GREAT LAKES FISHERY COMMISSION
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Ecology of recruitment in sea lamprey--summary

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GREAT LAKES FISHERY COMMISSION

Project Completion Report

Unusual sex ratios in larval sea lamprey, *Petromyzon marinus*, from Great Lakes tributaries

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Gonads of sea lamprey (*Petromyzon marinus)* larvae in 14 streams tributary to the Great Lakes were examined for sexual differentiation. Sex ratios varied between 0 and 70.8 % female. 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.

Sea lamprey, *Petromyzon marinus*, invaded the Great Lakes prior to the 1950's and their rapidly increasing populations contributed to the collapse of many native fish populations (Lawrie, 1970). Chemical control of sea lamprey was established by the early 1960's with 3-trifluoromethyl-4-nitrophenol (TFM) and occasional use of 2'5-dichloro-4'-nitrosalicylanilide (Bayer 73) as a synergist (Smith and Tibbles, 1980). During the initial invasion by and subsequent control of sea lamprey populations in the Great Lakes shifts were noted in sex ratios of both adult and larvae. During the period of high lamprey abundance sex ratios of adults in the Upper Great Lakes were skewed to favour males (Heinrich et al., 1980). However with the decline of populations associated with chemical control sex ratios shifted to favour females. A shift from 35% females in 1958 to 61% in 1967 was noted for larval populations in some Lake Superior tributaries following drastic reductions in their numbers (Purvis, 1979). Adult lamprey populations also shifted to favour females (Smith, 1971; Heinrich et al., 1980). The shifts in population sex ratios in the Great Lakes suggests that the process of sexual differentiation may be labile.

Environmental sex determination (ESD) has been demonstrated in both invertebrates, including isopods (Williams and Franks, 1988), nematodes (Ellenby, 1954) and euchiuird worms (Jaccarini et al., 1983) and lower vertebrates, including turtles (Pieau and Dorizzi, 1981; Mohanty-Hejmadi and Dimond, 1986) alligators (Ferguson and Joanen, 1982) and teleost fish (Lindsey, 1962; Conover and Kynard, 1981; Rubin, 1985). Temperature-dependent sex determination is commonly observed. Incubation temperature can skew sex ratios in several species of turtles (Pieau and Dorizzi, 1981; Mohanty-Hejmadi and Dimond, 1986) and alligators (Ferguson and Joanen, 1982). Water pH also affects sex ratio as it is directly related to an increase in male offspring for some species of cichlids (Rubin, 1985). Sex differentiation in the European eel, *Anguilla anguilla*, is thought to be particularly sensitive to environmental influence due to the long period during which the gonad remains undifferentiated. D'Ancona (1950) suggested that increased crowding of *Anguilla* favoured the production of males and Grassi (1919) associated variation in sex ratios with salinity and nutrition. Larval lamprey also remain sex undifferentiated for an extended period of time (Hardisty, 1965a). ESD has been described in southern brook lamprey, *Ichthyomyzon gagei* (Beamish, 1993) and least brook lamprey, *Lampetra aepytera* (Docker and Beamish, 1994). Sex ratios of several populations of both species varied directly with larval growth rates and inversely with pH and mean annual temperature.

Populations of larval landlocked sea lamprey in the Great Lakes experience a wide range of stream conditions. The Great Lakes Drainage Basin encompasses a range of geographic and climatic conditions in which streams display a considerable range in, growing season, water quality, such as pH, hardness and alkalinity and lamprey larval densities. The present study examined 14 populations of landlocked sea lamprey from a large portion of their geographical distribution within the Great Lakes to establish the effect of environmental factors on the sex ratios of larvae.

METHODS AND MATERIALS

Study streams were carefully selected based on the presence of three year classes of sea lamprey larvae, a range in temperature and pH, and stream accessibility. Based on these requirements a preliminary list of streams was provided by sea lamprey control agents (Department of Fisheries and Oceans, Sault Ste. Marie, Ontario and Amherst, New York and from U.S. Fish and Wildlife Service, Marquette Michigan). The selection criteria were such that 14 streams were suitable for sampling (Figure 1).

Population size of sea lamprey larvae in each stream was estimated using a modified Zippen's depletion method (Zippen, 1956) and/or a Peterson mark recapture method (Ricker, 1975). Initially Zippen's estimates were used as only one stream visit is required, however due to a subsequent study, population estimates based on the Peterson mark recapture method were available for some additional tributaries in the Great Lakes Basin. The depletion method was applied to a maximum of three randomly selected sites per kilometre of stream inhabited by sea lamprey. At each site of 100 m^2 electro fishing passes were repeated until no larvae were captured or a maximum of six passes. If no larvae were captured in the first two passes a population of zero was assigned to that site. The mean population estimate for the depletion sites was extrapolated to estimate population of larvae over the area of inhabited stream.

The mark-recapture method was applied on seven streams. The number of larvae captured varied among streams from 252 in Harris Creek to 3826 in Cannon Creek with a mean (±SD) of 1413 ±1137. Of these, all larvae >55 mm total length were marked with wire tags and released. Tags were inserted into the muscle on the dorsal lateral surface, just posterior to the insertion of the dorsal fin. In a subset of streams larvae were double tagged using a combination of a coloured elastomer and wire tags. In double marked larvae, coloured elastomer was injected beneath the skin along the dorsal lateral surface immediately posterior to the branchiopores. The actual number of larvae marked averaged 63% of all larvae captured but, varied from 29% in

Harris Creek to 91% in West Root River. The interval between marking and recapturing was about 40 days. Tagged larvae were identified using a metal detector and by visual examination for elastomer marks. Mean number of larvae recaptured for all streams was 16.6 ±6.7% of those marked and varied from 6% in Ogontz River to 25% in Cobourg Brook. Population size and 95% confidence intervals were calculated with Peterson's inverse estimator (Ricker, 1975).

Relative population density (larvae/m^2 of inhabited stream) was estimated for each stream by dividing the population estimate, using the mark-recapture method when available, by area of lamprey inhabited stream. Chemical characteristics including, pH, alkalinity and total hardness were measured directly in the field (APHA, 1989) in a riffle within the lamprey distribution for each stream. Chemical characteristics were measured during each visit to the stream. In addition, temperature of each stream was monitored daily for approximately 18 months using calibrated automated temperature recorders. This data, in combination with information obtained from the Ontario Ministry of the Environment was compiled into an estimate of annual temperature as degree days over a period of one year.

Lamprey larvae captured by electrofishing were immediately killed with an overdose of MS222, identified (Vladakov, 1960) and total length measured (±1 mm). Most larvae were preserved in a solution of 5% formalin for sexing. A subsample representing the range of sizes present in a stream was frozen (-20 °C) for later removal of statoliths for age determination.

Lamprey were aged from the banding patterns on statoliths (Volk, 1986). Otic capsules were dissected and the largest statolith, the sacculus removed. Statoliths were cleared in 100% glycerin for between 5 and 15 days to intensify the banding pattern. Larval age was established by counting under a dissecting microscope the number of dark bands on a statolith. In Cannon

Creek and West Root River statoliths could not be used for aging due to aberrations (Barker et al., 1997).

Age-class discriminations for all fourteen streams were established using a combination of length-frequency distributions smoothed by a moving average over 7 mm and statolith banding patterns (Beamish and Medland, 1988) when possible. Modal lengths were then assigned to each age class using hand fitted curves and mean length (mm) at age (days) was established. A common hatch date of July 1 was used for all streams as actual hatch dates were not known. The hatch date was based on spawning occurring most frequently in early to mid June (Scott and Crossman, 1973) and hatching occurring approximately 10-15 days later (Wigley, 1959; Piavis, 1961). Larval age in days was based on the time between the common hatch date and collection date. A linear regression was fitted to mean length at age data for all streams and the slopes were used to indicate the rate of change in total larval length (mm) over time (days).

Larvae were sexed by examination of histological transverse sections cut at 10 μm thicknesses. A transverse section of tissue was cut 2 mm anterior to the insertion of the dorsal fin, dehydrated in increasing concentrations of ethanol (50-100%) and embedded in paraffin. Sectioned tissue was stained with Harris' haematoxylin and counterstained with eosin (Humason, 1972). Criteria for sexing larvae were consistent with that used by Wicks et al. (1997). Sex was assigned to larvae >90 mm based on gonad shape and cell composition. Individuals with undifferentiated gonads could be recognized by small gonad size compared to differentiated males and females, very few isolated germ cells, and an entire gonad margin (Hardisty, 1965b).

Data were analysed using multiple linear regression, with proportion of females, males and intersexuals as dependent variables and pH, temperature, growth rate and density as independent variables. Multivariate regression analysis was performed on percentage males and intersex regressed against combinations of pH, temperature, growth rate and density (Wilkinson, 1990). Linear regression analysis included all interaction effects as well as the quadratic effects for all independent variables. Sex ratio percentages were logit transformed and tested for normality using Lilliefor's test (Wilkinson, 1990). Analysis of covariance was used to compare slopes and elevations of the growth rate regression curves for each stream. Unless otherwise stated all analysis was at a significance level of $p<0.05$.

RESULTS

Data on stream characteristics were collected from all 14 streams (Table 1). The pH range among streams was not large, but representative of that among tributaries to the Great Lakes, from 6.4 in the Ogontz River to 8.9 in Proctor's Creek (Table 1). Temperature, as degree days for the 14 streams ranged between 1484 for Carp River, a Lake Superior tributary, to 4097 for Mayhew Creek, tributary to Lake Ontario (Table 1). Population size was estimated for all sample streams (Table 2). Reliable confidence intervals were not calculated for Lynde Creek due to the small number of larvae examined for marks. Population size was estimated by both Peterson's mark recapture and the depletion methods in four streams. In two streams, Farewell and Cannon creeks, population estimates were quite similar with the two methods. Differences were larger for estimates of larval abundance in Harris Creek and West Root River. Larval densities were calculated based on Peterson mark recapture population estimates when possible for each stream and ranged from 0.1 to 4.18 larvae/m^2 for those portions of the stream inhabited by lamprey (Table 3).

Larval age from length-frequency distributions was supported by that from statolith banding patterns. For example, larvae collected from Sturgeon River had mean total lengths (±SD) for one, two and three years of age the basis of statolith banding patterns of 36.4 ±10.9 (n=16), 60.3 ±9.5 (n=16) and 97.2 ±9.2 mm (n=5). Modal lengths derived from the length-frequency distribution of larvae collected during the same sampling period were 30, 58 and 93 mm. Similar results were noted in all study streams (Table 4). A growth equation was derived for each stream based on the length of larvae at a given age. The slope of these equations was used to reflect rate of growth as a daily change in total length in mm for each population (Table 3). Analysis of covariance showed a significant interaction term suggesting that the slopes or growth rates were significantly different in at least one stream. Scheffe's multiple comparison test indicated that growth rates were significantly different between some streams ($p<0.1$; Table 3).

Larval sex could be determined at lengths >90 mm in all but two streams, Harris Creek and West Root River. In both streams larvae between 90-100 mm total length had undifferentiated gonads and most larvae collected from these two streams were in that size range. Undifferentiated gonads were characterized by an entire gonad margin and only a few primordial germ cells that were either isolated or in clusters (Hardisty, 1965a). Thus, establishing sex ratios for these streams was not possible. Females were recognized by the presence of a horse-shoe shaped ovary, consisting of finger-like lobes containing nucleated basophilic oocytes (Figure 2; Docker, 1992). The gonad of male larvae has a shallowly clefted angular shape, a smaller area in cross section and is comprised of stromal tissue and germ cells which are either isolated or clustered in cell nests (Figure 3; Hardisty, 1965b). Some males contained oocytes, but oocytes were on average 18 μm maximum diameter, significantly smaller than those in females (Figure 3).

Oocytes in male testes rarely exceeded six per transverse section.

All streams contained larvae that did not fit in the typical male or female category and were classified as intersexual (Figure 4,5 ; Wicks et al., 1997). Intersexual larvae ranged in size from 90 to 160 mm total length in all streams examined.

Ratios of males, females and intersexual larvae >90 mm total length varied significantly among streams. The proportion of females varied between 0 % and 70.8 ±6.1% of the total larvae examined (Table 5). Mayhew Creek had the largest number of females and Richardson's Creek the smallest. Sex ratios excluding intersexual larvae were not significantly different from parity in Farewell Creek and Cobourg Brook with the percentage of females being 47.5 ±8.9 and 42.5 ±11.3 ($p<0.05$). The proportion of females was significantly higher than parity in all remaining streams except Gordon's and Richardson's Creeks which were lower containing, 18.4 ±10.8 and 0% females respectively ($p<0.05$). Intersexual larvae comprised between 8.1 and 100% of the larvae examined in all 12 streams. In Richardson's Creek all larvae (n=33) contained an intersexual gonad and thus was excluded from the analysis of male and female sex ratios.

Multiple regression analysis was used to examine the relationship between stream characteristics and the percentage of females in a population (Wilkinson, 1992). The combined effects of both larval density and growth and pH and temperature on the percentage of females in a population did not provide a significant linear model. A strong correlation between pH and total hardness and conductivity was established; thus only pH was used to represent stream chemistry due to limited degrees of freedom. Interaction and quadratic effects were also examined with no significant results. The best relationship was indicated by an increasing trend in the proportion of females as larval density increased although the regression of percentage females on larval density was not significant ($r=0.31$, $p=0.27$, $df=9$, Figure 6).

Similarly a significant relationship was not found between the percentage of males in a population and stream characteristics. Again the combined effects of both larval density and growth and pH and temperature on the percentage of females in a population did not provide a significant linear model. However, corresponding to the increasing trend noted in females with increasing density, male proportions showed a decreasing trend when intersexual larvae were excluded. The regression of percentage males in a population on larval density was not significant ($r=0.31$, $p=0.27$, $df=9$). Similar trends were noted for both males and females when intersexual larvae were included in the ratio calculations.

Multiple regression analysis was also used to examine the relationship between stream characteristics and the percentage of intersexual larvae in a population (Wilkinson, 1992). The combined effects of both larval density and growth and pH and temperature on the percentage of females in a population did not provide a significant linear model. The percentage of intersexual larvae in a population was not significantly related to any stream characteristics or larval density. However, a significant direct relationship was established between growth rate, and the proportion of intersexual larvae at $p<0.1$ (Figure 7) . The relationship is described by the regression:

$$I = 1218.8G - 68.2 \qquad (n = 13,\ r = 0.536,\ p=0.06)$$

where I is the percentage of intersexual larvae and G is the growth rate (mm/day).

DISCUSSION

Sex ratios of sea lamprey in the Great Lakes have been found to vary widely. Following the initial invasion of the Great lakes when sea lamprey abundance was high, adult males comprised as much as 70% of the population in the Upper Great Lakes (Heinrich et al., 1981). When populations were dramatically reduced through chemical control a shift towards a preponderance of females was noted (Smith, 1971; Purvis, 1979; Heinrich et al., 1981). For example the larval populations in Huron River, a Lake Superior tributary shifted dramatically from from 36% to 84% female between 1958 and 1965 . A similar shift was found in the sex ratios of recently metamorphosed larvae in Whitefish River, a Lake Michigan tributary with the number of female larvae increasing from 33 % to 91% between 1962 and 1966 (Purvis, 1979). Differential toxicity of TFM to the sexes was not thought to be the cause for shift in sex ratios.

Sex ratios determined for streams in this study show significantly more females than males in eight of twelve streams. Two streams had equal numbers of males and females. The preponderance of females generally found in this study corresponds with that earlier noted especially for adults (Purvis, 1979; Heinrich et al., 1981) following reduced abundance through chemical control. However, the proportion of females within populations did not vary significant with larval density among streams as might be predicted from the earlier observations in the Great Lakes (Heinrich et al., 1981; Purvis, 1979) and as found for several species of brook lamprey (Beamish, 1993; Docker and Beamish, 1994). Interestingly, a trend towards increasing numbers of females with increased density was noted, however, the relationship was not statistically significant. Perhaps sea lamprey numbers are now so severely controlled that other stream characteristics have a more significant effect on the direction of sex differentiation. For example, Docker and Beamish, (1994) noted a reversal of the relationship between the proportion of females and larval density in populations of southern brook lamprey under conditions of decreased growth rates. However, no significant relationship was found in this study between the proportion of females and any of the stream characteristics measured. It is possible that relationships noted for lamprey populations in the past, such as direct relationships between pH and the proportion of males were not found in this study as a result of a relatively narrow range in environmental quality found in the tributaries to the Great Lakes examined in this study

The incidence of intersexual larvae in Great Lakes sea lamprey was first reported in three streams by Wicks et al. (1997). Examination of a further 12 streams study supports the existence of large numbers of intersexual sea lamprey larvae in other tributaries to the Great Lakes. Studies on brook lamprey suggest that two types of testicular development may occur. Fukayama and Takahashi (1983) described male differentiation in the sand lamprey, *L. reissneri,* as being characterized by either a gonad having a lobulated margin and containing few germ cells or having some of the characteristics of a typical ovary. The more ovarian like testes contain many degenerating oocytes of similar size to those found in ovaries and are in transition from ovaries to testes. Ovarian type male development was noted through a large range of sizes with approximately 10 to 20% of all male sand lamprey developing in this manner. Fukayama and Takahashi (1982) and Hardisty (1965a) report similar findings for both the Japanese river lamprey, *L. japonica,* and the brook lamprey, *L. planeri*, respectively.

Based on the large cross sectional area of the gonad and presence of substantial numbers of oocytes observed in transverse sections of larval lamprey examined in this study many larvae may be undergoing ovarian type male development. If the intersexual larvae from each stream examined are in fact undergoing a type of male development and are combined with other males then sex ratios indicate that all but four streams have predominately male populations. Proportions of males in a given stream could be as high as 80-100%. Such large proportions of male larvae are inconsistent with reports of sex ratios that favour female for both adult spawning and larval populations in the Great lakes after the commencement of TFM treatments (Heinrich et al., 1980)

Interestingly a positive relationship was noted between number of intersexual larvae and larval growth rate. In the past 30 years sea lamprey larvae have been chemically eliminated from Great Lakes' streams on a regular treatment cycle. Hence, it is reasonable to assume that many of the sea lamprey that reproduce are individuals that have either survived chemical treatment or completed the stream dwelling phase of their life history before a treatment occurs. If the latter is true then a regular chemical treatment schedule may select for individuals with accelerated growth rates. In support of this suggestion, most metamorphosing larvae examined in a companion study were three to four years of age (unpublished data). Prior to chemical treatment, age-at-metamorphosis was reported at three to seven years (Potter, 1980). It is interesting to speculate that due to dramatic selective pressure, which a rigorous chemical control cycle has imposed on sea lamprey, that the species is moving towards a nonparasitic life cycle. Hardisty (1969) suggested that speciation towards a nonparasitic form may be indicated for *P. marinus* based on differences in gonadogenesis between the anadromous and landlocked forms. Landlocked sea lamprey have significantly lower potential fecundity than the anadromous counterpart resulting from an apparent acceleration in gonadal development relative to somatic growth (Hardisty, 1969). A similar relationship exists between parasitic species and their presumed nonparasitic derivative (Hardisty, 1971) with the latter form having the lower fecundity (Hardisty, 1969). Hardisty et al. (1992) suggests that sexual differentiation in nonparasitic lampreys is more indirect, with transitional phases being expressed more frequently than in parasitic species. He further suggests that nonparasitic species which commence sex differentiation earlier than parasitic lampreys may not produce sufficient concentrations of those substances that control oocyte development in males. In parasitic species which remain sexually undifferentiated for a longer period Hardisty suggests the inhibitory factors are present at levels that prevent oogenetic development in males. The eventual sex of the intersexual individuals examined in this study remains in question as reported adult sex ratios (Heinrich et al., 1981) contradict the larval sex ratios reported in this study.

Heteromorphic sex chromosomes have not been found in the phylogenetically primitive lamprey. There are a large number of diploid chromosomes in lamprey on which genes for determining sex may be distributed. Polygenic sex determination is thought to occur by environmental stimuli acting on a large number of genes that influence sex differentiation. Absence of specific sex chromosomes and the extended period during which larval lamprey gonads remain undifferentiated (Hardisty, 1965a, 1965b; Lewis and McMillan, 1965) suggests that sex determination in lamprey may be labile. Results of this study did not reveal any significant relationships between sex determination and the environmental characteristics measured including stream temperature regime, pH, alkalinity and larval density. However, a strong increasing trend was noted between larval density and proportion of females. This trend is opposite to that found with a decrease in larval abundance following chemical control of sea lamprey in the Great Lakes (Purvis, 1979). It is possible however that a reduction in the population size of sea lamprey through chemical control has lowered larval densities in streams to a point that density no longer has a significant effect on sex differentiation. Thus, the increasing trend may result from the combination of density and other as yet unidentified variables which could include both environmental and xenobiotic substances.

The high incidence of intersexual larvae may also influence the analysis of the interaction between sex ratio and environmental factors. Intersexual larvae had not been reported in *P. marinus* prior to 1997 (Wicks et al., 1997) and it was suggested that lability of lamprey sex differentiation in combination with xenobiotic substances may be the cause of variation in gonadal development. Based on results of this study one might suspect that the larval lampricide TFM is responsible for disruption of sexual development patterns. TFM has been implicated as an estradiol agonist in rainbow trout, where it works in a manner similar to p-nonylphenol (Hewitt et al., 1997). However, TFM is applied to streams only for short durations of approximately 16-48 hours, and rapidly photo degrades. It is therefore unlikely that subsequent future larval recruits would be exposed directly to TFM. There is also a large degree of variation noted in proportions of intersexuals found among streams even though all have been treated with TFM . Alkyl phenolic compounds are also commonly found in stream sediments and have been implicated as estrogenic substances (Ahel et al., 1987; Jobling et al., 1996). It is possible that other or combinations of xenobiotics perhaps in concert with natural environmental stimuli may act on the direction of sex differentiation in the Great lakes sea lamprey.

In summary, the present study provides further evidence that sex differentiation in *P. marinus* is indeed labile based on the variable sex ratios and presence of intersexual larvae.

Although no significant relationships were noted between the sex ratios of larval populations in the Great Lakes and environmental characteristics, extremely high incidences of gonadal variation were established. The proportion of intersexual larvae was significantly related to growth rate in individual streams which may support the theory of speciation of sea lamprey to a nonparasitic form. Alternatively gonadal variation may result from xenobiotic stimuli or manmade disruptions of the sea lamprey life cycle. Both theories provide new and exciting avenues of research on the landlocked sea lamprey.

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Table 1. Abiotic characteristics of study streams, 1995/1996.

Lake	Stream	pH	Alkalinity ($mg/L\ CaCO_3$)	Hardness ($mg/L\ CaCO_3$)	Temperature (degree days)
Huron	Cannon Cr.	7.5	17	18	2933
Huron	Gordon's Cr.	7.4	80	66	2216
Huron	Harris Cr.	6.8	22	22	2685
Huron	Richardson's Cr.	8.0	166	121	2214
Huron	Spragge Cr.	6.8	19	16	2549
Huron	Sturgeon R.	8.0	194	193	3200
Huron	West Root R.	7.1	27	14	2763
Michigan	Ogontz R., West	6.4	42	49	2600
Ontario	Cobourg Br.	8.3	213	245	3245
Ontario	Lynde Cr.	8.4	210	254	3889
Ontario	Farewell Cr.	8.8	200	340	3862
Ontario	Mayhew Cr.	7.5	180	227	4097
Ontario	Proctor's Cr.	8.9	222	246	3241
Superior	Carp R.	8.0	83	145	1484

Table 2. Population estimates of sea lamprey larvae using Petersen mark-recapture (Ricker 1975) and depletion method (Zippen 1956) in tributaries to the Great Lakes 1995/1996.

Stream	Mark-Recapture			Depletion Method		
	N	$N_{upper95\%}$	$N_{lower95\%}$	N	$N_{upper95\%}$	$N_{lower95\%}$
Farewell Creek	4449	5195	3890	3468	5167	1770
Lynde Creek	13722	na	na	na	na	na
Cobourg Brook	3196	3690	2819	na	na	na
Ogontz River	22442	30607	17716	na	na	na
Harris Creek	1814	4621	1129	496	1330	-338
West Root River	7319	7679	6959	15010	39005	-8985
Cannon Creek	18983	20628	17581	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
Carp River	na	na	na	7571	12677	2465

Table 3. Stream area and density and growth rate of sea lamprey larvae in 14 tributaries to the Great Lakes 1995/1996. Scheffe's test indicates those streams with significantly different growth rates ($\propto$=0.1).

Stream	Area m^2	Density larvae/m^2	Growth rate 10^{-2} mm/day	Growth rate different from stream
1. Farewell Creek	30148	0.12	9.0	5/6/7/10/14
2. Lynde Creek	52955	0.10	9.8	5/10
3. Cobourg Brook	19250	0.32	10.4	
4. Ogontz River	8750	4.18	9.4	
5. Harris Creek	4200	0.12	6.8	1/2/11/13
6. West Root River	63080	0.24	7.0	1
7. Cannon Creek	25833	0.81	8.5	1
8. Mayhew Creek	23823	1.26	7.4	
9. Proctors Creek	3300	1.00	9.1	
10. Sturgeon River	49500	0.67	8.4	1/2/11/13
11. Spragge Creek	2100	0.29	12.7	5/10
12. Gordon's Creek	3600	0.28	9.2	
13. Richardson's Creek	8707	0.12	10.9	5/10
14. Carp River	30591	0.25	8.8	1

Table 4. Total length at age ±standard deviation in populations of sea lamprey larvae using both statolith banding patterns and length frequency histograms in tributaries to the Great Lakes.

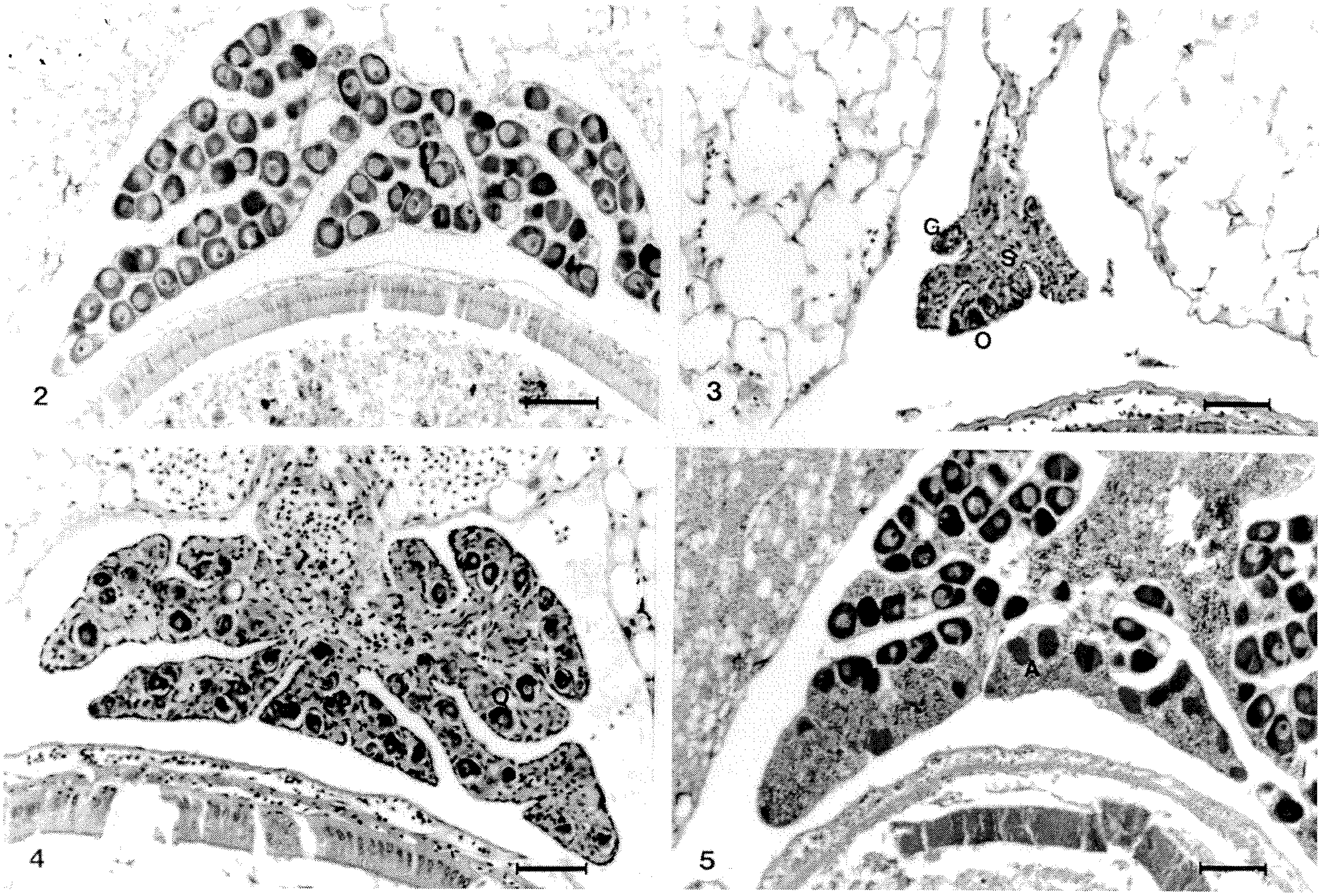
	Total Length (mm) At Age (months)						
Stream	Statoliths			Length Frequency			
	12	24	36	12	24	36	n
Farewell Creek	51 ±6 (22)	84 ±14 (9)	124 ±35 (12)	74	109	145	1189
Lynde Creek	na	93 ±11 (21)	93 ±45 (8)	53	97	134	839
Cobourg Brook	49 ±11 (8)	91±13 (9)	105 ±41 (7)	45	92	121	650
Ogontz River	35 ±29 (6)	74 ±13 (10)	115 ±9 (5)	40	81	108	1352
Harris Creek	35 ±7 (9)	54 ±6 (7)	72 ±3 (9)	45	67	86	172
West Root River	54 ±8 (5)	93 ±20 (5)	119 ±22 (5)	48	70	108	1864
Cannon Creek	48 ±11 (8)	71 ±17 (8)	128 ±4 (3)	48	80	119	3960
Mayhew Creek	45 ±16 (9)	76 ±10 (16)	98 ±6 (5)	52	80	106	694
Proctor's Creek	38 ±4 (11)	73 ±21 (15)	100 ±8 (5)	38	80	112	1006
Sturgeon River	36 ±11 (16)	60 ±10 (16)	97 ±9 (5)	30	58	93	236
Spragge Creek	na	57 ±20 (8)	80 ±8 (7)	67	85	163	223
Gordon's Creek	55 ±3 (2)	84 ±27 (12)	123 ±17 (19)	54	80	124	570
Richardson Creek	53 ±12 (6)	81 ±34 (6)	125 ±14 (2)	55	90	127	57
Carp River	43 ±6 (9)	69 ±9 (10)	98 ±9 (13)	45	68	98	264

Table 5. Sex ratios of sea lamprey larvae sampled from twelve streams tributary to the Great Lakes. The 95% confidence limits are given in brackets.

		Percent	of Total	
STREAM	Number sexed	♀	♂	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

List of Figures

FIGURE 1 BJW). BTM. LAB. FWHB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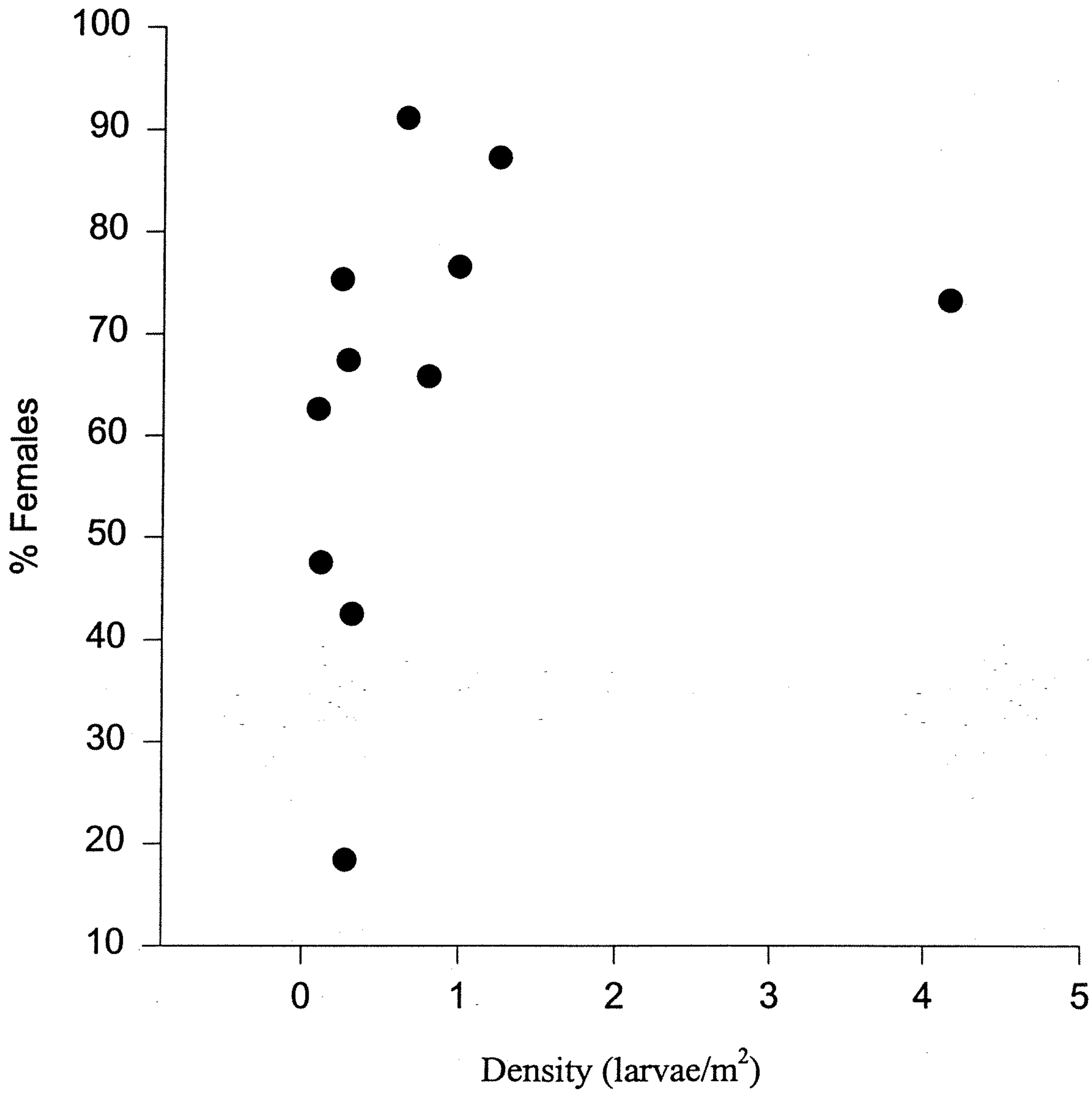

FIGURE 6 BJW. RJM. LAB. FWHB

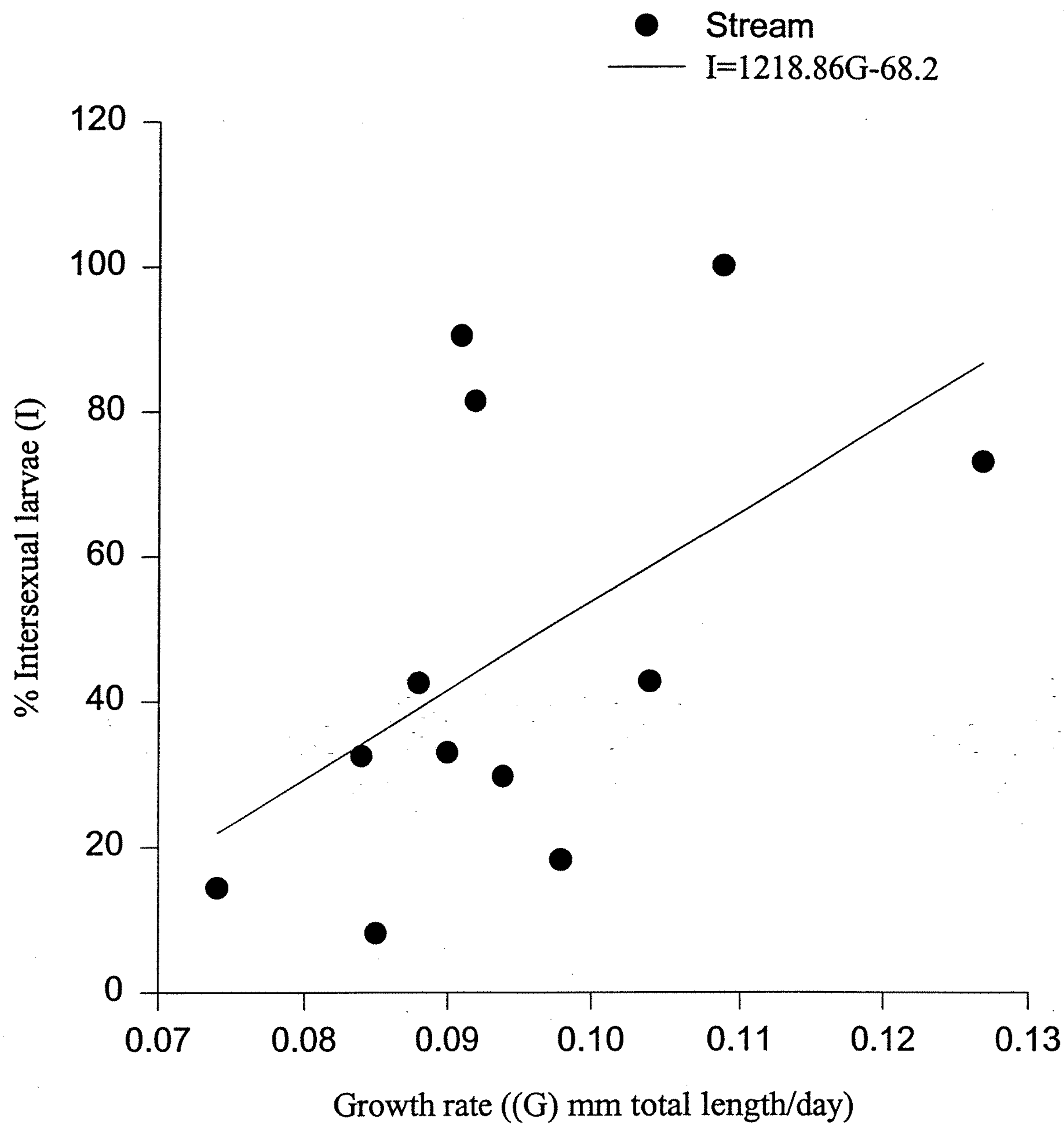

FIGURE 7. BTW. BTM. LAB. FWHB

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