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Distribution and Factors Affecting Survival of Sea Lamprey Eggs In and Out of Nests

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Distribution and Factors Affecting Survival of Sea Lamprey Eggs In and Out of Nests

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Project Completion Report

Lake Champlain Basin Program

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Executive summary

Management of sea lamprey in the Lake Champlain basin is currently dependent upon use of larval lampricides and barriers to block spawning migrations. The management agencies in the basin are dedicated to reduction of lampricide use, focusing on exploration of alternative methods of sea lamprey control. We have constructed a stage-based population viability model for sea lamprey that yields an estimate of reductions in the number of parasitic lamprey resulting from a variety of alternative control methods, used alone or in combination. Preliminary work on the model has highlighted gaps in our understanding of lamprey life history. Without an adequate understanding of survival constraints at each life stage, it is impossible to accurately predict changes in population size resulting from management efforts. One of the biggest gaps in our knowledge is egg survival. The purpose of the proposed work was to quantify factors that affect egg survival, particularly retention in the nest, the distance eggs drift from the nest, substrate type on which the eggs come to rest, and egg predation by fish in relation to current and substrate type. The data from this study will be used in the completed, stochastic version of the model to provide stream-specific estimates of parasite production under different management scenarios using current and alternative control methods. The objectives of this study were to:

1. Estimate the numerical and spatial distribution of lamprey eggs in and out of the nest after spawning, related to stream current during the spawning period.
2. Determine the survival probability of sea lamprey eggs in and out of nests in relation to substrate type.
3. Quantify fish and crayfish predation on sea lamprey eggs in the laboratory in relation to presence or absence of current, substrate type, and predator species.

Four sea lamprey nests in tributaries to Lake Champlain were excavated to enumerate all eggs and estimate survival. Numbers of egg and prolarvae in nests averaged 10,142, ranging from 4,440 to 21,856; this represents 6.6 to 32.5% of eggs from a single female. Survival of eggs in nests averaged 72.7% for all nests, ranging from 55.6 to 94.3%. Field sampling demonstrated that natural densities of sea lamprey eggs on spawning gravel directly downstream from nests was low (1.9 eggs/m^2) and density on depositional areas was 105.7 eggs/m^2; viability of these eggs was near 0. Egg loss from exclosure boxes seeded with eggs was less in spawning gravel (65.6% ± 7.4%) than in silt (93.4% ± 5.3%; $p < 0.0001$); egg loss was not impacted by the presence of a cover to exclude larger fish predators. Average hatching success for all eggs introduced to spawning gravel was 3.4%; no eggs survived to hatch on silt. Egg loss appeared to be related to stream discharge, such that more eggs are displaced during periods of high flow. In the lab, predation was examined on different substrates, (no substrate, silt, sand, spawning gravel, and cobble) and by different species; crayfish (six replicates), logperch (three replicates), creek chub (three replicates), and white sucker (four replicates). Substrate type had no effect on the numbers of eggs consumed by predators, but different predators consumed significantly different numbers of eggs; crayfish consumed an average of 74% of available eggs, creek chub consumed an average of 47.2%, white sucker consumed an average of 8.7%, and logperch consumed an average of 3.0%. Survival of eggs reared in laboratory flumes was significantly different among substrates (F-ratio = 27.74, df = 2, $p< 0.0001$). Egg survival on silt (69.2%) and sand (50.8%) was significantly higher than survival on spawning gravel (19.1%). The contradiction between field and laboratory survival of eggs on silt is likely due to the ‘ideal’ conditions in the laboratory; in the flumes there was little organic material and no low-flow areas that might have generated low oxygen levels that would suffocate eggs. Results indicate that predation rates on sea lamprey eggs outside the nest are high and that, in the laboratory, substrate type alone has little impact on egg hatching success. Given the low retention of eggs in nests, egg mortality is likely a primary determinant of year class strength. Any production of sea lamprey outside of the nest likely occurs under low stream discharge conditions from eggs that are deposited on spawning gravel.

Parameters generated from this work (proportion of eggs remaining in the nest, survival of eggs in the nest, survival of eggs outside the nest, all expressed as ranges) will be used as inputs for the life history model for sea lamprey in Lake Champlain. Future studies to better quantify the relationship between stream discharge and egg retention in nests would be valuable. This may require several years of data collection in order to adequately sample high- and low-flow conditions in streams, which were more extreme than we could replicate in the laboratory. Field observations over a number of years suggest that recruitment from a single stream could, in years of very high flow, be eliminated due to nest destruction. Measurement of dissolved oxygen directly at the substrate:water interface in depositional areas would be valuable for understanding the low survival of lamprey eggs in these areas.

Status

The project was completed in fall, 2005; the laboratory and field studies are presented in separate report sections, below, and will be submitted for publication in a peer-reviewed journal in April, 2006.

FACTORS AFFECTING SEA LAMPREY (*PETROMYZON MARINUS*) EGG SURVIVAL, AS MEASURED IN THE LABORATORY

Abstract

Sea lamprey (*Petromyzon marinus*) are a nuisance parasitic fish that have hindered efforts to restore salmonid populations in Lake Champlain. Control efforts benefit from improved understanding of factors that affect recruitment. For example, the majority (85%) of sea lamprey eggs are washed out of the nest; survival rates of these eggs are currently unknown. We used laboratory studies to examine predation and incubation habitat as factors affecting sea lamprey egg survival outside of the nest. Predation was examined on different substrates, (no substrate, silt, sand, spawning gravel, and cobble) and by different species; crayfish (six replicates), logperch (three replicates), creek chub (three replicates), and white sucker (four replicates). Predators were introduced to aquaria containing 100 or 200 eggs and allowed to forage for 18 h. Results show that substrate type has no effect on the numbers of eggs consumed by predators, but different predators do consume significantly different numbers of eggs (F-ratio = 11.12, df = 3, $p < 0.0001$). Crayfish consumed an average of 74% of available eggs, creek chub consumed an average of 47.2%, white sucker consumed an average of 8.7%, and logperch consumed an average of 3.0%. We examined survival of sea lamprey eggs to stage 12 on three different substrates: silt, sand, and spawning gravel. Survival of eggs was significantly different among substrates (F-ratio = 27.74, df = 2, $p < 0.0001$). Egg survival on silt (69.2%) and sand (50.8%) was significantly higher than survival on spawning gravel (19.1%). Results indicate that predation rates on sea lamprey eggs outside the nest are high and that, in the laboratory, substrate type alone has little impact on egg hatching success. Given the low retention of eggs in nests, egg mortality is likely a primary determinant of year class strength.

Introduction

The sea lamprey (*Petromyzon marinus*) has been implicated in the decline of fish stocks in the Great Lakes and impeding efforts to restore salmonid populations in Lake Champlain by causing increased fish mortality (Smith and Tibbles 1980; Marsden et al. 2003). Sea lamprey are a parasite primarily on soft-scaled fishes such as lake trout (*Salvelinus namaycush*) and salmon (*Salmo* and *Oncorhynchus* spp.). Various forms of population control have been employed since the early 1950s in an effort to reduce parasitic populations in the Great Lakes and Lake Champlain. Currently, lamprey control follows an integrated pest management approach, applying all feasible control techniques. Primary control methods are chemical treatments with larvicides (3-trifluoromethyl-4-nitrophenol (TFM) and 2'5-dichloro-4'nitrosalicylanilide (5% granular Bayluscide)) and barriers in tributaries to block and remove spawning runs of sea lamprey. Population modeling has become a useful tool to evaluate population response to multiple control techniques (Jones et al. 2003; Howe et al. 2004). A better understanding of the population dynamics during early life history is required to explain the variable stock recruitment relationship in sea lamprey populations (Jones et al. 2003).

To better understand recruitment dynamics, we need a thorough understanding of mortality rates of eggs and larvae. Past studies of the early life history of sea lamprey have documented fecundity, spawning behavior, and larval production (Applegate 1950; Wigley 1959; Manion 1968; Manion1972; Manion and Hanson 1980). Sea lamprey spawn in nests constructed in stream gravels; however, only a small proportion (10-15%) of eggs remain in the nest for incubation (Manion and Hanson 1980; unpublished data). No attempts have been made to account for the majority of the eggs produced by sea lamprey that are not retained in the nest. Mortality of eggs and larvae can be caused by abiotic factors including temperature, oxygen availability, rearing habitat, or turbulence, and biotic factors including predation and food availability. Predation presents a serious threat to the survival of sea lamprey eggs and prolarvae, particularly those that have been washed from the protection of the nest. The small size of the eggs (1mm) makes them vulnerable to many species of fish as well as benthic invertebrates such as crayfish (*Orconectes* spp.; Paradis et al. 1996). Predation also has the potential to be the major cause of mortality in emerging larvae; because sea lamprey larvae filter microorganisms and organic detritus from the water, starvation in this stage is unlikely. Year class strength in many fish populations is determined in the early life stages (Werner and Gilliam 1984; Wootton 1998). The dynamics of the early life history of sea lamprey populations therefore should be an important factor in establishing the year class strength of the parasitic population. Studies have attempted to estimate the larval production of adult sea lamprey, however previous efforts have focused only on those surviving offspring within or emerging from individual nests and ignored the high proportion of eggs that are not deposited in the nest (Applegate 1950; Manion 1968; Manion and Hanson 1980). Even low survival in the high proportion of eggs washed from the nest could be a significant addition to the future parasitic population.

The purpose of this study was to identify potential biotic and abiotic sources of sea lamprey egg mortality in a laboratory setting. In particular, we focused on predation and the effect of substrate on egg incubation. Predator species were chosen for inclusion in this experiment based on their abundance as bycatch in sea lamprey traps in tributaries of Lake Champlain. Sea lamprey are trapped annually in several Lake Champlain tributaries as part of annual control efforts. Traps are placed downstream and within 1 km of sea lamprey spawning substrates. Species captured in high numbers in the traps were assumed to be present on the sea lamprey spawning grounds and thus are potential predators of eggs that drift downstream from the nests as well as eggs in nests. Substrates used duplicated the range of substrate types found in spawning streams.

Methods

All experiments were conducted at the Rubenstein Ecosystem Science Laboratory, University of Vermont, Burlington, Vermont.

Egg predation

Species included in egg predation experiments were creek chub (*Semotilus atromaculatus*) (59 – 122 mm total length), logperch (*Percina caprodes*) (52 – 98 mm total length), white sucker (*Catostomus commersoni*) (77 – 125 mm total length), and crayfish (*Orconectes spp*.) (16.7 – 28.3 mm carapace length). The common shiner (*Luxilus cornutus*) is also abundant as bycatch in sea lamprey traps, but was not included in this experiment due to difficulties in keeping this species in the lab. Logperch used in experimental trials were captured by net in nearshore waters of Lake Champlain. All other fishes, including female sea lamprey, were collected in sea lamprey traps used by the U. S. Fish and Wildlife Service as part of annual control efforts. Crayfish used in experimental trials were captured in spawning streams with a backpack electrofishing unit. Predators were held in 190 L aquaria for less than 10 d prior to being used in experimental trials. Species held in the lab were fed commercial fish food every other day; food was not withheld prior to the onset of egg predation experiments to avoid artificially high levels of predation due to starvation.

Experimental units were 23 cm x 35.5 cm x 22 cm, 19 L plastic containers. Each of five substrate types, no substrate, silt, sand, spawning gravel, and cobble, were added to two experimental containers. Silt consisted of particles < 300 μm approximately 3 cm deep, sand was standard playground sand approximately 3 cm deep, sea lamprey spawning gravel was 31 mm – 83 mm in diameter with a mean of 53 mm, and cobble consisted of larger gravels averaging 101 mm in diameter across the longest axis. An air stone was added to each aquarium to supply oxygen. Approximately 30 min prior to the start of each trial, 100 unfertilized sea lamprey eggs that previously had been stripped from a ripe female were added to each of the ten aquaria. Predators were then haphazardly selected from the holding tank and measured (total length of fish, carapace length of crayfish), then randomly assigned to one of the tanks in each pair of substrates via coin flip. Predators were allowed to acclimate in a large aquarium net in the experimental chamber for 15 minutes before being released. Only one predator was added per treatment container. Covers were placed on the experimental containers to prevent escapement. Predators were left in the experimental aquaria for 18 h, from 1515 to 0900 the following day. This period of 18 hours encompassed four potential feeding periods light, dusk, dark, and dawn. Predators were then removed, and all substrates were sieved to retrieve all remaining eggs. Treatments that did not contain predators were used to assess efficiency of egg retrieval. Three trials were conducted with logperch and creek chub, four trials with white sucker, and six trials were conducted with crayfish. Two hundred eggs were used in the final four crayfish experiments because nearly 100% were consumed in the first two trials conducted with 100 eggs.

Egg survival

An experimental hatching system of stream troughs was constructed using rain gutters with a recirculating water supply system to examine egg survival in relation to substrate. Each stream trough was approximately 1.5 m long and 13 cm wide and was divided by 363 μm nitex mesh panels into four chambers. Three chambers were 30 cm in length, and the fourth, upper-most chamber contained the water inflow and was not used for experimentation. The complete system was composed of four stream troughs and thus 12 chambers capable of holding substrate. Hatching success of sea lamprey eggs was tested on three of the substrates used in the predation experiment: silt, sand, and sea lamprey spawning gravel. Cobble was not used because the cobbles were too large to fit sufficient numbers into the troughs. Approximately 2 cm of silt, sand, or a monolayer of spawning gravel was placed in the chambers of the first three stream troughs following a Latin square design, with one substrate in each position in each stream trough (Figure 1). In the fourth stream trough, silt was placed in the center chamber, sand was placed upstream, and spawning gravel was placed downstream. The fourth stream trough was set up to test the effect of silt on the other substrates in the event that the water flow transported large amounts of silt downstream. Silt was added to all stream troughs first so that the other chambers could be cleaned before substrates were added to prevent silt from fouling the other treatments.

Spawning sea lamprey were collected by hand from nests in Lewis Creek, VT, on June 1, 2005 and transferred to the laboratory where they were held in circular 1500 L tanks. The first trial was initiated on June 3, 2005. A ripe female lamprey was removed from the tank and eggs were stripped directly into an 18 cm glass culture dish containing approximately 200 ml of water. Two mature male lamprey were removed from the tank and milt stripped directly into the dish containing the eggs. After the second male was stripped, the bowl was swirled to achieve thorough mixing of gametes (Languille and Hall 1988; Ciereszko et al. 2000). After thorough mixing, eggs were washed with fresh dechlorinated water and 1 ml of eggs measured in a 10 ml graduated cylinder was added to each chamber in the hatching system. Silt and sand treatments were stirred after eggs were added to simulate burial by deposition. Three 1-ml samples of eggs were preserved to estimate the number of eggs in each chamber. A 1-ml sample of eggs was also added to the uppermost chamber in each stream trough to act as a control treatment for each stream trough. Temperature was monitored daily to ensure that it remained in the optimal range for sea lamprey egg development (16–25ºC; McCauley 1963; Piavis 1961, 1971). During the rearing period, temperature was maintained between 18 and 22 ºC. Eggs were allowed to incubate for seven days before the substrate in each chamber was removed and sieved to recover all eggs. Once eggs were free of substrate they were preserved in 5% formalin for later examination. Eggs were examined under a stereomicroscope and deemed dead or alive using developmental staging criteria described by Piavis (1961, 1971). By the seventh day surviving embryos were in stage 12 (head formed) or 13 (pre-hatching). Embryos that had not progressed from stage 10 were considered dead. The experiment was repeated on June 24, 2005. The second trial lasted 10 days to allow eggs to incubate until hatching. To keep results consistent, all embryos that had progressed to stage 12 were considered alive.

Statistical methods

All analyses were conducted using JMP (version 5.1.2; SAS Institute, Inc., Cary, NC, 1989-2005) software with significance levels set at $\alpha = 0.05$ (SAS Institute 2004). Despite the fact that the hatching experiments were designed as a Latin square, data were analyzed as fractional factorial designs so that data from all 12 chambers could be analyzed together and because high order interactions were assumed to be 0. Predation experiments were also analyzed as a fractional factorial using ANOVA to test the main effects of substrate, species, and length on consumption rate as well as the length-species interaction. The dependent variable, percent of eggs consumed, was arcsine transformed to meet normality assumptions of the ANOVA. Tukey’s HSD was used to test all pairwise comparisons between species.

A one-way ANOVA was used to test the main treatment effects of substrate on hatching success using stream trough number and control hatching success as co-variants. The dependent variable percent alive was square root transformed to meet normality assumptions of the ANOVA. Tukey's HSD test was used to test all pairwise comparisons between substrates.

Results

Egg predation

The overall ANOVA testing substrate, species, length, and length-species interaction effects on egg consumption was significant (F-ratio = 12.14, df = 11, p <0.0001). The effect of substrate type was not significant at the 0.05 level (F-ratio = 1.6, df = 4, p < 0.187). Different species consumed significantly different proportions of available eggs (F-ratio = 11.1, df = 3, p <0.0001). Length (F-ratio = 6.9, df = 1, p <0.011) and species*length interaction (F-ratio = 5.0, df = 3, p <0.003) were also a significant factors in the model (Table 1). Multiple comparison tests highlighted the differences in consumption rates between species (Table 2). Across all substrates, crayfish (mean consumption rate of 74%) and creek chub (mean consumption rate of 47.2%) consumed a significantly higher proportion of available eggs than logperch (3.0%) and white sucker (8.7%). Multiple comparison tests also showed that substrate types were not significantly different from one another with respect to consumption rates. Though predator size was significant in the overall model, its effects are largely due to length differences in crayfish. When crayfish are removed from the model, length and the length*species interaction were no longer significant (F-ratio = 1.322 df = 1, p< 0.257; F-ratio = 0.3826 df = 2, p< 0.685). Control treatments indicated that all eggs were easily recovered from experimental aquaria (88 - 100% recovered) and there was no need to correct consumption proportions for eggs lost due to recovery error (Figure 2).

Egg survival

Mean survival of eggs was 17.5% on spawning gravel, 47.4 % on sand, and 67.5% on silt. The overall ANOVA testing effects of substrate type and stream trough on hatching success was significant (F-ratio = 10.18, df = 6, $p < 0.0001$). Effects tests showed that stream trough effects were not significant (F-ratio = 0.73, df = 3, $p \leq 0.548$), but substrate had a significant effect on hatching success (F-ratio = 27.74, df = 2, $p < 0.0001$; Table 3). Multiple comparison tests revealed that egg survival on silt (67.5%) and sand (47.4%) was significantly different from egg survival on spawning gravel (17.5%), but egg survival was not significantly different between silt and sand (Table 4).

Discussion

Our results indicate that both predators and rearing environment can significantly affect sea lamprey egg survival. Predation has the potential to be a major factor in sea lamprey egg mortality, and may affect the highly variable stock recruitment relationships that are present in sea lamprey populations (Jones et al. 2003). Previous investigators suggested that predation and rearing environment could be factors in sea lamprey egg survival, but did not provide quantitative data (Applegate 1950; Manion 1968; Manion and Hanson 1980). Manion (1968) noted logperch and small rainbow trout as egg predators during spawning and sampling. Applegate (1950) also notes the vulnerability of eggs not deposited in the nest to "predation by small fishes" and "suffocation by silt deposition." The results of this study show that predation by small stream fishes and crayfish could be a major source of egg mortality.

Gape limitation is likely not a major impediment to predation, even by small fishes, due to the small size of sea lamprey eggs (~ 1 mm), and our results that confirm that length of predator is not a significant effect in predicting predation rate. Among the species tested here, crayfish are the greatest consumers of sea lamprey eggs, capable of consuming at least 200 eggs in an 18-h period. Creek chubs also consumed nearly 50% of those eggs available to them in an 18-h period. Contrary to the findings of Savino and Miller (1991), who found that substrate size had an effect on consumption rates of crayfish, (*Orconectes virilis*), feeding on lake trout eggs and larvae, we found that substrate had no effect on consumption rates; therefore, eggs could be vulnerable in any habitat.

The species composition of the system in which sea lamprey eggs are deposited could have a major impact on survival. Sea lamprey spawning tributaries in the Lake Champlain basin appear to vary with respect to species composition. Anecdotal evidence suggests that some streams have an abundance of crayfish (Stonebridge Brook and Malletts Creek) while others appear to have low abundance of crayfish, but high abundance of other species such as logperch (Mill Brook) (USFWS Lake Champlain Fish and Wildlife Resources Office, unpublished data). Results suggest that the species composition of the spawning tributary could have a great impact on egg survival, which could in turn affect recruitment.

The results of this study also show that the habitat in which eggs are deposited may not have adverse effects on survival. Sea lamprey eggs that were incubated buried in fine silt survived at a higher rate than those incubated without substrate. This finding indicates that suffocation by silt may not be a major factor influencing mortality of sea lamprey eggs. The stirring up of fine silt and sand particles during the spawning act may be an important process used to separate eggs from one another, functioning to help prevent mortality due to fungus in the nest. Eggs sampled from sea lamprey nests often are covered with fine particles of silt and sand (personal observation). Other studies have shown that eggs of walleye (*Sander vitreus*) do survive to hatch when deposited on silt and detritus, but survival rates are lower than when deposited on sand and gravel (Corbett and Powles 1986). Increased mortality of eggs reared in spawning gravel in this study may be the result of increased fungal growth due to clumping of the eggs; deeper gravel layers may reduce clumping. Though silt alone may not be a factor in egg mortality, this study did not test the effects of oxygen deprivation, due to decomposition of organic material, which may occur in depositional areas in spawning streams. Sea lamprey eggs collected by the authors in depositional areas containing organic material did show high mortality. Future studies should also consider the effect of stream turbulence as well as oxygen deprivation on egg mortality.

Acknowledgements

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Table 1. Analysis of variance table from predation experiments: effects of species type, substrate type, length, and length species interaction on consumption of sea lamprey eggs by four species of egg predator.

Source	DF	Sum of Squares	F-Ratio	P-value
Species	3	3.95	11.1	≤ 0.0001
Substrate type	4	0.753	1.6	≤ 0.187
Length	1	0.818	6.9	≤ 0.011
Species*length	3	1.78	5.0	≤ 0.003
Error	67	7.93		
Total	78	23.7		

Table 2. Results of multiple comparison test to identify differences in proportion of sea lamprey eggs consumed between species. Mean is arcsine transformed % eggs consumed. Species not connected by the same letter are significantly different.

Species				N	Mean
Crayfish	A			6	0.9651
Creek chub		B		3	0.5899
White sucker		B	C	4	0.1237
Logperch			C	3	0.0300

Table 3. Analysis of variance table for hatching experiments: effect of substrate type, stream trough, and control rates on hatching success of sea lamprey eggs.

Source	DF	Sum of Squares	F-Ratio	P-value
Control	1	0.034	2.40	≤ 0.140
Stream trough	3	0.031	0.73	≤ 0.548
Substrate	2	0.787	27.74	≤ 0.0001
Error	17	0.241		
Total	23	1.11		

Table 4. Results of the multiple comparison tests to identify differences in hatching success on different substrate types. Mean is square root transformed survival rate. Substrates not connected by the same letter are significantly different.

Substrate			N	Mean
Silt	A		4	0.3852
Sand	A		4	0.6802
Spawning gravel		B	4	0.8196

Figure Captions

Figure 1. Schematic of sea lamprey egg rearing experimental design. Arrows represent recirculating water flow.

Figure 2. Effects of substrate treatment on mean number of eggs remaining in experimental units after 18 hours for both control (no predator) and treatment (predator) conditions for each species tested a. (logperch), b.(white sucker), c (creek chub), and d.(crayfish). Error bars represent standard error.

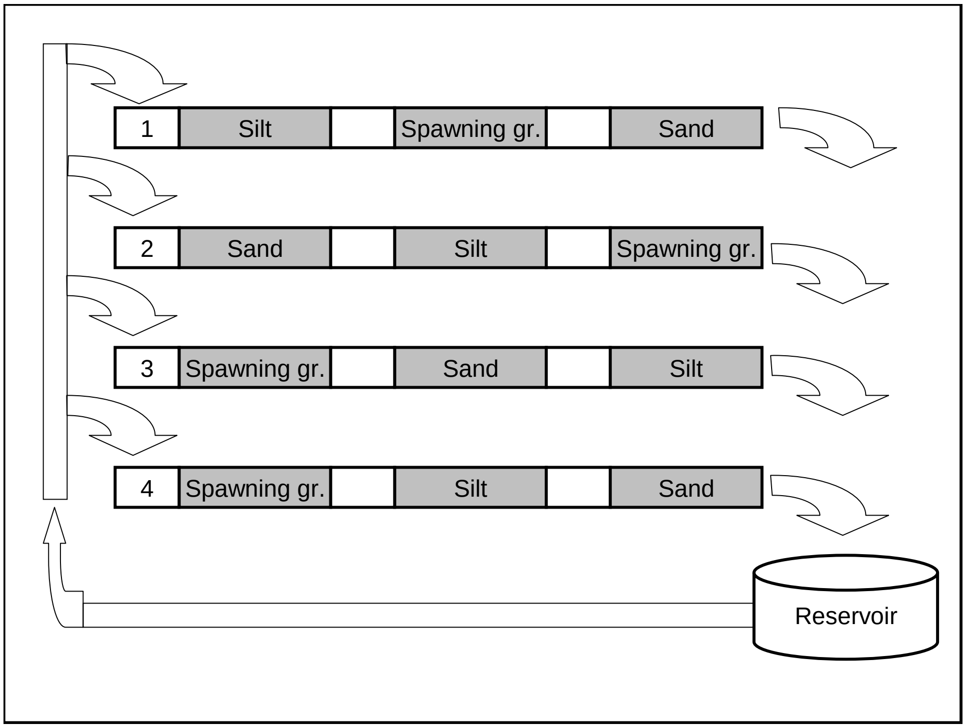
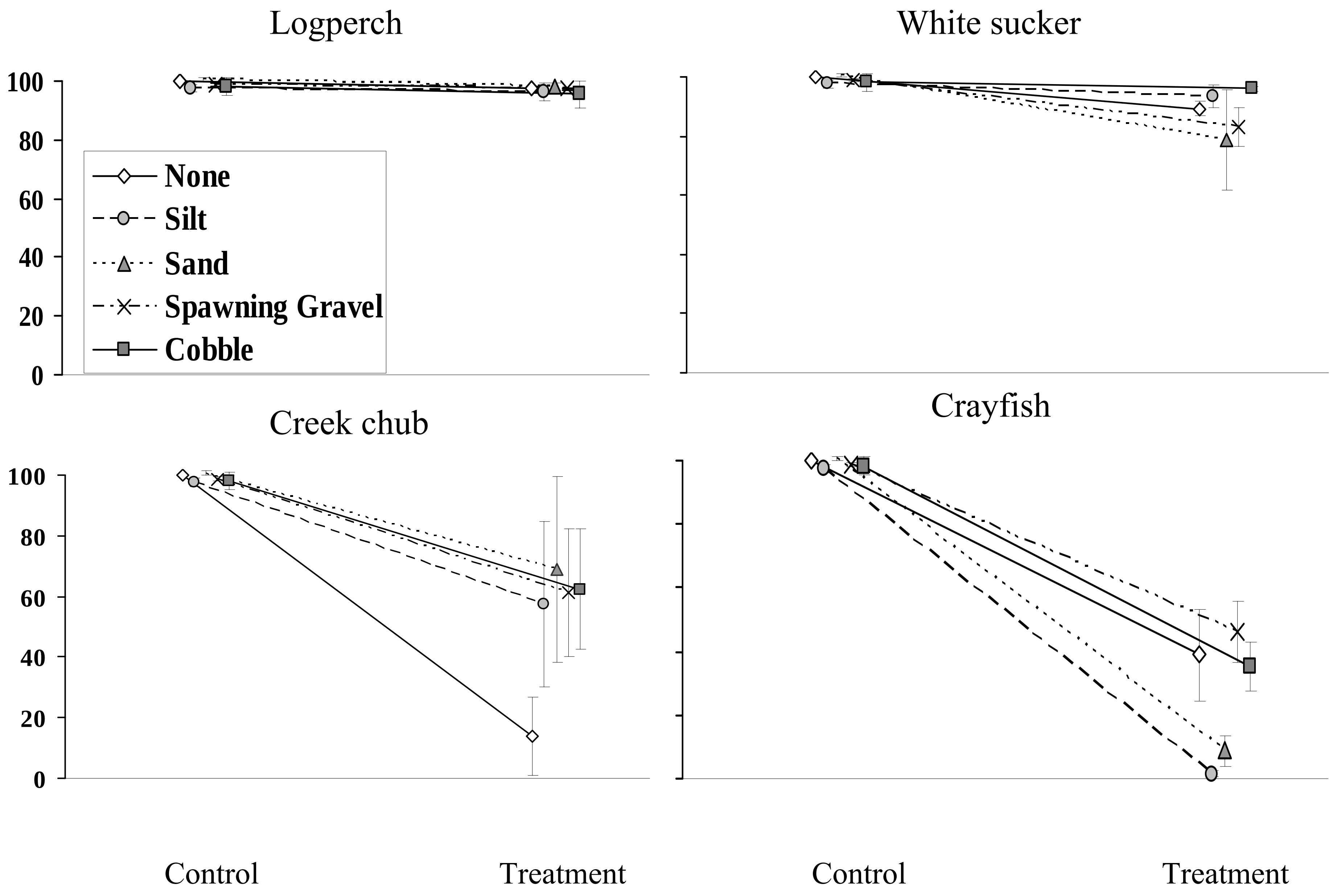

1
Silt
Spawning gr.
Sand
2
Sand
Silt
Spawning gr.
3
Spawning gr.
Sand
Silt
4
Spawning gr.
Silt
Sand
Reservoir

Figure 1.


Logperch
White sucker
100
80
60
40
20
0
None
Silt
Sand
Spawning Gravel
Cobble
Creek chub
Crayfish
100
80
60
40
20
0
Control
Treatment
Control
Treatment

FATE OF SEA LAMPREY (*PETROMYZON MARINUS*) EGGS DEPOSITED OUTSIDE NESTS

Abstract

Sea lamprey (*Petromyzon marinus*) populations in Lake Champlain continue to be detrimental to the restoration of salmonid populations. As part of a continued effort to better understand and model sea lamprey populations field trials were conducted to improve our understanding of the dynamics of the early life history of sea lamprey, specifically survival of eggs that are spawned but not deposited in nest, and survival of eggs in nests. Four sea lamprey nests in tributaries to Lake Champlain were excavated to enumerate all eggs and estimate survival. Numbers of egg and prolarvae in nests averaged 10,142, ranging from 4,440 to 21,856; this represents 6.6 to 32.5% of eggs from a single female. Survival of eggs in nests averaged 72.7% for all nests, ranging from 55.6 to 94.3 %. We sampled spawning habitat directly downstream from sea lamprey nests (5.3m² total area), and in depositional areas (1.4 m² total area) with a Hess sampler to obtain natural egg densities and viability outside of nests. We also used exclosure boxes to introduce sea lamprey eggs to stream substrates to investigate viability and rates of egg loss due to predation and/or stream currents. Twenty pairs of stream boxes were deployed in Lewis Creek on each of two substrate types, spawning gravel and silt. Stream discharge data were used as factors in deposition and disappearance. Hess samples indicate that natural densities of sea lamprey eggs outside of nests on spawning gravel is low (1.9 eggs/m²) and that densities on depositional areas were 105.7 eggs/m² and viability of these eggs is near 0. Exclosure box results indicate that egg loss was less in spawning gravel (65.6% ± 7.4%) than in silt (93.4% ± 5.3%; $p < 0.0001$) and that egg

loss was not impacted by the presence of a cover to exclude larger fish predators. Data also indicate that stream discharge may have an effect on egg loss. Any production of sea lamprey outside of the nest likely occurs under low stream discharge conditions from eggs that are deposited on spawning gravel.

Introduction

The sea lamprey (*Petromyzon marinus*) is a nuisance parasitic fish in the Great Lakes and Lake Champlain which continues to affect important sportfish populations despite efforts to minimize their abundance. Currently, sea lamprey control in Lake Champlain, as in the Great Lakes, follows an integrated pest management approach centered on treatment of tributaries with chemical pesticides. Several sea lamprey-producing tributaries in the Lake Champlain basin are not treatable with pesticides due to concerns over threatened or endangered brook lamprey populations (*Ichthyomyzon fossor* and *Lampetra appendix*). Researchers have created a population model of sea lamprey populations in Lake Champlain to assess potential non-chemical control options on all sea lamprey producing tributaries (Howe et al. 2004). Accurate population modeling depends on accurate population parameter estimates especially in early life history when slight differences in rates of survival can have large impacts on modeling results.

Several studies have examined aspects of the early life history of sea lamprey (Applegate 1950; Manion 1968; Manion and Hanson 1980). Sea lamprey are semelparous; in landlocked populations sea lamprey ascend tributaries in the spring of the year and construct a nest in suitable gravel for spawning. Investigations have included a general description of spawning behavior, determination of fecundity, number of eggs deposited in the nest, and survival of eggs deposited in the nest. These studies indicate that only approximately 14 % of eggs remain in the nest after spawning and that a high proportion of these survive to hatch (85-90%). These studies do not, however, examine the survival of the eggs that are spawned, but not deposited in the nest. Both Applegate (1950) and Manion (1968) noted the potential vulnerability of eggs not deposited in the nest to predation by small stream fishes and suffocation by silt deposition. All eggs that were not deposited in the nest were assumed to be dead. Neither study further examined the possibility that the lost eggs might contribute to production, despite the fact that several other stream-spawning species are successful broadcast spawners. Walleye (*Sander vitreus*), white sucker (*Catostomus commersoni*), and lake sturgeon (*Acipenser fulvescens*) all spawn by broadcasting large numbers of small eggs over stream substrates (Scott and Crossman 1973). The spawning strategy of sea lamprey is unusual. Why would an organism develop a strategy that requires high parental investment (nest construction) while potentially wasting more than 80% of the reproductive output? Eggs may in fact have high survival under certain conditions; nest building may be a strategy to ensure survival of some eggs in years in which environmental conditions, such as flow, do not favor survival of eggs broadcast outside a nest. Examination of egg survival outside of the nest is necessary to ensure that population models account for all production. Egg survival outside of the nest also has potential impacts on future control strategies. If the nest is responsible for all larval production then control efforts could be focused there. If survival is occurring outside of the nest, control efforts aimed at nest production may be ineffective.

The purpose of this study was to examine the survival of sea lamprey eggs outside of the nest under natural conditions. We first set out to locate naturally spawned sea lamprey eggs outside of nests to examine their viability. Artificially spawned eggs were also introduced to experimental stream boxes in spawning streams to examine egg loss due to predation and water current as well as egg survival on different substrate types. Because the study stream, Lewis Creek, is monitored by a USGS gauging station, average daily discharge could be used as a cofactor in analyses examining the disappearance of introduced eggs.

Methods

Nest sampling

Four sea lamprey nests were sampled using a device similar to that described by Manion (1968), consisting of a 25 x 69 cm opening with 61 cm long x 25 cm high metal wings on either side connected to a 363 µm mesh plankton net. The device was positioned approximately 0.5 m downstream from the crest of the nest with wings extending upstream to enclose the nest. Each nest was sampled by manually disrupting all of the gravel in the nest to release eggs from the substrate. Successive excavations were conducted and collected in separate containers until the number of eggs and/or larvae in the sample diminished to close to zero. Nests sampled were on Lewis Creek, VT, LaPlatte River, VT, Malletts Creek, VT, and Mullen Brook, NY. Retention of eggs in the nest was calculated to be the total number of eggs collected from each nest divided by the Lake Champlain fecundity estimate, 66,286 (unpublished data), of the average weight (169 g, N=305) female sea lamprey collected by U.S. Fish and Wildlife Service during annual control efforts (USFWS Lake Champlain Fish and Wildlife Resource

Office, unpublished data). Sub-samples from each nest were examined for viability. Survival was determined using developmental staging criteria (Piavis 1961, 1971).

Hess sampling

Hess sampling was carried out during the spawning seasons of 2004 and 2005 to locate and determine the density of naturally spawned eggs outside of the nest. Samples were collected 5 to 10 days after spawning had taken place in four tributaries: Lewis Creek, Malletts Creek, and Laplatte River, Vermont, and Mullen Brook, New York. Date of spawning was determined by the developmental stage of the eggs collected from the target nest according to Piavis (1961, 1971). Hess samplers are a 33 cm diameter steel cylinder with a 363 μm mesh net attached to the side; the sampled area is 0.85 m^2. The sampler was used by burying the cylinder 10 cm deep into the substrate, then sifting all substrate within the sampler (0.085 m^2) to a depth of 8 cm by hand so that any eggs would be carried by the current into the collection container at the end of the net. In areas where the substrate prevented the use of the Hess sampler, a stream drift net was used to sample 0.09 m^2 of stream substrate to emulate the Hess sampler. In 2004 we collected 62 samples (5.3 m^2 total area) within 10 m downstream from four individual nests. Samples were taken in a line at 1-m intervals directly downstream of the nest for a total distance of 10 m. Pairs of lateral samples were taken, generally at 6 and 9 m to document lateral drift of eggs. In 2005, a total of 16 samples (1.4 m^2 total area) was collected between June 3 and June 6 in depositional areas within a stream section containing considerable sea lamprey spawning activity in Lewis Creek. Samples were preserved in 5% formalin for later examination. All eggs were removed from sediment and examined for viability. Samples were not taken in spawning gravels in 2005 due to the extremely low number of eggs found in these areas in 2004.

Stream boxes

Experimental *in situ* exclosure boxes, similar to those used by Bouwes and Luecke (1997), were constructed in 2005 to allow sea lamprey eggs to be introduced to stream substrates and later retrieved. Boxes were 21 cm^2 and 6.5 cm deep with fine (< 363 μm) mesh bottoms and high-density polyethylene walls. Wire mesh (5 mm^2) was used for box covers to exclude larger fish predators, while allowing stream flow to move eggs. Small fish and invertebrate predators were likely able to invade the covered stream boxes. Stream boxes were buried in stream substrate so that the top of the box was level with the adjacent substrate. Lewis Creek, Vermont was monitored daily in spring of 2005 to determine the onset of sea lamprey spawning. The first nesting sea lamprey were observed on May 30 when stream temperatures reached 19° C. On May 31 ten pairs of stream boxes were deployed in spawning gravel in Lewis Creek. Paired boxes were placed throughout a section of spawning habitat, directly adjacent to one another in sea lamprey spawning gravel. After both boxes were buried, a 70-cm dia tall cylinder was placed around each box to block stream flow so that 1 ml (~750) of fertilized sea lamprey eggs could be introduced to each box. This density of eggs was intentionally elevated to unnatural levels to ensure that some eggs would remain in order to quantify egg loss. Bouwes and Luecke (1997) found no significant difference in proportion of egg loss between different egg density treatments in exclosure experiments. Sea lamprey eggs were obtained by hand-capturing spawning lamprey, then stripping and mixing gametes in a glass vial in the field. Two males were used to fertilize all eggs to lessen the chance of using an infertile male. After the eggs were added, a cover was placed on one of the pair of boxes chosen by coin flip and the flow diversion was removed. Three boxes, without covers or added eggs, were placed throughout the array acting as control boxes to determine the number of eggs that might be added to each box by natural spawning. The following day, June 1, the procedure was repeated and ten pairs of stream boxes were deployed in the same stream section in depositional areas. After seven days, boxes were removed from the stream and contents were sieved to retrieve remaining eggs. Eggs were preserved in 5% formalin to be counted and to estimate survival at a later date. Additional replicate trials with five pairs of stream boxes on each substrate type, spawning gravel and silt, were conducted on June 10 to June 21, and June 29 to July 7. Eggs for replicate trials were obtained from female sea lamprey being held in the lab and were not fertilized.

Stream discharge

Historical discharge data for Lewis Creek were obtained from USGS water data archives and examined to determine annual variation in discharge during sea lamprey spawning. Detailed records of spawning activity are unavailable; however, limited spring water temperature data and sea lamprey trapping data are available (USFWS Lake Champlain Fish and Wildlife Resource Office, unpublished data). The timing of sea lamprey spawning can be estimated based on these data.

Statistical methods

All analyses were conducted using JMP (version 5.1.2; SAS Institute, Inc., Cary, NC, 1989-2005) software with significance levels set at $\alpha = 0.05$. Viability of Hess sampled eggs is reported simply as percentage of total eggs that appear viable. Stream box data were analyzed using an ANOVA with substrate (spawning gravel or depositional sediments), presence of a cover, the cover*substrate interaction, and average discharge during the trial as factors. The percentage of eggs remaining in each box was natural log transformed to meet the normality assumptions of the ANOVA.

Results

Nest sampling

The total number of eggs recovered per nest was 4,440 in Lewis Creek, 5,071 in Mullen Brook, 9,201 in LaPlatte River, and 21,856 in Malletts Creek. Nest retention estimates ranged from 6.7 to 33.0 %, and averaged 15.3 %. The high number of eggs in Malletts Creek suggests that more than one female may have spawned in the nest; thus, the retention estimate of 33% from this stream may be an overestimate. Survival estimates of eggs in the nest averaged 72.7% for all nests, ranging from 55.6% in the Laplatte River to 94.3 % in Lewis Creek.

Hess sampling

Hess samples collected in 2004 contained very few sea lamprey eggs; a total of 10 eggs was collected from 62 samples. This sample corresponds to a density of 2.0 ± 0.64 eggs/m^2 ± standard error. Of these eggs, 4 (40%) were found in lateral samples. Because of the small sample, viability estimates were not calculated. Hess sampling in 2005 produced a sufficient number of sea lamprey eggs (N = 148) for viability analysis; egg density in depositional areas was 108.8 ± 53.0 eggs/m^2. Over 90% of these eggs were fertilized; however, none appeared to be viable.

Stream boxes

The overall ANOVA testing the effects of cover, substrate, cover*substrate interaction, and mean stream discharge was significant (F-ratio = 14.32, df = 4, $p < 0.0001$). Effects tests showed that presence of a cover (F-ratio = 4.78, df = 1, $p < 0.033$), substrate type (F-ratio = 53.8, df = 4, $p < 0.0001$), and mean stream discharge (F-ratio = 8.19, df = 1, $p < 0.006$) were all significant effects of the mode (Table 1). The substrate*cover interaction was not a significant effect. Upon further analysis it became clear that the three trials were not comparable with respect to mean stream discharge and that this difference might be affecting the analysis. Mean stream discharge during the three trials was 0.92 m^3/sec (trial 1), 5.27 m^3/sec (trial 2), and 1.21 m^3/sec (trial 3). Because discharge during trial two was high and only half of the stream boxes deployed during that trial were retrieved, the analysis was repeated omitting the second trial and the interaction term that was insignificant in the first analysis. The reanalysis showed that the overall model remained significant (F-ratio = 15.22, df = 3, $p < 0.0001$), but the presence of a cover and mean stream discharge were no longer significant. Substrate type remained a significant effect of the model (F-ratio = 44.4, df = 1, $p < 0.0001$; Table 2). Spawning gravel retained more eggs with or without a cover (34.4% ± 7.4%, 95% CI) than did silt (6.6% ± 5.3%, 95% CI; Figure 1).

Viability analysis was limited to the first trial when fertilized eggs were used. Hatched pro-larvae were found in all boxes placed in spawning gravel. Average hatching success for all eggs introduced to spawning gravel was 3.4%. No eggs survived to hatch on silt.

A total of 250 eggs was found in the stream boxes acting as controls that were not seeded with eggs. All of these eggs were found in the three control boxes placed in spawning gravel during trial one. The high number of eggs is a result of one box that contained 230 eggs; after this box was deployed a sea lamprey nest was constructed 1.5 m upstream. The other two control boxes contained 8 and 12 eggs each, averaging 1.3% of the number that was added to each treatment box. Because no treatment boxes were located in close proximity to active nests, numbers were not adjusted to account for natural egg introduction.

Stream discharge

Examination of sea lamprey trapping and temperature data suggests that spawning in Lewis Creek generally occurs between May 15 and June 15 when average daily stream temperatures approach 16 ºC. Average discharge during this period is variable from year to year (0.83 - 5.8 m^3/sec). In 2004 and 2005, when spawning was monitored closely, peak spawning took place under substantially different discharge conditions (Figure 2).

Discussion

Sea lamprey populations have highly variable stock recruit relationships, resulting from a variety of factors that affect the survival of early life stages (Jones et al. 2003). Predation, water currents, and loss of eggs from the nest certainly play a role in this variable survival. Our nest sampling data indicate that an average of 15.3% of eggs remain in nests, confirming the estimate of Manion and Hansen (1980). Hess sampling indicated that sea lamprey eggs were very sparse in areas downstream from nests in 2004. Although four (40%) eggs were collected in lateral samples, it is difficult to construe dispersion from these limited data. Unquantified observations of drifting eggs suggest that eggs leaving the nest move rapidly downstream for substantial distances (> 40m), so that the majority of eggs would not be found in a straight path within 10 m of the nest. The small sample size suggests that most of the eggs from each nest either traveled further downstream than 10 m, or were consumed by predators before sampling occurred.

Depositional areas did contain sea lamprey eggs, but viability was near zero. Naturally spawned eggs collected via Hess sampling in depositional areas in 2005 were often buried in coarse particulate organic material, which may have concealed them from predators that have the potential to remove high densities of eggs; individual crayfish can consume over 200 sea lamprey eggs in 18 h (S. Smith, University of Vermont, unpublished data). Low viability of eggs in Hess samples suggests that depositional areas are inhospitable environments for egg incubation, despite results from lab experiments showing high survival of sea lamprey eggs on silt substrates (S. Smith, unpublished data). Organic material may be concentrated in depositional areas, leading to low dissolved oxygen that would be detrimental to egg incubation.

Exclosure experiments indicate that eggs deposited on silt substrate are highly vulnerable to predation and/or drift. Our results suggest that covers used in exclosures were not adequate to exclude all egg predators, or that other factors such as water flow are also important factors in egg loss. Sea lamprey eggs are less vulnerable to disappearance caused by any factor on spawning gravel than on depositional silt. When sea lamprey eggs were artificially deposited on silt substrates, less than 10% remained after seven days compared to 34% that remained on spawning gravel. Gravel may protect eggs from predation as well as drift, as seen in salmonids eggs spawned on cobble (e.g., Fitzsimons et al. in review) This result, in combination with low viability of eggs on silt substrates, suggests that most out of nest production likely comes from eggs deposited in spawning gravel. We were unable to obtain robust estimates of egg deposition outside of nests in spawning gravel in 2004. The relatively low discharge conditions during the 2005 spawning season may have increased out of nest deposition on suitable spawning habitat (Figure 2). The presence of naturally spawned eggs in the control stream boxes suggests that some eggs lost from the nest can be deposited in spawning gravel substrates. This result is contrary to findings in 2004 when very few eggs were collected in over $5m^2$ of spawning habitat sampled directly downstream from nests. Data from uncovered stream boxes on spawning gravel confirm that increased flows cause high levels of egg disappearance. Only 4.1% of eggs remained in open stream boxes during trial two when stream discharge averaged 5.27 m^3/sec, compared to trials one and three when 29.6% of eggs remained and stream discharge averaged 0.92 m^3/sec and 1.21 m^3/sec respectively.

Retention of eggs in nests is likely to be related to stream flow, as nests are frequently completely destroyed in high flow events (unpublished observations). If low discharge during the spawning season allows eggs lost from the nest to hatch, and increases retention of eggs in the nest, potentially large year classes could be produced during low-water years. This type of temporal environmental variation could be a driving force in the early life history dynamics of sea lamprey populations. The nest structure constructed by sea lamprey may be an adaptation of semelparity to protect a small percentage of the eggs from environmental variability that occurs in spawning streams from year to year. The adaptation of nest building ensures that some of the offspring, those deposited in the nest, will survive in years when stream flows do not favor broadcast spawning. A spawning strategy has evolved in sea lamprey that protects a small percentage of offspring in a suitable habitat, the nest, and scatters the remainder to land where the current takes them. The broadcasting of part of the clutch could also be viewed as a bet-hedging strategy for spatially variable environments (Winemiller and Rose 1993). The spreading of over half of the eggs produced by sea lamprey could help to ensure that some of the eggs are located in favorable locations, such as the interstitial spaces in spawning gravel.

In summary: eggs that leave the nest disperse mostly directly downstream, and have a high probability of being consumed by a variety of predators; eggs that settle on silty substrates have high mortality, probably due to suffocation. Egg densities are artificially high in depositional areas, as these areas concentrate eggs; egg densities in other substrates represent deposition minus losses due to predation. Eggs remaining in the nest have higher survival than those outside the nest, but in high flows more eggs may leave the nest, or the nest may be entirely destroyed.

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Table 1. Analysis of variance table for stream box field trials: effects of cover, substrate type, and mean stream discharge on the percentage of eggs remaining in each stream box.

Source	DF	SS	F-Ratio	P-value
Cover	1	8.85	4.78	≤ 0.033
Substrate	1	99.5	53.8	≤ 0.0001
Substrate*Cover	1	0.163	0.09	≤ 0.768
Mean stream discharge	1	15.1	8.19	≤ 0.006
Error	50	92.5		
Total	54	198		

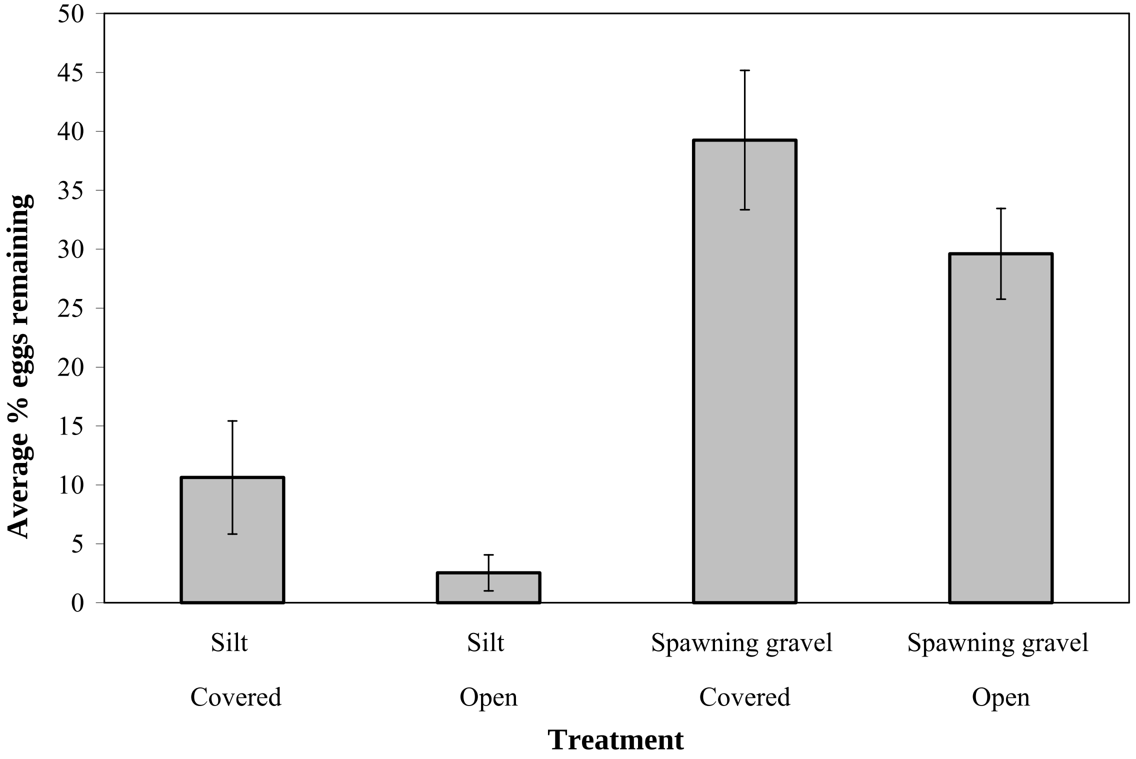
Table 2. Analysis of variance table for stream box field trials: effects of cover, substrate type, and mean stream discharge on the percentage of eggs remaining in each stream box excluding trial two.

Source	DF	SS	F-Ratio	P-value
Cover	1	4.20	2.23	< 0.143
Substrate	1	83.7	44.4	< 0.0001
Mean water flow	1	1.41	0.746	< 0.393
Error	42	79.1		
Total	45	165		

Figure Captions

Figure 1. Mean percentage of sea lamprey egg remaining in Lewis Creek stream boxes relative to treatment type, excluding trial two. Error bars represent standard error.

Figure 2. Stream discharge data from Lewis Creek, Vermont. (A) Average discharge from May 10 through June 10 all years from 1990 to 2005 measured in cubic meters per second. (B) Comparison of discharge (m^3/sec) between study years 2004 and 2005, with peak spawning indicated by heavy vertical lines. Stream box trials are indicated by colored vertical lines.


50
45
40
35
30
25
20
15
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Average % eggs remaining
Silt
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Covered
Spawning gravel
Open
Treatment

Figure 1.

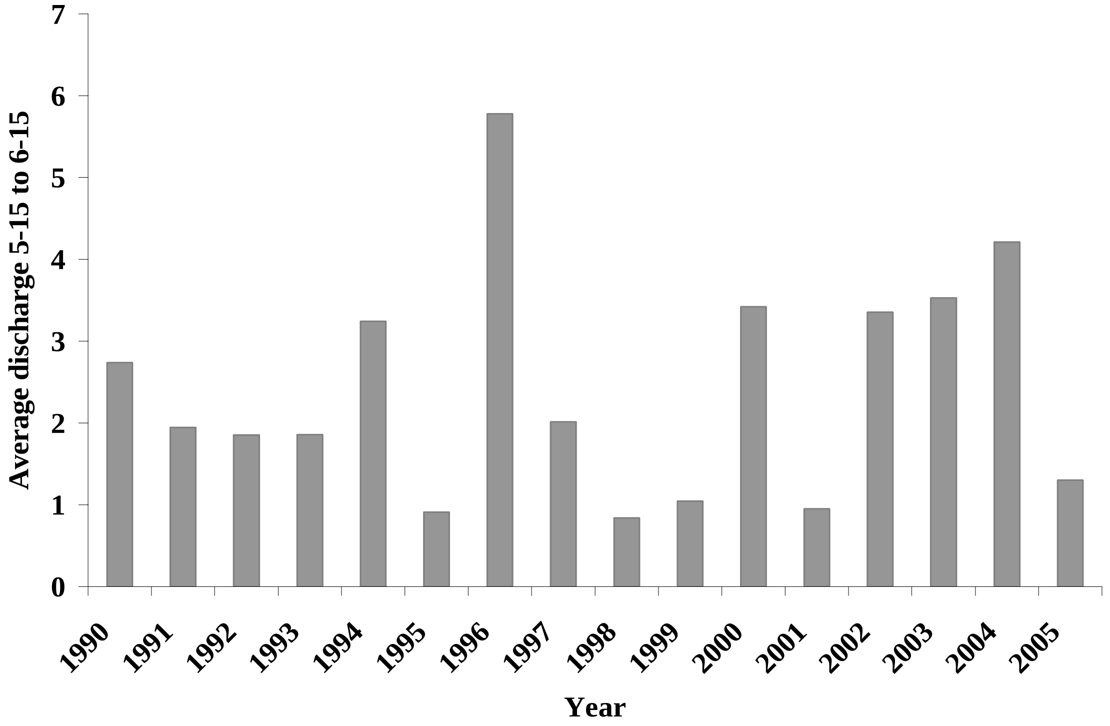

Figure 2. A.

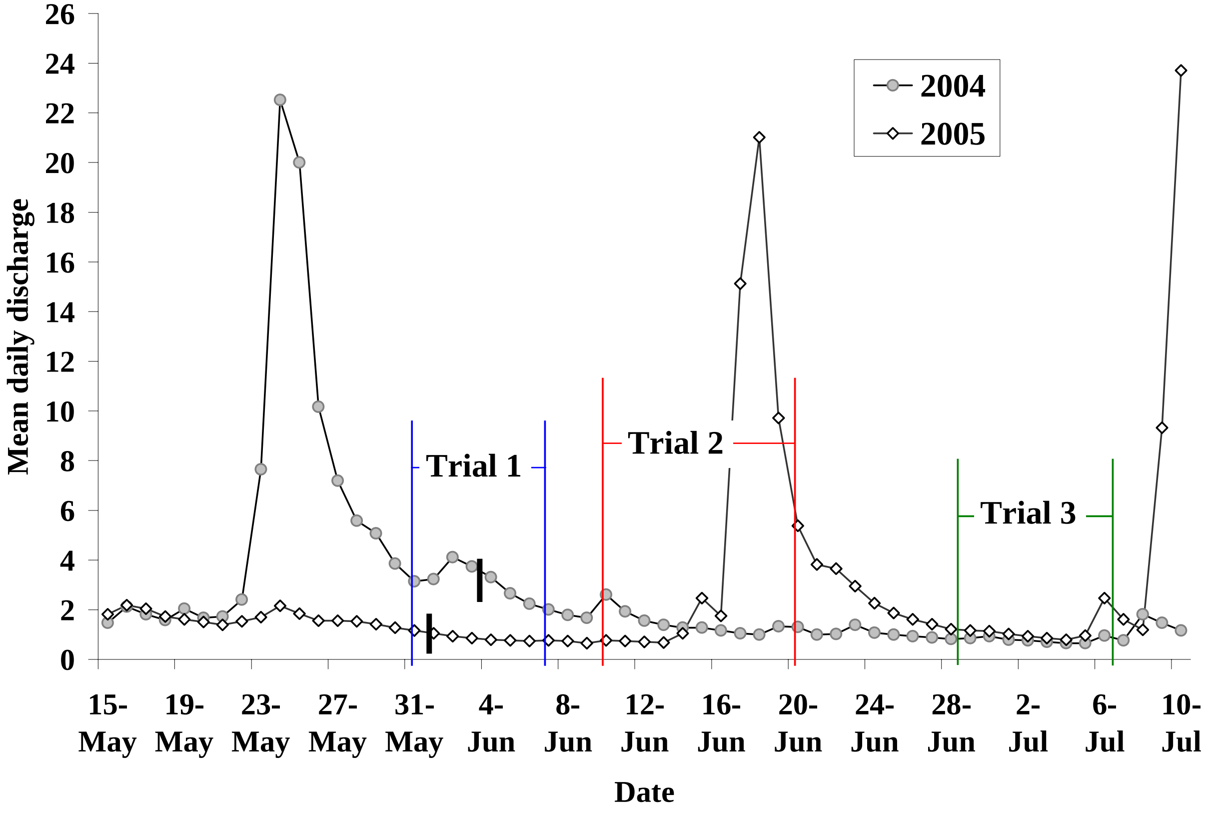

Figure 2. B.