FACTORS AFFECTING THE BEHAVIOR OF GREAT LAKES SEA LAMPREY (*PETROMYZON MARINUS*) AT TRAPS

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Thesis submitted to the Faculty of the
University of Michigan-Flint
in partial fulfillment of the
requirements for the degree of
Master of Science in Biology

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April 2014

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Department of Biology

2014

ABSTRACT

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Sea Lamprey (*Petromyzon marinus*) is a parasitic species that have affected Great Lakes fisheries in many ways. Control of sea lamprey populations through binational efforts started in 1950s and continues today. The primary technique used to control sea lamprey is the application of lampricides to streams to kill larvae before they become parasites. The Great Lakes Fishery Commission is looking for an alternative method of control to complement lampricides to reduce sea lamprey abundance.

Trapping adult sea lamprey as they migrate upstream is used for assessment of spawning population in the stream. Trapping efficiency needs to be improved before this method could be used as an alternative method of control. Thus, the understanding of sea lamprey behavior at traps is important to try and improve trap success. A male mating pheromone component (3kPZS) used as an attractant in traps has been shown to increase trap capture. Also, other external factors are likely to affect the behavior of sea lamprey at traps. Video was used to record sea lamprey behavior at five traps across five migration seasons, with one trap being baited with 3kPZS. I found sea lamprey are 31% more likely to enter after approaching the trap when it was baited with pheromone. I found additional environmental factors that affected the probability that a sea lamprey would enter and be retained in a trap.

Dedication

I would like to dedicate this completed thesis to my family and friends for their continuous support of furthering my education and my love to studying nature.

Acknowledgements

I would like to first thank my advisor Dr. Heather Dawson for all of her support and guidance throughout my graduate program. Her guidance, encouragement, and assistance through every step through the process and helped me with my confidence on just keep pushing me forward on my writing. I would also like to thank my committee members Dr. Kevin Tang and Teresa Yoder-Nowak for their support, advice, and total confidence in me every step of the way. Thank you also to Danielle Potts, and John Cohoon for their help in setting up the trapping site the first year. Thank you also to Alex Maguffee, and Josh Creed for the endless video watching and data entry that took place.

Thank you to Larry Atherton from University of Michigan-Flint for all of his help in obtaining funding, and the unlimited paperwork that he assisted with.

I would also like to thank everyone at the USGS Hammond Bay Station for all of their advice, assistance, and support, especially Nick Johnson. I am grateful to Nick Johnson for providing me with housing and a vehicle to drive to the study site. Thanks to Gale Bravener from Fisheries and Oceans Canada for providing cameras, DVR equipment for Carp Lake Outlet as well as information for chapter 2 about St. Mary's River traps.

A special thanks to my family and friends for the patience and pushing me to finishing my thesis to move to the next step in my life.

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Overall Introduction

Sea lamprey (*Petromyzon marinus*) are an invasive fish species that invaded the Laurentian Great Lakes triggering negative cascading effects to the aquatic ecosystem (Lark 1973; Smith and Tibbles 1980). Sea lamprey were a contributing factor in the collapse of lake trout (*Salvelinus namaycush*), whitefish (*Coregonus clupeaformis*), deep water cisco (*Leucichthys Coregonus*) and blackfin cisco (*Coregonus nigripinnis*) populations in the Great Lakes during the 1940s and 1950s (Morman et al. 1980; Page et al. 2013). Sea lampreys entered the Great Lakes from the Atlantic Ocean through a series of shipping canals that were built to connect the Upper Great Lakes with the Atlantic Ocean (Morman et al. 1980). They had invaded all of the Great Lakes by 1938, and by the early 1960s lake trout fishery harvests had declined to 2% of pre-invasion levels (Schneider et al. 1996). Management efforts to control sea lamprey populations throughout the Great Lakes region started in the 1950s and continue today. Due to destruction of valuable fish stocks and the adverse effect of sea lamprey on the ecological balance of fish species in the Great Lakes, the Great Lakes Fishery Commission (GLFC) was established in 1955 by a treaty between Canada and the United States (GLFC 2002). Their mission is to coordinate efforts to formulate and implement a program to eradicate or minimize sea lamprey populations in the Great Lakes (Pearce et al. 1980).

The sea lamprey life cycle in the Great Lakes begins in tributaries where fertilized eggs hatch into small, wormlike larvae called ammocoetes which burrow into the soft bottoms of streams to filter-feed on detritus for 3 to 6 years (Potter 1980). After ammocoetes reach appropriate size, they metamorphose into juveniles that migrate downstream and into the Great Lakes where they parasitize fish for 12 to 20 months. Juvenile sea lamprey do their damage by attaching to large fish with their suction-cup mouth and rasping a hole through the fish's scales and skin with their teeth, so they can feed on its blood and body fluids. During its parasitic lifetime, a single sea lamprey has been estimated to destroy 6.6 to 18.9 kg of host species (Swink 2003). After the juvenile period, maturing adults migrate back into tributaries to find a mate, spawn and die. Depending on the productivity of the system, the complete life cycle of sea lamprey from egg to adult, takes an average of 5 to 8 years to complete.

Sea lamprey control employs an integrated pest management strategy, which includes defining targets for control that optimize benefits, using quantitative methods and systems approaches, and applying alternative methods of control that consist of using lampricides to eliminate larval lamprey, barriers to limit access to productive spawning habitat, and traps to reduce reproductive potential of the adult population (Christie and Goddard 2003) The primary technique of control involves applying a lampricide, 3-trifluoromethyl-4-nitrophenol (TFM), to streams to kill ammocoetes while they are burrowed in the stream bottom. Lampricides are effective at killing ammocoetes, and have a minimal impact on other fish species, aquatic plants, invertebrates, and wildlife (Dahl et al. 1980). Alternative control methods are used despite the obvious success of lampricides because of public concern about pesticide use and the rising costs of lampricides. In their recent mission statement, GLFC stated that they wish to decrease the use of lampricides, and implement an alternative control method while still maintaining sea lamprey abundance at or below target levels (GLFC 2011). The true effectiveness of alternative control methods, which targets adults, depends on the ability to overcome compensation and recruitment variation (Dawson and Jones 2009). Thus, spawners need to be reduced to the point where few or no high recruitment events will occur.

Pheromones have been found to play a role in different stages of the sea lamprey life cycle. Ammocoetes release a pheromone which activates in the water column to indicate the habitat quality for spawning adults and induce migration of adult lamprey to the mouths of water systems (Moore and Schleen 1980; Bjersulius et al 2000; Wagner et al 2009). Adult sea lamprey pheromones start to play roles in the migration of lamprey as they migrate upstream. Adult sea lampreys have been found to be attracted to 7α,12α, 24-trihydroxy-3-one-5α-cholan-24-sulfate (3kPZS), a component of a pheromone known to be released by mature males, and traps baited with this male mating pheromone component have been found to capture more sea lampreys than unbaited traps (Johnson et al.2009; 2013). Male sea lamprey pheromones have been found to improve trapping efficiency in various stream systems (Johnson et al. 2009).

In addition to pheromones, there could be various external factors that could contribute to sea lamprey entering and being retained in a trap. Sea lamprey, Pacific lamprey *(Entosphenus tridentatus)*, and European river lamprey (*Lampetra fluviatilis*) vary their migratory activity in response to increased discharge, whereas nightly variation in migratory activity in European brook lamprey (*L. planeri*) has been attributed to both temperature and discharge (Applegate 1950; Skidmore 1959; Malmquist 1980; Almeida et al. 2002; Luzier and Silver 2005; Masters et al. 2006; Andrade et al. 2007). For example, a curvilinear relationship was found between sea lamprey migratory activity and water temperature, with temperatures between 10°C and 18°C stimulating activity (Applegate 1950). Various other factors could play a role in the behavior of sea lamprey at traps, such as the location and design of the trap, time of night, and time of season.

Even though pheromone-baited traps have been shown to capture more sea lamprey on average than unbaited traps (Johnson et al. 2013), there are few data at traps on the actual entrance and retention rate of sea lampreys and numbers of sea lamprey approaching traps. Although pheromone-baited traps could be a promising alternative control method, this method still needs to be evaluated. Additionally, by evaluating various external factors that could contribute to the attraction and retention of sea lamprey in traps, I could potentially make recommendations to managers on how to trap more sea lamprey with or without the use of pheromones. To address these issues, this study proposes: 1) to evaluate sea lamprey behavior at a trap which was either pheromone baited or unbaited through analysis of video, and 2) to evaluate external factors which could also influence entrance and retention rates of sea lampreys at traps including water temperature, discharge, time of season, time of night, trap, and interactions between these factors.

Chapter 1: THE INFLUENCE OF THE APPLICATION OF A SYNTHESIZED MALE MATING PHEROMONE ON THE BEHAVIOR OF SEA LAMPREY AT A TRAP

Abstract

Great Lakes sea lamprey is an invasive species that has had an impact on game fish populations. Methods of control alternative to lampricides are currently being investigated. Teeter (1980) and colleagues were the first to demonstrate that the pheromones emitted by a nesting male sea lamprey function as an attractant to ovulating females. A male pheromone compound (3-keto Petromyzonol sulfate: "3kPZS") was identified, synthesized, and was shown to lure up to 60% of females into traps in controlled field environments (Johnson et al. 2009). That research has led to management-scale tests of the synthesized mating pheromone, 3kPZS, as bait in trapping systems operated by sea lamprey control agents. To be trapped, individual sea lamprey must first encounter, then enter, and then be retained in traps. Entrance and retention rates of sea lamprey in traps may be influenced by application of pheromones to a trap. A trap near Mackinaw City, Michigan, was baited with pheromone every other night during the 2011 and 2012 spawning seasons, and behavior of sea lamprey at the trap was video recorded. Entrance and retention rates of sea lamprey were determined through video analysis. The data indicated that sea lamprey that approached the trap were more likely to enter the trap when it was baited with 3kPZS. Environmental factors were also found to play a role in the probability of entry and retention of sea lamprey in traps.

Introduction

Sea lamprey traps are currently only used for assessment purposes, but if the efficiency of traps could be increased they could also function to help control sea lamprey (GLFC 2011). Managers currently use traps to perform mark-recapture studies for estimate populations of adult spawning sea lamprey to assess the effectiveness of the control program from previous years (Mullet et al 2003). Current trapping operations, where used, only remove about 40% of the adult population from tributaries throughout the Great Lakes (Sullivan and Adair 2012), which is too low to suppress sea lamprey recruitment (McLaughlin 2007). However, by observing sea lamprey behavior at traps, I may be able to determine how traps can capture and retain larger percentages of the individuals that encounter them. The trapping process could be viewed as individual movements through certain behavioral states as Bravener and McLaughlin (2013) stated in a conceptual model that consists of four phases: unavailable, available, trapped and removed. A sea lamprey is "unavailable" during the spawning run where those individuals do not encounter a trap. A sea lamprey becomes "available" to be trapped when coming into close proximity to a trap. A sea lamprey is "trapped" when that individual navigates through the funnel into the trap and stays in the trap to be "removed" by the control agents. Sea lamprey behavior can affect durations in and transitions between states (Bravener and McLaughlin 2013). This study, in part, is interested in the behavior of sea lamprey after they become "available" to be trapped and before being "removed" by control agents. These sea lamprey can choose to not enter the trap, enter the trap and be retained and therefore "removed", or enter the trap but later escape and therefore not be "removed". All of these behaviors could be quantified by analyzing video recorded at sea lamprey traps during the adult migratory season. Probabilities of entrance and retention can depend on the physical features of a trap or its location, the locomotor and sensory capabilities of the individual sea lamprey, and environmental conditions that influence lamprey behavior (Bravener and McLaughlin 2013).

One of the factors that may affect trap efficiency is the use of attractants. By using natural sea lamprey pheromones as a trap attractant the efficiency of traps to capture and retain adult sea lamprey could be increased. Many attractants have been used to bring animals into certain locations for different purposes. Teeter (1980) and colleagues were the first to demonstrate that the odor emitted (pheromones) by a nesting male sea lamprey functions as an attractant to ovulating females (Johnson 2009). The male mating pheromone has been identified with several other components as mainly a bile acid: 7α, 12α, 24-trihydroxy-3-one-5α-cholan-24-sulfate (3kPZS; Li et al. 2002). Subsequent efforts focused principally on ascertaining whether the pheromone may be used effectively as trap attractants (Johnson et al. 2005, 2009; Wagner et al. 2006). Scientists synthesized the male mating pheromone, which was subsequently shown to attract sexually immature and mature lamprey upstream to the pheromone's source (Siefkes et al. 2005) and into 3kPZS-baited traps (Johnson et al. 2009; 2009; Luehring et al. 2011).

Research is currently underway to assess whether the pheromones sea lamprey use to communicate can be exploited to capture individuals effectively on a management-level scale. In a natural environment, larval migratory pheromones have been primarily responsible for directing spawning adults to certain habitat rich systems, then as adults migrate upstream, 3kPZS also has elevated upstream migratory activity of pre-ovulated females (Moore and Schleen 1980; Bjerslius et al. 2000); Wagner et al. 2009). Immature sea lamprey may be exposed to 3kPZS if spawning habitats are inhabited by mature spermiating males. In those cases, the presence of 3kPZS may be an indicator of suitable spawning habitat within a stream, thereby triggering increased migratory activity and priming of the neuroendocrine system of immature lamprey

(Chung-Davidson et al. 2013). The pheromone, 3kPZS, drives upstream movement toward the nest, but still unidentified components retain females on nests and induce spawning behaviors (Johnson et al. 2012a). Most recent research on 3kPZS has been conducted in the laboratory, mimicking the natural environments with manipulated subjects and no pheromone competition from free ranging males (Johnson et al. 2010).

The aforementioned research has led to management-scale tests of synthesized 3kPZS as bait in trapping systems operated by United States Federal Wildlife Service (USFWS) and Fisheries and Ocean Canada (DFO. Management-scale field trials conducted by Johnson et al. (2009, 2013) in ten U.S. streams indicated that efficiency of capture at sites where 3kPZS was applied as trap bait increased by an average of 10% compared to the 10-year historical average. Increases were found to be variable, with some sites experiencing increases of over 25%.

As well as pheromones, there could be various external factors that could contribute to lamprey entering and being retained in a trap. Several lamprey species' nightly movements appear to be due to environmental variation in the system but none have been found to be important (Applegate 1950; Skidmore 1959; Malmquist 1980; Almeida et al. 2002; Luzier and Silver 2005; Masters et al. 2006; Andrade et al. 2007). There was a curvilinear relationship between water temperature and migratory activity, being optimum between 10°C and 18°C and decreasing above and below those temperatures for Great Lakes sea lamprey. (Applegate 1950). Landlocked sea lamprey also showed a relationship between migratory activity and water temperature with changes in water temperature more important than absolute water temperature (Skidmore 1959). The migratory activity of other species of lamprey has been found to increase due to stream discharge and water temperature (Masters et al. 2006; Malmqvist 1980). If factors that can be manipulated by control agents (i.e., trap design, attractants) affect trapping efficiency then this can lead to improved trapping success.

With improvements in trap design and deployment, and the potential for using pheromones to increase trap capture rates, trapping may become a key element of control in the future and even surpass barriers as the primary alternative to lampricides (Jones 2007). Quantifying sea lamprey behavior at traps will help fine tune trap design to improve overall trapping efficiency. Underwater video is a valuable method for evaluating trap efficiency because, unlike other methods such as simple trap counts, it allows the observer to record the behavior of all individuals that encounter the trap, regardless of whether they enter the trap or not, or enter and then escape. In this chapter, underwater video was used to determine how baiting traps with synthesized 3kPZS changes the effect of physical, temporal, and environmental factors on sea lamprey behavior at traps. I predicted that 3kPZS application to traps and surrounding waters will improve trap performance by increasing the probability of a lamprey entering a trap upon encounter, while not decreasing the probability of a lamprey being retained in a trap. I also predicted that when a trap was baited with 3kPZS, the probability of sea lamprey entering a trap upon approach 1) increases with time of night, 2) increases with time of season, 3) increases with water temperature, and 4) increases with stream discharge.

Methods

Study Site

Video was collected at a permanent sea lamprey trap on the Carp Lake Outlet during May through Mid-June in 2011 and May through Mid-June in 2012. The permanent trap is located on the Carp River at a low head barrier dam near Mackinaw City, MI USA that is a tributary of

Lake Michigan (Figure 1). The permanent trap has six separate entrances oriented vertically on the front of the trap. The trap openings are 88.9 mm x 88.9 mm with fingers 12.7 mm apart in one funnel that was 1181.1 mm high x 228.6 mm wide x 304.8 mm deep (Figure 2). These fingers consist of 4 metal appendages that drape over the back of the funnel. The fingers are used to inhibit the exit of sea lamprey from the trap allowing them to be retained. The fingers only open inward into the trap and cannot be pushed outward. The fingers rest into toothed metal grooves to keep them positioned correctly in the trap opening. During the study period, synthesized 3kPZS was applied to the trap every other night. Video was recorded nightly at a permanent trap using a Digital Video Recorder (DVR). Sea lampreys move primarily at night, so video was recorded from 21:00 to 05:00 each day. Video was recorded during the entire sea lamprey migration season occurring in the beginning of May to mid-June when sea lamprey travel up Great Lakes tributaries to find suitable habitat in which to spawn.

2011 Trapping season

There were two traps, one permanent and one portable, with two underwater video cameras (Lorex Cvc6990 B&W submersible camera) attached to each trap. Cameras were secured to a 2 x 4 that was fastened to the outer enclosure and included a 10-watt halogen light to illuminate the view of each camera (Laguna PowerGlo Mini Pond Light Kit PT-1550). In field studies, no consistent differences have been found in the numbers of sea lampreys caught in lit versus unlit traps (Stamplecoskie 2012). The cameras were positioned 30 cm from trap entrance to record sea lamprey behaviors but to not occlude the entrances to the traps. The lights were connected to a 12 V transformer (Laguna PowerGlo Mini Pond Light Kit PT-1550) that switched them on at dusk. Video was set to record from 21:00 to 5:00 each night using a Digital recorder

(DVR, Lorex 8 channel Pentaplex Network DVR). The lights, video cameras, and DVR were powered by two 12 V marine Batteries (Everstart Maxx 29 deep-cycle marine). Video was downloaded twice, during the middle and end of the season, to an external hard drive. Batteries were checked and replaced daily to maximize the video recording during the night. Video cameras were checked daily and readjusted as needed to get the best video quality of the trap entrance.

The synthesized form of 3kPZS was applied every night to either the permanent trap or the portable trap by a battery operated, programmable peristaltic pump (Admiral Reef Dosing Pump, Norwich, CT) that applied 3kPZS at the dosage of 10^{-12} M. This concentration of 3kPZS delivers the highest capture efficiency of ovulated females in baited traps (Johnson et al. 2009) and is within the detection of olfactory threshold of pre-ovulated females (Siefkes and Li 2004). The 3kPZS batch # 183-EJH-290-3 synthesized in February 2010 (Bridge Organics), was applied to the trap. The batch had purities greater than 99% based on high pressure liquid chromatography and mass spectrometry.

Due to the poor video quality of the portable trap, only the permanent trap video was analyzed. All the recorded video was watched using playback of the video in ten minute increments via Digiclient 6.0 (Digimerge 2006). All video recorded during the study was observed by one reviewer that was blind to the baiting schedules of each trap. Each time a sea lamprey entered the field of view of a camera the observer recorded the date and time. If a sea lamprey entered the trap the observation was recorded as "entered" and the date and time of the entry was recorded. If a sea lamprey did not enter the trap the observation was recorded as "did not enter" and the date and time of the lamprey leaving the field of view of the camera was recorded. If a sea lamprey entered the field of view by escaping out the trap entrance the observation was recorded as "escaped" and the date and time of the escape was recorded.

2012 Trapping Season

In 2012, only the permanent trap was used for video analysis. Two underwater video cameras (Security Labs Waterproof Color Cameras with infrared and 8 LED built in lights, Security Labs, Inc., www.security-labs.com) were secured to the permanent trap on a 2 X 4 fastened to the outer enclosure, which was positioned 30 cm from trap entrance to record sea lamprey behaviors but to not occlude the entrance to the trap. Video was set to record from 21:00 to 5:00 each night using a Digital recorder (Q-see Security Surveillance, 4 Ch. H.264 network DVR, Digital Peripheral Solutions). The video cameras, and DVR were powered by two 12 V marine Batteries (Everstart Maxx 29 deep-cycle marine) that were paralleled to get maximum video during the night. Video was downloaded daily on to an external hard drive. Batteries were checked and replaced daily to maximize the video recording during the night. Video cameras where checked daily and readjusted as needed to get the best video quality of the trap entrance.

The polymer form of 3kPZS known as polyethylene glycol (PEG) was placed into a polyvinyl chloride plastic pipe (average weight was 18.3g) with each consisting of about 11.3 g of polymer/3kPZS mixture. PEG was placed in an Automatic pet feeder with a LCD Clock that was set to drop the PEG at 21:00 into a mesh bag that extended down into the water. The amount of 3kPZS needed to achieve 10^{-12}M was determined daily by using discharge rating curves (Gore 2006). When water levels were above those used to develop the rating curves, stream discharge was manually estimated using the velocity area method (McMahon et al. 1996).

The 3kPZS batch # 183-EJH-290-3 synthesized in February 2010 (Bridge Organics), was used to make the emitters. The batch had purities greater than 99% based on high pressure liquid chromatography and mass spectrometry.

All the recorded video was watched using playback of the video in two hour increments, via "EFPlayer HD". All video recorded during the study was observed by two reviewers blind to the baiting schedules of the trap. Behavior of sea lamprey was quantified in the same manner as in the video recorded during 2011.

External factors

Other factors were measured to see whether they affected entrance and retention rates of sea lampreys. Water temperature was recorded two ways, by a water temperature data logger (2011), and daily by the trap operators with a mercury thermometer that was held in the water for two minutes to get an accurate temperature (2012). Gauge height was recorded every day to be inputted into a discharge equation that outputs the discharge by using a discharge curve. The video was divided into different hours of the night ranging from 1-8 corresponding with the hour of recording; for example 21:00-21:59 would be recorded as hour 1, 22:00-22:59 as hour 2, etc. All observations within the hour of the night would receive the corresponding number to account for all the observations in the data set. The total catch was recorded every day by the control agents in which the agents sorted the sea lamprey as male or female that were captured during the night. The total catch amounts were summed for males and females each day for the entire migratory season. Time of season was divided into four equal divisions based on total catch (i.e., time of season 1 included the dates in which 0- 25% of the total trap catch occurred during the season).

Data analysis

Retention was calculated on an hourly basis as$\left(\frac{\text{Entries}-\text{Escapes}}{\text{Entries}}\right)$. All statistical analyses were conducted using (SPSS® version 20; IBM Corp., 2011), unless stated otherwise. To test the predictive ability of factors affecting the probability of entry we conducted a logistic regression using all of the video observations of lamprey approaching a trap with the following full model to test:

$log\left(\frac{Trap\ entry}{1-Trap\ entry}\right) = \alpha + \beta_1$year + $\beta_2$pheromone baited + $\beta_3$time of night + $\beta_4$time of season + $\beta_5$water temperature + $\beta_6$stream discharge + $\beta_7$year x pheromone baited + $\beta_8$year x hour of night + $\beta_9$year x pheromone baited x hour of night + β_{10}year x pheromone baited x water temperature

We created a model that included all predictor variables that were useful in predicting the response variable by conducting a stepwise method (backward: likelihood ratio).

To test the predictions on the factors affecting the probability of retention we conducted a linear regression on all of the data testing the same factors and interactions used in the aforementioned model. We created a model that included all predictor variables that were useful in predicting the response variable by conducting a stepwise method (backward: likelihood ratio).

Results

In 2011, we recorded 46 hours and 31 minutes of video over 21 nights, yielding 742 observations during the migratory period. Video was only recorded between 21:00 and 02:00 due to issues with lighting and power. The majority of observations (96%) were recorded in times of season 2 and 3. In 2012, we recorded 321 hours and 5 minutes of video over 44 nights yielding, 13,135 observations during the migratory period. The majority of observations (70%) were recorded in times of season 2 and 3. Video was recorded between 21:00 and 05:00.

Probability of entry

The best model to significantly explain probability of entry included the following factors and interactions: pheromone baited, hour of night, time of season, discharge, pheromone baited by year, hour of night by year, pheromone baited by hour of night by year, and pheromone baited by year by water temperature (Table 1). Sea lamprey were 1.31 times more likely to enter the trap when it was baited with pheromone (χ^2=44.346, df=1, p<0.0001) (Figure 3). Hour of night significantly explained some of the variance in probability of entry with entry more likely to occur later in the night/early morning (χ^2=70.893, df=7, p<0.0001) (Table 2, Figure 4). Probability of entry in hours of night 5,6,7,and 8 (midnight and later) was significantly different than in hour 1, entry rate in hours 2, 3, and 4 were not significantly different from hour 1. The probability that a sea lamprey would enter the trap upon approach decreased from the beginning to the end of the season (χ^2=642.328, df=3, p<0.0001) (Figure 5). Sea lamprey were less likely to enter the trap as stream discharge decreased (χ^2=21.424, df=1, p<0.0001). As the main effects were added to the model some hours of night changed from significant predictors to non-significant predictors, indicating other factors can statistically explain differences in probability of entry (Table 2).

Pheromone by year interaction was significant with sea lamprey more likely to enter the trap when it was baited than when it was not baited during both 2011 and 2012 (χ^2=21.425, df=2, p<0.0001) (Figure 6). Hour of night by year interaction significantly explained probability of entry (χ^2=19.854, df=4, p=0.001) in both 2011 and 2012. In 2011, probability of entry was highest in hour 3 (23:00-00:00) and decreased to hour five (01:00-02:00) (Figure 7). In 2012, hour 5 had the highest probability of entry and hour 3 had the lowest (Figure 7). Pheromone baited by hour of night by year interaction significantly explained proability of entry (χ^2=55.836, df=11, p<0.0001). In 2011, the highest probability of sea lamprey entering the trap when baited with pheromone occurred in hour 5, but when the trap was not baited with pheromone the lowest proability of entry occurred in the same hour (Figure 8). In 2012, when the trap was baited with pheromone probability of entry was highest in hour 6 (2 am-3 am), and lowest in hour 3 (11 pm-midnight) (Figure 8). The interaction between pheromone and year and water temperature significantly explained probability of entry (χ^2=135.887, df=4, p<0.0001).

Probability of Retention

The best model to significantly explain probability of retention included the following factors and interactions: hour of night, total trap catch, hour of night by year, time of season by year, water temperature by year, hour of night by pheromone baited by year, and time of season by year by pheromone baited (Table 3). Hour of night significantly explained retention (χ^2=10961.039, df=7, p<0.0001), with retention decreasing after 00:00 (Figure 9). Time of season was a significant factor influencing the retention of sea lamprey in the trap (χ^2=1328.619, df=3, p<0.0001). The retention rate decreased from time of season 1 to 2 then increased again (Figure 10). For the change in significance as main effects were added to the model refer to table 4.

The interaction between hour of night and year significantly explained variation in retention (χ^2=1950.224, df=5, p<0.0001). Both years had a similar pattern of retention over the night, with higher retention observed early in the evening (hours 1-3; 21:00-00:00), then a decrease in retention (Figure 11). The time of season by year interaction significantly explained some of the variation in proability of retention (χ^2=31.975, df=3, p<0.0001), with sea lamprey more likely to be retained during the entire 2011 season when compared to 2012 (Figure 12). Water temperature by year significantly explained some of the variation in proability of retention with an increase in retention with increasing water temperature . (χ^2=323.443, df=2, p<0.0001). The interaction between hour of night and year and pheromone baited helped to significantly explain probability of retention (χ^2=403.415, df=13, p<0.0001). In 2011, retention showed a decrease after midnight for both baited and non-baited nights (Figure 13). In 2012, retention showed a large decrease from midnight to 5 am on both baited and non-baited nights.(Figure 13). In 2011, retention is higher overall. However, in 2011 no video was recorded between 02:00 and 05:00 when probability of retention was observed to be lowest in 2012. (Figure 13). The interaction between time of season and year and pheromone baited significantly explained retention (χ^2=991.234, df=5, p<0.0001). In 2011, probability of retention remained constant across times of season 2, 3, and 4 whether the trap was baited or not baited (Figure 14). In 2012, proability of retention when the trap was pheromone baited was highest in time of season 1 and lowest in 2 (Figure 14).

Discussion

The use of sea lamprey pheromone increased the probability of entry into a trap when baited with synthesized 3kPZS versus when the trap was not baited (Figure 3). While looking at the interaction of pheromone baited with year, in both 2011 and 2012 when the trap was baited with pheromone the probability of entry was increased vs. when the trap was not baited. In 2011, as also reported in Johnson et al. (2013), sea lamprey observed approaching the trap were 68% (confidence interval = 24%–128%) more likely to enter when the trap was baited with 3kPZS than when not baited. In 2012, sea lampreys were 31% more likely to enter when the trap was baited with 3kPZS then when not baited. However, in 2011 there were much fewer observations recorded compared to 2012 due to the lack of quality video, battery life, and problems with cameras and lighting, with most observations occurring from 21:00 to 00:00 (Table 5 and 6). In a previous study, 3kPZS-baited traps captured significantly more prespermiated, pre-ovulated, and ovulated sea lampreys than paired unbaited traps (Johnson et al. 2013). My research indicates that 3kPZS-baited traps are more effective due to the fact that sea lampreys approaching a trap are more likely to enter when the trap is baited with 3kPZS.

The probability of a sea lamprey entering a trap increased as the night continued into the early morning hours (Figure 4). Movement of sea lamprey coincides with photoreceptors that limit movement during diurnal times and restricts movement to night time (Binder et al 2008). Interaction of hour of night by year indicated a different pattern in probability of entry between 2011 and 2012. In 2011, probability of entry declined after midnight, while in 2012 probability increased into early morning. However, during the 2011 season video was recorded only until 02:00 (five total hours), while during 2012 video was recorded until 05:00 (eight total hours). As lamprey movement continues into early morning the lamprey were more likely to enter the trap.

The different times of season in the spawning migration of sea lamprey affected the likelihood of entry, with entry being more likely at the beginning of the season than at the end of the season (Figure 5). Spawning migration is mainly controlled by the temperature of the surrounding waters which controls the start of movement of sea lamprey upstream as well as the presence of larval pheromone to identify existing quality spawning grounds (Wagner et al 2009).

The decrease in probability of entry towards the end of the spawning season could be contributed to the lack of energy/fat stores that propels the whole migration and spawning activity in lamprey (Beamish 1974). Thus, weakened lamprey may desist from exhibiting strong directed upstream movements. As the time of spawning approaches lampreys have been observed to reverse course and head downstream to locate spawning habitat and mates (Wagner et al. 2010).

Water discharge is negatively correlated with the probability of a sea lamprey entering the trap. Increased discharge from smaller streams may cause sea lamprey to locate the larval pheromone plume easier and faster to locate quality spawning habitat. Stronger rheotactic cues help determine suitable habitat to spawn for optimum larval success. Discharge has been found to be a significant factor on smaller streams but less of a factor in larger systems (Binder & McDonald 2010). Carp Lake Outlet is considered a small to medium system compared to St. Mary's River.

Interaction between multiple factors influenced the probability that a sea lamprey would enter the trap. The interaction of pheromone baited by year by hour of night significantly explained some of the variance in probability of entry. Probability of entry was not always higher when the trap was baited with pheromone compared to when it was not baited, and this relationship changed with the hour of night. This could be due to the fact that 3kPZS is only a single component of the complete mating pheromone released by adult male sea lamprey (Johnson et al. 2012). An additional significant predictor of probability of entry was the interaction between pheromone baited by year by water temperature with probability of entry increasing with water temperature. Temperature modulates upstream migration, general health, and sexual maturation in all lamprey (Binder and McDonald 2008; Clemens et al. 2009; Keefer et al. 2009), so it follows that behavior of sea lamprey would change in response to these factors.

The other important component of the trapping process is retention of the individuals that enter the trap. Hourly retention was significantly lower after midnight in both years (Figure 11). This is likely due to the fact that there are more lampreys in the trap, and some have been in the trap longer which increases the likelihood that they will find an escape route. Midnight could be the best time to remove the greatest number of reproductive and immature individuals from the system before the majority of the lamprey leave the trap. Some traps in the St. Mary's River are emptied between midnight and 1 am and again at approximately 9 am as research has shown an increase in catch with the additional trap check (Jean Adams, U.S. Geological Survey, unpublished data). Retention was greatest at the end of the spawning season (Figure 10). Lack of fat stores towards the end of the season could result in individuals not leaving the trap because they do not have the energy to disperse to find a partner to reproduce before perishing. Alternatively, the motivation of lamprey to try and escape the trap may be influenced by the density of sea lamprey in the trap; less lamprey (in late season) may result in higher retention. While 2011 had a higher probability of retention than 2012, both years show a similar pattern (Figure 12).

Interactions between various factors influenced the probability of retention. Water temperature by year significantly explained variation in the retention of sea lamprey with probability of retention being higher in 2011. Pheromone baited by year by hour of night indicated retention increasing and decreasing throughout the night with no obvious pattern detected. In 2011, the only difference in retention between hours of night occurred in hour 5 (01:00 -02:00) when retention was significantly higher when the trap was baited vs. unbaited. Probability of retention was highest in both years before midnight, but individuals were more likely to be retained in 2011 (Figure 11). Pheromone baited by year by time of season indicates a difference in the pattern of retention throughout the season between years and between baited and unbaited nights. Pheromone baited by year by water temperature and pheromone baited by year by discharge were significant interactions that explained some of the variance in retention, but clear patterns were difficult to discern.

Pheromone baiting proved to be successful in attracting sea lamprey to enter the trap, but it did not have an effect on retaining the individuals in the trap. Even though 3kPZS might be used as an attractant, and has been known to stimulate upstream movement in immature and mature sea lamprey (Johnson et al. 2013), it does not help retain the individuals in the trap. Probability of entry was higher later in the night, while probability of retention was lower later in the night. Probability of entry was higher at the beginning of the season, and retention was higher at the end of the season. Some sea lamprey traps on the St. Mary's River do night traps checks between midnight and two in the morning, which could be beneficial by yielding more lampreys being taken from the water system before lampreys start to escape from the traps. Sea lamprey entrance rates were influenced mainly by main effects and interactions between pheromone, hour of night, and water temperature. Retaining those individuals that entered the trap is more complex with many different factors contributing (through main effects or interactions) to the retention of sea lamprey.

The results found in this research could help sea lamprey control agents maximize the adult population that could be captured in traps if traps were going to start being used as a removal method in their control plan. Synthesized 3kPZS proved to increase the probability of sea lamprey entering a trap, just as previous studies suggested that in the field and in control settings, lamprey were attracted to baited traps (Johnson et al 2013; Li et al 2012; Luehring et al 2011). Larval pheromone still must be present to attract sea lamprey into a particular stream where the synthesized pheromone can be discharged from a trap, as 3kPZS has not been shown to increase the rate at which sea lamprey encounter traps. As sea lamprey mature in streams they become harder to trap, as they begin moving back down stream and are not lured to the barrier-integrated trap with just 3kPZS. A male sea lamprey on a nest excreting the complete pheromone would retain a mature female because it has the complete components of pheromones to keep that female versus having just one component. As 3kPZS is the primary component to induce upstream movement to the spawning nest (Johnson et al 2012a), and other components of the complete pheromone are beginning to be identified (Li et al 2012). In pheromone systems of fish and insects, mixtures of compounds are used to present certain messages to the receiver but when partial components of fish and insect pheromones are used in traps capture rates vary and often can be lower than when all components are used (Johnson et al. 2006; Howse et al. 1998). If additional components of the mating pheromone could be identified and synthesized it could increase the effectiveness of barrier-integrated traps. If components of the pheromone released by larvae to attract adult sea lamprey to quality habitat could be identified and synthesized then the rate at which adults encounter traps could likely be increased.

Other environmental factors such as water temperature were shown to increase the likelihood of lamprey entering and being retained in a trap. Water temperature is an important factor, with optimum temperatures for trapping being just below optimum temperatures for the development of sea lamprey embryos (Binder et al. 2010). More sea lamprey can be removed at the beginning to the middle of the season versus the end. In order for trapping to be used as an alternative method for control of adult sea lampreys, it must be efficient enough to reduce reproductive potential (i.e., animals are removed at a greater rate than they can replace themselves). Trapping can improve assessment of program effectiveness and fits within the framework of integrated pest management (Christie and Goddard 2003). Traps baited with 3kPZS could be one of the first of several tactics used to enhance the overall effectiveness of the control program by modifying behavior with chemosensory cues (Twohey et al. 2003). Integrating the use of pheromone cues to lure more sea lamprey into streams that are more effective to treat could be especially beneficial for the control program (Miller and Cowles 1990; Wagner et al 2012; Hassanalie et al 2008). The cost of 3kPZS to be applied to traps operated by control agents, and the cost to synthesize 3kPZs has decreased 40 fold in the past decade (Johnson et al. 2013). Therefore, the GLFC is registering the pheromone with the Environmental Protection Agency and Health Canada through the North American Free Trade Agreement as the first vertebrate pheromone ever used for pest control (Johnson et al 2013). Further research is needed on other components of the male pheromone to determine how components besides 3kPZS impact sea lamprey migratory behavior.

Table 1. Main factors and interactions that significantly explained probability of entry of sea lamprey with Wald Chi-Square, degrees of freedom, and significance reported.

Tests of Model Effects

Source	Type III		
	Wald Chi-Square	df	Sig.
(Intercept)	3.458	1	0.063
Pheromone.baited	4.611	1	0.032
Hour.of.night	30.016	7	0.0001
Time of season	574.282	3	0.0001
Discharge.cms	8.545	1	0.003
Pheromone.baited * Year	35.949	1	0.0001
Hour.of.night * Year	20.020	4	0.0001
Pheromone.baited * Hour.of.night * Year	94.124	11	0.0001
Pheromone.baited * Year * Water.temp	135.887	4	0.0001

Dependent Variable: Entered

Model: (Intercept), Pheromone.baited, Hour.of.night, Time of season, Discharge.cms, Pheromone.baited * Year, Hour.of.night * Year, Pheromone.baited * Hour.of.night * Year, Pheromone.baited * Year * Water.temp

Table 2. Sea lamprey entry factors showing parameter coefficients (B),standard errors (SE), significance (Sig.), and odds ratio (OR) as factors were added to the model.

	Model 1				Model 2				Model 3				Model 4			
Variables	B	SE	Sig.	OR	B	SE	Sig.	OR	B	SE	Sig.	OR	B	SE	Sig.	OR
Pheromones	0.274	0.0411	0.0001	1.315	0.254	0.0416	0.0001	1.29	0.282	0.0447	0.0001	1.326	0.273	0.0448	0.0001	1.314
Hour of nights 8					0.381	0.146	0.009	1.46	0.296	0.151	0.05	1.344	0.237	0.1518	0.118	1.268
Hour of nights 7					0.524	0.1244	0.0001	1.69	0.464	0.1287	0.0001	1.591	0.411	0.1296	0.002	1.508
Hour of nights 6					0.513	0.1131	0.0001	1.67	0.467	0.1171	0.0001	1.595	0.415	0.1179	0.0001	1.514
Hour of nights 5					0.556	0.101	0.0001	1.74	0.537	0.1048	0.0001	1.711	0.503	0.1054	0.0001	1.654
Hour of nights 4					0.166	0.0921	0.071	1.18	0.185	0.0959	0.054	1.203	0.165	0.0962	0.086	1.18
Hour of nights 3					0.124	0.0871	0.154	1.13	0.138	0.0911	0.129	1.148	0.122	0.0914	0.183	1.129
Hour of nights 2					0.121	0.0855	0.156	1.13	0.108	0.0891	0.225	1.114	0.098	0.0894	0.274	1.103
Hour of nights 1					0				0	.		1	0	.		1
Time of season=4									-1.617	0.0953	0.0001	0.198	-1.786	0.1021	0.0001	0.168
Time of season=3									-0.388	0.0944	0.0001	0.679	-0.483	0.0966	0.0001	0.617
Time of season=2									-0.471	0.0916	0.0001	0.624	-0.547	0.0931	0.0001	0.578
Time of season=1									0	.		1	0	.		1
Discharge													-0.438	0.0946	0.0001	0.645

Table 3. Main factors and interactions that significantly explained retention of sea lamprey with Wald Chi-Square, degrees of freedom, and significance reported.

Tests of Model Effects

Source	Type III		
	Wald Chi-Square	df	Sig.
(Intercept)	7.213	1	0.007
Hour.of.night	3800.081	7	0.000
Time of season	6.933	3	0.074
Hour.of.night * Year	134.425	4	0.0001
Time of season * Year	19.120	3	0.0001
Year * Water.temp	719.357	2	0.0001
Hour.of.night * Year * Pheromone.baited	441.976	11	0.0001
Time of season * Year * Pheromone.baited	991.234	5	0.0001

Dependent Variable: Retention.hourly

Model: (Intercept), Hour.of.night, Time of season, Hour.of.night * Year, Time of season* Year, Year * Water.temp, Hour.of.night * Year * Pheromone.baited, Time of season* Year * Pheromone.baited

Table 4. Sea lamprey entry factors showing parameter coefficients (B), standard errors (SE), significance (Sig.), and odds ratio (OR) as factors were added to the model.

	Model 1				**Model 2**			
Variables	**B**	**SE**	**Sig.**	**OR**	**B**	**SE**	**Sig**	**OR**
Hour of nights 8	-0.566	0.022	0.0001	0.568	-0.547	0.021	0.0001	0.579
Hour of nights 7	-0.621	0.0195	0.0001	0.537	-0.598	0.0187	0.0001	0.55
Hour of nights 6	-0.671	0.0178	0.0001	0.511	-0.628	0.0171	0.0001	0.534
Hour of nights 5	-0.71	0.0165	0.0001	0.492	-0.671	0.0158	0.0001	0.511
Hour of nights 4	-0.633	0.0157	0.0001	0.531	-0.602	0.0151	0.0001	0.547
Hour of nights 3	-0.015	0.0152	0.321	0.985	0.021	0.0146	0.148	1.021
Hour of nights 2	0.043	0.0152	0.005	1.044	0.07	0.0146	0.0001	1.072
Hour of nights 1	0a			1	0a	.	.	1
Time of season=4					0.062	0.0134	0.0001	1.064
Time of season=3					-0.036	0.0129	0.005	0.964
Time of season=2					-0.218	0.0128	0.0001	0.804
Time of season=1					0a	.		1

Table 5 . The hours of sea lamprey video watched by the observer in 2011.

Carp Lake Outlet		2011		
			Time	
Date	Hours	Minutes	Start - End	Observations
May 3	2	2	21:00 - 23:29	
4	2	59	21:00-23:59	2
5	1	53	00:00-1:15 & 21:00-21:38	
8	0	25	21:00-21:25	
13	3	0	21:00-24:00	
14	6	30	00:00-5:00 & 21:00-22:30	
17	0	35	21:00-21:35	
19	0	35	21:00-21:35	1
23	0	25	21:00-21:25	5
25	0	30	21:00-21:30	2
26	1	36	22:24-24:00	12
27	4	23	00:00 – 2:40 & 21:00 - 22:43	2
29	3	0	21:00 - 24:00	160
30	4	55	00:00-1:55 & 21:00 - 24:00	278
31	4	19	00:00 – 1:19 & 21:00 - 24:00	251
June 1	1	35	21:00-22:35	6
5	1	2	21:00-22:02	
10	0	47	21:00-21:47	
12	3	0	21:00-24:00	9
13	0	25	00:00-00:25	
14	2	23	21:00-23:23	18
	46	**31**		**742**

Table 6. The hours of sea lamprey video watched by the observers in 2012.

Carp Lake Outlet			2012	
			Time	
Date	Hours	Minutes	Start - End	Observations
May 1	3	8	20:52 - 24:00	10
2	4	33	0:00-0:33 & 19:00-24:00	2
3	1	50	0:00-1:50	0
5	3	1	20:59-24:00	14
6	8	1	0:00-5:01 & 21:00-24:00	3
7	7	23	0:00-4:23 & 21:00-24:00	0
8	8	0	00:00-5:00 & 21:00-24:00	25
9	8	0	00:00-5:00 & 21:00-24:00	82
10	8	0	00:00-5:00 & 21:00-24:00	46
11	8	0	00:00-5:00 & 21:00-24:00	539
12	8	0	00:00-5:00 & 21:00-24:00	120
13	8	0	00:00-5:00 & 21:00-24:00	95
14	8	0	00:00-5:00 & 21:00-24:00	1403
15	8	0	00:00-5:00 & 21:00-24:00	897
16	8	0	00:00-5:00 & 21:00-24:00	67
17	8	0	00:00-5:00 & 21:00-24:00	27
18	8	0	00:00-5:00 & 21:00-24:00	1206
19	8	0	00:00-5:00 & 21:00-24:00	1186
20	8	0	00:00-5:00 & 21:00-24:00	1871
21	8	0	00:00-5:00 & 21:00-24:00	53
22	8	0	00:00-5:00 & 21:00-24:00	262

23	8	0	00:00-5:00 & 21:00-24:00	1082
24	8	0	00:00-5:00 & 21:00-24:00	1116
25	8	0	00:00-5:00 & 21:00-24:00	529
26	8	0	00:00-5:00 & 21:00-24:00	304
27	8	0	00:00-5:00 & 21:00-24:00	19
28	8	0	00:00-5:00 & 21:00-24:00	969
29	8	0	00:00-5:00 & 21:00-24:00	327
30	8	0	00:00-5:00 & 21:00-24:00	35
31	8	0	00:00-5:00 & 21:00-24:00	25
June 1	8	1	00:00-5:01 & 21:00-24:00	3
2	8	1	00:00-5:00 & 20:59-24:00	16
3	8	2	00:00-5:02 & 21:00-24:00	93
4	8	1	00:00-5:01 & 21:00-24:00	88
5	8	1	00:00-5:01 & 21:00-24:00	331
6	7	1	00:00-4:01 & 21:00-24:00	140
7	8	0	00:00-5:00 & 21:00-24:00	85
8	8	0	00:00-5:00 & 21:00-24:00	43
9	6	2	00:00-5:00 & 21:00-22:02	2
10	3	0	21:00-24:00	14
11	8	0	00:00-5:00 & 21:00-24:00	18
12	8	0	00:00-5:00 & 21:00-24:00	3
13	8	0	00:00-5:00 & 21:00-24:00	2
14	5	0	00:00-5:00	
	321	**5**		**13135**

Figure 1. Location of the Carp Lake Outlet.

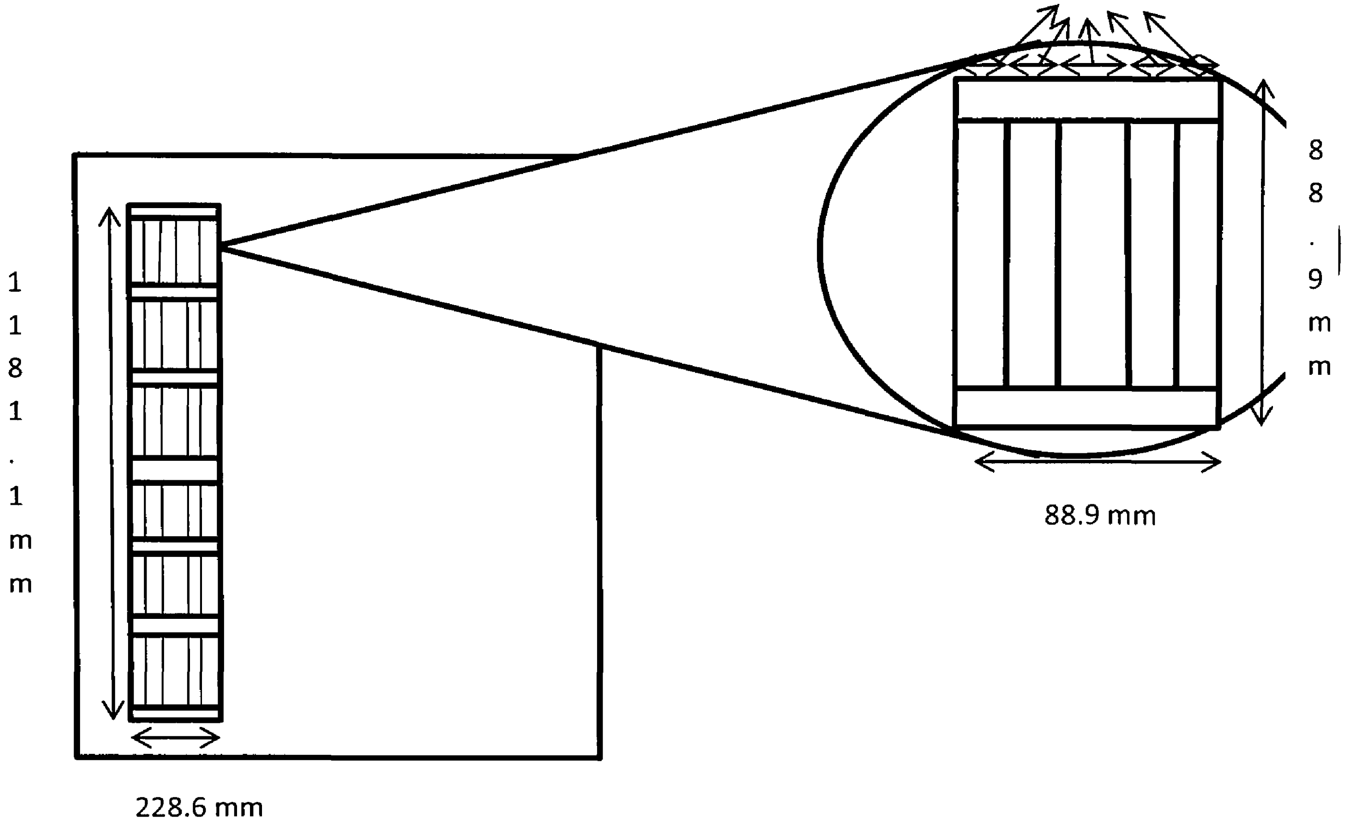


Figure 2. . Drawing of the permanent trap with measurements of the trap dimensions.

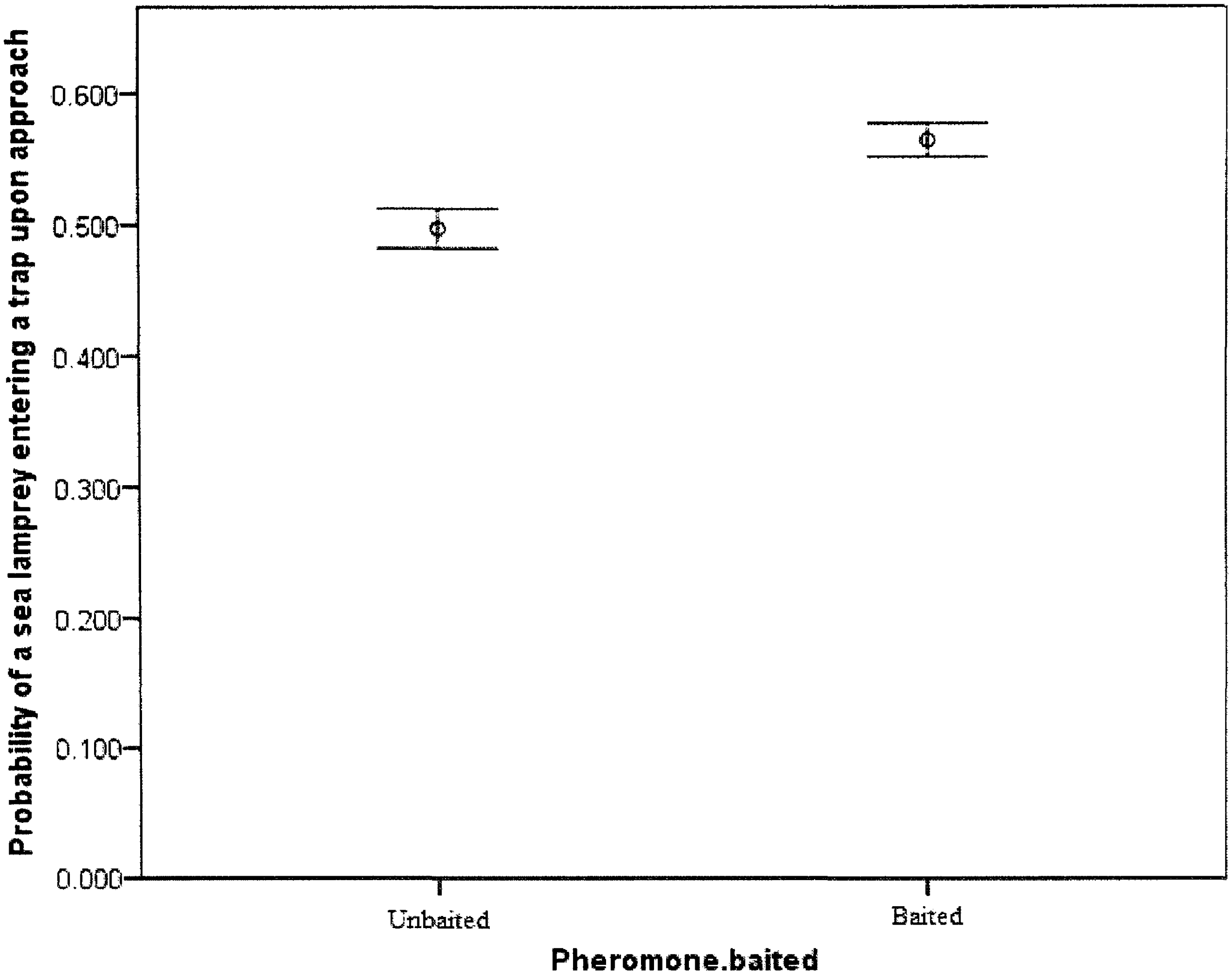


Figure 3. Sea lamprey probability of entry when the trap was unbaited and baited. Error bars indicate 95% confidence intervals.

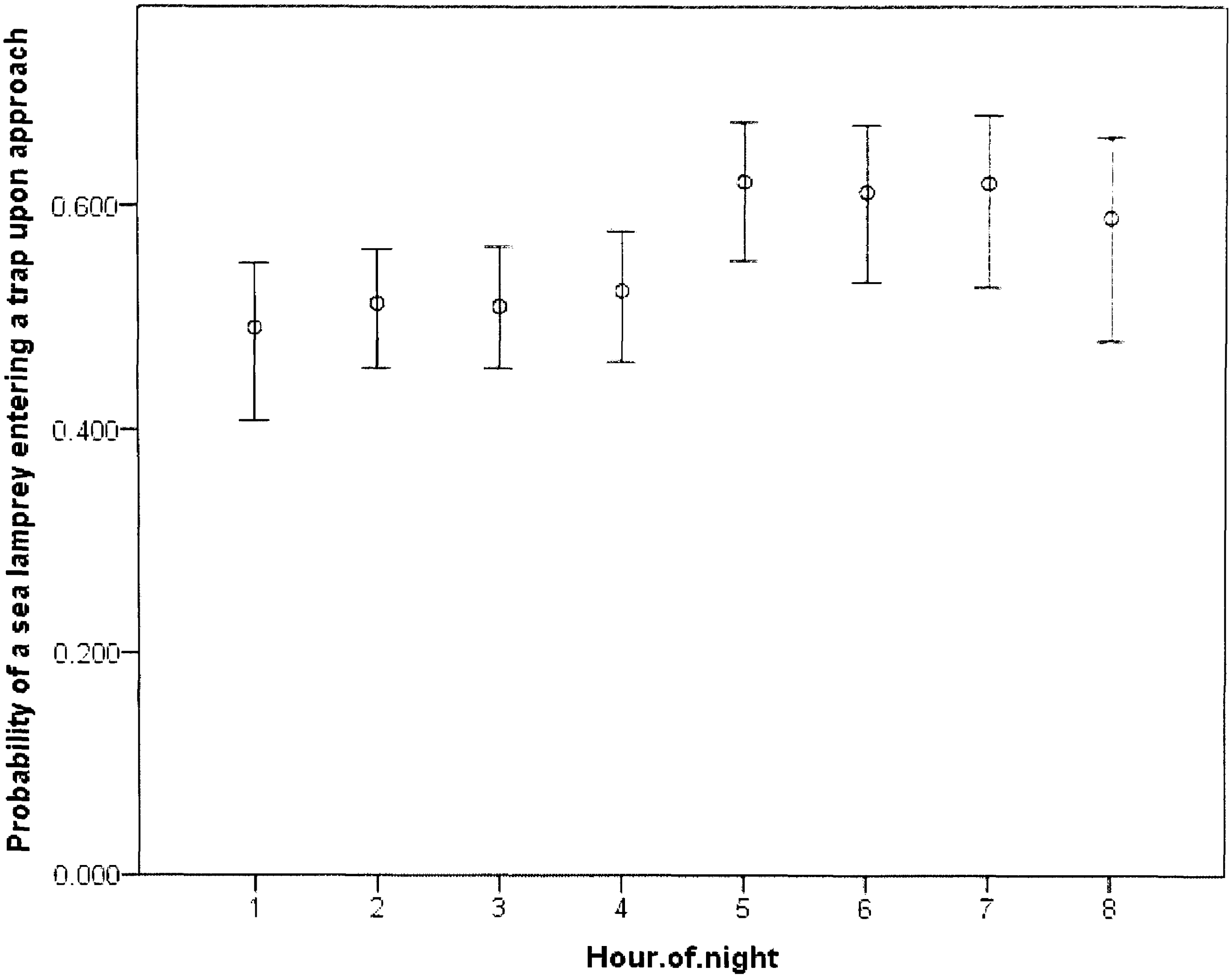


Figure 4. Hourly probability of sea lamprey entry. Error bars indicate 95% confidence intervals.

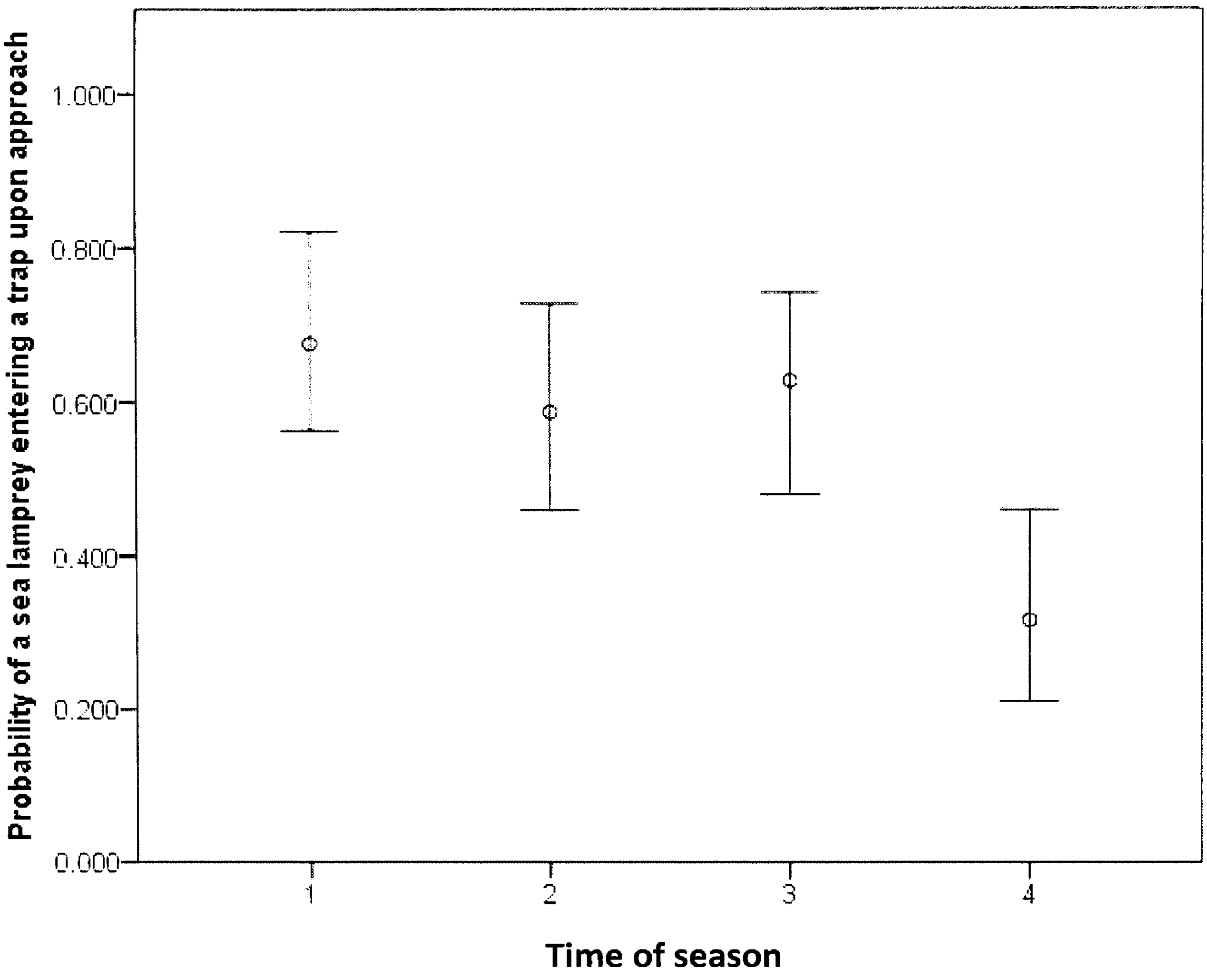


Figure 5. Probability of sea lamprey entry at different times of season. Error bars indicate 95% confidence intervals.

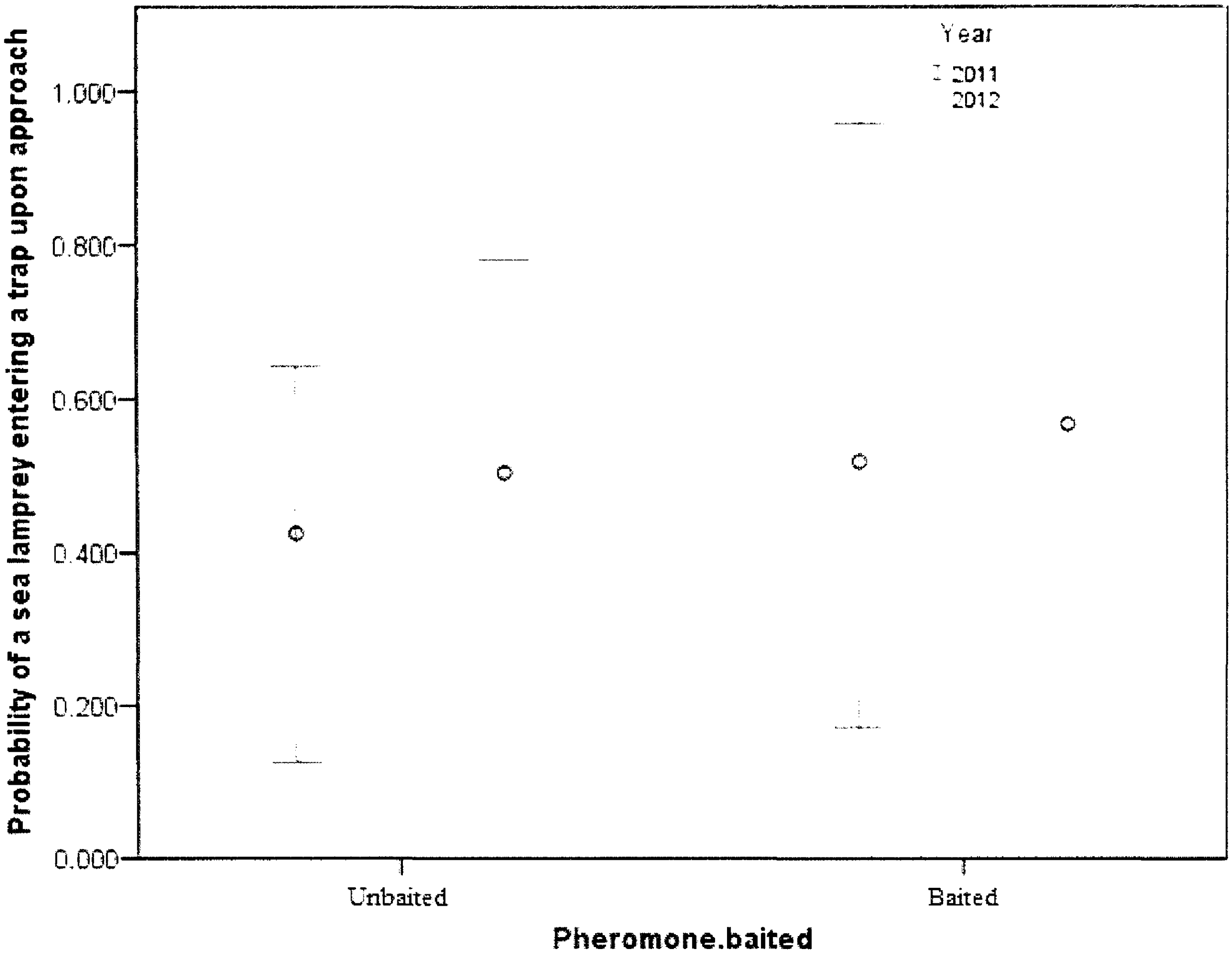


Figure 6. Probability of entry between unbaited and baited nights in 2011 and 2012. Error bars indicate 95% confidence intervals.

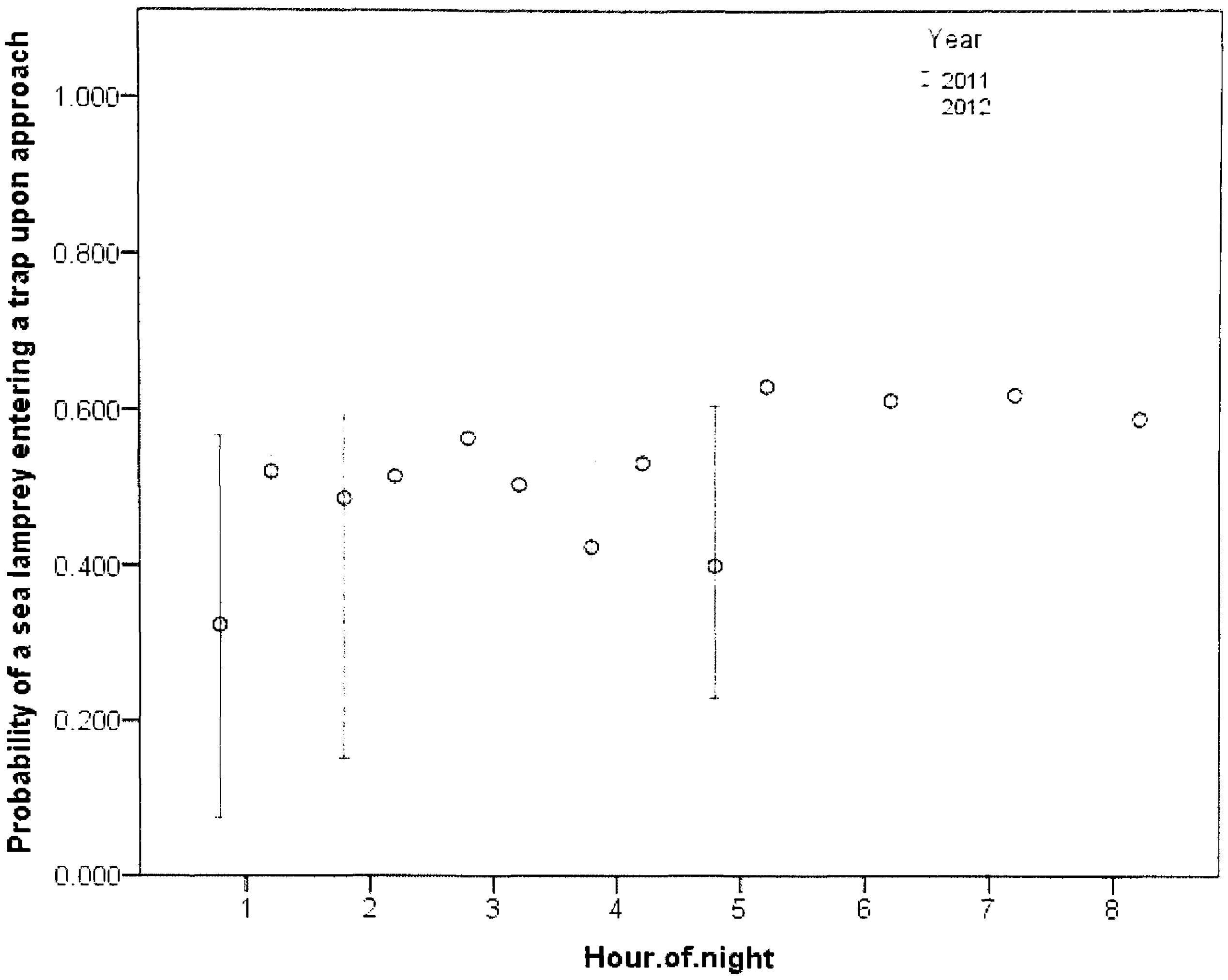
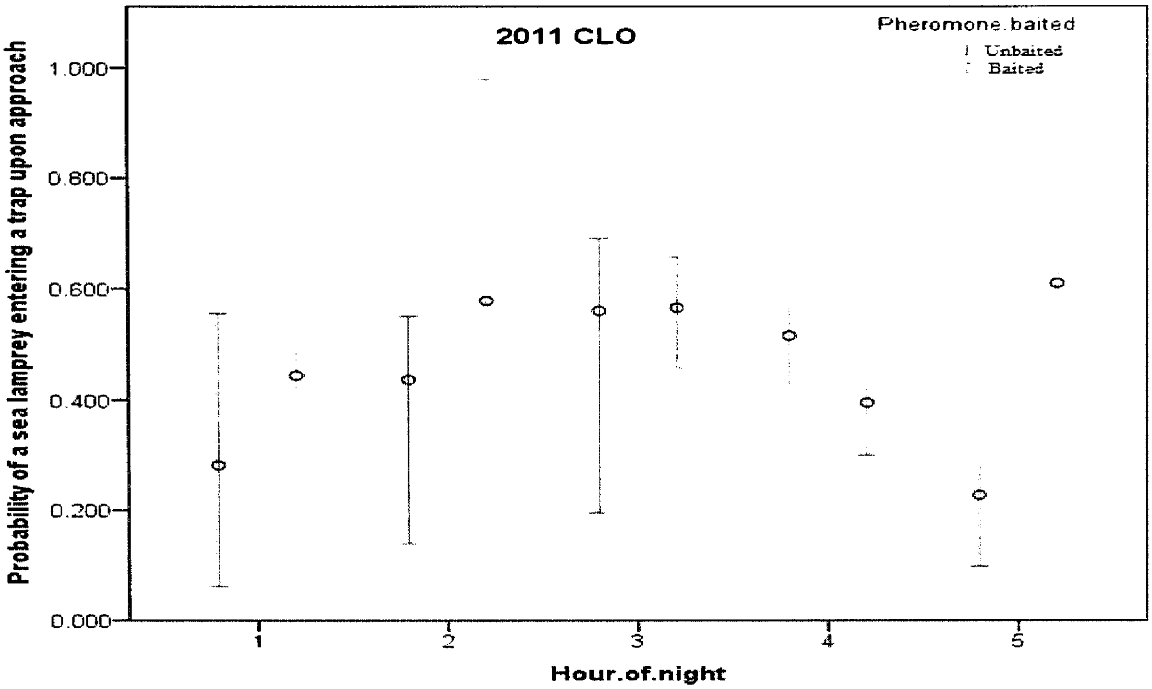


Figure 7. Hourly probability of sea lamprey in 2011 and 2012. Error bars indicate 95% confidence intervals.



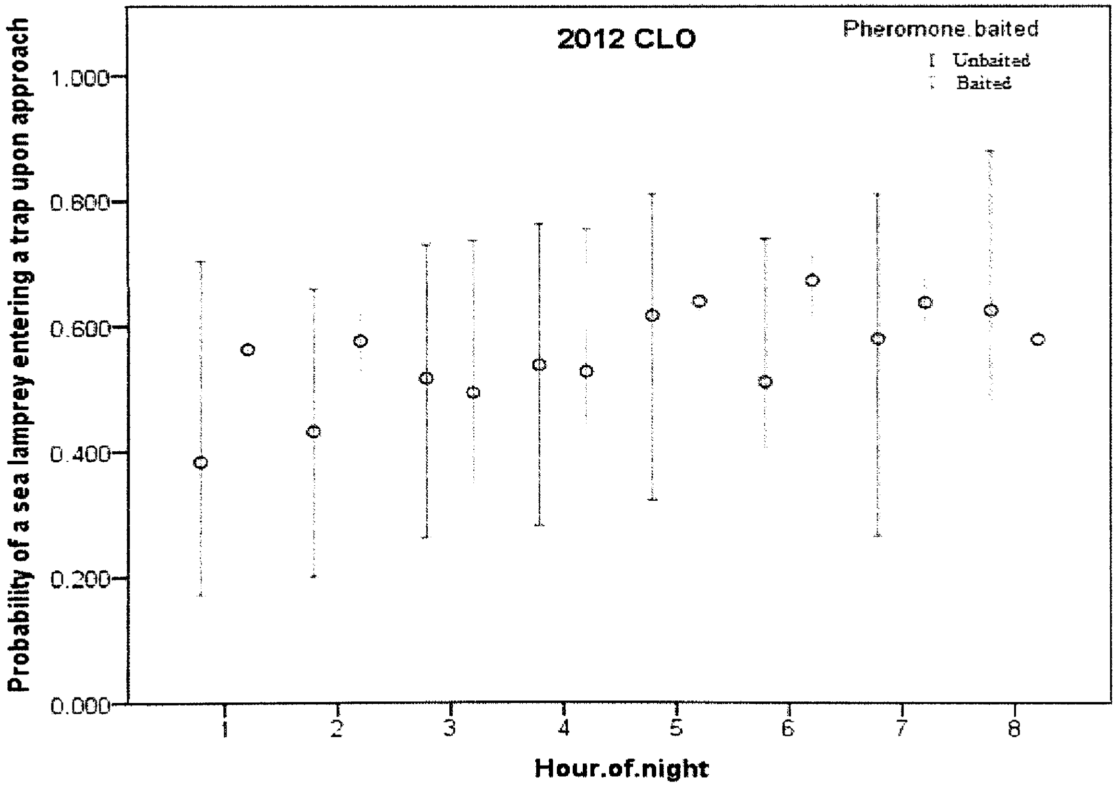


Figure 8. Three-way interaction showing probability of entry with between unbaited and baited nights in 2011 and 2012. Error bars indicate 95% confidence intervals.

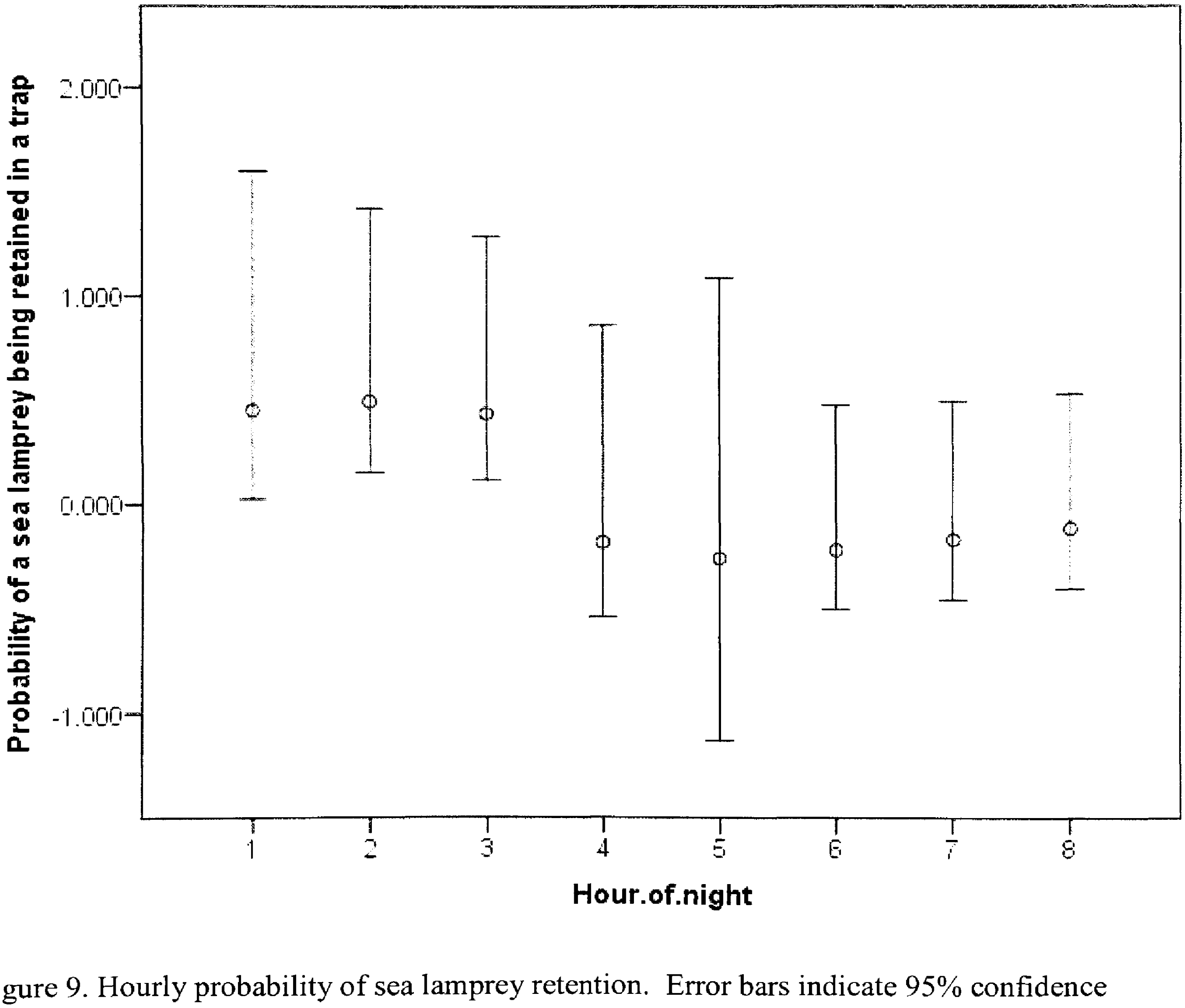


Figure 9. Hourly probability of sea lamprey retention. Error bars indicate 95% confidence intervals.

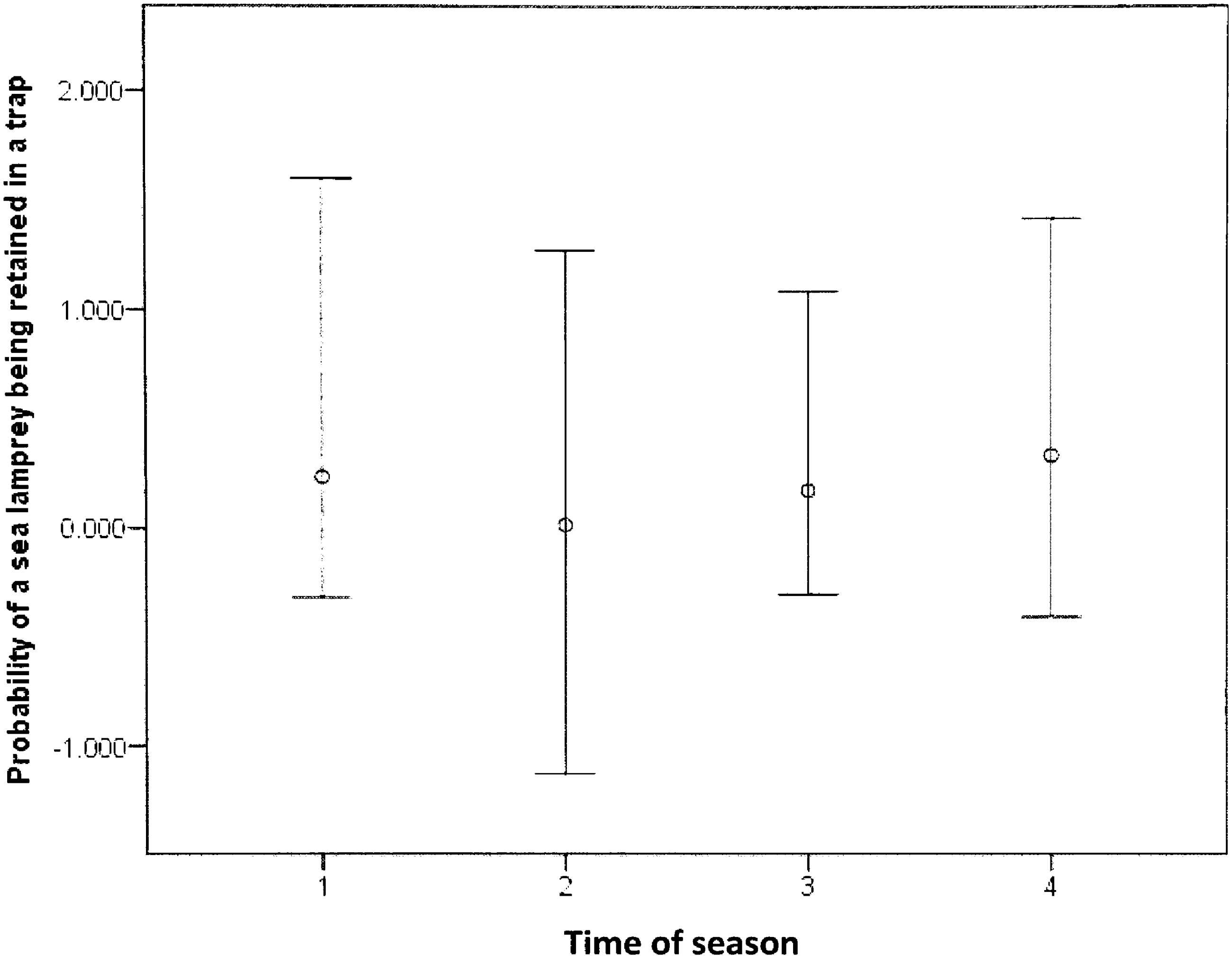


Figure 10. Probability of sea lamprey retention at different times of the season. Error bars indicate 95% confidence intervals.

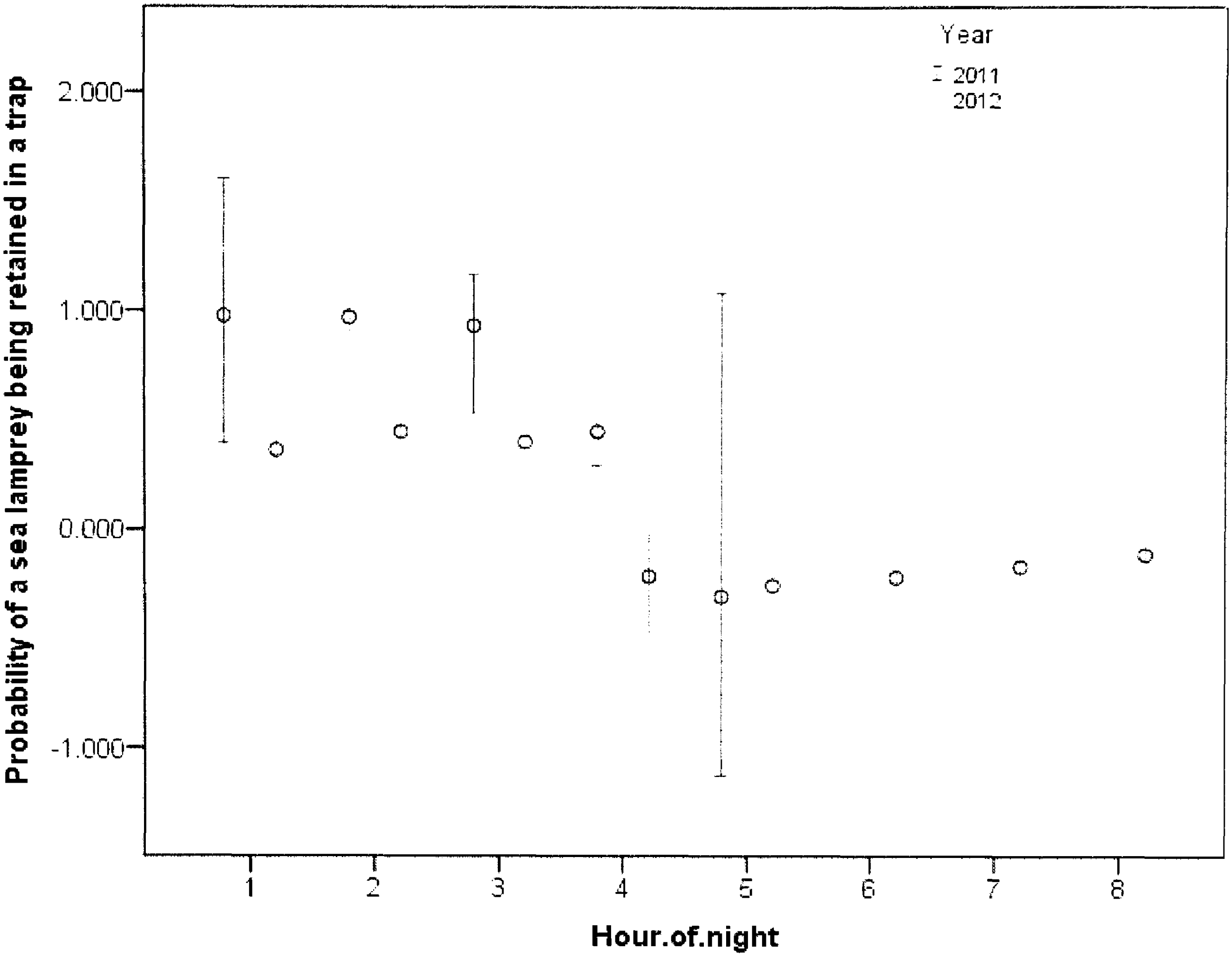


Figure 11. Hourly probability of sea lamprey retention in 2011 and 2012. Error bars indicate 95% confidence intervals.

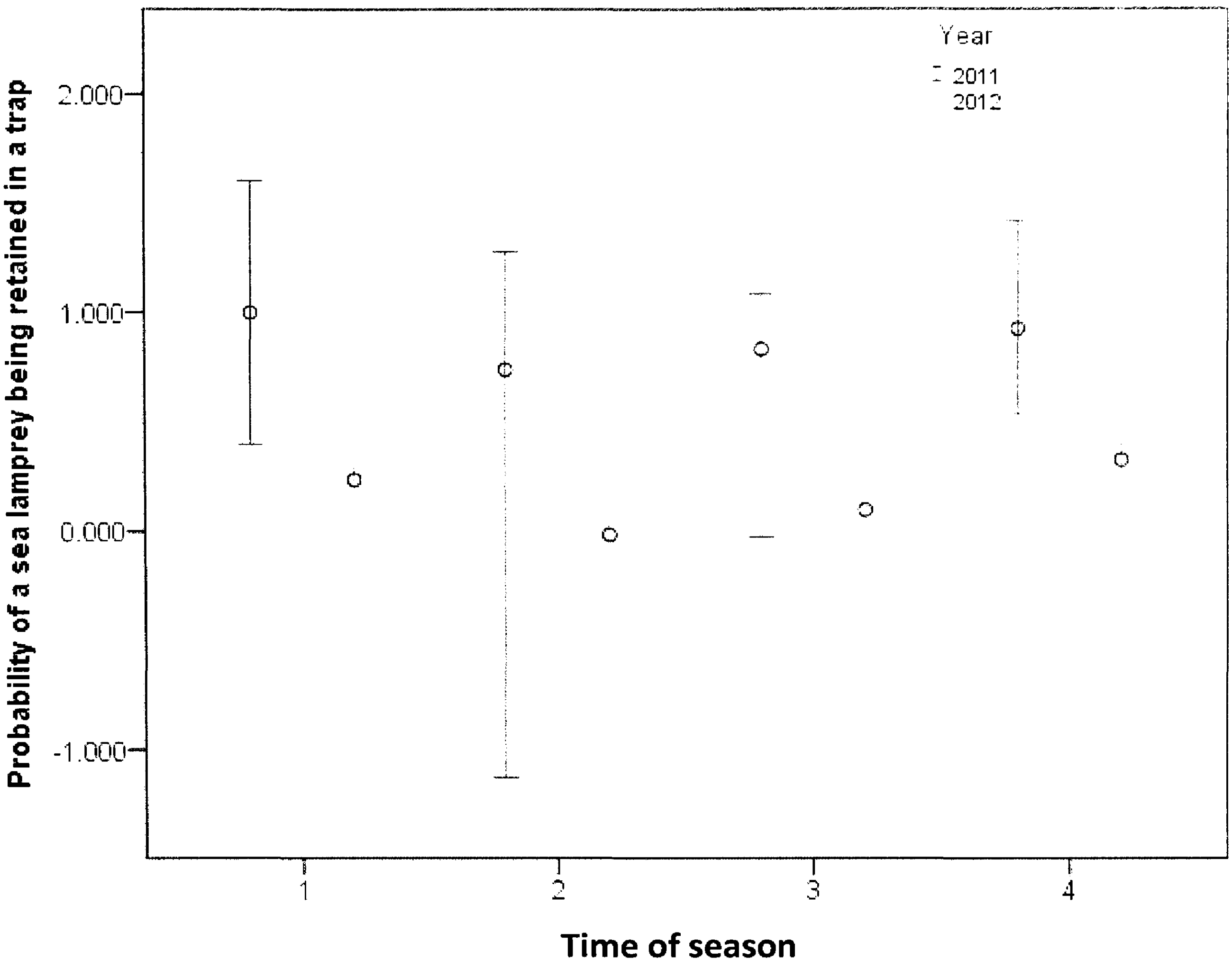


Figure 12. Probability of sea lamprey retention at different times of the season in 2011 and 2012. Error bars indicate 95% confidence intervals.

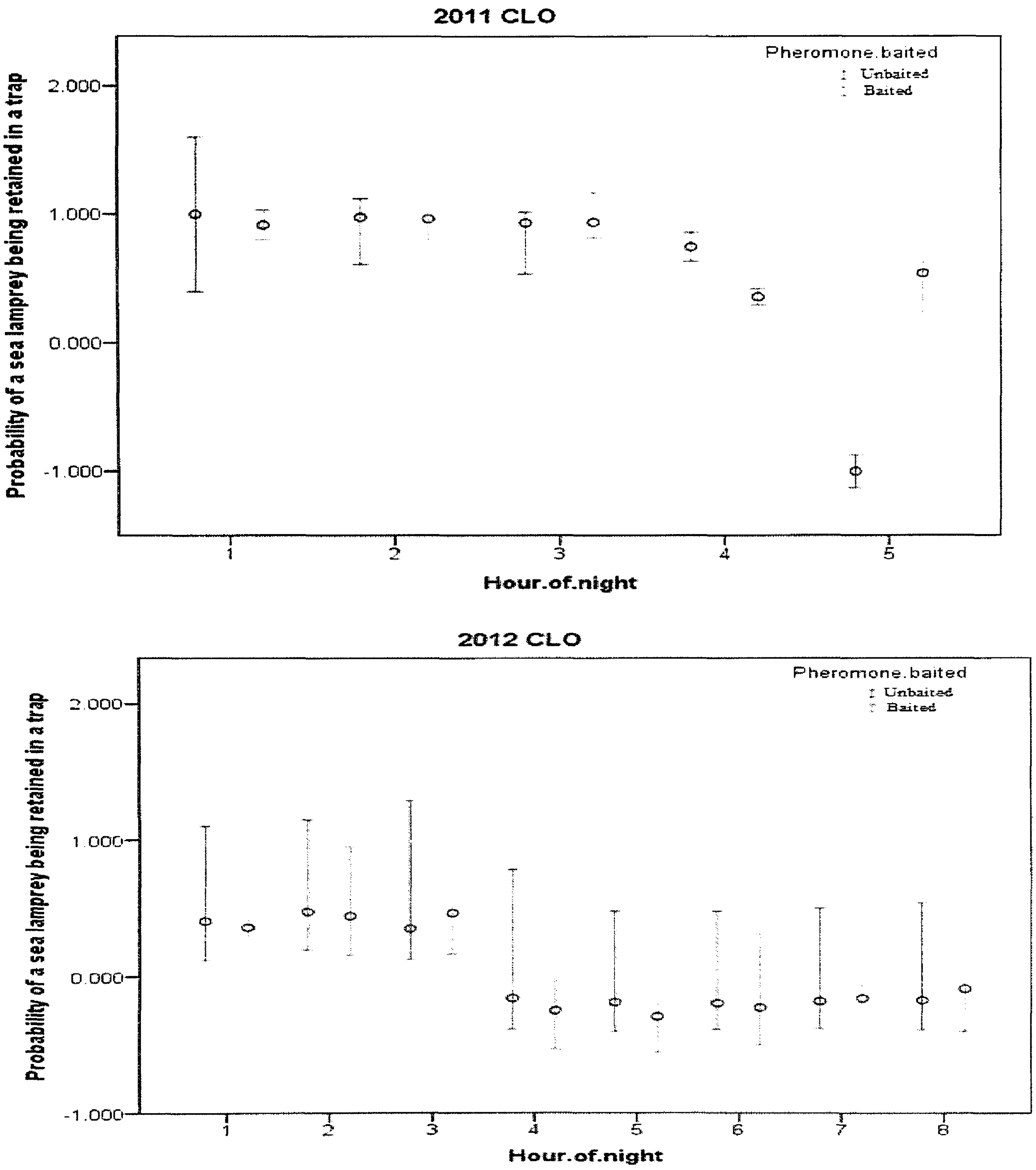


Figure 13. Three-way interaction showing hourly probability of sea lamprey retention between unbaited and baited nights in 2011 and 2012. Error bars indicate 95% confidence intervals.

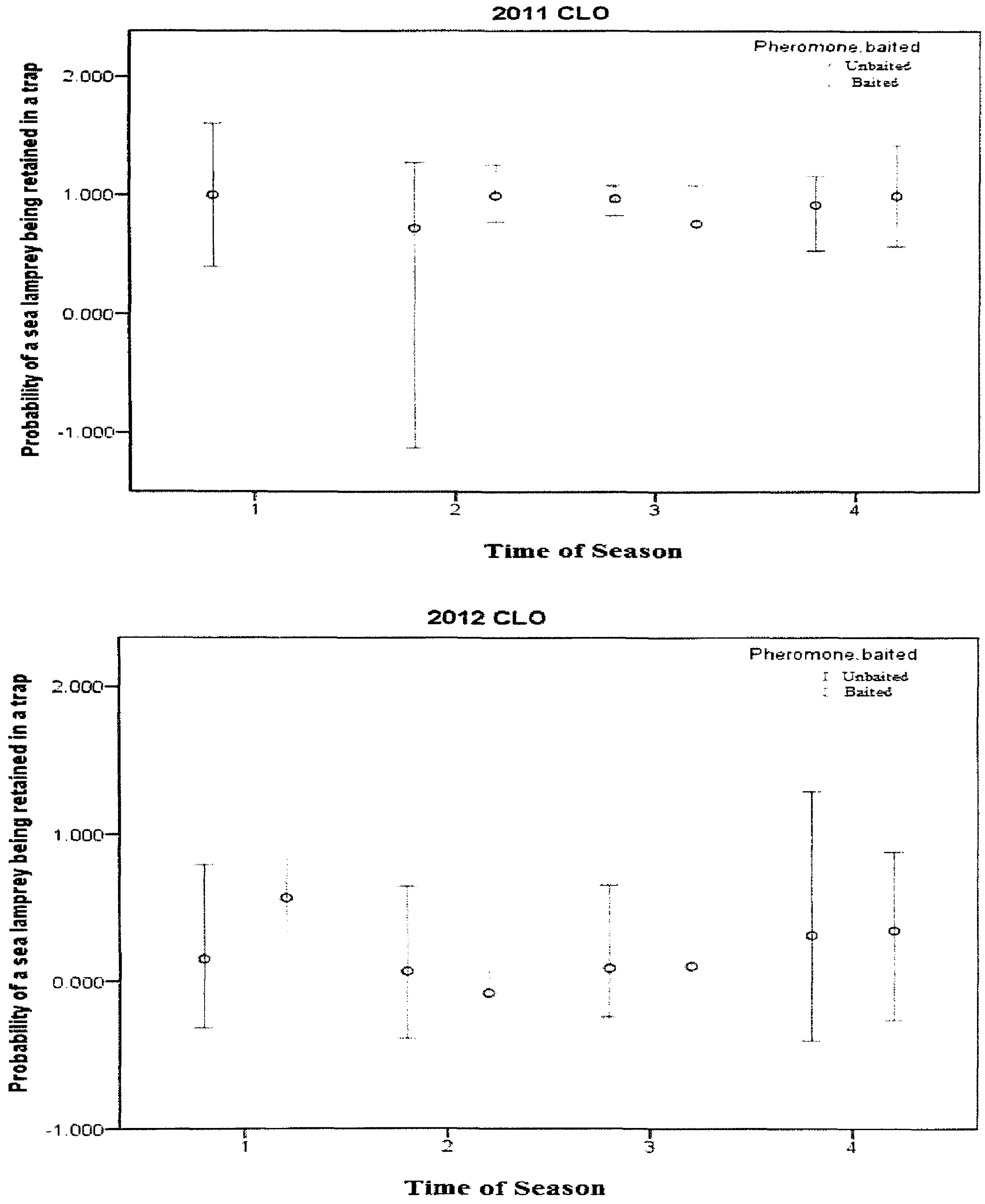


Figure 14. Three-way interaction showing probability of sea lamprey retention at different times of the season between unbaited and baited nights in 2011 and 2012. Error bars indicate 95% confidence intervals.

Chapter 2: **FACTORS INFLUENCING THE ENTRANCE AND RETENTION RATES OF SEA LAMPREY AT TRAPS IN TWO GREAT LAKES TRIBUTARIES**

Abstract

Trapping of sea lamprey has been used only for assessment purposes and to provide specimens for research purposes. In order for trapping to be used as a control method, the efficiency of traps needs to be improved. By studying the behavior of sea lamprey at traps, we may be able to determine important factors that affect trapping success. Traps vary in size, shape, and type. Along with the different trap types, environmental factors play a role in the entry and retention of sea lamprey. Entrance and retention rates of sea lamprey at a trap on the Cheboygan River and three traps on the St. Mary's River were determined through video analysis. The data indicated that sea lamprey entry was linked to time of season and the interaction of trap and water temperature, whereas there were multiple different physical and environmental factors playing a role in the retention of sea lamprey in traps.

Introduction

Sea lamprey traps have been used to capture migrating adult lamprey in streams as they are seeking reproductive habitat (Applegate 1950). The Great Lakes Fishery Commission (GLFC) is looking for alternative methods to reduce the use of lampricides; trapping could be one of those alternative methods (GLFC 2001a). Trapping efficiency would need to be improved to be considered as a viable alternative or complement to lampricide control (GLFC 2011). There are many factors that could potentially contribute to improved trapping such as different trap designs, placement of traps, and environmental factors.

Sea lamprey traps in the Great Lakes vary in their capture efficiency. There are different trap designs, ranging in size and type (i.e., permanent or portable; GLFC 2001a). Some traps are integrated with a barrier, or otherwise placed strategically to intercept sea lamprey on their spawning migration. Permanent traps are concrete or steel, usually square or rectangular in shape, built into a permanent barrier (Mclaughlin et al 2007). Portable traps are rectanglar or circular in shape, with either one or both sides containing a funnel guiding the lamprey toward the trap entrance. The funnel of portable traps can be oriented at the bottom, middle, or top of the entrance. Permanent traps often have no funnel, and the entrance is usually oriented vertically. Along with differences in trap design, the placement of those traps in streams can affect the rate at which sea lamprey encounter and enter the traps.

Environmental factors are important variables affecting behavior of sea lamprey during the migratory and spawning season, and could have potential effects on the entrance and retention of sea lamprey in traps. Sea lamprey begin migrating upstream when temperatures reach 10 °C (Applegate 1950), with peak migrations occurring in water temperatures of 15 °C (Binder et al 2005). Sea lamprey migratory behavior could also be affected by stream discharge. When water discharge is high, their ability to navigate could be compromised due to their poor swimming ability (Beamish 1974). Increased discharge from smaller streams may increase the probability that sea lamprey will locate the larval pheromone plumes in streams to find acceptable spawning habitat (Wagner et al 2009). Later in the season, sea lamprey movement starts increasing during daylight due to high water temperatures, poor health, and the physical determination to spawn before perishing (Binder and McDonald 2008), but, little to no research has observed how sea lamprey move throughout the entire migratory and spawning season.

The sea lamprey trapping process can be considered as individual movements that begin with a sea lamprey being unavailable when it is at large in the river. When a sea lamprey comes in close proximity to a trap it becomes available to be trapped. A sea lamprey is trapped when it enters the trap opening, and then is either lost due to escape or is retained (Bravener and McLaughlin 2013). The final step is sea lamprey being removed from the trap by control agents. Behavior of lamprey as they are moving through the different stages can be observed and quantified by analyzing video recorded at traps during the spawning migration. The use of video could provide insight into the movements of the lamprey as they are interacting with the traps, and potentially help us determine what improvements could be made to enhance the trapping process for agents to use trapping as a control method.

Sea lamprey trapping needs to be improved for the GLFC to use trapping as more of a suppression tool, rather than its current use as an assessment tool. Researching the factors that affect the probability of sea lamprey entering and/or being retained in a trap can help improve trapping efficiency. I examined the effects of trap design/location, and environmental factors like water temperature, water discharge, different times of the season and night, on probability of entrance and retention of sea lamprey in traps using video. Based on behavioral studies and the opinion of control agents, predictions were made as to how sea lamprey behavior around traps would change with physical and environmental factors. The predictions were 1) probability of entrance varies by trap, 2) probability of entrance increases as water temperature increases, 3) probability of entrance increases later in the season 4) probability of entrance increases later in the night 5) probability of retention varies by trap, 6) probability of retention decreases as water temperature increases, 7) probability of retention decreases later in the season; and 8) probability of retention decreases later in the night.

Methods

Study sites

This study was conducted at Cheboygan River(one trap), and St. Mary's River (three traps) during four migratory seasons (Figure 1). Video was collected at a trap in the Cheboygan River at the lock and dam near Cheboygan, Michigan during 2006. This trap was one of four traps operating in a spillway in 2006, and historically had the largest trap catches of all four traps. The trap had two entrances, both of which were funnels stacked one on top of the other with dimensions of 622.3 mm high x 685.8 mm wide x 660.4 mm deep, with a 196.85 mm x 165.1 mm rectangular opening, and 12.7 mm between the fingers. The trap was checked in the morning daily, and at that time any fish in the trap were counted and removed.

Video was collected at three different traps in the St. Mary's River, which is the stream that connects Lakes Superior and Huron between Sault Ste Marie, Ontario and Sault Ste. Marie, Michigan. All traps at the St. Mary's River were located in the tailrace of the Clergue Generating Station (GS). Video was collected at the North Attractant Water trap (SM NAWT) during 2008, 2009, the South Attractant Water trap (SM SAWT) during 2009, and the North Central Portable (SM NCP) during 2009. The SM NAWT and the SM SAWT are permanent traps that are located on the north and south side of the tailrace, respectively. The SM NCP trap is one of three portable traps that were suspended by chains and positioned between the permanent traps along the generating station wall. The SM NAWT and SM SAWT traps had water introduced into the holding chamber so that the water flowing through the trap opening acts as an attractant for sea lamprey to enter, whereas the SM NCP traps was placed in an area of high flow. The SM NAWT trap has two entrances, both of which are funnels 1524 mm high x 863.6 mm wide x 660.4 mm deep, with a rectangular opening of 1524 mm x 82.55 mm and 12.7 mm between fingers. The SM SAWT trap has two cages of identical size. Both cages have two entrances – one that faces downstream and one that faces toward shore. The downstream facing openings are rectangular without a funnel, 2032 mm high, 139.7 mm wide and 12.7 mm between fingers. The SM NCP trap has 2 funnels, both of which are 812.8 mm high, 812.8 mm wide, 660.4 mm deep, with a 76.2 mm diameter circular opening, and 19.05 mm" between fingers. The three traps were checked each morning around 0600 hours during times of high sea lamprey activity. The SM NCP was also checked at night (around 02:00) during the peak of sea lamprey migratory activity. At the time of trap check any fish in the trap were counted and removed. Checking portable traps at night was thought to improve trap efficiency by maximizing retention and therefore, total catch. During times when sea lamprey activity was lower, and trap catches minimal, traps were checked most days but not necessarily early in the morning.

Video recordings

In the Cheboygan River, an underwater video camera (Lorex Cvc6990 B and W Submersible Camera) was positioned 61 cm from the trap entrance so as to record sea lamprey behaviors, but not occlude the entrance to the trap. A 10-watt halogen light positioned above the trap illuminated the inside. The light was connected to a 12 V DC photoswitch (Flexcharge Night Watchman) that switched the light on after dark. In field settings, no consistent differences have been found in the numbers of sea lampreys caught in lit versus unlit traps when LED lights were used (Stamplecoskie 2012). Video was recorded at this trap using a Digital Video Recorder (JSA HQ400 8 channel DVR). The light was powered by a 12 V battery (7.2 Ah Sealed Lead Acid Rechargeable Battery), and the cameras and DVR were powered by 12 V deep-cycle marine batteries. Behavior of sea lampreys during three partial nights (between 21:00 and 24:00, with two nights during the peak of the migration season) was observed.

Sault Ste Marie trap entrances were outfitted with CCTV black and white waterproof bullet cameras (Speco Technologies, Amityville, NY). Cameras were mounted and oriented to view the outside of each trap entrance. Floodlights with red filtering were mounted above each trap entrance to illuminate the area for video observations. Red lighting has been shown to have minimal effect on fish behavior compared to white or other colors (Widder et al. 2005; Binder and McDonald 2007). Video was recorded using either a DVR or a VCR with quad processor to split the camera feeds. Power was available at these sites and used to power all equipment required to obtain video recordings. The method of video subsampling at the St. Mary's traps differed for each year. This is because sea lamprey behavior at these sites was initially quantified to test different hypotheses. For 2008, two times were randomly selected from each of six nights, between 21:00 to 05:00, and behavior of the first five sea lampreys after each selected time was recorded. For 2009, the behavior of one untagged sea lamprey within seven minutes prior and following every observation of a PIT-tagged sea lamprey was recorded. For 2010, all sea lamprey behavior was recorded that occurred between 21:00 and 05:00 on every other night for four nights.

External factors

Factors that were measured which may affect entrance and retention rates of sea lamprey were water temperature, stream discharge, time of night, and time of season. For Cheboygan, water temperature was collected daily by control agents using a mercury thermometer. For St. Mary's, water temperature was recorded by a temperature logger (HOBO Water Temp Pro, Onset Computer Corporation, Bourne, MA, USA) every two hours during the study. For Cheboygan, no discharge was collected, as the trap was located in the spillway of a dam where effects of discharge were likely minimal. For St. Mary's, hourly discharge data at Clergue GS were provided by staff at Brookfield Renewable Energy. To analyze specific sea lamprey behavior in accordance with time of night and season, video data were divided into different hours of the night ranging from 1 to 8 and different times of the trapping season ranging from 1 to 4. Video recordings were usually made from 21:00 hours until 05:00 hours each night during the study period. This represented the period when migrating sea lamprey were expected to be most active near the traps (Binder and McDonald, 2007). Hours of night corresponded with the hour of recording. For example, 21:00–21:59 would be recorded as hour 1; hour of night 2 was 22:00–22:59, etc. All observations within the hour of the night would receive the corresponding number to account for all the observations in the data set. Time of season was divided into 4 equal divisions based on total catch. The total catch was recorded every day by the control agents then summed and divided equally. Time of season 1 included the dates in which 0–25% of the total trap catch occurred during the season, time of season 2 included the dates in which 26–50% of the total catch occurred, etc.

Data Analysis

Retention was calculated on an hourly basis as$\left(\frac{\text{Entries}-\text{Escapes}}{\text{Entries}}\right)$. All statistical analyses were conducted using SPSS (version 20 (IBM Corp., 2011) unless stated otherwise. To test the predictive ability of factors affecting the probability of entry, a logistic regression was conducted using all of the video observations of lamprey approaching a trap with the following full model to test:

$$log\left(\frac{Trap\ entry}{1-Trap\ entry}\right) = \alpha + \beta_1\text{year} + \beta_2\text{trap and location} + \beta_3\text{time of night} + \beta_4\text{time of season} + \beta_5\text{water temperature} + \beta_6\text{stream discharge} + \beta_7\text{trap x time of night} + \beta_8\text{trap x time of season} + \beta_9\text{trap x water temperature} + \beta_{10}\text{trap x stream discharge}$$

I created a model that included all predictor variables that were useful in predicting the response variable by conducting a stepwise method (backward: likelihood ratio).

To test the predictions on the factors affecting the probability of retention I conducted a linear regression on all of the video observations of lamprey and tested the same factors and interactions used in the aforementioned model. I created a model that included all predictor variables that were useful in predicting the response variable by conducting a stepwise method (backward: likelihood ratio).

Results

Behavior of sea lamprey during three nights between 21:00 and 24:00 was observed for a total of 1260 observation in the Cheboygan River. Over 2008 and 2009, the three St. Mary's traps yield 122 (SM NAWT), 120 (SM SAWT), and 104 (SM NCP) observations.

Entrance

The best model to explain probability of entry included the following factors and interactions: time of season and trap x water temperature (Table 1). When just using trap as an explanatory variable, the Cheboygan River and St. Mary's River SM NCP traps were significantly different. But, when additional variables are included in the model, trap does not help to explain probability of entry (Figure 2). Lamprey are less likely to enter a trap in the final fourth of the season (χ^2=35.059, df=1, p<0.0001) (Figure 3; Table 2). Only time of season 3 and 4 had data for all four traps, so time of season 1 and 2 were excluded from the data set. The probability of entry was not observed to change with hour of night. There was a significant trap by water temperature interaction which explained some of the variance in probability of entry (Figure 4; Table 1) (χ^2=9.511, df=4 ,p<0.050). As water temperature increased the probability of entry increased for SM NAWT and SM SAWT, but the true correlation is hard to tease out for all the traps (Figure 4). The probability of entry increases later in the season but the likelihood of sea lamprey entry is low.

Retention

The best model to significantly explain probability of retention included the following factors and interactions: hour of night, water temperature, hour of night by trap, trap by time of season, and trap by water temperature (Table 3). Hour of night proved to be a significant factor in retaining sea lamprey in traps (χ^2=293.494, df=7, p<0.0001) (Table 3). The probability of sea lamprey being retained in traps decreased from the first hour (Table 4; Figure 5). Water temperature appeared to be a significant factor in retaining sea lamprey in traps (χ^2=5.162, df=1,

$p<0.023$) (Table 4). The probability of retention decreased as water temperature increased (Table 4).

There were several interactions that explained the retention of sea lamprey in traps. The probability of a trap retaining sea lamprey decreases as the night goes on in some traps as indicated by the significant trap by hour of night interaction ($\chi^2=1475.338$, df=15, $p<0.0001$) (Table 3; Figure 6). The interaction of trap by time of season was significant in explaining retention of sea lamprey in traps ($\chi^2=37.533$, df=3, $p<0.0001$), with SM NAWT having the lowest retention, although highly variable (Figure 7). The other traps had similar retention in the two time periods of the season. The interaction of trap and water temperature was significant, but the interaction proved difficult to interpret ($\chi^2=67.243$, df=3, $p<0.0001$) (Figure 8; Table 3).

Discussion

Probability of entry varies by trap when the interaction of water temperature and trap are considered. The rate at which sea lamprey enter a trap did not differ between traps, when the main effect of trap was tested. Probability of entry increased as water temperature increased among traps. Probability of entry did not increase later in the season, but rather decreased later in the season. The probability that a sea lamprey would enter a trap did not change with hour of night.

The significant factors that influence entry into traps are time of season and the interaction of trap and water temperature. The different times of season in the spawning migration of sea lamprey affected the likelihood of entry, with sea lampreys being more likely to enter the trap in the third quarter of the season rather than the last quarter of the season (Figure 4). In this study, sea lamprey were observed only in the second half of the migratory season (times of season 3 and 4), and sea lamprey energy reserves towards the end of the migratory season are depleted (Beamish 1974). Time of season is related to water temperature, as temperatures change throughout the season. As water temperatures increased, the likelihood of sea lamprey entering the SM NAWT and SM SAWT traps increased. Spawning migration of sea lamprey has been linked to the temperature of the surrounding waters, which controls the start of movement upstream (Wagner et al 2009) until they reach barriers. Lamprey that reach the barrier pool remain there until spawning actually begins, then reverse their movement to locate the spawning grounds downstream (Wagner et al. 2010).

Probability of retention varied when there were interactions between trap and other factors. Probability of retention decreased as water temperatures increased Probability of retention decreased later in the season for SM NCP and Cheboygan trap. Probability of retention decreased later in the night for some traps.

The significant factors that influence retention of sea lamprey in a trap are hour of night, water temperature, hour of night by trap, trap by time of season and trap by water temperature. The probability of sea lamprey being retained in traps starts to decrease after midnight (Figure 5). The Cheboygan trap lacked observations after midnight, while retention varied greatly for the other traps (Figure 6). Sea lamprey caught earlier in the evening were more likely to escape; they are more likely to find the escape route the longer they exhibit active searching behavior in the trap Servicing traps at night is currently being employed in some traps in the St. Mary's River to increase the capture rate of adult sea lamprey in that system.

The retention of sea lamprey decreased as water temperature increased, but this trend was not observed across all traps (Figure 8). Water temperature is linked to many sea lamprey behaviors during the spawning season because temperature helps initiate the beginning of the migration season, as well as the act of spawning with the help of other cues like pheromones (Binder and McDonald 2008). Movement of lamprey during the migratory season is most pronounced between 15°C and 20°C (Binder et al. 2011), with 18°C being the optimum development for embryos of sea lamprey. This movement occurs when water temperature and stream flow increase during the spring (Binder and McDonald 2010, Hardisty and Potter 1971, Robinson and Bayer 2005), so an increase in searching behavior should result in a greater probability of escapement.

The variability in retention was partially explained by interactions between additional factors such as the interaction between time of season and trap and hour of night and trap. The retention rate of sea lamprey at traps decreased from season 3 to season 4 (Figure 7). The motivation to spawn before dying may be an important factor later in the season, which may decrease the ability of traps to retain sea lamprey. Sea lamprey is less likely to be retained later in the evening at many traps. Trap catch may be increased if traps are checked twice a day to reduce the number of sea lamprey escaping the traps.

General conclusions

The only variable in common which significantly affected both entry and retention was the interaction between trap and water temperature. A study conducted during the 2011 trapping season on the St. Mary's River traps observed in this study and two other traps in the river, determined that daily mean water temperature, water temperature^2, and the two-day change in temperature explained 85% of the variability in the log-transformed trap catch (Barber et al. 2012). Control agents already track water temperature carefully to determine when to begin setting sea lamprey traps across the Great Lakes basin.

Explaining retention was more complex than explaining probability of entry, with multiple interactions and factors contributing to retaining sea lamprey. The different trap designs may be a key in explaining the different rates of retention. There is evidence to suggest that there is likely a trade-off between entrance and retention rate relating to trap design (Bravener and McLaughlin 2013). For example, the Carp Lake Outlet trap (see Chapter 1) had a relatively high entrance rate and low retention rate compared to the St. Mary's and Cheboygan traps. Trap designs with three entrance funnels caught significantly more crawfish (*Procambarus clarkia* and *P acutus acutus*) in Louisiana ponds than did trap designs with one or two funnels (Pfister and Romaire 1983). Conversely, the retentive ability of the trap designs was inversely related to the number of entrance funnels of crawfish (Pfister and Romaire 1983).

A limitation of this chapter is the lack of observations of sea lamprey behavior across the entire migratory season. Most traps did not have observations in the first half of the season, so observations from only the second half of the season were used to inform my conclusions. Additionally, the video of sea lamprey behavior were subsampled differently for all of the traps. However, this study was able to help us understand some of the variables affecting the likelihood that a sea lamprey will enter and be retained in a trap. Much research is currently being done to understand sea lamprey migratory pathways in streams (Bravener 2011), to improve trap placement, and determine attractive water flows which maximize trap success (Barber et al. 2012). Other research is ongoing into new trap designs, such as the use of eel-ladder traps to trap sea lampreys (McDonald and Desrochers 2012).

Table 1. Main factors and interactions that significantly explained probability of entry of sea lamprey with Wald Chi-Square, degrees of freedom, and significance reported.

Tests of Model Effects

Source	Type III		
	Wald Chi-Square	df	Sig.
(Intercept)	8.575	1	0.003
Time of season	12.431	1	0.000
Trap * Water.temp	9.511	4	0.050

Dependent Variable: Entered

Model: (Intercept), Time of season, Trap * Water.temp

Table 2. Sea lamprey entry factors showing parameter coefficients (B),standard errors (SE), significance (Sig.), and odds ratio (OR) as factors were added to the model.

	Model 1				Model 2			
Variables	B	SE	Sig.	OR	B	SE	Sig.	OR
Time of Season	-0.854	0.1443	0.0001	0.426	-1.314	0.3728	0.0001	6.74
Interactions								
SM NCP*Water temperature					0.095	0.0683	0.164	1.1
SM SAWT*Water temperature					0.074	0.0643	0.251	1.077
SM NAWT*Water temperature					0.139	0.0777	0.073	1.149
Cheboygan*Water temperature					0.074	0.0588	0.208	1.077

Table 3. Main factors and interactions that significantly explained probability of retention of sea lamprey with Wald Chi-Square, degrees of freedom, and significance reported.

Tests of Model Effects

Source	Type III		
	Wald Chi-Square	df	Sig.
(Intercept)	88.563	1	0.000
Hour.of.night	221.739	7	0.000
Water.temp	3.846	1	0.050
Hour.of.night * Trap	752.819	14	0.000
Trap * Time of season	10.946	3	0.012
Trap * Water.temp	67.243	3	0.000

Dependent Variable: Retention.hourly

Model: (Intercept), Hour.of.night, Water.temp, Hour.of.night * Trap, Trap * Time of season, Trap * Water.temp

Table 4. Sea lamprey retention factors showing parameter coefficients (B), standard errors (SE), significance (Sig.), and odds ratio (OR) as factors were added to the model.

	Model 1				Model 2			
Variables	B	SE	Sig.	OR	B	SE	Sig.	OR
Hour of night=8	-0.054	0.0381	0.158	0.948	-0.063	0.0382	0.101	0.939
Hour of night=7	-0.057	0.0228	0.012	0.944	-0.067	0.0232	0.004	0.935
Hour of night=6	-0.25	0.0175	0.0001	0.778	-0.261	0.018	0.0001	0.771
Hour of night=5	-0.025	0.0152	0.105	0.976	-0.037	0.0162	0.021	0.963
Hour of night=4	-0.071	0.0121	0.0001	0.931	-0.082	0.013	0.0001	0.921
Hour of night=3	0	0.0089	0.956	1	-0.003	0.009	0.697	0.997
Hour of night=2	0.001	0.0082	0.921	1.001	0	0.0082	0.953	1
Hour of night=1	0a			1	oa			1
Water temperature					-0.002	0.001	0.023	0.998

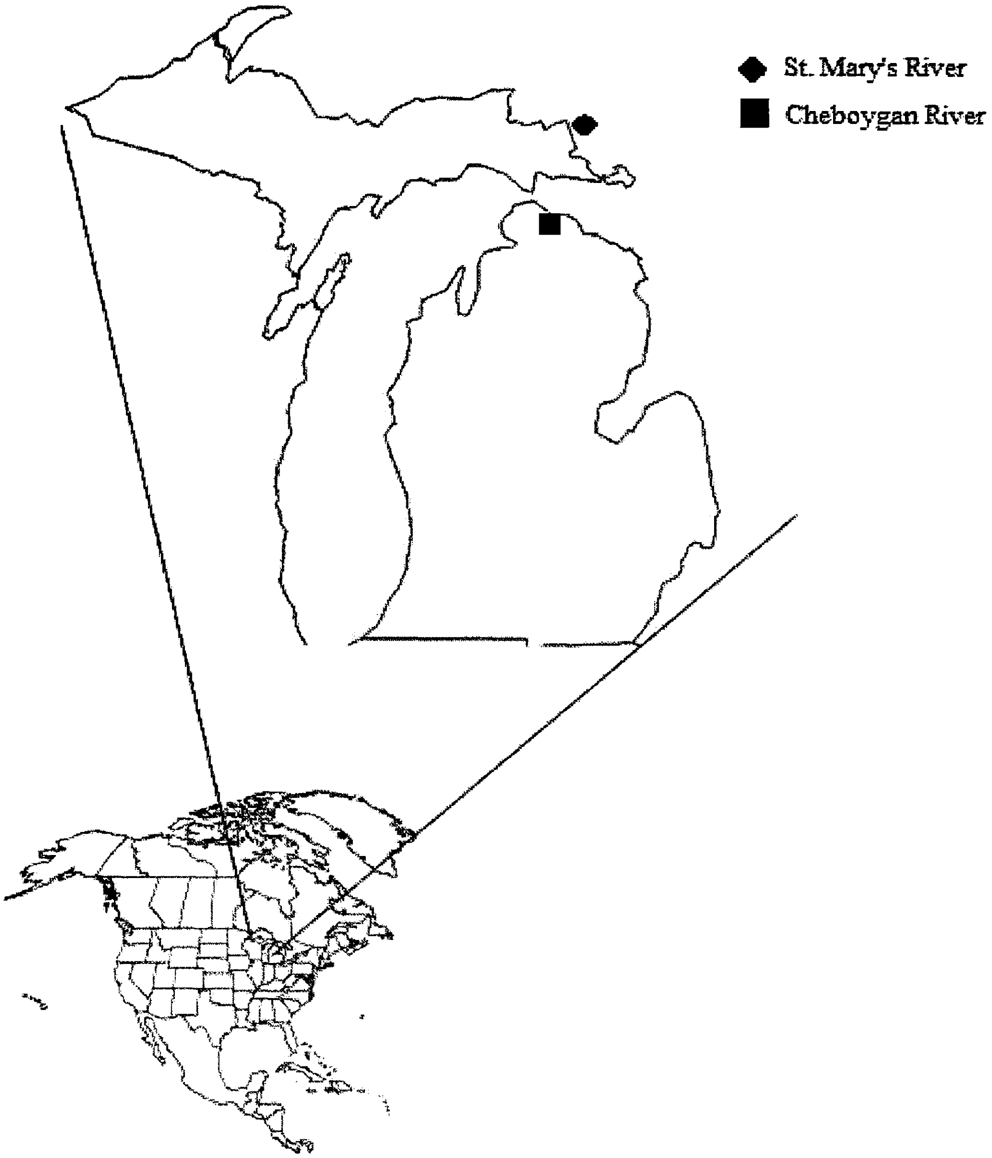


Figure 1. Locations of Cheboygan River and St. Mary's River.

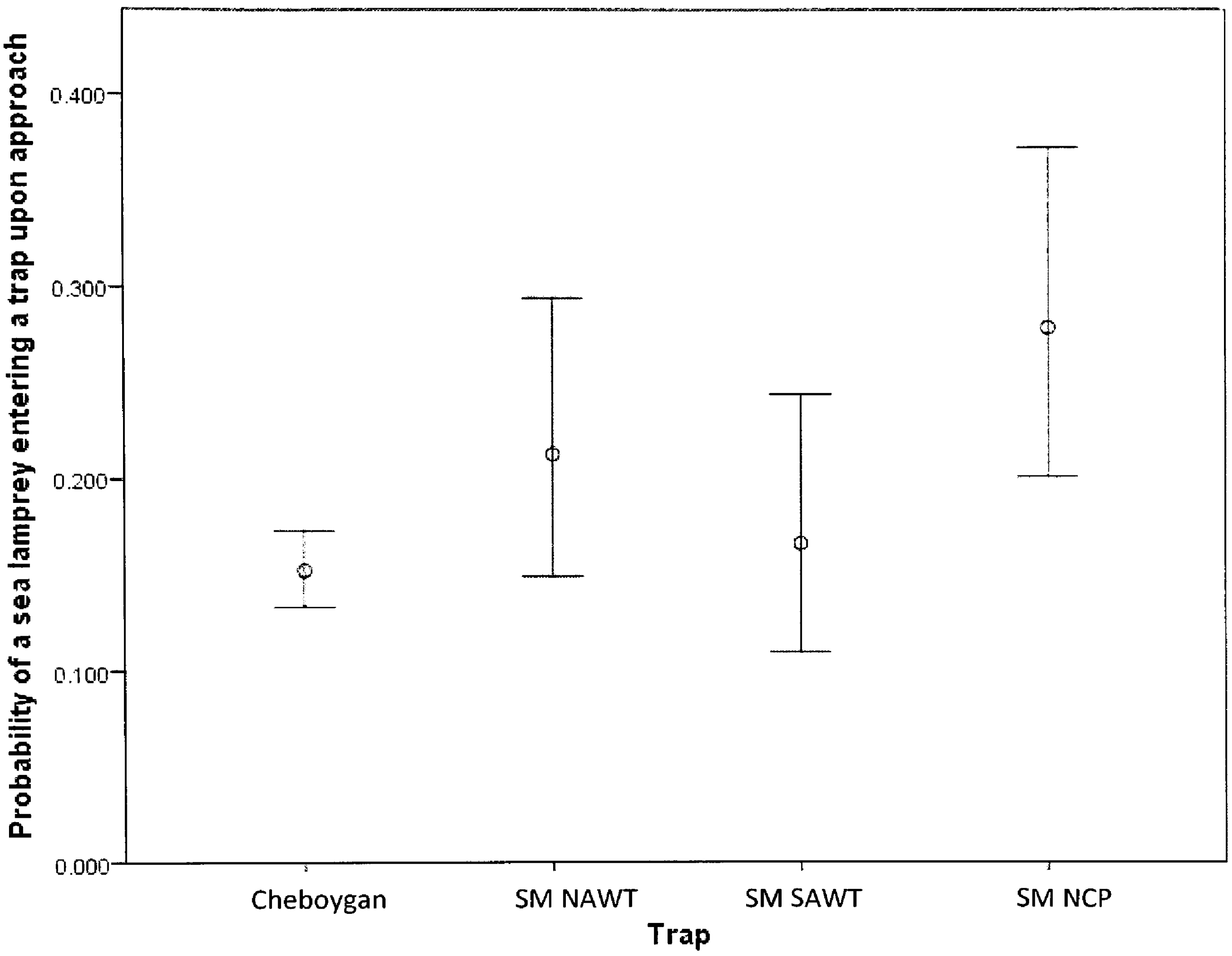


Figure 2. The relationship between trap and the probability of a sea lamprey entering a trap. Error bars indicate 95% confidence intervals.

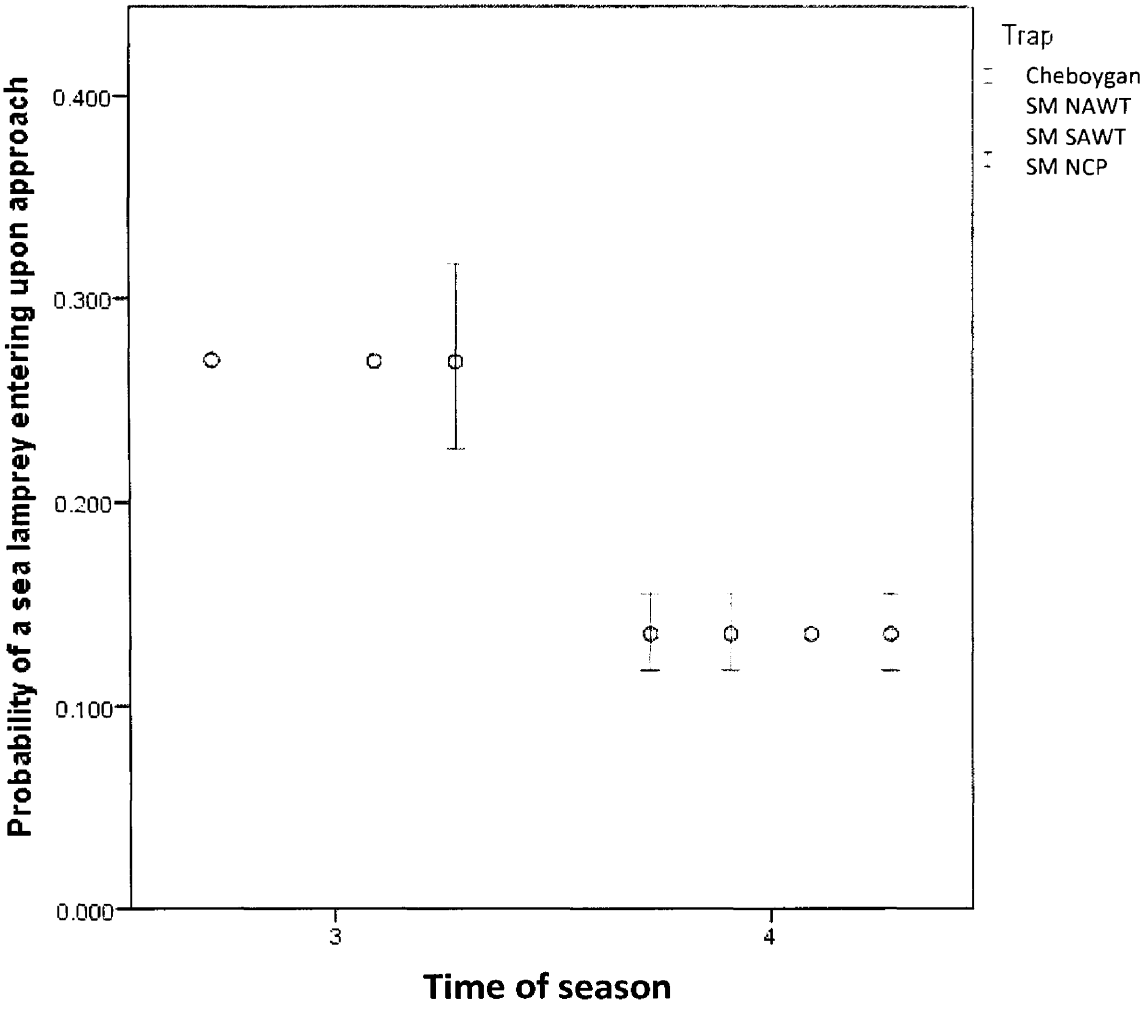


Figure 3. Probability of sea lamprey entering different traps during different times of the season. Error bars indicate 95% confidence intervals.

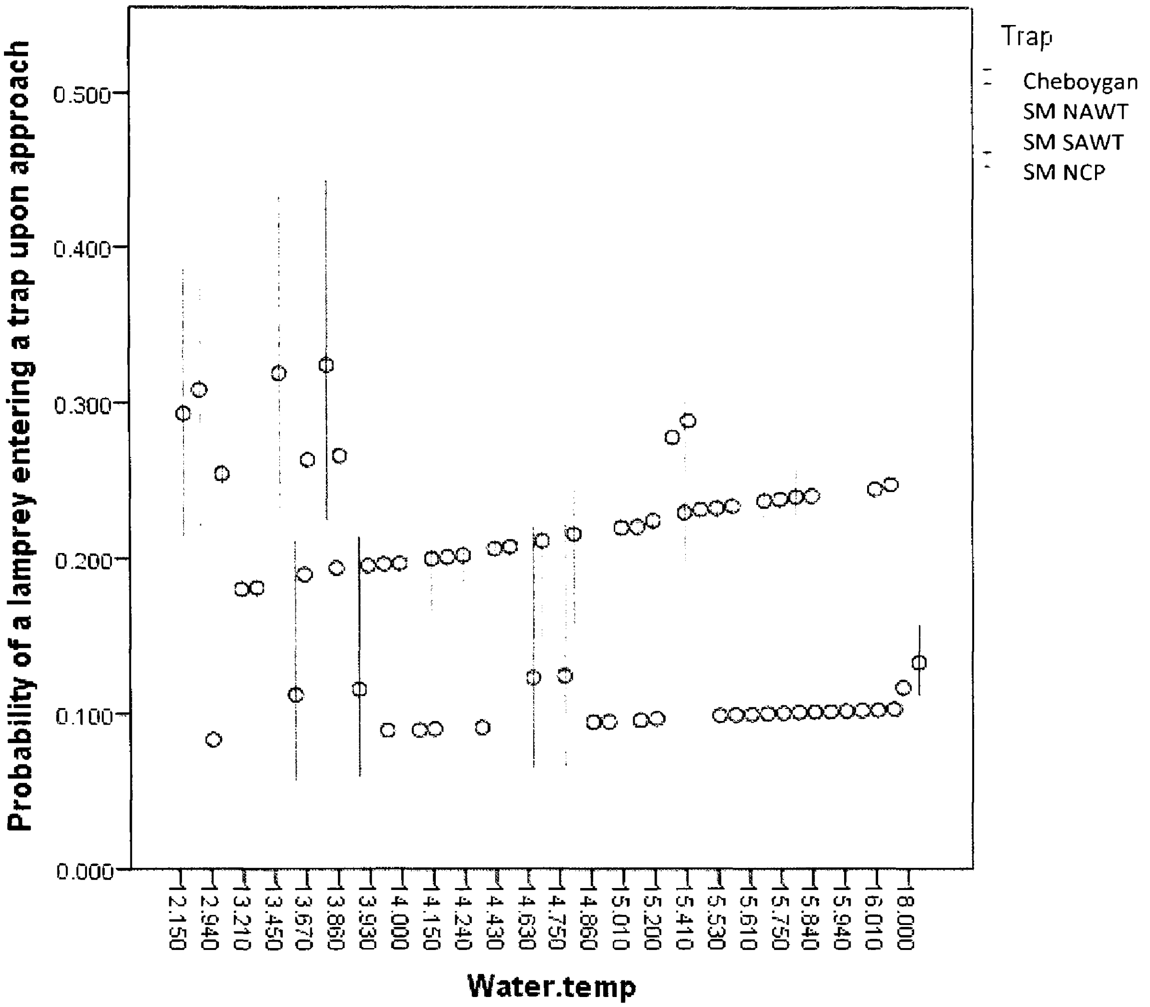


Figure 4. The relationship between water temperature and the probability of entry at different traps. Error bars indicate 95 % confidence intervals.

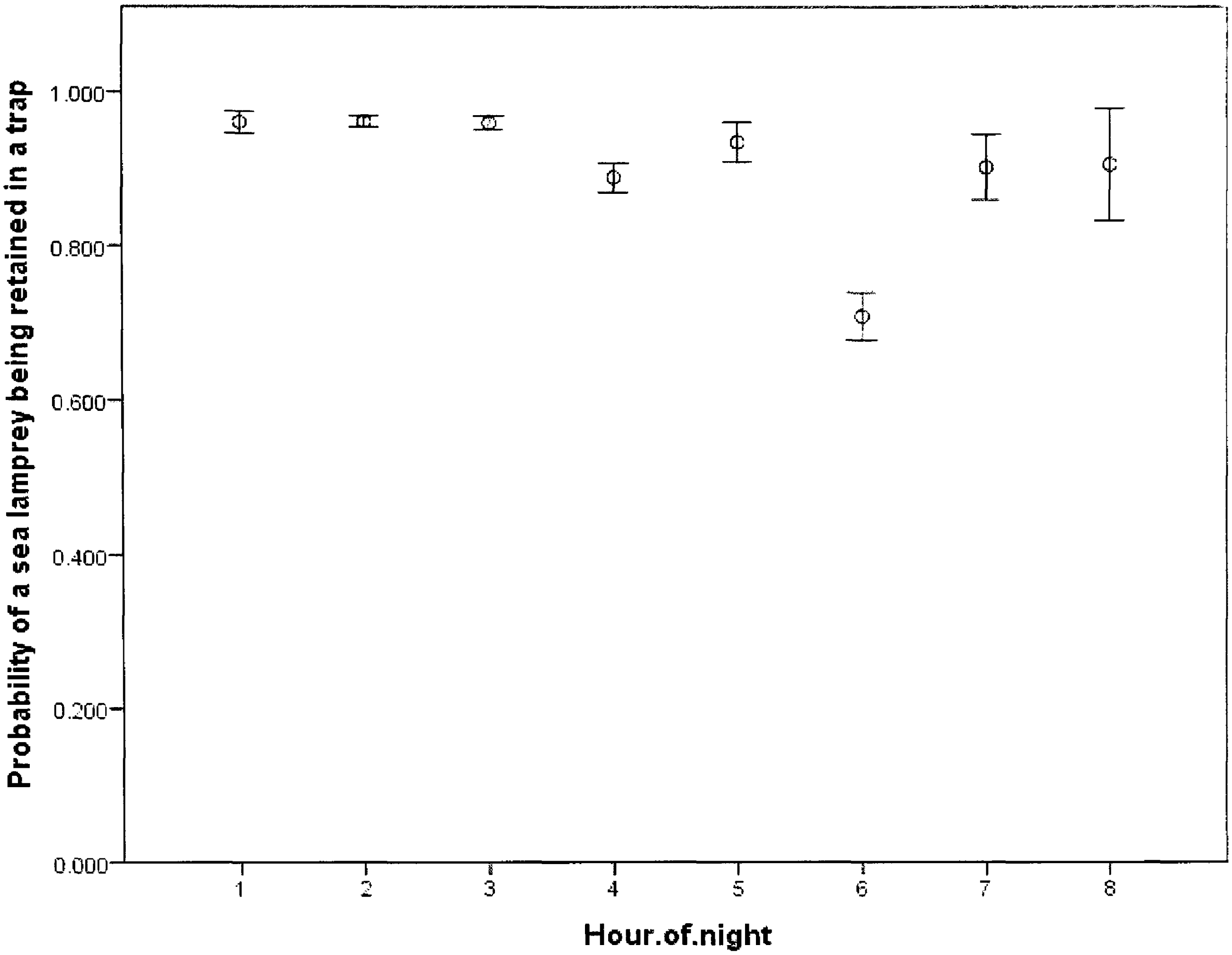


Figure 5. The probability of sea lamprey being retained during different hours of night.

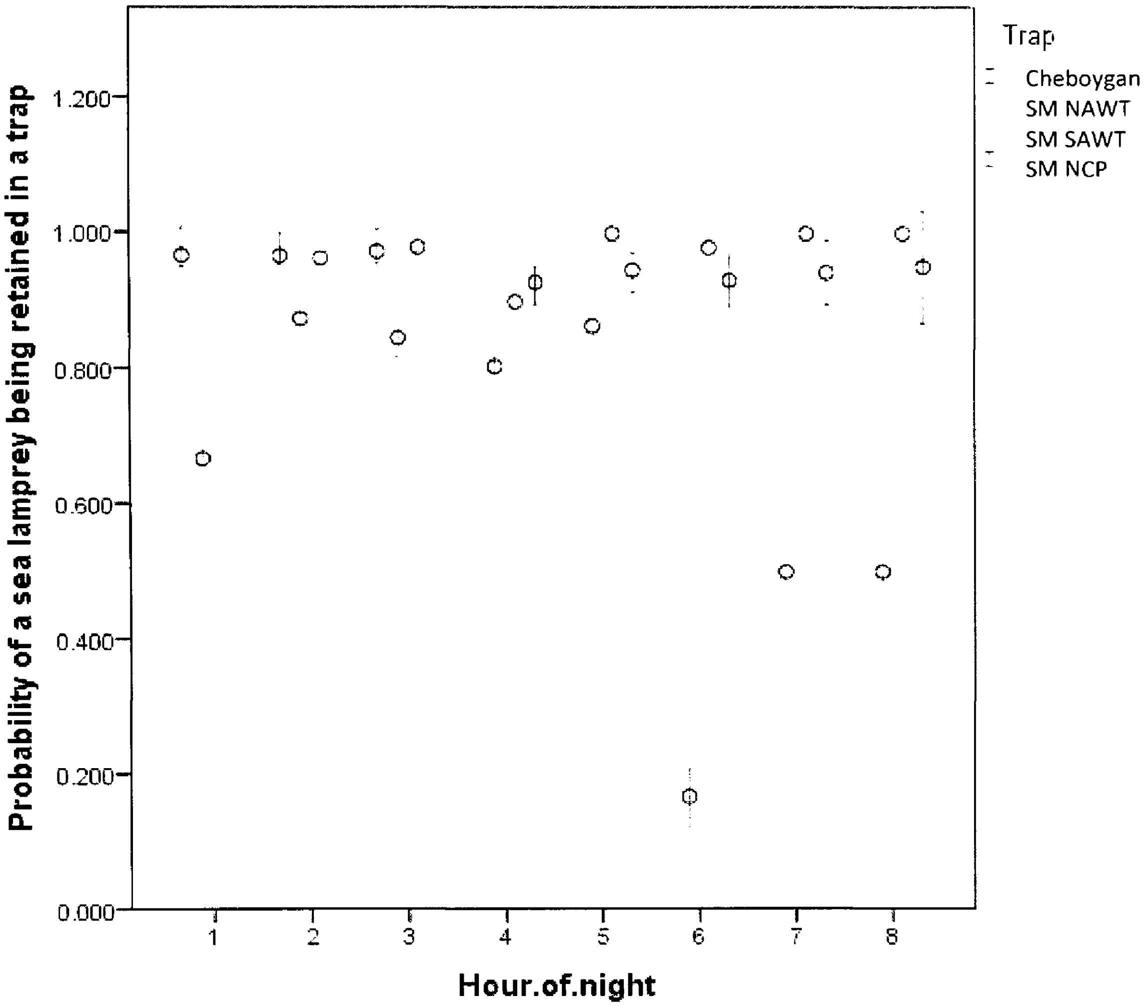


Figure 6. The relationship between hour of night and the probability of retention at different traps. Error bars indicate 95% confidence intervals.

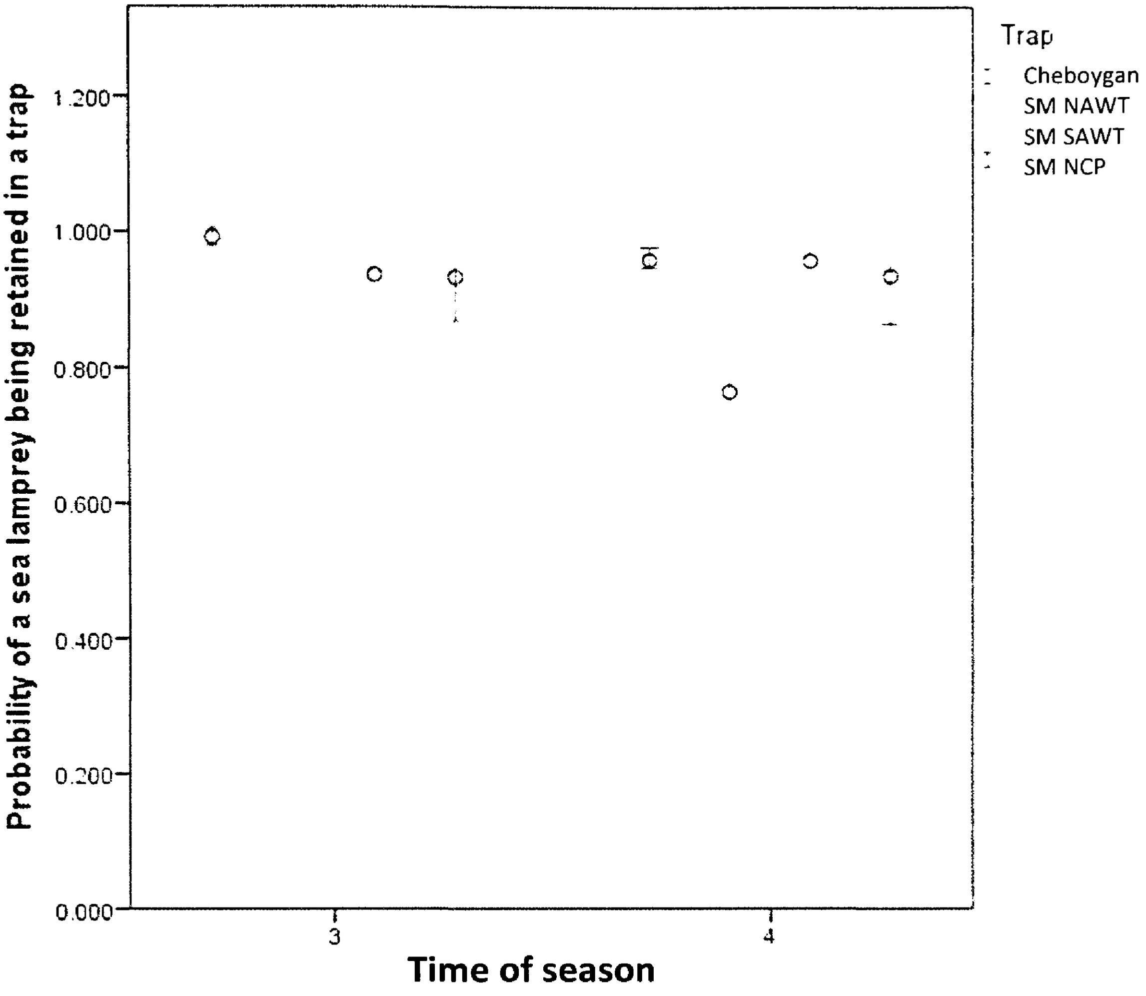


Figure 7. The probability of sea lamprey being retained at different traps in two different times of season. Error bars indicate 95% confidence intervals.

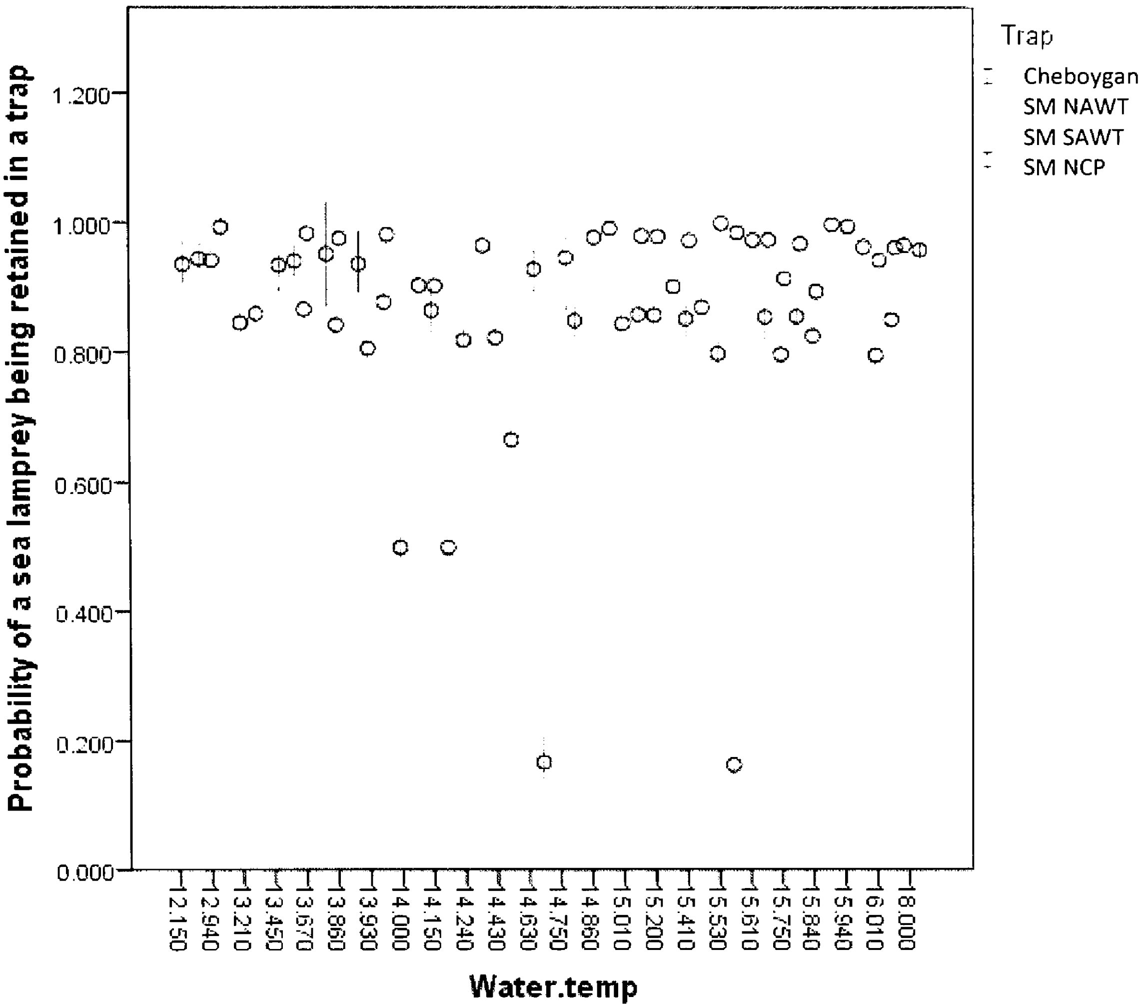


Figure 8. The relationship between water temperature and the probability of sea lamprey being retained at different traps. Error bars indicate 95% confidence intervals.

References

Almeida, P.R., Quintella, B.R., and Dias, N.M. 2002. Movement of radio-tagged anadromous sea lamprey during the spawning migration in the River Mondego (Portugal). Hydrobiologia, 483; 1-8.

Andrade, N. O, Quintella, B.R, Ferreira, J, Pinela, Povoa. I, Pedro. S, and Almeida, P. R. 2007. Sea lamprey (*Petromyzon marinua L.*) spawning migration in the Vouga River basin (Portugal): poaching impact, preferential resting sites and spawning grounds. Hydrobiologia 582:121-132

Applegate, V.C. 1950. Natural history of the sea lamprey (*Petromyzon marinus*) in Michigan. U.S. Fish Wildl. Serv. Spec. Sci. Rep. Fish. Serv. 55.

Barber, J.M., Adams, J.V., Bravener, G., Hrodey, P., Rous, A., McLaughlin, R.L., and Siefkes, M.J. 2012. Enhanced St. Marys River sea lamprey control. 2012 Project Completion Report. Great Lakes Fishery Commission, Ann Arbor, Mich.

Beamish, F.W.H. 1974 Swimming performance of adult sea lamprey, *Petromyzon marinus*, in relation to weight and temperature. Trans. Am. Fish. Soc. 103: 355-358

Beamish, F.W.H. 1979. Migration and spawning energetics of the anadromous sea lamprey, *Petromyzon marinus.* Env. Biol. Fishes 33:381-387.

Binder, T.R., and McDonald, D.G. 2007. Is there a role for vision in the behavior of sea lampreys (*Petromyzon marinus*) during their upstream spawning migration? Can. J. Fish. Aquat. Sci. 64(10): 1403–1412. doi:10.1139/f07-102.

Binder, T. R., and McDonald, D. G. 2008. The role of temperature in controlling diel activity in upstream migrant sea lampreys (Petromyzon marinus). Can. J. Fish. Aquat. Sci. 65: 1113–1121.

Binder, T.R., and McDonald, D.G. 2008. The role of dermal photoreceptors during the sea lamprey (*Petromyzon Marinus*) spawning migration. Journal Comp. Physiol A. 194:921-928.

Binder, T.R., Mclaughlin, R.L., and McDonald, D.G. 2010: Relative importance of water temperature, water level, and lunar cycle to migratory activity in spawning-phase sea lampreys in Lake Ontario. Trans. Am. Fish. Soc. 139(3): 700-712.

Bjerselius, R., Li, W., Teeter, J.H., Seeley, J.G., Johnsen, P.B., Maniak, P.J., Grant, G.C., Polkinghorne, C.N., and Sorensen, P.W. 2000. Direct behavioral evidence that unique bile acids released by larval sea lamprey (*Petromyzon marinus*) function as a migratory pheromone. Can. J. Fish. Aquat. Sci. 57(3): 557-569.

Bravener, Gale A., and Robert L. Mclaughlin. 2013. A Behavioural Framework for Trapping Success and Its Application to Invasive Sea Lamprey. Can. J. Fish. Aquat. Sci. 70.10: 1438-446.

Christie, G.C. and Goddard, C.I. 2003. Sea Lamprey International Symposium (SLIS II): Advances in the integrated management of sea lamprey in the Great Lakes. J. Great Lakes Res. 29(Suppl. 1): 1-14.

Chung-Davidson, Y-W., Wang, H., Siefkes, M.J., Bryan, M.B., Wu, H., Johnson, N.S., and Li, W. 2013. Pheromonal bile acid 3-ketopetromyzonol sulfate primes the neuroendocrine system in sea lamprey. BMC Neurosci. 14: 11.

Clemens, Benjamin J., Thomas R. Binder, Margaret F. Docker, Mary L. Moser, and Stacia A. Sower. 2010. Similarities, Differences, and Unknowns in Biology and Management of Three Parasitic Lampreys of North America. Fisheries 35.12: 580-94.

Dahl FH, McDonald RB. 1980. Effects of control of the sea lamprey (*Petromyzon marinus*) on migratory and resident fish populations. Canadian Journal of Fisheries and Aquatic Sciences 37:1886-94.

Dawson, H.A., and Jones, M.L. 2009. Factors affecting recruitment dynamics of Great Lakes sea lamprey (*Petromyzon marinus*) populations. J. Great Lakes Res. 35:353-360.

EF Media Player. Free Download Center. N.p., n.d. Web. 5 Mar. 2014. <http://www.freedownloadscenter.com/Multimedia_and_Graphics/MPEG_Audio_Players_and_Editors/EF_Media_Player_Max.html>

Gore, J.A. 2006. Discharge measurement and streamflow analysis. *In* Methods in Stream Ecology. Revised Second Edition. *Edited by* F.R. Hauer and G.A. Lamberti. Academic Press, San Diego, pp. 53-74.

Great Lakes Fishery Commission. 2001. Strategic vision of the Great Lakes Fishery Commission for the first decade of the new millennium. Ann Arbor, MI, USA.

Great Lakes Fishery Commission. 2011. Strategic Vision of the Great Lakes Fishery Commission 2011-2020. Great Lakes Fishery Commission, Ann Arbor, Mich.

Hardisty, M. W. and I. E. Potter. 1971. The Biology of Lampreys, Volume 1. Academic Press, London, New York. 1-200.

Hardisty, M. W. and I. C. Potter. 1971. The Biology of Lampreys, Volume 2. Academic Press, London, New York. 287-300.

Hassanali, A., Herren, H., Khan, Z.R., Pickett, J.A., and Woodcock, C.M. 2008. Integrated pest management: the push-pull approach for controlling insect pests and weeds of cereals, and its potential for other agricultural systems including animal husbandry. Phil.Trans. R. Soc. B. 363: 611-621.

Home and Business Surveillance Systems. Surveillance Systems for Homes and Businesses. N.p., n.d. Web. 05 Mar. 2014. <http://www.q-see.com/>

Howse, P.E., Stevens, I.D., and Jones, O.T. 1998. Pest Management. Chapman & Hall, New York.

Johnson, N.S. and Li, W. 2010. Understanding behavioral responses of fish to pheromones in natural freshwater environments. J. Comp. Physiol. A. 196: 701-711.

Johnson, N.S., Luehring, M.A., Siefkes, M.J., and Li, W. 2006. Pheromone induced behavior and pheromone reception in ovulating female sea lampreys. N. Am. J. Fish. Manage. 26: 88-96.

Johnson, N. S., Siefkes M.J., and Li, W. 2005. Capture of ovulating female sea lampreys in traps baited with spermiating male sea lampreys. N. Am. J. Fish. Manage. 25: 67-72.

Johnson, N.S., Yun, S-S., Thompson, H.T., Brant, C.B. and Li, W. 2009. A synthesized pheromone induces upstream movement in female sea lampreys and summons them into traps. P. Natl. Acad. Sci. USA. 106(4): 1021-1026.

Johnson, N.S., Yun, S-S., Buchinger, T.J., and Li, W. 2012. Multiple functions of a multi-component mating pheromone in sea lamprey. J. Fish Biol. 80: 538-554.

Johnson, N.S., Siefkes, M.J., Wagner, C.M., Dawson, H.A., Wang, H., Steeves, T., Twohey, M., and Li, W. 2013. A synthesized mating pheromone component increases adult sea lamprey (*Petromyzon marinus*) trap capture in management scenarios. Can. J. Fish. Aquat. Sci. 70: 1101-1108.

Jones, M.L., Hansen, G.A., Liu, W., Irwin, B., Treble, A.J., and Dawson, H.A. 2007. Sea lamprey population dynamics: updating demographic models and application to a novel control strategy. 2007 Project Completion Report. Great Lakes Fishery Commission, Ann Arbor, MI.

Jones, M.L. 2007. Toward improved assessment of sea lamprey population dynamics in support of cost-effective sea lamprey management. J. Great Lakes Res. 33(Supplement 2): 35-47.

Keefer, Matthew L., Mary L. Moser, Charles T. Boggs, William R. Daigle, and Christopher A. Peery. 2009. Effects of Body Size and River Environment on the Upstream Migration of Adult Pacific Lampreys. N. Am. J. Fish. Manage. 29.5: 1214-224.

Lark, J.G.I. 1973. Early Record of Sea Lamprey (*Petromyzon marinus*) from Lake Ontario. J. Fish. Res. Board Can. 30(1): 131-133.

Li, K., Siefkes, M.J., Brant, C.O., and Li, W. 2012. Isolation and identification of petromyzestrosterol, a polyhydroxysteroid from sexually mature male sea lamprey (*Petromyzon marinus* L.) Steroids. 77: 806-810.

Li, W., Scott, A.P., Siefkes, M.J., Yan, H.G., Liu, Q., Yun, S-S. and Gage, D.A. 2002. Bile acid secreted by male sea lamprey that acts as a sex pheromone. Science. 296(5565): 138-141.

Luehring, M.A., Wagner, C.M., and Li, W. 2011. The efficacy of two synthesized sea lamprey sex pheromone components as a trap lure when placed in direct competition with natural male odors. Biol. Invasions. 13(7): 1589-1597.

Luzier, C., and Silver, G. 2005. Evaluate habitat use and population dynamics of lampreys in

Cedar Creek, 2004. Annual report for Bonneville Power Administration, Project 200001400, Vancouver, Washington.

Malmqvist, B. 1980. The spawning migration of the brook lamprey, *Lampetra planeri* Bloch, in a south Swedish stream. J. Fish Biol. 16:105-114

Masters, J. E. G., Jang, M. H., Ha, K.,Bird, P. D., Frear, P., and Lucas. 2006. The commercial exploitation of a protected anadromous species, the river lamprey (*Lampetra fluviatilis* (L.)), in the tidal River Ouse, north-east England. Aquatic Conservation: Marine and Fresh. Eco. 16:77-92

McDonald, D.G., and D. Desrockers. 2012. Using an Eel Ladder-trap to Trap Sea Lampreys: Proof of Concept. GLFC Completion Report.

McLaughlin, R.L., Hallett, A., Pratt, T.C., O'Connor, L.M., and McDonald, D.G. 2007. Research to guide use of barriers, traps, and fishways to control sea lamprey. J. Gt. Lakes Res. 33(Sp2): 719.

McMahon, T.E., Zale, A.V., and Orth, D.J. 1996. In Fisheries Techniques Second Edition. Edited by B.R. Murphy and D.W. Willis. American Fisheries Society, Maryland. pp. 83-120.

Miller, J.R. and Cowles, R.S. 1990. Stimulo-deterrent diversionary cropping: a concept and its possible application to onion maggot control. J. Chem. Ecol. 16: 3197-3212.

Moore, H.H. and Schleen, I.P. 1980. Changes in spawning runs of sea lamprey (*Petromyzon-marinus*) in selected streams of Lake Superior after chemical control. Can. J. Fish. Aquat. Sci. 37: 1851-1860.

Morman, R. H., Cuddy, D. W. & Rugen, P. C. 1980. Factors influencing the distribution of sea lamprey (*Petromyzon marinus*) in the Great Lakes. Can. J. Fish. Aquat. Sci. 37: 1811–1826.

Mullett, K.M., Heinrich, J.W., Adams, J.V., Young, R.J., Henson, M.P., McDonald, R.B., and Fodale, M.F. 2003. Estimating lake-wide abundance of spawning-phase sea lampreys (*Petromyzon marinus*) in the Great Lakes: extrapolating from sampled streams using regression models. J. Great Lakes Res. 29(Suppl. 1): 240-252.

Page, L. M., H. Espinosa-Pérez, L. T. Findley, C. R. Gilbert, R. N. Lea, N. E. Mandrak, R. L. Mayden, and J. S. Nelson. 2013. Common and Scientific Names of Fishes from the United States, Canada, and Mexico. 7th ed. Bethesda, MD: American Fishery Society.

Pearce W.A., Braem, R.A., Dustin, S.M., and Tibbles, J.J. 1980. Sea lamprey (*Petromyzon marinus*) in the lower Great Lakes. Canadian Journal of Fisheries and Aquatic Sciences 37: 1802-1810.

Pfister, V.A. and Romaire, R.P. 1983. Catch efficiency and retentive ability of commercial crawfish traps. Aquacultural Engineering 2:101-118.

Potter, I.C. 1980. Ecology of larval and metamorphosing lampreys. Can. J. Fish. Aquat. Sci. 37: 1641-1657.

Robinson, C. T., and Bayer, J.M. 2005. Upstream Migration of Pacific Lampreys in the John Day River, Oregon: Behavior, Timing, and Habitat Use. Northwest Science 79: 106-119.

Schneider C.P., Owens, R.W., Bergstedt, R.A., O'Gorman, R. 1996. Predation by sea lamprey (*Petromyzon marinus*) on lake trout (*Salvelinus namaycush*) in southern Lake Ontario, 1982-1992. Can. J. Fish. Aquat. Sci. 53:1921-1932.

Siefkes, M. J. & Li, W. 2004. Electrophysiological evidence for detection and discrimination of pheromonal bile acids by the olfactory epithelium of female sea lampreys (Petromyzon marinus). J. Compar. Phys. A. 190: 193–199.

Siefkes, M.J., Winterstein, S.R., and Li, W. 2005. Evidence that 3-keto petromyzonol sulphate specifically attracts ovulating female sea lamprey, *Petromyzon marinus*. Anim. Behav. 70: 1037-1045.

Skidmore, J. F. 1959. Biology of spawning-run sea lampreys (*Petromyzon marinus*) in the Pancake River, Ontario. Master's Thesis. University of Western Ontario, London.

Smith, B.R. and Tibbles, J.J. 1980. Sea Lamprey (*Petromyzon marinus*) in Lakes Huron, Michigan, and Superior - History of Invasion and Control, 1936-78. Can. J. Fish. Aquat. Sci. 37(11): 1780-1801.

Stamplecoskie, K., Binder, T.R., Lower, N., Cottenie, K., McLaughlin, R.L., and McDonald, D.G. 2012. Response of migratory sea lampreys to artificial lighting in portable traps. N. Am. J. Fish. Manage. 32: 563–572.

Swink WD. 2003. Host selection and lethality of attacks by sea lamprey (*Petromyzon marinus*) in laboratory studies. J. Great Lakes Res. 29(Suppl. 1): 307-319..

Teeter, J. 1980. Pheromone Communication in Sea Lampreys (Petromyzon-Marinus – Implications for Population Management. Can. J. Fish. Aquat. Sci. 37(11): 2123-2132.

Twohey, M., Sorensen, P.W., and Li, W. 2003. Possible applications of pheromones in an integrated sea lamprey management program. J. Great Lakes Res. 29(Suppl. 1): 794-800.

Wagner, C.M., Twohey, M.B., and Fine, J.M. 2009. Conspecific cueing in the sea lamprey: do reproductive migrations consistently follow the most intense larval odour? Anim. Behav. 78: 593-599.

Wagner, Michael C., Adam F. Thomas, Michael Twohey, Roger Bergstedt, Rod McDonald, and Weiming Li. A Full-scale Field Test of the Efficacy of the Male Mating Pheromone Compound 3-ketopetromyzonal-sulfate in Trapping-for-control Scenarios. GLFC completion report, Ann Arbor, MI.

Wagner CM, Jones ML, Twohey MB, Sorensen PW .2006. Afield test verifies that pheromones can be useful for sea lamprey (Petromyzon marinus) control in the Great Lakes. Can J Fish Aquat Sci 63:475–479