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Review

Achieving Sea Lamprey Control in Lake Champlain

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Abstract: The control of parasitic sea lamprey in Lake Champlain has been a necessary component of its fishery restoration and recovery goals for 30 years. While adopting the approach of the larger and established sea lamprey control program of the Laurentian Great Lakes, local differences emerged that shifted management focus and effort as the program evolved. Increased investment in lamprey assessment and monitoring revealed under-estimations of population density and distribution in the basin, where insufficient control efforts went unnoticed. As control efforts improved in response to a better understanding of the population, the effects of lamprey on the fishery lessened. A long-term evaluation of fishery responses when lamprey control was started, interrupted, delayed, and enhanced provided evidence of a recurring relationship between the level of control effort applied and the measured suppression of the parasitic sea lamprey population. Changes in levels of control efforts over time showed repeatedly that measurable suppression of the parasitic population required effective control of 80% of the known larval population. Understanding the importance of assessment and monitoring and the relationship between control effort and population suppression has led to recognition that a comprehensive, not incremental, approach is needed to achieve effective control of sea lamprey in Lake Champlain.

Keywords: population suppression; lampricide; fishery restoration; sea lamprey; Lake Champlain

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1. Introduction

Sea lamprey (*Petromyzon marinus*) parasitism is a limiting factor to both the restoration [1] and recovery [2] of fish populations in Lake Champlain. The preferred host species of the lake include lake trout (*Salvelinus namaycush*), land-locked Atlantic salmon (*Salmo salar*), and lake sturgeon (*Acipensir fulvescens*). While sea lamprey do parasitize other species in the lake, the parasitic load on these species and the level of induced mortality place sea lamprey more in the role of a predator than parasite. The origin of sea lamprey in Lake Champlain has been the subject of debate. A series of genetic studies [3–5] concluded that they were endemic to the lake and likely remnants of the Champlain Sea, when the basin was contiguous with the Atlantic Ocean in following the last glacial event approximately 10,000 years ago. Eshenroder [6,7] challenged the assumptions of the genetics models using historical collections and canal construction timelines to propose that sea lamprey entered Lake Champlain through the New York State canal system when it joined the Hudson River to Lake Champlain through a series of connections during the end of the 19th century. Regardless of origin, Atlantic-native sea lamprey have proven to be a nuisance species in Lake Champlain and incompatible with its freshwater hosts.

Lake Champlain was historically home to lake trout and landlocked Atlantic salmon populations [8–10]. During 19th-century industrialization, the damming of tributaries and deforestation degraded riverine habitat [9]. This loss of habitat in concert with over-exploited fisheries led to the extirpation of native stocks of both species between approximately 1850 and 1900 [10]. A programmatic effort to restore these native species and introduce other salmonids began in 1973 with the formation of the Lake Champlain Fish and Wildlife Management Cooperative (Cooperative); the Cooperative comprises the

New York Department of Environmental Conservation, the Vermont Fish and Wildlife Department, and the U.S. Fish and Wildlife Service. In 1977, the Cooperative set goals to reestablish a lake trout and Atlantic salmon fishery and establish a rainbow trout (steelhead) fishery by 1985 [11]. As efforts to improve the fishery moved forward, parasitic sea lamprey populations surged. It became clear to the Cooperative that meeting fishery restoration and recovery goals would require efforts to suppress sea lamprey population.

In developing a program to control Lake Champlain sea lamprey, the Cooperative followed the existing Laurentian Great Lakes (Great Lakes) model [12,13] in establishing three fundamental management components. First, basin-wide assessments determine densities and distributions of larval sea lamprey and direct selection and implementation of control efforts. Second, as part of an integrated pest management approach, both chemical and physical control methods target larval and adult life history stages. Because the larvae of Lake Champlain consistently spend four years maturing in tributaries before emigrating to the lake as parasites, four year classes can be eliminated effectively once every four years using lampricides (selective piscicides) applied to tributaries and their associated deltas [14]. The active ingredient of the liquid and bar formulations of lampricide applied to rivers is 4-nitro-3-(trifluoromethyl)phenol (IUPAC nomenclature) and commonly referred to as TFM. The active ingredient of the lampricide applied to deltas in a granular formulation and occasionally applied to rivers in a liquid formulation as a synergist with TFM is 5-chloro-*N*-(2-chloro-4-nitrophenyl)-2-hydroxybenzamide (IUPAC nomenclature) and commonly referred to as niclosamide. All formulations of these lampricides are restricted-use pesticides and manufactured solely for application by designated federal and state government agencies. While manufacturers have refined product formulations at times, the two active ingredients used for controlling sea lamprey have remained the same for the entirety of the control program.

Second, physical control methods such as dams, temporary barriers, and screens serve to block and trap migrating adults before they reach habitat suitable for spawning [15–17]. The program benefits from dams on ten tributaries (labeled 1, 2, 4, 15, 16, 17, 19, 21, 24, 25; Figure 1) built for purposes other than lamprey control where they serve to limit the length of river accessible to adult sea lamprey migrating upstream to spawn. The program uses temporary, seasonally-installed barriers on seven tributaries that block adult sea lamprey during their spring spawning season (April–June), but are removed for the other nine months of the year (labeled 10, 11, 19, 20(2), 22, 26; Figure 1). These temporary barriers include traps which allow adult sea lamprey to be removed and killed and other aquatic species to be removed and passed above the barrier. The effectiveness of physical control methods in Lake Champlain varies from 100% with large hydropower dams to occasionally 0% with small temporary barriers subject to failure when overcome by high water events. When feasible, lampricides are a more effective, reliable, and consistent method of control. However, especially where lampricide use is restricted, physical control methods have a role in the program.

Third, we monitor and evaluate control efforts using a wounding rate index [18,19] to track changes in the frequency of lamprey parasitism on host species of interest. The wounding rate index is not a direct measure of parasitic lamprey abundance. Characteristics of host species and their population dynamics affect it in ways that are difficult to quantify [20,21]. Despite the limitations of the wounding rate index to provide direct point estimates of abundance, its consistent and standard usage over time [18,22] in Lake Champlain and the Great Lakes provides opportunities to compare general trends in the relationship between sea lamprey and host abundances.

The population dynamics of sea lamprey and the effort necessary to suppress their population has been studied and modeled by Great Lakes researchers to develop and refine their control program [23]. However, understanding the stock recruitment relationship of sea lamprey has proven challenging because of the uncertainty associated with density independent recruitment and compensation from density dependent survival [24–26]. Defining and establishing consistent or standardized levels of control effort required to achieve desired levels of lamprey population suppression have therefore also proven difficult. While long-term successful suppression of populations has been satisfactory for decades, Jones and Adams [27] propose that population eradication remains possible. We share these interests and seek to add experience from the Lake Champlain sea lamprey control program to further the understanding of how lamprey populations respond to increasing levels of control effort. The smaller scale of Lake Champlain and availability of a 30-year data set present an opportunity to consider these dynamics in ways that may lead to new insights as lamprey control efforts continue to evolve.

2. Management Phases

When the Cooperative evaluated progress toward its fishery restoration goals in 1985, approximately half of the lake trout and Atlantic salmon collected were found to be the target of sea lamprey parasitism as measured using the standardized wounding rate index [18,22]. Experience from the Great Lakes and Lake Champlain fishery data showed that efforts to restore these salmonid species would not be successful without suppression of the sea lamprey population. In 1990, the Cooperative began an 8-year experimental control program (ECP) under the guidance and in coordination with the Great Lakes program. At that time, assessments documented larval lamprey in 19 tributaries [28]. The ECP used lampricide to control populations in 13 tributaries (labeled 1, 4–8, 10, 13–15, 17, 22, 23; Figure 1) while trapping migrating adults on three others [29]. The ECP was designed as a pilot program to determine whether the model of sea lamprey control used in the Great Lakes could be applied to Lake Champlain to suppress the lamprey population. After eight years, the evaluation of both sea lamprey suppression and fishery responses led the Cooperative to pursue further and continuing sea lamprey control to support its fishery goals [29].

To transition from the ECP to a long-term control program (LTCP), a federal Environmental Impact Statement (EIS) was required. The process of writing and approval of this document took three years. Several groups opposed the use of lampricide and filed lawsuits challenging the EIS. The Cooperative ultimately received approval of the EIS in 2001 [30] and made plans to resume the control of sea lamprey in 2002 as the LTCP began. The period (1998–2001) between the ECP and LTCP has been termed the partial control program (PCP). During that time, lampricide treatments remained on schedule in New York where available state funds effectively extended the ECP there. Continued treatment of Vermont tributaries required federal funds that remained unavailable until approval of the EIS. During the PCP, the nine New York tributaries treated during the ECP remained controlled while of the four Vermont tributaries treated during the ECP, two were trapped (labeled 22, 23; Figure 1), and two were left uncontrolled (Table 1). At the time, the Cooperative believed that a reduction in control efforts during PCP would sustain some lesser level of population suppression, but would avoid surrendering all progress made during the ECP.

With the EIS in place to begin the LTCP, lampricide treatments resumed in Vermont in 2002 and continued in New York. Sea lamprey wounding rates of 25 per 100 lake trout and 15 per 100 Atlantic salmon were set as goals that the Cooperative believed could support fishery restoration goals [30] based on experience from the Great Lakes and the ECP [29]. Although the EIS enabled the LTCP to proceed, issues on individual rivers resulted in further permitting challenges. As the LTCP resumed in 2002, assessments documented larval lamprey populations in 20 tributaries in need of control [30]. Of those, nine were treated with lampricide and five were trapped (Table 1) [30]. As work progressed toward meeting the requirements for the inclusion of new and existing lamprey-producing tributaries, sea lamprey control efforts languished and wounding rates climbed higher until implementation of a more comprehensive approach. The LTCP authorized by the EIS [30] has continued to the present day. As the program progressed and incorporated experience to affect changes and improvements, the LTCP of 2020 has grown and now documents larval lamprey in 26 tributaries, controlled presently using 19 lampricide treatments and five barriers with traps.

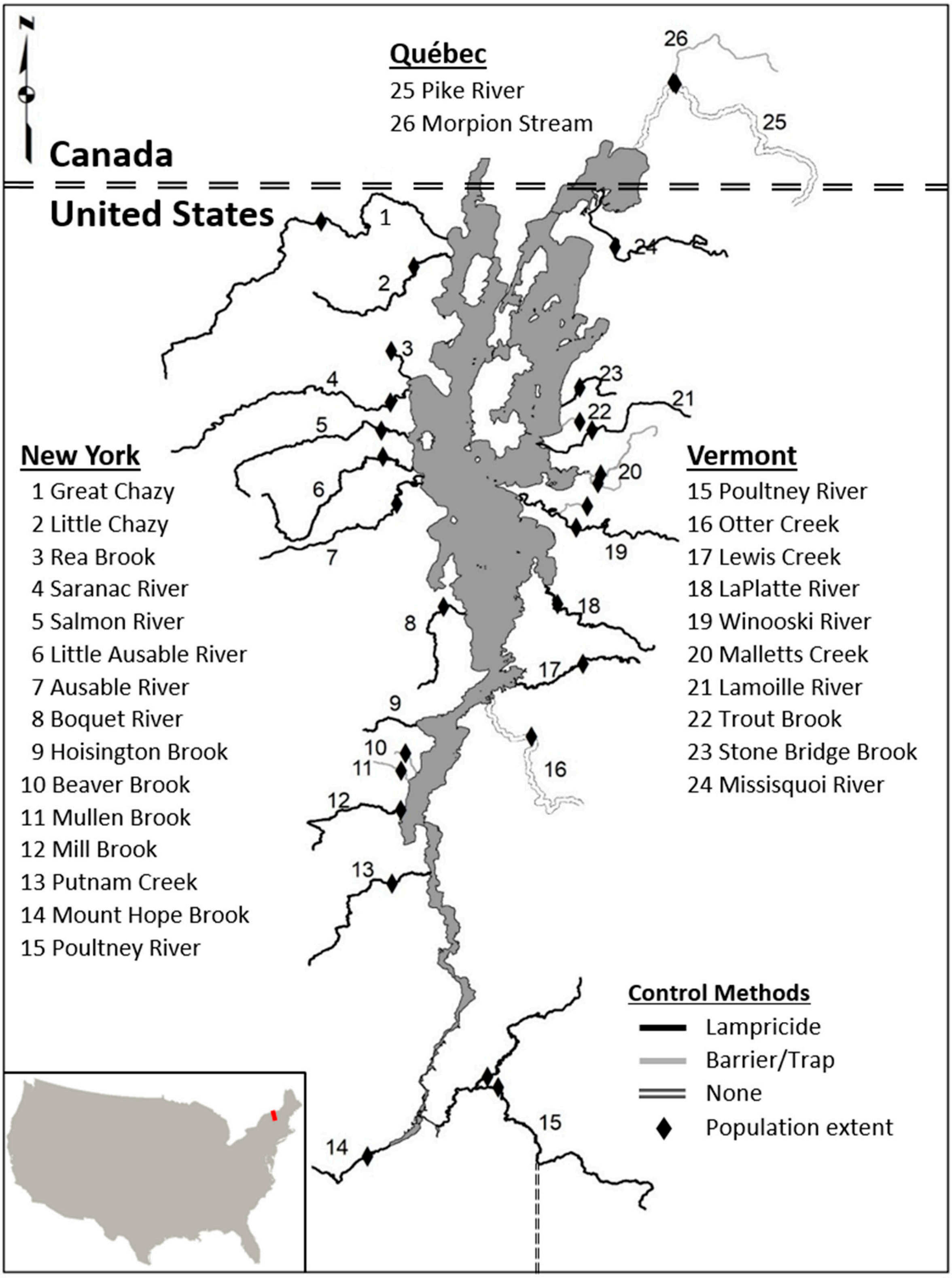

Figure 1. Lake Champlain and its 26 tributaries with currently known larval sea lamprey populations, controlled as indicated. The lake map represents the red-colored region on the inset United States map. Lamprey-producing subordinate tributaries controlled concurrently with mainstem tributaries are not included in counts.

Table 1. Historical levels of chemical (lampricide) and physical (barriers with traps) sea lamprey control efforts used on Lake Champlain. Lamprey-producing subordinate tributaries controlled concurrently with mainstem tributaries are not included in counts. ECP = experimental control program; PCP = partial control program; LTCP = long-term control program.

Year	Management Phase	Tributaries with Lamprey	Lampricide Control	Trapping Control	% of Tributaries Controlled
1992	ECP	19	13	3	84
2000	PCP	19	9	5	74
2002	LTCP	20	9	5	70
2009	LTCP	20	14	5	95
2020	LTCP	26	19	5	92

These three differing periods of Lake Champlain lamprey control unintentionally provided insight into the relationship between the lamprey population of Lake Champlain and the effort required to suppress it. Over 30 years, lamprey densities have fluctuated in individual tributaries, populations have expanded to new tributaries, control efforts have adjusted and sometimes been delayed, and technological advancements have enabled new and improved approaches to control. When viewing these programmatic adaptations over the long term, patterns emerged that lead to a better understanding of how to successfully control sea lamprey in Lake Champlain.

3. Management Review

The Lake Champlain lamprey control program presents opportunities for reviewing both short- and long-term population responses to control efforts. The lamprey control program set forth as a management initiative, not an ecological experiment [11,28,30]. Variables were not controlled, measures were coarse, and replication exists only in the form of a time series. Despite the inability to apply statistical models or tests, some general trends and patterns emerged over time that demonstrate relationships and emphasize aspects of the program in ways that will inform managers when making decisions in years to come.

By 2005, the Cooperative began questioning why the level of control effort was not showing the same type of anticipated response in lamprey reduction seen during the experimental program. With the implementation of the LTCP in 2002, fishery managers anticipated similar positive results based on the responses seen during the experimental program. The Cooperative distilled explanations for why wounding rates reached record highs in the period 2004–2006 into three general categories that led to further investigations into the need for: (1) control of additional known sources of larval production, (2) locating and controlling unknown sources of larval production, and (3) improved lampricide treatments that reduce the number of residual (surviving) larvae. While most agreed that the reason for rising wounding rates was some combination of these three, determining where to focus efforts required more data.

At the inception of the experimental program, it was logical and appropriate to believe that because Lake Champlain had a parasitic sea lamprey problem consistent with what the Great Lakes program manages, that if the Cooperative implemented the same control techniques and methodologies as the Great Lakes successfully employed, Lake Champlain would experience the same positive results. The immediate responses seen during the experimental program did appear to validate that approach as application of standard lamprey control techniques showed an expected reduction in sea lamprey wounds (Figure 2) [29]. As time passed, it became increasingly clear that while the general approach to sea lamprey control was capable of working in Lake Champlain as it does in the Great Lakes, there were nuanced differences that had not been recognized or accounted for and undermined existing assumptions.

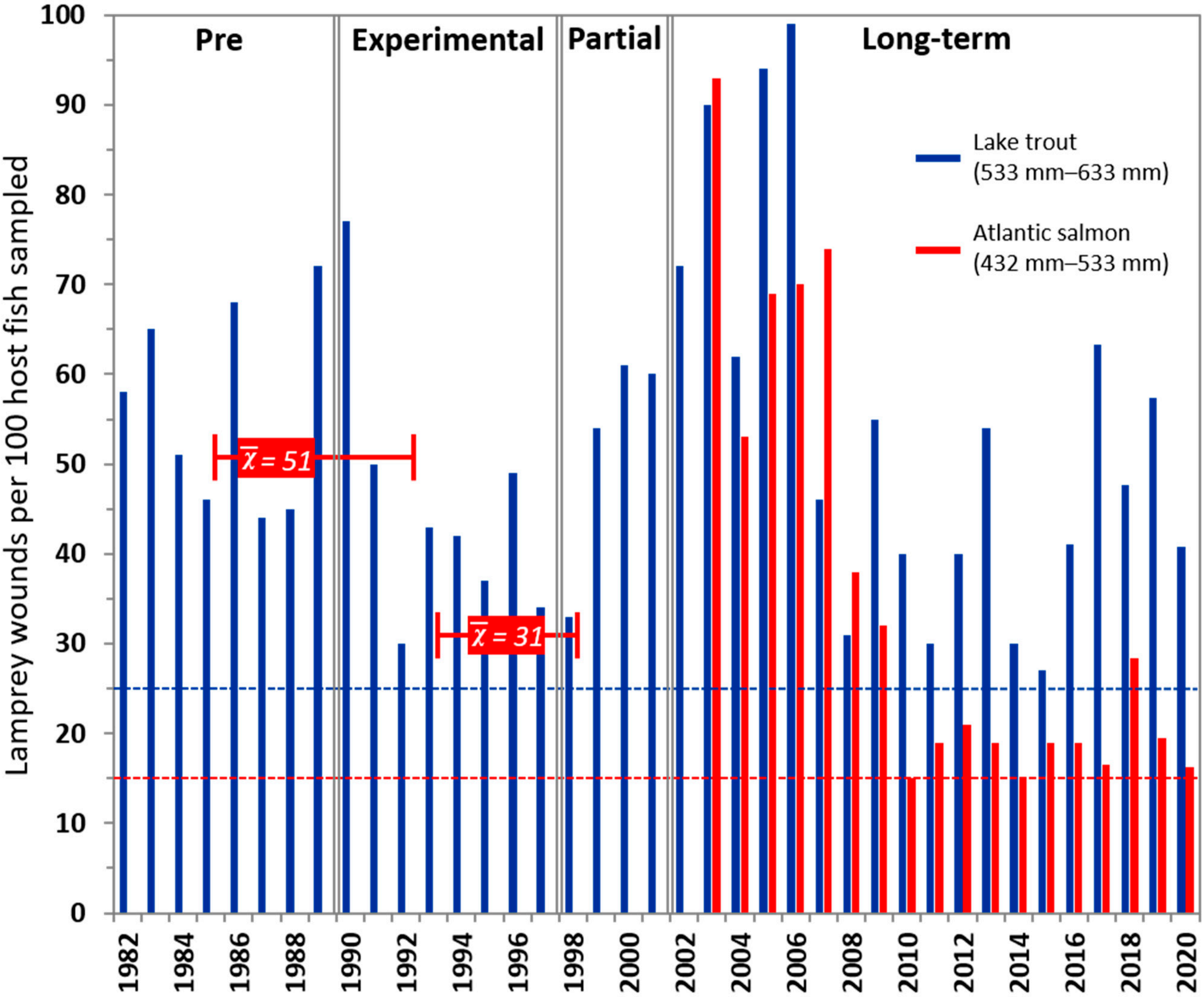

Figure 2. Sea lamprey wounding rates on lake trout and Atlantic salmon measured as number of wounds per 100 fish [18]. The vertical double lines separate the periods before lamprey control (Pre), the 8 year experimental control program (Experimental), the period of partial control (Partial), and the long-term control program (Long-term). Non-standardized collection effort among years for Atlantic salmon wounding data, prior to the Long-term program, led to grouping and averaging available data across the years 1985–1992 and 1993–1998 to approximate and reflect the time-lag responses to lamprey parasitism during the Pre and Experimental control periods, respectively. Horizontal dashed lines indicate the management goals for lake trout (25) and Atlantic salmon (15).

The three areas of concern shared a common need for more assessment and monitoring data. Enhancement of existing control actions was a simpler, more direct, a more convenient solution, and might ultimately prove necessary. However, such determinations required a more detailed understanding of the density and distribution of the larval population in the basin and site-specific measures of control efficacy. The Great Lakes program affirmed this need for enhanced assessment and its critical importance as they also placed attention on assessment in developing more effective control strategies [31,32]. Any broadly applied attempts focused on increasing existing control efforts were unlikely to address all remaining sources of lamprey production that contributed to the parasitic population. With increased attention paid, Lake Champlain assessment and monitoring developed into a more systematic approach, where quadrennial surveys provided comprehensive coverage of all tributaries in the basin for the detection of new and emerging larval populations. Implementation of standardized surveys that both preceded and followed every lampricide treatment became a permanent method for determining effectiveness. Regular surveys on tributaries with barriers and traps verified the effectiveness of the method used at each site. The data gained from these increased assessment and monitoring efforts provided new insights and helped to isolate the reasons that the LTCP was not matching the success of the ECP.

3.1. Discontinuity

3.1.1. Partial Control

During the four years of the PCP, lake trout wounding rates rose sharply from 33 in 1998 to 77 in 2002 (Figure 2). The Cooperative expected that a reduction in control effort during the PCP would result in higher wounding rates, but the resurgence of lamprey during this period to even higher wounding levels on lake trout than seen prior to the ECP was unexpected (Figure 2). A rebound effect appeared underway that partial control efforts failed to slow or lessen. While treatments continued on the nine New York tributaries treated during the ECP, the PCP did not include delta treatments previously associated with four of those tributaries during the ECP. We cannot quantify the contribution of those untreated deltas, but it amounted to further reduction in the cumulative control effort expended during the PCP. The four Vermont tributaries controlled during the ECP were not disproportionately large lamprey producers, based on larval population survey data. In fact, larval survey data indicate the nine treated New York tributaries accounted for more than a commensurate 69% of the total larval production among the 13 tributaries treated during the ECP. In light of the success of the recent ECP, expectations were that partial control efforts would produce partial population suppression and, at the very least, keep the lamprey population from returning to previous levels. Yet despite the treatments conducted in New York and attempts to trap two (labeled 22, 23; Figure 1) of the four Vermont tributaries treated during the ECP, the lake trout wounding rate incline that began during the PCP in 1998 continued to rise through the early years of the LTCP (Figure 2). The Cooperative did not track Atlantic salmon wounding data during the PCP, but once those measures resumed in 2003, they showed the same sharp increase in wounding rate as seen for lake trout (Figure 2).

3.1.2. Delayed Control

After the approval of the EIS, some local citizens continued to express concern and objection to the use of lampricide to control sea lamprey on the Poultney River (Figure 1). Through engaged conversation, the Cooperative chose to negotiate an agreement to delay chemical control for five years on that river. The agreement led to the creation of Federal Advisory Committee Act (FACA) group whose charter was to work toward alternative methods to control sea lamprey that circumvented the use of lampricides on the Poultney River. The 5 year delay ended in 2007 at which time no feasible alternatives had emerged that could effectively control the larval population estimated at over 163,000 in 2006. The wounding rates for both lake trout and Atlantic salmon in 2006 had reached a record high point (Figure 2) and led the Cooperative to proceed with application of lampricide to the Poultney in 2007. Following that treatment, wounding rates that had remained elevated even after the start of the long-term program in 2002, began to decline (Figure 2). The decline could not be attributed solely to the treatment of the Poultney River because other program improvements were also underway. The program treated the Winooski River with lampricide for the first time in 2004, making it the largest treated Vermont tributary at that time. The level of control effort applied across the basin was rising which included bringing the Poultney River back into the program. The end of the Poultney 5 year delay and other initiatives begun in 2006 marked a turning point, as seen in Figure 2.

3.2. Enhanced Assessment and Monitoring

From 1990 through 2005, we evaluated lampricide treatment effectiveness primarily by counting visible lamprey mortality the day following a treatment. Those observations provided evidence of dead lamprey that validated reasonable assumptions of treatment effectiveness. However, when wounding rates remained higher than expected and without a clear cause, we questioned whether qualitative observations of dead larvae following treatments missed quantitative measures of actual treatment effectiveness. To evaluate that, we added a new regular aspect to the assessment program in 2006. The summer following each fall lampricide treatment, assessment crews began performing post-treatment assessments for comparison to pre-treatment assessments.

Post-treatment surveys provided a new way to evaluate and understand the effectiveness of treatments. We found that measurements of treatment effectiveness based on the comparison of pre- and post-treatment assessments were a more nuanced and river-specific metric than previously understood. Perhaps the most surprising finding was that when we observed relatively large numbers of dead lamprey following some treatments, we occasionally found substantial numbers of larvae that simultaneously survived those same treatments. This led to further investigations and refinements in lampricide application approach and methodology.

When looking into the reasons that some treatments were highly successful and others were not, we discovered multiple factors that contributed to varying levels of larval lamprey survival during some treatments. We understood and addressed variables affecting dose, alkalinity, pH, seasonality, and stream-specific requirements based on toxicity testing. We were also aware of and accounted for variables affecting exposure, discharge, attenuation, dilution, channel morphology, and others. We found that the ineffective treatments were not the result of program-related miscalculations or technical errors. Instead, river-specific characteristics had been missed which required applying a more nuanced control approach to each river.

After evaluating all lampricide-controlled tributaries, post-treatment assessments revealed that most treatments had indeed been successful. However, some did show a consistent presence of residual larvae following treatments. The Ausable River and Putnam Creek (labeled 7, 13; Figure 1) provide two examples of how we identified and corrected ineffective treatments. The Ausable River has a mean annual discharge of 715 cubic feet per second (CFS), making it the second-largest New York tributary to Lake Champlain. Larval lamprey population estimates have averaged more than 600,000 over the past 15 years, not including its associated delta population, thereby ranking the Ausable as the largest producer of sea lamprey in Lake Champlain. Assuming that recruitment of larvae to the parasitic population of the lake is density independent [26] and similar to that of other tributaries in the basin, ineffective treatments there yield more considerably more net lamprey production than would ineffective treatments in smaller and lower populated tributaries. This recognition reemphasized that the importance and consequences of successful lampricide treatments increased as the size of the larval lamprey population increased.

We found that two factors in the Ausable were responsible for its insufficient treatment effectiveness. One was river morphology on the day of treatment. The Ausable splits into two mouths near its terminus. Large portions of the larval population reside in each mouth. Depending on the discharge of the river on the day of treatment, or changes in channel morphology from year to year, we found that disproportionate volumes of the mainstem followed one mouth or the other. Under ideal conditions, lampricide reaches both mouths in volumes proportional to their channel volumes. When conditions are not ideal, one mouth becomes a disproportionate route for lampricide-treated water traveling downstream and leads to sub-lethal lampricide exposure for the population of the mouth receiving lower flow.

To address this in the short term, selected portions of river that received sub-lethal doses during the 2006 and 2014 fall treatments received supplemental retreatments in the following springs (2007 and 2015). Increased secondary applications of backwaters and the addition of a supplemental downstream lampricide application point, contingent on discharge at the time of treatment, also improved delivery of lethal doses of lampricide to lamprey infested habitat. These additional steps used during lampricide applications are common, but the need to place additional application points along the river are usually obvious and arranged when first designing a treatment. The new development here was using the post-treatment assessment as a tool to identify a problem that was not otherwise recognized. For over a decade prior, presence of dead larvae following treatments served as sufficient indication of successful treatments of the Ausable. It was not until resolute post-assessment surveys identified the presence of residual survivors and their locations that we were able to isolate and address the issue. When first performed on the Ausable in 2011, that post-treatment assessment revealed the 2010 treatment had been 47% effective. Since that time, following improvements to application methodology, post-treatment assessments showed that the 2014 treatment and 2015 supplemental retreatment were cumulatively responsible for raising treatment effectiveness to 94%. The 2019 post-assessment survey of 2018 treatment found that it successfully eliminated 72% of the larval population.

Putnam Creek presented a much different set of circumstances. Despite being smaller with a mean annual discharge of 80 CFS, the abundant preferred habitat of this tributary provides conditions that support a larval population consistently estimated at over 150,000 during the last 15 years. Treatment monitoring data consistently showed that lampricide concentration and other water chemistry parameters fell within the bounds of successful treatments. However, once we started post-assessment surveys, we discovered despite seeing numerous dead larvae following treatments, there were often still large numbers of residual larvae the following year. Because larvae distribute themselves and drift over time [33], identifying any specific point sources leading to treatment survival proved difficult. Following several investigations, we discovered groundwater influence was the likely source of residual larvae in Putnam Creek. A portion of the river is in an area where groundwater routinely seeps from the banks. Through an additional series of spatial measurements in the channel using a temperature probe, we found a groundwater sublayer present within the channel sediment as well. Though this groundwater was not a substantial contributor to the overall discharge of Putnam Creek and did not affect measured treatment concentrations, we believe it provided microrefugia to sediment-dwelling larval lamprey. Fresh water recharge from below the sediment water interface countered the lethal treatment concentration present above that interface during treatments resulting in a net sub-lethal and survivable exposure in that section of the tributary. We have not yet developed a way to fully negate groundwater influence that leads to treatment residuals, but detecting its presence and extent have allowed treatments to be fine-tuned to better address the specific areas now presumed to provide lamprey with refuge during treatments.

Before post-treatment assessments began in 2006, numerous dead lamprey led managers to believe treatments were successful. The examples in the Ausable River and Putnam Creek show how that assumption led to incorrect expectations that control effort equated to control effectiveness. Until we quantified and monitored control effectiveness with additional assessment effort, remaining sources of production like these two tributaries went unnoticed. There are additional tributaries in the basin found to need river-specific adjustments to treatment strategy as well. The importance of post-treatment assessments and the way they inform control effectiveness has led us to make them a standard part of the control program.

3.3. Aggressive Programmatic Expansion

As post-treatment assessments revealed sources of residual larval lamprey production in need of additional attention, the Cooperative sought to eliminate lamprey populations in additional tributaries where assessments had detected their presence. The EIS from 2001 had prescribed plans for how and where to control the population as part of the LTCP. Unfortunately, it did not include provisions for the addition of newly colonized tributaries in the future. As efforts continued to control all known sources of production, the detection of new larval populations led to the need for a federal Environmental Assessment (EA) in 2008 to authorize the inclusion of the Lamoille River and Pond Brook in Vermont and Mill Brook in New York into the LTCP [34]. Continued annual larval assessments later found new populations of lamprey in the Little Chazy River and Rea Brook in New York (Figure 1). To keep pace with larval lamprey colonization, these two tributaries warranted production of another EA in 2018 that added them to the LTCP [35]. Following yet another detected new colonization, a third EA added Hoisington Brook in New York (Figure 1) to the LTCP in 2019 [36]. Experience from the PCP, when partial control allowed the population to expand, factored heavily into the decision to maintain an aggressive approach to addressing all sources of production. While EA's were required to expand the LTCP and deliver control at those locations, another tributary identified in the original EIS [30] showed new evidence of an emerging population. The LaPlatte River (Figure 1) did not warrant control throughout the ECP and LTCP, but when surveys showed an emerging population, the Cooperative chose to initiate lampricide treatments there in 2016.

Morpion stream and the Pike River in Québec (Figure 1) were both known sources of production, but as Canadian tributaries to Lake Champlain, they are not subject to jurisdiction under the EIS issued by the United States. Requests made to Québec provincial officials to treat both tributaries with lampricide were not successful, leaving both as uncontrolled sources of lamprey production. Through a long process of evaluating potential alternatives to using lampricide, an innovative seasonally-removable, modular screen barrier structure was designed and installed in Morpion Stream 2014. Morpion stream is approximately 10 m wide and up to 1.5 m deep at the barrier site. Each spring, prior to lamprey spawning season, seven flow-through screen modules are set into place on a concrete base laid into the sediment. Each module is composed of 5 m height aluminum frame containing a bottom-hinged screen. Each screen locks in place upright using a float barrel mechanism that lifts during flood conditions to release the top of the screen to pivot on its bottom hinge and fall flat and flush to the sediment. This feature prevents debris buildup or extreme flows from turning the flow-through screen barrier into a dam that would flood surrounding lands. When locked in place and operating, the 13-mm spaced grates on each screen block lamprey from migrating upstream, but allow the river to flow through with minimal impoundment upstream of the barrier. The barrier is also angled between banks which naturally directs sea lamprey searching for passage into a trap where they are collected. This design is a unique solution to blocking sea lamprey in a river where discharge is too high to use small-scale (channel width < 5 m) barrier solutions and where lampricide usage is prohibited. While being a smaller tributary to the larger Pike River, the larval population of Morpion Stream has been estimated as high as 135,000 and warrants control. Following installation of the barrier, larval population estimates have averaged under 50,000 with recent technical improvements expected to result in additional declines. The Pike River remains uncontrolled and is a known producer of sea lamprey. At this time, we have no options available to control lamprey there. Its size and migratory non-target species concerns preclude consideration of a barrier or lampricide. As new technologies are developed, we hope to find an agreeable form of control to use in the Pike River in the future.

4. Discussion

After 30 years of perspective since the start of the ECP, factors that influenced the long-term success of sea lamprey control in Lake Champlain have been recognized, addressed, and used to steer decisions on where to focus resources efficiently. Periods of discontinuance resulted in a disproportionate population resurgence. Insufficient attention to assessment and monitoring led to misinformed assumptions. Control techniques executed soundly and according to plan suffered from cryptic sources of unaccounted variation. The examples presented do not provide particularly novel or noteworthy management actions. The fine-tuning of sea lamprey control has been ongoing in the Great Lakes for over 70 years [12,13]. However, with 26 lamprey-producing tributaries among a watershed with 226, Lake Champlain may offer a scale where the dynamics between sea lamprey parasitism and its effects on the fishery produce detectable effects among a relatively few sources of lamprey production. With lamprey found in 450 of the 5400 tributaries of the

Great Lakes [13], changes in individual streams become less pronounced and detectable in a control program of nearly 20 times the scale. When considering the many changes to control efforts over the length of the Lake Champlain program, when they occurred, and their various effects on the lamprey population, we have formed two conclusions that we believe offer insight into sea lamprey control efforts into the future.

First, we assert that the relationship between control effort and population reduction is non-linear based on the measurements of wounding rates following changes in the control program. The wounding rate index is not a direct measure of the parasitic population and cannot be used to make empiric estimations of that relationship. Attempts to understand the relationship are therefore limited to general qualitative observations of this relationship rather than quantitative descriptive models. Even with that limitation, we believe the wounding rate data can reflect changes in trends and serve in part as a lesser surrogate measure of relative abundance to indicate when substantial changes in the lamprey population occur or are sustained over time. The relationship between control effort and population suppression appears to follow an inverse sigmoidal relationship depicted in the conceptual diagram in Figure 3. The long-term wounding rate data (Figure 2) show instances during the PCP and during the start of the LTCP when wounding rates failed to decline until additional and more effective control was administered to sources of lamprey production. If the relationship was linear, then some fractional decline should have been detected during the PCP when 69% of the tributaries controlled during the ECP continued to be treated. As the LTCP began and added tributaries to the original 13 treated during the ECP, there was an expectation of decline that failed to materialize for the first five years of the LTCP. When additional assessments and monitoring began in 2006 and led to improvements in control effectiveness, along we the resumption of delayed treatments and inclusion of new ones, the benefits of control efforts began to exceed costs as represented by point 1 on Figure 3.

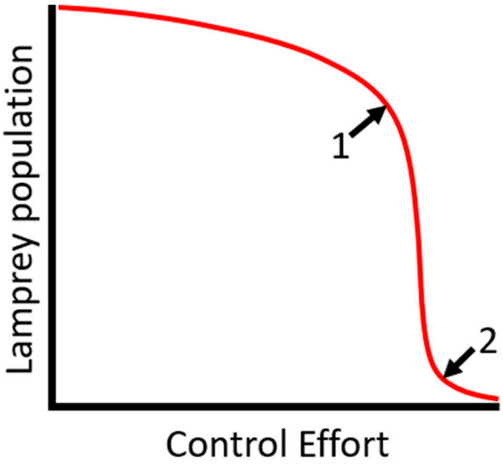

Figure 3. Conceptual representation of the relationship between the Lake Champlain sea lamprey population and efforts to control it. Point 1 indicates where benefits of population suppression begin to exceed the costs of control efforts. Point 2 indicates the beginning of diminishing returns where the costs of additional control efforts yield limited additional population suppression benefits.

Second, we found that achieving a conceptual 50% reduction point in wounding rate requires considerably more than a 50% control effort. Thus, not only is the relationship non-linear, it also skews toward the need for a disproportionately higher level of control effort to achieve desired reductions in lamprey populations. To suppress the lamprey population into the region between points 1 and 2 on Figure 3, control efforts needed to address more than 80% of the known sources of larval sea lamprey production in the basin. That same required level of control effort appeared consistently and repeatedly during the ECP, PCP, and the LTCP (Table 1). We do not suggest that the observed percentages constitute specific numeric management benchmarks, but we do think the long-term data reflect the existence of a threshold for required control effort, below which measurable reductions in the Lake Champlain lamprey population cannot be achieved.

Evaluation of sea lamprey control efforts is indirect where the larval and adult life history stages receive control while assessment of those efforts focuses on the juvenile (parasitic) stage. This indirect evaluation prevents immediate determinations of population suppression measures corresponding to applied effort. The cumulative effects (changes in wounding rates) of individual control efforts are also not observable until at least one year following implementation. These control program characteristics make comparisons between sea lamprey and other fish species controlled by removal and assessment of the same life history stages tenuous when looking for common relationships between control effort and population response. So while other long-term invasive fish control programs have modeled and quantified relationships between direct species removal and measured population responses [37–39], we hesitate in seeking to relate our findings to theirs because of the differences in target species life histories, niche, and control and assessment methodologies.

Relating our findings to other sea lamprey control efforts are complicated by scale and management focus. The Great Lakes program has historically used different measures and models [40–42] to prioritize their allocation of limited resources to achieve the greatest benefits across their larger scale. Lake Champlain differs in that limits to control have historically been the result of socio-political issues rather than limited resources. This difference and the 20× smaller scale enables the Lake Champlain program to control a higher proportion of its lamprey-producing tributaries. Currently, the Great Lakes regularly controls 166 of their 450 (37%) lamprey-producing tributaries with lampricides [13]. Those 166 do represent a large portion (more than 37%) of the total basin-wide larval population, yet it compares to 19 of 26 (73%) lampricide treated tributaries in Lake Champlain. Despite the apparent advantage Lake Champlain has in proportional control effort, lamprey wounding rates on lake trout in lakes Superior, Michigan, Huron, and Erie have remained under 20 since at least the year 2000 and under five in Lake Ontario since 1985 [43]. This compares to Lake Champlain lake trout wounding rates that have remained above the management target of 25 since recording began in 1982 (Figure 2). There are many presumed reasons for this [20,21], yet aside from the causes, the differences in response relative to control highlights how control effort and population responses can differ widely between two similar programs that focus on the same target species. This leads us to conclude that our specific findings may have limited applicability to Lake Champlain or similar, smaller watersheds.

5. Conclusions

The differing phases of Lake Champlain sea lamprey control over 30 years offered an occasion to evaluate trends and anomalies during periods of cessation, adjustment, and improvement. With 26 current lamprey-producing tributaries in the basin, the potential for each to exert influence on the population forces managers to remain vigilant in assessing larval population densities and distributions. It also requires validation that implemented control efforts meet management expectations. We learned that fractional efforts do not correspond to fractional reductions and that the minimum effort required to successfully control sea lamprey falls closer to the maximum end of the range. In recent years, we began referring to our approach as “comprehensive” to imply that we have come to realize the need to address all sources of lamprey production in the basin. Ignoring even a few or one source of lamprey production can negate gains that have taken years to achieve.

As sea lamprey control continues to serve as a tool to facilitate the restoration and recovery of native fish stocks in Lake Champlain, further refinement of current methodologies and the development of new approaches are both needed to ultimately meet the management targets for sea lamprey population suppression. Continued reliance on thorough larval assessment is critical to keeping pace with expanding colonization of new tributaries. We also look to shift the assessment of the parasitic population from exclusive reliance on wounding rates to a more inclusive and direct measure of lamprey abundance used by the Great Lakes [44,45]. Having established the level of assessment and control effort required to achieve and sustain population suppression during the previous three decades of the Lake Champlain sea lamprey control program, we expect further reductions during the ensuing fourth decade to require additional approaches, not just additional effort.

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