GREAT LAKES FISHERY COMMISSION
Project Completion Reports[1]

Ecology of recruitment in sea lamprey--summary

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GREAT LAKES FISHERY COMMISSION

Project Completion Report Summary

Ecology of Recruitment in Sea Lamprey

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Sea lamprey (Petromyzon marinus) have adapted extremely well to an entirely freshwater existence in the Great Lakes. Compared to their anadromous counterpart the landlocked sea lamprey have a shortened juvenile period (Beamish 1980), smaller size at maturity (Beamish and Potter 1975), lower fecundity (Hardisty 1979) and perhaps, oscillating sex ratios (Houston and Kelso 1990). The reduction of landlocked sea lamprey larval densities through the cyclic use of chemicals may create favorable conditions for epigenetic responses including enhanced growth, shortened larval life and an increased proportion of females.

This study first investigated the cumulative environmental influence on larval growth rates and sex ratios as well as the duration of the larval period for established populations (3-6 year classes) in twelve streams regularly treated with chemicals. This was referred to as a stationary study. A second investigation followed larval life history traits before and after chemical (3-trifluoromethyl-4-nitrophenol or TFM) treatment. Particular attention was paid to potential fecundity, mortality, growth and age-at-metamorphosis among residual (those remaining) larvae in eight streams after chemical treatment. The population characteristics studied are all potential compensatory mechanisms. This report summarizes information described more fully in the accompanying manuscripts as well as preliminary estimates of mortality. Reliable mortality rates of residual larvae will require an additional year or two beyond the tenure of this contract, as anticipated in the initial proposal.

Table 1. Sea lamprey (Petromyzon marinus) study streams' abiotic characteristics in 1996. Streams in boldface are monitored before and after chemical treatment.

Great Lake	Stream	pH	Alkalinity ($mgl^{-}CaCO_3$)	Hardness ($mgl^{-}CaCO_3$)	Conductivity (μS)	Degree days
Huron	**Cannon Cr.**	6.5	13	17	39	2933
Huron	Gordon's Cr.	7.4	54	57	146	2216
Huron	**Harris Cr.**	6.4	11	17	56	2685
Huron	Richardson's Cr.	7.4	143	154	373	2214
Huron	Spragge Cr.	6.3	13	11	39	2549
Huron	Sturgeon R.	na	na	na	na	3200*
Huron	**West Root R.**	6.3	12	13	49	2763
Michigan	**Ogontz R., West Branch**	6.5	42	49	98	2600
Ontario	**Cobourg Br.**	8.1	213	245	743	3245
Ontario	**Lynde Cr.**	8.4	224	262	992	3889
Ontario	**Farewell Cr.**	8.8	229	303	1011	3862
Ontario	Mayhew Cr.	7.5	180	227	950	4097
Ontario	**Oshawa Cr.**	8.2	257	260	795	3313
Ontario	Proctor's Cr.	7.9	189	249	1097	3241
Superior	Carp R.	na	na	na	na	1484

Streams were selected based on the number of year classes of sea lamprey larvae, pH, temperature, accessibility and TFM treatment schedule (Table 1). Thermal characteristics of each stream were monitored using Optic Stowaway automated temperature loggers (Onset 1995). Temperature was expressed as degree days and represents the sum of the mean daily temperature throughout the year.

The stationary study estimated population size using a modified Zippens depletion method (Zippens, 1956). This involved the random selection of a maximum of three $100m^2$ sample sites per kilometre. These sites were then subject to depletion using electrofishing passes. The mean population estimate for the depletion sites was then extrapolated to estimate the entire streams' larval population. The second study used a Petersen mark-recapture method (Ricker, 1975). The population size and 95% confidence intervals were calculated with Petersen's estimator (Ricker, 1975). Larval populations in some streams, common to the two studies, were estimated using both methods.

Sea lamprey larvae were captured by electrofishing, sedated using MS-222, measured (total length mm) and marked. All sea lamprey greater than 55 mm were marked using wire tags and elastomer except in 1995 when only wire tags were used. Larvae less than 55 mm were considered too small to mark. After marking, larvae were allowed to recover from sedation before being released to the approximate area of capture. Young-of-the-year were not represented as an independent group because of collecting difficulties and lack of quantitative accountability.

Larvae were allowed at least ten days after being tagged and released before a stream was electrofished a second time to estimate population size. Tagged larvae were identified using a metal tag detector and by visual examination for elastomer marks. Larvae from reduced populations were marked in the spring following chemical treatments and first resampled approximately 20 days later for population and mortality estimates.

Age class structure of each reduced population was consistent with that prior to TFM treatment. Percent age class composition for each stream's larval population was estimated using MIX3.1A (Macdonald and Pitcher, 1979). Statolith banding patterns from a subset of larvae were examined (Volk, 1986; Beamish and Medland, 1987) which provided more precise mean length for age class estimates.

In Farewell Creek and West Root River, recolonizing larvae were not observed in the year following treatment (1996). In Cannon Creek, recolonizing larvae were not observed in the two years following treatment (1996, 1997). Young-of-the-year larvae were not included in estimates of mortality because of small sample sizes.

The morphology and development of gonads and the determination of sex were studied in all investigations. Subsamples of larvae captured in each stream were preserved for the assignment of sex. Ten transverse sections were taken from the mid-region of the larvae and examined for sex analysis. Sex was assigned to each individual according to established criteria; the number and diameter of oocytes and gonadal morphology (Hardisty, 1965; Lewis and McMillan, 1965; Docker, 1992).

Results

General

The stationary study examined 15 streams around the Great Lakes (Table 1). Zippens' population estimates varied greatly from 496 in Harris Creek to 33,009 in the Sturgeon River (Table 2). These streams also varied in lamprey species composition. Larval densities for streams inhabited only by sea lamprey varied from 0.12 to 7.09 larvae/m^2 (Table 3). Tributaries that contained more than one species of lamprey in addition to sea lamprey had combined densities ranging from 0.20 to 9.54 larvae/m^2.

Populations of larvae in the eight reduction streams before TFM treatment varied widely from 2,400 larvae in Harris Creek to 22,000 larvae in the West Branch of the Ogontz River (Table 2). Densities of larvae similarly exhibited considerable variation ranging from 0.10 to 2.48 larvae/m^2 in the West Branch of Lynde Creek and the West Branch of the Ogontz River, respectively (Table 3). Metal tag loss over a 16 to 20 day period in the Lake Ontario tributaries was minimal (0 in all but Cobourg Brook which was <2%) but variable in northern streams (Ogontz River 10%, Cannon Creek 32% and West Root River 43%). These metal tag loss results concur with those observed in a laboratory experiment completed in 1996. The lab experiment found in metal tag losses of 33, 20 to 17% for small (>54 and <80 mm), medium (>79 and < 95 mm) and large (> 95 mm) larvae, respectively. An important observation from the laboratory study is that tag loss stabilized within six weeks after tagging.

Table 2. Population estimates of sea lamprey (Petromyzon marinus) larvae before chemical reduction using Petersen mark-recapture (Ricker, 1975) and depletion method (Zippen, 1956) in Tributaries to the Great Lakes.

Stream Name	Population Estimates					
	Mark-Recapture			Depletion Method		
	N	$N_{upper95\%}$	$N_{lower95\%}$	N	$N_{upper95\%}$	$N_{lower95\%}$
Farewell Creek	4431	5608	3502	3468	5167	1770
Lynde Creek-West	1879	3540	1095	1839	3103	575
Lynde Creek	7047	10244	5022	na	na	na
Cobourg Brook	3196	3690	2819	na	na	na
Oshawa Creek	7825	1845	1682	na	na	na
Ogontz R. West Branch	21670	27727	16938	na	na	na
Harris Creek	2385	5612	1208	496	1330	-338
West Root River	9424	12034	7380	15010	39005	-8985
Cannon Creek	17548	19051	16165	20868	47510	-5774
Mayhew Creek	na	na	na	29957	76109	-16195
Proctor's Creek	na	na	na	15550	37379	-6279
Sturgeon River	na	na	na	33009	135952	-69934
Spragge Creek	na	na	na	602	1583	-379
Gordon's Creek	na	na	na	1020	2273	-233
Richardson Creek	na	na	na	1020	2954	-914
Little Gravel River	na	na	na	2000	5000	101
Carp River	na	na	na	7571	12677	2465

Table 3. Stream area and density of sea lamprey in 16 tributaries to the Great Lakes.

* indicates reduction streams. Density [1] represents those calculated from Petersen mark-recapture and density [2] represents those calculated from Zippen depletion method

Stream Name	Area(m^2)	Density[1] (#/m^2)	Density[2] (#/m^2)
Farewell Creek*	30148	0.15	0.12
Lynde Creek West Branch	17955	0.10	0.10
Lynde Creek*	52955	0.13	na
Cobourg Brook*	19250	0.32	na
Oshawa Creek*	72000	0.11	na
Ogontz R. West Branch*	8750	2.48	na
Harris Creek*	4200	0.57	0.12
West Root River	63080	0.15	0.24
Cannon Creek	25833	0.68	0.81
Mayhew Creek	4225	na	7.09
Proctors Creek	3300	na	1.00
Sturgeon Creek	49500	na	0.67
Spragge Creek	2100	na	0.29
Gordon's Creek	3600	na	0.28
Richardson Creek	8707	na	0.12
Little Gravel River	22500	na	0.09
Carp River	30591	na	0.25

Nominal residual population size in the eight streams following treatment with TFM were set at 5% of pretreatment numbers but actual residual populations were 2.0% in Harris Creek, 10% in Cobourg Brook, 12% in Oshawa Creek and approximately 5% in the other streams (Table 4).

Metamorphosis of sea lamprey in the southern streams prior to chemical treatment occurred at ages three and four with the majority of larvae metamorphosing at age three. In the northern streams, metamorphosis, based on very few observations, occurred mostly at age four with some at age five. These northern streams showed peculiarities in statolith morphology especially in metamorphosing larvae and this presented a problem with the aging of some individuals.

Diversity in statolith morphology

Diversity in statolith morphology and size (length) was examined in larval and metamorphosing sea lampreys from four streams in Ontario. In mid-summer statolith lengths were similarly and positively correlated with larval total lengths in the four streams. Statoliths from larval and metamorphosing lampreys collected from Lynde and Farewell Creeks in June and September displayed typical alternating opaque and translucent bands. The number of opaque bands, or annuli, provided reliable age estimates when compared to length-frequency distributions. In July and September, statoliths from some larval and metamorphosing lampreys collected from West Root River and Cannon Creek were either absent or did not have typical bands, hence not

Table 4. Populations of sea lamprey reduced by 95% of the original population before chemical reduction in 8 tributaries to the Great Lakes, Ontario, Canada.

Stream name	5% reduced population estimated (actual)
Farewell Creek	222 (223)
Lynde Creek	352 (387)
Harris Creek	119 (48)
West Root River	471 (366)
Cannon Creek	877 (950)
Cobourg Brook	296 (339)
Oshawa Creek	391 (963)
Ogontz River, West Branch	1084 (1070)

always providing reliable ages. The diversity of statoliths appears to be related to ambient calcium ion concentrations, especially during periods of rapid larval growth. The use of statoliths is sometimes the only method to age some populations of sea lampreys due to ambiguity of length-frequency distributions. The absence of statoliths, as found in this study, has potential management implications when determining age-at-metamorphosis.

Growth

Growth rates of sea lamprey larvae were equated to a change in total length over time and compared among 17 streams. Both anadromous and landlocked populations of lamprey were examined, the latter before and after the commencement of chemical treatment 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. Differences were found among some regression intercepts. A trend of increasing hatch dates with latitude was observed as well as an inverse relationship between larval length-at-age and latitude and stream discharge. In recent years the larval period in landlocked populations is completed in approximately 3 or 4 years in southern streams and 4 years in northern streams. The larval period appears to have been 5 years in those streams examined in this study before chemical treatment and 5 or 6 years in anadromous populations.

Table 5. Location of tributary streams sampled for sea lamprey (*Petromyzon marinus*) larvae.

Basin Tributary	Province or State	Location Latitude	Longitude
North West Atlantic			
Terra Nova	NFLD	48°40'	50°00'
Petitcodiac	NB	46°01'	65°04'
Lake Champlain			
Lake Chazy	NY	44°50'	73°25'
Oneida Lake			
Fish	NY	43°13'	77°42'
Great Lakes			
St. Mary's			
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 6. Mean observed and estimated (parentheses) dates for migration, reproduction and hatch of sea lamprey (Petromyzon marinus).

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)
Peticodiac	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

Mortality

Preliminary estimates of mortality have been made only for larvae in the Ogontz River. Before chemical treatment, instantaneous mortality rate for all year classes combined was -0.817, based on the interval July to October, 1996. Changes in population size of residual larvae, all year classes combined, was measured on three occasions between the time of chemical treatment, October 6, 1996 and September 6, 1997. This is described by the regression:

$$\ln N = 6.846 - 0.575\ t \qquad (r = 0.69)$$

where N is population size and t, time in years. It is noteworthy that instantaneous mortality is appreciably lower in residuals than in larvae before treatment. Changes in population of residuals in the Ogontz River, Cannon Creek and West Root River will be followed over the next year or two to more confidently describe larval mortality before and after chemical treatment.

Gonadal variation in sea lamprey larvae

The observation of atypical gonads in land-locked sea lamprey larvae from several streams tributary to the Great Lakes led to this descriptive study on typical male and female gonads, as well as atypical gonads. Typical male and female gonads examined in the present study have similar characteristics to those observed in the past; however, larvae with atypical gonads have some characteristics of both male and female larvae (Table 7). Many of the atypical larvae had an unusual number of germ cells, or many atretic oocytes. Based on quantitative evaluation of several gonadal characteristics of male, female and

atypical larvae, it was possible to verify atypical status of 88% of the larvae which had been qualitatively assigned the atypical sex (Table 8). The slowing of gonadogenesis, or the diversion of energy for somatic development are possible causes of the atypical gonads observed in this study.

Unusual sex ratios in larval sea lamprey

Gonads of sea lamprey larvae in 14 streams tributary to the Great Lakes were examined for sexual differentiation. Sex ratios varied between 0 and 70.8% female (Table 9). All streams contained larvae deemed intersexual and varied in proportion between 8 and 100% among streams. Intersexual gonads were significantly different than gonads of typical females and males on the basis of cross-sectional area of gonad, shape and cell composition and organization. Sex ratios from each stream were evaluated with respect to biotic and abiotic characteristics, including larval density, temperature, pH, and larval growth rates. A trend was noted with the proportion of females increasing with larval density. Proportion of intersexual larvae had a significant direct relationship to larval growth rates. This study reports a high incidence of intersexual larvae and supports the theory of environmental sex determination in lamprey.

Potential fecundity of sea lamprey with typical and atypical gonads

Lampreys produce a fixed number of oocytes early in larval life, which represents their total reproductive potential or potential fecundity. In this study transverse sections from the mid-region of the body were examined histologically and categorized as males,

females or atypical based on criteria established earlier. A sub-sample of these larvae from each of three streams, Cannon, Cobourg and Gordon's Creek, was examined for potential fecundity.

Table 7. Ranges of gonadal characteristics for male, female and typical sea lamprey larvae, Petromyzon marinus, examined from Cobourg Brook, Ontario. Values given are means of measurements made from 10 transverse sections per larvae.

Gonadal Characteristics	Sex		
	Male (N = 22)	Female (N = 22)	Atypical (N = 47)
Germ cell number	4 - 598	0 - 159	4 - 1372
Oocyte number	0 - 8	75 - 190	0 - 167
diameter (μm)	13 - 22	46 - 77	16 - 79
Number of atretic oocytes	0	0	0 - 84
Gonad area (mm^2)	0.014 - 0.077	0.216 - 0.823	0.032 - 0.715
perimeter (mm)	0.88 - 2.35	4.75 - 11.02	1.21 - 9.30
shape (P^2/A)	56 - 164	106 - 149	45 - 140

Table 8. Tolerance limits for each gonadal characteristic measured on male and female larval sea lampreys, Petromyzon marinus, from Cobourg Brook. The tolerance limits are given for germ cell number, oocyte number, oocyte diameter, number of atretic oocytes, gonad area, gonad perimeter and gonad shape for three total length ranges; 106 - 120 mm, 121 - 135 mm and greater than 136 mm.

Gonadal characteristic	Larval length range (mm)	Male Tolerance limit	Female Tolerance limit
Germ cell number	106 - 120	-418, 1157	-81, 193
	121 - 135	-81, 700	-413, 658
	> 135	-413, 658	-22, 36
Oocyte number	106 - 120	0	47, 172
	121 - 135	-1.2, 1.9	64, 216
	> 135	-8.8, 10.2	30, 238
diameter (μm)	106 - 120	-	42.9, 53.6
	121 - 135	14.7	38.7, 73.5
	> 135	11.9, 17.7	46.1, 93.6
Number of atretic oocytes	106 - 120	0	0
	121 - 135	0	0
	> 135	0	0
Gonad area (mm^2)	106 - 120	0.013, 0.06	0.123, 0.449
	121 - 135	0.036, 0.039	0.064, 0.752
	> 135	-0.033, 0.098	0.066, 1.120
perimeter (mm)	106 - 120	0.50, 2.40	3.24, 8.61
	121 - 135	0.20, 3.22	2.90, 10.83
	> 135	0.11, 3.03	2.15, 14.79
shape (P^2/A)	106 - 120	19, 80	64, 161
	121 - 135	-87, 266	64, 173
	> 135	-4, 152	43, 205

Table 9. Sex ratios of sea lamprey larvae sampled from twelve streams tributary to the Great Lakes.

Stream	Number sexed	Percent of Total		
		Female	Male	Intersex
Cannon Cr.	172	60.5 ± 7.3	31.4 ± 6.9	8.1 ± 4.1
Carp R.	127	43.3 ± 8.6	14.2 ± 6.1	42.5 ± 8.6
Cobourg Br.	110	24.5 ± 8.0	32.8 ± 8.8	42.7 ± 9.2
Farewell Cr.	179	31.8 ± 6.8	35.2 ± 6.9	33.0 ± 6.9
Gordon's Cr.	264	3.4 _ 2.2	15.2 ± 4.3	81.4 ± 4.7
Lynde Cr.	297	51.2 ± 5.7	30.6 ± 5.2	18.2 ± 4.4
Mayhew Cr.	216	70.8 ± 6.1	14.8 ± 4.7	14.4 ± 4.7
Ogontz R.	202	51.5 ± 6.9	18.8 ± 5.4	29.7 ± 6.3
Proctor's Cr.	177	7.3 ± 3.8	2.3 ± 2.2	90.4 ± 4.3
Richardson Cr.	33	0	0	100
Spragge Cr.	159	18.2 ± 6.0	8.8 ± 4.4	73.0 ± 6.1
Sturgeon R.	83	61.4 ± 13.9	6.1 ± 5.1	32.5 ± 10.1

Potential fecundity of typical female larvae ranged from $33 \cdot 10^3$ to $129 \cdot 10^3$ (Table 10). Of this total, germ cell numbers ranged from $0.5 \cdot 10^3$ to $80 \cdot 10^3$ and oocytes from$19 \cdot 10^3$ to $65 \cdot 10^3$. Atresia of oocytes was not observed.

Larvae with atypical gonads were placed into four groups based on gonad area, oocyte diameter, gonad morphology and cell composition (Table 11). Potential fecundity of Type 1 and 3 gonads was within the range found for typical larvae but in these instances the gonads displayed unusual characteristics. Type 3 gonads had a typical horseshoe-shaped gonad with lobes, however a large amount of stromal tissue was present and some lobes did not contain oocytes.

Potential fecundity varied widely among atypical larvae (Table 10). In some larvae with atypical gonads, germ cell numbers were unusually high. Some of the atypical larvae examined appeared to be males, with the gonad differentiation through an ovarian, then transitional gonad before the testis develops. In other larvae with atypical gonads, potential fecundity was within the range found for typical larvae; however, the oocytes were comprised of only first stage oocytes. Perhaps these larvae are indeed females, with the gonad initially differentiating as a testis, followed by ovarian differentiation.

Overall, larvae with atypical gonads displayed a slowing of gonadogenesis, as evidenced by the persistence of germ cells into larger, older larvae. This may indicate they are diverting a disproportionate amount of energy to somatic growth at the expense of gonadal development, thereby allowing them to shorten the larval period. Gonadal

Table 10. Quantitative characteristics of typical gonads and the four groups of atypical gonads measured on sea lamprey larvae (Petromyzon marinus) collected from streams tributary to the Great Lakes. Values given are ranges over the total lengths examined.

Characteristic	Gonad Type				
	Typical	Atypical			
		1	2	3	4
Germ cells Number ($\times 10^3$)	0.5--80	0—27	10--5300	0--20	27--4100
Oocytes Number ($\times 10^3$)	19--65	12--40	8--51	22--39	19--25
Diameter (μm)	56--88	15--18	33--46	52--58	39--56
Gonad Length (mm)	50--64	49--57	48--57	44--56	48--58
Area (mm^2) ($\times 10^{-2}$)	32--117	4--6	14--63	39--72	20--56

Table 11. Morphology and condition of typical and four groups of atypical gonads from landlocked sea lamprey larvae (Petromyzon marinus) collected from streams tributary to the Great Lakes.

Gonad type	Total length (mm)	Sample size	Gonad morphology and composition
Typical female	115-165	8	horseshoe-shaped, prominent lobes, no atresia, second stage oocytes only, oocytes arranged in pairs
Atypical 1	120-129	4	angular-shaped, no lobes, no atresia, 1st stage oocytes only, oocytes only present around perimeter of gonad
Atypical 2	116-137	4	horseshoe-shaped, no lobes, atresia (2,000-10,000), 2nd stage oocytes only, many germ cell clusters, oocytes scattered individually
Atypical 3	122-146	3	horseshoe-shaped, lobes, no atresia, excess stromal tissue and few oocytes in some lobes
Atypical 4	119-141	4	horseshoe-shaped, lobes, atresia (5,000-40,000), many germ cell clusters, 1st and 2nd stage oocytes

development presumably resumes during the juvenile period which follows the larval period and the non-trophic interval of metamorphosis. Growth of atypical larvae may well be faster than typical larvae, however, growth of larvae prior to treatment with TFM appears to be similar to the growth of larvae since TFM treatments. In our analysis of growth, we did not separate larvae based on their sex. Since we used modal lengths and did not consider sex, any difference in growth rates may have been masked.