GREAT LAKES FISHERY COMMISSION

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Comparison of Larval Sea Lamprey (*Petromyzon marinus*) Population Dynamics in Lampricide Treated and Untreated Tributaries of Lake Champlain

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GREAT LAKES FISHERY COMMISSION
RESEARCH COMPLETTION REPORT

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Comparison of Larval Sea Lamprey (*Petromyzon marinus*) Population Dynamics in Lampricide Treated and Untreated Tributaries of Lake Champlain.

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Abstract

In Lake Champlain, an eight-year experimental control program began in 1990 to control the exotic sea lamprey (*Petromyzon marinus*). In this study, the effects of sea lamprey control (lampricide application) on larval lamprey life-history characteristics were compared between a treated stream, Lewis Creek, four and five years after treatment, and the untreated Pike River and Morpion Stream. In each stream, sea lamprey habitat was measured at approximately 100 transects during 1999 and ammocoete density was determined using an electro fisher at pre-selected transects during 1999 and 2000. In 1999 and 2000, larval sea lamprey density was highest in Lewis Creek, intermediate in Morpion Stream and lowest in Pike River. During 1999, transformers were larger on average and older in Pike River/Morpion Stream (143 mm, 100% age 5) than in Lewis Creek (130 mm, 100% age 4; $p<0.05$). During 2000, the age distribution at metamorphosis in the untreated Pike River/Morpion Stream was 12.5% age 4, 75% age 5+ and 12.5% age 6 and in the treated Lewis Creek age at metamorphosis was 26% age 4+ and 74% age 5. Condition factor ($\text{weight} \times 10^5/\text{length}^3$) of age 4 Lewis Creek transformers during 1999 and age 4 Lewis Creek and Pike River transformers during 2000 was higher than age 4 ammocoetes from Lewis Creek, Morpion Stream and Pike River. Estimated survival in Pike River and Morpion Stream from age 1 to 4 was >100% and 4 to 5 was 74%. Estimated survival in Lewis Creek was 85% from age 1 to 2, 89% from age 2 to 3 and 62% from age 3 to 4. In Lewis Creek, estimated survival from age 4 to 5 was greater than 100%. The results of this study suggest that the first re-establishing year class after lampricide application may have enhanced growth and may experience early metamorphosis.

Introduction

Sea lamprey (*Petromyzon marinus* Linnaeus) is a primitive vertebrate that has gained attention because of its detrimental effects as an exotic species in freshwater ecosystems. The sea lamprey has an unusual life history: as larvae the sea lamprey lives as a burrowing filter feeder in stream sediments; the larvae then metamorphose into parasitic adults that inhabit cool, deepwater lakes or the Atlantic Ocean, and return to tributaries to spawn and then die (Applegate 1950). During the nineteenth century, it is believed sea lamprey gained access from the Atlantic Ocean to Lake Ontario, the Finger Lakes, and Lake Champlain via the shipping canals; from Lake Ontario, sea lamprey gained access to the upper four Great Lakes via the Welland Canal during the last century (Lawrie 1970). It has also been argued that sea lamprey could be endemic to Lake Ontario, the Finger Lakes and Lake Champlain, having entered these lakes via the St Lawrence River (Smith 1972; Daniels 2001).

Commercial and recreational fish populations and other native fish species have been adversely affected in these freshwater ecosystems as a result of the invasion of the sea lamprey (Applegate and Moffett 1955; Aron and Smith 1971). The decline of fish populations has led to efforts to control the sea lamprey in the 1950s in the upper three Great Lakes with the goal of reducing or eradicating their populations. Since the beginning of the sea lamprey control program, efforts of governmental agencies have evolved into a multi-million dollar program, expanding to the lower Great Lakes, the Finger Lakes, and Lake Champlain.

Sea lamprey control is largely dependent on reduction of larval densities in streams through use of 3-trifluoromethyl-4-nitropheno (TFM). Current control strategies apply TFM in tributaries every three to four years based on the predicted cost-per-kill of metamorphosing ammocoetes (transformers) produced in a tributary (G. Christie, unpublished data, Great Lakes

Fishery Commission). Reducing densities of larval sea lamprey via a control program has important management implications if, at low densities, sea lamprey begin metamorphosis to the parasitic phase in a shorter period of time (Walters et al. 1980). Larval sea lamprey at reduced densities may have accelerated growth, higher survival, increased proportion of females in the population and may begin metamorphosis earlier (Purvis 1980; Morman 1987; Holmes and Yousen 1997). Understanding the effects of density reductions on larval sea lamprey development is critical for evaluating the efficacy of a long-term sea lamprey control program.

Metamorphosis of landlocked sea lamprey typically begins at three to seven years when the ammocoete has attained an adequate length and weight (Applegate 1950; Potter 1980; Yousen et al. 1993). Age at metamorphosis is primarily dependent on growth and evidence indicates that some variation in age at metamorphosis exists within a year class (Potter 1980; Purvis 1980). Purvis (1979) proposed the hypothesis that sea lamprey ammocoetes were "self-regulating", responding to density by altering growth and survival. Changes in growth and survival that maintain a long-term average population biomass are known as compensatory mechanisms (Everhart and Youngs 1981).

Sea lamprey ammocoete life history characteristics are not well understood in streams before treatment with lampricides. In Lake Champlain, several streams that contain sea lamprey have not yet been treated with lampricide. The purpose of this study was to understand the response of sea lamprey ammocoete populations in streams after lampricide treatment. Specifically, the objectives of the study were as follows:

1. Compare population dynamics of larval sea lamprey (density, growth rates, survival, and age at metamorphosis) in treated and untreated streams.
2. Compare number of returning adult spawning sea lamprey in treated and untreated streams.

We compared density, growth, survival, sex ratio, and age and size at metamorphosis of sea lamprey ammocoetes in the untreated Pike River and Morpion Stream to a similar treated stream, Lewis Creek, four and five years after treatment. Additionally, we quantified adult spawning sea lamprey abundance using nest counts in each of these three streams.

Methods

Study sites

Pike River is a tributary of the northeastern end of Lake Champlain that drains into Missisquoi Bay, Quebec, Canada (N 45° 04” 50’, W 73° 06” 12’; Figure 1). Morpion Stream is a tributary of the Pike River; their confluence occurs at Notre Dame-de-Stanbridge, Quebec, Canada (N 73° 2.5” 32’, W 43° 10” 58’). Lewis Creek is a tributary of east central Lake Champlain and drains into Hawkins Bay, Vermont (N44° 14" 47', W73° 16" 42'). Lewis Creek was first treated with TFM in 1990 and was treated a second time in 1994. Pike River and Morpion Stream have never been treated with lampricides. The elevation of Pike River and Morpion Stream at their confluence is 43 m above lake level and the elevation of Lewis Creek at the upstream end of the study section is 60 m above lake level. Each of the streams has a riffle/pool sequence and agricultural riparian zone; some channelization has occurred in Pike River and Morpion Stream. The average width of Pike River is 41m, Lewis Creek is 12 m, and Morpion Stream is 5 m. Average conductivity and temperature measured during the study period in Pike River was 368 ohms and 71 ^{0}F, Lewis Creek 245 ohms and 70 ^{0}F, and Morpion Stream 411ohms and 69 ^{0}F.

Larval assessment

Sea lamprey habitat in the wadable sections (< 0.8 m deep) was classified perpendicular to flow at 106 transects in the Pike River in 1998, 86 transects in Morpion Stream and 107 transects in Lewis Creek in 1999 using the methods described by Twohey et al. (1996; Appendix A). Distance between transects was random, although numbers were bounded by + or - 50% of the distance if 100 transects were spaced evenly. In the field, transects were located using a hip chain.

At each transect, habitat was classified into one of four habitat types: type I, optimum ammocoete habitat; type II, adequate, although not preferred ammocoete habitat; type III, unsuitable ammocoete habitat; and type IV, adult sea lamprey spawning habitat. Habitat was identified by feeling the substrate and extent of habitat was measured across the transect to the nearest 0.04 m (Twohey et al. 1996).

Larval lamprey were sampled with an ABP-2 backpack electro-fisher at standard settings (O'Neal 1987). Larvae were sampled from type I habitat at every other transect and from type II habitat at every eighth transect. Sampling plots had an area of 2.5-5 m^2 and each plot was electro-fished in one pass at 1.5 m^2/min. In 1999, larval lamprey were sampled from Morpion Stream from July 20 to August 5, Lewis Creek from August 9-19, and Pike River from August 18 to September 28. In 2000, larval lamprey were sampled from Morpion Stream from July 17 to August 8, Lewis Creek from July 19 to August 25 and Pike River from August 14 to October 1.

The non-wadable portions of Pike River and Lewis Creek were sampled with a deep-water electro-fisher during 1999; however, the sampling was judged to be ineffective. Only data from the wadable sections of each stream are reported.

Temperature and conductivity were measured and recorded at each transect sampled for larval lamprey. Conductivity was measured with a Corning handheld conductivity meter. All lamprey collected were placed in a plastic freezer bag and stored at - 5 ^{0}C for two to four months until processed.

Age, sex determination and growth

Larval sea lamprey were measured (total maximum length) to the nearest millimeter and weighed (wet weight) to the nearest 0.01 gram. After measurement, each lamprey was assigned an age based on their statoliths as described by Volk (1986). Statoliths were removed from each animal and stored in a Falcon Becton Dickinson flexible 96 well flat bottom tray. Each well was filled with 2 ml of 100% glycerol. Ages were assigned within four weeks after dissection. After the head of the ammocoete was removed for statolith dissection, the bodies of each transformer and ammocoete >120 mm were stored in 10% formalin for later sex determination. Sex of these sea lamprey was determined by examining a cross-section of the gonads under a dissecting microscope.

One person assigned ages to each lamprey using a dissecting microscope. Age was interpreted by counting the number of opaque bands (annuli). One year was added to the assigned age of metamorphosing ammocoetes because larvae do not deposit an annulus during the year of metamorphosis (Medland and Beamish 1991). Growth curves were constructed for length and weight using assigned ages of larvae for each stream.

Ammocoete density and survival

Ammocoete density was estimated for type I and type II habitat. Efficiency of the electro-fishing gear was estimated for each plot using a logistic regression model as described by Steeves (2000). This model estimates probability of capture for each ammocoete captured in a sampling plot based on the length of the ammocoete, an initial estimate of ammocoete density, and mean depth and conductivity of the sampling plot. If native lamprey were captured in a plot, density for native and sea lamprey were estimated separately, using an initial density estimate of native and sea lamprey combined because the presence of native lamprey in a plot would affect the probability of capture for all lamprey species. The density estimate for native and sea lamprey for a plot was summed to estimate total ammocoete density. Native lamprey densities were reported because evidence suggests interspecific density dependent competition between lamprey species (Murdoch et al. 1991).

Ammocoete density of sea lamprey, native lamprey, and total ammocoete density was log transformed (Ln + 1) to calculate standard error (SE) and 95% confidence intervals (CI). Log transformation was successful in normalizing the density data for a stream; however, the transformations did not equalize variances between streams. A one-way Kruskal-Wallis ANOVA was used to determine whether sea lamprey ammocoete density in type I and type II habitat was different between the three streams for 1999 and 2000. If the Kruskal-Wallis ANOVA indicated significant differences between streams, a Dunn's multiple comparison test was used to determine which streams were significantly different from each other. A *t*-test assuming unequal variances was used to determine if sea lamprey ammocoete density in a stream was different between 1999 and 2000, and for type I and II habitats.

The abundance of each year class of sea lamprey was estimated for Pike River, Morpion Stream and Lewis Creek in the wadable water section during 1999 and 2000. Larval density for each year class was estimated for each plot as the total number of all lamprey species captured; however, the total number of all lamprey species captured for the plot was used as the initial starting density in the logistic regression model. Abundance of a year class was extrapolated from the mean year class density for type I and type II habitats for the total amount of type I and type II habitat present in a stream. Ammocoete survival was estimated from the change in abundance of each age class from 1999 to 2000 in Lewis Creek (Everhart and Youngs 1981). In the Pike River and Morpion Stream, survival was estimated as the change in abundance of each age class for both streams combined because sea lamprey ammocoetes from Morpion Stream could migrate downstream into the Pike River.

Length and weight of transformers during 1999 was compared between Pike River and Morpion Stream combined (due to small sample size) and Lewis Creek using a *t*-test assuming unequal variances. During 2000, length and weight at metamorphosis was compared using a one-way ANOVA for Lewis Creek, Pike River and Morpion Stream. Size at metamorphosis for different ages at metamorphosis during 2000 was compared using a one-way ANOVA. If an overall ANOVA was significant, a Tukey honest significant difference (HSD) multiple comparison test was used to determine which means were significantly different.

A one-way ANOVA was used to compare ammocoete length and condition factor (weight/length^3*10^6; Youson et al. 1993) for age 4 transformers and ammocoetes from Lewis Creek, and age 4 ammocoetes from Pike River and Morpion Stream during 1999. A one-way ANOVA was used to compare ammocoete length and condition factor for age 4 transformers and ammocoetes from Lewis Creek and Pike River, and ammocoetes from Pike River and Morpion

Stream. If the overall ANOVA was significant, a Tukey HSD multiple comparison test was used to determine which means were significantly different. A sufficient sample size of age 5 ammocoetes was not collected for a comparison during 1999 and 2000.

Adult Assessment

Adult spawning population were not obtained during 1999 and 2000 due to high stream discharge and poor capture efficiency of the portable assessment traps (PATs) used to collect adult lamprey as they ascended streams. To obtain an alternative index of adult lamprey abundance, sea lamprey nests were counted in Pike River, Morpion Stream and Lewis Creek. A crew of two to three people walked the wadable section of the Pike River and Lewis Creek, counting each nest. In Morpion Stream, a crew of one or two people counted nests beginning at the confluence of Morpion Stream and Pike River, and ending at the origin of the stream. All counts were made at the end of the spawning season. Counts on Pike River and Lewis Creek were completed in one day and Morpion Stream was completed in a week; each section of stream was surveyed only once, to avoid counting nests more that once.

Results

Sea lamprey habitat

Percent of each type of sea lamprey habitat in the wadable waters section of each stream was similar except for spawning habitat in Lewis Creek (8.2% greater than spawning habitat in the Pike River and 5.5% greater than in the Morpion Stream) and type I habitat in Pike River (12.1% less than Morpion Stream and 9.7% less than Lewis Creek) (Table 1). Lewis Creek has

23,468 m^2 of habitat (Type I and II) available to lamprey ammocoetes in the wadable water section, relative to 69,442 m^2 in the Pike River and 41,200 m^2 in Morpion Stream.

Ammocoete density

Sea lamprey ammocoete density in type I habitat was significantly different among Pike River, Morpion Stream and Lewis Creek in 1999 ($H=15.926$, $P<0.001$) and in 2000 ($H=12.557$, $P<0.001$; Table 2). In both years sea lamprey ammocoete density in type I habitat was significantly higher in Lewis Creek than in Morpion Stream and Pike River ($P<0.05$).

Sea lamprey ammocoete densities in type II habitat was highest in Lewis Creek (1.37 larvae/m^2), intermediate in Morpion Stream (0.39 larvae/m^2) and lowest in Pike River (0.25 larvae/m^2) during 1999, although these differences were not significantly significant ($H=4.218$, $P<0.121$). In 2000, sea lamprey ammocoete density in type II habitat was significantly different among the three streams ($H=8.666$, $P<0.013$). Sea lamprey ammocoete density in type II habitat was significantly higher in Lewis Creek (2.90 larvae/m^2) than Morpion Stream (0.60 larvae/m^2; $P<0.05$). Sea lamprey ammocoete density in the Pike River was higher in type II habitat during 2000 than 1999 ($t = -4.20$, $P<0.003$).

Silver lamprey ammocoete density in Lewis Creek was 0.26 larvae/m^2 in type I habitat and 0.06 larvae/m^2 in type II habitat during 1999. Silver lamprey ammocoete density in Lewis Creek was 0.32 larvae/m^2 in type I habitat and 0.07 larvae/m^2 in type II habitat during 2000. American brook lamprey ammocoete density in Morpion Stream was 0.30 larvae/m^2 in type I habitat during 1999. American brook lamprey were not captured in type II habitat in Morpion Stream during 1999. In Morpion Stream, American brook lamprey ammocoete density was 0.25

larvae/m^2 in type I habitat and 0.26 larvae/m^2 in type II habitat during 2000. No native lamprey were captured in the Pike River.

Age and size at metamorphosis

In 1999, transformers in Lewis Creek were one year younger (100% age 4) than transformers in Pike River (100% age 5) and Morpion Stream (100% age 5). Transformers collected from Lewis Creek during 1999 were 8.8% shorter and weighed 30% less than those transformers from Pike River and Morpion Stream

(t = - 4.49, $P<0.002$; t = - 2.84, $P<0.022$).

In 1999, age 4 transformers from Lewis Creek, and age 4 ammocoetes from Pike River, Morpion Stream and Lewis Creek were not significantly different in mean length (ANOVA; F = 2.693, $P<0.054$; Figure 2). However, condition factor of age 4 transformers from Lewis Creek, and age 4 ammocoetes from Pike River, Morpion Stream and Lewis Creek was significantly different (ANOVA; F = 9.142, $P<0.0001$). Condition factor of Lewis Creek transformers was 24% higher than ammocoetes from Lewis Creek ($P<0.0001$), 24% higher than ammocoetes from Morpion Stream ($P<0.001$), and mean condition factor was 4% higher than ammocoetes from Pike River, although this difference was not significant ($P<0.276$).

In 2000, 26% of the transformers collected in Lewis Creek were age 4 and 74% were age 5, whereas 17% of the transformers collected in Pike River were age 4, 73% age 5 and 10% age 6, and in Morpion Stream 12.5% of the transformers collected were age 4, 75% age 5 and 12.5% age 6. Transformer length was significantly different in Pike River, Morpion Stream, and Lewis Creek during 2000 (ANOVA, F = 9.672, $P<0.0001$). Pike River transformers were 6% longer than Lewis Creek transformers ($P<0.004$), while Morpion Stream transformers were 10% longer than Lewis Creek transformers (P<0.001). Morpion Stream transformers were not significantly longer than Pike River transformers (P<0.216). Length of transformers was not significantly different among ages within streams (P<0.298).

In 2000, age 4 transformers from Lewis Creek and Pike River, and age 4 ammocoetes from Pike River, Morpion Stream and Lewis Creek were significantly different in mean length (ANOVA; F = 10.387, P<0.0001; Figure 3). Mean length of Lewis Creek transformers was 12.6% higher Lewis Creek ammocoetes (P<0.031). There was no significant difference between Lewis Creek transformers and Morpion Stream ammocoetes (P<0.211), Pike River ammocoetes (P<1.000), and Pike River transformers (P>0.999). Mean length of Pike River transformers was 21.5% higher than Lewis Creek ammocoetes (P<0.0001), 21% higher than Morpion Stream ammocoetes (P<0.001) and 15.2% higher than Pike River ammocoetes (P<0.001). Pike River ammocoetes were 7.6% higher than Lewis Creek ammocoetes (P<0.0001).

Condition factor of age 4 transformers from Lewis Creek and Pike River, and age 4 ammocoetes from Pike River, Morpion Stream and Lewis Creek was significantly different during 2000 (ANOVA; F = 7.043, P<0.0001). Condition factor of Lewis Creek transformers was 13% higher than ammocoetes from Lewis Creek (P<0.043). Lewis Creek transformers were not significantly different than ammocoetes from Morpion Stream (P>0.999) and Pike River (P<0.869), and transformers from Pike River (P<1.000). Condition factor of ammocoetes from Lewis Creek was 12.8% less than ammocoetes from Morpion Stream (P<0.002), 5.8% less than ammocoetes from Pike River (P<0.015) and 12.8% less than transformers from Pike River (P<0.037). Condition factor of Pike River transformers was not significantly different than ammocoetes from Morpion Stream (P<0.349) and Pike River (P<0.642).

Growth and survival

Ammocoete growth, represented by length was linear for each stream, whereas growth represented by weight was exponential (Table 4). Growth was not consistently higher for all age classes in any one stream.

During 1999, the average age of ammocoetes in Lewis Creek was 2.0, in Pike River 3.1 and in Morpion Stream 2.1 (Figure 4). During 2000, the average age in Lewis Creek was 2.5, in Pike River 4.0, and Morpion Stream 2.7. Estimated survival in Lewis Creek was 85% from age 1 to 2, 89% from age 2 to 3 and 62% from age 3 to 4. In Lewis Creek, estimated survival from age 4 to 5 was >100%. In Pike River and Morpion Stream, the abundance of each year class was higher during 2000 than 1999 for ages 1 to 4, suggesting high ammocoete survival during the study period. Estimated survival in Pike River and Morpion Stream from 4 to 5 was 74%.

Sex ratio in Lewis Creek

During 1999 in Morpion Stream, 88% of the ammocoetes > 120 mm were female (n=17) and 75% of transformers collected were female (n=4). In Pike River, 81% of the ammocoetes were female (n=30) and 66% of the transformers were female (n=3). In Lewis Creek, 61% of ammocoetes were female (N=31) and 44% of transformers were female (n=18).

During 2000 in Morpion Stream, 55% of the ammocoetes were female (n=31) and all transformers collected were female (n=6). In Pike River, 72% of the ammocoetes were female (n=74) and 87% of the transformers were female (n=30). In Lewis Creek, 44% of ammocoetes were female (n=36) and 52% of transformers were female (N=23).

Nest Counts

During 1999, 347 nests were counted in the Pike River, 221 in Morpion Stream and 930 in Lewis Creek. During 2000, 502 nests were counted in the Pike River, 253 in Morpion Stream and 1,562 in Lewis Creek.

Discussion

Quantitative information on larval sea lamprey survival, growth, and age and size at metamorphosis, as related to population density, is essential for the long-term success of the sea lamprey control program in the Great Lakes and Lake Champlain. Life history characteristics, lengths, weights and density have been documented for larval populations (Applegate1950; Gersmehl and Baren 1985); however, these characteristics have not been accurately quantified in response to changes in population density as related to sea lamprey control. If sea lamprey populations respond to changes in density by altering life history characteristics to maintain their population level, certain control strategies that reduce ammocoete density may have lower effectiveness than anticipated. In this study, we quantified population dynamics of sea lamprey ammocoete populations in the untreated Pike River and Morpion Stream and compared those dynamics to a similar stream that has been treated twice with lampricide.

Sea lamprey ammocoetes, in the treated Lewis Creek, entered metamorphosis at a smaller length and earlier age, four years after treatment, than in the untreated Pike River and Morpion Stream. Ammocoetes undergoing early metamorphosis in Lewis Creek were the first year class to re-establish after the last lampricide treatment in 1994. Sampling for this study began during 1999 when ammocoetes of the first re-establishing year class were age 4+. Due to the time frame of this study, we were unable to determine if the 1995 year class began metamorphosis earlier than age 4. Ammocoetes have been documented to enter metamorphosis as early as 2 and 3 years of age (Purvis 1979; Morkert et al. 1998). In 2000, approximately 75% of transformers in Lewis Creek, Pike River and Morpion Stream were age 5. Only in Pike River and Morpion Stream were age 6 transformers collected. The different assigned ages of transformers in Pike River, Morpion Stream, and Lewis Creek in 2000 is consistent with previous studies documenting variation in age at metamorphosis (Purvis 1979, 1980)

Early metamorphosis in Lewis Creek during 1999 and in Lewis Creek and Pike River during 2000 was associated with higher ammocoete weight compared to ammocoetes of the same age class in those streams that did not enter metamorphosis. Energy required to complete the morphological and physiological changes of metamorphosis comes from an accumulated lipid supply (Lowe et al. 1973; Youson 1980). Typically, the minimum length and weight at which sea lamprey begin metamorphosis is 120 mm and 3.0 g with a condition factor of 1.5 (condition factor, CF = weight/length^3 x 10^5; Youson et al. 1993; Holmes and Youson 1994).

In streams in Lake Superior and Lake Michigan, growth (measured in length) of the first age class to re-establish in streams after lampricide treatment was higher compared to succeeding year classes (Purvis 1979). Jones (unpublished data, Michigan State University) determined that the first year class to re-establish after treatment experienced higher growth compared to succeeding year classes in 12 of 34 Great Lakes streams. Re-analysis of data from (Purvis 1979) determined that high growth of the first re-establishing year class was not consistent among streams (M. Jones, unpublished data, Michigan State University). In the present study, length-at-age was not significantly higher for transformers that were the first re-establishing year class after treatment in Lewis Creek compared to the same age class that did not enter metamorphosis in Lewis Creek, Pike River and Morpion Stream. However, early age transformers from this year class had a higher condition factor.

Low ammocoete density did not appear to be the factor that regulated metamorphosis in this study, because ammocoete density in the treated stream with early metamorphosis was approximately three times higher than in the untreated streams with older transformers. The presence of native lamprey in Lewis Creek and Morpion Stream may influence density dependent effects in these streams based on intraspecific competition between lamprey species (Murdoch et al. 1991). When all lamprey species are considered as part of ammocoete density in these streams, ammocoete density in Lewis Creek is still substantially greater than the other streams. High ammocoete densities in Lewis Creek may be a function of: (1) stream productivity, (2) number of returning adult spawners per unit of ammocoete habitat, or (3) re-established ammocoete populations exceeding the carrying capacity. Overall stream productivity appears to be higher in Pike River and Morpion Stream than Lewis Creek based on observations of primary productivity and measurements of conductivity. We did not quantify adult abundance, but believe adult spawning populations are higher in Lewis Creek based on nest counts. Higher ammocoete densities may have occurred in Lewis Creek because the population exceeded its carrying capacity. In several streams in the Great Lakes, ammocoete densities were higher after treatment than before treatment (Torblaa and Westman 1980). During the eight-year experimental sea lamprey control program in Lake Champlain, seven stream reaches were treated twice with lampricides at a four-year interval (Lake Champlain Fisheries Technical Committee 1999). During the second treatment, four of the seven streams had more dead sea lamprey ammocoetes.

High growth of the first re-established year class following treatment suggests that this year class had greater access to resources, in the absence of competition from older year classes, than did subsequent year classes. In our study, the first year class to re-establish after treatment was not numerically dominant over succeeding year classes, suggesting that there was either low spawning density after re-establishment, migration out of the study area possibly due to earlier metamorphosis, or low subsequent survival. Sea lamprey that re-established a population in the year following treatment in Lake Ontario was the dominant year class throughout the treatment interval and had constant survival, whereas the following year classes were lower in abundance and experienced higher mortality (Weise and Pajos 1998).

Survival estimates in the three streams in this study suggests that mortality was low for ammocoetes. In Lewis Creek, survival was higher for age 1 to 3 than age 4 ammocoetes. As ammocoetes become older and larger, downstream movement increases (Hardisty and Potter 1971). Large size and increased movement may increase chances of mortality due to predation. Drossier (unpublished data, Michigan State University) has determined that as ammocoetes increase in size, high density conditions will stimulate movement into new habitat. In the Pike River and Morpion Stream, mortality could not be estimated because each year class, except for the oldest year class, increased in abundance from one year to the next. This suggests that ammocoete survival is high. It appears that a high percentage of ammocoetes in Morpion Stream migrate downstream into the Pike River at age 4.

Limiting factors for sea lamprey ammocoetes growth and survival may include habitat and food. Production of algae in a stream has been compared to the overall consumption by a sea lamprey population; data support the hypothesis that algae are produced in excess and that food is not a limiting factor for ammocoetes (Moore and Beamish 1973). If food is not the factor directly limiting the ammocoete population, habitat/space may be limiting in streams where there is abundant spawning habitat and the number of spawners produce more larvae than can occupy the ammocoete habitat. Yap (1995) determined gut content at high and low density of ammocoetes was similar, although assimilation of food resources by ammocoetes decreased with increasing density. It is believed that reduced assimilation is due to disturbance on ammocoetes as density increases (S. Bowen, pers. com., Michigan Technological University, 2000).

Great Lakes adult sea lamprey populations have shifted from a nearly equal sex ratio or a greater proportion of males to a preponderance of females after sea lamprey control (Heinrich et al. 1980). Treated streams in the Great Lakes also have a higher proportion of female ammocoetes (Purvis 1979). In this study, the treated Lewis Creek had a lower proportion of females compared to the untreated Pike River and Morpion Stream. Our results are similar to studies of the least brook lamprey (*Lampetra aepytera*) and the southern brook lamprey (*Ichthyomyzon gagei*) where the proportion of females in streams was inversely related to relative ammocoete density (Beamish 1993; Docker and Beamish 1994). Before sea lamprey control in Lake Champlain, streams with high relative ammocoete density had small transformers and were45 to 50% females, compared to streams with low relative density that had large transformers and were 70 to 80% females (Gersmehl and Baren 1985). Low density conditions may stimulate ammocoetes to become female because of greater assimilation of resources; typically, female gonads are more costly than male gonads. Sex specific mortality as an explanation for sex ratio differences in ammocoetes was not detected in the least brook lamprey and no evidence of sex specific mortality occurred during a three-year study of sea lamprey ammocoetes maintained at different densities (Docker 1992; Docker and Beamish 1994). Surprisingly, there was no significant difference between the size of male and females transformers at high or low density before treatment, although female transformers at high density were slightly larger than males. In past studies, female transformers were larger than male transformers (Applegate and Thomas 1965). Currently, no information exists on age structure of male and female sea lamprey transformers at high and low densities.

Transformers collected four years after treatment had a higher number of males than females. If Lewis Creek was overpopulated and had scarce resources, conditions may have promoted a tendency towards a higher proportion of males due to the lower cost associated with male gonads. An alternative explanation is that male ammocoetes transformed at a younger age than females or had higher mortality. This seems probable because five years after treatment, there was an approximately equal sex ratio similar to the sex ratio before treatment.

Given the differences in density among our study streams, it is curious that Pike River and Morpion Stream ammocoetes did not enter metamorphosis at an earlier age than Lewis Creek. Purvis (1979) found that by increasing ammocoete density in a Lake Superior stream, metamorphosis was stimulated. Crowding conditions may stimulate early metamorphosis because of reduced growth and survival. However, in this study younger transformers had a higher condition factor, which was initiated during 1998 or possibly earlier when larval density in Lewis Creek was presumably lower.

Our results suggest that sea lamprey ammocoete growth may increase after treatment of stream tributaries, which may reduce the time required to enter metamorphosis. Sea lamprey control managers must be aware that if application of lampricides creates conditions for early metamorphosis and selects for those traits, the efficacy of a long-term sea lamprey control program would be reduced because of higher costs associated with more frequent application of lampricides. It is critical that treatment intervals are adaptive to changes in growth and age at metamorphosis so that transformers do not leave Lake Champlain and Great Lakes tributaries. The impact on non-target species could also be increased due to increased frequency of exposure to lampricides. More quantitative information is required from the untreated and treated sea lamprey populations in Lake Champlain streams that have different environmental variables, ammocoete densities and adult spawning abundance in order to determine if the increased growth as observed was a local response to Lewis Creek. Additionally, if the Pike River and Morpion Stream are treated with lampricides, this study needs to be repeated after treatment to determine the response of the re-established sea lamprey population in these streams.

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Table 1. Area (m^2) and percentage area of sea lamprey habitat types from the wadable water sections of Pike River, Morpion Stream and Lewis Creek.

	Habitat Type			
Tributary	Type I	Type II	Type III	Spawning
Pike River				
Area (m^2)	16,972	52,470	258,007	5,828
% of total area	5.1	15.7	77.4	1.7
Morpion Stream				
Area (m^2)	21,538	19,662	78,005	5,503
% of total area	17.2	15.8	62.6	4.4
Lewis Creek				
Area (m^2)	10,772	12,696	41,966	7,222
% of total area	14.8	17.5	57.8	9.9

Table 2. Mean sea lamprey, and sea lamprey and native lamprey ammocoete density for type I and II habitat (± SE, number in parentheses represent sample size), with population estimates for sea lamprey, and native lamprey and sea lamprey density for type I and II habitat for Lewis Creek, Pike River and Morpion Stream during 1999 and 2000. NP indicates absence of native lamprey.

Density (larvae/m^2)	Lewis Creek[a]	Pike River	Morpion Stream[b]
1999			
Sea Lamprey			
Type I	3.65±0.22 (32)	0.76± 0.10 (32)	1.03±0.15 (30)
Type II	1.37±0.22 (14)	0.25±0.06 (12)	0.39± 0.17 (7)
Population Estimate	56,711	26,017	29,852
Native/Sea Lamprey			
Type I	3.91±0.22	NP	1.39±0.17
Type II	1.43±0.23		0.39±0.17
Population Estimate	60,274		37,606
2000			
Sea Lamprey			
Type I	4.74±0.22 (16)	1.14±0.10 (14)	1.28±0.18 (19)
Type II	2.90±0.24 (19)	0.96±0.10 (19)	0.60±0.20 (8)
Population Estimate	87,878	69,920	39,366
Native/Sea Lamprey			
Type I	5.06±0.23	NP	1.53±0.18
Type II	2.97±0.24		0.86±0.20
Population Estimate	92,213		49,865

[a] Native lamprey included in density estimate are silver lamprey

[b] Native lamprey included during 1999 are American brook lamprey and in 2000 are American brook lamprey and silver lamprey.

Table 3. Mean total length (mm) and wet weight (g) (± SE), and sample sizes (n) for transformers by age for Lewis Creek, Pike River and Morpion Stream during 1999 and 2000.

	Age at metamorphosis		
	Age 4	Age 5	Age 6
1999			
Lewis Creek			
Length	131±2.01		
Weight	4.19±0.16		
n	18	0	0
Pike River			
Length		140±1.76	
Weight		5.58±0.68	
n	0	3	0
Morpion Stream			
Length		145±2.18	
Weight		5.31±0.57	
n	0	4	0
2000			
Lewis Creek			
Length	134±3.98	138±1.83	
Weight	4.56±0.36	4.86±0.16	
n	6	17	0
Pike River			
Length	145±4.06	144±1.86	145±6.43
Weight	5.92±0.45	5.37±0.17	5.46±0.42
n	5	22	3
Morpion Stream			
Length	145	150±3.83	157
Weight	5.18	6.48±0.45	7.43
n	1	6	1

Table 4. Mean total length (mm) and wet weight (g) (± SE), and sample size (n) for ammocoetes by age for Lewis Creek, Pike River and Morpion Stream during 1999 and 2000.

	Age class				
	1	2	3	4	5
1999					
Lewis Creek					
Length	59±0.57	79±0.66	104±1.09	130±1.99	
Weight	0.38±0.01	0.89±0.02	1.98±0.07	3.85±0.18	
n	236	396	203	27	
Pike River					
Length		88±3.55	108±1.33	121±2.39	
Weight		1.50±0.17	2.26±0.08	3.19±0.2	
n		12	96	27	
Morpion Stream					
Length	53±1.25	86±2.31	103±2.0	132±5.91	
Weight	0.26±0.02	1.06±0.08	1.85±0.11	3.78±0.52	
n	34	42	51	11	
2000					
Lewis Creek					
Length	52±0.52	75±1.03	93±0.83	117±1.66	
Weight	0.29±0.01	0.80±0.05	1.44±0.04	2.72±0.11	
n	148	137	230	71	
Pike River					
Length	44	72±2.50	112±4.02	126±1.27	135±17
Weight	0.18	0.77±0.11	3.52±0.84	3.59±0.10	4.37±1.22
n	1	2	23	95	2
Morpion Stream					
Length	61±3.49	81±1.94	100±3.58	119±4.55	105
Weight	0.59±0.10	1.23±0.08	2.22±0.31	3.17±0.29	2.36
n	13	43	41	13	1

Figure 1. Lewis Creek, Vermont and Pike River and Morpion Stream Quebec, Canada, Lake Champlain.

Figure 2. Length and condition factor (± SE) for age 4 ammocoetes from Pike River, Morpion Stream and Lewis Creek and age 4 transformers from Lewis Creek during 1999.

Figure 3. Length and condition factor (± SE) for age 4 ammocoetes from Pike River, Morpion Stream and Lewis Creek and age 4 transformers from Lewis Creek and Pike River during 2000.

Figure 4. Estimated abundance (± SE) of each age class in Lewis Creek, and Pike River and Morpion Stream (combined) during 1999 and 2000.

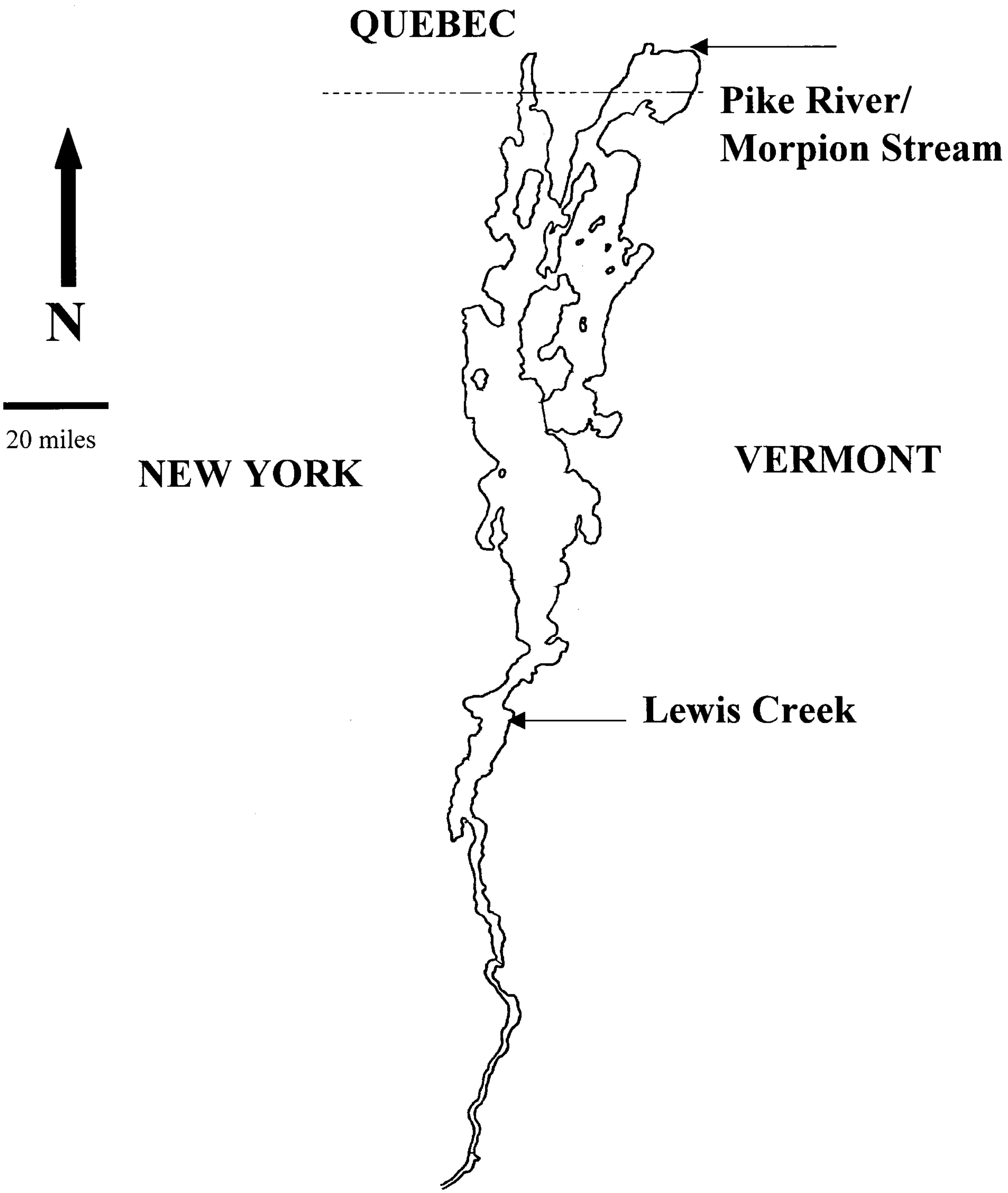

QUEBEC
Pike River/
Morpion Stream
N
20 miles
NEW YORK
VERMONT
Lewis Creek

Figure 1.

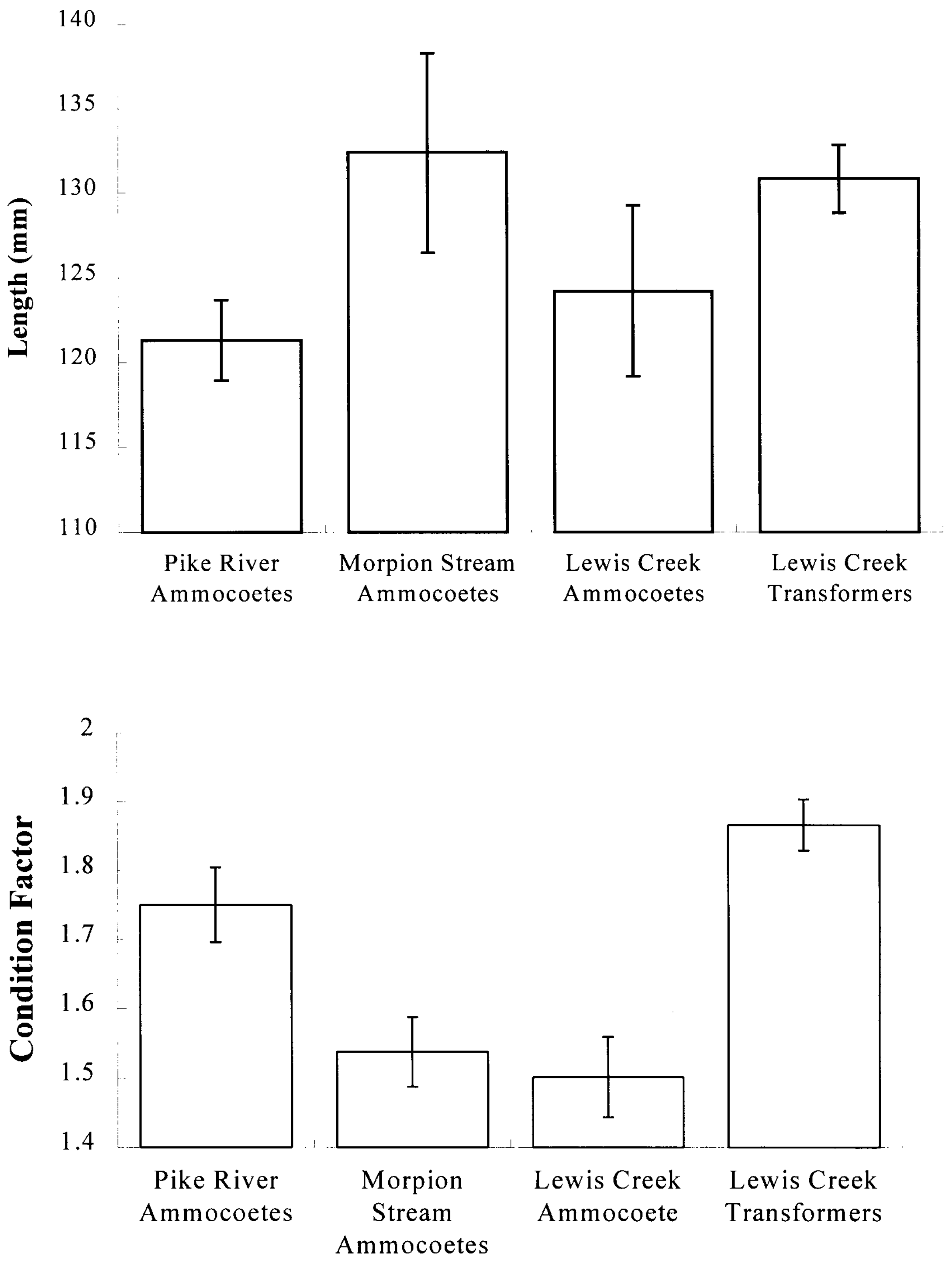
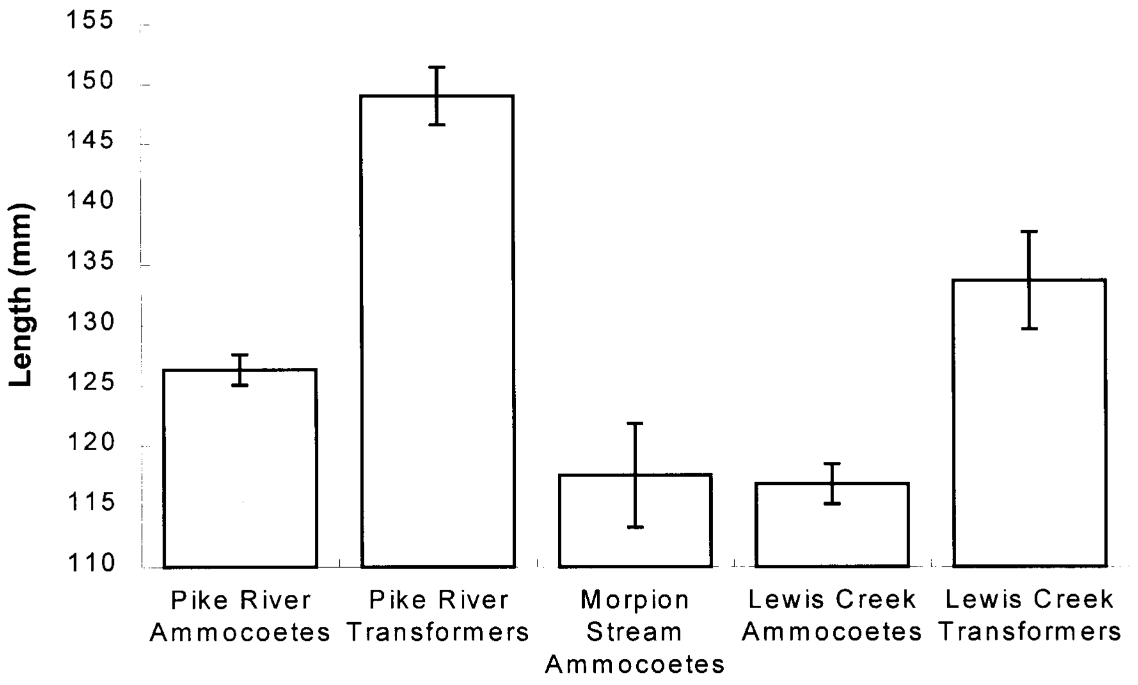
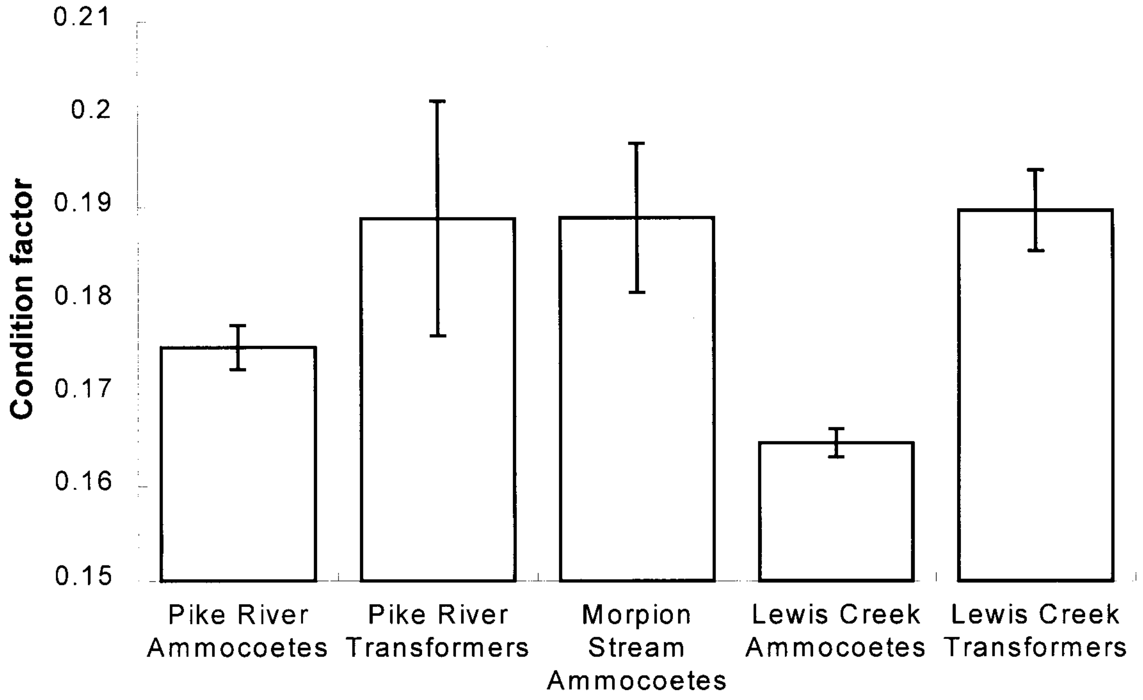

Length (mm)
140
135
130
125
120
115
110
Pike River Ammocoetes
Morpion Stream Ammocoetes
Lewis Creek Ammocoetes
Lewis Creek Transformers
Condition Factor
2
1.9
1.8
1.7
1.6
1.5
1.4
Pike River Ammocoetes
Morpion Stream Ammocoetes
Lewis Creek Ammocoete
Lewis Creek Transformers

Figure 2.



155
150
145
140
135
130
125
120
115
110
Length (mm)
Pike River Ammocoetes
Pike River Transformers
Morpion Stream Ammocoetes
Lewis Creek Ammocoetes
Lewis Creek Transformers



0.21
0.2
0.19
0.18
0.17
0.16
0.15
Condition factor
Pike River Ammocoetes
Pike River Transformers
Morpion Stream Ammocoetes
Lewis Creek Ammocoetes
Lewis Creek Transformers

Figure 3.

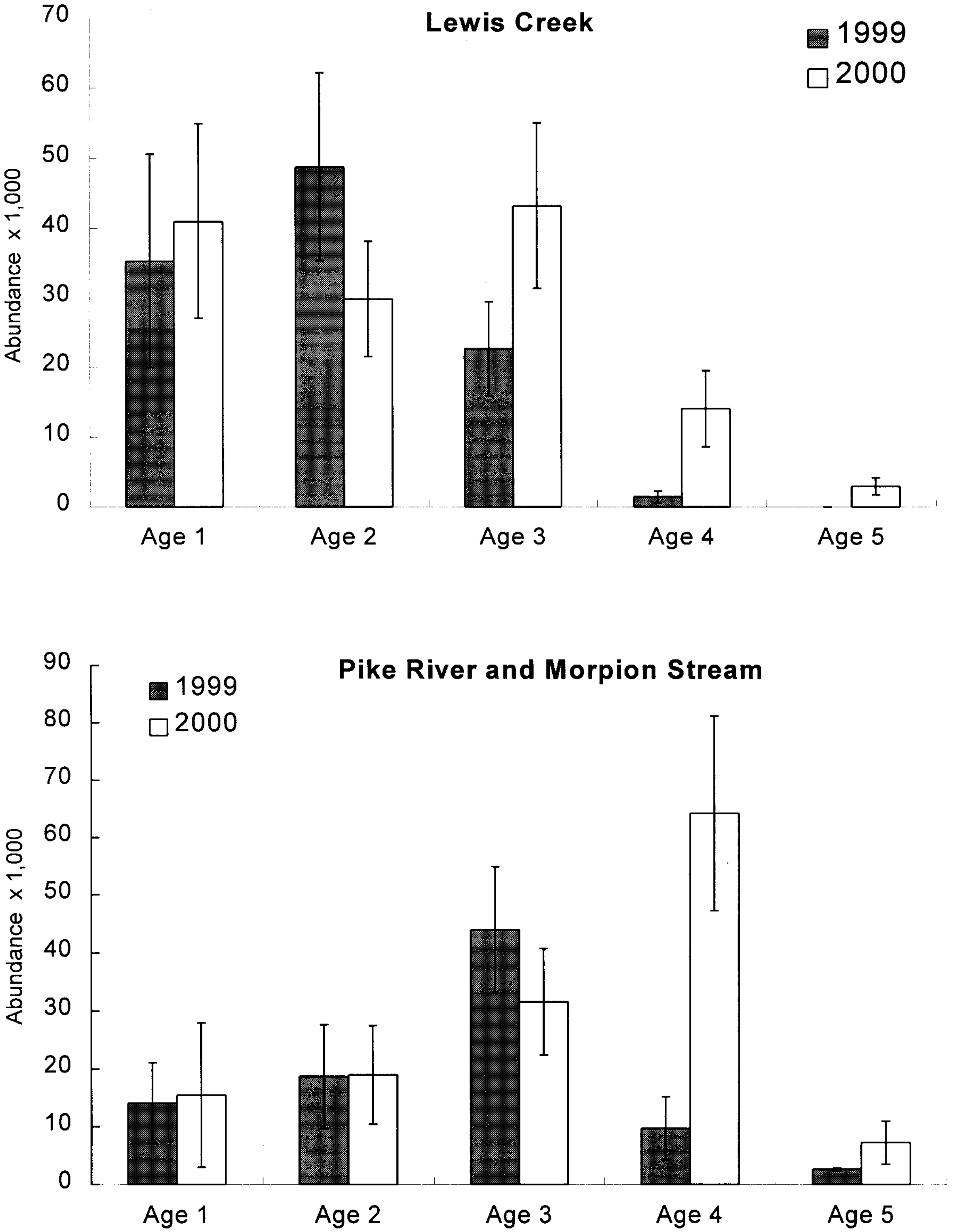

Lewis Creek
1999
2000
Abundance x 1,000
70
60
50
40
30
20
10
0
Age 1
Age 2
Age 3
Age 4
Age 5
Pike River and Morpion Stream
1999
2000
Abundance x 1,000
90
80
70
60
50
40
30
20
10
0
Age 1
Age 2
Age 3
Age 4
Age 5

Figure 4.

APPENDIX A

Non-Wadable Water Sections of Pike River and Lewis Creek

Deep-water section

In the non-wadable waters section, 16 transects for Pike River and 40 transects for Lewis Creek were allocated evenly (287.5 m apart for Pike River and 15 m for Lewis Creek) and perpendicular to flow as locations for habitat classification and estimation of larval density (Fodale et al. 1998). The transects began 143.8 m (1/2 the distance spaced between two transects) below the beginning of the non-wadable water section on the Pike River. In Lewis Creek transects began 7.5 m below the beginning of the semi-wadable waters section. Transects were located with a hand-held GPS receiver in the deep water electro-fishing boat. At each transect, an Echman dredge was used to obtain substrate at five points equally spaced across the transect.

At each transect in the non-wadable water section larval lamprey were collected using a standard non-wadable water electro-fisher at standard settings (Bergstedt and Genovese 1994; Fodale et al. 1998). GPS coordinates, temperature and conductivity were recorded at each plot. All lamprey captured were stored using the same techniques as in the wadable waters section.

Semi-wadable waters section

In Lewis Creek a stream reach between the wadable and non-wadable waters section was too deep to classify habitat using the wadable waters protocol and would not provide passage for the deep water electro-fishing boat because it was obstructed by debris. In this semi-wadable reach 10 transects were allocated using the wadable waters protocol, except if a transect location was not wadable the transect was moved to the closest wadable points. At each transect lamprey were sampled using the wadable waters section protocol.

Table 1. Area (m^2) and percentage area represented by each sea lamprey habitat type for the non-wadable water section of Pike River, and the non-wadable waters section and semi-wadable waters section of Lewis Creek.

	Habitat Type		
Tributary	Type I	Type II	Type III
Pike River			
Area (m^2)	251,563	28,750	7,188
% of total area	87.5	10	2.5
Lewis Creek – non-wadable			
Area (m^2)	69,825	3,675	0
% of total area	95	5	0
Lewis Creek – semi-wadable			
Area (m^2)	12,224	5,199	749
% of total area	67.3	28.6	4.1

Table 2. Mean sea lamprey ammocoete density and mean total ammocoete abundance for the non-wadable water section of Pike River, and the non-wadable waters section and semi-wadable waters section for Lewis Creek. Sample sizes were too small for calculation of confidence intervals.

Tributary/habitat type	Mean density (larvae/m^2)	Total area (m^2)	Total abundance
Pike River			
Type I	0.005	251,563	1,258
Lewis Creek – non-wadable			
Type I	0.01	69,825	698
Lewis Creek – semi-wadable			
Type I	2.08	12,224	25,426
Type II	0.21	5,199	1,092