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EARLY LIFE HISTORY OF SEA LAMPREY LARVAE: EMERGENCE, DISPERSAL, AND EFFECTS OF DENSITY ON MOVEMENTS.

By

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ABSTRACT

EARLY LIFE HISTORY OF SEA LAMPREY LARVAE:
EMERGENCE, DISPERSAL, AND EFFECTS OF DENSITY ON MOVEMENTS.

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Since the invasion of sea lamprey into the Great Lakes, there has been a major effort to control their populations. Managers want to decrease their reliance on chemical control methods and increase their reliance on alternative control methods, such as: increased trapping, continued use of barriers, and the sterile male release program. To determine the potential effectiveness of these alternative control methods more information is needed on the life cycle of sea lamprey, especially during the first year of life. I investigated emergence of sea lamprey from nests, their dispersal away from nests during their first growing season using field and microsatellite methods, and the relation between density and movements after settlement in age-0 sea lamprey. Emergence occurred over a short period of time, between 8 and 14 days and during the darkest hours of the night, between 1200 and 0300. The numbers of prolarvae produced from nests was quite variable and ranged from 87 to 20,713. Despite the potential for large numbers of prolarvae emerging over a short period of time, densities of age-0 sea lamprey were low, on average between 4 and 10 per m^2. The low densities of age-0 sea lamprey seen in the field may be in part due to their ability to disperse widely, at least 874 m. Density independent dispersal or movements were seen during warmer temperatures, possibly allowing individuals to establish low densities such that density-dependent dispersal seen during cooler temperatures is not very prevalent.

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General Introduction:

Since the invasion of sea lamprey into the Great Lakes, there has been a major effort to control their populations. The main control method used is a chemical called 3-trifluoromethyl-4-nitrophenol (TFM), which is used to treat streams to kill larvae (Smith, 1971, Meyer and Schnick, 1983). This method is very effective and has been used since the early 1960's (Torblaa and Westman, 1980). However due to increasing costs of the chemical and public concerns about using chemicals in streams, the Great Lakes Fishery Commission wants to reduce the reliance on chemical controls (Strategic Vision of the Great Lakes Fishery Commission, 1992 and 2001). To do this, managers will need to rely more heavily on alternative control methods such as: increased trapping, continued use of barriers, and the sterile male release program.

These alternative control methods may not be as effective as chemical control however. Chemical controls target the larval stage of sea lamprey, whereas the alternative control methods target reproduction. This difference in targeted life stages complicates effective control. Chemical controls reduce the population just before the parasitic life stage, while with using alternative control methods there are many life stages between when the population is reduced and when they become parasites, allowing time for compensatory

mechanisms to play out. Compensatory mechanisms are density-dependent demographic responses that effectively increase population growth at low densities and decrease population growth at high densities. There is evidence to suggest that compensatory mechanisms exist in sea lamprey populations (Smith, 1971; Purvis, 1979; Heinrich et al., 1980; Morman, 1987; Murdoch et al., 1992), yet the evidence is far from conclusive (Jones et al., in review). To effectively control sea lamprey populations using alternative control methods, managers need to determine at what life stages compensatory mechanisms exist and their magnitude. If sea lamprey populations are not able or only slightly able to compensate, the effectiveness of the alternative control methods may not be compromised. But if compensatory mechanisms are strong, control efforts using alternative methods may not decrease the population sufficiently to justify the decision. To determine the potential effectiveness of these alternative control methods more information is needed on the demographics of sea lamprey particularly during reproduction and larval life stages.

The life cycle of the sea lamprey is anadromous. Adult sea lamprey migrate into streams in April and May and begin spawning when mean water temperatures reach around 11 °C (Applegate, 1950). Sea lamprey spawn in cobble and gravel areas, generally riffles, where water velocities are between 0.5 and 1.5 m/s (Manion and Hanson, 1980). Males start the construction of nests, which consist of a depression and a perpendicular ridge of cobble downstream; nest construction can take 1 to 3 days (Manion and Hanson, 1980). Once a female joins a male, spawning commences. Eggs are released in the depression and carried by the water current into the interstices of the cobble ridge (Applegate, 1950).

The adults kick up sand with their tails to help cement eggs into the ridge. Eggs hatch after approximately 10 to 13 days when held at a constant water temperature of 18 °C (Piavis, 1961); once hatched they are considered prolarvae. Prolarvae are able to burrow 17 to 33 days after fertilization. The burrowing stage is termed developmental stage 17 (Piavis, 1961), and is the point at which they are assumed to emerge from nests. Prolarvae become larvae after burrowing and when the yolk is passed through the gut and the digestive system is functional; this occurs 33 to 40 days after fertilization (Piavis, 1961).

The larval stage of the sea lamprey can last from 3 to 12 years depending on the productivity of the stream. Larvae live in depositional areas of streams and filter-feed on detritus (Sutton and Bowen, 1994). When larvae reach a length of around 120 mm they begin to metamorphose into parasites. Following metamorphosis, they migrate downstream into the lakes or ocean, between September and May, and begin feeding on fish, such as salmon and trout. They grow quickly and spend only about 12 to 20 months feeding as parasites, after which time they become adults and migrate back into streams to complete the life cycle.

The early life stages of fish are generally thought to heavily influence recruitment (Cushing, 1996; Wootton, 1990). Hjort (1914) proposed that the greatest mortality occurs during the early life of fish and coined this the critical period. Recent authors suggest that this critical period occurs during transitions (Benoît and Pepin, 1999), such as hatching, emergence, and the shift from endogenous (yolk) to exogenous (active) feeding (Lasker, 1981; Diana, 1995). Sea lamprey fecundity is estimated to be high,

producing between 55,000 and 69,000 eggs per female (Manion and Hanson, 1980). However, typical age-1 and older larval densities are reported to be around 2 per m^2 (Jones et al., in review), suggesting that mortality is high during the first year of life.

Little is known of the first year of life of the sea lamprey. Sea lamprey at this stage are small (4-20 mm in length, 1-2 mm in width) and hence difficult to sample. The embryological development has been fully described, as have some aspects of the emergence stage. Because of the lack of information on age-0 sea lamprey and the apparent importance of the first year of life in determining recruitment in fish, I chose to explore three aspects of age-0 sea lamprey ecology. I chose to expand on the description of emergence that has been reported by Applegate (1950) and Manion and McLain (1971), by following emergence from 10 nests in each of two streams. I also investigated age-0 sea lamprey dispersal or distributions during the first growing season, which has not been done in the past. I also examined movements of larvae after settlement in relation to density and temperature / season.

Chapter 1:
Sea lamprey emergence from nests.

Introduction

Recent authors suggested that the greatest mortality in fishes occurs during transitions (Benoît and Pepin, 1999), such as hatching, emergence, and the shift from endogenous (yolk) to exogenous (active) feeding (Lasker, 1981; Diana, 1995). Many freshwater fish hatch within nests but do not emerge for some time after, often just before the switch from endogenous to exogenous feeding. The timing and pattern of emergence will therefore determine the conditions that larvae experience before and during their first feeding. The timing of emergence also determines the length of the first growing season (Elliott and Hurley, 1998) and thus the size that age-0 fish reach before entering their first winter. Hence, emergence can be a key stage in a fish species' life history and knowledge of this stage may provide insight into processes affecting early larval survival.

Although sea lamprey emergence from nests has been previously investigated, a full description of this stage is lacking. Applegate (1950) followed only 3 nests from fertilization to emergence, and reported the number of larvae emerging each day. Emergence occurred 19 to 20 days after fertilization. Manion and McLain (1971) monitored 48 nests but only reported the average (22 days) and the maximum (34 days) number of days it took for prolarvae to emerge. These authors did not describe the

duration (Elliott, 1984; Snucins et al., 1992) or the diel pattern (Field-Dodgson, 1988; Kempinger, 1988) of sea lamprey emergence. If emergence is spread over a relatively long period of time, then that species may be bet hedging (Hopper, 1999); the risk of all larvae emerging during a period when environmental conditions are poor is lessened. On the other hand, if emergence happens over a relatively short period of time, the emerging larvae may experience reduced mortality due to swamping of predators. Because lamprey larvae are more or less passively transported to burrowing habitats (Applegate, 1950), this latter strategy may also create localized high densities, resulting in intense intra-specific competition, dependent upon the numbers emerging.

One common method used for reporting the duration of developmental stages is degree days (Casselman, 1995; Kamler, 1992; Elliott, 1984; Kempinger, 1988; Ross and Merritt, 1978), but this has yet to be used for sea lamprey. This index combines both the numbers of days development takes to reach different stages and the fluctuating temperatures to which eggs and prolarvae are exposed during this period. This index can be easily compared among locations and among species. In addition, if emergence can be quantified using degree days, managers could use this information to more effectively treat streams because eggs are not vulnerable to TFM (cite).

Applegate (1950) is the only author that reports the lengths of sea lamprey emerging from nests. He provided a histogram of lengths for one nest (222 individuals, average length = 8.54 mm). Lengths of larvae at emergence are commonly reported (Field-Dodgson, 1988; Randall, 1982), and needs to be further explored in sea lamprey. Looking across

nests and streams may provide insight into the ecology of larvae at this life stage. Larger larvae may enjoy a competitive advantage over smaller larvae. This advantage may be caused by large eggs via larger females (Kamler, 1992).

The objective of this component of my study was to expand on the previous descriptions of sea lamprey emergence. Specifically I set out to: (1) describe emergence relative to spawning activity; (2) examine the diel pattern of emergence; (3) compare the numbers and size (lengths) of prolarvae produced in individual nests and between streams; (4) quantify the duration of the emergence period; and (5) determine if emergence timing can be predicted using degree days.

To address these objectives, I conducted a field study, a laboratory experiment, and a secondary analysis of published data. Ten nests, in each of two streams, were monitored from nest construction to prolarval emergence. Eggs were raised in the laboratory until prolarvae burrowed into a sand substrate (similar to Piavis, 1960), to test whether prolarvae burrow at the same time as prolarvae emerge from nests. To supplement these two components, data from Applegate (1950) and Piavis (1961) was reanalyzed to calculate degree days.

Methods

Study Streams

A tributary to Lake Huron, the Trout River is located just north of Rogers City in Presque Isle County, Michigan. It has a catchment size of 36.8 mi^2. There is a sea lamprey barrier on the river; my study nests were located below the barrier within a 160 m reach

(Figure 1). The instream habitat is suitable for both sea lamprey spawning (cobble, gravel) and for larval rearing (depositional, fine sediments). This stream is regularly treated with TFM, and was treated while eggs were incubating in nests but before emergence began.

The Black Mallard River is also a tributary to Lake Huron and is about 20 mi north of Rogers City. The catchment size is 27.4 mi^2. The Black Mallard River is also a known sea lamprey producer and is regularly treated with TFM. There is less spawning and larval habitat in the Black Mallard River than in the Trout River and water levels are often quite low by mid-summer. Applegate (1950) also used this river as a study stream, at that time it was named Carp Creek. Study nests were within a 175 m section of the river (Figure 2).

Field sampling

A continuous temperature monitor (HOBO, Onset Computer Corp., Pocasset, MA) was installed in each stream to record daily water temperatures (every 12 min) throughout the spawning and emergence period. The daily water levels during the emergence period were recorded using a temporary staff gauge in each stream.

Study streams were walked daily, starting on May 20, 2000 to locate sea lamprey nests and monitor spawning activity. Monitoring began before any nesting activity had taken place in the study reach. When a nest was found it was marked with a flag and the following data were recorded: 1) the date it was first located, 2) dates spawners were

present, 3) the sex of adults was recorded, and 4) it was noted if the nest looked like it had been re-worked. When a nest is first built, it is easy to locate because the rocks creating the nest have been turned over and are clean (no periphyton) and hence brighter than the surrounding rocks. After a couple of days, the rocks in the nest become covered in periphyton again. Therefore, if a nest is re-worked a few days after first being built, by either the same adult or a different adult, it is noticeable. A sample of eggs was collected a few days after a nest was found to confirm successful deposition and the stage of embryological development (Piavis, 1961). Eggs were staged following Piavis' (1961) description of sea lamprey development and an expected hatch and emergence date was calculated. Drift sampling began immediately after the expected hatch date but well before the expected emergence date.

Prolarvae were collected below nests using a rectangular drift net, 45.5 x 15 cm, with a mesh size of 350 μm. The drift nets were set less than 2 m downstream from 10 nests in each stream, approximately every other night from June 8 to July 13, 2000 in the Black Mallard River, and June 19 to July 14, 2000 in the Trout River. Young-of-the-year sea lamprey ammocoetes drift mainly at night (Johnston, 1997; Bennett and Ross, 1995). To confirm emergence followed this diel pattern, I conducted a preliminary study. Drift nets were set below two nests in Weldon Creek, Mason County, Michigan, from July 5 to July 24, 1998. Of the 105 emergent prolarvae collected, only one was collected during the daylight hours (0900 to 1600 h). Therefore, in both study streams, nets were set for three 3 h periods (9 h total) each night, beginning between 20:30-21:30 (before dusk) and

ending between 05:30-07:30 hrs (after dawn). Prolarvae caught in each net were either counted on site or preserved in 70% ethanol for later enumeration.

Prolarval lengths were measured using a dissecting scope attached to a monitor to digitize prolarvae. The program OPTIMAS version 4.10 (BioScan, Inc., 1987-1993) was used to calculate lengths. Approximately 1000 prolarvae were measured from each stream, stratified by nest.

Laboratory experiments

Prolarvae were raised in the laboratory from sea lamprey spawned June 10 – 13 and June 16-17, 2000. Eggs and milt were removed from ripe sea lamprey and spawned into a beaker with approximately 1 liter of filtered Lake Huron water. After 30 minutes, beaker water was changed several times and eggs were introduced into a 10 liter glass battery jar; each spawning was placed in a different battery jar. Eggs were arranged in a single layer. Battery jars were placed in an insulated water bath, and held at a constant temperature of 18 °C (optimal temperature for development according to Piavis, 1961). Four days after fertilization, dead eggs were removed. Water was changed with filtered water every other day.

After eggs hatched, prolarvae were transferred to 100 ml beakers in the water bath. Each beaker was filled with approximately 20 ml of sand and 80 ml of water. For each spawning date, 10 prolarvae were introduced into each of three replicate beakers. Each day the water was changed and the number of prolarvae remaining on the surface of the sand was counted; those missing were assumed to have burrowed.

Secondary analysis

I reanalyzed data from Applegate (1950) and Piavis (1961) by converting daily water temperatures into cumulative degree days to emergence (Applegate) or to stage 17 (Piavis). From Applegate's study I used the data reported for three nests from the Ocqueoc River, in Presque Isle County, Michigan: the date spawning was completed, the mean date prolarvae were captured in plankton nets, and the number of prolarvae collected. The appendix to his work listed mean daily stream temperatures. For the Piavis publication, I used trials with rearing temperatures of 15.5, 18, and 21 °C. He recorded the time to reach each developmental stage; I used stage 17 as a surrogate for emergence.

Data analysis

I calculated cumulative degree days (CDD) using the following equation: $DD=\sum (t - 7)$, where t is the average daily stream temperature (°C), and the constant, 7, is the temperature below which no development occurs (Piavis, 1961). The estimated fertilization date was used as the starting point for the calculation of cumulative degree days.

All data were analyzed using parametric statistical methods in Statistica (Statsoft, Inc. 1998). I calculated the cumulative percent of prolarvae that emerged each day; those dates and CDD that corresponded most closely to the 10^{th}, 50^{th}, and 90^{th} cumulative percentiles were defined as the start, peak, and end dates and CDD. All differences were considered significant if the p-value was less than 0.05.

I tested the null hypotheses that: 1) prolarval lengths were the same for all nests within a stream and between streams; 2) the beginning, peak, and end CDD for the emergence period were the same for both streams; 3) the peak of emergence (CDD) was the same for my field data and Applegate's (1950) data; 4) the peak of burrowing (CDD) was the same for my laboratory study and Piavis's (1961) study; and 5) there was no difference between the peak of emergence in the field studies and burrowing in the laboratory studies. Many of these hypotheses provide insight into whether CDD can be used to predict prolarval emergence.

Results

Field sampling

Water temperatures were similar between the two streams during spawning; average daily temperatures ranged from 15-18 °C in the Black Mallard River (Figure 3A) and 13-19 °C in the Trout River (Figure 3B). The average water temperature during emergence was 20.6 °C (range 15.5-23.9 °C) in the Black Mallard River (Figure 3A) and 21.7 °C (range 17.6-24.3 °C) in the Trout River (Figure 3B). The relative water stage increased in the Black Mallard River just after drift sampling began due to heavy rains, then gradually decreased over the sampling period (Figure 3A). The Trout River's stage remained relatively constant, with a slight decline over time (Figure 3B). The heavy rains, corresponding rapid drop in water temperature, and increased flow in the Black Mallard River, provided a contrast to the more stable Trout River.

Nests were found in the Black Mallard River from May 22 to May 30, but no spawners were seen on nests. However, adults were seen late in the season. Upstream of nest 10 a new nest was built by a male and two females on June 23 (mean water temperature = 20.3 °C), nest 9 was reworked on June 23, and nest 6 was reworked on July 1 (mean water temperature = 21.3 °C). Spawning occurred in the Trout River study reach from May 23 to June 12; spawners were seen on most nests (Table 1).

Emergence tended to be concentrated during the middle (darkest hours) of the night. Approximately 24 – 30 % of prolarvae emerged between 2100 h and 2400 h, 66 – 68 % emerged between 2400 h and 0300 h, and 3 – 7 % of prolarvae emerged after 0300 h (Figure 4).

The number of prolarvae produced from nests was quite variable and generally showed a unimodal distribution (Figure 5 and 6). In the Black Mallard and Trout Rivers, 6,037 prolarvae (range 87 – 1,900 per nest) and 83,541 prolarvae (range 346 – 20,713 per nest) were collected, respectively (Table 2). The maximum number of prolarvae collected in one net over a 3 h period was 736 in the Black Mallard River and 8,348 in the Trout River. For the Trout River, where adults were observed on nests, there is no relationship between the number of spawners seen on a nest and the number of prolarvae produced (Figure 7).

Prolarvae emerging from nests were on average smaller in the Black Mallard River than those in the Trout River ($p<0.05$, $t=17.77$, $df=2390$). The average length of emerging

prolarvae in the Black Mallard River was 7.96 mm (range 4.86 – 12.45 mm; Figure 8A) and in the Trout River, 8.65 mm (range 4.69 – 12.80 mm; Figure 8B). Within streams there were significant differences in lengths between nests (Black Mallard River: $p < 0.05$, $F_{9,818}=12.28$; Trout River: $p < 0.05$, $F_{4,1388}=188.11$). No trend in prolarval lengths was seen over time (Figure 9), although there appears to be more scatter or variability in lengths as the emergence period progressed. Larger individuals were collected later in the season but some of these animals looked as though they had been feeding and hence were not emerging prolarvae but rather ammocoetes that were re-distributing.

Emergence began in the Black Mallard River on average 23 days (range 18-26 days) after the nest was constructed and at a mean CDD ($\pm$ standard deviation) of 254 ± 24 (Table 3). Cumulative degree days in the Black Mallard River were calculated using catches before July 1, because prolarvae collected after were assumed to be from later spawnings (June 23 and July 1) than the ones I was following (May 22 to May 30). The Trout River began emerging 22 days (range 18-25 days) after fertilization and at an average CDD of 318 ± 37, which was significantly greater than the Black Mallard River ($p < 0.05$, $t= 4.58$, $df=18$).

The Trout River also took longer to reach the peak of emergence than the Black Mallard River ($p<0.05$, $t=5.09$, $df=18$). The Black Mallard River peaked at an average of 26 days (range 23-28 days) or 290 ± 17 CDD (Table 3). The Trout River emerged 31 days (range 26-39 days) after fertilization or 370 ± 47 CDD.

Emergence ended in the Black Mallard River at a mean of 29 days (range 23-35 days) or 338 $\pm$ 28 CDD after fertilization. Emergence ended in the Trout River after 36 days (28-41 days) and at an average of 432 $\pm$ 53 CDD. Again, emergence in the Black Mallard Creek ended earlier than the Trout River ($p<0.05$, $t=4.9$, $df=18$) (Table 3).

On average, prolarvae in the Black Mallard River emerged over a 7 day period (range 3-12 days) and a mean of 83 $\pm$ 38 CDD. The Trout River prolarvae emerged over 8 days on average (range 4-14 days) or 113 $\pm$ 41 CDD. The emergence period was not different between the two streams (days: $p=0.28$, $t=1.12$, $df=18$; CDD: $p=0.11$, $t=1.67$, $df=18$).

Laboratory experiment

Prolarvae began to burrow in the laboratory experiments at an average CDD of 261 (range 242 – 286), similar to the field results, and finished burrowing at an average of 294 CDD (range 253 – 396). The peak of burrowing occurred at an average of 24 days (range 22-28 days) after fertilization or 267 $\pm$ 12 CDD. The CDD to peak emergence in the Black Mallard and Trout River's were greater than the peak of burrowing in the laboratory experiments (Black Mallard: $p<0.05$, $t=3.00$, $df=15$; Trout River: $p<0.05$, $t=5.68$, $df=15$), i.e. larvae in the study streams took more heat to emerge (Figure 10).

Secondary analysis

The peak of emergence in Applegate's (1950) study nests occurred 19 to 20 days after fertilization or 303 $\pm$ 3 CDD. Prolarvae began emerging around 274 CDD and finished

emerging around 319 CDD. There were no significant differences between when 50% of prolarvae emerged in Applegate's nests and in the Black Mallard River nests ($p < 0.25$, t=t.21, df=11). However in the Trout River, CDD's to peak emergence was greater than in Applegate's data ($p<0.05$, t=2.43, df=11). Prolarvae in my laboratory experiments burrowed earlier than prolarvae emerged in Applegate's nests ($p<0.05$, t=4.86, df=8) (Figure 10).

In Piavis's experiments, prolarvae reared in 15, 18, and 21 °C water temperatures began burrowing at 214, 193, and 212 CDD, respectively. Using the middle day that stage 17 occurred as 50% burrowed, I calculated a mean CDD of 248 $\pm$ 41. There were no differences between the CDD to 50% burrowed in my laboratory experiments and Piavis's experiments ($p = 0.2769$, t=1.17, df=8). There was also no difference between when prolarvae emerged in Applegate's nests and when prolarvae burrowed in Piavis's experiments ($p=0.08$, t=2.29, df=4). Both of my study streams had greater CDD at peak emergence than did Piavis's experiments (Black Mallard: $p<0.05$, t=2.68, df=11; Trout River: $p<0.05$, t=4.06, df=11).

Discussion

Water temperatures needed for sea lamprey spawning and emergence are quite broad. The temperatures seen in my study streams during both spawning (13-19 °C) and emergence (15-24 °C) are similar to those reported by other authors (11-24 °C: Applegate, 1950; 10-18.5 °C: Manion and McLain, 1971). The late spawnings in the Black Mallard River (20-21 °C) occurred with in the range of reported spawning temperatures. Applegate (1950) also witnessed spawnings late into the season.

The distributions of catch over time are generally unimodal, but some nests showed additional peaks suggesting late spawnings. As an example, nest 6 was reworked on July 1 and showed an additional peak in the emergence distribution (< 10 individuals) around July 12. This date corresponds to 176 CDD and is likely the start of the emergence period for the prolarvae spawned on July 1. Hence, the later peaks in the emergence distributions were removed when analyzing CDD.

The patterns of emergence for sea lamprey are similar to those of other species. Emergence occurs predominately during the darkest hours of the night (1200 – 0300 h) and declines sharply after 0300 h. Studies sampling drift or movements of stream young-of-the-year fishes have also reported increased drift around midnight and a decline towards dawn. (Brown and Armstrong, 1985; Bennett and Ross, 1995; Johnston, 1997). The overall duration of the emergence period is short, on average it took 8 to 14 days for 80% of prolarvae to emerge; Applegate (1950) reported duration's of 3 to 4 days. This difference is likely due to water temperature variations; even slight changes in temperatures over time can drastically change the heat accumulated. Chinook salmon also exhibit a short emergence duration, where the majority of fry emerge, on average, in 11 days (Field-Dodgson, 1988), despite a much longer incubation period.

The numbers of emergent prolarvae varied greatly from nest to nest and stream to stream. The Trout River produced 5,569 prolarvae per female seen, on average and the Black Mallard Creek produced 604 prolarvae per nest, on average. No correlation was evident

between the numbers of females present and the numbers of prolarvae produced. Applegate (1950) collected only 222 – 622 prolarvae from individual nests. Manion (1968) dismantled 19 nests before emergence and reported 1,763 to 10,545 prolarvae per nest. He also noted that on average, a single nest (one pair of spawners) produced 3,240 prolarvae and a double nest (two pairs of spawners) produced 7,531 prolarvae. It is possible that the numbers of prolarvae collected in my study are under-estimates because prolarvae may have drifted around the mouth of the drift nets. Although Applegate (1950) constructed enclosed raceways around nests to collect all emerging prolarvae, his numbers may also be under-estimates. The raceways may have changed the water flow to the nest and perhaps increased nest mortality. Regardless, the numbers of prolarvae produced in nests and streams varied greatly, but can be large. Variations in nesting success may in part explain the large amount of density independent variation in recruitment success observed by Jones et al. (in review).

With such recruitment variation of emerging prolarvae, it is possible that high densities could occur after settlement. Due to their small size, prolarvae are not good swimmers and rely on water currents to move them to burrowing habitats (Applegate, 1950). I collected over 4,000 prolarvae in a single net in a 3 hr time period (maximum of 8,000 / 3 h) on multiple occasions. Again, it is possible that these are under-estimates of the true numbers of prolarvae emerging. These large emergence events and the concentration of emergence in a short period of the night suggest that large numbers of prolarvae could be deposited in the same habitat patch. This overcrowding could potentially affect their

feeding rates (Yap and Bowen, in review), growth rates (Morman, 1987; Murdoch et al, 1992), movements (Chapter 3) and hence survival.

The Trout River produced larger numbers of prolarvae per nest than the Black Mallard River. This difference could be due to the heavy rains and subsequent high water levels in the Black Mallard River that possibly decreased the efficiency of the drift nets. However, the plotted data (Figure 5B-K) for each nest in the Black Mallard River, suggests that the peak catches did not occur until well after the high waters started to subside, indicating that this difference is not likely due to inefficient sampling. Therefore the difference in production between my two study streams is more likely due to other factors, such as egg or female size or water-quality.

In addition to producing more prolarvae, the Trout River prolarvae are on average larger (8.65 mm, range 4.69 – 12.80 mm) than those in the Black Mallard River (7.96 mm, range 4.86 – 12.45 mm) and they emerged later (Trout River: 370 CDD; Black Mallard: 290 CDD). Water temperatures between the two streams are relatively similar and hence this seems unlikely to be the reason for these differences. One possibility is that larger females spawned in the Trout River compared to the Black Mallard River. The Trout River had more adults in the system possibly creating higher competition for mates, allowing only the larger females to spawn. Or possibly, the Trout River attracted larger and better-conditioned females due to water-quality. The size of a female will influence the size of the offspring produced (Benoit and Pepin, 1999; Kamler, 1992; Elliott and Hurley, 1998) and possibly their survival (Diana, 1995). Larger eggs tend to have longer

developmental periods in fishes (Ware, 1975; Economou, 1991). Furthermore, the rate of yolk absorption tends to be high in small eggs and lower in larger eggs (Kamler, 1992). Therefore, prolarvae in the Black Mallard River possibly absorbed their yolk and had to emerge earlier to begin exogenous feeding. In contrast, the Trout River prolarvae possibly had more yolk reserves due to larger eggs and hence higher survival. These results suggest that knowledge about the linkage between condition of parents (Oconnor, in review), egg size, and timing of emergence may provide more insight into larval recruitment.

With the addition of the secondary analysis, my evidence suggests that cumulative degree days to emergence are different in the field than in the laboratory. The Black Mallard and Trout River's cumulative degree days to emergence were higher than in my laboratory study and Piavis' study (1961). It took more degree days to reach peak emergence in the field, when temperature fluctuated, than in the laboratory, when it was held constant. Traditionally, emergence is estimated to occur about 22 days after fertilization (Piavis, 1961). However, my results show that laboratory results are generally under-estimates of what is happening in the field.

The main control strategy in sea lamprey management relies on the chemical treatment of streams with TFM. While in the nests, eggs and possibly prolarvae are less vulnerable to TFM. Due to time constraints of the control agents, streams are now treated without regard to when the current year-class in a stream will emerge. For some costly-to-treat streams, it would be useful and more cost effective to know when the majority of

prolarvae have emerged so that an extra year-class can be targeted, thereby increasing the time interval between costly treatments. Other stream sections require frequent treatments because they are close to lakes and hence there is concern that lentic populations could accumulate. These lentic areas can not be treated effectively. My results from Chapter 2 suggest that larvae disperse widely and soon after emergence. If managers want to effectively treat these short stream sections they need to treat soon after emergence when age-0 ammocoetes are vulnerable, but not before emergence is complete. Knowledge of the timing of emergence is therefore important. The results presented herein could be used to estimate the optimal timing for treatments. If managers want to target an additional year-class it may be wise to wait to treat until 36 days or at least 432 CDD after the spawning period. Unfortunately, to apply these results knowledge of the timing of spawning is needed; spawning surveys are uncommon on lamprey producing streams. On the other hand, many rivers have adult traps on them, and if the relationship between the numbers of adults collected in traps and the timing of spawning were available, this emergence work could be used more broadly to better target optimal treatment times.

Table 1: Dates that nests were first located and the dates and numbers of male and female spawners seen on nests in the Trout River. (* denotes that nest was re-worked but no spawners were seen, - denotes no spawners were seen)

Nest	Located	Active	Males	Females
1	6/01	6/01	1	2
		6/04	1	1
		6/07	*	
2	6/01	6/01	1	3
3	5/25	5/25	1	1
		5/31	1	1
4	5/25	5/25	1	1
		5/31	1	1
5	5/30	-	-	-
6	5/25	5/25	1	1
		6/05	1	1
7	5/30	-	-	-
8	5/23	5/30	1	2
		6/05	1	1
9	5/23	5/31	1	1
10	5/25	6/07	1	1

Table 2. Total number of prolarvae collected in each nest for each stream, the total number of prolarvae collected by stream, the mean number of prolarvae collected per nest, and the standard deviation of prolarvae collected per nest.

Nest	Black Mallard River	Trout River
1	87	346
2	267	14,880
3	201	1,316
4	535	12,015
5	1,900	1,044
6	164	14,632
7	109	3,986
8	768	11,093
9	666	3,516
10	1,340	20,713
Total	6,037	83,541
Mean	604	8,354
Std Dev	600	7,190

Table 3: Mean (and standard deviation) for the beginning, peak, and end of prolarval emergence (or burrowing) for all study components.

	Field Studies			Laboratory Studies	
	Black Mallard River	**Trout River**	**Applegate's Data**	**Laboratory Exp.**	**Piavis's Lab Study**
Beginning	254 ± 24	318 ± 37	--	--	--
Peak	290 ± 17	370 ± 47	303 ± 3	267 ± 12	248 ± 41
End	338 ± 28	432 ± 53	--	--	--

Figure 1: Schematic diagram of nest locations in the Trout River, nest numbers are in bold, and inset showing river location (not to scale).

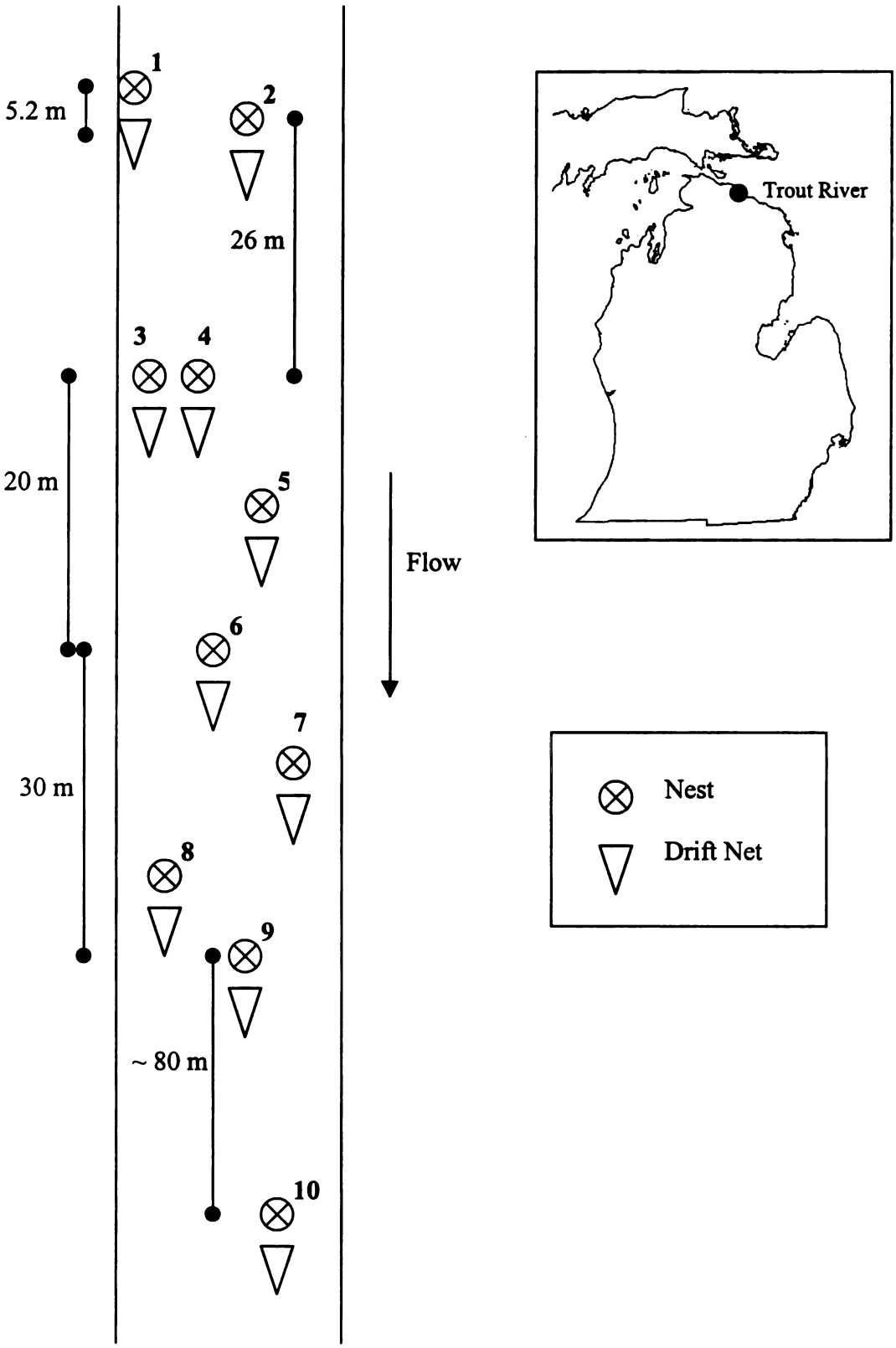


Figure 2: Schematic diagram of nest locations in the Black Mallard River, nest numbers are in bold, and inset showing river location (not to scale).

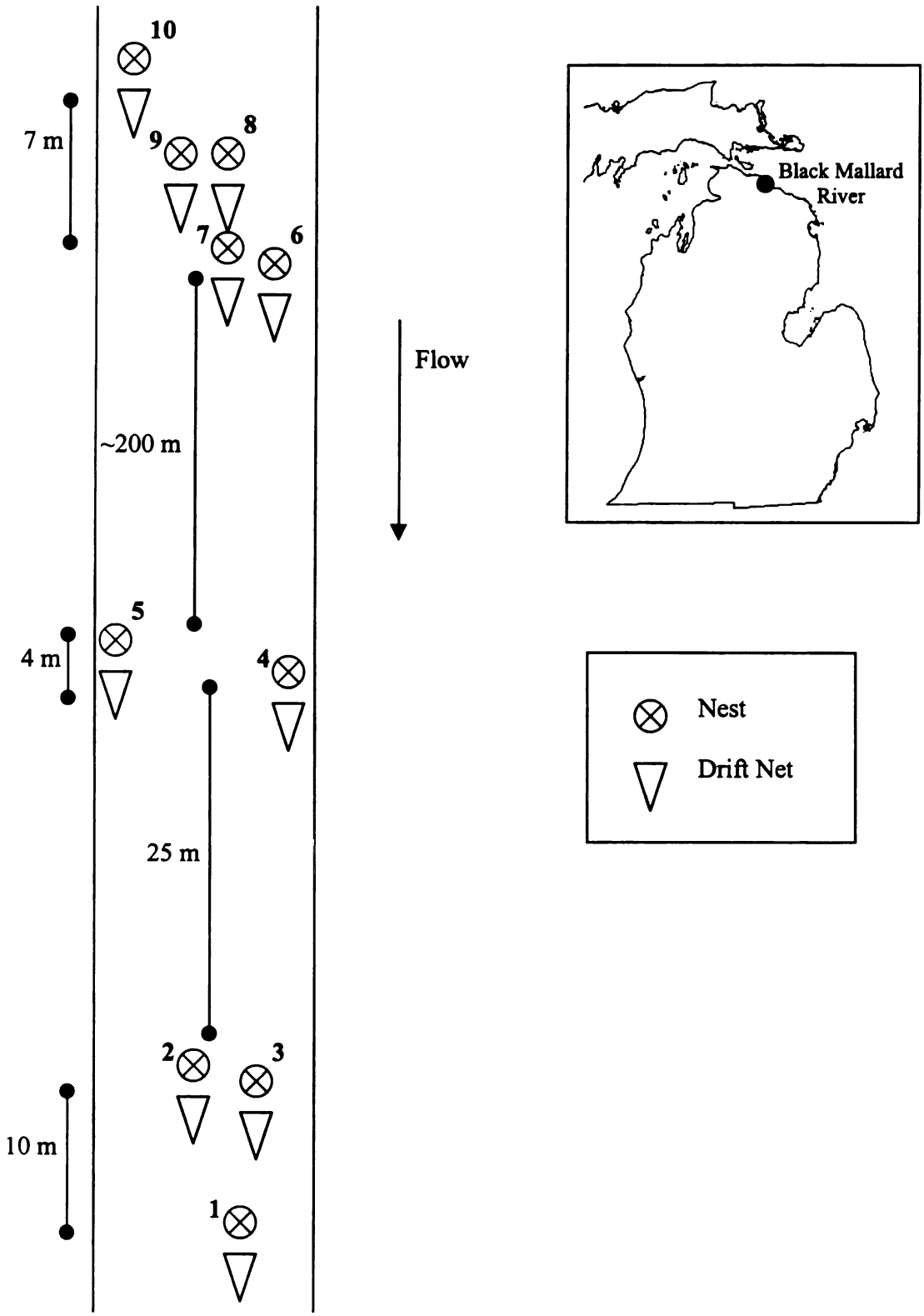
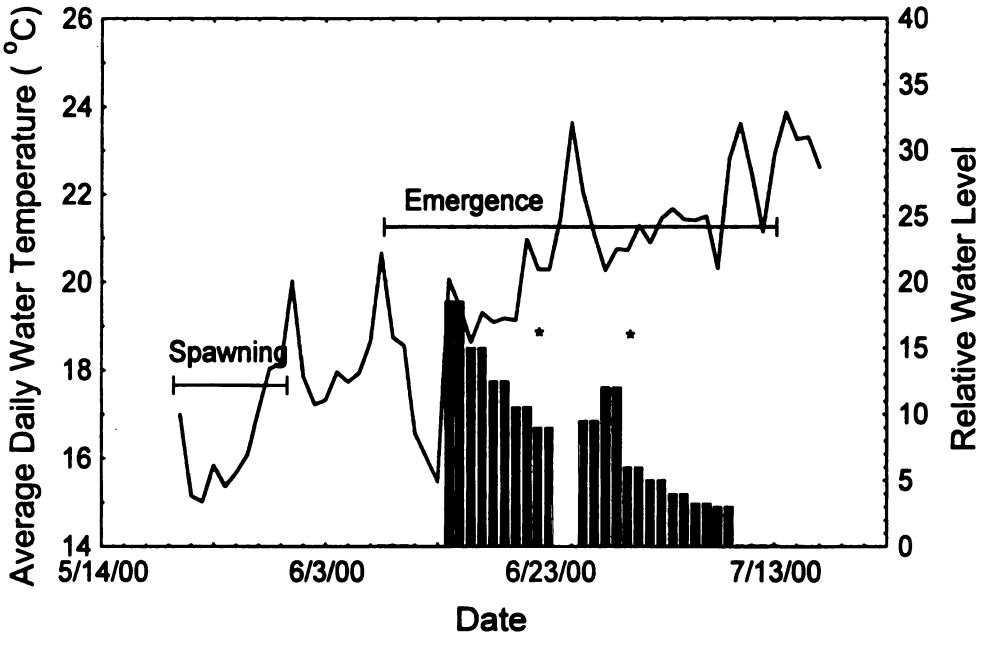


Figure 3: Average daily stream temperatures in the Black Mallard River (A) and the Trout River (B) during the spawning and emergence period and relative water level during the emergence period. (*denotes late spawnings)

A.



B.

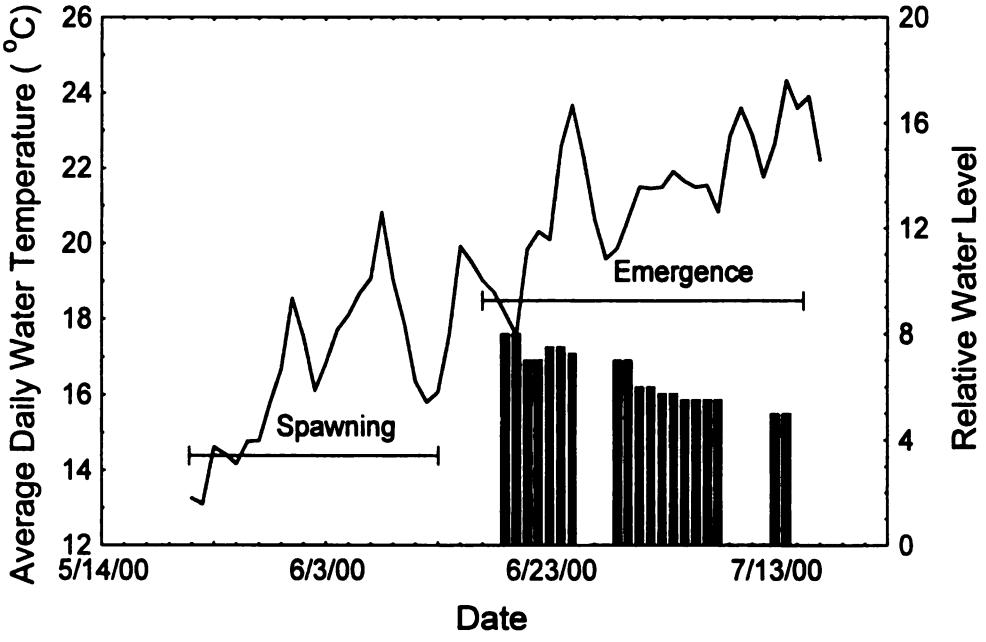


Figure 4: Box plot of the percent of emergent prolarvae collected during set 1 (2100-2400 h), set 2 (2400-0300 h), and set 3 (after 0300 h). The whiskers show the minimum and maximum values, the box depicts the 25 and 75 % quartiles, and the dash the median.

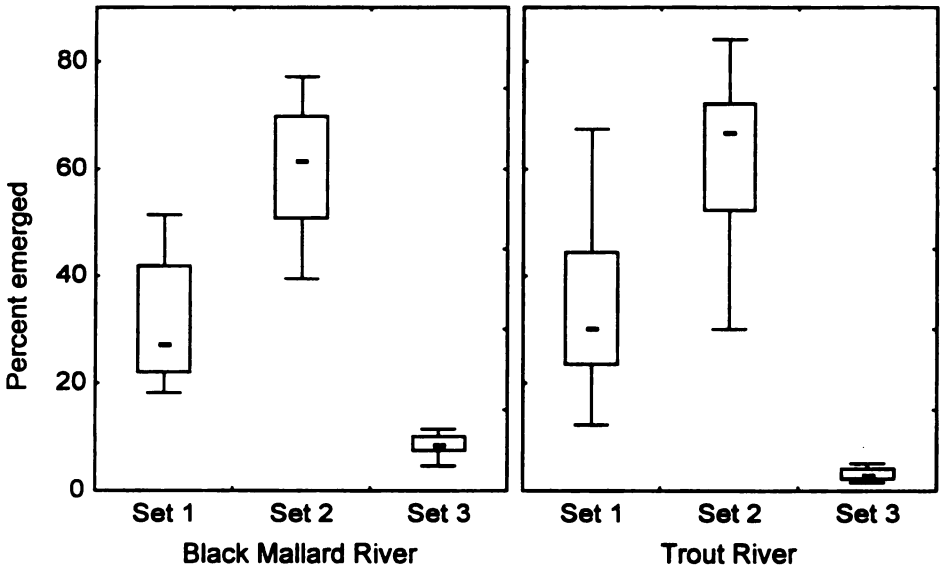


Figure 5: The number of prolarvae collected each day by nest for the Black Mallard River and the average daily stream temperatures and relative water levels during the emergence period.

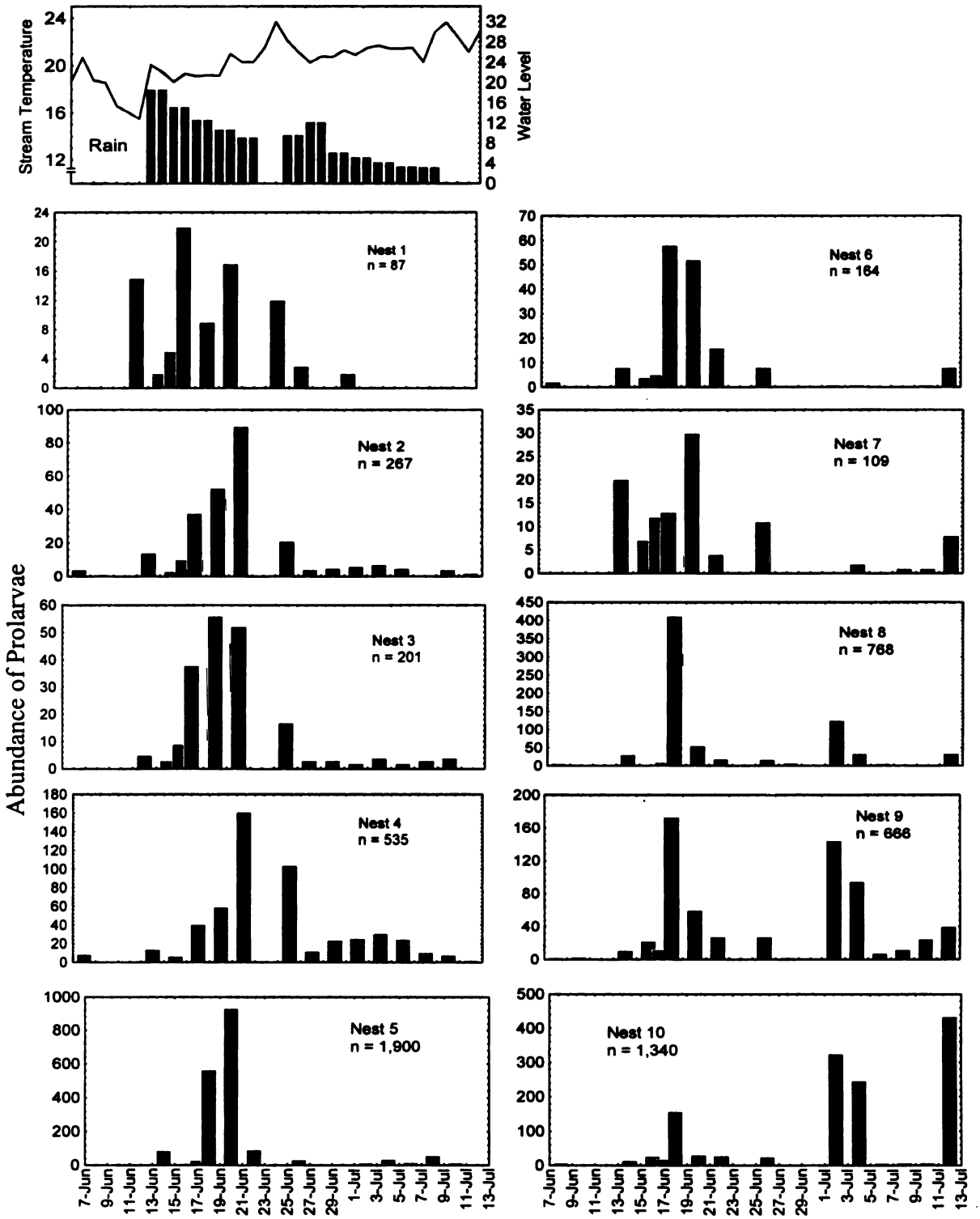


Figure 6: The number of prolarvae collected each day by nest for the Trout River and the average daily stream temperatures and relative water levels during the emergence period.

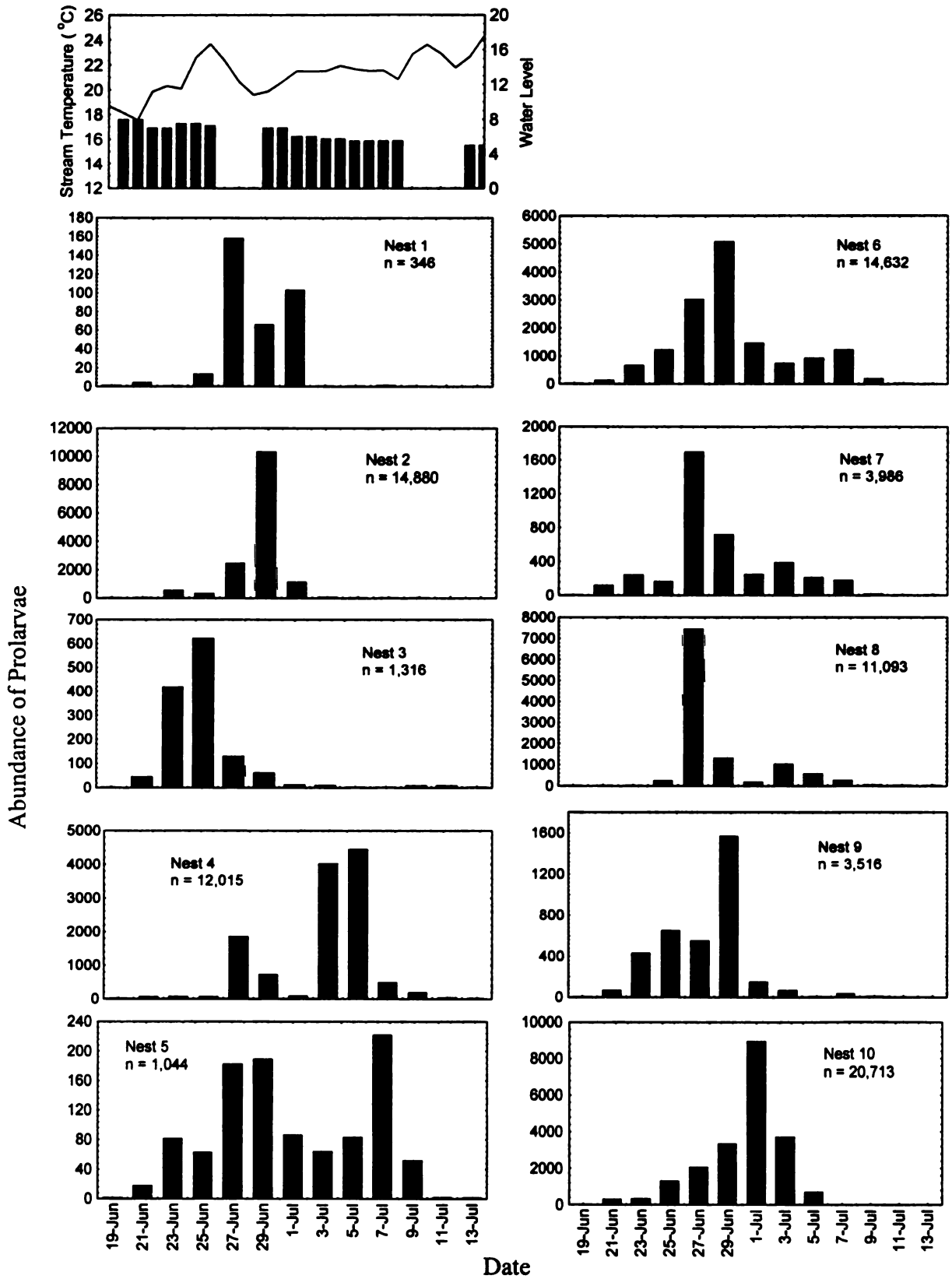


Figure 7: Scatterplot of the number of prolarvae produced vs. the number of spawners seen on nests in the Trout River.

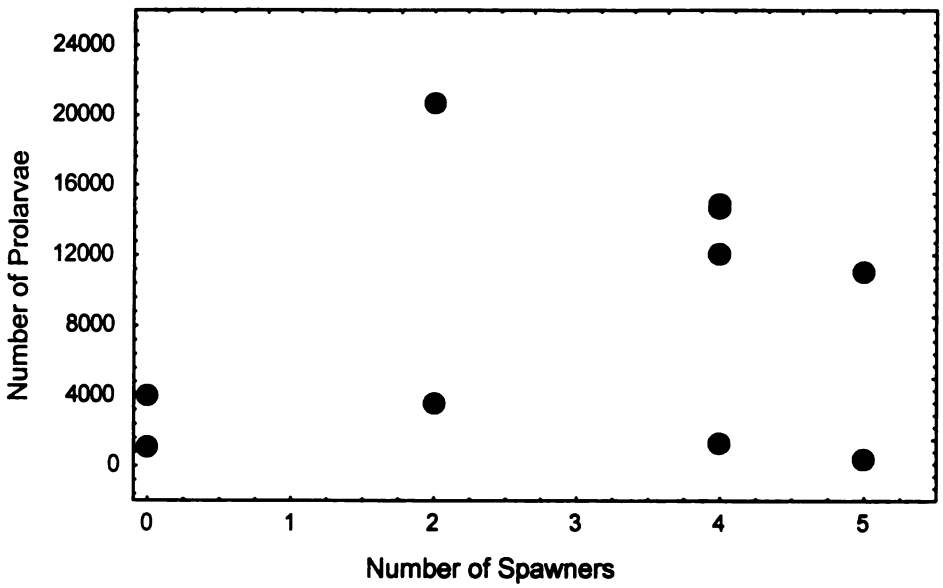
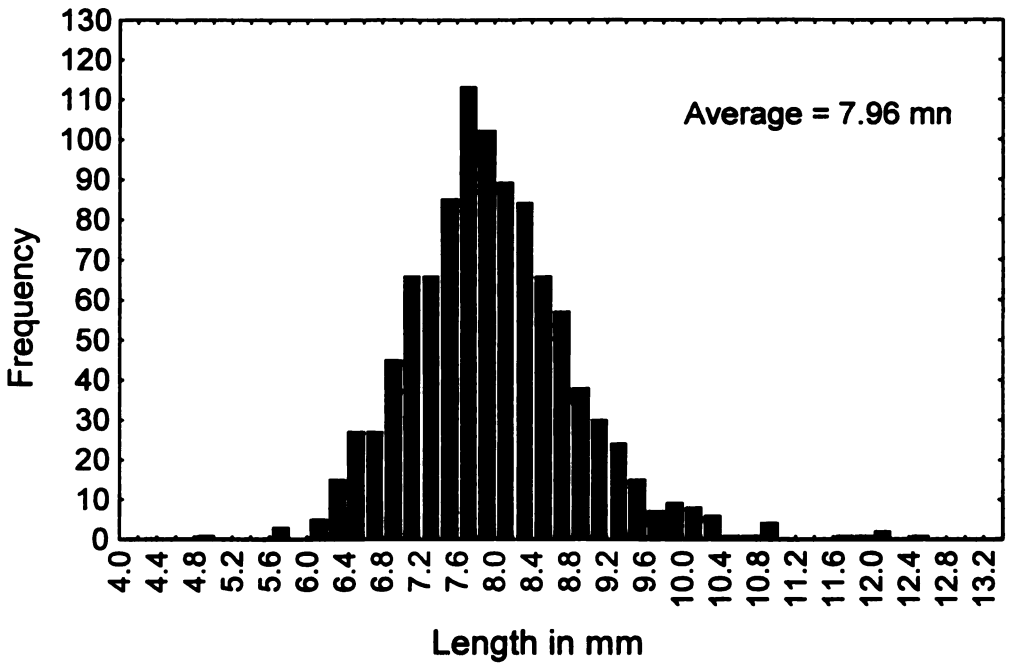


Figure 8: Distribution of lengths for emerging prolarvae for each stream, the Black Mallard River (A) and the Trout River (B).

A.



B.

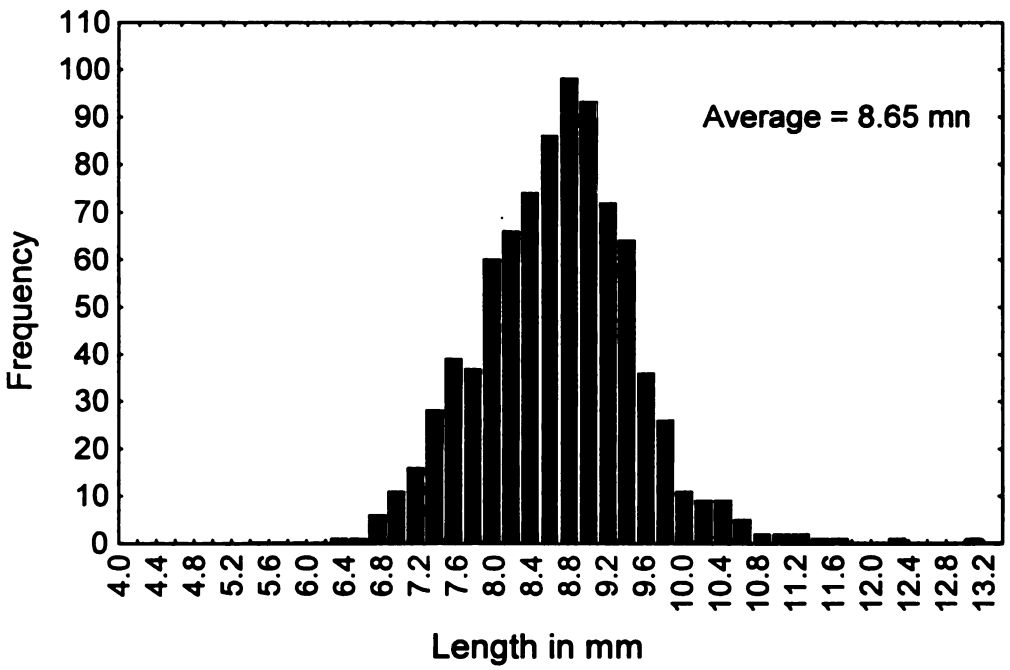
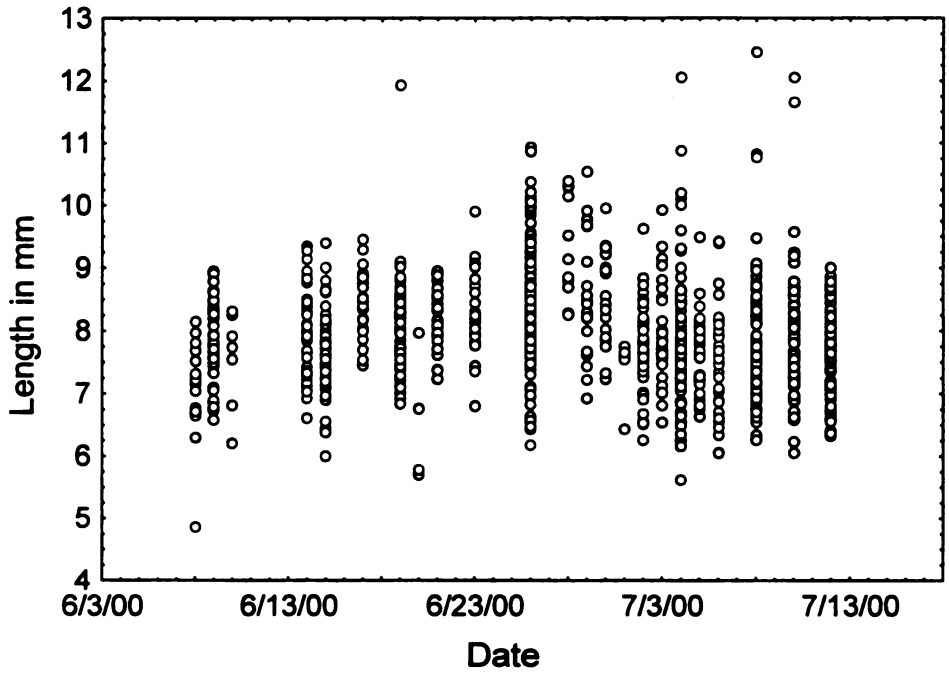


Figure 9: Scatterplot of lengths for emerging prolarvae over time in the Black Mallard River (A) and in the Trout River (B).

A.



B.

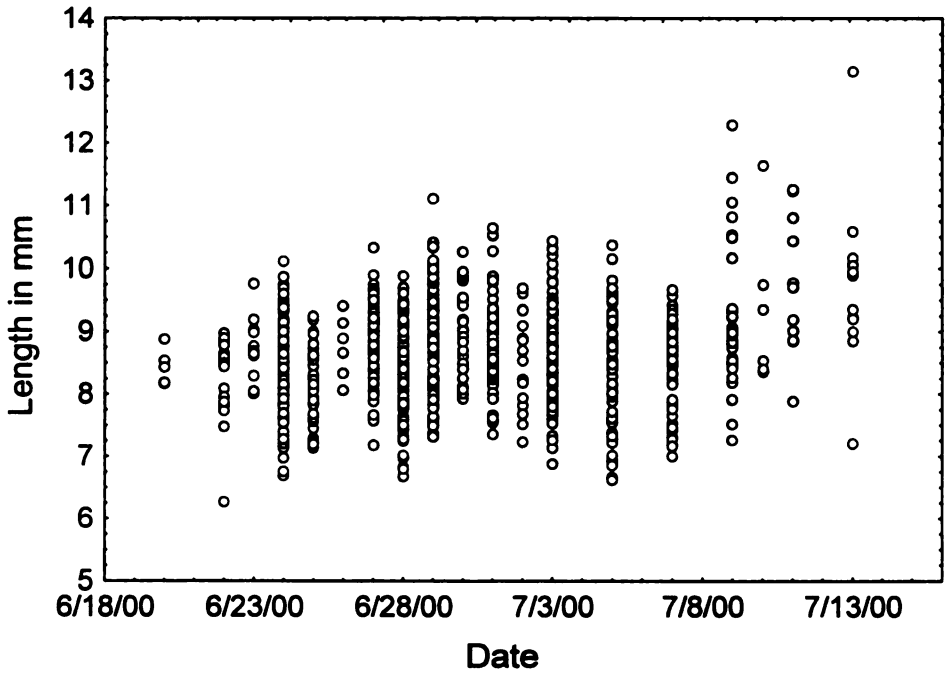
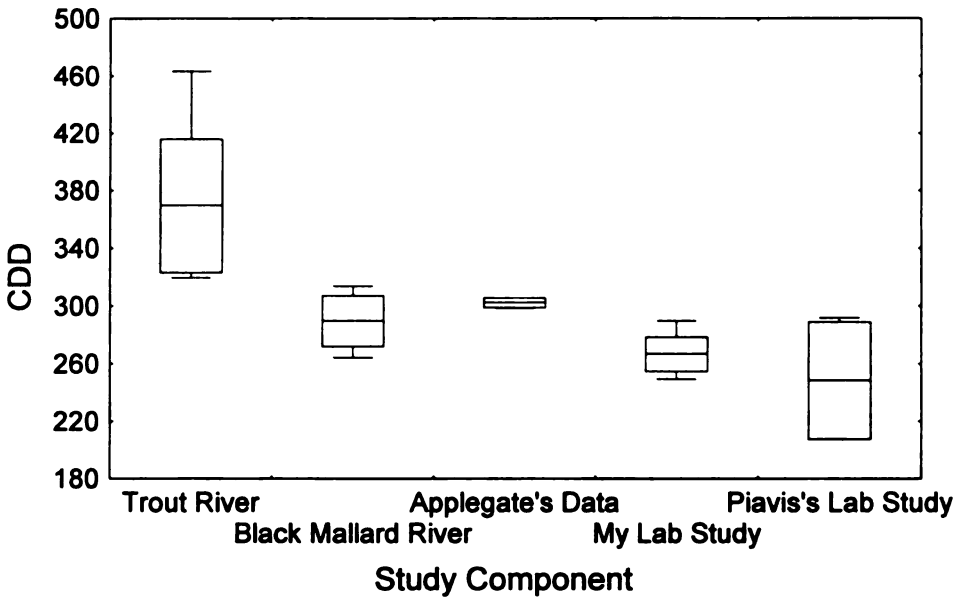


Figure 10: Boxplot of cumulative degree days for the peak of prolarval emergence for each study component, the line is the mean, the box represents the standard deviation, and the whiskers are the minimum and maximum values.



Chapter 2:
Dispersal of age-0 sea lamprey during the first growing season.

Introduction

Dispersal of larval fish away from spawning habitat seems likely to be a critical process in determining the habitat conditions and level of intra-specific competition (Howard, 1960) experienced by young-of-the-year (age-0) fish and thus their survival rates. If dispersal is passive, age-0 fish may be found in sub-optimal habitats and may clump together (Robinson et al., 1998). If dispersal is active, individuals may become more evenly spaced (Robinson et al., 1998) or may continue dispersing to find optimal habitats. Competition may be a driving factor in determining recruitment if dispersal is limited. Yet, physical transport processes may be more important if dispersal is wide or unlimited (Economou, 1991). Of course a combination of these may be more likely. However, as dispersal distances increase so does the risk of not finding suitable habitat (Economou, 1991), becoming prey, and depleting energy reserves (Kamler, 1992). Understanding the extent to which fish disperse can provide valuable insight into recruitment processes.

Hardisty (1961) and Hansen and Hayne (1962) state that sea lamprey dispersal from nests during their first growing season is a very vulnerable time, but that little is known about this life stage. Densities are generally at a maximum at this stage and fish are at their

smallest and most vulnerable size. Manion and McLain (1971) report that ammocoetes remain close to spawning areas and then gradually scatter. Beamish and Lowartz (1996) mention that age-0 ammocoetes move to nursery habitats after emerging from nests and then within a few months 'join the remainder of the population'. It is suggested that dispersal is largely dependent on heavy rainfalls (Hardisty, 1961), yet no study has looked specifically at this process in age-0 sea lamprey and no quantitative estimates for distances moved have been reported.

Densities of age-0 ammocoetes have also not been documented, despite routine stream assessments by the Sea Lamprey Control Program. Because of their small size, age-0 ammocoetes are not collected or reported. High densities decrease growth rates for age-1 and older ammocoetes in the laboratory (Morman, 1987; Murdoch et al., 1992) and in the field (Weise and Pajos, 1998), but the effect of density on growth rates of age-0 ammocoetes is unknown.

Because age-0 sea lampreys are not often sampled, methods and sampling designs are not documented. I expected age-0 ammocoetes to be difficult to find and clumped when found. Adaptive sampling is an innovative approach to compensate for the potentially inefficient sampling of rare and clustered populations (Thompson, 1992; Thompson and Seber, 1996). Adaptive sampling allows for the flexibility to increase sampling intensity in areas that have the object of interest, in this case age-0 ammocoetes.

The objectives for this study component were to: (1) document densities of age-0 ammocoetes; (2) determine if age-0 ammocoetes cluster close to nests of origin or if they disperse widely; (3) look for evidence in the field of density affects on growth of age-0 ammocoetes; and (4) determine the efficiency of adaptive sampling for estimating densities of age-0 ammocoetes.

Methods

Study design

To address these objectives, I needed to be able to associate ammocoetes collected in the stream with a specific source nest. This could be accomplished by restricting nests to a few widely separated locations or by marking prolarvae to uniquely identify their nest of origin. I tried to restrict spawning areas by installing cages in streams and introducing adults into them. However, this was unsuccessful, adults escaped and no nesting occurred within these cages. Tagging prolarvae is not practical because of their size (4.5 – 12 mm). Therefore, I chose to introduce small numbers of adults above barriers in two streams which otherwise were not accessible to sea lamprey. I then identified nests that were isolated and conducted surveys to estimate age-0 densities at a range of distances downstream of nests. To further enhance my ability to associate ammocoetes with source nests I also collected DNA samples from adults and larvae and used microsatellite methods to assign larvae to parents and determine siblings.

Study streams

Ogemaw Creek is a tributary to the Rifle River in Ogemaw County, Michigan (Figure 1). The stream has a barrier at the mouth that sea lampreys cannot traverse. The stream is approximately 6 m wide and 3 km long. The Carp River is a tributary to Lake Superior and is located near Pancake Bay in Ontario, Canada (Figure 1). The Carp River has a mean width of approximately 10 m and a length of 8 km. It too has a barrier to sea lampreys. Twelve pairs of adults were stocked into each stream above the barrier.

Field methods

No previous studies have investigated age-0 ammocoete movements; therefore I conducted a preliminary study to explore how far downstream of nests ammocoetes might disperse. In Ogemaw Creek in 1998, I located nests and electrofished 32 randomly selected transects. These data suggested that age-0 ammocoetes seemed to be within 200 m of nesting areas. Using these preliminary data, I created regions or zones below nests to determine if ammocoetes clump near nests or if they disperse widely. I established three sampling zones (Figure 2) downstream of two nests in each stream. The first sampling zone was considered near the nest and started at the nest and extended downstream 50 m. The next zone extended from 55 to 155 m downstream of a nest and was called the middle zone. The third zone included habitats between 160 m and 310 m downstream from the nest, and was called the far zone. A 5 m buffer between each zone was not sampled. Catches of ammocoetes were compared between zones to determine dispersal. If ammocoetes were principally collected in the near zone then they were

considered to be limited dispersers. If ammocoetes were commonly found in the far zone, they were considered widely dispersed.

To determine successful deposition and embryological development stage (Piavis, 1961), a sample of eggs was collected from each nest and preserved in 70% ethanol. The developmental stage was used to determine the timing of the first sampling event, to be sure that ammocoetes had left nests.

A small backpack gold-mining dredge (Keene Equipment, CO) with a 4 cm diameter suction hose was used to collect age-0 ammocoetes. Sample plots were 25 x 25 cm^2 and were delineated using a plexi-glass frame with solid sides and an open top and bottom, to prevent escape of ammocoetes during dredging. Bottom sediments were excavated using the dredge to a depth of approximately 6 cm and collected in a bucket with a 590 μm screen bottom. Material that did not pass through the screen was hand-picked in the field to collect ammocoetes. All age-0 ammocoetes were preserved in 70% ethanol, later identified to species, and measured. Sampling occurred in Ogemaw Creek on July 20 – 22 (event 1), August 12 – 13 (event 2), and September 5 – 6 (event 3). Sampling occurred in the Carp River on August 2 – 5 (event 1), August 23 – 24 (event 2), and September 24 – 25 (event 3).

Initially, six random plots were sampled within each zone below nests. I conducted a power analysis with data collected using the same dredge technique (L. O'Connor and J. Kelso, Department of Fisheries and Oceans, Ontario, Canada, unpublished data). I calculated that six samples would provide sufficient power (α=0.05 and β=0.3; Merritt

and Cummins, 1996) to detect a difference of twelve ammocoetes per m^2 between zones. Random sample plots were located by generating random transects within each zone and then sampling the closest preferred larval habitat or type I habitat, which consists of a mixture of sand, silt, and detritus, to the transect.

Following the adaptive sampling approach, if an age-0 ammocoetes was collected in a random plot, additional neighborhood plots were sampled. The neighborhood samples in this study consisted of one 25 x 25 cm^2 plot upstream and downstream of the random plot (Figure 3). During the first sampling event, neighborhood plots were sampled until no age-0 ammocoetes were collected; hence the number of neighborhood plots could consist of more than two additional plots. This was changed to only one neighborhood plot upstream and downstream during the second and third sampling event because of time constraints.

Microsatellite methods

Microsatellite loci are 'nuclear DNA with short repeated core sequences scattered throughout the nuclear genome' (Wirgin and Waldman, 1994). These sequences are relatively prevalent in the genome and can be inherited, but do not seem to be used in gene expression, that is they do not code for specific functions or protein products (Scribner and Pearces, 2000). Because these sequences are not used in gene expression, they do not appear to be under selective pressures and so generally have more variation than gene expression sequences (Wirgin and Waldman, 1994). The number of different alleles that is seen at a locus across individuals characterizes this variation. By using

multiple loci, relatedness can be assessed using likelihood estimates of parent and offspring genotypes.

Fin clips were taken from all adults stocked into Ogemaw Creek and preserved in tissue buffer. DNA was extracted from tissue samples of fin clips and age-0 ammocoetes using Puregene® DNA extraction kits (Gentra Systems, Inc.). Additional ammocoetes were collected for this analysis. Once extracted, sample concentrations were obtained using flourometry and then diluted to 20 ng/ml. Polymerase chain reactions (PCR) were used to amplify targeted microsatellite loci within the DNA. Primers used in the PCR include: SLGA210F / Kim210R, FGT3, Spl120, SLGA38F / 3SLGA38R, GISE5, and GISB15. Primers are the different reagent mixtures to cut and amplify specific loci. These flourescently labeled PCR products were run onto 6% denaturing polyacrylamide gels and scanned using a FM BIO II (Hitachi, Inc.) scanner to produce a picture of the alleles associated with each loci. Each gel was run with not only my samples but also a ladder marking sizes down the gel and individuals of known genotypes. From the gel pictures, alleles were scored, thereby genotyping each individual.

Data analysis

Field data were analyzed using parametric statistical methods in Statistica (Statsoft, Inc. 1998). I explored the following questions: 1) are densities of age-0 ammocoetes different between zones and 2) does density affect age-0 ammocoete length.

In adaptive sampling the mean of a zone (û) is calculated from (Thompson and Seber, page 98, 1996):

$$w_i = \frac{1}{m_i} \sum_{j \in Ai} y_j$$

$$\hat{\mu} = \frac{1}{n} \sum_{i=1}^{n} w_i$$

where A_i denotes the network which includes random plot *i*,

m_i is the number of plots within network A_i, not including edge plots,

y_j is the number of ammocoetes in sample *j*, and

n is the number of initial random sample plots.

A network is a cluster of plots that includes the random and neighborhood sample plots. An edge plot is a neighborhood sample plot where the condition was not met, i.e. no age-0 ammocoetes were collected. If the random sample plot contains no ammocoetes then m is equal to 1, m is also equal to 1 if the neighborhood sample plots do not contain any age-0 ammocoetes.

The variance for a zone is calculated from (Thompson, p. 271, 1992):

$$\text{var}(\hat{\mu}) = \frac{(N-n)}{Nn(n-1)} \sum_{i-1}^{n} (w_i - \hat{\mu})^2$$

where N is the total number of possible sample plots within a zone. N was calculated by multiplying the area of a zone by an estimate of the percent of type I habitat in the

stream, which is estimated from habitat transect data collected during larval assessments, and then dividing by 0.0625 m^2, which is the size of a single sample plot.

The microsatellite data were analyzed using CERVUS 2.0 (Marshall et al., University of Edinburgh, 1998-2001), a likelihood-based parentage analysis program, to associate ammocoetes with parents thereby determining siblings. In addition to determining the maximum distance separating siblings, I used the data to address two other questions. First, I wanted to determine if different families occur below different nests. If ammocoetes do not disperse widely one would expect to find ammocoetes of different mothers or fathers below different nests. To explore this question I compared the distributions of siblings found below the two nests. Second, I wanted to determine if siblings clump in habitat patches (i.e. are siblings found more often in the same habitat patch than would be expected by chance?). To test this, I used a randomization test (Sokal and Rohlf, 1995) to determine if the total number of siblings observed co-occurring in habitat patches was significantly greater than what could occur randomly. The observed number of sibling pairs in each habitat patch was counted and summed over all habitat patches. Then all the siblings from all patches were randomly re-assigned to habitat patches and the total number of sibling pairs was counted; this simulation was repeated 1000 times. I compared the observed number of sibling pairs in my data to the simulated random distribution to determine the probability of obtaining the observed number of sibling pairs by chance.

To determine whether the adaptive cluster sampling (acs) is more efficient than a simple random sampling (srs) design for age-0 ammocoete populations, the ratio of the acs variance and the srs variance was calculated. If the ratio is less than 1 then the acs was more efficient, whereas if the ratio is greater than 1 the simple random sampling design with sample size n* was more efficient. The variance of a simple random sample is calculated as (Thompson, page 275, 1992):

$$\text{var}(srs) = \left(\frac{\sum_{i=1}^{N} (y_i - \mu)^2}{n^* - 1} \right) \frac{(N - n^*)}{(Nn^*)}$$

where n* is the number of plots sampled, in this case the number of random plots sampled.

Results

In Ogemaw Creek, a total of 141 plots were sampled and 40 age-0 ammocoetes (range per plot: 0 – 5) were collected. Ten age-0 ammocoetes were collected in Ogemaw Creek downstream of nest 1, and 30 age-0 ammocoetes downstream of nest 2. In the Carp River, 172 plots were sampled and 251 age-0 ammocoetes (range per plot: 0 – 23) were collected. In the Carp River, 160 and 91 age-0 ammocoetes were collected downstream of nest 1 and nest 2, respectively. Out of the 313 plots sampled in both streams, age-0 ammocoetes were found in only 74 (Figure 4). These data do not follow a Poisson distribution ($\chi^2 = 181.86$, df=2, $p<0.05$), suggesting that age-0 ammocoetes are not distributed randomly but are aggregated.

Mean densities of age-0 ammocoetes varied between 0 and 44 per m^2 (Table 1). There were no significant differences in age-0 ammocoete densities between zones or between events (Two-way ANOVA: Zones – $F_{2,27}$=0.47, p=0.63; Event – $F_{2,27}$=1.66, p=0.21; interaction – $F_{4,27}$=0.45, p=0.77) (Figure 5). Yet the far zone in the Carp River does on average have higher densities than the other two zones and there appears to be a downward trend by the last sample event (Figure 6).

Six loci were used to determine parentage in Ogemaw Creek, however the number of alleles within each locus was small, ranging from 2 to 8 (Table 2). Expected heterozygosity values ranged between 0.32 and 0.726, values less than 0.5 are generally not useful for large-scale parentage analysis (Cervus 1998-2001). Locus SLGA38 had a relatively high null allele frequency (>0.05). A null allele is an allele that can not always be detected with the primer being used because of mutations in the binding sites such that the allele is not amplified sufficiently (Cervus, 1998-2001). Despite the high null allele frequency estimate, SLGA38 did not cause major problems with mismatches in genotyping between adults and ammocoetes and hence was kept in the analysis.

Ammocoetes from the second and third sampling events were genotyped. The low allelic diversity made it difficult to identify siblings with much confidence. Eight females produced the 42 ammocoetes collected. Cervus (1998-2001) analyzes parents separately. When males were used as the unknown parent, nine ammocoetes were attributed to a father with greater than 60% confidence, while only one of those was attributed to a father at a confidence of 80% or greater. When females were used as the unknown

parent, twelve ammocoetes were attributed to a mother with greater than 60% confidence, and three of those were attributed to a mother at a confidence of 80% or greater. Because ammocoetes were attributed to mothers with greater confidences than the fathers, mothers were used in the analysis. In those cases where confidences were below 60%, the most-likely mother was used. Notwithstanding the low confidence in sibling identification, in the analysis presented below I assume that parental assignments are correct.

Siblings were found in the near zone of the upstream nest and the far zone of the downstream nest, by the second sampling event siblings were 820 m apart and by the third sampling event 874 m apart. There is no evidence that distinct groups of siblings are associated with the two different nests, their distributions are similar (Figure 7).

The randomization test suggests that pairs of siblings are more likely to be found in the same habitat patch than would be expected by chance. The randomization's produced a mean number of sibling pairs around 9 (Figure 8), while my data indicated 20 sibling pairs. Only four out of 1000 simulations produced 20 or greater sibling pairs, suggesting that ammocoetes appear to aggregate with siblings. However, it must be emphasized again that these results are conditional on a low confidence of assignment of parentage.

Ogemaw Creek ammocoetes were on average larger than those in the Carp River. In Ogemaw Creek the average length of ammocoetes during the second sampling event was 12.69 mm and 17.21 mm in the third sampling event (sample event 1 was not recorded). In the Carp River, ammocoetes averaged 11.40, 13.54, and 15.59 mm in length during the

first, second, and third sampling event, respectively. There were significant length differences between streams during the second sampling event ($F_{1,96}$=7.04, $p<0.05$) but not during the last sampling event ($F_{1,21}$=3.32, p=0.08); however only 5 ammocoetes were collected in the Carp River at this time. There were no length differences between zones in either of the streams except during the second sampling in the Carp River, the average length of ammocoetes in the near zone was 14.03 mm, in the middle zone was 13.15 mm, and in the far zone was 12.89 mm ($F_{2,68}$=3.66, $p<0.05$). There also appears to be no strong relationship between density and length within streams (Figure 9).

Although the data suggest that age-0 ammocoetes aggregate, the adaptive-cluster sampling (acs) was generally not more efficient than a simple random sampling (srs) design. Efficiency values ranged from 0.29 to 10.03 (Table 3); those values < 1 indicate that the adaptive sampling design was more efficient. On seven occasions the acs did better than the srs, however on 17 occasions they were the same. Essentially, a simple random sampling design with 6 plots estimated the population density just as accurately as an adaptive cluster sampling design.

Discussion

Fine-scale densities of age-0 ammocoetes can be very high (384 / m^2), although average densities were low, 4 and 10 ammocoetes per m^2 in Ogemaw Creek and the Carp River, respectively. Densities reported here are not much higher than those seen for older ammocoetes. Other authors report densities of age-1 and older ammocoetes in the field between 0 and 10 per m^2 (Manion and McLain, 1971, Jones et al., in review), most

yearling densities range between 0 and 2 per m^2 (Jones et al., in review). Given the large numbers of ammocoetes expected to emerge from nests (range 87 – 20,713 prolarvae per nest, as reported in Chapter 1) and the relatively small amount of habitat, I expected high densities to be prevalent. Yet these results suggest that age-0 ammocoetes are generally found in low densities. I estimated the overall abundance of age-0 ammocoetes by multiplying the average density below nests by the amount of larval habitat (type 1 = fine, depositional sediments). In Ogemaw Creek, estimated abundance's are relatively low (Table 4). This could be due to low nesting success as seen in the Black Mallard River in Chapter 1, or it could be due to early mortality of recently emerged larvae, wide dispersal, gear efficiency, or a combination of all four. Abundance estimates in the Carp River (Table 4) are relatively high during the first two sampling events and suggest high nesting success as was seen in the Trout River in Chapter 1. However, by the last sampling event, the abundance estimate drops sharply suggesting either mortality later in the season or continuing dispersal. Due to the study design used, i.e. introducing low numbers of spawning adults, the densities reported here may be lower than in naturally occurring populations.

Both the field and microsatellite data suggest that age-0 ammocoetes do not clump near nests but disperse widely. These results suggest that siblings can disperse at least 874 m apart in the first growing season; this is a minimum estimate of dispersal distance because my study area only extended 974 m downstream of the upstream nest. Manion and McLain (1971) suggested that age-0 ammocoetes initially remained close to spawning areas and then generally scattered. In their study, adults were introduced into stream

reaches that were separated by either falls or installed dams. The most downstream reach did not receive any adults. Ammocoetes were not found in the most downstream reach until the next spring. The reach above the most downstream reach was 1.3 km long, suggesting that ammocoetes dispersed less than that during their first growing season. Hardisty (1961) suggested that age-0 ammocoetes are dependent on heavy rains to help them disperse; however I do not believe this to be the case and present evidence in Chapter 3 that ammocoetes disperse readily early in the first growing season.

The microsatellite work supported the field data, however, most of the ammocoetes were assigned to parents with confidences below 60% and it seems likely that fewer females spawned. Only three nests were located in the study area and upstream of the study area in Ogemaw Creek. One pair of adults was seen spawning on a nest and all nests were small. Generally when there are multiple adults on a nest the downstream end of the nest become less horse-shoe shaped and more ridge shaped, this was not the case in Ogemaw Creek. Furthermore, O'Connor et al. (in review) suggest that it is likely that less than 50% of adults spawn.

The low polymorphism of the loci used in my analysis severely limited the use of these data. Other studies successfully assigning parents to offspring use loci that range in the number of alleles from 2 to 30 (Norris et al., 2000), more commonly 20-30 alleles (Letcher and King, 1999). The more variable the loci, generally the easier it is to assign parentage, especially in a small population such as the ones created in this study. Norris et al. (2000) assigned parentage using only 4 loci and correctly identified parents 94.3%

of the time. However, sea lamprey show similar variability to the endangered wood stork, which have on average 2 alleles at a loci (Van Den Bussche et al., 1999). It is possible that this low variability of alleles is due to the founder effect, where relatively few adults created the population. Research is continuing to identify other sea lamprey loci that exhibit greater polymorphism. If such loci can be found, this method would be invaluable by allowing researchers to explore in more detail the population dynamics of sea lamprey.

I found no evidence for the suggestion that young ammocoetes segregate from the rest of the population (Beamish and Lowartz, 1996). In the plots from which I collected age-0 ammocoetes, about half (31 of 74) also had older ammocoetes in them.

Ogemaw Creek ammocoetes were larger than those in the Carp River and also grew more between sampling events. Age-0 ammocoetes grew about 2 mm between sampling events in the Carp River, whereas they grew about 4.5 mm in Ogemaw Creek. The Carp River had much higher densities than were found in Ogemaw Creek. The scatter plot of length by density (Figure 7) does show a slight downward trend as densities increase in the Carp River. Increasing density affects growth rates of older ammocoetes (Murdoch et al., 1992; Mallatt, 1983; Morman, 1987) over longer periods of time. However, these differences are just as likely due to cooler water temperatures in the Carp River and possibly a shorter growing season because of its more northerly location.

Ammocoete distributions are aggregated, yet the adaptive cluster sampling design did not decrease the variance of the density estimates more so than a simple random design. This inefficiency of the adaptive design is likely due to age-0 ammocoetes not aggregating to the extent expected. They were not found in high concentrations; in Ogemaw Creek the maximum number collected in a plot was five and in the Carp River, a maximum of 23 were collected in a plot. Therefore, a simple random sampling design is sufficient for estimating densities of age-0 ammocoetes. However, one advantage to the adaptive cluster design is the increased number of animals collected (Thompson, 1992). The neighborhood samples in the Carp River had a higher catch per unit effort (0 – 3.12) than did the random sample plots (0.12 – 0.95); in Ogemaw Creek the catch per unit efforts between the neighborhood and random plots were essentially the same. Hence, if individuals are needed for other parameters of interest, this design can be very effective.

The dredge was an effective device to sample the early age-0 ammocoetes and generally did not kill them. However, processing the dredge material was time consuming and the technique is fairly destructive to the habitat. For these reasons, I do not suggest using this method as a sole means for sampling age-0 ammocoetes. Age-0 ammocoetes are susceptible to the traditional AbP-2 electrofishing method by late summer (mid to late August). With fine mesh paddles, electrofishing is a relatively effective way of sampling these small fish. Hence, I suggest using the dredge method to capture the early age-0 ammocoetes for intense research activities and the AbP-2 electrofisher for routine assessments.

Table 1: Mean densities of age-0 ammocoetes (per m^2) within zones by nest and sampling event.

		Event 1			Event 2			Event 3		
Stream	Nest	A	B	C	A	B	C	A	B	C
Ogemaw	1	0	0	2.67	5.33	0	2.67	2.67	4.00	0
	2	2.67	6.40	2.67	6.67	0	10.67	5.33	9.78	5.33
Carp	1	2.67	10.67	44.27	16.89	35.56	2.67	2.67	0	8.00
	2	5.33	0	3.56	10.67	13.33	24.61	0	0	1.45
Average:		2.67	4.27	13.29	9.89	12.22	10.15	2.67	3.44	3.69

Table 2: Summary of microsatellite loci used in analysis: H(O) is the observed heterozygosity, H(E) is the expected heterozygosity, Excl(1) is exclusionary power without any known parent, Excl(2) is the same as Excl(1) but when one parent is known.

Locus	Number of alleles	H(O)	H(E)	Excl(1)	Excl(2)	Null allele frequency
SGLA210	2	0.485	0.502	0.124	0.187	+0.0135
FGT3	3	0.409	0.366	0.066	0.154	-0.0629
Spl120	2	0.545	0.500	0.123	0.186	-0.0476
SLGA38	8	0.621	0.726	0.301	0.470	+0.0699
GISB15	3	0.385	0.327	0.053	0.160	-0.1001
GISE5	5	0.524	0.466	0.111	0.244	-0.0639
Mean number of alleles per locus: 3.83			Total exclusionary power (first parent): 0.577 Total exclusionary power (second parent): 0.811			

Table 3: Efficiency values for Ogemaw Creek and the Carp River by zone and sampling event.

		Event 1			Event 2			Event 3		
Stream	Nest	A	B	C	A	B	C	A	B	C
Ogemaw	1	--	--	1.00	1.00	--	1.00	1.00	0.56	--
	2	1.00	1.00	1.00	0.63	--	1.00	1.00	0.29	1.00
Carp	1	1.00	0.33	0.38	10.03	0.91	1.00	1.00	--	1.00
	2	1.00	--	4.00	4.00	1.00	0.93	--	--	1.00

Table 4: Estimated abundance's of age-0 ammocoetes in sampling reaches below nests.

Stream	*Nest*	Event 1	Event 2	Event 3
Ogemaw Creek	1	106	318	265
	2	466	689	813
Carp River	1	4,166	3,986	772
	2	643	3,517	105

Figure 1: Locations of study streams.

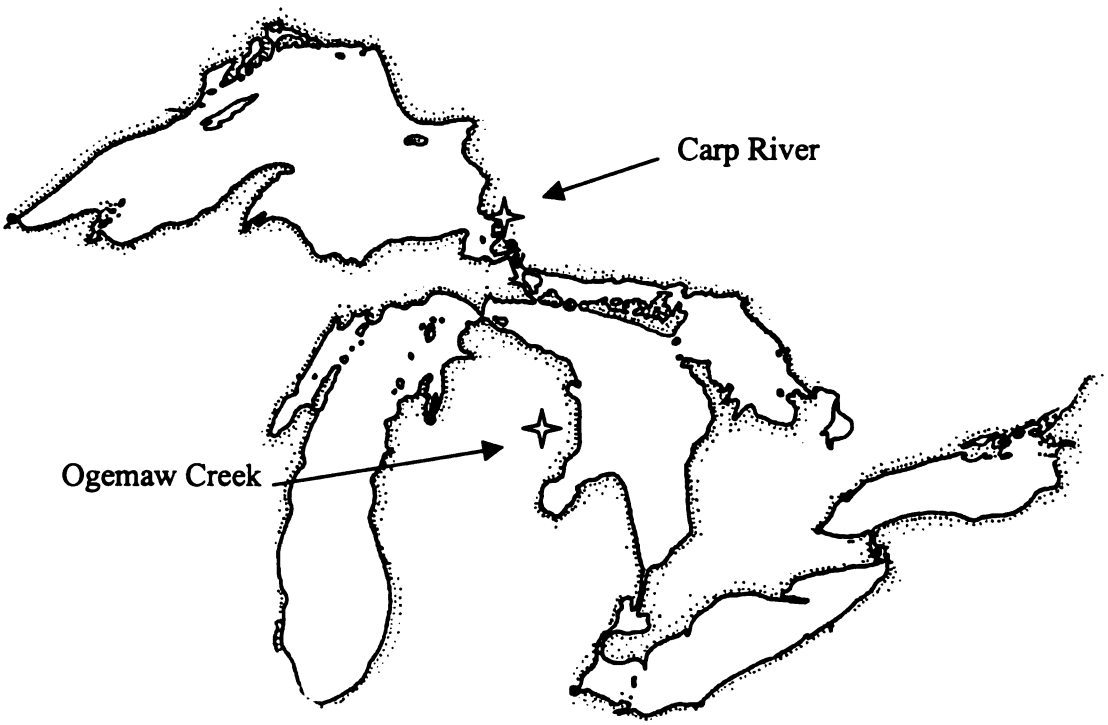


Figure 2: Schematic showing sampling zones. The near zone extends from the nest to 50 m downstream, the middle zone extends from 55 to 155 m downstream from the nest, and far zone extends from 160 to 310 m downstream from the nest. There is a 5 m buffer between each zone.

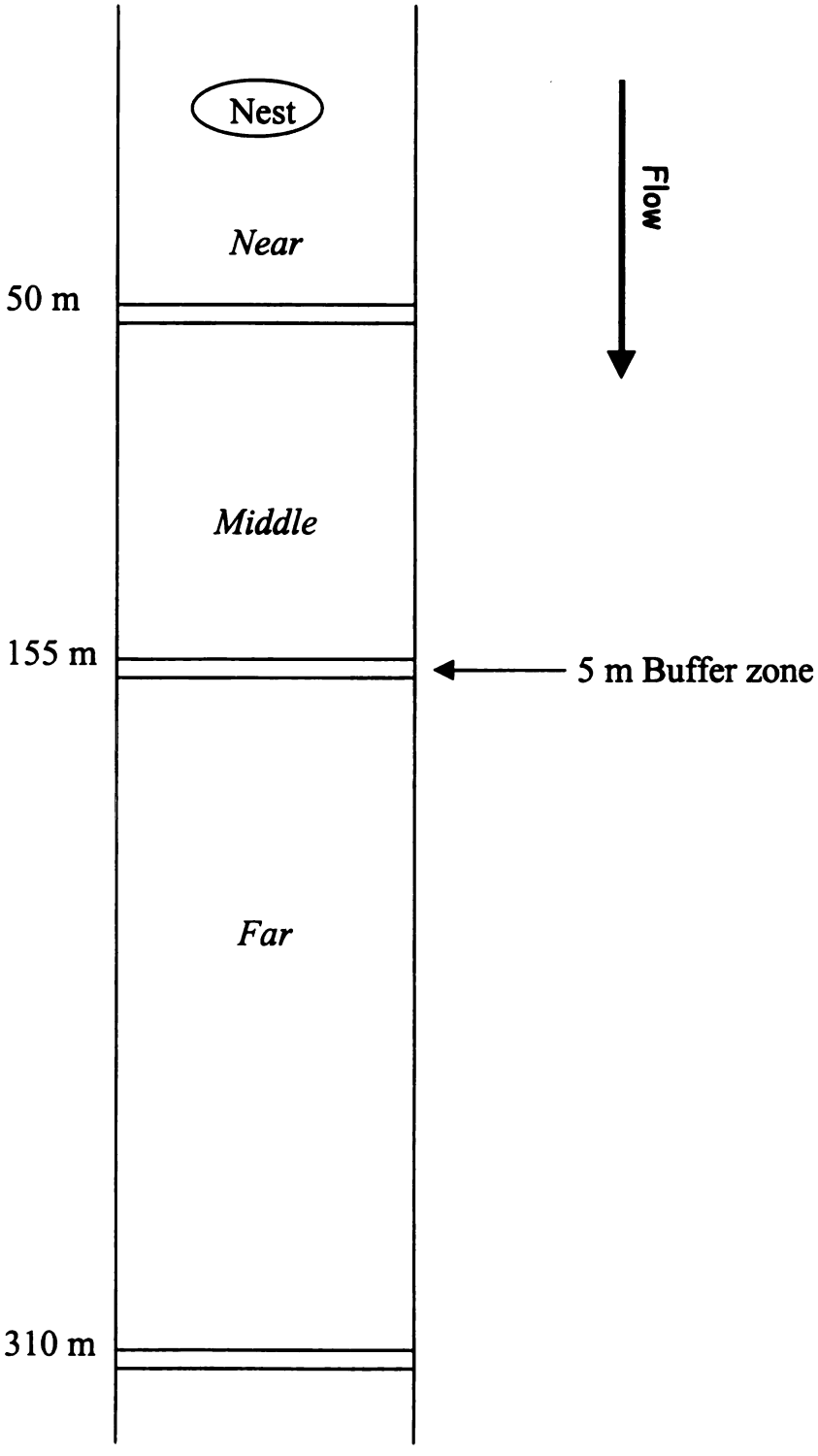


Figure 3: Schematic of adaptive sampling design. Figure A shows the six initial random plots sampled, boxes in gray indicates that at least one age-0 ammocoete was collected, i.e. the condition was met. Figure B shows those same six random plots with the additional sampled neighborhood plots in black.

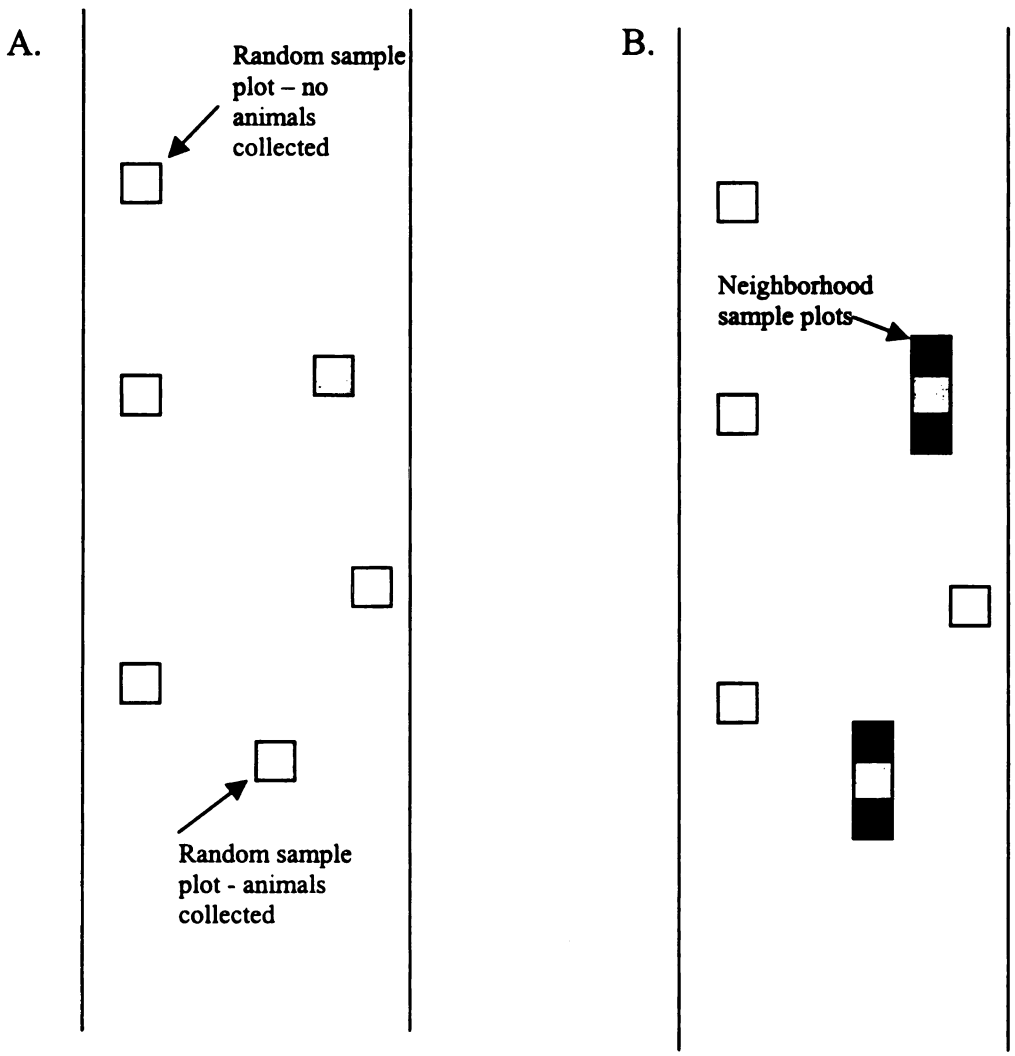
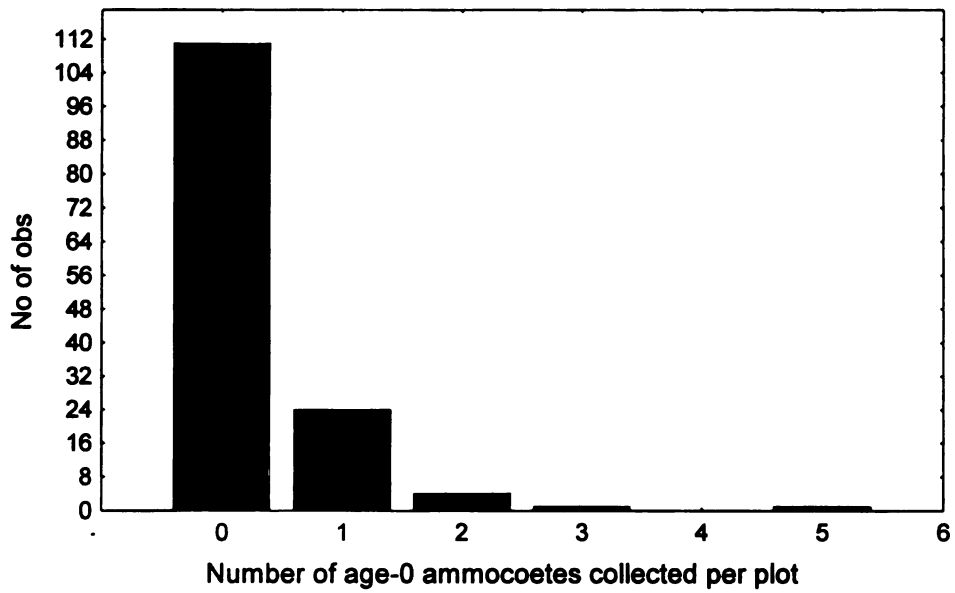


Figure 4: Histograms of ammocoetes collected in Ogemaw Creek (A) and the Carp River (B).

A.



B.

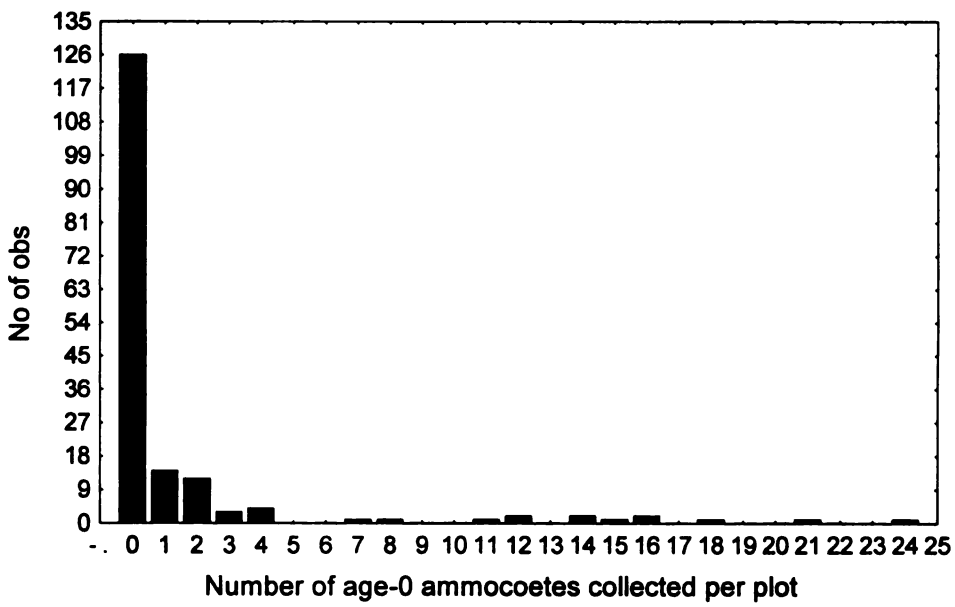


Figure 5: Box plots of the mean densities of age-0 ammocoetes per m^2 by zone for Ogemaw Creek (white boxes) and the Carp River (shaded boxes). The box represents the 25^{th} and 75^{th} quartile, the line the mediam and the whiskers the minmum and maximum.

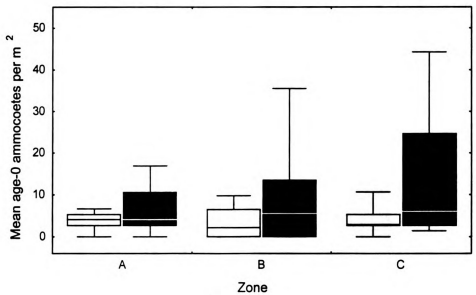


Figure 6: Box plots of the mean densities of age-0 ammocoetes per m^2 by sample event for Ogemaw Creek (white boxes) and the Carp River (shaded boxes). The box represents the 25^{th} and 75^{th} quartile, the line the mediam and the whiskers the minmum and maximum.

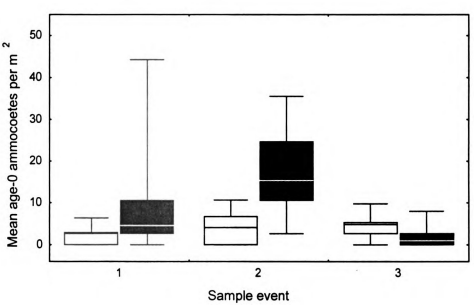
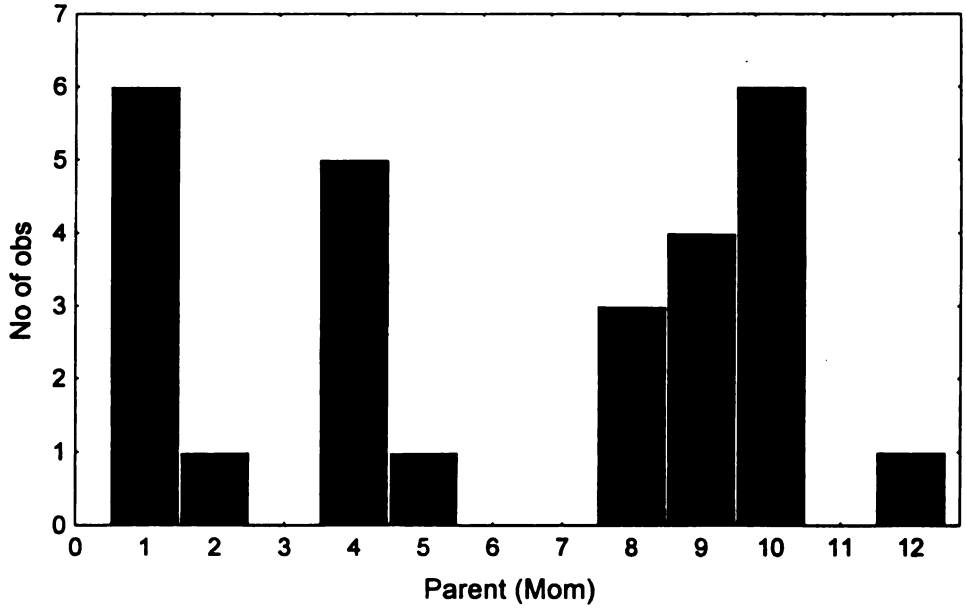


Figure 7: Histogram of the number of ammocoetes associated with each male parent for upstream most nest (A) and downstream most nest (B).

A.



B.

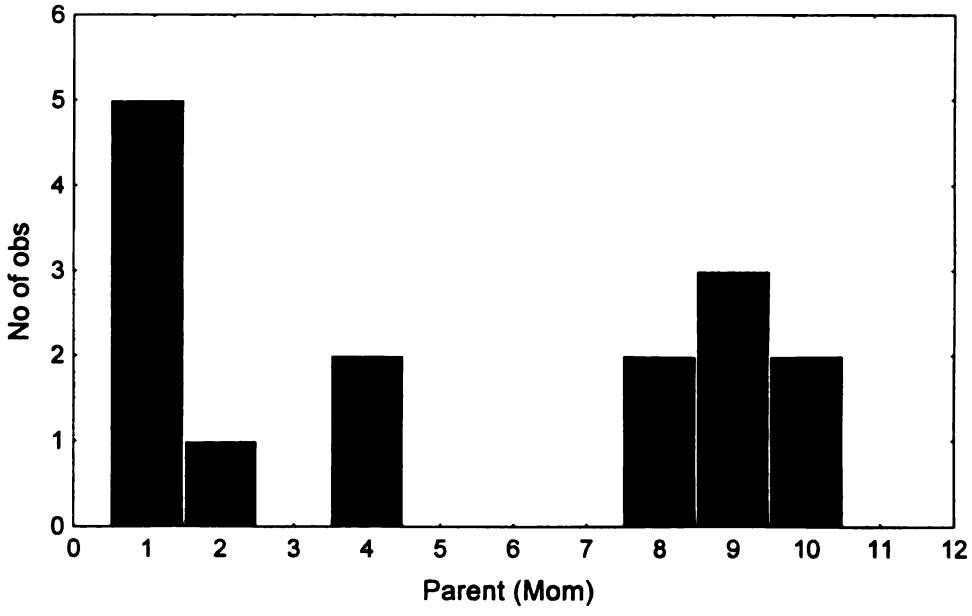


Figure 8: Histogram of values for randomly distributed nest-mate pairs, 1000 simulations. Asterisk denotes the number of nest-mate pairs in observed data.

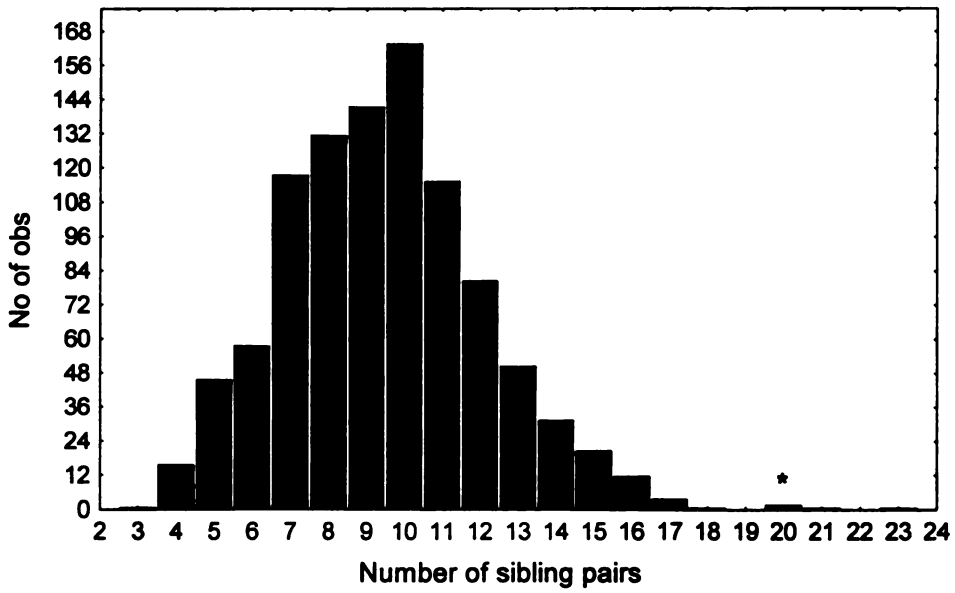
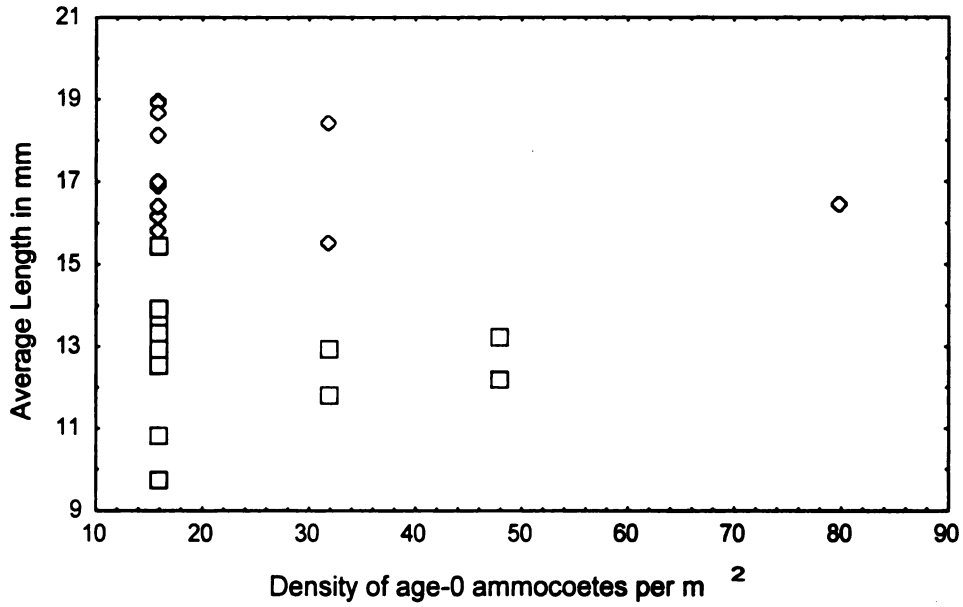
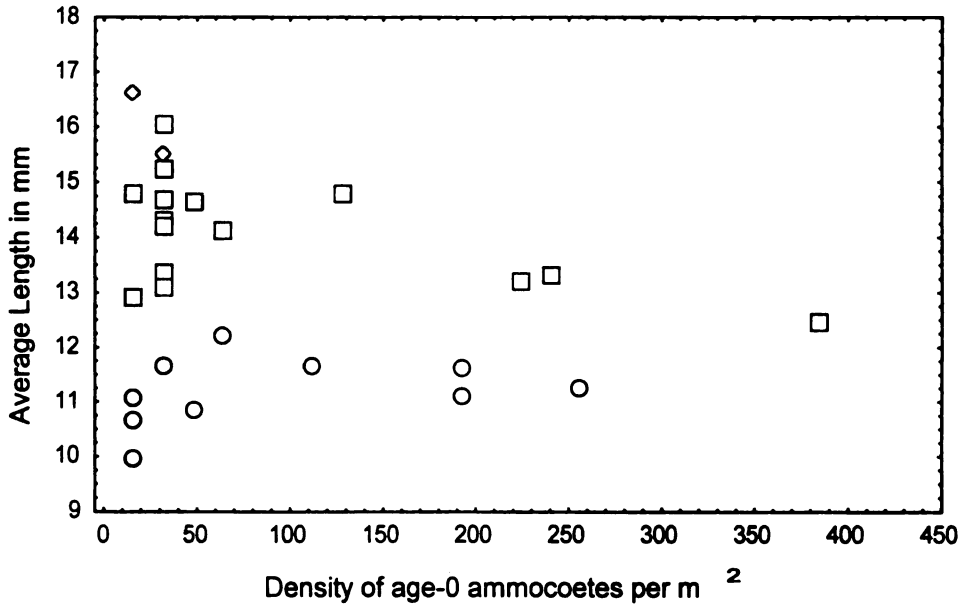


Figure 9: Scatterplot of average ammocoete lengths in mm in relation to the density of the habitat patch in Ogemaw Creek (A) and the Carp River (B). The circles represent ammocoetes during the first sampling event, the squares the second sampling event, and the diamonds the third sampling event.

A.



B.



Chapter 3:
The effects of density on the movements of sea lamprey larvae in the laboratory.

Introduction

The relation between growth and density of sea lamprey ammocoetes is density dependent in aquaria and cages (Mallatt, 1983; Morman, 1987; Murdoch et al., 1992). However, field observations are inconclusive as to the presence or degree of density effects on growth (Jones et al., 2001). These contrary conclusions may be due to the limitations of the enclosed experiments as they do not allow for dispersal. Dispersal may be an important mechanism in lessening the demographic effects of density. To date, no studies have investigated ammocoete dispersal and its relationship to density.

Density is an important mechanism determining dispersal in both fish and aquatic insects (Hume and Parkinson, 1987; Fonseca and Hart, 1996; Kerans et al, 2000). Ammocoetes are benthic suspension feeders and burrow into soft sediments, a behavior similar to suspension feeding stream insects. Stocked steelhead fry dispersal was shown to generally increase with high densities (Hume and Parkinson, 1987). Several insect taxa show density-dependent drift (stoneflies: Walton et al., 1977; black flies: Fonseca and Hart, 1996; Gersabeck and Merritt, 1979; caddisfly: Kerans et al., 2000). Kerans et al. (2000) investigated how density, velocity, and substrate affected dispersal in the

caddisfly *Hydropsyche slossonae* and found it to be conditional on season. Dispersal was density dependent in the spring, however in the fall dispersal increased but was density independent. Understanding the degree to which ammocoetes disperse and the factors affecting dispersal may link laboratory and field studies on growth, and provide managers with a better understanding of sea lamprey population dynamics and behavior.

I examined the following questions: 1) do ammocoetes move / disperse at any density; 2) does density of ammocoetes affect their likelihood of moving; and 3) are there seasonal differences in movement. I conducted trials using age-1 and older ammocoetes (age 1+) but concentrated on age-0 ammocoetes. Densities are highest during the first year of life and hence may be subjected to greater density effects than later stages. In addition, this early life stage often determines population size in fishes (Trippel and Chambers, 1997).

Experimental Design:

Dispersal may be hard to discern from mortality (Le Cren, 1973). Studies in natural systems often can only report the difference in numbers of animals from one time period to the next and generally label this as mortality. Tagging methods can be used to monitor dispersal in the field, however age-0 ammocoetes are too small to use these techniques. In laboratory aquarium experiments, only mortality can be assessed due to the constrained environment.

Therefore, an experimental design was required to monitor movements of individual animals or small groups of animals and to be able to manipulate densities. Because of the

difficulties of conducting this in the field, I designed a laboratory study (adapted from Fonseca and Hart, 1996) that:

1. allowed for movement of ammocoetes,
2. simulated natural stream conditions,
3. and allowed easy monitoring of movement by creating source areas with ammocoetes and sink areas without.

Ammocoetes were placed in replicate artificial streams at three randomly assigned densities: 5, 15, and 30 per experimental unit, equivalent to 80, 240, and 480 ammocoetes per m^2 respectively. The two lower densities are similar to those used in previously published growth and density studies (Mallatt, 1983; Morman, 1987; Murdoch et al., 1992). I conducted thirty replicates for each density of age-0 ammocoetes between August and September 2000. These two time periods were chosen to examine summer and fall seasonal effects. Fifteen replicates were completed for each density of age-1+ ammocoetes from July to September. Fewer trials using age-1+ ammocoetes were conducted because of the emphasis on age-0 ammocoetes, and hence seasonal effects were not tested.

Experimental methods:

Age-0 ammocoete trials:

Age-0 ammocoetes (8 – 26 mm in length) were collected using drift nets (350 μm mesh, for 3 h sets) and an electrofisher (AbP2-backpack electrofisher, University of Wisconsin) in the Trout River, Presque Isle County, a tributary to Lake Huron, in northern Michigan.

Approximately 75 age-0 ammocoetes (11–26 mm in length) were held in each of two 38 L (10-gal) aquaria or holding tanks, filled with sand to a depth of 6 cm. These holding tanks were kept in a water bath at a constant temperature of 18°C. The aerated water in the holding tanks was replaced every other day with filtered Lake Huron water. Every other day, ammocoetes were fed suspended sediments collected from depositional stream habitats that were sieved through a 125 μm mesh screen.

Three oval raceway tanks (Frigid Units, Inc., Toledo, Ohio) were used to create stream-like conditions. The raceways were 2.9 m in length, 40 cm wide, and the overall unit width was 1.6 m (Figure 1). A near-shore pump circulated unfiltered Lake Huron water to produce low flow conditions (~15 cm/sec) in the raceways similar to field conditions. The water was 17 cm deep and water temperature was recorded daily. Natural lighting was not controlled, but was provided from windows around tanks. Four plastic trays (25.5 x 28.5 x 9 cm) filled with 2 cm of beach sand were placed in each tank to provide habitat for ammocoetes. One tray served as a source tray and the other three trays served as sinks to collect dispersing ammocoetes. The sand was replaced with dry sand before each trial. The trays were positioned 50-60 cm apart, with the first (source) tray 1 m away from the water input (Figure 1).

Ammocoetes were introduced into the source tray using an open top and bottom plexis-glass introduction box (20 cm wide x 20 cm long x 22 cm tall), to ensure that all ammocoetes burrowed into the sand before each trial started. The introduction box was sunk into the sand and was only removed after all ammocoetes had burrowed. Trials

began in late afternoon (1400 – 1700 h) and ended the next morning (0800 – 1200 h). Preliminary observations indicated that ammocoetes moved only at night and that movement tended to occur after a single night. Contents of trays were hand-sieved after each trial to find ammocoetes. The number of ammocoetes found in each tray was recorded. Ammocoetes were then returned to the holding aquarium and not reused until 2 days later to reduce stress on the animals.

Age 1 and older ammocoete trials:

Age-1+ ammocoetes (range 33 - 116 mm) were obtained from the US Geological Survey's Hammond Bay Biological Station. These ammocoetes were fed a yeast mixture every other day, which is standard practice for raising age-1+ ammocoetes. Age-0 ammocoetes were not feed yeast because previous studies had shown that they did not feed well on the yeast (W. Swink, USGS, Hammond Bay Biological Station, personal communication). Methods for trials were the same as that described for age-0 ammocoetes (see above).

Data analysis:

The fraction of the initial population that were in each tray was computed. Attempts to normalize these data using an arcsine square root transformation (Neter et al., 1996) were unsuccessful. Hence, I analyzed the data by comparing the fraction in the source and sink trays among densities and season, using a Kruskal-Wallis non-parametric test (Gibbons, 1993; Statistica, StatSoft, Inc., 1998), unless otherwise noted. I tested the null hypotheses that: (1) the fraction of ammocoetes that moved out of the source tray was the

same for each density and season and (2) the fraction of ammocoetes that burrowed into the three sink trays were the same for each density and season. P values less than <0.05 were considered significant.

Results

Age-0:

In August, age-0 ammocoete movement out of the source tray was not different between the density trials ($p>0.8$, $n=33$) (Figure 2). The average percent of ammocoetes that moved out of the source tray ($\pm$SE) was 27.3 ± 7.8 % in the low-density trials, 20.6 ± 4.8 % in the medium-density trials, and 26.4 ± 5.4 % in the high-density trials. Of the ammocoetes that moved, 83.1% were not found in any sink tray and assumed to have been lost down the drain. In the low density trials, ammocoetes were found only in the first sink tray. In the medium and high density trials, ammocoetes were found in all sink trays but in decreasing numbers with increasing distance away from the source tray. The numbers of ammocoetes found in sink trays were not significantly different from each other within each density treatment ($p>0.3$, $n=99$) (Table 1).

In September, age-0 ammocoete movement among the density trials (Figure 2) was significantly different ($p=0.03$, $n=57$). The average percent of ammocoetes that moved out of the source tray ($\pm$SE) was 4.2 ± 1.9 % in low-density trials, 6.3 ± 2.5 % in medium-density trials, and 10.7 ± 2.6 % in high-density trials. Of the ammocoetes that moved in September, 30.1% were missing and assumed to have been lost down the drain. The distribution of ammocoetes in the sink trays was similar to that seen during the

August trials. There were no significant differences ($p>0.3$, $n=171$) in the number of ammocoetes found in sink trays in the different density trials (Table 1).

Movement was generally less in September than in August (Figure 2), moreover, there was a general decline in movement in all densities as temperatures decreased (Figure 3). Of the ammocoetes that moved from the source tray, a significantly larger proportion were found in sink trays in September than in August (Mann-Whitney u test, $p < 0.0001$, September $n=57$, August $n=33$). Ammocoetes were rarely found swimming freely in the raceways at the end of a trial.

Age-1+:

On average, 20 % of age-1+ ammocoetes moved regardless of density ($p>0.9$, $n=45$). Age-0 movements in August were not significantly different than the age-1+ movements (Mann-Whitney U test, $p=0.24$), however age-0 movements in September were significantly different (Mann-Whitney U test, $p<0.05$). Again, there was a general decline in movement in all densities as temperatures decreased (Figure 3). Of the age-1+ ammocoetes that moved, 6.8 % were missing, this was significantly less than in the age-0 August trials (Mann-Whitney U test, $p<0.01$), however it was not different than the number missing in the age-0 September trials (Mann-Whitney U test, $p=0.10$).

Discussion

Approximately a quarter (20 - 25 %) of ammocoetes moved out of the source tray in July and August, regardless of density. Ammocoete movements in all densities were greater

when temperatures were warmer, suggesting that density-independent dispersal predominates, regardless of age. Other fishes also have high drift or movement rates soon after emergence (Atlantic salmon, white sucker, and sea lamprey: Johnston, 1997; multiple species: Copp and Cellot, 1988; Brown and Armstrong, 1985). These results suggest a possible mechanism for the wide dispersal observed in chapter 2. The dispersal process may assist in moving ammocoetes away from nests to discourage clumping.

My data suggest that dispersal differs with water temperatures and possibly season. Because temperature and lighting were not controlled in the experiments, temperature is presumed to be an indicator for seasonal changes, although other factors, such as day length and barometric pressure, may confound these results. Kerans et al. (2000) found that the caddisfly larvae *Hydropsyche slossonae* (fifth instar) exhibited density-independent dispersal in the fall, and density-dependent dispersal in the spring. This caddisfly pupates in late spring and being heaviest at this time do not disperse as frequently. Age-0 ammocoetes showed the opposite pattern in that, dispersal seemed to be controlled by density-independent processes in warm temperatures (e.g. summer) and density-dependent processes in cooler temperatures (e.g. fall). Observations of age-1+ ammocoetes in warm temperatures were similar. Similar to *H. slossonae*, ammocoete movements were greater when density-independent dispersal predominated. Life cycle characteristics may also explain ammocoetes tendency for density-dependent dispersal in cooler temperatures (e.g. September). Early winter is suggested to be a critical time for fish as they seek to build up energy reserves to assist in overwinter survival at a time when food supply is limited. Yap and Bowen (2001, in review) reported that the northern

brook lampreys available food and assimilation efficiency declined from May through August, but increased briefly in September. Cunjak (1988) examined brown and brook trout energy stores over winter and found that in early winter (November – December), both lipid and serum protein levels decreased rapidly, even though food supply was sufficient. Gardiner and Geddes (1980) reported similar results in Atlantic salmon from October to December. The amount of fat or energy stored in tissues before the early winter period may determine the overwinter survival of fish. These observations suggest that when food is more limiting, ammocoete dispersal may be more sensitive to density.

Body size is a major factor in determining overwinter survival, especially for young-of-the-year fish because they are at their smallest size (Shuter and Post, 1990). Because sea lampreys hatch in mid- to late-summer and grow relatively slowly, the fall may be a crucial time for ammocoetes to feed. As previously mentioned, growth is affected by density when ammocoetes (age-1+) are confined to tanks or cages (Mallatt, 1983; Morman, 1987; Murdoch et al., 1992). Mallett (1983) found that even at high food concentrations, increasing density inhibited ammocoete growth, and suggested that ammocoetes might release "some growth-inhibiting compound into the surrounding sediments". Bowen (personal communication) proposes that ammocoetes' assimilation efficiency decreases with increasing density, causing a decline in growth rates. The density-related-dispersal behavior shown in my experiments may increase or enhance survival by allowing ammocoetes to more efficiently feed before winter by finding lower densities of ammocoetes. Such dispersal may also provide decreased interactions between ammocoetes during winter; these interactions could increase activity levels and

consequently deplete energy reserves faster, as shown in pumpkinseeds (Bernard and Fox, 1997).

The average densities of age-0 ammocoetes reported in Chapter 2 (5 to 10 per m^2) are low compared to the low density used in these experiments (80 per m^2). Densities were reported as high as 384 per m^2 (Chapter 2), but infrequently. It is possible that the process of density-independent dispersal early in the season and ammocoetes ability to disperse widely, allow individuals to establish low densities such that density-dependent dispersal is not very prevalent. The densities reported in Chapter 2 from streams where the spawning population size was kept very low may be much lower than is seen in streams open to adult migrations, however.

A limitation of my experiments is the use of sub-optimal habitat (sand) in the source and sink trays. It is possible that larvae may be able to withstand higher densities in more optimal habitats (type 1 = fine, depositional sediments). However, because of the short time period (1 night) over which I saw ammocoete movement and Mallett's (1983) observations of decreased growth even with high food concentrations, it seems unlikely that more optimal habitat would have had any major effect to change these results. In addition, the results of this study suggest that the ability to gain body mass, and possibly the accumulation of lipids, as water temperatures decline may be an important factor in overwinter survival. I proposed that larvae move more at high densities because they do not grow freely, and furthermore suggest that this growth and hence accumulation of fats, i.e. lipids, determines survival. If proven, percent lipids in age-0 ammocoetes in the fall

could provide a key variable in determining recruitment for that year-class. Further work is needed to test this hypothesis.

Table 1: Number of ammocoetes that moved out of source trays and where they settled for each density and month.

Month	Density	Number of trials	Total individuals used	Number moved	Destination			
					Sink tray 1	Sink tray 2	Sink tray 3	Missing
August	Low	11	55	15	1	0	0	14
	Medium	11	165	34	3	0	2	29
	High	11	330	87	7	5	5	70
September	Low	19	95	4	1	0	0	3
	Medium	19	285	18	5	3	3	7
	High	19	570	61	18	16	12	15
Summary (August + September)	Low	30	150	19	2	0	0	17
	Medium	30	450	52	8	3	5	36
	High	30	900	148	25	21	17	85

Figure 1: Diagram of raceway tanks and layout of the source and sink trays.

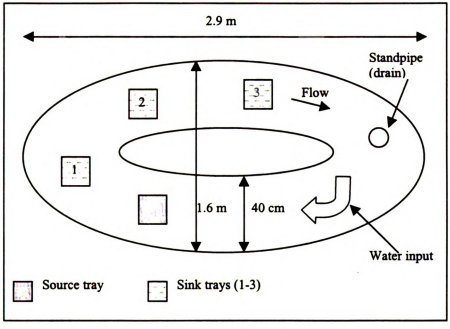


Figure 2: Average percent of ammocoetes that moved out of the source tray in August (n=11) and September (n=19) for each density. Error bars represent ± 1 standard error.

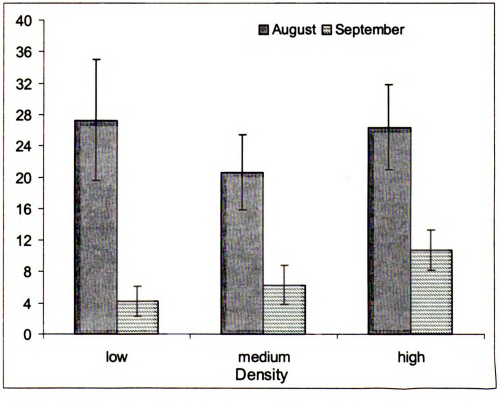
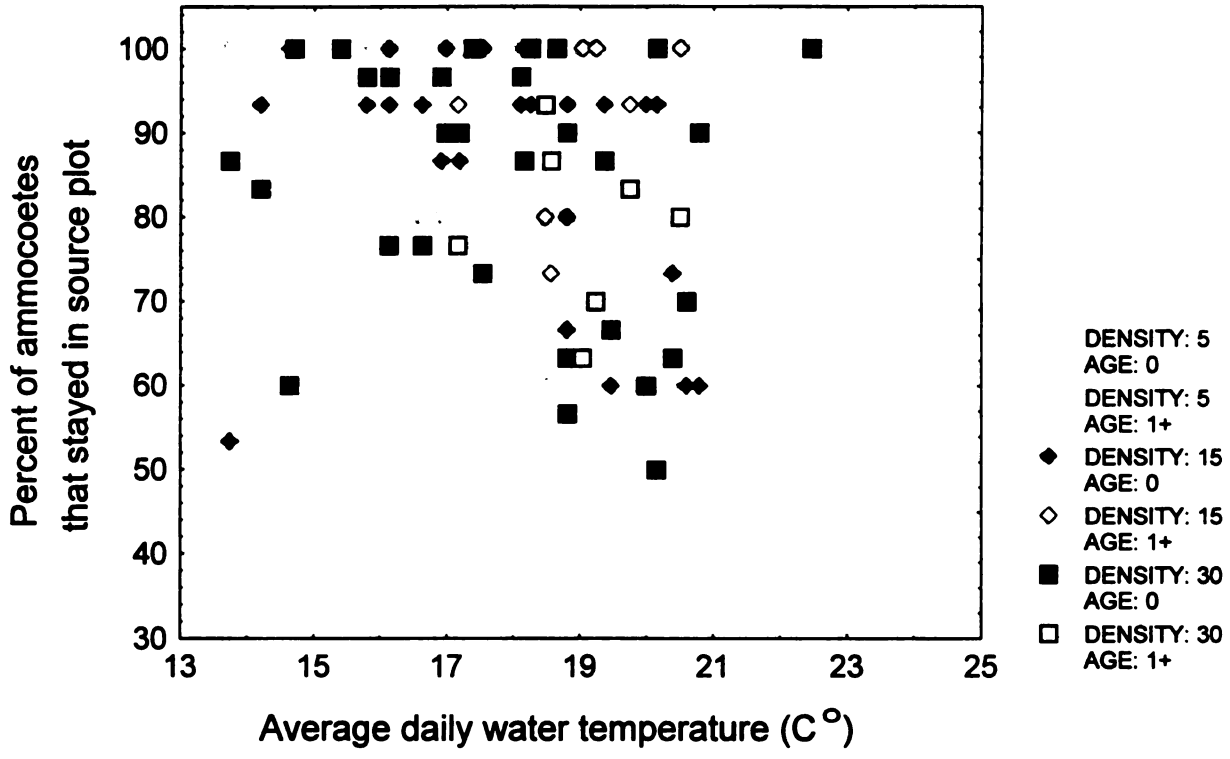


Figure 3: Percent of ammocoetes that did not move out of source tray by average daily water temperature for all densities and ages.



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