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Review

The evolution of sea lamprey control in the St. Marys River: 1997–2019

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A B S T R A C T

The St. Marys River was historically the single largest sea lamprey (*Petromyzon marinus*) producer in the Great Lakes. Rehabilitation of the once thriving Lake Huron fishery that had collapsed due to overfishing and habitat degradation was significantly inhibited by this uncontrolled source of sea lamprey. In 1997, the Great Lakes Fishery Commission implemented an integrated control strategy that incorporated lampricide control (granular Bayluscide spot treatments), sterile male release technique (SMRT), and enhanced trapping during the spawning migration. A decrease in the abundance of juvenile sea lamprey in the St. Marys River and a decline in lake trout wounding rates in Lake Huron following large-scale granular Bayluscide treatments in 1998, 1999, 2010 and 2011 indicated that lampricide control was most effective in controlling larval sea lamprey abundance in the river. The effects from the SMRT and adult trapping, however, could not be fully determined. Uncertainty in the efficacy of these alternative control techniques and in stock-recruitment relationships, ultimately led to the termination of the integrated control strategy. Since 2012, sea lamprey in the St. Marys River have been controlled exclusively with granular Bayluscide to treat areas with high densities of larvae. An adaptive management approach that considers the best available data has been incorporated to monitor and evaluate the effectiveness of ongoing control strategies. The evolution of sea lamprey control in the St. Marys River has resulted in a 90% reduction in sea lamprey from the river and contributed to recovery of the Lake Huron fish community.

Contents

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Introduction

The St. Marys River is a large international channel that originates in Whitefish Bay in eastern Lake Superior and then meanders for approximately 112 km before emptying into Lake Huron. The river is the largest tributary to Lake Huron with a mean annual discharge of approximately 2140 m^3/s that is closely regulated by the International Joint Commission (IJC) (Duffy et al., 1987; Morse et al., 2003; Ripley et al., 2011). The St. Marys River is a complex system with a set of rapids near the outflow from Lake Superior that eventually divides into a series of channels and embayments (e.g., Lake George, Munuscong Bay); this complexity gives rise to a multitude of habitat types that support a highly diverse fish community comprised of salmonines, coregonines, castastomids, percids, cyprinids, and burbot (Fielder et al., 2007). The rapids near the riverhead provide excellent spawning habitat for multiple fish species, including the invasive sea lamprey (*Petromyzon marinus*). Throughout the river, there are extensive areas with clay, silt, and sand substrate that provide exceptional nursery habitat for larval sea lamprey (Ripley et al., 2011).

Sea lamprey invaded the upper Great Lakes from the Atlantic Ocean in the mid-1930s (Smith and Tibbles, 1980). They were first detected in Lake Huron and Lake Superior in 1937 and 1938, respectively, and it is likely that they invaded the St. Marys River during this same time period (Kauss, 1991; Young et al., 1996). The first larval sea lamprey in the St. Marys River was captured in 1962 during dredging operations (Eshenroder et al., 1987). The distribution and survival of sea lamprey larvae in the St. Marys River initially may have been hindered by poor water quality, and spawning habitat was sparse or inaccessible as a result of navigational and hydroelectric projects. Enactment and enforcement of environmental regulations and intensive stream restoration efforts in the 1970s and 1980s, coupled with increased host abundance in Lake Huron, stemming from lake trout (*Salvelinus namaycush*) rehabilitation efforts and establishment of Pacific salmonid (*Oncorhynchus* spp.) populations to provide sportfishing opportunities and predatory control of invasive planktivorous fishes, enabled the St. Marys River to quickly become the largest source of sea lamprey in the Great Lakes (Ripley et al., 2011; Young et al., 1996).

Although the establishment of sea lamprey had negligible effect on the riverine fish community, the production of sea lamprey from the St. Marys River prevented rehabilitation of a once diverse and healthy fish community in Lake Huron that was decimated in response to habitat destruction and overfishing (Morse et al., 2003). Efforts to control sea lamprey in most infested Lake Huron tributaries was initiated by 1970; however, control efforts in the St. Marys River using the conventional treatment approach of applying the lampricide TFM (3-trifluoromethyl-4-nitrophenol) to kill sea lamprey larvae was precluded by the complexity of the system and high stream discharge (Eshenroder et al., 1987; Schleen et al., 2003). As a result, the river harbored an uncontrolled population of sea lamprey that soon became a detriment to salmonine management in both Lakes Huron and Michigan.

The high frequency of wounded lake trout in northern Lake Huron, near the outflow of the St. Marys River, compared to other regions of the Great Lakes was an assumed indicator of an untreated source of sea lamprey in the region. Sea lamprey reproduce in streams near the St. Marys River and in tributaries that flow directly into the St. Marys River; however, these sources were treated with TFM regularly and their contribution to the abundance of sea lamprey in Lake Huron was believed to be relatively insignificant (Table 1; Nowicki et al., 2021). Soon it became apparent that the high rate of sea lamprey induced mortality on lake trout observed in Lake Huron could be attributed to the sea lamprey population produced in the St. Marys River (Adams et al., 2003). In 1994 efforts to rehabilitate lake trout were discontinued in northern Lake Huron until a plan was established to effectively control sea lamprey in the St. Marys River (Morse et al., 2003).

The aim of this paper is to summarize the coordinated response by the Great Lakes Fishery Commission (GLFC) and its partners to develop and implement an integrated sea lamprey control strategy in response to the unchecked population of sea lamprey in the St. Marys River, and how this strategy evolved over time as additional information became available. In presenting this case study, we synthesize results from more than two decades of sea lamprey control effort in the St. Marys River and discuss achievements, failures, and limitations of the integrated control strategy implemented in the river from 1997 to 2011.

Table 1
Survey timing, when sea lamprey were last found (last positive), larval sea lamprey production, and treatment frequency and timing in tributaries to the St. Marys River. Median larval estimates are derived from Quantitative Assessment Surveys conducted in the U.S. and Canada from 1995 to 2014.

Stream	Last surveyed	Last positive	Median larval estimate	Mean treatment cycle (years)	Last treated
Waiska River	2019	2019	15,856	5.5	2016 (scheduled 2021)
Mission Creek	2016	2004	No recent recruitment	Never treated	Never treated
Frechette Creek	2016	1981	No recent recruitment	Never treated	Never treated
Ermatinger Creek	2016	2012	No recent recruitment	Never treated	Never treated
Charlotte River	2017	2017	1848	Irregular	2011
Little Munuscong River	2019	2019	46,473	4.2	2016
Munuscong River	2019	2019	44,260	3.8	2019 (scheduled 2021)
East Davignon Creek	2018	1972	Not available	Irregular	1972
West Davignon Creek	2018	2016	2274	4	2014
West Davignon Diversion Channel	2018	2015	Not available	Irregular	1989
Little Carp River	2017	2016	297	5.1	2016
Big Carp River	2017	2007	8349	4.6	2007
Whitefish Channel	2019	2019	15,333	4	2016 (scheduled 2020)
Root River	2017	2019	Not available	4	2016 (scheduled 2020)
Garden River	2015	2019	718,564	3	2020
Echo River	2017	2019	53,488	4	2015 (scheduled 2020)
Bar River	2017	2011	30,110	Irregular	2011

Response to the St. Marys River sea lamprey crisis

In 1991, the GLFC, upon recommendation by its advisory board, the Sea Lamprey Integration Committee (SLIC), responded to the sea lamprey crisis in Lake Huron by establishing the St. Marys River Control Task Force (SMRCTF), which was charged with developing a sea lamprey control strategy for the river (Schleen et al., 2003). The SMRCTF was comprised of sea lamprey experts from Fisheries and Oceans-Canada (DFO), U.S. Fish and Wildlife Service (USFWS), and U.S. Geological Survey (USGS), as well as fishery experts from the Lake Huron Committee (LHC), Lake Huron Technical Committee, and other external agencies and universities. In developing its strategy, the SMRCTF considered multiple control options, including the application of lampricides, low-head barriers, trapping, and the sterile-male release technique (SMRT). Control options were considered both independently and in combination with other options as part of an integrated strategy and were evaluated based on projected reductions of larval sea lamprey abundance in the river, reductions of parasitic juvenile sea lamprey in Lake Huron, estimated total cost, cost-effectiveness, and confidence in predicted outcomes (Schleen at al., 2003). Sea lamprey and lake trout models were used to predict the effects of the strategies on abundances of larval and parasitic juvenile sea lamprey and lake trout in Lake Huron (Schleen et al., 2003; Sitar et al., 1999).

In 1997, the GLFC approved a 5-year integrated control strategy that combined lampricide treatments using granular Bayluscide (5, 2′ –dichloro-4′-nitrosalicylanilide) to reduce abundance of larval sea lamprey in the St. Marys River prior to their metamorphosis into parasitic juveniles combined with trapping and the SMRT to reduce the effective number of spawning adults in the river. The envisioned strategy was that large-scale granular Bayluscide treatments of the St. Marys would occur in 1998 and 1999 after which control would focus on SMRT and trapping so that the effectiveness of these actions could be assessed independently and not confounded with the effects of lampricide treatment (Adams et al., 2003; Schleen et al., 2003). Construction of a low-head barrier to block sea lamprey access to spawning areas in the river was considered and initially seemed feasible, but ultimately was deemed too expensive and potentially detrimental to the migration and habitat of valuable fish species (Bray, 1993; Schleen et al., 2003). The integrated control strategy was to also include a comprehensive assessment plan that estimated the production of sea lamprey from the river, its predicted effects on the Lake Huron fishery, and an evaluation of the costs and benefits for potential control strategies (Adams et al., 2003; Schleen et al., 2003).

The integrated control strategy developed by the SMRCTF for the St. Marys River was projected to reduce larval abundance in the river by 97% and the abundance of parasitic juvenile sea lamprey in Lake Huron by 85%. The theoretical reduction would support the fish community objectives established by the LHC and align with milestones identified in the *Strategic Vision of the Great Lakes Fishery Commission for the Decade of the 1990s* (Great Lakes Fishery Commission 1992).

Fig. 1. St. Marys River. Larval sea lamprey distribution extends from Izaak Walton Bay (upstream of the navigation locks, at the south-eastern end of Lake Superior) downstream through the main channel to the south end of Neebish Island and through the west channel to the south end of Lake George. Infested (positive) tributaries are numbered to correspond with streams as ordered in Table 1.

Implementation of the integrated sea lamprey control strategy (1997–2001)

Larval assessment/Lampricide control

The integrated control strategy in the St. Marys River was initiated with an extensive assessment of larval sea lamprey populations in the river. Granular Bayluscide surveys conducted in the 1980s were used to generate an initial estimate of larval sea lamprey abundance in the river and define the geographic extent of the larval infestation. The total larval abundance estimated at that time was 6.8 million larvae, with the distribution of larvae extending approximately 70 km from the outlet of Izaak Walton Bay downstream to Munuscong Lake and through the North Channel to the south end of Lake George (Fig. 1; Fodale et al., 2003). In the early 1990s, as part of the larval assessment effort, sea lamprey control agents began using a Ponar dredge to classify benthic habitat in the St. Marys River as acceptable or unacceptable for larval sea lamprey (Mullett and Bergstedt, 2003; Slade et al., 2003). Concurrently, deep-water electrofishing (DWEF) methodology was developed and used to refine the infestation of larval sea lamprey in the St. Marys River, allowing for increased spatial coverage and more reliable quantitative estimates of larval abundance (Bergstedt and Genovese, 1994).

Between 1993 and 1996, larval sea lamprey assessment was considerably increased to further refine population estimates and larval distribution within the river. Density was assessed at nearly 12,000 georeferenced locations. A gear-correction was applied to the DWEF catch as it was found to be more selective for smaller sea lamprey. The gear-corrected catch was used to identify plots with the highest densities. Catches at each location were then incorporated with depth and habitat to map the distribution and produce estimates of larval abundance. Using this approach, the river-wide population during 1996 was estimated at 5.2 million larvae, with the highest densities located in the portion of river immediately downstream of the St. Marys River rapids (Fodale et al., 2003).

Polygons identifying areas for potential spot treatments with granular Bayluscide were delineated and the cost to treat each of the polygons was calculated. The most cost-effective treatment strategy was determined by weighing the cumulative number of larvae killed against treatment cost, then ranking individual polygons by the expected cost/kill ratio of larval sea lamprey. Small areas where the density estimates were driven by only a few larvae were excluded from the ranking process. Using this approach, an area of 880 ha targeting 76% of the larvae in the stream was recommended for treatment with granular Bayluscide (Fig. 2). Efficacy studies on test plots and previous treatments conducted with gran-

Fig. 2. St. Marys River larval assessment sampling area. Shaded polygons indicate high-density plots that are annually ranked for treatment with granular Bayluscide. Location of the nest study, trap sites, and sterile-male release site are also displayed.

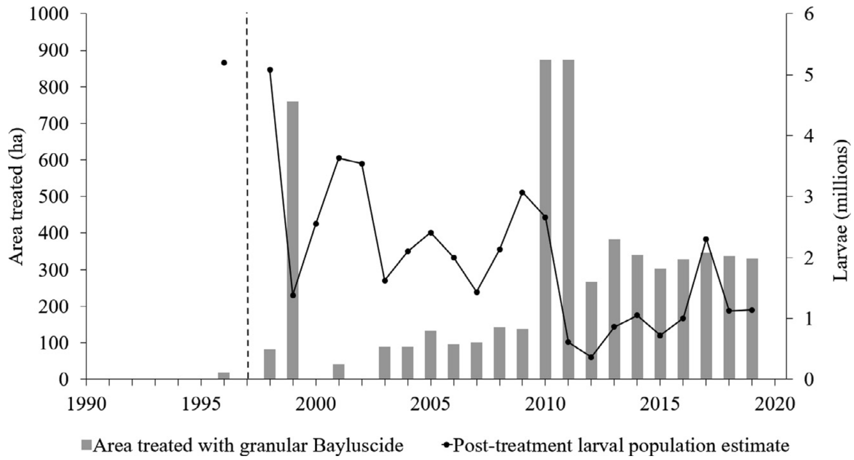

Fig. 3. Treatment effort (area treated) and St. Marys River larval sea lamprey population estimate. Pre-control abundance of sea lamprey larvae was estimated at 5.2 million. Vertical dashed line indicates implementation of the integrated control strategy.

ular Bayluscide in Seneca Lake, New York estimated the efficacy of granular Bayluscide at approximately 75% (Fodale et al., 2003). When this rate of efficacy was applied, the number of larvae predicted to be killed in the recommended treatment area was approximately 3 million. To incorporate other components of the integrated control strategy, it was decided that 42 ha of the delineated treatment plots initially would not be treated to serve as a control area for the SMRT (discussed below), reducing the predicted number of sea lamprey larvae killed to 2.6 million at an expected treatment cost of $4.1 million (Fodale et al., 2003).

The large-scale granular Bayluscide treatment of the St. Marys River was approved in 1997 and required support from multiple partner agencies. Funding for the treatment included federal appropriations from both U.S. and Canadian governments as well as a $3 million USD contribution from the State of Michigan. A pilot study was conducted in 1998 on 82 ha of the recommended treatment area to test procedures. The primary aerial granular Bayluscide treatment of 759 ha was conducted in 1999 by a contracted pesticide application firm and sea lamprey control agents from the DFO and USFWS. Staff from USGS and the Michigan Department of Natural Resources assisted with monitoring for mortality of non-target organisms, and the Chippewa Ottawa Resource Authority, an inter-tribal management program that coordinates fishery management issues for member tribes within 1836 Treaty boundaries of the Great Lakes, provided temporary storage for the substantial amounts of granular Bayluscide required for treatment.

The 1998 and 1999 treatment efforts were considered a collaborative success. Results from stratified-random sampling for sea lamprey larvae conducted pre- and post-treatment in 1998 and 1999 estimated that larval densities in the targeted plots were reduced by 76% and 88%, respectively. Granular Bayluscide treatments were not intended to continue past 1999 to allow for more rigorous evaluation of the SMRT and trapping as control actions. However, the 42 ha of larval habitat near the rapids, originally set aside to monitor the effects of the SMRT and trapping, was treated in 2001, as effects from the SMRT and trapping could not be measured with adequate statistical power and there was a lingering concern about increasing larval densities. Post-treatment sampling results indicated a total reduction in larval abundance from 5.2 to 1.4 million larvae over a 5-year period (Fig. 3). Additionally, although granular Bayluscide is less selective for sea lamprey than TFM, treatment effects on non-target organisms appeared minimal (Klar and Schleen, 1999; Schleen and Klar, 2000).

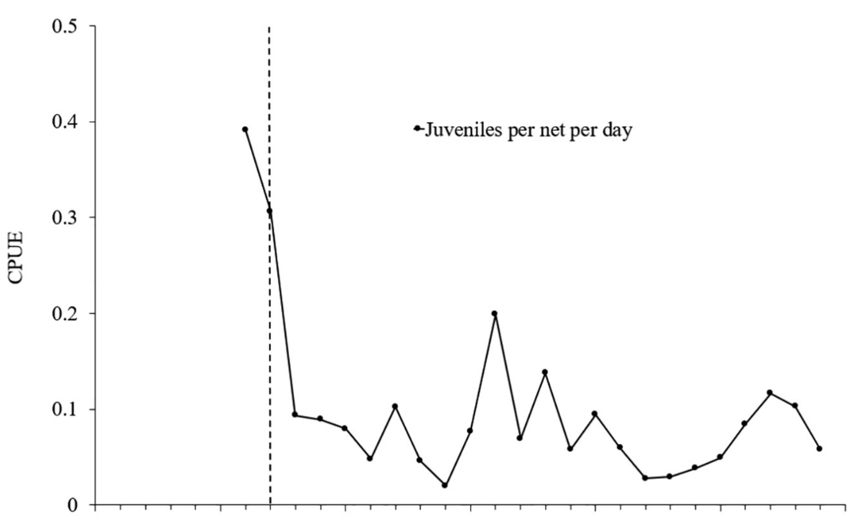

Fig. 4. Annual catch rate of out-migrating juvenile sea lamprey in the St. Marys River. Vertical dashed line indicates implementation of the integrated control strategy.

Juvenile assessment

An annual out-migrating juvenile index survey was initiated in the St. Marys River in 1996. Approximately one dozen nets were regularly fished from mid-October through the end of November annually. These 1.8-m x 1.2-m floating nets were attached to navigational buoys in the middle and east Neebish channels. Nets were checked for sea lamprey approximately three times per week. Catch per unit effort (CPUE) was relatively high at 0.39 and 0.31 out-migrating juveniles per net day during 1996 and 1997, respectively, but decreased substantially in subsequent years (Fig. 4).

Alternative control

Alternative control methods implemented to further suppress the larval sea lamprey population in the St. Marys River included enhanced trapping and implementation of the SMRT. Trapping adult sea lamprey in the St. Marys River was conducted annually during the spawning migration (late May to mid-July). Trap size and configuration varied among sites, but trap design and placement were generally similar. Traps were large enough to hold thousands of sea lamprey, but differed in volume (1 to 5 m^3), number of entrances (two or more), and size and shape of entrances (from 5-cm diameter circular to 10-cm × 200-cm rectangular entrances). Traps were initially located at the Clergue Generating Station in Canada and at the U.S. Army Corp of Engineers (USACE) hydroelectric facility (Fig. 2). The traps were either permanently attached to hydroelectric facility tailrace walls, or were portable and suspended in the water from chains or steel cables along the tailrace walls where flow was favorable (Schuldt and Heinrich, 1982). Traps were operated to exploit the tendency for sea lamprey to seek flow, either by deploying traps in areas of high flow or by pumping water into the holding chamber so that the water flowing through the trap opening acted as an attractant for sea lamprey (Bravener 2011).

Sea lamprey trapping was initiated in 1975, and the estimated abundance of adult sea lamprey migrating upstream ranged from 10,000 to 40,000 during the 1970s to 1990s (Mullett et al., 2003; Schleen et al., 2003). Improvements to trapping, along with the initiation of the SMRT program in 1991, appeared beneficial to reducing reproduction in the St. Marys River (Schleen et al., 2003). Trapping results (number captured and abundance estimate) were used in conjunction with the number of sterile males released for the SMRT to estimate the theoretical reduction in reproduction due to both trapping and the SMRT (Twohey et al., 2003). Since sea lamprey do not exhibit natal homing behavior, the abundance estimates were also used, along with estimates in other streams, for monitoring trends in sea lamprey abundance in Lake Huron (Adams et al., 2021).

Trapping efficiency, calculated as total catch divided by the abundance estimate, provides an indication of the annual removal rate and therefore the effectiveness of trapping as a control technique. Trapping efficiencies between 1987 and 1991 averaged 40%. The traps used at this time were simple, portable traps. In 1992 it was predicted that adding new and improved traps could increase the capture effectiveness to as much as 70% (Schleen et al., 2003). More traps were installed during 1994 to 1996 and several more design, structural, and operational modifications were incorporated from 1997 to 2001; however, despite these improvements, trapping efficiency remained close to 40% (Fig. 5).

Trapping in the St. Marys River was also conducted to supply male sea lamprey for control through the SMRT. The principle behind the SMRT is to release large numbers of reproductively sterile males into wild populations so that they compete with fertile males and reduce the effective spawning population of wild females (Knipling 1955). Research on the application of the SMRT in sea lamprey control began in the 1970s, was tested in Lake Superior tributaries and the St. Marys River from 1991 to 1996, and then fully implemented in the St. Marys River in 1997 (Twohey et al., 2003). The evaluation of the SMRT in the St. Marys River from 1991 to 1996 involved the release of between approximately 2700 and 7500 sterile males. Males used for the SMRT program on the St. Marys River were captured during their spawning migrations from 25 tributaries to Lakes Superior, Michigan, Huron, and Ontario. Sterile males were released from shore in Sault Ste. Marie, Michigan, approximately 5 km downstream of the St. Marys River rapids (Fig. 2), as the upper river was considered to be the primary spawning location (Bravener and Twohey, 2016).

Beginning in 1997, all available sterile males (17,000) were released into the St. Marys River, increasing the number that had been released into the river between 1991 and 1996 (mean = 4600 males). By 1999, the number of sterile males released annually reached 26,000 (Fig. 6; Bravener and Twohey, 2016). Estimated reduction in reproduction from the combination of trapping and the SMRT between 1997 and 2001 ranged from 80 to 92%; however, measuring the true effect of these alternative control methods was challenging (Bravener and Twohey, 2016). The SMRT was assessed using nine hypotheses that outlined key milestones

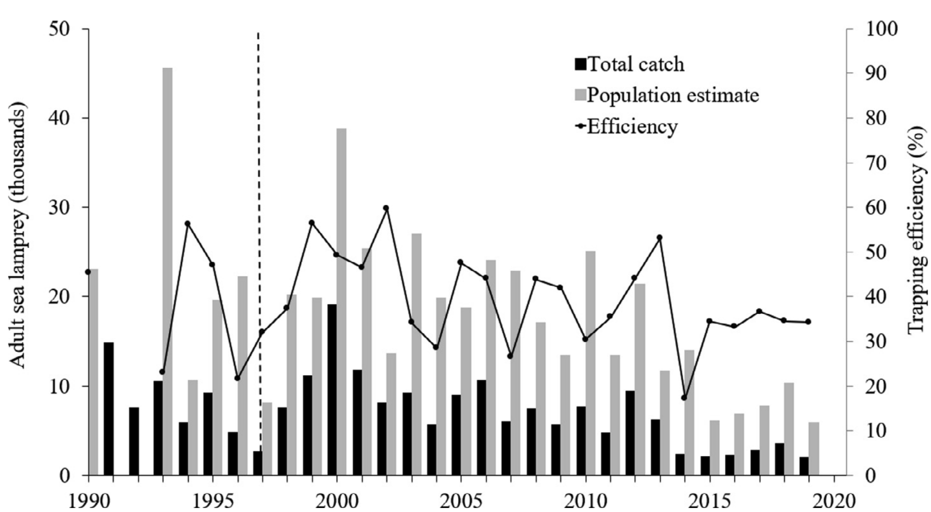

Fig. 5. St. Marys River adult sea lamprey trapping results (1985–2019). Vertical dashed line indicates implementation of the integrated control strategy.

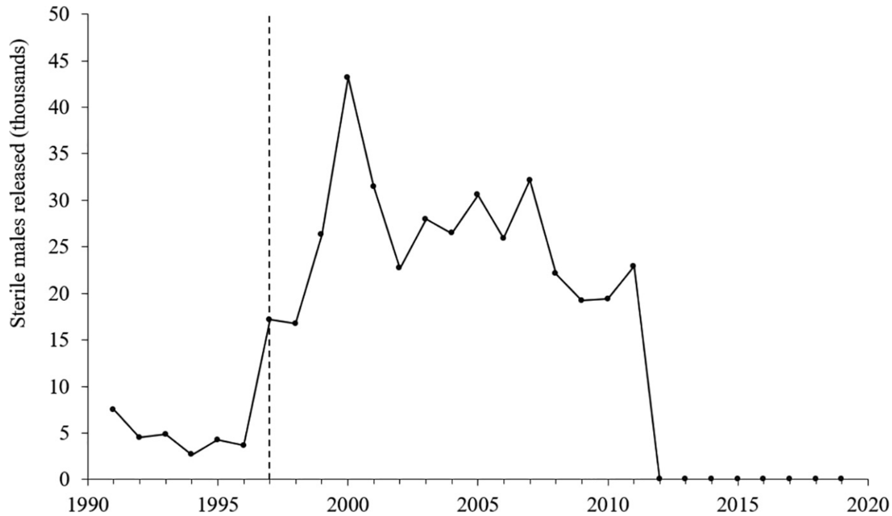

Fig. 6. Number of sterilized male sea lamprey released per year into the St. Marys River. Fewer sterile males were released into the St. Marys between 1991 and 1996 as part of an experiment in this river and select Lake Superior tributaries. When the integrated control strategy began in 1997, the Lake Superior experiment ended and all sterile males available were released into the St. Marys River (dashed vertical line). The SMRT portion of the integrated control strategy was discontinued after 2011 (solid vertical line).

that needed to be reached for it to successfully reduce damage to the fish community (Twohey et al., 2003). Surveys were conducted annually in the St. Marys River in July and August to determine sterile:fertile male ratios, and sea lamprey nests were sampled at the time of hatch to determine embryo viability, measured as the proportion of all embryos in the nest that were still alive (Bergstedt et al., 2003). The overall reduction in reproduction due to trapping and the SMRT combined was based on the reduction in effective females spawning. That metric was calculated using known values (sterile males released, males and females captured and removed), and estimated values (fertile males and females remaining in the system, based on population estimates and trapping efficiency). Reducing the number of effective females was assumed to reduce reproduction (number of larvae produced).

Evaluation of the St. Marys River integrated control strategy

The first 5-year phase of integrated sea lamprey control in the St. Marys River was completed in 2001. Each component of the control strategy was evaluated by the SLIC in 2002 when a decrease in the abundance of sea lamprey, and consequently a decrease in lake trout wounding in Lake Huron, should have been detectable. A summary of the evaluation and a recommendation for continued sea lamprey control in the St. Marys River beyond 2002 were presented at the GLFC interim meeting in December 2002. The comprehensive discussion focused on evaluating the assessment plan, a review of trap efficiency, the contribution of the SMRT, the effectiveness of granular Bayluscide treatments, and the results from integrated population assessment and simulation modeling efforts conducted by Haeseker et al. (2007), Haeseker et al. (2003). Cost effectiveness of each individual control option and how to incorporate sea lamprey control in the St. Marys River into the basin-wide treatment program were also considered.

Stratified random assessments conducted prior to and after the granular Bayluscide treatments conducted during 1998–2001 indicated an obvious and immediate reduction in larval abundance. Conversely, the direct effects of alternative controls on larval recruitment were difficult to evaluate due to variation in year-class abundance and confounding lampricide control actions. Other indices used to evaluate the effects of the integrated control strategy were also challenging to interpret due to lack of statistical power and variability in the data. For instance, although the number of sea lamprey trapped in the St. Marys River in 2002 suggested that the relative abundance of adult sea lamprey in the St. Marys River had decreased, this was not evident in estimates of abundance of sea lamprey in Lake Huron. While the abundance of sea lamprey in Lake Huron was somewhat lower than observed during the previous 20 years, it still remained higher than targets established by the LHC and specified in the fish community objectives for Lake Huron. Adams et al. (2003) discussed the statistical power and limitations of six indices used to determine the effects of the integrated control strategy on sea lamprey abundance and lake trout populations in northern Lake Huron: 1) abundance of adult sea lamprey estimated using mark-recapture methods; 2) relative abundance of parasitic juvenile sea lamprey using incidental catch in commercial nets; 3) annual mortality of lake trout; 4) abundance of adult sea lamprey in the St. Marys River; 5) age-specific relative return rates of lake trout; 6) sea lamprey wounding rates on lake trout. The results for all indices were consistent with the expected effect of the control strategy; however, with the exception of wounding on lake trout, several more years of data were necessary to have sufficient statistical power to evaluate the significance of sea lamprey control efforts on lake trout populations in Lake Huron (Adams et al., 2003).

Haeseker et al. (2003) constructed an age-structured integrated assessment model for sea lamprey in the St. Marys River that incorporated multiple data sources, including out-migrating juvenile CPUEs, adult abundance estimates for the St. Marys River, Lake Huron adult abundance estimates, and larval length composition in the St. Marys River. The aim of the modeling effort was to estimate abundance at age of sea lamprey and quantify the stock-recruitment relationship in the river as well as the effectiveness of the various control methods. Haeseker at al. (2007) incorporated estimates of the age-structured integrated assessment model in a decision analysis project designed to quantify the effects of different St. Marys River sea lamprey control strategies on the parasitic juvenile sea lamprey population in Lake Huron. To initiate the decision analysis project, Haeseker et al. (2007) organized a series of workshops involving sea lamprey and fishery managers, scientists, and stakeholders to identify management goals and objectives, alternative courses of management actions, and sources of major uncertainty. The results from these workshops were then incorporated in a simulation model to evaluate what management actions were most likely to achieve the identified management goals and objectives in light of the uncertain elements. Ten management options were explored that included various levels of trapping, SMRT, and granular Bayluscide treatments. Haeseker et al. (2007) concluded that management strategies that included enhanced levels of trapping (70%) and the SMRT (7:1 ratio of sterile to fertile males) in addition to granular Bayluscide treatments were most likely to achieve the stated management goals and objectives even when considering uncertainties associated with sea lamprey population dynamics, stock-recruitment relationships, implementation uncertainty, and effectiveness of treatment options.

Logistics to successfully implement the proposed management strategy were examined by multiple task forces including the SMRT Task Force (established 1984), the Pheromone and Trapping Task Force (established 2002), and the Large River and Connecting Channels Task Force (formerly the SMRCTF). By 2002, an adequate number of sterile males were released each year to significantly lower embryo viability and to theoretically create a 6.5:1 fertile male ratio, suggesting that the 7:1 ratio of sterile to fertile males could be achieved with minimal additional effort and would conceivably produce the desired effect (Bergstedt et al., 2003). Although average trapping efficiency was consistent at approximately 40% from 1997 to 2001, an increase to 58% in 2002 suggested that with further design modifications the goal of a 70% trapping efficiency might be attainable. Furthermore, preliminary results from telemetry studies conducted in 2001 and 2002 showed consistent patterns in sea lamprey movement in the St. Marys River, which could allow sea lamprey control agents to identify the most effective trapping location, improve trap construction, and re-evaluate trap placement (Schleen and Klar, 2002). Overall, the likelihood of achieving the enhanced level of alternative control was deemed promising. Consequently, the SLIC, with support from the various task forces, made the recommendation to continue the integrated control strategy (with enhanced levels of trapping and the SMRT) that based on the results of the Haeseker et al. (2007) decision analysis project, would provide the most cost-effective sea lamprey control in the St. Marys River and afford the best protection of the Lake Huron fish community.

Continuation of the St. Marys River integrated control strategy (2002–2011)

Larval assessment/Lampricide control

Although the larval sea lamprey abundance in the St. Marys River during the 2000s never rebounded to levels observed previously (Bergstedt and Twohey, 2007), abundance remained high enough that small (range 42–143 ha; mean 74 ha) granular Bayluscide treatments continued to be annually implemented as part of the integrated control strategy for the river. The annual treatments were a deviation from the original plan described in Schleen et al. (2003) that included only the initial granular Bayluscide treatment followed by annual trapping and the SMRT (Adams et al., 2003). The treatment plots continued to be selected using a stratified systematic sampling design where approximately 900 geo-referenced sites (1.44 m^2/drop, totaling approximately 2200 m^2) were sampled each year (Fig. 2). The strata included high-density areas considered for treatment as well as areas typically not considered for treatment due to low larval densities. Sampling intensity differed between the two strata; within treatment areas, one sample was collected every ha whereas in outside treatment areas one sample was collected every 9 ha. The extent of the sampling included the area just downstream of Whitefish Island, near the International Bridge, down to 46°26′N latitude, near 6 Mile Point. Adaptive sampling that required modification of sampling effort and intensity contingent on sea lamprey catch rates of any given sample was adopted in 2000 to better delineate the patchy distribution of sea lamprey larvae. However, to make planning, field collection, and data processing logistics more straightforward, this sampling methodology was discontinued in 2009.

Despite annual granular Bayluscide treatments and continued application of the SMRT and enhanced trapping, in 2009 larval sea lamprey abundance in the St. Marys River had increased to a level comparable to that observed prior to implementation of the integrated control strategy (Riley, 2013). Additionally, marking rates on lake whitefish (*Coregonus clupeaformis*) and cisco (*Coregonus artedi*) in northern Lake Huron increased, which elevated concerns about rising sea lamprey induced mortality on the Lake Huron fish community (Marsden and Siefkes, 2019; Nowicki et al., 2021). Consequently, a large-scale treatment strategy was implemented in tributaries to Lake Huron's North Channel in 2010 to reduce sea lamprey abundance in Lake Huron (Symbal et al., 2021). As part of this large-scale strategy, 900 ha of high-density larval habitat in the St. Marys River were treated in 2010 and 2011 (Fig. 3). Whereas large-scale treatments conducted in 1998 and 1999 involved aerial applications, the treatments in 2010 and 2011 (and beyond) were conducted using highly technical, GPS-enabled spray boats designed by Leistner Aquatic Services, Inc. The spray boat methodology mimicked commercial land-based agriculture pesticide applications and allowed for increased efficiency of application and more even lampricide coverage (Sullivan et al., 2021).

Alternative control

Juvenile sea lamprey abundance in the St. Marys River (Fig. 4) and lake trout wounding rates in Lake Huron began exhibiting a downward trend in 2002 and 2004, respectively. Additionally, natural reproduction of lake trout was documented in Lake Huron in 2005, and expectations were that with a continued aggressive level of integrated sea lamprey control in the St. Marys River, the population of naturally produced lake trout would continue to increase (Nowicki et al., 2021). The Reproduction Reduction Task Force (RRTF), a combination of the former SMRT and Pheromone and Trapping task forces, was established in 2003 and charged with improving and developing innovative alternative controls that would further suppress the St. Marys River sea lamprey population to a level that would continue to support lake trout rehabilitation in Lake Huron. Specifically, the RRTF was assigned to re-evaluate the role of trapping as an alternative control technique, review and improve the effectiveness of the SMRT, and to coordinate and facilitate research required to incorporate pheromone-based control methodology into the integrated control strategy.

In a persistent attempt to incorporate trapping as an effective control method and to achieve the longstanding goal of 70% trapping efficiency identified in the Haeseker et al. (2007) modeling analysis, efforts to increase trap efficiency in the St. Marys River were continued between 2002 and 2011. Structural changes were made including modification of traps to increase catch rates and ease of operation, and construction of new large permanent traps. For example, the northernmost permanent trap in the Clergue Generating Station tailrace (the north attractant water trap) was modified in 2006 so that a removable cage, containing sea lamprey that entered the trap, could be easily lifted and emptied. New traps were constructed at the Cloverland Electric Cooperative Hydroelectric Plant in 2006 and Clergue Generating Station in 2009. These locations were chosen based on observations of radio tagged sea lamprey during a radio telemetry study in 2000–2001 (Sea Lamprey Control Centre, unpublished data).

Operational changes included a) checking some of the traps at the Clergue Generating Station at night from 2005 to 2011 to minimize escapement from the traps, b) installing one-way swinging metal bars on portable trap entrances at the Clergue Generating Station in 2010 so that sea lamprey could enter but not escape, and c) in 2006, decreasing the number of sea lamprey marked and released for mark-recapture population estimates (from 10% daily to 5%) to reduce the amount of reproduction from adults that were not recaptured.

Hydroacoustic surveys, including those that incorporated video or dual-frequency identification sonar (McCann et al., 2018), and several additional radio, acoustic and PIT telemetry studies were also conducted to better understand adult sea lamprey behavior and movements relative to trap positioning (Barber et al., 2012; Bravener et al., 2013; Holbrook et al., 2016; Holub, 2019; Rous et al., 2017).

Sea lamprey control agents additionally began placing water level loggers near traps in the St. Marys River to evaluate the effects of water level on trapping efficiency. Once it was determined that water level was strongly correlated with trap efficiency, the RRTF began collaborating with the IJC, which regulates discharge in the St. Marys River, to investigate ways to manipulate flow during the sea lamprey trapping season. In 2010, the IJC incorporated flow manipulation for sea lamprey control into their revised water allocation plan. Results from field experiments conducted by control agents in subsequent years suggested that manipulating flow at the compensating gates significantly increased trap catch at several of the trapping locations. However, despite all of the efforts between 1992 and 2011, the overall average trap efficiency in the St. Marys River did not significantly increase (Fig. 5; Adair and Sullivan, 2012; Bravener and Twohey, 2016).

During this same time period, efforts were underway to improve effectiveness of the SMRT program. Bergstedt and Twohey (2007) recommended several modifications including new methods of sterilization, enhancement to the attractiveness of sterilized males, and identifying new sources of males to bolster the SMRT program. The efficacy of sterilizing females was also explored (Symbal et al., 2011). However, when the SLIC directed another review of the integrated control strategy in 2011 that included an examination of the effectiveness of the SMRT and the inclusion of more recent data in the decision analysis model, concerns were identified related to the uncertainty in the stock recruitment relationship and the ability to evaluate the effectiveness of the SMRT. Although the sterilization process was deemed effective, it appeared that the adult abundance in the St. Marys River was larger than previously estimated, and it was unlikely that enough sterile males could be released to significantly reduce recruitment (Holbrook et al., 2016). Because of compensation in the stock-recruitment relationship for St. Marys River sea lamprey, it was even possible that reduction in the effective number of spawning females could at least initially lead to higher larval abundances (Haeseker et al., 2003). Additionally, despite consistent sterile male releases between 2004 and 2011, embryo viability had increased (higher survival) during that time, becoming similar to what was believed to be the "baseline viability" before the SMRT was applied (Fig. 7). This observation suggested that the SMRT program was not adequately suppressing embryo survival. Based on these conclusions, the SMRT was no longer considered a cost-effective means of sea lamprey control in the St. Marys River, and the GLFC made the decision to remove it from the control strategy beginning in 2012. Funding was re-allocated to increase lampricide treatment on the river, with the predicted response being an immediate and continued reduction in larvae after 2011 (Bravener and Twohey, 2016).

The decision to discontinue the SMRT program in the St. Marys River was supported by updates to the Haeseker et al. (2007), Haeseker et al. (2003) integrated assessment and simulation modeling analyses conducted by Jones et al. (2015). The integrated assessment and simulations models used by Jones et al. (2015) were similar to those of Haeseker et al. (2007), Haeseker et al. (2003) although they incorporated additional data sources (e.g., larval abundance and age-composition post-Bayluscide treatment in some years), additional years of observations, and modifications to the population model to reflect improvements in understanding of sea lamprey demographics and assessment methods (e.g., incorporation of aging error, acknowledgement of uncertainty in adult trapping efficiency in the river) or enactment of integrated control policies (e.g., trapping, SMRT application). The modeling analyses conducted by Jones et al. (2015) found that while granular Bayluscide treatments remained critical for sea lamprey control in the St. Marys River, the effectiveness of trapping and the SMRT was min-

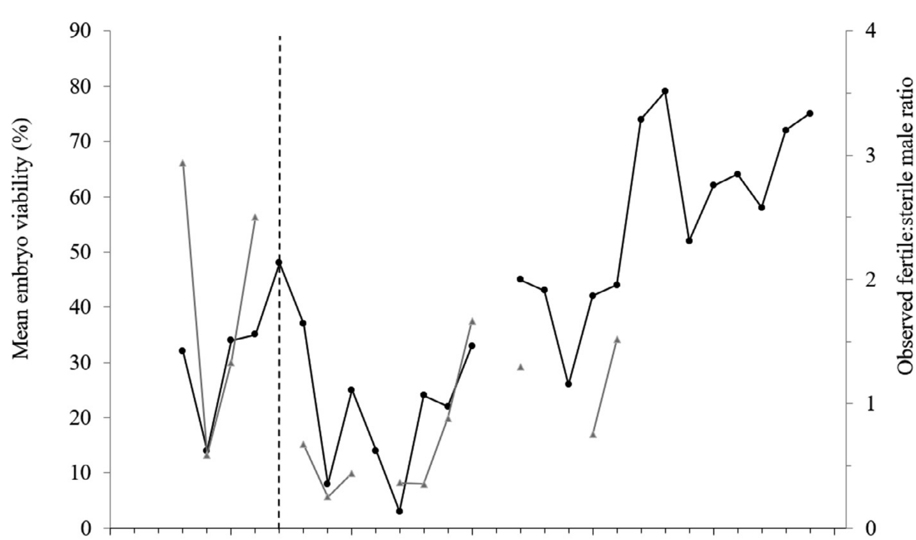

Fig. 7. St. Marys River mean embryo viability (black circles) and ratio of observed males in the rapids (gray triangles), 1993–2019. Line breaks indicate data were not obtained during at least one year. Sterile male releases occurred between 1991 and 2011. Integrated control strategy was implemented in 1997 (vertical dashed line) and was terminated after the 2011 trapping season (vertical solid line).

imized because of high recruitment compensation in the river. The finding by Jones et al. (2015) that alternative control policies like trapping and the SMRT did not necessarily improve sea lamprey control in the St. Marys River differed from the modeling results from Haeseker et al. (2007); this discrepancy was due in part to Jones et al. (2015) assuming a lower trapping efficiency and sterile:fertile male ratios than what was assumed by Haeseker et al. (2007), which reflected insight gained on sea lamprey trapping in the St. Marys River after the initial modeling work. Because of the high cost associated with granular Bayluscide treatments, Jones et al. (2015) recommended advancement of strategies to improve trapping success to increase the effectiveness of alternative methods of control.

Experimental evaluations of pheromone baiting showed promise for increasing trapping efficiencies and potentially disrupting spawning behavior of sea lamprey in the St. Marys River. Li et al. (2002) identified a male sex pheromone component, 7α,12α,24-tri hydroxy-3-one-5α-cholan-24-sulfate (3kPZS), which could be used to lure ovulated females upstream (Siefkes et al., 2005) and into traps (Johnson et al., 2009). Barrier-integrated traps were placed at terminal locations because sea lamprey congregate at dams or hydropower facilities where they may repeatedly encounter a trap (Bravener et al., 2013; Rous et al., 2017). During 2009–2011, 3kPZS was applied to traps located in eight U.S. tributaries to test whether the application of a pheromone component could increase sea lamprey trap catch (Johnson et al., 2013). In the St. Mary River, 3kPZS was applied to traps at the USACE Unit #10 hydropower plant during 2009–2010, but not 2011 due to river discharge allocation manipulations. While results indicated that trapping efficiency was significantly higher across all experimental streams during years when 3kPZS was applied, the mean percent change in trap efficiency in the St. Marys River was only 1%. Overall study results showed marginal increases in trap efficiency (0–30%) with the greatest increases occurring when applied to larger streams with few adult sea lamprey (Johnson et al., 2015a, 2015b).

Changes to the St. Marys River sea lamprey control strategy (2012-present)

With the discontinuation of the SMRT, the need for trapping was also lessened as one of the primary aims of trapping was to provide male sea lamprey for sterilization. Additionally, trapping alone was deemed unlikely to result in meaningful reductions in the abundance of adult sea lamprey in the St. Marys River. The decision to forego trapping as a standalone means for alternative control was also supported by the modeling results from Haeseker et al. (2007) and Jones (2015). Haeseker et al. (2007) explicitly suggested in cases where the effectiveness of control options designed to reduce the number of spawners was uncertain, it would be prudent to primarily focus on control options that targeted larval sea lamprey. Trapping of adult sea lamprey still occurred in the St. Marys River, although the primary purpose of trapping transitioned to continuation of the mark-recapture analysis in the river to provide a means for indexing sea lamprey abundance in Lake Huron. Although the mark-recapture analysis continued, in 2018 the analysis shifted from a Schaefer method to a simpler Petersen method (Adams et al., 2021). The pooled Petersen estimator performed better than the modified Schaefer estimator in terms of accuracy and precision with large sample sizes and was more accurate than the Schaefer estimator with small sample sizes (Harper et al., 2018; Lewandoski et al., 2020). Historical population estimates obtained from all index streams between 1980 and 2018 were updated accordingly (Adams et al., 2021).

The discontinuation of the SMRT and use of trapping as a means of reducing effective number of spawners in the St. Marys River meant that an integrated control strategy was no longer being pursued. Rather, since 2012, the strategy for controlling sea lamprey in the St. Marys River has been primarily focused on granular Bayluscide application to reduce larval abundance. Between 2012 and 2019, the total area treated with granular Bayluscide ranged from roughly 270 to 380 ha, although where the granular Bayluscide is applied in the river changes annually based on the size and location of the plots that rank for treatment.

The sampling design for estimating larval sea lamprey abundance in the St. Marys River and to rank plots for treatment has been consistent since 2009, although approximately every five years the sampling scope is expanded to include additional areas downstream to the north end of Munuscong Lake, an area of approximately 80 km^2. The expansion in sampling area provided a more complete river-wide population estimate and enabled detection of potential changes in low density areas. Furthermore, to ensure the most effective treatment strategy, since 2015 plots with high densities of larval sea lamprey have been re-ranked after a theoretical treatment with 75% efficacy is applied. If the cost:kill ratio of the re-ranked plots is lower than single-treatment plots, the high-density plots are re-treated to eliminate residual larvae. Since 2015, this process has resulted in 22 plots (245 ha) being treated twice in the same year.

After the transition from an integrated to a lampricide-based control strategy, the decision to treat approximately 300 ha of high-density larval habitat annually was based on modeling results. The same modeling framework used by Jones et al. (2015) was used to evaluate a range of granular Bayluscide treatment strategies, including six constant strategies (e.g., 100 ha/yr), seven intermittent strategies (e.g., 300 ha/yr for 3 yrs followed by 900 ha/yr for 2 yrs), and three feedback strategies (e.g., 300 ha/yr with back-to-back 900 ha/yr if age 1 + abundance > 1.0 million). Based on best understanding of the effectiveness of granular Bayluscide treatment and St. Marys River sea lamprey population dynamics, the results of the forecasting exercise suggested that application of granular Bayluscide to 300–400 ha of larval habitat each year was the most cost-effective treatment strategy for the St. Marys River. Higher treatment levels would increase cost, but not be expected to result in meaningful reductions in larval sea lamprey abundance because when treatment exceeds 400 ha the areas being treated had relatively low densities of sea lamprey (T. Brenden, unpublished data). These results also explain why it was found more cost-effective to treat 300 ha annually rather than 900 ha every 3 years.

The sea lamprey control program uses several indices, including those modeled by Adams et al. (2003), to measure success of the St. Marys River control strategy (Great Lakes Fishery Commission, 2019). Between 2015 and 2019, the average estimated abundance of adult sea lamprey returning to spawn in the St. Marys River was the lowest recorded since the modern mark-recapture methods began in 1985. Additionally, larval abundance and juvenile production from the river was significantly lower than before the integrated control strategy was initiated. Larval abundance during 2019 was about 1.1 million, which was slightly greater than the abundance estimated between 2010 and 2016, but overall low and stable. The lowest historical estimate of 360,000 sea lamprey larvae in the St. Marys River was observed in 2012 after the large-scale granular Bayluscide treatments occurred in 2010 and 2011 (Fig. 3). Given the proximity of the St. Marys River, trends in adult sea lamprey abundance and its effect on lake trout in both Lakes Huron and Michigan are used to measure the success of sea lamprey control efforts in the river. The mean of the most recent three years is used to determine status relative to targets. In Lake Michigan, both the adult sea lamprey index and marking rates on lake trout were below targets and at historic lows in 2019. In Lake Huron, both the adult sea lamprey index and marking rates on lake trout were slightly above targets and near historic lows in 2019. Lake trout abundance has been stable or increasing in Lakes Huron and Michigan, respectively (Steeves and Barber, 2020). Additionally, the index of abundance (CPUE) of incidentally captured juvenile sea lamprey from select northern Lake Huron commercial fisheries (Hume et al., 2021) was near historic lows between 2014 and 2017.

Summary and recommendations for 2020 and beyond

The development and implementation of an integrated pest management strategy to control sea lamprey in the St. Marys River formed the basis for rehabilitation of lake trout and other fish in Lakes Huron and Michigan (Schleen et al., 2003). However, in 2012, sea lamprey control in the St. Marys River transitioned from an integrated to a lampricide-based control strategy that is best described as an adaptive management approach. When it comes to pest management, not all control methods are practical, effective, economically feasible, or environmentally sound (Sawyer, 1980). Furthermore, in circumstances where an effective form of alternative control has not been identified or demonstrated, some invasive organisms can only be effectively controlled with pesticides. In the case of sea lamprey control in the St. Marys River, there was a considerable amount of uncertainty in the efficacy of the alternative control methods applied, and the immediate and obvious reduction in larval abundance as a result of lampricide control drove the decision to eliminate the SMRT and use trapping solely as an assessment tool.

Although lampricide control has proven to be the most effective method to control sea lamprey in the St. Marys River, the environmental fate of lampricides and their potential effects on non-target organisms is a growing area of concern, not only in the St. Marys River, but throughout the Great Lakes. Consequently, the need to develop alternative and/or supplemental control techniques remains a high priority for the GLFC (Siefkes et al., 2021). As an example, lake sturgeon *(Acipenser fulvescens)*, which are currently listed as threatened in Michigan and known to be sensitive to lampricides, have recently begun to recruit in the St. Marys River; non-chemical methods to control sea lamprey could provide protection of young-of year lake sturgeon and support the multi-agency effort to rehabilitate lake sturgeon in the system. There have also been recent concerns that sea lamprey in the Great Lakes region could be developing resistance to lampricides as a result of ongoing exposure through the control program (Dunlop et al., 2018). While development of lampricide resistance to TFM has not been conclusively demonstrated, and the risk of developing resistance to Bayluscide is reduced due to its less selective nature, the potential for resistance is nevertheless an issue of concern regarding the future of sea lamprey control in the St. Marys River and throughout the Great Lakes region.

Until feasible alternative control methods are developed, the lampricide-based control strategy currently applied to the St. Marys River should continue to evolve and incorporate the best information to guide management decisions. From a lampricide control perspective, the most appropriate treatment strategy continues to be explored using the previously discussed modeling framework and cost-benefit analysis developed by Jones et al. (2015). There remains a great deal of uncertainty as to the precise relationship between the total treatment area of the St. Marys River and the expected population-level mortality rate that will result from that amount of treatment. This relationship is a function of granular Bayluscide treatment effectiveness, how larvae are spatially distributed through the St. Marys River, and where granular Bayluscide is applied in the river. Because it is expected that modeling will continue to be used to inform treatment strategies for the St. Marys River, work is ongoing to enhance the assessment and forecasting models from Jones et al. (2015) to account for larval distributions in the St. Marys River and where granular Bayluscide has been and will be applied so that forecasted results are more accurate. Research confirming results from previous studies showing a 75% efficacy rate for granular Bayluscide would also be beneficial for the modeling efforts.

Recently, the Larval Assessment and Lampricide Control task forces have been charged with determining what metric might initiate a change in the amount of larval sea lamprey habitat recommended for treatment in the St. Marys River (i.e., increased larval populations in St. Marys River, adult sea lamprey abundance greater than target in Lake Huron, etc.). It will also be important to monitor habitat improvement projects for other fishes, such as the Little Rapids Restoration Project, and the removal of beneficial use impairments that have potential to increase availability of spawning habitat and survivability of sea lamprey in the St. Marys River (https://www.epa.gov/great-lakes-aocs/st-marys-river-aoc#stlouisbuis).

Despite the uncertainty of the alternative controls applied in the St. Marys River, the complexity of the system has provided a platform for continuous research into innovative pest management techniques. The SMRT program was more thoroughly reviewed by Bravener and Twohey (2016); they concluded that the method may have had some suppressive effect on embryo viabilities in the St. Marys River. The mean post-SMRT viability (67%) has been significantly higher than the mean during-SMRT viability (32%) (Fig. 7). However, the observed sterile:fertile male ratios were lower than expected, and the St. Marys River was not ideal given the relatively large fertile male abundance being targeted compared to number of males that could be sterilized and released each year. Recent evidence from a telemetry study confirmed that the adult sea lamprey population in the St. Marys River was likely greater than initially estimated (Holbrook et al., 2016), suggesting that the suppressive effect of the SMRT was likely lower than predicted. The effect of the SMRT on the larval population was difficult to measure due to the combination of techniques employed, the difficulty in assigning ages to captured larvae, and the large variation in the stock-recruitment relationship (Dawson and Jones, 2009; Jones et al., 2003). Despite this, implementation of the SMRT on the St. Marys River demonstrated that the methodology ostensibly has merit if applied in an appropriate system, most importantly a stream with low adult abundance so that high sterile:fertile male ratios can be achieved (Bravener and Twohey, 2016). The SMRT is currently being tested in such a system, the Cheboygan River in Lake Huron (Johnson et al., 2021)

Lessons learned from the continuous effort to improve trapping efficiency in the St. Marys River have been highly beneficial when considering trap design and deployment in other systems. For example, traps incorporating an eel ladder that were first deployed in the St. Marys River are now used effectively in the Cheboygan and Ocqueoc rivers. Telemetry and hydroacoustic studies conducted in the St. Marys River have provided valuable information about sea lamprey movement and spawning behavior that can be applied to other streams. Pheromone research continues to show promise for influencing sea lamprey behavior during migratory and mating periods if applied in the appropriate scenario.

Overall, the sea lamprey control program in the St. Marys River is considered a success and the reductions in the number of parasites produced from this system has contributed to the resurgence of lake trout in Lake Huron, including increased lake trout biomass, reductions in mortality rates, and increased proportion of fish of wild origin (Johnson et al., 2015a, 2015b). Determining precisely the extent that Lake Huron lake trout have benefitted from the success of sea lamprey control in the St. Marys River is challenging because concurrent to these successes there have been numerous other changes that have occurred in Lake Huron, including dramatic reductions in abundance of invasive planktivores (Riley et al., 2008) and overall decreases in lake productivity (Dunlop and Riley, 2013; Riley and Dunlop, 2016), which have also affected the lake trout population. Information learned from the St. Marys River control program is now proving useful in designing control strategies for the Huron-Erie Corridor, which has recently been determined to be a source of sea lamprey in Lake Erie and faces many of the same challenges (large, complex system with high discharge) that were encountered on the St. Marys River (Grunder et al., 2021). While not all control techniques proved useful in the St. Marys River for reducing sea lamprey abundance, the information learned has proven beneficial for considering how these techniques can be successfully implemented in other sea lamprey producing tributaries in the Great Lakes region.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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