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Tradeoff between Assessment and Control of Aquatic Invasive Species: A Case Study of Sea Lamprey Management in the St. Marys River

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Abstract
    Allocating resources between the gathering of information to guide management actions and implementing those actions presents an inherent tradeoff. This tradeoff is evident for control of the Sea Lamprey *Petromyzon marinus* in the St. Marys River, connecting Lakes Huron and Superior and a major source of parasitic Sea Lampreys to Lake Huron and northern Lake Michigan. Larval Sea Lampreys in the St. Marys River are controlled through the application of Bayluscide, which is applied to areas of high larval density. Bayluscide applications are guided with an annual deepwater electrofishing survey to estimate larval Sea Lamprey density at relatively fine spatial scales. We took a resampling approach to describe the effect of sampling intensity on the success of the larval Sea Lamprey management program and explicitly incorporated the economic tradeoff between assessment and control efforts to maximize numbers of larvae killed in the St. Marys River. When no tradeoff between assessment and control was incorporated, increasing assessment always led to more larvae killed for the same treatment budget. When the tradeoff was incorporated, the sampling intensity that maximized the number of larvae killed depended on the overall budget available. Increased sampling intensities maximized effectiveness under medium to large budgets (US$0.4 to $2.0 million), and intermediate sampling intensities maximized effectiveness under low budgets. Sea Lamprey control actions based on assessment information outperformed those that were implemented with no assessment under all budget scenarios.

Managers of natural resources should ideally seek to maximize the effectiveness of an action (e.g., pests killed, habitat restored, ecosystem services provided) while minimizing costs. Costs play a fundamental role in natural resource management (Clark 2005; Fenichel and Hansen 2010), and the

need to formally incorporate these costs into the decision-making process has become increasingly important (Shogren et al. 1999; Hansen and Jones 2008a; Fenichel and Hansen 2010). An inherent tradeoff exists between the gathering of information (assessment or sampling) to guide management actions

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and the implementation of those actions (Mehta et al. 2007). Costs associated with gathering information to advise management include the cost of data collection and the opportunity costs, but these resources could be used to gather information that could be used in some other way to improve management (Hansen and Jones 2008b). While many authors note the importance of incorporating this tradeoff into the management process, in most instances the tradeoff is not explicitly considered (Mehta et al. 2007; Hansen and Jones 2008a; Fenichel and Hansen 2010). Explicitly considering the effect of allocating budgetary resources on the success of management actions should make the management process more effective and efficient.

Determining the appropriate level of sampling is an important consideration for management programs that require the assessment of populations. This consideration is especially important for invasive species control where population assessment is used to inform control actions (Nally 1997; Mehta et al. 2007). If data collected via sampling programs are the basis for control decisions, then the intensity at which sampling is conducted can influence the success of a management program. If sample data are used to target areas for a management action and too few samples are collected, the ability to differentiate between areas of high and low abundance may be reduced, causing some areas with high abundance to go undetected. Determining the appropriate sampling intensity is especially important when species distributions are patchy, zero catches are common, or the probability of missing high-abundance patches is high. Conversely, intensive sampling programs are costly, and there may be a point of diminishing returns, at which adding more samples will only lead to small increases in identification of areas of high abundance. Consideration of appropriate sampling intensities is also important when the resources allocated to sampling reduce resources available for the management actions they are intended to inform. The program to control Sea Lampreys *Petromyzon marinus* in the Laurentian Great Lakes is an example of a management program where sampling data are used to target actions to suppress this invasive species. The effectiveness of Sea Lamprey control actions are affected by both the influence of sampling intensity on accuracy and the opportunity costs associated with data collection.

The invasion of Sea Lampreys into the upper Laurentian Great Lakes (Lakes Superior, Huron, and Michigan) in the early 20th century has resulted in major ecological and economic impacts (Smith 1971; Christie and Goddard 2003; Lupi et al. 2003). A program of control was initiated in the late 1950s, and the success of that effort to reduce Sea Lampreys and the mortality they cause on salmonids has contributed to the valuable Great Lakes' sport fishery, worth over US\$7 × 10^9 to the regional U.S. economy each year (USFWS 2006; Southwick Associates 2008; Great Lakes Fishery Commission 2012). These large-scale efforts to control Sea Lampreys continue throughout the Great Lakes with an U.S. annual budget of over \$15 million (Hansen and Jones 2008b). The majority of these control efforts use chemicals that target the sedentary larval life stage in stream sediments. In most streams, the liquid lampricide TFM (3-trifluoromethyl-4-nitrophenol) is applied to entire stream flows to control the larval stage burrowed in the stream sediment (Christie and Goddard 2003). In lentic areas and large rivers TFM application is not feasible due to the large volume of water, greater depths, and cost associated with treatment, so spot treatments are carried out in areas of high larval density using a granular, bottom-release formulation of Bayluscide (2′,5-dichloro-4′-nitro-salicylanilide; Fodale et al. 2003).

The St. Marys River is one of the largest producers of Sea Lampreys to Lake Huron and northern Lake Michigan due to good spawning habitat and a large amount of high-quality larval habitat, making it an important system for larval control (Fodale et al. 2003; Schleen et al. 2003). Sea Lampreys produced in the St. Marys River were once so numerous that significant damage was effected on valued fish stocks in Lake Huron and Lake Michigan, impeding management objectives for those stocks (Morse et al. 2003). Sea Lamprey control efforts in the St. Marys River have a positive net value in terms of economic benefits to recreational angling in Lake Huron (Lupi et al. 2003), and continued suppression of the St. Marys River Sea Lamprey population remains critical to fish management and restoration (Bronte et al. 2003; Madenjian et al. 2003; Dobiesz et al. 2005).

The application of TFM is impractical for the St. Marys River because of its large size, so targeted application of Bayluscide in areas of high larval density is the only direct method of control (Schleen et al. 2003). Decisions of which and how many areas to treat with Bayluscide are made on an annual basis and are analogous to decisions about which and how many streams to treat with TFM (Hansen and Jones 2008a). Seventy-one areas (plots) of good larval habitat, and thus, high larval abundance, have been identified in river and are considered annually for Bayluscide application. In most years, the budget available for control is much less than would be needed to treat all plots in the river, so sampling data are used to decide which plots to treat. An annual deepwater electrofishing survey is conducted to estimate larval abundance in the plots (Fodale et al. 2003). These survey data are used to decide which plots to treat so as to maximize the number of larvae killed per hectare treated. The larval Sea Lamprey assessment program in the St. Marys River is costly, and resources allocated to sampling reduce the resources available for larval control.

Hansen and Jones (2008a) showed that reduced assessment in smaller lamprey-producing streams could lead to increases in the number of Sea Lampreys killed by reallocating resources from assessment to control efforts. A similar tradeoff between assessment and control resources might also exist in the St. Marys River. The likelihood of treating those plots with the highest larval density should increase as sampling intensity

increases, resulting in higher numbers of larvae killed per treated hectare. Given nearly perfect knowledge of larval density (i.e., very high sampling intensity), the expectation is that the cumulative number of larvae killed per treated hectare would increase rapidly at first and then level off as areas with lower larval densities were treated. However, catches of larval Sea Lampreys in the survey are highly variable because of their heterogeneous spatial distributions and the relatively small area covered by an individual deepwater electrofishing sampling event (2.44 m², Bergstedt and Genovese 1994). At low sampling intensities, estimates of larval abundance and selection of plots with the highest larval density would probably be very inaccurate, resulting in a suboptimal number of larvae killed per hectare. When the economic tradeoff between resource allocation to assessment and control is considered, there is likely to be a point of diminishing returns, above which more assessment data will not increase the number of larvae killed because of the loss of control resources, and this leads to an optimal level of sampling effort. This optimal level of sampling effort will probably vary with overall budget levels.

The continued suppression of the Sea Lamprey population in the Great Lakes is critical to achieving future fish management and restoration goals (Bronte et al. 2003; Madenjian et al. 2003; Dobiesz et al. 2005), and the success of the larval management program in the St. Marys River depends on the ability to successfully prioritize plots for treatment. Identifying sampling intensities that maximize the number of larval Sea Lampreys killed by the control program and explicitly incorporating economic tradeoffs between assessment and control should result in improved suppression of larval Sea Lampreys in the St. Marys River.

In this study, we examined the effect of sampling intensity on the efficiency of the Sea Lamprey management program in the St. Marys River by resampling independent, intensive deepwater electrofishing survey data to simulate the plot selection and treatment process and predict levels of Sea Lamprey suppression. We explicitly incorporated the tradeoff between the costs of assessment and control to maximize kill of larval Sea Lampreys in the St. Marys River. The specific objectives of this work were to (1) relate the efficiency of larvae killed (larvae killed per treated hectare) to varying levels of sampling intensity and examine the potential for increased sampling to improve the efficiency of the treatment program, and (2) to explicitly consider the tradeoff between resource allocation to assessment versus control efforts to identify sampling intensities that will maximize the number of larvae killed under different overall budgets.

METHODS

In the St. Marys River 71 treatment plots (830 ha total) ranging in size from 1.2 to 27.5 ha have been selected for the purposes of conducting the deepwater-electrofishing surveys

to assess larval Sea Lamprey density as related to applying Bayluscide for larval control (Figure 1). Bayluscide application occurs in late spring and early summer and is followed by annual posttreatment deepwater-electrofishing surveys that drive treatment decisions in the following year. Treatment plots ("in-plot") were defined based on areas observed with high larval density during 1993–1996 (Fodale et al. 2003). A large area of the river (6,980 ha) is characterized by low larval density ("out-of-plot"), which Bayluscide are not subjectdd to treatment does, but where electrofishing is conducted at a reduced intensity of 0.02 samples/ha (Robinson et al. 2013).

Field data.—The cost and time associated with intensively sampling all 71 plots in the St. Marys River was prohibitive, so we chose to represent the population based on a subsample of plots. In addition to the usual posttreatment survey of larval Sea Lampreys in the St. Marys River, several plots were selected to receive high-intensity pretreatment deepwater electrofishing surveys in 2010 (16 plots) and 2011(10 plots), based on the methods described in Bergstedt and Genovese (1994). Surveys were conducted at a much higher intensity that averaged 5.2 samples/ha, or 8 times that of normal sampling intensity (0.66 samples/ha in 2011). Sampling areas were randomly selected within each plot, and a range of historically high, medium, and low density plots were included to approximate the range of larval densities in the St. Marys River. Data from the 2010 and 2011 intensive surveys were combined to create a 26-plot pseudo-population, based on the assumption that the range of larval densities and plot sizes in the St. Marys River was represented in the 26 plots sampled (Table 1). The pseudo-population was contained in an area 31% of the size of the in-plot portion of the St. Marys River.

The larval capture efficiency of the deepwater electrofishing gear decreases as larval Sea Lamprey length increases (Bergstedt and Genovese 1994), so a length-based gear-selectivity correction was applied to all larval catch data:

$$C = \sum_i \left[1 + e^{(0.0229L_i - 1.732)} \right], \quad (1)$$

where C is the adjusted catch for an individual electrofishing sample, L is the length of a larva (mm), and i is an index for the individual Sea Lampreys captured and measured in the sample (Robinson et al. 2013). Selectivity-adjusted catch data from the intensive survey were used to calculate plot-level larval density estimates for the pseudo-population:

$$D_p = \frac{10,000}{n_p 2.44} \sum_{j=1}^{n_p} C_{j,p} \quad (2)$$

where D is the density (larvae/ha), n is the sample size in each p plot, 2.44 is the area of each sample (m²), and j is an index for each individual electrofishing sample in a plot. Plot-level
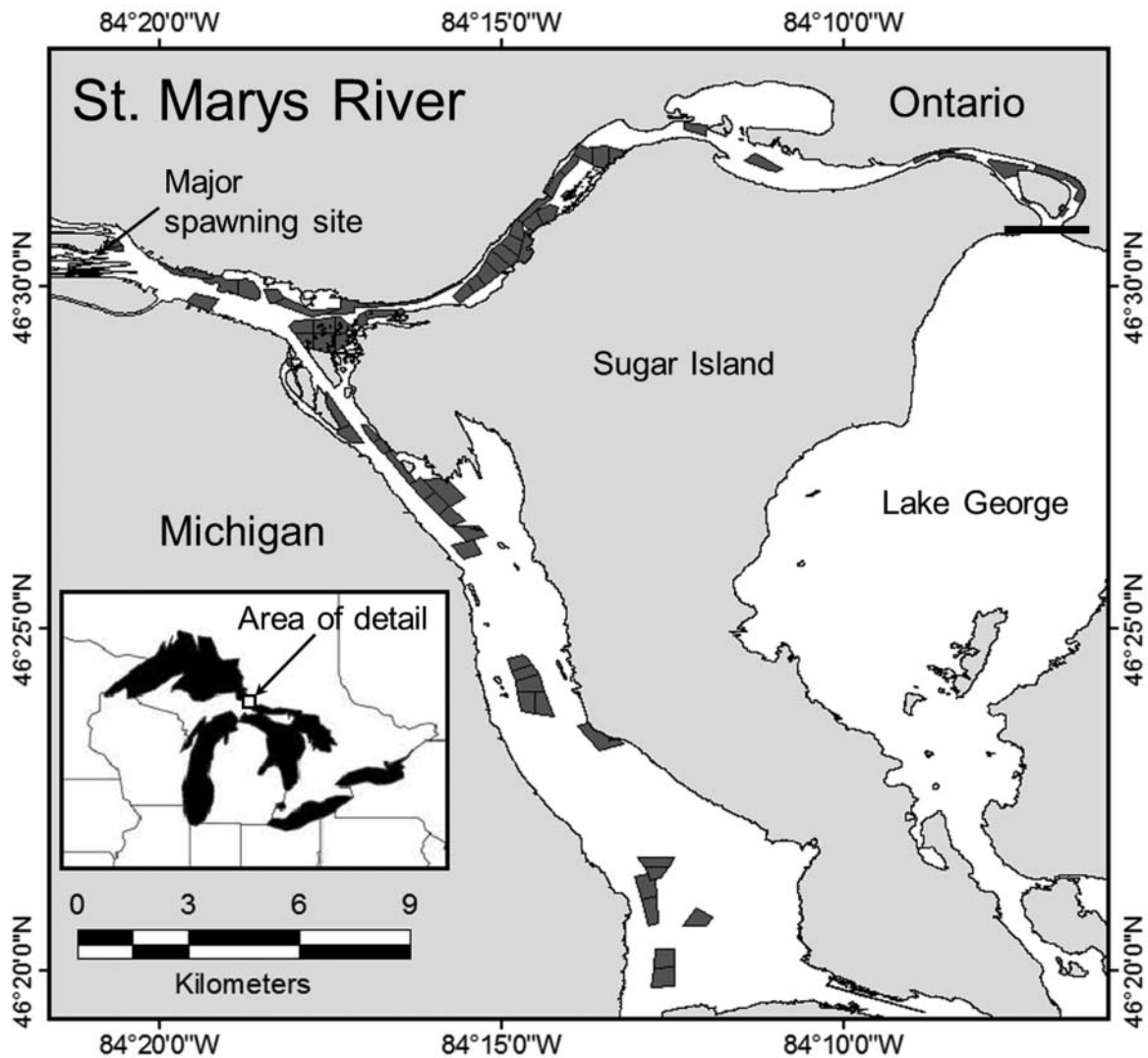
FIGURE 1. The St. Marys River from the navigational locks in Sault Ste. Marie, Michigan and Ontario, to the southern end of Sugar Island, showing all plots that are regularly assessed and considered for treatment (shaded gray areas) and out-of-plot area that are not treated (white areas). A small area that is surveyed but was not included in the figure is near the southern end of Sugar Island. The major spawning area (as designated) is located in the rapids north of the navigational locks. Inset shows location in the Great Lakes Region.

larval abundance was calculated by multiplying the density estimates by plot areas. The density and abundance estimates calculated using the field data from the intensive deepwater electrofishing survey were considered the most precise estimates of larval abundance in the St. Marys River available at that time.

Larvae killed relation.—A kill relation (larvae killed per treated hectare) was developed for the pseudo-population to represent the best possible treatment efficiency under the maximum available sampling intensity (i.e., the high-intensity sampling). This relation offered a best-case scenario to which kill relations derived from lower sampling intensities could be compared. To develop the kill relation based on the high-intensity sampling, plots were ranked in descending order

based on larval density estimates. Then a Bayluscide treatment was simulated by applying an estimated percent mortality of 51% for an individual treatment event (Robinson et al. 2013) to the estimated larval abundance for each plot, starting with the highest density plot. Treatment mortality was applied without error. Cumulative number of larvae killed and cumulative area treated were calculated following the application of treatment mortality to each additional plot.

Resampling.—Five deepwater electrofishing sampling intensities were simulated by resampling the selectivity-adjusted catch data from each plot in the pseudo-population 1,000 times for each sampling intensity. In-plot sampling intensity used during the 2011 annual deepwater electrofishing survey conducted by the Department of Fisheries and Oceans

TABLE 1. Larval Sea Lamprey and sample data for the St. Marys River plots sampled in 2010 and 2011.

Plot identity number	Plot area (ha)	Number of samples	Sample density (samples/ ha)	Larval density (larvae/ha)	Larval abundance per plot
2010					
1	2.2	32	14.4	1,211	2,684
3	3.3	12	3.6	18,702	61,510
5	6.2	50	8.1	2,518	15,558
16	1.2	9	7.3	2,111	2,591
18	11.7	59	5.0	447	5,227
20	13.0	56	4.3	10,961	142,356
24	17.9	46	2.6	1,140	20,393
30	7.1	44	6.2	4,189	29,757
31	3.5	27	7.8	0	0
40	15.2	59	3.9	419	6,360
172	6.1	35	5.7	1,556	9,567
363	11.9	60	5.0	2,101	25,042
365	13.8	57	4.1	807	11,153
422	15.7	60	3.8	279	4,383
532	8.7	50	5.7	557	4,868
4,001	13.7	60	4.4	4,206	57,765
2011					
1	2.2	15	6.8	4,727	10,473
3	3.3	21	6.4	3,469	11,408
20	13.0	47	3.6	523	6,789
21	8.7	44	5.0	880	7,679
22	15.6	47	3.0	657	10,212
111	17.0	49	2.9	1,925	32,704
112	17.0	50	2.9	2,322	39,382
152	13.1	49	3.7	379	4,960
153	10.4	40	3.8	561	5,858
154	6.8	40	5.9	665	4,510

Canada are indicative of the sampling intensity in recent years (0.66 samples/ha) and were used to inform the simulated sampling intensities. We simulated five sampling intensities at 25, 50, 100, 150, and 200% of the average 2011 sampling intensity (0.66 samples/ha), resulting in sampling intensities of 0.15, 0.33, 0.66, 0.99, and 1.32 samples/ha. All of the simulated sampling intensities were considerably lower than those used to develop the pseudo-population (Table 1). The number of samples collected from each plot was calculated for each level of sampling intensity by multiplying the plot area (ha) by the desired sampling intensity (samples/ha) and rounding to the nearest integer. The minimum number of samples that could be collected in each plot was set to 1, ensuring that each of the 26 representative plots received at least one sample at each sampling intensity.

Estimates of plot-level larval density were calculated for each simulated plot-level deepwater electrofishing survey,

providing 1,000 density estimates for each plot for each sampling intensity. The 26 plots were ranked in descending order based on density for each of the 1,000 simulated survey events. The kill relations (larvae killed per treated hectare) were then developed based on each simulated survey event and by applying Robinson et al.'s (2013) 51% treatment mortality to the abundance estimate for each plot calculated using all field data (Table 1). Cumulative larvae killed and cumulative area treated were then calculated following the simulated treatment of each additional plot. Kill relations were also developed for a "no information" scenario, which was designed to simulate the treatment of plots in the river with no sampling information. In this scenario, plots were randomly selected, and a simulated treatment event was applied. As with the other sampling intensities, this process was repeated 1,000 times.

Mean kill relations were characterized for each sampling intensity and for the no-information scenario using locally weighted regression scatter plot smoothing (loess curves; Neter et al. 1996). Loess curves were estimated with cumulative larvae killed in each plot as the dependent variable and cumulative area treated as the independent variable, resulting in 26,000 data points for each loess curve. The loess method is nonparametric and fits successive linear regression functions from predetermined data point neighborhoods into a single curved line. To prevent the loss of information, loess curves were fitted with relatively small neighborhoods (20% of data points per neighborhood).

Optimizing resource allocation.—We assumed that the overall budget for Sea Lamprey control in the St. Marys River was exclusive, such that resources spent on assessment reduced the funds available for control. The cost of collecting an electrofishing sample in the St. Marys River is US$ 80.11 per 2.44-m^2 sample, and the cost of treating one hectare of river bottom with Bayluscide is $4,395.50, which includes staff time, equipment costs, and the cost of Bayluscide (Mike Steeves, Great Lakes Fishery Commission, personal communication). These values were used to describe the effect of the tradeoff between assessment and control resources on numbers of Sea Lampreys killed under different budgets. We considered 11 realistic total annual control budgets for the St. Marys River ranging from $100,000 to $2,000,000. The $2 million budget would be enough to treat roughly half the plots in the St. Marys River if no resources were allocated to assessment. Because the area of the pseudo-population was 31% of total St. Marys River in-plot area, the total river budget levels corresponded to pseudo-population budget levels ranging from $ 31,000 to $622,000.

The cost of assessment for each sampling intensity was calculated by multiplying the cost of a single sample by the number of samples required to achieve the desired simulated sampling intensities for the 26 plot pseudo-population. The cost of collecting 50 additional samples (31% of the 5-year out-of-plot average sample size) was added to every assessment

budget to account for the out-of-plot sampling that occurs in the river each year. The out-of-plot sampling level did not change with the in-plot sampling intensities based on the assumption that the out-of-plot areas would continue to be sampled at their present intensity, regardless of in-plot assessment decisions. The area that could be treated under each budget was calculated by subtracting the sampling budget from the total budget and dividing by the cost to treat 1 ha.

The fitted loess curves for each sampling intensity were used to predict the mean number of larvae that would be killed as a result of treating a given area. Numbers of larvae killed in the pseudo-population were predicted for each sampling intensity, under each budget. We approximated a 90% confidence interval around the estimated number of larvae killed by calculating the 0.05 and 0.95 quantiles for the number of larvae killed for a given area treated (± 5 ha) from the resampling data. The 10-ha range was necessary to ensure that enough data points were available to properly calculate the quantiles. For example, if 100 ha were treated the quantiles were calculated based on the number of larvae killed from 95 to 105 ha treated. All data analyses were performed using the statistical software R (R Development Core Team 2012).

RESULTS

High-intensity pretreatment deepwater electrofishing surveys ranged in sampling intensity from 2.6 to 14.2 samples/ha (Table 1). Estimates of plot-level larval Sea Lamprey density (larvae/ha) ranged from 0 to18,700, and larval abundance estimates ranged from 0 to 142,000 (Table 1). The kill relation developed using the intensive field data predicted a rapid increase in the number of larvae killed as very high density plots are treated, followed by a gradual reduction in larvae killed per hectare as medium and low density plots are treated (Figure 2).

Intensive field-data curves of mean larvae killed per treated hectare for each simulated sampling intensity fell below the curve, indicating a less efficient treatment application in terms of larvae killed for each additional hectare treated (Figure 2). The distance between the curves based on the resampling data and the curves based on the intensive field data decreased as simulated sampling intensity increased, indicating increasing treatment efficiency with increasing sampling intensity. The curve for the no-information scenario was approximately linear and was the most inefficient. The greatest distance between the curves for low-intensity resampling and high-intensity field sampling occurred at medium levels of treatment effort (i.e., half of the area treated) and were smallest at the extremes of treatment effort (i.e., none or all of the area treated). As the maximum number of hectares treated is approached (i.e., the far right side of the Figure 2 curves) differences between the curves become negligible, except for the difference between some sampling and no sampling. Variability in the number of larvae predicted to be killed by a simulated treatment event
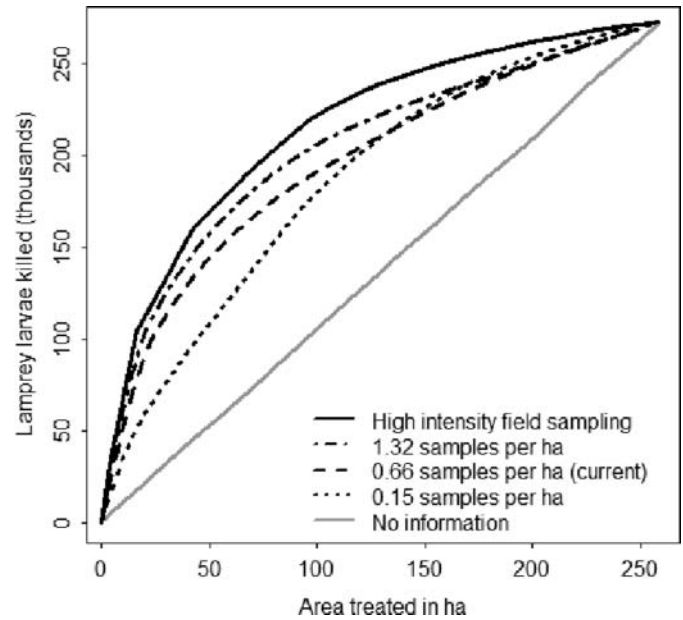

FIGURE 2.   Loess curves fitted to St. Marys River larval Sea Lampreys killed per treated hectare as derived from resampling data at three sampling intensities and under a no-information scenario. The solid black line is the kill relation (larvae killed/treated hectare) based on the high intensity field sampling and represents the most efficient kill relation. The 0.99 and 0.33 samples/ha loess curves were not included in the figure to prevent crowding.

increased as the sampling intensity decreased for the survey data upon which treatment decisions were based (Figure 3A–E). The no information scenario, in which plot-level treatment events were simulated in random order, produced the greatest variability (Figure 3F).

Explicitly including a budgetary tradeoff between assessment and control efforts changed the shape of the relation between number of larvae killed and the sampling intensity upon which treatment decisions were based (Figure 4A). As a result, the sampling intensity that maximized numbers of larvae killed changed as the overall budget changed. Larvae killed was never maximized under a no-information scenario (0 samples/ha), and the greatest change in the number of larvae killed occurred between the no-information scenario and the lowest sampling intensity scenario (0.15 samples/ha) at all budget levels. Under very small budgets ($0.1–0.2 million) larval kill was maximized from 0.15 to 0.66 samples/ha. As the overall budget increased, larval kill was maximized at the highest sampling intensity included in the analyses (1.32 samples/ha). However, the difference between larval kill at low verses high sampling intensities was relatively small, especially under the largest budgets. Differences between numbers of larvae killed for each incremental increase in the overall budget also decreased as the size of the budget increased. Uncertainty around the number of larvae killed decreases as the sampling intensity increased at all budget levels (Figure 4B). At medium and high budget levels, the minimum number of Sea Lamprey larvae expected to be killed increased
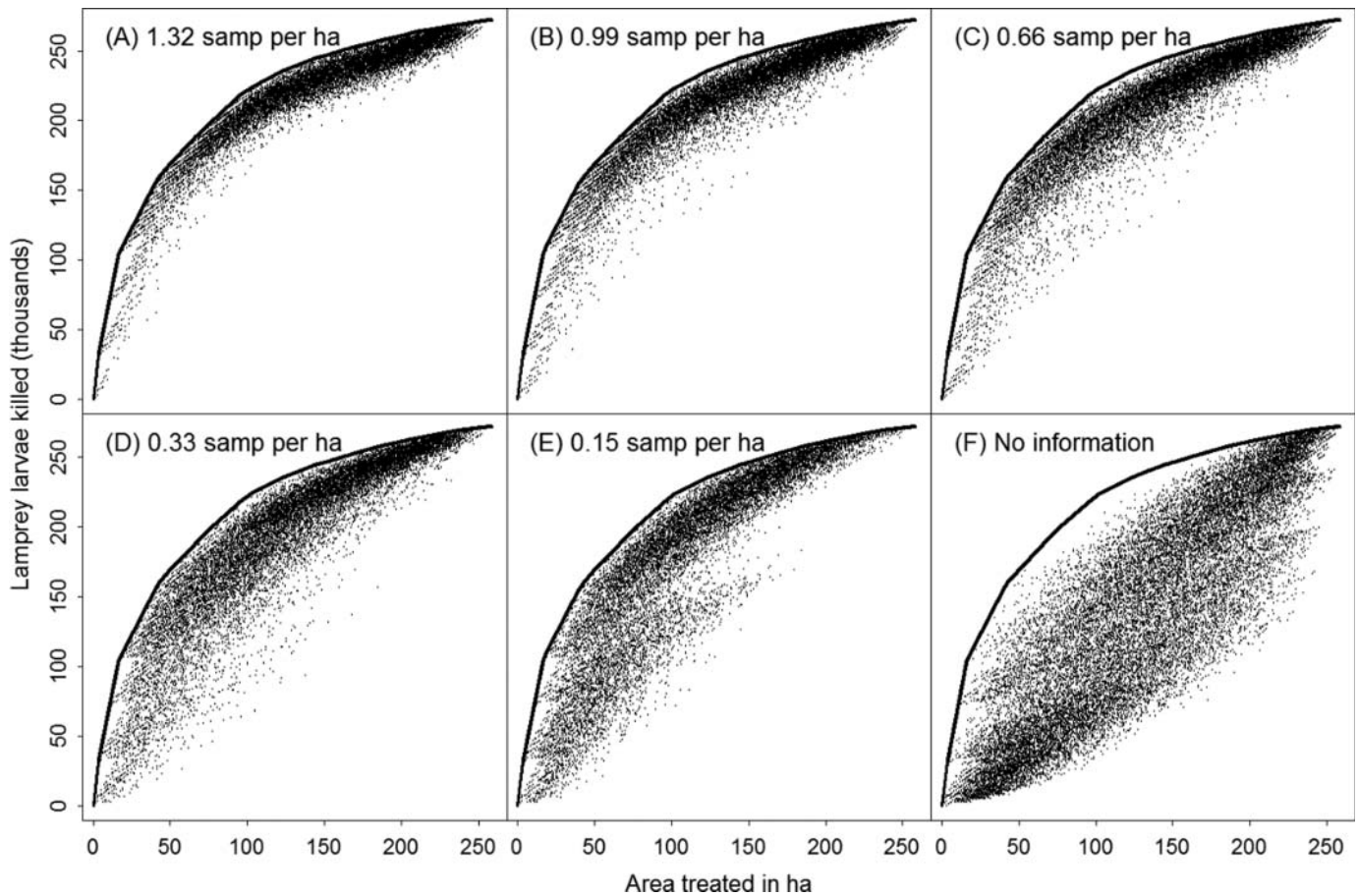
FIGURE 3. Estimates of Sea Lamprey larvae killed per treated hectare (black points) based on resampling of field data at five sampling intensities (**A–E**) and a no-information scenario (**F**). The solid black line is the kill relation (larvae killed/treated hectare) based on the high-intensity field sampling. The expected number of larvae killed is based on abundance estimates from the field data and the estimate of treatment effectiveness from Robinson et al. (2013).

with increasing sampling intensity. For example, at a budget of $0.4 million and a sampling intensity 0.15 samples/ha there was a 95% chance of killing at least 21,400 larvae compared with 66,600 at a sampling intensity of 1.32 samples/ha. At a budget of $1.8 million and a sampling intensity 0.15 samples/ha there was a 95% chance of killing at least 145,000 Sea Lamprey larvae compared with 205,000 Sea Lampreys at a sampling intensity of 1.32 samples/ha.

DISCUSSION

The tradeoff between resource allocation to data collection versus control actions has important implications for the effectiveness of management. Taking a simulation approach, we explicitly incorporated the economic tradeoff between assessment and control efforts to maximize the effectiveness of larval Sea Lamprey management in the St. Marys River, one of the most important and challenging areas for Sea Lamprey control in the Great Lakes. The sampling intensity that maximized the number of Sea Lampreys killed depended on the budget available, higher sampling effort being beneficial under

larger overall budgets. Additionally, simulated Sea Lamprey control actions based on sampling outperformed those that were implemented without sampling under all scenarios. Explicitly incorporating the economic tradeoff between resource allocation to assessment and control in the St. Marys River and elsewhere should result in more efficient and effective control of Sea Lampreys in the Great Lakes, given the limited resources available.

Although the resources available for assessment and control in the St. Marys River are linked, it is worthwhile to consider a scenario under which resources allocated to assessment are separate from control. When no tradeoff between assessment and control is incorporated, increasing assessment always leads to more effective control, but approaches a point of diminishing returns as sampling intensity becomes high. The benefit of increased sampling is additionally diminished at very high or low treatment levels (i.e., treatment of only a small area or treatment of the entire river). This occurs because the few areas of very high larval density can be identified with relatively low levels of sampling; therefore, a high sampling intensity is not necessary to effectively identify a
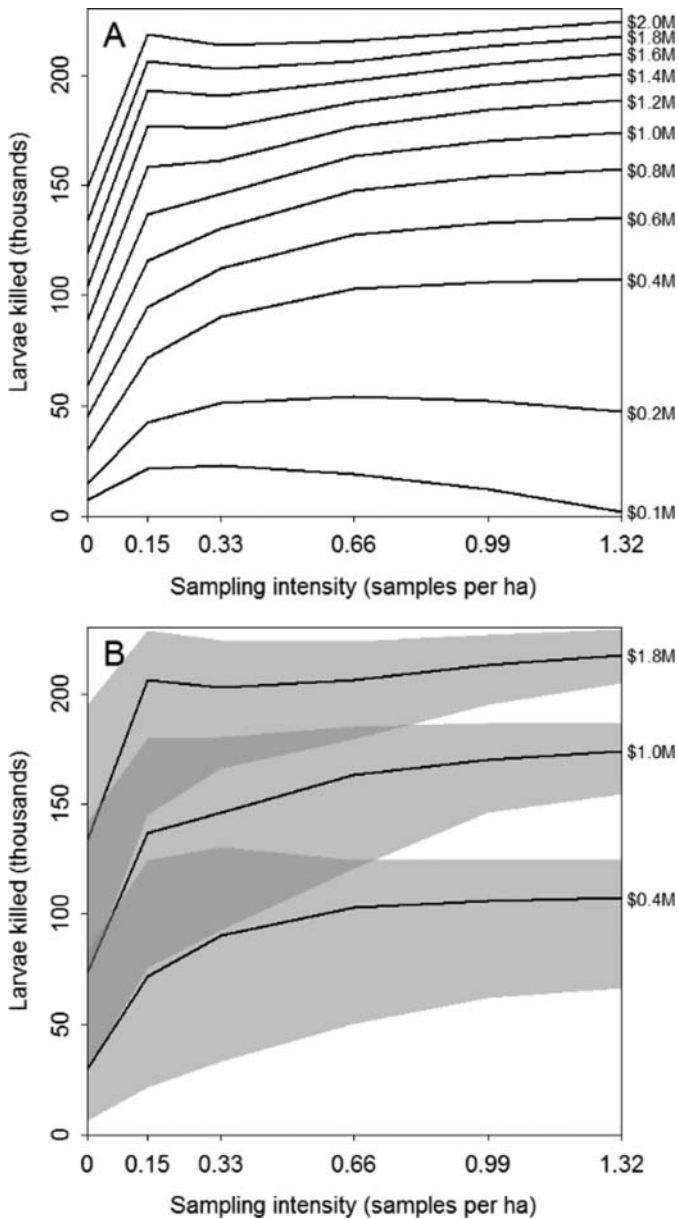
FIGURE 4. The relation between sampling intensity and Sea Lamprey larval kill at various budget levels: **(A)** 11 scenarios (M = million), and **(B)** subset of 3 scenarios. Estimated numbers of larvae killed apply only to the 26-plot pseudo-population at one point in time, but the budget levels are labeled at the scale of the St. Marys River. Each line represents a fixed budget for assessment and control; as assessment increases the area treated decreases. The grey shaded areas in panel B represent the range between the 5th and 95th percentiles.

few high-density plots. Conversely, if a very large portion of the river is to be treated, the number of larvae killed will necessarily be maximized, greatly reducing the benefits of high sampling intensity.

Explicitly including the economic tradeoff between resource allocation to assessment and control changes how sampling intensity impacts the success of the treatment

program. The effectiveness of treatment efforts does not necessarily increase with increased sampling intensity if the tradeoff is included. If the budget is small, low sampling intensity frees up resources for treatment while still allowing identification of high density plots. Under very large budgets low sampling intensity is also adequate because resources are available to treat nearly all plots, removing the need to differentiate between plots of high, medium, and low density. Increasing sampling intensity is most beneficial at intermediate budget levels, when differentiating between plots of medium and low density becomes necessary to avoid wasting treatment resources in areas containing few Sea Lamprey larvae. At higher budget levels the estimated number of larvae killed was similar for all nonzero sampling intensities. However, there is still a benefit to high sampling intensities under high budgets because the minimum number of larvae expected to be killed increases as sampling intensity increases. Regardless of the budget level, collecting some information rather than none resulted in greater numbers of larvae killed.

Maximizing the number of larval killed is the primary goal of the Sea Lamprey management program, but it is not the only benefit of the sampling program and is therefore not the only consideration when determining appropriate sampling intensity. Defining goals in terms of population thresholds and sampling at intensities that will allow detection of the desired changes is also an important consideration. Although a low level of sampling may maximize the number of larvae killed, it may also be important to accurately estimate the number of Sea Lampreys killed, as well as the current population level. Without this knowledge, it would be difficult to know when to suspend or scale back the control program in the St. Marys River and allocate resources to other areas in the Great Lakes that produce Sea Lampreys. The sampling program may also identify new areas of high larval density outside the current plots, or in-plot areas that have had historically low larval populations, resulting in changes in the plot structure. These issues represent opportunity costs that could result from inadequate sampling, but were not explicitly included in the analysis.

Our analyses have several potential sources of uncertainty that are important to consider. Ideally, the analyses would have included all of the treatment plots in the St. Marys River to ensure that the larval Sea Lamprey population was accurately characterized. However, the cost of sampling the entire population at a very high intensity was prohibitive, so we chose to represent the population based on a subsample of plots (pseudo-population). The most likely potential issue with using a subsample of plots is that the frequency of plots of high, medium, and low density in the pseudo-population may be different than the actual St. Marys River population. Plots of very low density are most likely underrepresented in the pseudo-population; Robinson et al. (2013) showed that there have been a high number of such plots in the St. Marys River in recent years. We compared the frequency distributions of the plot densities in the pseudo-population to that of Robinson

et al. (2013) and found them be very similar. However, under-representing low-density plots in the pseudo-population would result in underestimating the potential benefit of increasing sampling intensity at higher budget levels. Variability in the effectiveness of individual treatment events is also a source of uncertainty that was not accounted for in our analysis. Robinson et al. (2013) estimated a Bayluscide induced treatment mortality of 51% with a 90% credible interval of 0.37–0.64. As a result, the true variability around larval kill was underestimated.

We considered the tradeoff between assessment and control for a single year's treatment event, which reflects the current method of assessment and treatment. If the information gained in assessment can help inform decisions in future years, the value of assessment could be higher than presented in our analyses. Prior information could be used to inform the plot selection or assessment process, although prior information is currently only included qualitatively through selection of "expert judgment" plots for treatment in the Sea Lamprey management program in the St. Marys River. One potential method for including information from previous years is to include plots for treatment that have been identified as having very high larval densities in past years. However, our analysis indicates that low sampling intensities are successful in identifying plots with the highest densities, so this method is unlikely to significantly alter the relation between sampling intensity and the success of the control program. A model-based approach that incorporates previous years' data could also be used to identify plots for treatment. Robinson et al. (2014) found that averaging plot-level density estimates produced using a generalized linear model with those based on the survey data, would result in more effective plot selection than sampling alone.

The effect of sampling and assessment practices, and the tradeoff between resource allocation to assessment and control, have been considered in smaller Sea Lamprey-producing streams (Hansen and Jones 2008a; Hansen et al. 2003). Hansen et al. (2003) recommended that sampling in smaller lamprey-producing streams (i.e., TFM-treated streams) should be expanded to include suboptimal habitats and that reducing uncertainty surrounding stream-specific Sea Lamprey production could improve control efforts. In contrast, Hansen and Jones (2008a) showed that reducing effort allocation to assessment in smaller lamprey-producing streams would result in a reduction in the accuracy of population estimate but that the subsequent increase in resources available for stream treatment would result in more larval Sea Lampreys killed overall. Our results agree with those of Hansen and Jones (2008a) for small St. Marys River control budgets, but the benefit of reducing sampling intensity was not apparent as budget size increased.

Our work quantifies the tradeoff between assessment and control of an invasive species and supports previous theoretical and empirical evidence demonstrating the importance of including economic tradeoffs in invasive species management (Mehta et al. 2007; Hansen and Jones 2008b; Fenichel and Hansen 2010). Additionally, this study illustrates the potential for budget constraints to change the optimal assessment or sampling strategy. Explicitly incorporating tradeoffs between assessment and control into invasive species management will help to identify the optimal allocation of resources to achieve desired objectives. The general approach implemented here should be considered when making decisions about resource allocation to assessment and management actions. The patterns we observed probably apply to spatially targeted control efforts for other lamprey species and for other invasive or nuisance organisms, but the specific results are probably dependent on the distribution of density among treatment plots.

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