

'Growth and mortality parameters
      wkmax = 74  'mm
      rhomax = .55
      kwk = 100 'ind/sq m.
      krho = 100 'ind/sq m.
      zmmin = .2   '1/yr
      zmmax = 2   '1/yr
      kzm = 10 ^ 2 'ind/sq m.
      FOR k = 0 TO 6
          READ ztmax(k)    '1/yr
      NEXT k
      DATA 4.6, 4.6, 4.6, 4.6, 4.6, 4.6, 4.6
'Transformation probabilities
      mintransize = 125     'mm
      ptmax = 1
      kpt = 25 ^ 2            'mm
'Migration
      pmn = 3             ' power of migration function
      pmu = .05           'upstream migration fraction
      pmd = .2            'downstream migration fraction
      FOR k = 0 TO 6
          cpm(k) = .05    'minimum migration probability
          pmax(k) = .55   'maximum migration probability
          kpm(k) = 20     'ind/sq m.
      NEXT k

'       Initial Variable Values
        xbar = 0
        'size at age
        age0len = 20   'mm
        l(0) = age0len
        FOR k = 1 TO 6
            l(k) = l(k - 1) * rhomax + wkmax
        NEXT k
```

```
        'numbers by cell and age (including transformers

        FOR i = 1 TO cel
          initnum = 15000
          FOR k = 0 TO 6
             FOR j = 1 TO 6
                nm(i, j, k) = 0
                nmx(i, j, k) = 0
                IF ca(i, j) > 0 THEN
                   isize = -(xbar >= 125) - (xbar >= 80)
                   nm(i, j, k) = initnum *
                                      cpref(i, j, isize)
                   nmx(i, j, k) = l(k)
                END IF
             NEXT j
             initnum = initnum * .5
          NEXT k
      NEXT i

'Annual Loop
FOR time = 0 TO 20

        'Treatment decison (treat=1 for treatment) &
treatment mortality
        treat = 0
        'IF INT(time / 4) * 4 = time AND time > 0
           THEN treat = 1
        FOR k = 0 TO 6
            ztm(k) = ztmax(k) * treat
        NEXT

        'Determine hatch abundance
        'RANDOMIZE TIMER
        'r = RND * 2 - 1
        'z = LOG((1 + r) / (1 - r)) / 1.82
        'hatch = avghatch + std * z


        'Distribute hatch and ammocoetes within each cell
        FOR i = cel TO 1 STEP -1  'stream cell index
            trans(i) = ptrans(i) * ttrans
```

```
FOR k = 0 TO 6   'ammocoete age index
    'distribute hatch to each cell

  IF k = 0 THEN
    newtotal = hatch * hdp(i)
    xbar = age0len

  ELSE
 'calculate new mean sizes due to admixture
    newtotal = 0
    xbar = 0

    sz = -(mx(i,k) >= 125) - (mx(i,k)>=80)
    IF cpreff(i, sz) = 0 THEN
        IF i = 1 THEN
            m(i, k) = 0
            mx(i, k) = 0
        ELSE
            kmig = m(i, k) + m(i - 1, k)
            IF kmig > 0 THEN
                mx(i - 1, k) = (m(i, k) *
                   mx(i, k) + m(i - 1, k) *
                   mx(i - 1, k)) / kmig
                m(i - 1, k) = kmig
                m(i, k) = 0
                mx(i, k) = 0
            ELSE
                m(i, k) = 0
                mx(i, k) = 0
            END IF

        END IF
    END IF
    FOR j = 1 TO 6
        xbar = nm(i, j, k) * nmx(i, j, k)
              + xbar
        newtotal = newtotal + nm(i, j, k)
    NEXT j
    xbar = xbar + (m(i, k) * mx(i, k))
    newtotal = newtotal + m(i, k)
    IF newtotal > 0 THEN
        xbar = xbar / newtotal
    ELSE xbar = 0
    END IF
    m(i, k) = 0
    mx(i, k) = 0

  END IF
```

```
                 'redistribute ammocoetes

                 FOR j = 1 TO 6
                   isize = -(xbar>=125) - (xbar>=80)
                   nm(i,j,k)=newtotal*cpref(i,j,isize)
                   nmx(i, j, k) = xbar
                 NEXT j

            NEXT k

         NEXT i
        ttrans = 0

IF time = 20 THEN
FOR i = 1 TO cel
    FOR j = 1 TO 6
     IF ca(i, j) > 0 THEN

       FOR k = 1 TO 6

            IF nmx(i, j, k) <= 80 THEN
                nul80(i) = nul80(i) + nm(i, j, k)
            ELSEIF nmx(i, j, k) >= 125 THEN
                nug125(i) = nug125(i) + nm(i, j, k)
            ELSE nubet(i) = nubet(i) + nm(i, j, k)
            END IF

        NEXT k
     END IF

  NEXT j

  PRINT #3, USING
"#####.##,";nul80(i);nubet(i);nug125(i);
  PRINT #3, i

NEXT i
END IF

'Store data according to survey technique
'Determine average abundance per cell by age
        FOR k = 0 TO 6
            avgabund(k) = 0
            avgsize(k) = 0
            nsize = 0
            FOR i = 1 TO cel
                FOR j = 1 TO 6
                    IF nm(i, j, k) > 0 THEN
                      nsize = nsize + 1
                      avgabund(k) = nm(i, j, k)
                                   + avgabund(k)
```

```
                   avgsize(k) = nm(i, j, k) *
                     nmx(i, j, k) + avgsize(k)
                 END IF
             NEXT j
         NEXT i
         avgsize(k) = avgsize(k)/(avgabund(k) + 1E-6)
         avgabund(k) = avgabund(k) / (nsize + .000001)

     NEXT k

     avgtrans = 0
     FOR i = 1 TO cel
         avgtrans = avgtrans + trans(i)
     NEXT i
     avgtrans = avgtrans / 20
     FOR k = 0 TO 6
         PRINT #2, USING "##.####^^^^ "; avgabund(k);
     NEXT k
     PRINT #2, USING "##.####^^^^ "; avgtrans


' FOR ifile = 1 TO 4
 '    i = 5 * ifile - 4
  '   FOR j = 1 TO 5
   '       FOR k = 0 TO 6
    '         IF nm(i, j, k) > 0 THEN
    '            PRINT #ifile, USING "#.###^^^^, ";
                                       nm(i, j, k);
    '         ELSE
    '            PRINT #ifile, nm(i, j, k); ",";
    '         END IF
    '
    '         IF nmx(i, j, k) > 0 THEN
    '            PRINT #ifile, USING "### , ";
                                 nmx(i, j, k);
    '         ELSE
    '            PRINT #ifile, nmx(i, j, k); ",";
    '         END IF
    '     NEXT k
    ' NEXT j
    ' PRINT #ifile, trans(i)
 'NEXT ifile

     'screen information
     CLS
     LOCATE 1, 1: PRINT "time: "; time
     FOR row = 2 TO 7
        LOCATE row, 5
```

```
     PRINT USING "Age # abundance: ##.####^^^^
        size: ####.#"; row - 1; avgabund(row - 1);
        avgsize(row - 1)
    NEXT row
    LOCATE 9, 5: PRINT "Transformer Abundance: ";
                                              avgtrans

'   Update Density, Growth, and Transformation
'   Age Population

    FOR i = 1 TO cel    'stream cell index
      FOR j = 1 TO 6 'substrate index
       IF ca(i, j) > 0 THEN

        ammden = 0
        FOR k = 1 TO 6
          ammden = ammden + nm(i, j, k)
        NEXT k
        'set up substrate specific parameters
        ammden = -ammden / (ca(i, j) + 1E-6) *
                                    (ca(i, j) > 0)

        wk = wkmax * (1-ammden / (ammden + kwk))
        rho = rhomax * (1-ammden / (ammden+krho))
        zm = zmmin + zmmax * ammden^2 /
                        (ammden^2 + kzm)


       'grow and remove dead from oldest age group
        FOR k = 0 TO 6
         nm(i,j,k) = nm(i,j,k)*EXP(-zm - ztm(k))
         nmx(i, j, k) = wk + rho * nmx(i, j, k)

          'calculate transformer production
          IF nmx(i, j, k) > mintransize THEN
             sizdif = (nmx(i, j, k) -
                          mintransize)^2
             ptrans = ptmax * sizdif
                        / (sizdif+kpt)
             ttrans = ttrans + nm(i,j,k)
                         * ptrans
             nm(i,j,k) = nm(i,j,k) *
                         (1- ptrans)
          END IF

        NEXT k
        'age survivors
        nmx(i,j,6) = (nmx(i,j,6) * nm(i,j,6) +
                        nmx(i,j,5) * nm(i,j,5))
        nm(i, j, 6) = nm(i, j, 6) + nm(i, j, 5)
        nmx(i,j,6) =nmx(i,j,6)/(nm(i,j,6)+ 1E-6)
```

```
                FOR k = 5 TO 1 STEP -1
                    nm(i, j, k) = nm(i, j, k - 1)
                    nmx(i, j, k) = nmx(i, j, k - 1)
                NEXT k
              'Calculate migration for next time interval
                FOR k = 1 TO 6
                    pmig = cpm(k)+pmax(k) * ammden^pmn/
                          (ammden ^ pmn + kpm(k) ^ pmn)
                    xbar = nmx(i, j, k)
                    isize = -(xbar >= 125) - (xbar >= 80)
                    IF pref(isize,j)<.9 THEN pmig=pmax(k)

                    nummig = pmig * nm(i, j, k)
                    m(i, k) = m(i, k) + nummig
                    nm(i, j, k) = nm(i, j, k) *
                                  (1 - pmig)
                    mx(i,k) = nmx(i,j,k) * nummig +
                              mx(i,k)
                NEXT k
              END IF

            NEXT j

            FOR k = 1 TO 6
                mx(i, k) = mx(i, k) / (m(i, k) + .000001)
            NEXT k

        NEXT i
'Cause ammocoetes to migrate
        FOR i = cel TO 1 STEP -1

            FOR k = 1 TO 6
                IF i = cel THEN
                    m(i - 1, k) = m(i,k) * pmd + m(i-1,k)
                    m(i, k) = m(i, k) * (1 - pmd)
                    mx(i-1,k) = mx(i,k) * pmd + mx(i-1,k)
                    mx(i, k) = mx(i, k) * (1 - pmd)

                ELSEIF i = 1 THEN
                    m(i+1,k) = m(i,k) * pmu + m(i+1 k)
                    m(i, k) = m(i, k) * (1 - pmu - pmd)
                    mx(i+1,k) = mx(i,k) * pmu + mx(i+1,k)
                    mx(i, k) = mx(i, k) * (1 - pmu - pmd)

                ELSE
                    m(i+1,k) = m(i,k) * pmu + m(i+1,k)
                    m(i-1,k) = m(i,k) * pmd + m(i-1,k)
                    m(i, k) = m(i, k) * (1 - pmu - pmd)
                    mx(i+1,k) = mx(i,k) * pmu + mx(i+1,k)
                    mx(i-1,k) = mx(i,k) * pmd + mx(i-1,k)
                    mx(i, k) = mx(i, k) * (1 - pmu - pmd)
```

```
                END IF
            NEXT k

            NEXT i
NEXT time
CLOSE
END
```