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Contribution of manipulable and non-manipulable environmental factors to trapping efficiency of invasive sea lamprey

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ABSTRACT

We identified aspects of the trapping process that afforded opportunities for improving trap efficiency of invasive sea lamprey (*Petromyzon marinus*) in a Great Lake's tributary. Capturing a sea lamprey requires it to encounter the trap, enter, and be retained until removed. Probabilities of these events depend on the interplay between sea lamprey behavior, environmental conditions, and trap design. We first tested how strongly seasonal patterns in daily trap catches (a measure of trapping success) were related to nightly rates of trap encounter, entry, and retention (outcomes of sea lamprey behavior). We then tested the degree to which variation in rates of trap encounter, entry, and retention were related to environmental features that control agents can manipulate (attractant pheromone addition, discharge) and features agents cannot manipulate (water temperature, season), but could be used as indicators for when to increase trapping effort. Daily trap catch was most strongly associated with rate of encounter. Relative and absolute measures of predictive strength for environmental factors that managers could potentially manipulate were low, suggesting that opportunities to improve trapping success by manipulating factors that affect rates of encounter, entry, and retention are limited. According to results at this trap, more sea lamprey would be captured by increasing trapping effort early in the season when sea lamprey encounter rates with traps are high. The approach used in this study could be applied to trapping of other invasive or valued species.

Introduction

Manipulating behavior as an approach to improve pest management requires understanding the behavioral ecology of the pest (Foster and Harris, 1997). When traps are used for control, trapping effectiveness can be increased by adopting a systematic approach whereby pest behavior is closely observed in response to manipulations of attractant use, trap design, and trap positioning. Trapping of insect pests has been improved by manipulating behaviors related to encountering, entering, and exiting traps (Rodriguez-Saona and Stelinski, 2009). Phillips and Wyatt (1992) determined that differences in the efficiency of traps in capturing German cockroaches (*Blatella germanica*) were explained by differences in individual behavior when contacting and entering traps. Vale (1982) created a quantitative approach to tsetse fly (*Glossina* spp.) trap development that provided a rationale for understanding specific design features and linking trap design to behavior of the target species. In ensuing years, many different designs of tsetse fly traps and targets were developed based on this approach, which played a significant role in the control of tsetse and human African trypanosomiasis (Kuzoe and Schofield, 2005).

The behavior of organisms approaching and entering, or not entering, fishing gear can be complex and not amenable to ad hoc approaches for seeking improvements (Phillips and Wyatt, 1992). Systematic studies of an animal's behavior are expected to be more effective for determining important variables and trapping components affecting trap capture. The process by which fish enter and are retained involves a complex sequence of behaviors in response to the fishing gear (Winger et al., 2010). Observing and understanding these behavior patterns represent a critical step in effective gear design (Winger et al., 2010). For example, recognition of the elaborate relationship between trawl design and fish behavior was first articulated in the 1960s (Okonski, 1969). Consequently, there have been significant improvements in the way trawls are designed

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and tested, not only to improve fish capture, but also reduce fuel costs, bycatch, and impact on the environment (Winger et al., 2010).

Improving methods for trapping invasive sea lamprey (*Petromyzon marinus*) is a strategic goal of the sea lamprey control program in the Laurentian Great Lakes (GLFC, 2011). A better understanding of the trapping process and factors affecting trapping efficiency could help improve trapping tactics, removal rate of adults prior to reproduction, and overall sea lamprey control (McLaughlin et al., 2007; GLFC, 2011). The Great Lakes Fishery Commission and its control agents, Fisheries and Oceans Canada and U.S. Fish and Wildlife Service (USFWS), control sea lamprey in the Laurentian Great Lakes using barriers that deny adults access to spawning habitat in tributaries and periodic applications of semi-selective pesticides (lampricides) to tributaries where larvae occur (Christie and Goddard, 2003). Trapping of adults migrating into tributaries to spawn could be a third control option if the proportion of population of sea lamprey trapped (trapping efficiency) was high enough to suppress recruitment. Current trapping operations conducted throughout the Great Lakes remove approximately 40% of the adult population prior to spawning (Adair and Sullivan, 2015), which is too low to suppress recruitment. Sea lamprey populations exhibit density-dependent survival (compensation) and high variability in density-independent recruitment (Dawson and Jones, 2009). A simulation model of the sea lamprey control program in Lake Huron suggested that trapping coupled with an ongoing lampricide control program could reduce sea lamprey spawning abundances by upwards of 100,000 individuals if 50–60% of adult sea lamprey were removed prior to spawning (Young, 2005). This would require increasing trapping effort to include the 10 largest sea lamprey producing tributaries not currently trapped and a 48% average trap efficiency across all streams (Young, 2005).

Trapping efficiency involves a complex interplay between sea lamprey behavior, environmental conditions, and trap design. Bravener and McLaughlin (2013) summarized the trapping process by considering sea lamprey as belonging to one of four distinct states (unavailable, available, trapped, and removed) separated by five probabilistic events (encounter, departure, entry, retention, or escape; Fig. 1). A sea lamprey is "unavailable" while migrating upstream when it is not in close proximity to a trap. A sea lamprey becomes "available" to be trapped when coming into close proximity to a trap (encounter). Upon encounter, a sea lamprey either does not enter the trap (departs) or moves through the funnel into the trap (entrance). Upon entrance, a sea lamprey either remains in the trap until being removed by trap operators (retention) or leaves the trap prior to being removed by trap operators (escape). Sea lamprey behavior affects both the duration within each state as well as the transitions between states (Bravener and McLaughlin, 2013). Sea lamprey which are not captured may never encounter a trap, never enter a trap upon encounter, or escape after entrance (Bravener and McLaughlin, 2013). Trapping efficiencies within a tributary ultimately depend on the rates of encounter, entrance, and retention with traps (Bravener and McLaughlin, 2013).

Understanding the interplay between sea lamprey behavior and environmental conditions would help identify aspects of the trapping process where improvements in trapping efficiency seem most promising. For example, the St. Marys River connecting Lakes Superior and Huron is one of the largest producers of sea lamprey in the Great Lakes, and through the use of passive integrated transponder tags and underwater video at traps, sea lamprey in this river were found to have low rates of encounter and entry with traps (Bravener and McLaughlin, 2013). Suggestions for improving trap placement have resulted from recent research investigating migratory pathways of sea lamprey approaching traps (Rous, 2014; Holbrook et al., 2015). Behavioral responses of sea lamprey to increases in water discharge (and presumably attractive flows eliciting positive rheotaxis during spawning migration) at locations where traps are located indicate that improving trapping success will require manipulation of stimuli other than discharge (Barber et al., 2012; McLean et al., 2015). Responses of sea lamprey to a synthesized mating pheromone used as bait in traps has resulted in increased trap captures in some streams but not others, which warrants further investigation (Johnson et al., 2013).

Identifying environmental factors that can be manipulated by trap operators to increase rates of encounter, entrance, and/or retention offers a promising way of directing research to improve trapping efficiency and to assess possible gains. Some environmental factors that can influence sea lamprey behavior, such as pheromone concentrations or stream flow near a trap, can be manipulated. Other environmental factors, such as water temperature (or rate of change) and season, cannot be manipulated or are not practical to manipulate. The potential to improve trapping efficiency will depend on the relative importance of factors that can be manipulated by the trap operators versus those that cannot be manipulated, and the degree to which probabilities of sea lamprey encounter, entry, and retention change in response to environmental factors that can be manipulated. Understanding whether and how sea lamprey respond to the interaction between manipulable and non-manipulable factors can also help guide the determination of the conditions under which trapping is most likely to be effective. Lastly, if environmental factors that cannot be manipulated are strong determinants of trap efficiency, overall efficiency could still be improved by increasing trapping effort during times when those factors are expected to increase trap encounter and entrance rates.

We identified aspects of the sea lamprey trapping process that represent candidates for improving trap efficiency. Our first objective was to test how strongly seasonal patterns in daily trap catches (a measure of trapping success) were related to rates of trap encounter, entry, and retention (outcomes of sea lamprey behavior). Our second objective was to assess the relationships between rates of encounter, entry, and retention with environmental features that control agents can manipulate (pheromone addition, discharge) and features the agents cannot manipulate (change in water temperature, season). Pheromone application was considered because baiting traps with a synthesized mating pheromone component can increase trap capture of adults (Johnson et al., 2013). Tributary discharge was considered because stream flow is potentially manipulable at some trap sites, and higher tributary discharge could stimulate sea lamprey activity and/or attract sea lamprey upstream and increase the probability of encountering traps (McLaughlin et al., 2007; Binder et al., 2010; McLean et al., 2015). Tributary discharge also affects the hydraulic conditions around a trap,

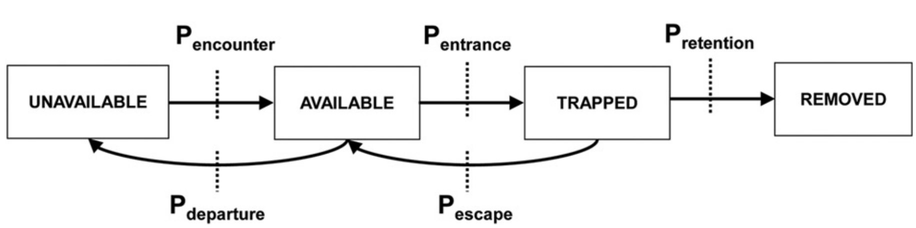

Fig. 1. Conceptual framework of the sea lamprey trapping process. Rectangles represent trapping states that a sea lamprey can occupy at a given time throughout the trapping season. Arrows represent transitions from one state to another and can depend on sea lamprey behavior (Px = transition probabilities).
Reproduced with permission from Bravener and McLaughlin (2013).

which can also influence the probability of a fish entering and being retained in a trap or fishway (Pratt et al., 2009). Daily change in water temperature was considered because trap catches at other tributaries have been strongly related to increasing water temperature (Binder and McDonald, 2008; Barber et al., 2012). Season was considered because rates of encounter and entrance have been found to vary over the season in other tributaries (Bravener and McLaughlin, 2013), and the number of sea lamprey swimming upstream has been observed to go down with Julian date which could be due to maturity changes over the season (Meckley et al., 2012). We conducted the study during an entire trapping season at a sea lamprey barrier and trap complex in a tributary with varying discharge and temperature, to which a synthesized mating pheromone was added every other night. This provided a unique opportunity to assess the importance of manipulable and non-manipulable factors in determining the trapping efficiency of sea lamprey, which has not been conducted in previous studies.

Materials and methods

Study site

This study was conducted at the USFWS sea lamprey barrier and trap complex in the Carp Lake River near Mackinaw City, Michigan (Fig. 2). This Lake Michigan tributary is approximately 9-m wide downstream of the barrier, which is located 500 m from the river mouth. The trap in this study had a single, funneled entrance that was approximately 118-cm high × 23-cm wide × 30.5-cm deep that tapered down to a series of six square openings oriented vertically on top of one another. In previous years another trap had been operated at this site as part of management-scale field trials of 3kPZS (Johnson et al., 2013, 2015a), but our study was the only one operating at this site in 2012. Each opening was approximately 8.25 cm^2. Vertically-hinged stainless steel rods set 1.25 cm apart and extending down inside and below the trap opening allowed sea lamprey to enter, but deterred sea lampreys from

Fig. 2. Location of Carp Lake River where video recording of sea lamprey at the study trap was conducted.

Table 1
Listing of a priori candidate models fit to trap catch and rates of encounter, entry, and retention. Also shown are the AICc values, AICc differences (ΔAICc), number of parameters (K), and AICc weights (ω) for each of the models. Models are presented in ascending order based on ΔAICc.

Explanatory variables	AICc	ΔAICc	K	ω
Trap catch				
Log_e encounters + entry	283.7	0.0	4	0.432
Log_e encounters + entry + retention	284.0	0.3	5	0.367
Log_e encounters + retention	285.9	2.2	4	0.144
Log_e encounters	287.7	4.1	3	0.057
Retention	334.6	51.0	3	<0.001
Entry + retention	336.9	53.3	4	<0.001
Intercept only	358.3	74.6	2	<0.001
Entry	359.8	76.2	3	<0.001
Trap encounter				
Change water temp + baited + season + $\log_e$ discharge	486.3	0.0	7	0.943
Change water temp + baited + season + baited × season + $\log_e$ discharge	492.0	5.6	9	0.056
Change water temp	501.6	15.2	3	<0.001
Baited + season + baited × season + $\log_e$ discharge	504.6	18.3	8	<0.001
Intercept only	507.8	21.5	2	<0.001
Baited + $\log_e$ discharge	509.8	23.5	4	<0.001
Trap entry probability				
Baited + $\log_e$ discharge	11,360.3	0.0	4	0.3844
Intercept only	11,360.6	0.3	2	0.3299
Change water temp	11,361.2	1.3	3	0.2033
Change water temp + baited + season + $\log_e$ discharge	11,364.2	3.9	7	0.0538
Baited + season + baited × season + $\log_e$ discharge	11,366.3	6.0	8	0.0195
Change water temp + baited + season + baited × season	11,367.8	7.5	9	0.0091
Season + $\log_e$ discharge				
Trap retention probability				
Change water temp	3374.5	0.0	3	0.4222
Change water temp + baited + season + $\log_e$ discharge	3374.9	0.4	7	0.3481
Change water temp + baited + season + baited × season	3377.2	2.7	9	0.1107
Season + $\log_e$ discharge				
Intercept only	3377.5	3.0	2	0.0960
Baited + $\log_e$ discharge	3380.8	6.3	4	0.0180
Baited + season + baited × season + $\log_e$ discharge	3383.4	8.9	8	0.0049

leaving the trap after entering. Sea lamprey behavior was observed by collecting video from 21:00 to 05:00 nightly, when sea lamprey are most active, over the period from May 1 to June 13, 2012. At approximately 09:00 each day, sea lamprey remaining in trap were removed and counted by USFWS personnel as the daily trap catch.

Video recording

Video recordings of sea lamprey behavior at the traps were made using two underwater video cameras (Security Labs Waterproof Color Cameras with infrared and 8 white LED built in lights, Security Labs, Inc., www.security-labs.com). The cameras were secured on a piece of wood (5.1 × 10.2 × 20.3-cm) fastened to the outer enclosure 30 cm from the trap entrance, allowing observation of sea lamprey behavior without obstructing the trap entrance. The field of view of the camera was such that the entire single-funneled entrance of the trap could be observed from approximately two sea lamprey body lengths from the camera position to the trap. Cameras were connected to a Digital Video Recorder (Q-see Security Surveillance, 4 Ch. H.264 network DVR, Digital Peripheral Solutions, www.q-see.com). The video cameras and DVR were powered by two 12-V marine batteries (Everstart Maxx 29 deep-cycle marine) wired in parallel. Lighting was required for sea lamprey to be observed on video. A previous study by Stamplecoskie et al. (2012) found no evidence that light attracted sea lampreys to trap funnels, improved entrance into traps, or improved retention inside traps when a lone trap was lighted in the field. Recorded video was downloaded daily.

Quantifying rates of encounter, entrance, and retention

Video recordings were observed using EF Player (GCL Project, Singapore, Malaysia). Observers playing back the time-stamped video recorded the time that a sea lamprey encountered the trap area, which was when a sea lamprey entered the camera view and times of three possible events afterward: did not enter, entered, or escaped. "Did not enter" was recorded if the entire sea lamprey left the field of view of the camera without entering the trap. "Entered" was recorded if the entire sea lamprey entered the trap. "Escaped" was recorded if the entire sea lamprey entered the field of view by exiting the trap. Each observation of a sea lamprey began when any part of a sea lamprey was observed in the field of view of the camera and culminated in one of these three events. An observation was recorded regardless of the length of time an individual was observed in the field of view.

Rates of encounter, entrance, and retention were calculated from the recorded observations. Encounter rate was calculated by summing all nightly observations of a sea lamprey approaching the trap, regardless of whether they entered or not. Entry rate was calculated by summing all nightly observations of sea lamprey entering the trap and dividing by the encounter rate. Retention rate was calculated by taking nightly totals of the number of entries and the number of escapes and calculating ((number of entries − number of escapes) / number of entries). Therefore, nightly entrance and retention rates varied continuously between 0 and 1.

Measurement/quantification of environmental factors

Pheromone attractant was emitted from the trap every other night. The pheromone attractant was a male mating pheromone component

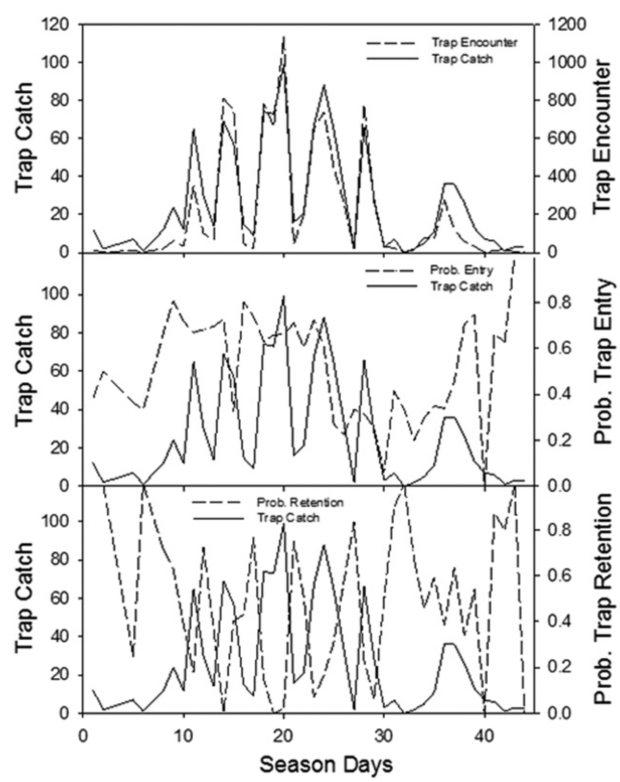

Fig. 3. Observed catch in relation to number of sea lamprey encounters, probability of trap entry, and probability of trap retention at the sea lamprey trap at Carp Lake River. Season days are numbered from 1 to 44, with day 1 being the first day the trap was fished and day 44 being the last.

identified as 7α,12 α,24-trihydroxy-3-one-5α-cholan-24-sulfate (3kPZS; Li et al., 2002). On nights when the Carp Lake River trap was baited, we used a controlled-release polyethylene glycol (PEG) 3kPZS emitter consisting of about 11.3 g of PEG and 20 mg of 3kPZS. 3kPZS batch # 183-EJH-290-3 synthesized during February 2010 (Bridge Organics). Batch purity exceeded 99% based on high pressure liquid chromatography and mass spectrometry. The 3kPZS emitter was placed in an automatic pet feeder with a LCD clock (KPF-04/05A/07/08) that was set to drop the PEG at 21:00 into a mesh bag that extended down into the water. The PEG 3kPZS emitter dissolved at a uniform rate over 10 h and, therefore, 3kPZS was applied at 2 mg/h. Two mg/h is approximately the rate 3kPZS was applied in an earlier study on the Carp Lake River (Johnson et al., 2013; conducted 2009–2011, present study occurred in 2012). Three nights of data were excluded due to issues with video not being recorded (two nights), or the 3kPZS emitter not dropping into the trap (one night). As a result, behavior of sea lamprey was observed when either the trap was not baited with 3kPZS during 21 nights or when the trap was baited with 3kPZS during 20 nights.

Tributary discharge, change in water temperature, and season were estimated or calculated throughout the trapping season. Daily tributary discharge was estimated from daily measurements of staff gauge height using the stage-discharge curve developed in a previous study by Johnson et al. (2013). Discharge is not manipulable at our specific study site, but is considered to be manipulable where dams and gates are used to regulate water flow. Water temperature was recorded every three hours using a temperature logger (HOBO Water Temp Pro, Onset Computer Corporation, Bourne, MA, USA) attached to the outside of the trap. Daily change in water temperature was calculated by subtracting the mean daily water temperature for a specific day from the mean water temperature the previous day. Season was considered by splitting the period the trap was fished into thirds of 15, 14, and 15 day durations corresponding with early, mid, or late periods in the season, respectively. We wanted to capture potential changes in sea lamprey behavior over a season because other studies have observed variation in rates of encounter and entrance in other tributaries (Bravener and McLaughlin, 2013). Season was an attempt to separate early, mid-season, and late migrating sea lamprey to compare potential differences in behavior between groups on average.

Data analysis

Objective 1: relating daily trap catches to rates of trap encounter, entry, and retention

To relate daily trap catch with rates of encounter, entry, or retention, we fit negative binomial regression models with a log-link function using the glm.nb function in the MASS package (Venables and Ripley, 2002). Rate of encounter (encounters each night) was $\log_e$ transformed prior to analysis because of skewness. For the negative binomial regression models, model fit was assessed by calculating a generalized R^2 for the best-performing (if there was only one model with ΔAICc values <10.0) or model-averaged (if there was more than one model with ΔAICc values <10.0) model. Generalized R^2 values were calculated as

$$R^2 = 1 - \left(\frac{L(0)}{L(\hat{\theta})}\right)^{2/n} / 1 - \left(\frac{L(0)}{L(S)}\right)^{2/n}$$

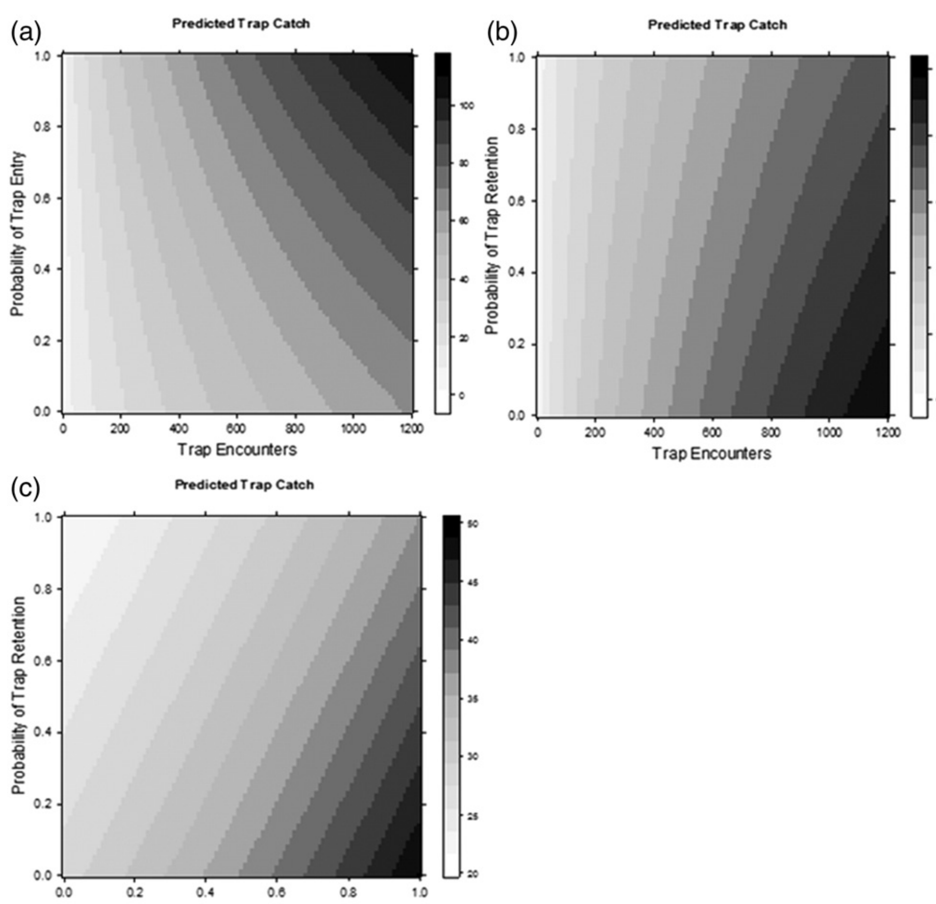

Fig. 4. Predicted trap catch at the Carp Lake River based on observed trap catch data, when including (a) probability of trap entry and number of sea lamprey encounters, (b) probability of trap retention and number of sea lamprey encounters, and (c) probability of trap retention and probability of trap entry.

where $L(0)$is the likelihood for an intercept-only model, $L(\hat{\theta})$ is the likelihood for the best-performing or model-averaged model, $L(S)$ is the likelihood for a saturated model, and n is the number of observations.

Akaike information criteria with small sample size correction (AICc) was used to evaluate the performance of each of the candidate models for a particular response variable (Burnham and Anderson, 2002). Empirical support for candidate models was evaluated via AICc difference (ΔAICc). Models with ΔAICc values <10.0 were considered to have strong plausibility as being the "best" model. If more than one candidate model had a ΔAICc value of <10.0, model-averaging based on Akaike weights of the candidate models with ΔAICc values <10.0 was conducted. Model averaging was conducted using the model.avg. function in the MuMIn package (Bartoń, 2015). All analyses were conducted in R (R Core Team, 2015).

Objective 2: assessing relationships between rates of encounter, entry, and retention with manipulable and non-manipulable factors

Negative binomial regression models also were used to relate nightly rate of encounter to season, discharge, pheromone addition, and change in water temperature, with model fit assessed as described in the previous section. We used mixed-effects logistic regression models to relate rates of entry and retention to season, discharge, change in water temperature, and pheromone addition. For each response variable, we a priori designated a set of candidate models that assessed the relative importance of factors that can be manipulated by the trap operators versus those that cannot be manipulated, and combinations of these factors known to affect sea lamprey behavior. The mixed-effects logistic regression models were fit by Laplace approximation using the glmer function in the lme4 package (Bates et al., 2015). Discharge was $\log_e$ transformed because of skewness in the data. For the mixed-effects logistic regression models, night was specified as a random effect, which resulted in night being treated as the experimental unit and individual observations of sea lamprey entering and escaping traps being treated as observational units. As a consequence of this model structure, there inherently was assumed to be a positive correlation among observations within a night, which helped account for the fact that the same sea lamprey could have been observed on multiple occasions.

For the mixed-effects logistic regression models, goodness of fit was assessed by calculating model accuracy, sensitivity, specificity, and area under the receiver operating characteristic curve (AUROC), which measures the probability that a predictor will rank a randomly chosen positive instance higher than a randomly chosen negative one and is a commonly used method for evaluating the discriminatory power of a logistic regression model. Goodness of fit measures for the mixed-effects logistic regression models were obtained using the confusion Matrix function in the caret package (Kuhn et al., 2015). All analyses were conducted in R (R Core Team, 2015).

Results

Key features of the sea lamprey spawning run (e.g., magnitude and timing of run, trap efficiency, range of water temperature) in our study year were similar to those of previous years. During 2012, USFWS reported that 1201 sea lamprey were captured with a trap efficiency (number of sea lamprey captured in the trap/total number of sea lamprey estimated in the river) of 51%. In years previous, an additional trap was located in the Carp Lake River, and the number of sea lamprey captured and combined trapping efficiency of tributary traps for the period 2007 to 2011 ranged from 269 to 3110 and 41% to 86%, respectively. Average daily water temperature ranged from 8.8 to 25.0 °C during the 2012 sea lamprey trapping season compared to 7.2 to 22.2 °C during the 2011 trapping season. Tributary discharge did differ between the 2012 and 2011 sea lamprey trapping seasons with a range of 0.42 m^3/s to 1.23 m^3/s during 2012 compared with a range of 0.77 m^3/s to 27.0 m^3/s during 2011.

Sea lamprey spent little time on average in the camera field of view. Over 90% of observations lasted 10 s or less with sea lamprey swimming into and out of the field of view, and only 1% of the observations recorded sea lamprey suctioning on to the side of the trap entrance for longer time periods. The average time sea lamprey spent in the field of view was 8 s (standard deviation = 31 s), with the maximum time spent in the field of view of just over 10 min. Sea lamprey that ultimately entered the trap spent an average of 3 s in the field of view, while those that did not enter the trap spent an average of 5 s in the field of view.

Objective 1: relating daily trap catches to rates of trap encounter, entry, and retention

Two findings emerged from our evaluation of how rates of encounter, entry, and retention were related to trap catch. First, trap catch was best predicted by a model including rates of $\log_e$ encounter and entry (Table 1). Three other candidate models had ΔAICc values <10.0 (Table 1). The next-best performing model included $\log_e$ encounter, rate of entry, and rate of retention as explanatory variables, whereas the third-best model included $\log_e$ encounter and rate of retention and the fourth-best model only included $\log_e$ encounter (Table 1). The generalized R^2 for the model that resulted from model-averaging the coefficients of the four best performing candidate models was 0.89. Second, trap catch was positively related to $\log_e$ encounter and probability of trap entry, but negatively related to probability of trap retention (Fig. 3). Trap catch was negatively related to trap retention because presumably more sea lamprey were likely to escape when more were captured. Trap catch was most strongly related to trap encounter, which was evident by examining the empirical relationship between catch and the explanatory variables (Fig. 4). Based on the model-averaged parameter estimate for trap encounter, every increase in 1

Table 2
AICc model-averaged regression coefficient estimates and upper and lower 95% confidence limits for models fit to sea lamprey trap encounter, trap entry, and trap retention rates. Model averaging was conducted over candidate models with ΔAICc value <10.0. The exponentiated estimates and upper and lower 95% confidence limits are also shown to facilitate understanding expected change in the response variables given change in explanatory variables while others are held constant.

Variable	Estimate	95% CL	Exp. estimate	Exp. 95% CL
Trap catch				
$\log_e$ encounter	0.56	0.46–0.67	1.76	1.58–1.95
Trap entry probability	0.57	-0.18–1.26	1.72	0.84–3.53
Trap retention probability	-0.25	-0.85–0.38	0.79	0.43–1.46
Trap encounter				
Change in water temp (°C)	0.46	0.27–0.66	1.59	1.31–1.93
$\log_e$ discharge (m^3/s)	-4.30	-6.48–-2.13	0.01	0.00–0.12
Baited (yes)	0.08	-0.68–0.84	1.08	0.51–2.31
Season (mid)	-0.84	-2.29–0.60	0.43	0.10–1.82
Season (late)	-2.55	-3.93–-1.18	0.08	0.02–0.31
Baited (yes) × season (mid)	0.03	-0.45–0.51	1.03	0.64–1.67
Baited (yes) × season (late)	0.04	-0.48–0.56	1.04	0.62–1.76
Trap entry probability				
Change in water temp (°C)	0.02	-0.09–0.13	1.02	0.92–1.14
$\log_e$ discharge (m^3/s)	0.53	-0.85–1.90	1.69	0.43–6.68
Baited (yes)	0.10	-0.35–0.55	1.11	0.70–1.74
Season (mid)	0.03	-0.36–0.42	1.03	0.70–1.52
Season (late)	0.00	-0.32–0.31	1.00	0.73–1.36
Baited (yes) × season (mid)	-0.01	-0.26–0.24	0.99	0.77–1.27
Baited (yes) × season (late)	-0.01	-0.25–0.24	0.99	0.78–1.27
Trap retention probability				
Change in water temp (°C)	-0.41	-0.87–0.05	0.66	0.42–1.05
$\log_e$ discharge (m^3/s)	0.83	-2.39–4.06	2.30	0.09–58.12
Baited (yes)	-0.19	-1.33–0.95	0.83	0.26–2.58
Season (mid)	-0.19	-1.99–1.61	0.83	0.14–5.01
Season (late)	0.76	-1.54–3.06	2.14	0.21–21.28
Baited (yes) × season (mid)	0.17	-1.20–1.55	1.19	0.30–4.69
Baited (yes) × season (late)	-0.01	-1.03–1.00	0.99	0.36–2.72

$\log_e$ encounter rate was expected to increase trap catch by approximately 76% (Table 2). Conversely, every 1% increase in rate of entry increased catch by 0.5% and every 1% increase in rate of retention decreased catch by about 0.2% (Table 2). However, there is uncertainty as to the exact relationship between these variables and trap encounter because the 95% confidence intervals for the model-averaged regression coefficients for both rate of entry and rate of retention included both positive and negative values (Table 2).

Objective 2: assessing relationships between rates of encounter, entry, and retention with manipulable and non-manipulable factors

Three key findings emerged from evaluations of how environmental factors relate to rates of encounter, entry, and retention. First, the best approximating model for each aspect of the trapping process included both environmental factors that could be manipulated and factors that could not. Second, the discriminatory power of the predictive models based on model-averaged coefficients was low across the three components of the trapping process. Third, the relative importance of the manipulable variables (pheromone addition and discharge) was poor relative to the variables that cannot be manipulated (change in water temperature and season).

The best approximating model of each component of the trapping process included manipulable and non-manipulable variables. For trap encounter, two of the candidate models had ΔAICc values <10.0 (Table 1). The best-performing model based on lowest AICc value included change in water temperature, $\log_e$ discharge, pheromone baiting, and season (Fig. 5; Table 1). The second-best model additionally included an interaction between baiting and season (Table 1). For probability of trap entry, all of the candidate models had ΔAICc values <10.0, so all models were included in the model-averaging procedure (Table 1). The best-performing model based on lowest AICc value included $\log_e$ discharge and pheromone baiting, and season. However, this model performed only slightly better than an intercept-only model (Table 1). The predicted probability of trap entry was positively related to $\log_e$ discharge, change in water temperature, and pheromone baiting (Fig. 6). For probability of trap retention, all of the candidate models had ΔAICc values <10.0, so all models were included in the model-averaging procedure (Table 1). The best-performing model included change in water temperature as an explanatory variable (Table 1). The second best-performing model included change in water temperature, $\log_e$ discharge, pheromone baiting, and season, which had a ΔAICc of 0.4 (Table 1). The predicted probability of trap retention was negatively related to change in water temperature and pheromone baiting, but was positively related to $\log_e$ discharge (Fig. 7).

Across the three components of the trapping process, the discriminatory power of the predictive models based on model-averaged coefficients was low. Thus, rates of encounter, entrance, and retention of sea lamprey were not well predicted by our models based on the environmental variables we tested. For the model predicting encounter rate, the generalized R^2 that resulted from model-averaging the coefficients of the four best performing candidate models was 0.51. Accuracy of the model predicting probability of entry based on the model-averaged coefficients was 67.9%, with a sensitivity and specificity of 80.2 and 53.3%, respectively. The positive and negative predictive value of the model was 67.1 and 69.4%, respectively. The AUROC of the model based on the model-averaged coefficients was 66.8%, which suggested that the discriminatory power of the model predicting probability of entry based on model-averaged coefficients was low. Accuracy of the model predicting probability of retention based on the model-averaged

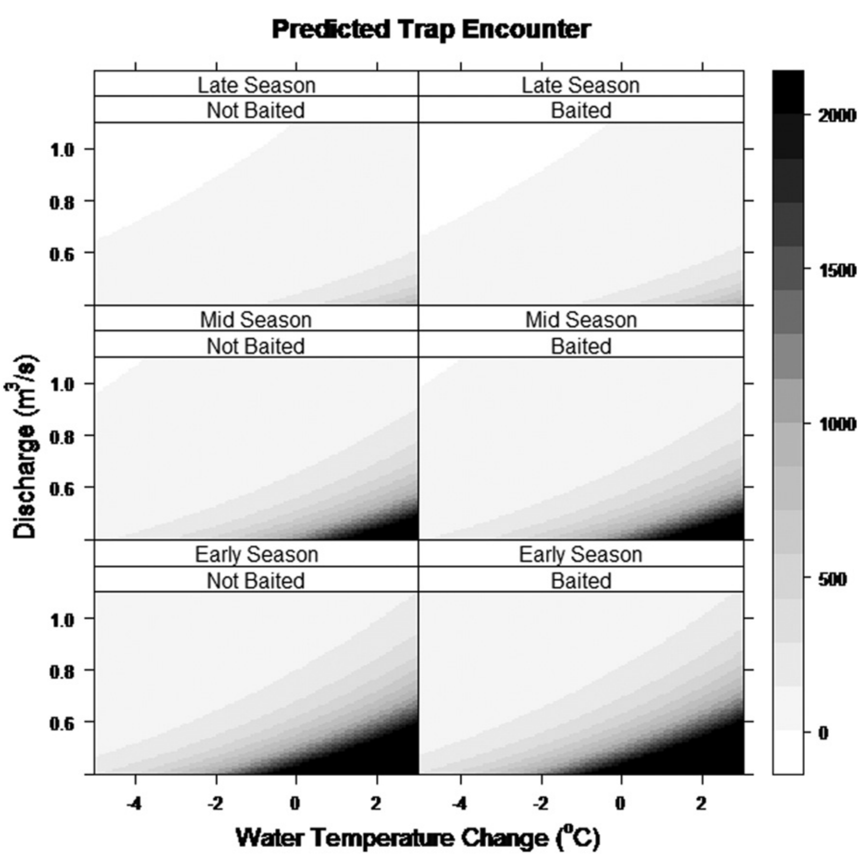

Fig. 5. Predicted number of sea lamprey trap encounters at the Carp Lake River in relation to discharge, change in water temperature, season, and whether the trap was baited with an attractant pheromone based on AICc model averaging of all candidate models with ΔAICc values <10.0 (see Tables 1 and 2 for listing of models and model-averaged coefficients).

coefficients was 85.4%, with a sensitivity and specificity of 38.1 and 95.4%, respectively. The positive and negative predictive value of the model was 63.8 and 87.9%, respectively. The AUROC of the best-performing model was 66.7%, which suggested that the discriminatory power of the model predicting probability of retention based on model-averaged coefficients was low.

The relative importance of the manipulable variables was poor relative to non-manipulable variables. Based on the model-averaged coefficient estimates, the likelihood of a sea lamprey encountering the trap was more influenced by a change in water temperature rather than a change in stream discharge. Rate of encounter was expected to increase by 59% for every 1 °C increase in water temperature, while every 0.1 $\log_e$ m^3/s increase in discharge was expected to decrease encounters by approximately 35% (Table 2). From a general standpoint, baiting increased encounter rate of sea lamprey depending on season (Table 2), but the effect of season was much stronger than the effect of baiting (Fig. 5). However, the 95% confidence intervals for the model-averaged coefficients for both season and pheromone baiting included both positive and negative values so there was uncertainty as to the exact relationship between these variables and trap encounter (Table 2). Probability of sea lamprey entering the trap increased slightly with discharge, baiting, a positive change in water temperature, and during mid-season (Fig. 6), but the exact relationship between trap entry and these explanatory variables was marked by a great deal of uncertainty. This was because the 95% confidence intervals for all of the model-averaged coefficients included both positive and negative values (Table 2). Probability of sea lamprey being retained in the trap increased during late season and with a negative change in water temperature (Fig. 7), but there was uncertainty as to the exact relationship between trap retention and these explanatory variables. Again, this was due to the fact that the 95% confidence intervals for all of the model-averaged coefficients included both positive and negative values.

Discussion

Two main conclusions emerged from this research. First, opportunities to improve daily trap catches at the Carp Lake River are expected to be greatest for changes to trap placement and operations designed to increase rates of trap encounter. Encounter rate was the strongest predictor of daily trap catch. Second, opportunities to improve rates of encounter, entrance, and retention by altering environmental factors are potentially limited, because measures of relative and absolute predictive strength were low for these manipulable variables. The best approximating model for each aspect of the trapping process included both environmental factors that could be manipulated and factors that could not. This suggests that improvement in trap efficiency will need to be achieved through increased trapping effort, which would be most effective with the addition of pheromone early in the season as water temperature increases.

Trap catch in this study was strongly affected by the rate at which sea lamprey encountered the trap, while probabilities of entry and retention had little effect on the overall trap catch. In trapping, variability in entrance only applies to those individuals that encounter, and retention only applies to those that enter. Sea lamprey encountering the trap were more likely to not enter the trap. Johnson et al. (2016) increased capture of adult sea lamprey in a portable trap by increasing the rate at which sea lamprey encountered the trap through the use of an electric lead (Johnson et al., 2016). However, Rous (2014) found little improvement in trap entrance and overall trap catch of sea lamprey in the St. Marys River in response to increasing nightly discharge, despite increased rates of encounter with the traps and 100% retention. But, encounter with, and entrance into, traps have been found to vary with sea lamprey class (fertile or sterilized), release date, and time of day (Bravener and McLaughlin, 2013). For example, while sea lamprey released in the St. Marys River earlier in the season were no more likely

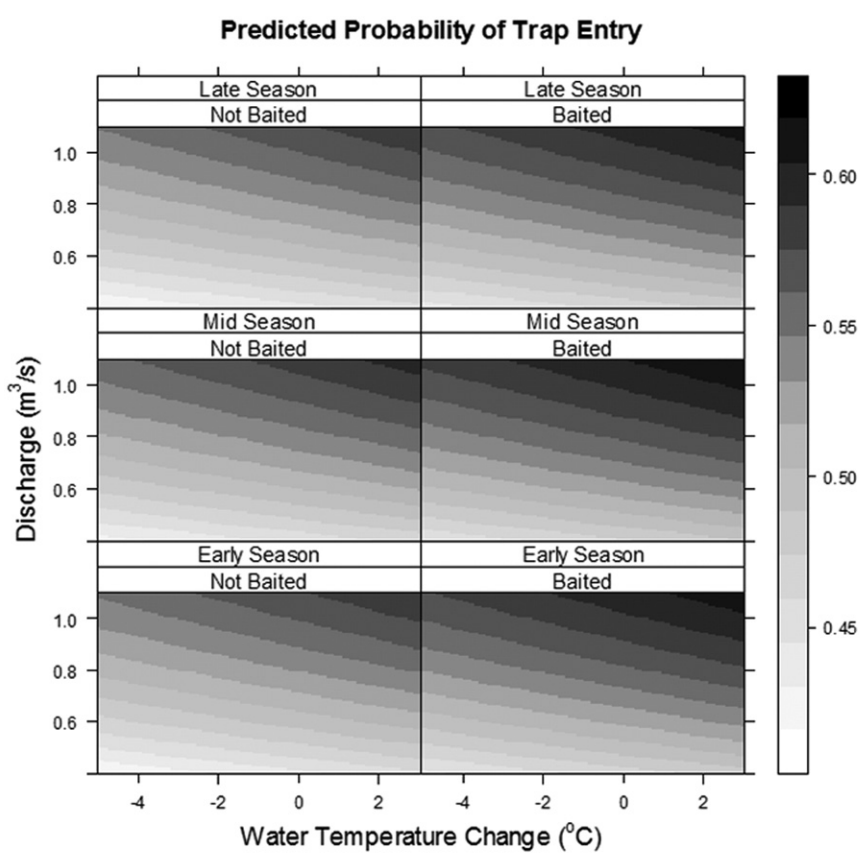

Fig. 6. Predicted probability of trap entry at the Carp Lake River in relation to discharge, change in water temperature, season, and whether the trap was baited with an attractant pheromone based on AICc model averaging of all candidate models with ΔAICc values <10.0 (see Tables 1 and 2 for listing of models and model-averaged coefficients).

to enter upon encountering a trap than those released later in the season, those released early had a greater number of encounters with traps (Bravener and McLaughlin, 2013). Based on the results of our study, research and management would see the most gains when improving encounter rate, rather than rate of entry or retention to increase trapping efficiency.

The addition of a partial mating pheromone to the trap marginally increased trapping success, which is consistent with previous studies. Mean sea lamprey catch and encounter were greater on nights the trap was baited versus unbaited [catch: 30.2 sea lamprey (baited) vs. 24.5 sea lamprey (unbaited); encounter: 265.2 sea lamprey (baited) vs. 177.1 sea lamprey (unbaited)]. Interestingly, a greater number of sea lamprey were captured per encounter on unbaited nights. We are not sure why this was the case, but in the end, the increase in encounter rate outweighed the reduction in rate of entry. Johnson et al. (2015a) found that pheromone-baited traps were most likely to catch large numbers of sea lampreys early in the trapping season, when water temperatures were increasing. Our results are consistent with Johnson et al. (2015a) because baiting generally increased encounter rate early in the season and entrance rate overall according to our predictive plots. However, there is some uncertainty as to the exact relationship between encounter and entrance rate and the addition of pheromone because of collinearity between pheromone application and other environmental variables. For example, change in water temperature was generally greater and discharge was lower on nights that traps were baited. Our study simply added a partial mating pheromone at a single concentration to an existing trap every other night for an entire trapping season and observed sea lamprey encounters, entries, and escapes. Sea lamprey traps still could be improved by optimizing pheromone application given different flow characteristics, trap entrances, trap materials, and substrate types around and in the trap, as well by determining the optimal location for deployment (Johnson et al., 2015a). Baiting traps with the full mating pheromone mixture released by males (spermiating male washings) rather than the partial mating pheromone would likely further increase trapping efficiency, as baiting traps in two Great Lakes tributaries with the full mating pheromone was found to capture significantly more sea lampreys than 3kPZS-baited traps (~10% increase; Johnson et al., 2015b).

In our study, there was no evidence of improvement in trapping success with increasing stream discharge. Rather, an inverse relationship between stream discharge and encounter rate was observed. McLean et al. (2015) found the probability of sea lamprey reaching a trap opening increased with increasing discharge after being observed by a camera 2 m away in the St. Marys River; however, they also found that changes in discharge did not influence the probability of entrance. Similarly, Bravener and McLaughlin (2013) were unable to detect a relationship between the probabilities of sea lamprey encountering or entering a trap in the St. Marys River and nightly discharge, although there was little nightly variation in discharge in their study. We may need to rethink how hydrodynamic conditions operate on behavior. For example, local hydrodynamic conditions near the trap opening (attractive flows at the trap opening eliciting positive rheotaxis) also warrant investigation because the effects of attraction stimuli can differ across large and small spatial scales (Foster and Harris, 1997).

Encounter rates could be improved by manipulating effort, and thus increasing trapping success. According to Bravener and McLaughlin (2013), the management responses to a low encounter rate of sea lamprey at traps are to add traps, improve trap placement, and/or add attraction to traps, bearing in mind that changes to the trap design and operation expected to improve a component of trapping may impact other components of trapping (Rous, 2014). Trapping efficiency in tributaries with low sea lamprey encounter rates like the Carp Lake River trap could be improved by increasing the number of traps, or adding physical or electrical leads to guide sea lamprey toward traps (Johnson et al.,

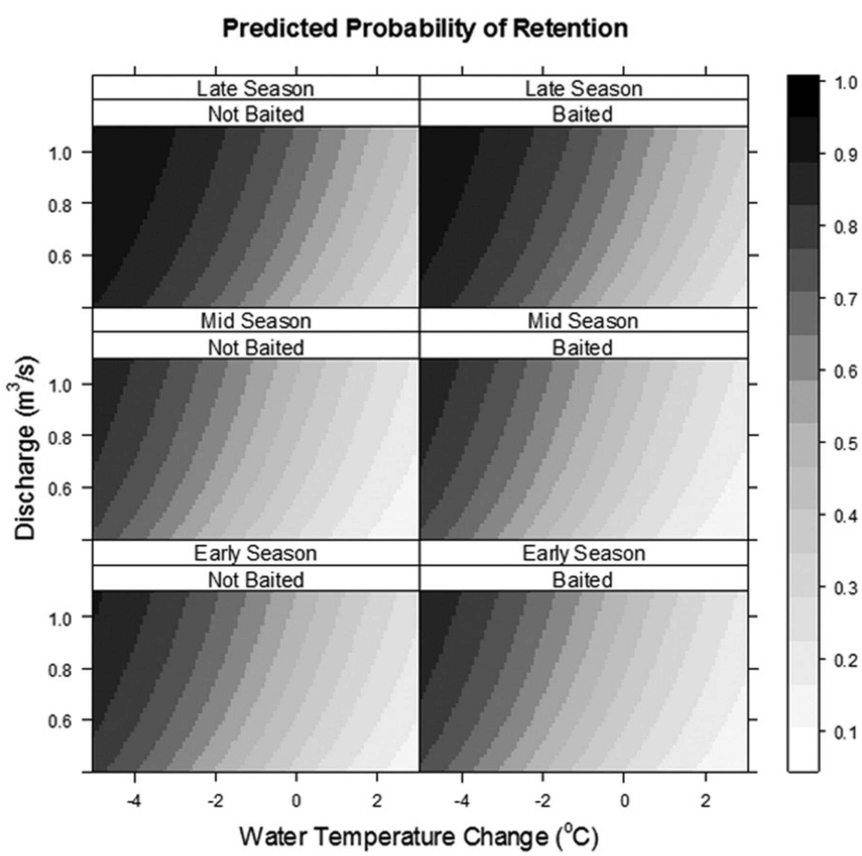

Fig. 7. Predicted probability of trap retention at the Carp Lake River in relation to discharge, change in water temperature, season, and whether the trap was baited with an attractant pheromone based on AICc model averaging of all candidate models with ΔAICc values <10.0 (see Tables 1 and 2 for listing of models and model-averaged coefficients).

2016). The Carp Lake River trap is integrated with a barrier so trap placement cannot be changed, but perhaps added traps could be placed near the river bottom where sea lamprey have often observed in trapping studies (Rous, 2014; Holbrook et al., 2015).

Emerging evidence supports the value of systematic evaluations of the trapping process, rooted in a conceptual framework considering the target animal's behavior (Bravener and McLaughlin, 2013; Rous, 2014; McLean et al., 2015; this study), rather than ad hoc manipulations of traps or trap operations to observe how catch changes. Our study provides a method to identify aspects of the capture process that represent candidates for improving efficiency that could also be applied to capture programs for other species. To our knowledge this is the only study directly assessing the importance of manipulable variables relative to non-manipulable variables in influencing trap capture. But, other studies have assessed the combination of manipulable and non-manipulable factors present that lead to the greatest trap efficiency. Phillips and Wyatt (1992) employed a systematic approach using direct observation of animals to understand the reasons why trap catch of the German cockroach was significantly different in traps of basically similar design. Jury et al. (2001) used video recordings of lobster behavior at traps to determine the mechanisms that lead to low trap efficiency; aggressive interactions between lobsters appear to be one of the dominant factors limiting both rate of entry into traps and rate of exit from traps. In the case of sea lamprey, the largest trap captures of sea lamprey was associated with a positive change in water temperature early in the season when partial pheromone was applied (this study; Johnson et al., 2015a).

This study has provided insights regarding how rates of encounter, entry, and retention affect overall trap efficiency, and how sea lamprey alter their behavior in response to changes in environmental factors that managers could manipulate or exploit to improve trapping efficiency. This kind of assessment can be costly in terms of time and money (Bravener and McLaughlin, 2013). However, the long-term costs of not assessing capture efficiency systematically, or pursuing improvements through trial and error, could potentially cost more (Williams et al., 2012).

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