GREAT LAKES FISHERY COMMISSION
Project Completion Reports[1]

Ecology of recruitment in sea lamprey--summary

by:

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March 1998

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GREAT LAKES FISHERY COMMISSION

Project Completion Report

Growth of larval sea lamprey from anadromous and landlocked populations

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March, 1998

Abstract

Growth rates of sea lamprey larvae were equated to a change in total length between hatch and the completion of the larval period and compared among 17 streams. Both anadromous and landlocked populations of lamprey were examined, the latter before and after the commencement of lampricide application to control abundance. Larval hatch dates were estimated from observations of riverine migration, reproduction and incubation. Growth rates within a stream were consistent among year classes. Significant differences in growth rates within streams were not found among larvae before chemical treatment, surviving residuals or newly recruited larvae as a consequence of reproduction the spring following chemical treatment. A natural logarithm transform was used to estimate growth coefficients or slopes which did not differ significantly among all populations. Length-at-age differed, in some cases significantly, among streams suggesting that variation in length-at-hatch may determine subsequent lengths-at-age throughout the larval period. A trend of increasing hatch dates with latitude was observed as well as an inverse relationship among larval length-at-age, latitude and stream discharge.

Most larvae within a stream completed metamorphosis at approximately the same age but it varied among streams from just over 3 to 6 years. The longest larval period was found for anadromous populations. Within the Great Lakes there was some suggestion that age-at-metamorphosis has been reduced since chemical treatment was first begun and that it is shorter by a year in southern than northern streams, however, this pattern was not consistent across all streams.

Introduction

Sea lamprey, *Petromyzon marinus*, occur as an ancestral anadromous form in the North Atlantic Ocean as well as a landlocked form which has invaded a number of freshwater lakes including the Great Lakes, Finger Lakes and Lake Champlain in North America (Hardisty and Potter, 1971; Scott and Crossman, 1973). Larvae, of both forms, burrow in the soft substrate of streams and feed mainly on biofilm and detritus (Moore and Mallatt, 1980; Sutton and Bowen, 1994). The duration of the larvae period is at least partly a function of the time required to reach a critical size and to accumulate the energy reserves required to complete the subsequent non-trophic stage of metamorphosis (Lowe et al, 1973; O'Boyle and Beamish, 1976; Youson & Holmes; Youson, 1980). Juvenile sea lamprey migrate from their natal stream to large water bodies and commence feeding on the body fluids and soft tissues of teleost fishes (Farmer, 1980).

Landlocked sea lamprey are economically important pests and are subject to control including the chemical treatment of streams to kill larvae (Smith and Tibbles, 1980). The lampricide, 3' trifluoromethyl 4' nitrophenol (TFM) is applied cyclically to maximize the number of larvae killed and to minimize the number that enter the destructive juvenile period. Shortly after TFM was in regular use, Purvis (1979) reported increases in larval growth, especially in the first year class to reestablish after a chemical treatment when densities are low. Sea lamprey larvae held in cages or aquaria at high densities also exhibited slower growth than larvae held at low densities (Mallatt, 1983; Morman 1987; Murdoch et al 1991).

The present study compared growth rates of sea lamprey between hatch and the completion of the larval period, from anadromous and landlocked populations, the latter since and prior to chemical control. The objective was to examine the extent to which larvae exhibit compensatory growth subsequent to chemical treatment and the potential modifying effects of other factors (Brett, 1979; Weatherley and Gill, 1987).

Methods

Sea lamprey larvae were collected from streams located throughout much of the species' geographic range in North America (Scott and Crossman, 1973; Lee et al, 1980; Dempson and Porter, 1993; Table 1.). Anadromous sea lamprey larvae were collected from two streams tributary to the North West Atlantic, Terra Nova and Petitcodiac Rivers. Larvae of landlocked sea lamprey were collected from 15 streams, 13 within the Great Lakes basin and one each from Lake Champlain and Oneida Lake. Within the Great Lakes, larvae were collected from six streams prior to the initial application of lampricide, Cheboygan, Ocqueoc, Jordan, Schmidt, Little Otter and Shelter Valley (Table 2.). Total lengths for a sample of larvae from each of the Cheboygan, Jordan and Schmidt rivers were provided by D. Lavis, U.S. Fish and Wildlife Service, Ludington, MI.

Larvae were collected also from streams previously treated with lampricide. Cobourg, Farewell, Lynde and Oshawa Creeks each had been treated 7-8 times prior to sampling whereas Cannon, West Branch of the Ogontz (hereafter referred to as the Ogontz) and West Root each had been treated 8 to 9 times (Table 2., Great Lakes Fishery Commission, unpbl.data). In these seven streams, a small sample of larvae, representing approximately 5 % of the population was removed and marked one to two weeks before a chemical treatment. After completion of the treatment, each sample, assumed to represent a residual population, was returned to it's natal stream. The residual populations were intended to simulate the larval population surviving an actual treatment because not all larvae can be expected to die during a chemical treatment. Age structure of the residual larval population was similar to that present before treatment because size-selective toxicity of lampricide has not been found. Population size was estimated using a Petersen mark-recapture method (Ricker, 1975) and age structure was estimated using length frequency histograms (Macdonald and Pitcher, 1979) and when available, analyses of banding patterns on statoliths (Medland and Beamish, 1987; Beamish and Medland, 1988).

Larvae were collected by either electrofishing or during a chemical treatment (Table 2.). After capture larvae were anaesthetized with 50 mg/l of tricaine methanesulfonate, unless killed by lampricide and total length (± 1 mm) measured. Larval growth was equated to change in total length over the period between hatch and the oldest larvae captured. Differences in growth among age classes within streams were assessed using ANCOVA and ANOVA (Draper and Smith, 1981).

Incubation time for sea lamprey eggs was estimated from earlier studies by Piavis (1961), Manion and McLain (1971) and Langille and Hall (1988). Piavis (1961) examined incubation success and time at constant temperatures from 7.2 to 26.6°C. Eggs hatched only between 15.5 and 21.1°C and incubation time varied from 13-17 days at 15.5°C and from 7-10 days at 21.1°C. Langille and Hall (1988) found a similar relationship between incubation time and temperature; 8 and 20 days at 21.0 and 15.0°C, respectively. Incubation times for sea lamprey eggs in the Big Garlic River, where daily water temperatures fluctuated between 10.0 and 18.3°C, ranged from 11-14 days (Manion and McLain, 1971). For this study, a single incubation time of 13 days which is the approximate mean found in earlier investigations was assigned to all populations.

Hatch dates were estimated from information on the timing of adult upstream migration, spawning and incubation time for eggs except for the population in Little Otter Creek for which a hatch date of June 1 was reported by Thomas (1962). When information on timing of spawning was available, hatch was estimated by adding 13 days for incubation to the mean date for the reproductive period. For the, Ocqueoc, Oshawa, Peticodiac and Terra Nova, information on spawning was available during the years when larvae were collected. For the, Cheboygan, Fish, Great Chazy, Jordan, and Shelter Valley information on spawning was gathered some years after larvae were collected.

Information on spawning in nearby streams was used to assign hatch dates for sea lamprey in Cobourg, Farewell, Lynde, Ogontz and Schmidt. Larvae in Schmidt Creek were assigned the same hatch date as those in nearby Ocqueoc River. For larvae in Farewell and Lynde Creeks, the same hatch date as those in Oshawa Creek was assigned as the three streams are only a few kilometres apart. Similarly, larvae in Cobourg Brook were assigned the same hatch date as those in nearby Shelter Valley Creek.

For two streams, Ocqueoc and Peticodiac, observations on both the timing of the upstream adult migration and spawning were available. This information was used to estimate the interval between the peaks of migration and spawning. The interval was then applied in the assignment of hatch dates for populations where information was available only for the upstream migration. Thus, for larvae in the Ogontz River, a hatch date was estimated from the timing of the adult migrations in two nearby streams, Fishdam and Sturgeon. The hatch date for larvae from both Cannon and West Root were estimated from observed upstream migrations of adult sea lamprey in Bridgeland Creek which was the nearest stream for which information was available.

Fertilized eggs from three sea lamprey captured in the Ocqueoc River in 1997 were incubated in the laboratory and the larvae photographed immediately after hatching (R.Bergstedt, U.S. Geological Service, Hammond Bay, MI). Total length of all larvae were then measured, to nearest 0.1 mm, using a digitizer. The normality of the distribution of larval lengths from each female sea lamprey was assessed using a Lilliefors non-parametric test (Wilkinson, 1990). Length of larvae at hatch was pooled among females and the mean length assigned as an observation, not a common intercept, for larvae in all streams.

For populations in Fish Creek, Peticodiac River and Shelter Valley Creek mean lengths at age were determined from length frequency histograms smoothed by a moving average of seven and subsequently hand-fitting normal curves to the histograms (Lowe et al, 1973; Potter and Beamish, 1975; O'Boyle and Beamish, 1977). Age of larvae for populations from the regularly treated streams and the Great Chazy River (Docker, 1992) was estimated also from statolith banding patterns.

The dominant metamorphosing age class was estimated from length frequency histograms or analysis of statolith banding patterns of both larvae and metamorphosing sea lamprey in all populations. In a number of streams, Cannon, Chazy, Cobourg, Farewell, Little Otter, Lynde, Ogontz, Oshawa and West Root, length frequency histograms and analyses of statoliths were used to determine age-at-metamorphosis. In three streams, Cheboygan, Jordan and Schmidt, no metamorphosing larvae were captured. Age-at-metamorphosis was predicted using the age of the oldest age class of larvae in these streams which were > 120 mm total length if sampled prior to July otherwise the age of the first older mode to show a substantial reduction in number was used (Hardisty, 1969; Beamish and Potter, 1975; Potter, 1980). In the remaining streams, Fish, Ocqueoc, Petitcodiac, Shelter Valley, and Terra Nova, the age-at-metamorphosis provided in previous studies was adopted for this investigation.

Chemical and physical characteristics for most of the streams were also measured or obtained (Applegate, 1950; R. Young, Department of Fisheries and Oceans, Sea Lamprey

Control, Sault Ste. Marie, Ont., unpbl. Data; D. Lavis, U.S. Fish and Wildlife Service, Ludington, MI., unpbl. Data; Table 3.). In thirteen streams, pH and conductivity were routinely measured with calibrated meters. Water temperature data for several streams was either continuously recorded or obtained from Environment Canada (1976). The number of degree·days above 0°C were estimated by computing the area under the mean daily temperature curve for each of eight streams (Table 3.). Mean annual discharge (m^3/s) was also obtained for several streams (Hansen and Hayne, 1962; Environment Canada, 1991, 1992).

Statistical analyses were computed in SAS (SAS Institute, 1985)or SYSTAT 7 (Wilkinson, 1990). Statistical significance was accepted at $p<0.05$ unless otherwise stated.

Results

Streams fluctuated widely in their general abiotic characteristics. Mean annual discharge varied by more than two orders of magnitude from 0.1 $m^3 \cdot s^{-1}$ for Cannon Creek to more than 36 $m^3 \cdot s^{-1}$ for the Terra Nova River (Table 3.). However, in most streams, discharge was less than 4 $m^3 \cdot s^{-1}$. Conductivity ranged from 16 to 522 μmhos with the lowest values in Terra Nova and highest in Little Otter Creek. A considerable variation was recorded in pH, from 5.6 in Terra Nova to 9.0 in Great Chazy. Water temperature ranged from a low of 2411 degree days in West Root River to a high of 3238 degree days in Lynde Creek.

A total of 75 samples of larvae were collected from the 17 streams, between 1947 and 1977. Number of samples collected within a stream varied from one to 10 (Table 2.). Mean sample size ranged from 143 to 1775 larvae (Table 2.). Sample size of larvae from streams subject to density reduction due to chemical treatment varied much more than other populations (Table 2.). For example, in Cannon Creek prior to reduction, sample size ranged from 947 to 3982 larvae whereas afterwards it varied from 84 to 248 lamprey.

Hatch date in the Terra Nova was based on the observation of spawning sea lamprey between July 10-23 (Dempson and Porter, 1993; Table 4.). In the Peticodiac, the adult migration occurred from June 8 to July 5 and peak spawning around June 25. Hatch dates were estimated to be July 8 in Peticodiac and July 26 in Terra Nova. For landlocked sea lamprey populations migration and spawning was observed only in the Ocqueoc. Migrations in the Ocqueoc occurred between April 30 and June 28, with peak spawning around June 16 and an estimated hatch date of June 28. The interval between mean migration and spawning was 21 days. This interval was used to estimate hatch dates for the remaining landlocked populations for which only migration was observed. Estimated hatch dates in southern streams ranged from

June 1 in Little Otter to June 21 in Shelter Valley. In northern streams, larval hatch dates ranged from June 15 in Ogontz River to June 29 in both Cannon and West Root rivers.

Generally, hatch dates were directly related to latitude. This relationship is described by the regression:

$$H = -166.18 + 7.56 \cdot L \quad (r = 0.93, n = 17, p < 0.05)$$

where H represents hatch date in days from January 1 and L, latitude in degrees (°). Thus larvae from a stream at 43° latitude can be expected to hatch, on average, 23 days earlier than those in a stream at 46°.

Mean length at hatch for the three groups of larvae, each from a different female, were 3.9 ± 0.5 (n = 49), 4.8 ± 0.8 (n = 54) and 4.9 ± 0 mm (n = 58). Within each group lengths for larvae at hatch (1 day, were normally distributed ($p = 0.21$). The pooled mean length at hatch was 4.6 ± 0.7 mm (n = 161).

Annual increases in total length were largest over the first year of the larvae period and progressively declined with age. This pattern was consistent among all populations. For example, in the Petitcodiac River total length increased 34 mm over the first year and 27, 23, 19 and 18 over the subsequent second, third, fourth and fifth years, respectively. Larvae in Lynde Creek increased 54 mm after one year and 34 and 30 mm after each of the second and third years.

Growth rates of larvae within a stream were consistent among year classes. Thus in Shelter Valley Creek, growth rates among year classes for the six age groups examined between 1969 and 1971 and represented by the regression coefficients, did not differ significantly (n = 56, df = 5, F = 0.27, p = 0.93). Further, intercepts of the regressions describing the relationship between total length and age by year class did not differ significantly (n = 56, df =

5, $F = 1.93$, $p = 0.11$). Similarly in Fish Creek, growth rates among year classes between 1973 and 1974 were not significantly different ($n = 42$, $df = 5$, $F = 0.02$, $p = 1.00$) nor were regression intercepts ($n = 42$, $df = 5$, $F = 0.16$, $p = 0.97$). In subsequent analyses of growth, year classes of larvae within each stream were combined.

Growth rates of larvae before chemical treatment, for surviving residuals and for newly recruited larvae as a consequence of reproduction the year after chemical treatment were examined in Cannon, Farewell, Lynde, Ogontz and West Root rivers. Newly recruited larvae were found in only three streams, Farewell, Lynde and West Root the year following treatment. In each stream significant differences in growth rate were not found among the groups of larvae (Table 5).

The relationship between the natural log of larval total length and the natural log of age was described by a linear regression for each stream. Growth rates did not differ significantly among the 17 streams ($n = 355$, $df = 6$, $F = 1.01$, $p = 0.45$) with a common value of 0.47 ± 0.01 (SE of estimates). However, significant differences were found among regression intercepts ($n = 355$, $df = 6$, $F = 5.51$, $p < 0.01$). Highest intercepts were found for growth equations for larvae from Farewell and Lynde Creeks which were significantly different from those from all other streams but not themselves. Larval growth for Farewell and Lynde creeks is described by the regression:

$$\ln TL = 1.50 \pm 0.06 + 0.47 \ln A \qquad (\pm \text{ SE of estimates})$$

where TL represents total length, mm, and A, age in days from hatch. Lowest intercepts were found for growth equations for larvae from Cheboygan, Ocqueoc and Petitcodiac which were significantly different from those for all other streams but not themselves. Larval growth in these three streams is described by the regression:

$$\ln TL = 1.17 \pm 0.07 + 0.47 \ln A$$

Regression intercepts for growth equations for larvae from the other 12 streams did not differ significantly among themselves. Larval growth in these 12 streams is described by the regression:

$$\ln TL = 1.33 \pm 0.07 + 0.47 \ln A$$

Large variations around lengths predicted for young larvae prompted comparison also by least square means (Table 6). While clear patterns of statistical significance based on least square means among streams are not obvious, lengths-at-age are again highest in Lynde and Farewell and lowest in Cheboygan, Ocqueoc, Petitcodiac and Terra Nova. The similarity in growth rates described earlier by a common regression slope for all populations in concert with the variation in least square means suggest persistent differences in larval length extending from the time of hatch. For example, length of larvae at hatch in Lynde Creek is predicted to be about 50% longer than that in the Cheboygan River. It is interesting as well to note the general trend of decreasing larval lengths-at-age with increasing latitude and stream discharge (Tables 1, 3 and 6). Thus 449 days after hatch, total length of larvae in the Terra Nova River, at a latitude of 48°40' and with a mean annual discharge of 36.7 $m^3 \cdot s^{-1}$ is predicted to be 52.5 mm whereas that in Oshawa Creek at 43°56' and 1.2 $m^3 \cdot 5^{-1}$ is estimated to be 74.4 mm. The relationship among larval total length 449 days after hatch, stream discharge and latitude is expressed by the regression:

$$TL_{449} = 146.10 - 1.78\ L - 0.25\ D \quad (df = 16,\ F = 3.83,\ p = 0.04)$$

where TL_{449} is larval mean total length 449 days after hatch and D, mean annual discharge, $m^3 \cdot s^{-1}$.

Most larvae within a stream commenced metamorphosis at approximately the same age but some individuals delayed post larval development by a year (Table 7). Age-at-metamorphosis varied from just over 3 to 6 years with anadromous sea lamprey displaying the longest larval period. Metamorphosing animals were captured from the Petitcodiac River and aged at 6 years (Beamish and Potter 1975) whereas in the Terra Nova River age-at-metamorphosis was estimated also at 6 years but on the basis of a larval length-frequency histogram.

Within landlocked populations there is some indication that age-at-metamorphosis before streams were treated with lampricide was greater than that since the commencement of regular TFM applications. However, relatively few streams and animals have been examined, considerable variation occurs among streams and no stream has been studied both before and after treatments have begun. Thus, most metamorphosing animals from the Great Chazy and Fish creeks (O'Boyle and Beamish 1977) were just over 5 years in age before lampricide was first applied to these streams. Within the Great Lakes' streams examined, metamorphosis was found to begin after a larval period of just over 3 to 5 years. In those streams regularly treated with lampricide most metamorphosing lamprey were just over 3 to 4 years. There was the suggestion among the 7 streams sampled that age-at-metamorphosis occurs mostly one year earlier in southern streams but again the number of streams and animals examined were small. It is worth noting that none of the marked residual lampreys have been captured after larval development from any stream. Age-at-metamorphosis before chemical treatment was introduced for control was mostly about 4 years but ranged from 3.1 to 5 years in the streams examined (Table 7). It is important to point out that until the past decade or so lamprey were aged on the basis of length-frequency histograms whereas statolith banding patterns have been used most recently. Neither method is without some concern although statoliths probably provide better estimates in most cases (see Barker, Morrison, Wicks and Beamish 1997).

None of the metamorphosing lamprey were staged according to the criteria described in Youson and Potter (1979). However, all were clearly beyond the early stages and exhibited extension of both the snout and disc. Indeed, total lengths of metamorphosing animals (Table 7) were clearly greater than those estimated for larvae immediately prior to the onset of external changes associated with metamorphosis. For example, in Lynde Creek, estimated length of larvae before metamorphosis was 122 mm, well below that of 147 mm found for the 37 metamorphosing individuals captured and measured. Similarly in Petitcodiac River, total length before metamorphosis was estimated at 120 mm and that among metamorphosing individuals, 139 mm. Clearly, the extension of the snout which occurs throughout all but the early stages of metamorphosis adds significantly to total length.

Table 1. Location of tributary streams sampled for sea lamprey (*Petromyzon marinus*) larvae

Basin Tributary	Location		
	Province or State	Latitude	Longitude
North West Atlantic			
Terra Nova	NFLD	48°40'	50°00'
Petitcodiac	NB	46°01'	65°04'
Lake Champlain			
Great Chazy	NY	44°50'	73°25'
Oneida Lake			
Fish	NY	43°13'	77°42'
Great Lakes			
St. Mary's R.			
Cannon	ON	46°34'	84°10'
West Root	ON	46°35'	84°17'
Lake Michigan			
Ogontz	MI	45°28'	86°51'
Lake Huron			
Ocqueoc	MI	45°15'	84°00'
Cheboygan	MI	45°38'	84°28'
Jordan	MI	45°06'	85°03'
Schmidt	MI	45°29'	84°00'
Lake Ontario			
Shelter Valley	ON	43°59'	78°00'
Farewell	ON	43°53'	78°49'
Lynde	ON	43°52'	78°58'
Cobourg	ON	43°58'	78°10'
Oshawa	ON	43°56'	78°54'
Lake Erie			
Little Otter	ON	42°45'	80°48'

Table 2. Sample information for sea lamprey (*Petromyzon marinus*) larval populations including collection dates, number of samples and sample size. The superscript 'E' indicates capture by electrofishing and 'C' indicates collection by chemical poisoning with 3' trifluoromethyl 4' nitrophenol.

Stream	Collection Date	Sample Information		
		Number of samples	Mean sample size	Standard deviation
Cannon	1995-97 $^{E, C}$	8	1205	1682
Cheboygan	1966 $^{E, C}$	3	244	184
Cobourg	1996-97 $^{E, C}$	4	488	367
Farewell	1995-97 $^{E, C}$	7	321	440
Fish	1973-74^{E}	8	166	49
Great Chazy	1985^{E}	1	1185	na
Jordan	1964 $^{E, C}$	1	733	na
Little Otter	1986^{E}	1	83	na
Lynde	1995-97 $^{E, C}$	6	237	313
Ocqueoc	1947-49^{E}	3	1162	193
Ogontz	1996-97 $^{E, C}$	5	744	567
Oshawa	1996-97 $^{E, C}$	3	1775	672
Petitcodiac	1973-74^{E}	5	428	177
Schmidt	1966 $^{E, C}$	2	190	186
Shelter Valley	1969-71^{E}	10	143	135
Terra Nova	1990,1993^{E}	2	339	68
West Root	1995-97 ^{E,C}	8	542	718

Table 3. Physical and chemical characteristics of streams in which larval sea lamprey (*Petromyzon marinus*) growth was measured.

Stream	Mean Annual Discharge (m^3/s)	pH	Conductivity (Fmhos)	Temperature EC@days
Cannon	0.1	6.4	43	2485
Great Chazy	3.5	9.0	185	na
Cheboygan	24.0	8.1	313	na
Cobourg	1.7	8.3	369	2746
Farewell	0.7	8.1	463	2985
Fish	10.6	7.5	142	na
Jordan	5.9	8.0	284	na
Little Otter	1.5	8.3	522	na
Lynde	0.9	8.3	420	3238
Ocqueoc	2.8	na	na	na
Ogontz	0.4	6.7	102	2635
Oshawa	1.2	8.3	433	2900
Petitcodiac	7.9	6.4	307	na
Schmidt	0.7	7.8	294	na
Shelter Valley	0.8	8.5	454	3343
Terra Nova	36.7	5.6	16	na
West Root	0.2	6.2	51	2410

Table 4. Mean observed and estimated (parentheses) dates for migration, reproduction and hatch.

Streams	Migration	Reproduction	Hatch
Cannon	(05/26, 05/04-07/05)	(06/16)	(06/30)
Great Chazy		06/09, 05/29-06/20	(06/21)
Cheboygan	05/26, 05/02-06/03	(06/16)	(06/30)
Cobourg	(05/18, 04/14-06/21)	(06/08)	(06/21)
Farewell		(06/03)	(06/15)
Fish	05/12, 04/24-06/23	(06/03)	(06/15)
Jordan	05/23, 04/30-06/29	(06/13)	(06/25)
Little Otter			(06/01)[1]
Lynde		(06/03)	(06/15)
Ocqueoc	05/25, 04/30-06/29	06/16, 06/10-06/23	(06/28)
Ogontz	(05/15, 04/04-07/15)	(06/04)	(06/17)
Oshawa		(06/03)	(06/16)
Petitcodiac	06/13, 06/08-07/05	06/25, 06/23-06/28	(07/08)
Schmidt	05/25, 04/30-06/29	(06/16)	(06/28)
Shelter Valley	05/18, 04/14-06/21	(06/08)	(06/21)
Terra Nova		07/13, 07/10-07/17	(07/26)
West Root	(05/26, 05/04-07/05)	(06/17)	(06/30)

[1] Thomas, M. L. 1962

Table 5. Comparison (ANCOVA) of growth rates of larvae before chemical treatment, surviving residuals and newly recruited larvae as a consequence of reproduction after treatment. Larvae from reproduction the year following treatment were not found in Cannon or Ogontz rivers. Modal lengths at age were derived from length frequency histograms (Macdonald and Pitcher 1979)

Stream	Sample Size	df	F	p
Cannon	34	1	1.01	0.32
Farewell	15	2	0.78	0.49
Lynde	12	2	1.36	0.33
Ogontz	9	1	2.81	0.17
West Root	18	2	3.30	0.07

Table 6. Comparison of least square means (± SE) for total length of larvae at a common age of 449 days. Vertical lines around each stream embrace those stream in which larval lengths did not differ significantly at $p < 0.05$.

<table>
<tr><th>Stream</th><th colspan="3">Least Square Mean</th><th colspan="17"></th></tr>
<tr><th></th><th>In TL</th><th>(SE)</th><th>TL mm</th><th></th><th></th><th></th><th></th><th></th><th></th><th></th><th></th><th></th><th></th><th></th><th></th><th></th><th></th><th></th><th></th><th></th></tr>
<tr><td>Lynde</td><td>4.35</td><td>(0.04)</td><td>77.5</td><td>x</td><td>|</td><td>|</td><td>|</td><td>|</td><td>|</td><td>|</td><td>|</td><td></td><td></td><td></td><td></td><td></td><td></td><td></td><td></td><td></td></tr>
<tr><td>Farewell</td><td>4.34</td><td>(0.04)</td><td>76.7</td><td>|</td><td>x</td><td>|</td><td>|</td><td>|</td><td>|</td><td>|</td><td>|</td><td></td><td></td><td></td><td></td><td></td><td></td><td></td><td></td><td></td></tr>
<tr><td>Oshawa</td><td>4.31</td><td>(0.06)</td><td>74.4</td><td>|</td><td>|</td><td>x</td><td>|</td><td>|</td><td>|</td><td>|</td><td>|</td><td>|</td><td>|</td><td>|</td><td></td><td></td><td></td><td></td><td></td><td></td></tr>
<tr><td>Schmidt</td><td>4.27</td><td>(0.07)</td><td>71.5</td><td>|</td><td>|</td><td>|</td><td>x</td><td>|</td><td>|</td><td>|</td><td>|</td><td>|</td><td>|</td><td>|</td><td>|</td><td>|</td><td>|</td><td></td><td></td><td></td></tr>
<tr><td>Fish</td><td>4.23</td><td>(0.03)</td><td>68.7</td><td>|</td><td>|</td><td>|</td><td>|</td><td>x</td><td>|</td><td>|</td><td>|</td><td>|</td><td>|</td><td>|</td><td>|</td><td>|</td><td>|</td><td></td><td></td><td></td></tr>
<tr><td>Jordan</td><td>4.22</td><td>(0.09)</td><td>68.0</td><td>|</td><td>|</td><td>|</td><td>|</td><td>|</td><td>x</td><td>|</td><td>|</td><td>|</td><td>|</td><td>|</td><td>|</td><td>|</td><td>|</td><td>|</td><td>|</td><td>|</td></tr>
<tr><td>Cobourg</td><td>4.21</td><td>(0.05)</td><td>67.4</td><td></td><td>|</td><td>|</td><td>|</td><td>|</td><td>|</td><td>x</td><td>|</td><td>|</td><td>|</td><td>|</td><td>|</td><td>|</td><td>|</td><td>|</td><td>|</td><td>|</td></tr>
<tr><td>Shelter Valley</td><td>4.19</td><td>(0.03)</td><td>66.0</td><td></td><td>|</td><td>|</td><td>|</td><td>|</td><td>|</td><td>|</td><td>x</td><td>|</td><td>|</td><td>|</td><td>|</td><td>|</td><td>|</td><td>|</td><td>|</td><td>|</td></tr>
<tr><td>West Root</td><td>4.17</td><td>(0.04)</td><td>64.7</td><td></td><td>|</td><td>|</td><td>|</td><td>|</td><td>|</td><td>|</td><td>|</td><td>x</td><td>|</td><td>|</td><td>|</td><td>|</td><td>|</td><td>|</td><td>|</td><td>|</td></tr>
<tr><td>Great Chazy</td><td>4.13</td><td>(0.08)</td><td>62.2</td><td></td><td>|</td><td>|</td><td>|</td><td>|</td><td>|</td><td>|</td><td>|</td><td>|</td><td>x</td><td>|</td><td>|</td><td>|</td><td>|</td><td>|</td><td>|</td><td>|</td></tr>
<tr><td>Cannon</td><td>4.11</td><td>(0.04)</td><td>60.9</td><td></td><td></td><td></td><td>|</td><td>|</td><td>|</td><td>|</td><td>|</td><td>|</td><td>|</td><td>x</td><td>|</td><td>|</td><td>|</td><td>|</td><td>|</td><td>|</td></tr>
<tr><td>Ogontz</td><td>4.10</td><td>(0.05)</td><td>60.3</td><td></td><td></td><td></td><td>|</td><td>|</td><td>|</td><td>|</td><td>|</td><td>|</td><td>|</td><td>|</td><td>x</td><td>|</td><td>|</td><td>|</td><td>|</td><td>|</td></tr>
<tr><td>Little Otter</td><td>4.09</td><td>(0.08)</td><td>59.7</td><td></td><td></td><td></td><td>|</td><td>|</td><td>|</td><td>|</td><td>|</td><td>|</td><td>|</td><td>|</td><td>|</td><td>x</td><td>|</td><td>|</td><td>|</td><td>|</td></tr>
<tr><td>Petitcodiac</td><td>4.05</td><td>(0.04)</td><td>57.4</td><td></td><td></td><td></td><td></td><td></td><td>|</td><td></td><td></td><td>|</td><td>|</td><td>|</td><td>|</td><td>|</td><td>x</td><td>|</td><td>|</td><td>|</td></tr>
<tr><td>Ocqueoc</td><td>4.01</td><td>(0.07)</td><td>55.1</td><td></td><td></td><td></td><td></td><td></td><td>|</td><td></td><td></td><td>|</td><td>|</td><td>|</td><td>|</td><td>|</td><td>|</td><td>x</td><td>|</td><td>|</td></tr>
<tr><td>Terra Nova</td><td>4.01</td><td>(0.07)</td><td>55.1</td><td></td><td></td><td></td><td></td><td></td><td>|</td><td></td><td></td><td>|</td><td>|</td><td>|</td><td>|</td><td>|</td><td>|</td><td>|</td><td>x</td><td>|</td></tr>
<tr><td>Cheboygan</td><td>3.96</td><td>(0.06)</td><td>52.5</td><td></td><td></td><td></td><td></td><td></td><td></td><td></td><td></td><td></td><td>|</td><td></td><td>|</td><td>|</td><td>|</td><td>|</td><td>|</td><td>x</td></tr>
</table>

Table 7. Total length and age of metamorphosing sea lamprey. Information for the Ocqueoc River was taken from Applegate (1950), for Fish Creek from O'Boyle and Beamish (1977), for Petitcodiac River from Beamish and Potter (1975) and for Shelter Valley Creek from Lowe, Beamish and Potter (1973). Ages assigned from statolith banding patterns are indicated by the superscript a, and those from length-frequency histograms by the superscript b.

Stream	Capture date (month/y)	Total Sample	Total Length (mm)	N	Age: Age at capture (y)	Age: Total length ± SD (mm)	Age at start of metamorphosis (y)
Cannon	08/95	59	152±12	4	4.2[a]	151±3[a]	4.1
				2	5.2	172	5.1
Great Chazy	10/85	475	165±29	4	4.3[a]	159±4	4.1
				13	5.3	161±4	5.1
Cobourg	07/96	4	152	1	4.1[a]	152	4.1
Farewell	09/95	14	147±9	14	3.3[a]	147±9	3.1
Fish	08-09/73	44	148±9	44	5.3[b]	148±9	5.1
Little Otter	10/86	10	139±7	8	4.4[a]	135±7	4.1
				2	5.4	143±1	5.1
Lynde	09/95	37	140±10	25	3.3[a]	137±10	3.1
Ocqueoc	10/48-03/49	749	136±12		3.4-3.9[b]		3.1
Ogontz	10/96	2	152	1	3.3[a]	156	3.1
				1	4.3	148	4.1
Oshawa	09/96	44	147±7	3	3.3[a]	136±8	3.1
Petitcodiac[a]	09/73	9	139±15	9	6.2[b]	139±15[b]	6.0
Shelter Valley	07-10/71	75	141±9	75	5.0-5.3[b]	141±9[b]	5.0
West Root	08/95	31	162±9	31	4.1[a]	162±9[a]	4.0

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