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Sea Lamprey Abundance and Management in Lake Superior, 1957 to 1999

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ABSTRACT. *The international sea lamprey* (Petromyzon marinus) *control program successfully laid the foundation for rehabilitation of lake trout* (Salvelinus namaycush) *in Lake Superior and was well coordinated among management agencies during 1957–1999. The lampricide TFM was the primary control tool, with recurring treatments in 52 larval-producing streams. Barriers and sterile-male-release, as alternative control technologies, were significant elements of the program. Barriers blocked spawning sea lampreys from substantial areas of habitat for sea lamprey larvae during 1966–1999, and the sterile-male-release technique was used to reduce larval production during 1991–1996. Sea lamprey control resulted in the suppression of sea lamprey populations in Lake Superior, as evidenced by the linear decline in spawner abundance during 1962–1999. However, sea lamprey abundance was not as low as the targets specified in the fish community objectives. Most of the parasitic sea lampreys in Lake Superior probably originated from survivors of lampricide treatments. Self-sustaining populations of lake trout were restored in most of the lake by 1996, although many were killed annually by sea lampreys. Economic injury levels for damage to fish populations by sea lampreys are being developed and will be used to distribute sea lamprey control resources among the Great Lakes.*

INDEX WORDS: *Lake Superior, sea lampreys, lake trout, TFM, lampricide, barrier, sterile-male-release.*

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INTRODUCTION

Sea lampreys (*Petromyzon marinus*) were first reported in Lake Superior in 1938 and their range quickly expanded throughout the lake during the 1940s and 1950s (Smith and Tibbles 1980). Parasitic-phase sea lampreys attacked lake trout (*Salvelinus namaycush*) and other fish. The significant reduction in predatory fish resulted in a secondary invasion of exotic forage fish species (Koonce *et al.* 1993).

The governments of Canada and the United States established the Great Lakes Fishery Commission (GLFC) in 1955 to coordinate fishery research, recommend measures to maximize sustained production of fish stocks, and implement programs to reduce sea lamprey populations in the Great Lakes (GLFC 1956). Smith and Tibbles (1980) documented the history of sea lamprey invasion and the sea lamprey control program through 1978.

The GLFC implemented an integrated management program for sea lampreys during the 1980s and 1990s (GLFC 1984) with the following objectives: (1) refocus the program from eradication to optimal suppression, (2) pursue and refine innovative lampricide control technologies, (3) emphasize development of non-chemical (alternative) control techniques, (4) develop and refine assessment techniques to support integrated control strategies, (5) integrate management of sea lampreys with management of fishery resources, and (6) enhance sharing of technical information among management agencies.

This paper summarizes sea lamprey management activities in Lake Superior during 1957–1999 including interagency coordinated fishery management and sea lamprey control and abundance. In addition, we evaluate the response of sea lamprey and lake trout populations to the integrated management of sea lampreys, and make recommendations for the future of integrated sea lamprey management in Lake Superior.

COORDINATED FISHERY MANAGEMENT

The Great Lakes Fishery Commission was formed in 1955 by the Convention on the Great Lakes between the United States and Canada. In 1965, the GLFC instructed the management agencies to establish a lake committee for each of the Great Lakes (GLFC 1967).

The role of the Lake Superior Committee (LSC) was to implement the joint strategic plan in Lake Superior. The LSC was established in 1965, and in 1999 consisted of representatives from the Chippewa/Ottawa Treaty Fishery Management Authority, Great Lakes Indian Fish and Wildlife Commission, Michigan Department of Natural Resources, Minnesota Department of Natural Resources, Ontario Ministry of Natural Resources, and Wisconsin Department of Natural Resources. During 1986–1994 the LSC developed fish community objectives and published state of the lake reports (Dochoda 1988; Busiahn 1990; Hansen 1990, 1994). The LSC developed targets for sea lamprey populations and control plans that were integrated with fishery goals.

In 1982, the Lake Superior Technical Committee (LSTC) was formed to focus on lake trout rehabilitation, including stocking and controlling mortality (GLFC 1982). In 1983, the LSTC was charged to develop a lake trout rehabilitation plan for Lake Superior (GLFC 1983a). The plan was adopted by the LSC in 1986 (GLFC 1986) and revised in 1996 (Hansen 1996).

The LSTC made five major contributions to sea lamprey management: (1) it established goals for the integrated management of sea lampreys (Christie and Goddard 2003), (2) it set target levels for parasitic sea lamprey abundance at a 50% reduction by 2000 and a 90% reduction by 2010 (Busiahn 1990), (3) it introduced the lake-wide assessment of sea lamprey populations, (4) it initiated the sterile-male-release technique as a lake-wide integrated control technique (Twohey *et al.* 2003), and (5) it incorporated sections describing the status of sea lampreys in state of the lake reports (Hansen 1990, 1994).

SEA LAMPREY-PRODUCING STREAMS

United States and Canadian biologists surveyed 1,915 streams that discharged into Lake Superior during 1950–1954 to identify those with the physical characteristics suitable for production of sea lampreys (Smith and Tibbles 1980). Of these, 424 had suitable characteristics and were considered to be potential sea lamprey-producing streams (Loeb and Hall 1952, Loeb 1953, Lawrie 1954). Larval habitat was classified into three groups according to stream substrate: Type I for preferred habitat, Type II for acceptable habitat, and Type III for unacceptable habitat (Mullett 1997, Mullett and Bergstedt 2003).

Sea lamprey larvae have been collected in 136 tributaries to Lake Superior. We separated the streams into three categories based on frequency of lampricide treatment during 1958–1999, reflecting the streams' productivity of sea lamprey larvae and transformers (from a modification of Hanson 1990). Streams treated every 5 or fewer years were in Category 1, those treated less frequently were in Category 2, and those not treated during 1990–1999 were in Category 3.

We classified 52 Category 1 streams as primary producers of parasitic sea lampreys in Lake Superior (Fig. 1). Category 1 streams contained suitable spawning and larval habitat, provided sufficient discharge, had annual recruitment of larvae to the population, and consistently had larvae that survived lampricide treatments. Larval population estimates for Category 1 streams ranged from 0 to 5.3 million animals; area of Type I habitat ranged from 0.09 to 41 ha (Fig. 2). We classified 19 Category 2 streams as secondary producers of parasitic sea lampreys in Lake Superior. Recruitment of larvae in these streams was sporadic and intermittent. Lampricide treatments averaged once every 8 years, and probably few larvae survived those treatments. We classified 65 Category 3 streams as those in which relatively few sea lamprey larvae ever existed. Generally, these streams had little or no suitable spawning or larval habitats. In addition to none of the 65 streams receiving lampricide treatment during 1990–1999, 6 of the 65 also were not treated during 1958–1989 because larvae were too sparse to justify treatment.

LAMPRICIDE CONTROL

The lampricide TFM (3-trifluoromethyl-4-nitrophenol, Applegate *et al.* 1961) was the primary sea lamprey control tool from 1957 to 1999. The general procedures used prior to 1979 (Smith *et al.* 1974, Smith and Tibbles 1980) have changed little, but instrumentation and techniques have improved (Johnson and Stephens 2003), including flow-through toxicity testing (Garton 1980, Bills and Johnson 1992, Johnson and Stephens 2003), toxicity regressions based on pH and alkalinity of stream water (Bills *et al.* 2003), and procedural improvements (Brege *et al.* 2003).

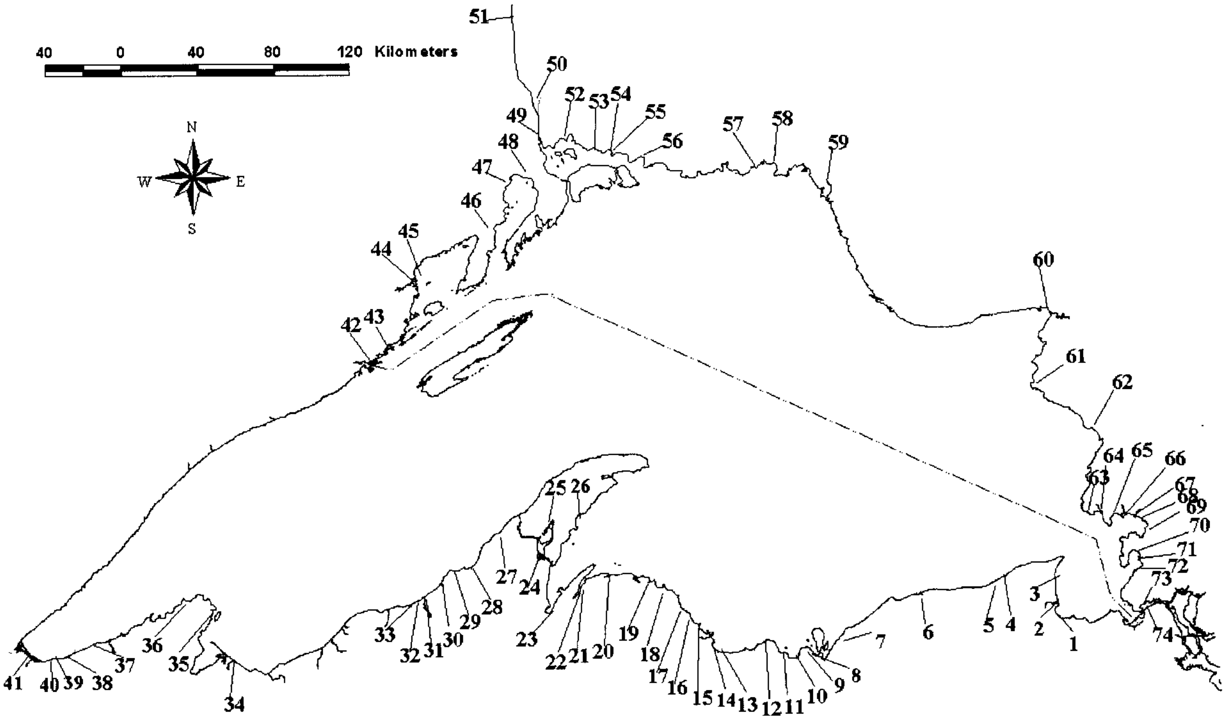
Treatment Effort

Smith and Tibbles (1980) detailed a summary of lampricide applications in Lake Superior tributaries during 1958–1978 that included 558 treatments with 365 t TFM and 2.4 t Bayluscide (5, 2′-dichloro-4′-nitrosalicylanilide) wettable powder (Howell *et al.* 1964). During 1979–1999, 399 treatments were conducted on tributaries of Lake Superior with 223 t TFM, 0.8 t of the solid-bar formulation of TFM (Gilderhus 1985), and 1.5 t Bayluscide wettable powder (Table 1).

The average number of Lake Superior tributaries treated per year declined 36%, from 25 streams during 1960–1969 to 16 streams during 1990–1999. The number of streams treated annually declined because (1) sea lampreys did not reestablish in 24% of streams following a first lampricide treatment, (2) the number of years between treatments increased in 15% of streams due to a better defined cost benefit ratio, and (3) the construction of barriers eliminated or reduced production of sea lampreys in several streams. Other measures of lampricide control effort also declined substantially during 1960–1999 (Fig. 3). The average amount of TFM applied annually (active ingredient) decreased from 21 t during 1960–1969 to 7.2 t during 1990–1999. The ratio of TFM used to stream discharge also decreased from 158 $kg \cdot m^{-3} \cdot s$ during 1960–1969 to 110 $kg \cdot m^{-3} \cdot s$ during 1990–1999. Area of Type I habitat treated declined during the 1970s and 1980s, yet increased to the 1960s level in the 1990s despite treatment of 40% fewer streams annually. We believe these trends in treatment effort reflect continual improvements in the control program. Advances in lampricide application techniques contributed to declines in the amount of TFM used to kill larval sea lampreys in streams. Quantitative stream assessments led to an improved process for selecting streams for treatment, enabling us to select and treat the most productive streams, which contributed to the increase in the amount of Type I habitat treated.

Nontarget Effects

Some of the effects of lampricide treatments on native lampreys (Schuldt and Goold 1980), resident and migratory fishes (Dahl and McDonald 1980), plants, invertebrates, and amphibians (Gilderhus and Johnson 1980, Torblaa 1968) were understood early in the program. A strategy for assessing effects on nontarget organisms was developed in part due to the recommendations of Maitland (1980) to expand research (GLFC 1983b). Also, lampricide registration requirements of Health Canada and the U.S. Environmental Protection Agency led to a $5 million (U.S. dollars) expenditure by the GLFC to determine environmental effects of sea lamprey control (Dawson 2003, Hubert 2003).



1. Galloway Cr.
2. **Tahquamenon R.** (a)
3. **Betsy R.** (a)
4. **Little Two Hearted R.**
5. **Two Hearted R.**
6. **Sucker R.**
7. **Miners R.** (a, b)
8. **Furnace Cr.** (a)
9. Five Mile Cr.
10. **AuTrain R.**
11. Rock R. (a)
12. Laughing Whitefish R.
13. **Chocolay R.** (a)
14. Carp R.
15. **Harlow Cr.**
16. **Little Garlic R.**
17. **Big Garlic R.** (a)
18. **Iron R.**
19. **Salmon Trout R.**
20. **Huron R.**
21. **Ravine R.**
22. **Silver R.** (a)
23. **Falls R.**
24. **Sturgeon R.**
25. Trap Rock R.
26. **Traverse R.**
27. **Salmon Trout R.**
28. **Misery R.** (a, b)
29. **East Sleeping R.**
30. **Firesteel R.** (a)
31. **Ontonagon R.** (a)
32. **Potato R.**
33. **Cranberry R.**
34. **Bad R.** (a)
35. **Red Cliff Cr.** (a)
36. Sand R.
37. **Brule R.** (a, b)
38. Poplar R.
39. **Middle R.** (a, b)
40. **Amnicon R.** (a)
41. **Nemadji R.**
42. **Pigeon R.**
43. Cloud R.
44. **Kaministiquia R.**
45. Neebing-McIntyre R. (a, b)
46. Pearl R.
47. **Wolf R.** (a, b)
48. **Black Sturgeon R.** (b)
49. **Stillwater R.**
50. Cash R.
51. **Nipigon R.** (a)
52. **Jackfish R.**
53. **Cypress R.**
54. **Little Gravel R.**
55. **Gravel R.**
56. Pays Plat R.
57. Prairie R.
58. Little Pic R.
59. Pic R.
60. **Michipicoten R.**
61. **Gargantua R.**
62. Agawa R.
63. Gimlet Cr. (a, b, t)
64. **Pancake R.**
65. **Carp R.** (a, b)
66. **Batchawana R.**
67. **Chippewa R.**
68. Harmony R.
69. Stokely Cr. (a, b, 3)
70. **Goulais R.**
71. Sheppard Cr. (b, t)
72. Cranberry Cr.
73. **Big Carp R.** (a, b)
74. **Little Carp R.**

FIG. 1. Location of 52 Category 1 (bold) and 19 Category 2 Lake Superior streams. Streams where assessment traps (a) were operated in 1999 and where barriers (b) were constructed during 1966–1999 are identified; they include one Category 3 stream designated by (3) and two tributaries to Category 1 streams designated by (t). The dashed line is the international boundary between the U.S. and Canada.

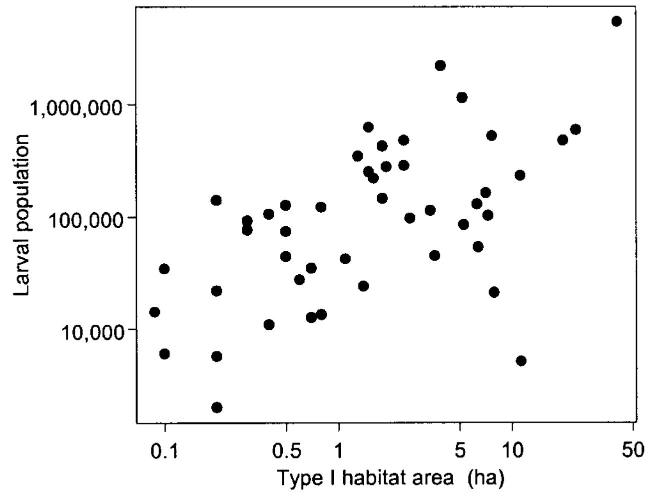


FIG. 2. Larval population and Type I habitat area of Lake Superior Category 1 streams based on recent estimates (1996–1999). Four streams were excluded from the plot because their population estimates were zero (Furnace, Falls, Silver, and Gravel rivers), and one was excluded because no recent estimate was available (Salmon-Trout River, I.D. 27 in Fig. 1).

The GLFC, through its contract agents, conducted several short- and long-term tests of the effects of lampricides on nontarget organisms. In general, TFM had no long-term effect on nontarget species in treated rivers (Boogaard and Bills 2003, Weisser *et al.* 2003).

During 1997–1999, the lake sturgeon (*Acipenser fulvescens*) was listed as threatened in Michigan and of special concern in Minnesota and Wisconsin. Lake sturgeon are nearly as sensitive to TFM as sea lampreys when they are shorter than 12 cm (Johnson *et al.* 1999). Four tributaries to Lake Superior were known areas of concern regarding the effect of TFM on lake sturgeon: St. Louis, Bad, Ontonagon, and Sturgeon rivers. Lake sturgeon shorter than 12 cm migrate downstream shortly after hatching in April–June, and young lake sturgeon migrate into the lake (Auer 1996). Yet field surveys during 1997–1998 commonly encountered lake sturgeon 8–23 cm in streams throughout August. Consequently, we reduced the application rate for lampricide treatments of the Bad, Ontonagon, and Sturgeon Rivers during 1997–1999 to protect juve-

TABLE 1. Summary of stream treatments to control sea lampreys in Lake Superior, 1979–1999. Lampricide quantities given for active ingredients.

Year	No. stream treated	Discharge at mouth (m^3/s)	Length of Stream treated (km)	TFM (kg)	TFM bar formulation (no. bars)	TFM bar formulation (kg)	Bayluscide powder (kg)
1979	19	200	584	15,386	0	0	179
1980	23	85	580	13,193	0	0	23
1981	19	134	537	16,122	6	1	131
1982	27	107	517	9,752	0	0	52
1983	25	165	418	17,336	0	0	199
1984	24	109	509	12,960	0	0	70
1985	24	83	534	11,271	346	72	27
1986	20	162	440	15,565	275	57	161
1987	24	106	987	11,808	269	56	71
1988	20	101	620	14,559	757	158	73
1989	20	39	185	4,827	354	74	21
1990	27	150	660	14,659	286	60	101
1991	16	29	468	4,927	0	0	0
1992	16	126	330	13,129	383	74	119
1993	11	31	189	3,047	200	40	0
1994	20	90	341	9,068	280	55	24
1995	10	101	477	7,256	163	33	52
1996	15	45	333	5,481	132	25	8
1997	15	83	296	8,513	143	27	89
1998	15	29	349	3,528	226	47	4
1999	13	139	367	10,526	71	14	82
Total	399	2,115	9,721	222,913	3,891	793	1,486

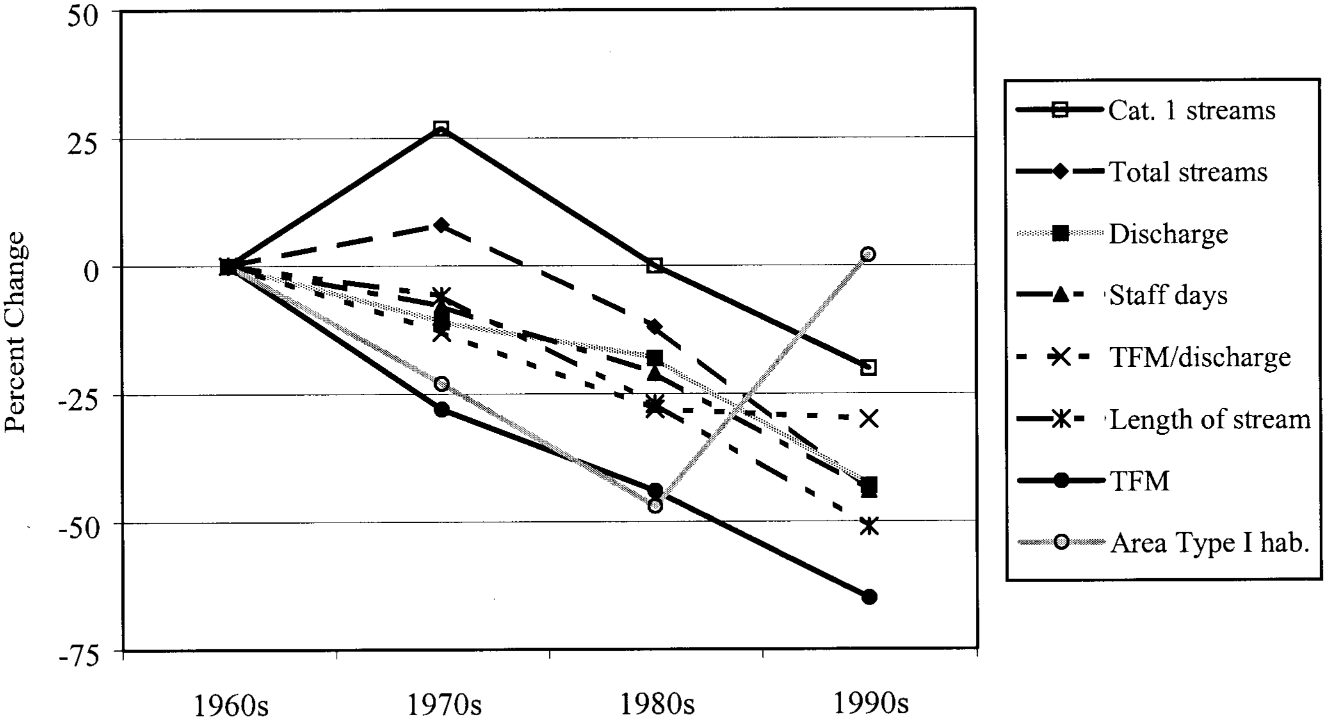


FIG. 3. Relative change in treatment effort from the1960s to the 1990s. Percent change is expressed for each decade relative to the 1960s means: 25 streams, 15 Category 1 streams, 1,900 staff days, 610 km of stream, 130 m^3/s discharge, 21 t TFM, 160 $kg/m^3/s$ TFM to discharge ratio, and 1,200 ha Type I habitat area.

nile lake sturgeons (the St. Louis River was not treated during 1997–1999).

ALTERNATIVE CONTROL

Barriers

The construction and modification of dams and other structures provided an operational alternative to lampricide treatments. During 1966–1999, barriers were built to block spawning sea lampreys in 12 tributaries of Lake Superior (Fig. 1, Table 2). Eleven of the 12 were low-head barriers that blocked sea lampreys because of their inability to jump more than 10 cm vertically. Ten of these low-head barriers were permanent structures that were effective in most years and required little maintenance. The other low-head barrier, in the Big Carp River, made use of an inflatable structure that allowed fish passage when lowered. The second type of barrier was an experimental velocity barrier in the Neebing-McIntyre River, the only velocity-type barrier in any Great Lakes tributary.

Since their construction, barriers have reduced or eliminated production of larval sea lampreys in most of the 307 km of stream and 46 ha of Type I habitat upstream of the barriers (Table 2). For all 12 streams combined, sea lamprey production was eliminated from 153 of 192 stream-years of operation during 1966–1999. Upstream sea lamprey production in 23 stream-years was due to field research on the efficacy of experimental sterile male sea lamprey release (Twohey *et al.* 2003). Discounting the effects of these experiments, the structures eliminated sea lamprey production upstream of the barriers in 91% of the stream-years.

Barriers in the Black, Sturgeon, and Brule rivers probably contributed to most of the reduction in recruitment of parasitic sea lampreys to the lake from these streams. Of the estimated 46 ha of Type I habitat that was blocked by the 12 barriers, 76% of the area was blocked by the barriers on these three rivers, and spawning sea lampreys did not produce larvae in the area upstream in 46 of 48 stream-years. The barriers on the Misery and Neebing-McIntyre rivers blocked an additional 17% of the

TABLE 2. Summary of barrier operations on Lake Superior streams, 1966–1999.

I.D.[1]	Stream	Year built	Stream Length (km)[2]	Type I habitat area (ha)[2]	Barrier operation (no. years)	No upstream sea lamprey production (no. years)	No lampreys placed upstream (no. years)	Barrier success rate (%)[3]
7	Miners R.	1978	2	0.6	21	21	21	100
28	Misery R.	1984	19	3.1	15	0	9	0
37	Brule R.	1984	72	14.0	15	13	15	87
39	Middle R.	1983	28	0.2	16	12	12	100
45	Neebing-McIntyre R.	1993	29	4.5	6	2	6	33
47	Wolf R.	1987	17	1.0	12	7	7	100
48	Black Sturgeon R.	1966	79	20.6	33	33	33	100
63	Gimlet Cr.	1979	5	0.2	20	20	20	100
65	Carp R.	1983	12	0.8	16	13	13	100
69	Stokely Cr.	1980	13	0.2	19	16	16	100
71	Sheppard Cr.	1984	14	0.4	15	15	15	100
73	Big Carp R.	1995	17	0.1	4	1	2	50
Total			307	45.7	192	153	164	91

[1] I.D. numbers refer to map locations in Figure 1.

[2] Stream length and habitat area upstream of barrier describes the portion of the stream treated with TFM prior to barrier construction.

[3] The success of each barrier is calculated as the number of years with no upstream lamprey production divided by the number of years in which sea lampreys were not placed upstream of the barriers as part of a controlled experiment.

total area, but they were effective in only 2 of 21 stream-years.

Barriers have effectively reduced habitat available for sea lamprey larvae, but they also affect streams by warming, sedimentation, blocking migrating fishes, and intangible aesthetic degradation from placement of an intrusive structure in a free-flowing stream (Lavis *et al.* 2003). Blocking upstream migrations of fish species has probably been the most significant effect because the barriers generally have been constructed in areas of steep gradient where the impounded area was relatively small lessening the chance of significant warming and sedimentation. Dodd *et al.* (2003) conducted extensive research on the species richness of fish in 12 Lake Superior streams, six with and six without barriers. The upstream portion of each stream had fewer species than the downstream portion, but the difference was greater for barrier streams by an average of two fewer species upstream. The species most consistently absent upstream and present downstream of a barrier was sea lamprey larvae (Noakes 2003). During 1995–1999, barriers constructed by the GLFC were either designed with an inflatable crest for seasonal operation or included fishways to facilitate migration of nontarget fish species.

Sterile-male-release

The sterile-male-release technique involves the release of male sea lampreys that have been sterilized but are capable of spawning. Successful application of the technique results in female sea lampreys laying eggs that are unfertilized or mutated.

In 1987, the GLFC approved Lake Superior as the primary application site for the sterile-male-release technique because of its low number of sea lampreys and relatively isolated population. During 1991–1996, an annual average of 16,100 sterile-male sea lampreys were released into 33 streams of Lake Superior (Twohey *et al.* 2003). The annual average number of estimated resident males in these streams was 10,600 leading to a theoretical 60% reduction in larval production.

In 1997, the GLFC shifted the use of sterile-male sea lampreys from Lake Superior to the St. Marys River, and releases into Lake Superior tributaries were discontinued (Schleen *et al.* 2003, Twohey *et al.* 2003). The effect of sterile-male-release on the long-term estimates of spawning sea lampreys and damage to the fishery will be evaluated with information gathered through 2004. Because the time from hatching to metamorphosis was estimated as 4–6 years for sea lampreys in Lake Superior tributaries (Christie *et al.* 2003), treatments during 1991–1996 would theoretically show reductions in parasitic-phase abundance during 1996–2003 and in spawning-phase abundance during 1997–2004.

Implementation of the sterile-male-release technique in Lake Superior had several initial successes followed later by two differing outcomes. Several of the initial successes were: (1) field tests during 1992–1995 showed the male sea lampreys were sterilized, competed with other males, mated with females, and reduced the production of larvae from nests and in streams (Twohey *et al.* 2003); (2) all cooperating fishery agencies and groups involved in Lake Superior supported and endorsed the implementation; (3) the capture, transport, and sterilization of male sea lampreys was well coordinated; and (4) the studies conducted in association with the technique advanced our understanding of compensation and stock-recruitment in sea lamprey populations. Yet, the mean relative abundance of spawning-phase sea lampreys in the lake during 1997–1999 was twice as high as the mean during the preceding 10 years ($t = 2.28$, $df = 11$, $p = 0.044$, Fig. 4), and Brege *et al.* (2003) showed that neither the quantity of lampricide nor frequency of treatments were reduced in the targeted streams during 1994–1999. These apparently conflicting results may have been caused by several factors: (1) increased survival of larvae after hatching, induced by the lower densities created by sterile-male-release; (2) increased survival of parasitic sea lampreys because of increased abundance of lake trout; or (3) changes in lampricide control treatment independent of sterile-male-release.

LARVAL SEA LAMPREYS

Assessment of larval sea lamprey populations changed substantially during 1979–1999. Stream assessments of larval sea lampreys were used to predict a stream's potential for production of parasitic sea lampreys, determine the priority of streams for lampricide treatment, and assess the effects of control actions. During 1958–1978, measures of relative abundance of larvae captured in electrofishing surveys were used to determine which Lake Superior streams needed treatment (Smith and Tibbles 1980). Several field and laboratory studies were conducted during 1979–1999 to advance the accuracy and precision of these estimates. Improved sampling equipment was developed along with estimates of sampling efficiency for that equipment (Bergstedt and Genovese 1994, Hintz 1993, Bowen *et al.* 2003, Weisser 1994). Systematic habitat-based estimation of larval sea lamprey abundance was initiated in 1988 (GLFC 1996). A lake-wide ranking system for prioritizing lampricide treatments was developed (Christie *et al.* 2003, Slade *et al.* 2003), and development of a decision support system advanced the prioritization of control actions (Christie and Goddard 2003).

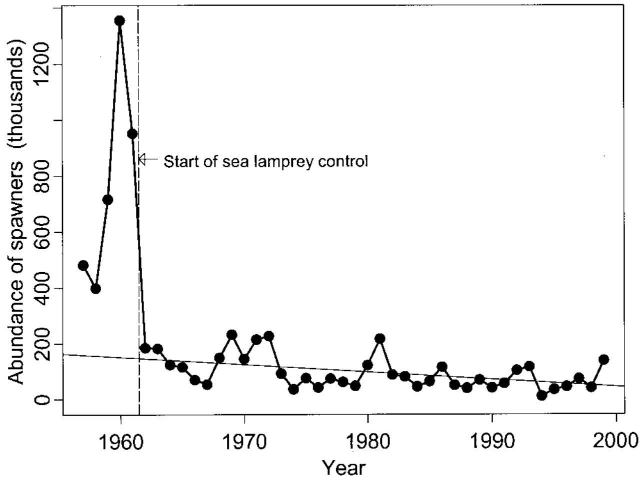


FIG. 4. Estimated abundance of spawning-phase sea lampreys in Lake Superior during 1957–1999. The regression line shows the trend over time from 1962 to 1999, since the start of sea lamprey control.

Relative Abundance in Streams 1960–1994

Streams were assessed more frequently during 1960–1994 than during 1995–1999. These assessments collected information for a variety of purposes and included determination of relative abundance and length of larvae to schedule lampricide treatments, determination of relative abundance of young-of-year larvae in index rivers, collection of larvae for bioassays, and growth and transformation studies. Although these assessments were designed to serve different purposes, they all included estimates of the time or area sampled and the number and length of larvae collected.

Population Estimation in Streams 1988–1999

Larval sea lamprey populations were estimated for 29 U.S. streams, including 27 of the 33 Category 1 streams in the U.S., using a habitat-stratified sampling method during 1988–1995 (GLFC 1996). Estimates were based on the amount of Type I and

TABLE 3. Lentic areas of Lake Superior, identified by their associated streams, where sea lamprey larvae were known to inhabit, 1957–1999. I.D. numbers refer to map locations in Figure 1 (Category 3 streams have no I.D.).

I.D.	Stream	Inhabited area (ha)	No. larvae	No. transformers	Year of estimation	Last year of known production
6	Sucker R.	0[1]	—	—	1987	1987
8	Furnace Cr.	2	0	0	1998	1984
21	Ravine R.	3	14,400	300	1999	1999
—	Slate R.	1	0	0	1991	1983
22	Silver R.	12	21,500	200	1999	1999
23	Falls R.	2	0	0	1999	1997
—	Mackenzie R.	30	12,000[2]	300[2]	1997	1999
51	Nipigon R.[3]	850	165,000	4,100	1999	1999
55	Gravel R.	11	3,900	400	1999	1999
66	Batchawana R.	13	151,400	3,800	1999	1999
67	Chippewa R.	4	3,800	< 100	1999	1999
	Total	928	371,000	< 9,200		

[1] Inhabited lentic area was destroyed by erosion in 1987.

[2] On-site estimate not conducted; estimate based on the proportion of larvae and transformers for the other six producing lentic areas.

[3] Inhabited lentic area was in Helen Lake 4 km upstream of Lake Superior.

II habitat and the density of larvae in each habitat type in each stream. Stream habitat was classified at equally spaced transects, distributed from the river mouth to the upstream limit of the river inhabited by larvae. Density of larvae was estimated by depletion sampling in 10.2 m^2 of Type I habitat at each transect and 10.2 m^2 of Type II habitat at every other transect (Armour *et al.* 1983, Zippin 1958).

The results of the assessment confirmed the importance of Type I habitat in the distribution of sea lamprey larvae. In those streams with at least 25 transects, larval abundance was significantly correlated with Type I habitat area ($r = 0.72$, $df = 22$, $p < 0.001$) and sea lamprey larvae were significantly more dense in Type I than Type II habitat ($t = 5.61$, $df = 23$, $p < 0.001$). We divided each stream in two, such that half of the transects were upstream and half were downstream, and used paired *t*-tests to compare the means for all streams. There were no significant differences between upstream and downstream means of larval density in Type I habitat ($t = 0.53$, $df = 23$, $p = 0.60$), density of large larvae (> 120 mm) in Type I habitat ($t = 0.73$, $df = 23$, $p = 0.47$), and Type I habitat area ($t = 0.11$, $df = 26$, $p = 0.92$).

During 1996–1999, all streams that were predicted to produce transformers the following year were assessed. The number of larvae that would metamorphose the following year was predicted from estimates of habitat composition, the density and size distribution of larvae in Type I habitat, and estimates of larval growth and transformation rates (Slade *et al.* 2003). Larval density in Type II habitat was assumed to be 10% of the density in Type I habitat, based on information collected in 29 U.S. streams during 1988–1995. There were many sources of bias and variance in these predictions, and improvements in the accuracy and precision of the estimates were ongoing (Hansen *et al.* 2003).

Both assessments indicated that most of the sea lamprey larvae and their preferred habitat were found in relatively few Lake Superior streams. Ensuring the suppression of larval populations in these very high production streams could greatly contribute to sea lamprey control lake-wide.

Population Estimation in Lentic Areas 1966–1999

Lentic areas offshore of 11 river mouths in Lake Superior had populations of sea lamprey larvae during 1957–1999. Of these 11 streams, 7 were predicted to have contributed parasitic sea lampreys to the lake in 1999 (Table 3). Although lentic areas are known producers of sea lamprey larvae, the direct treatment of lentic areas with lampricides was discontinued in 1989. The majority of the transformers

(86%) were produced by two areas: Helen Lake in the Nipigon River and the bay offshore of the Batchawana River. These and other lentic areas in Canada had been treated periodically with granular Bayluscide until 1988 when Environment Canada raised registration issues for the compound, and its use was discontinued. These areas probably contributed parasitic sea lampreys to Lake Superior in many years during 1989–1999.

A high frequency of stream treatments has proven to be an effective indirect control method for adjacent lentic areas. The Furnace, Falls, and Slate rivers were treated annually with TFM for several years to limit colonization of sea lamprey larvae in offshore lentic areas. Sea lampreys failed to recolonize the rivers, so TFM treatments were discontinued. The Silver River was also treated with TFM annually for many years. Because sea lampreys continued to recolonize the lentic area, we sustained the high frequency of treatments on the Silver River to suppress sea lamprey production in the lentic area. The lentic area offshore the Sucker River was once one of the largest lentic producers of sea lampreys in the U.S., but the area was destroyed by erosion in 1987 and was no longer productive.

Survival of Lampricide Treatment

As part of a study of production levels, populations of larvae that survived lampricide treatments in the Firesteel, Bad, and Ontonagon rivers were estimated 1 year after treatment (GLFC 1996). From 1991–1992, survival the year after treatment was estimated at 7% in the Firesteel River and 1% in the Bad River. From 1992–1993, survival after treatment was 4% in the Ontonagon River. These survival estimates did not take into account natural mortality and out-migration.

Mortality

The numbers of sea lamprey larvae were estimated annually in the Firesteel River during 1990–1991, and survival was estimated from July 1990 to September 1991 (GLFC 1992b, 1993). Age-1 and age-2 larvae were marked with pigment dye and released throughout the inhabited reach of the river in 1990 (N = 1,525) and 1991 (N = 5,035). During a lampricide treatment in September 1991, 13,857 dead and dying larvae were collected, of which 21 had been marked in 1990 and 134 in 1991. Based on the 2.7% recovery rate of those marked in 1991, the expected number of recaptures of those marked in 1990 was 41. Because only 21 of those marked in 1990 were recovered, we estimated annual mortality as 48% from 1990 to 1991.

Stream Ranking 1995–1999

During 1995–1999, a ranking system for sea lamprey-producing streams throughout the Great Lakes was developed based on the cost of lampricide treatments and the projected numbers of transformers in streams in the treatment year (Christie *et al.* 2003, Slade *et al.* 2003). Each of the assessed streams in the Great Lakes basin was ranked by the projected cost to kill a transformer, based on stream-specific treatment cost and projected transformer production from 1995–1999 assessments. The number of staff days needed to treat each stream was calculated based on historical effort and the top ranking streams (those with the lowest cost per kill) were selected until the cumulative total staff days was 4,700, the level of effort available from the control agents. The cost of lampricide treatments for Lake Superior streams during 1995–1999 ranged from $10,000 to $467,000, and the cost per transformer killed ranged from $2 to $300 (U.S. dollars).

SPAWNING-PHASE SEA LAMPREYS

Abundance of spawning-phase sea lampreys has been the key long-term measure of success of the sea lamprey control program. During 1953–1979, electric and mechanical barriers were used to remove spawning sea lampreys and monitor their relative abundance and biological characteristics (Heinrich *et al.* 1980). During 1953–1960, 55 weirs were operated in Lake Superior streams, but weirs were later replaced by lampricides as the primary control tool. By 1971, the number of weirs in Lake Superior was reduced to eight (Smith and Tibbles 1980), and the operation of these weirs was discontinued in 1980.

Assessment Tools

Portable traps were effective for capturing spawning-phase sea lampreys when placed at strategic locations below dams and natural barriers, and the resulting catches provided reliable long-term trend information (Schuldt and Heinrich 1982). During 1980–1985, 10 Lake Superior streams had portable traps, five had mechanical weirs, and two had permanent traps.

Permanent traps were first used in association with barriers constructed to block sea lamprey spawning migrations. They were generally constructed of concrete or steel sheet, and often were more efficient than portable traps.

Larger mechanical traps were briefly used in a few streams. For example, sea lampreys in the Sucker River were captured with a large wooden trap similar to the electric weir traps (McLain *et al.* 1965). This trap was set at the abandoned abutment of the discontinued electric weir. In most years from 1980 to 1992, too few sea lampreys were captured in these large mechanical traps to estimate abundance.

Capture of spawning sea lampreys in streams without a barrier was largely unsuccessful with traps and weirs. Portable and permanent traps were only effective near dams, and mechanical weirs were not cost-effective because of the high maintenance they required. Susquehanna hoop traps (Sterling Marine Products, Montclair, NY) proved effective in capturing spawning sea lampreys in streams without barriers in 1985 (Purvis and McDonald 1987). The hoop traps were developed to sample in shallow streams and were later replaced by D-ring nets (H. Christensen Co., Duluth, MN) during 1996 because the flat side of the D-ring rested better on the stream bottom than the round hoop traps.

In 1999, spawning-phase sea lampreys were captured from 23 streams to measure lake-wide abundance of sea lampreys and to monitor the long-term success of the control program (Fig. 1). Portable traps were operated in seven streams with an average capture efficiency of 20%. D-ring nets were used in eight streams with an average capture efficiency of 20%. Permanent traps were used in eight streams with an average capture efficiency of 66%.

Population Estimates 1957–1999

Weir data for 1957–1979 were combined with trap data for 1980–1999 to provide a continuous series of lake-wide abundance estimates of spawning sea lampreys. To estimate numbers of spawning-phase sea lampreys, mark-recapture studies were implemented in trapped streams (Heinrich *et al.* 1987, Purvis and McDonald 1987) beginning in 1986. During 1986–1999, an average of 17 streams was assessed annually in Lake Superior, and mark-recapture estimates were made using a modification of the Schaefer (1951) model (Mullett *et al.* 2003). Because trapping was relatively consistent from 1980 to 1999, the trap sampling efficiency was used to estimate sea lamprey abundance for 1980–1985 when trap catch information was available but mark-recapture estimates were not (Mullett *et al.* 2003). If neither mark-recapture nor sampling efficiency estimates were available for a river, we estimated sea lamprey abundance using a multiple linear regression estimator based on stream drainage area, geographic region of the lake, stream category (1 or 2), year, and the number of years since the last treatment (Mullett *et al.* 2003).

Because there was no measure of efficiency for the 1957–1979 weir data, we estimated a 66% trapping efficiency based on mark-recapture estimates at seven sea lamprey barriers with permanent traps during 1986–1999. We applied this efficiency to weir catches, and converted the catches to abundance estimates of spawning sea lampreys. A predictive model similar to that described above was developed for the combined weir and trap data that spanned 1957–1999. We then applied an adjustment factor to the 1957–1979 data that was based on the comparison of predictions from the two models for the 1980–1999 data.

Spawning-phase sea lamprey abundance averaged 558,000 sea lampreys annually during 1957–1961, prior to control, then declined to 77,000 sea lampreys annually during 1962–1999 (Fig. 4). During 1962–1999, the abundance of spawners in Lake Superior declined 1,500 per year ($F_{1,36}$ = 5.04, $p = 0.031$, $R^2 = 12\%$).

Fish Community Objective

The Lake Superior Committee fish community objective for sea lampreys was to achieve a 50% reduction in parasitic-phase sea lamprey abundance by 2000, and a 90% reduction by 2010 (Busiahn 1990). To assess our progress toward this objective, we used the abundance of spawning-phase sea lampreys as an indicator of parasitic-phase sea lamprey abundance, with an abundance benchmark based on the 1986–1989 average annual abundance of spawning-phase sea lampreys. The average number of spawning-phase sea lampreys from 1996–1999 (84,000) was greater than half the average number of spawning sea lampreys from 1986–1989 (26,000), although the difference was not significant ($t = 2.04$, $df = 6$, $p = 0.087$).

The probability of achieving the 2000 and 2010 fish community objectives may have been reduced by the increased budgetary constraints on the sea lamprey control program during the early 1990s, movement away from a reliance on lampricides, discontinuation of the sterile-male-release technique in Lake Superior tributaries, lags in construction of new sea lamprey barriers, and regulatory and permitting constraints on lampricides and barrier construction. Additionally, stocks of coregonids increased during the 1980s and 1990s (Bronte *et al. in review*) and this may have led to an increase in survival of sea lamprey transformers similar to that observed in northern Lake Huron (Young *et al.* 1996). During 1999–2000, the LSC reviewed the Lake Superior fish community objectives and initiated a revision of the sea lamprey objective to levels that would cause insignificant mortality of adult lake trout.

SOURCE OF PARASITIC-PHASE SEA LAMPREYS

There were several sources of parasitic-phase sea lampreys in Lake Superior since lampricide control began: (1) undetected populations of larvae, (2) known populations of larvae not treated with lampricide, (3) larvae in treated streams that recruited and transformed during the interval between treatments, (4) larvae that survived a lampricide treatment and transformed before the next treatment, (5) larvae produced because of ineffective barriers, and (6) parasitic-phase sea lampreys that migrated to Lake Superior from Lakes Michigan and Huron.

We reviewed each of the potential sources and believe that most of the parasitic-phase sea lampreys in Lake Superior since the start of lampricide control were from larvae that survived lampricide treatments. We predicted transformer production 2 years after treatment based on assessments conducted in 1995–1999, assuming an instantaneous lampricide mortality of 95%, and using a stream ranking model to forecast larval growth and transformation (Christie *et al.* 2003). Transformer production two years after treatment exceeded the level that originally triggered the treatment in 42% of the treated streams. Yet only 14 Lake Superior streams were treated every 2 years on average during 1958–1999, and eight of these were associated with lentic areas and were treated frequently to limit colonization of offshore areas. In streams with large larval populations, even a small fraction of treatment survivors can contribute large numbers of parasitic-phase sea lampreys to the lake during the years until the next treatment.

Other sources of parasitic-phase sea lampreys were not major contributors to the population. The probability of an unknown major source was small, because we conducted systematic assessments of all Lake Superior streams with the potential to produce sea lampreys. Although untreated streams (primarily Category 3 streams) and lentic areas (Table 3) contain stable populations of larvae, the contribution from these sources was relatively small. Streams that were treated with lampricide less frequently (Category 2 and 3 streams) had the potential to produce transformers during the interval between treatments, but these streams had long treatment intervals due to their limited recruitment of larvae and therefore their production of transformers between treatments was probably not a major contribution. Although larvae were produced upstream of sea lamprey barriers on the Big Carp, Misery, and Neebing-McIntyre rivers, their contribution was probably small because these upstream areas continued to be assessed and treated with lampricide when needed. Migration into Lake Superior from the other Great Lakes was insignificant according to many years of mark-recapture and coded-wire tagging experiments.

EFFECTS ON LAKE TROUT POPULATIONS

The combined effects of intensive fishing exploitation and sea lamprey predation resulted in the collapse of lake trout stocks and the closure of the fishery by 1962 (Pycha and King 1975, Pycha 1980). The annual harvest of lake trout was less than 1,000 t in 1879, when lake-wide harvest statistics were first available, peaked at 3,000 t in 1903, and averaged 2,000 t per year during 1913–1950 (Baldwin *et al.* 1979). The annual harvest of about 2,000 t suggested a sustainable annual yield during 1913–1950. However, abundance actually decreased 50% during this period and the yield resulted from a doubling of gill-net efficiency during the 1940s as nets and fishing methods improved (Pycha and King 1975). Fishing intensity, yield, and abundance then declined during 1953–1961, as sea lampreys invaded Lake Superior, increased in abundance, and preyed on remaining lake trout (Pycha and King 1975, Swanson and Swedberg 1980, Pycha 1980).

The strategy for restoring lake trout in Lake Superior was to increase recruitment by stocking, and to reduce total annual mortality by controlling sea lampreys and regulating fisheries (Lawrie and Rahrer 1972, 1973; Lawrie 1978; Hansen *et al.* 1995a). Several studies in the 1990s suggested that lake trout recovery had progressed far enough to cease stocking, so long as lake trout fisheries were prudently regulated (Hansen *et al.* 1995a, 1995b, 1996, 1997). More recent evidence supported these claims and indicated that wild lake trout stocks in Michigan waters were close to or exceeded historical abundance (Wilberg 2000) and that the stocks also were experiencing density-dependent compensation in survival (Doemel 2000), both indicators of stock recovery. Fishery managers on Lake Superior declared victory in their pursuit of lake trout restoration after more than 35 years of effort, and ceased stocking of lake trout in most waters of the lake in 1996. However, mortality by sea lampreys and demand by recreational, commercial, and tribal harvest continued to threaten the future of lake trout stocks in Lake Superior during 1997–1999.

Wounding

The incidence of sea lamprey wounds on lake trout in Lake Superior was derived from observed numbers of Type A, Stage-I, -II, and -III sea lamprey marks (King and Edsall 1979) on lake trout caught in April and May (Hansen *et al.* 1994). In 1986, a standardized method of calculating the sea lamprey wounding rate (wounds per 100 fish) was initiated by all fishery management agencies with jurisdiction on Lake Superior, with the exception that Minnesota did not report A-III wounds. Sea lamprey wounding of lake trout was determined from annual assessment fisheries in the U.S. and from catches of lake trout in commercial fisheries in Canada. Annual weighted-mean sea lamprey wounding of lake trout longer than 43 cm was defined as the number of sea lamprey wounds divided by the number of lake trout sampled in all management areas.

The average sea lamprey wounding rate across Lake Superior during 1986–1999 was five per 100 fish, but wounding rates were generally higher during 1989–1993 than either preceding or succeeding periods (Fig. 5). The average sea lamprey wounding rate in 1999 was similar to the 1986–1998 mean for all size-classes of lake trout. Average sea lamprey wounding rates increased with lake trout length (Fig. 6).

Mortality

The number of lake trout that died from sea lamprey attacks each year in Lake Superior was estimated from a statistical relation between the probability of surviving a sea lamprey attack, the sea lamprey wounding rate, and a model of lake trout interactions with sea lampreys (Hansen *et al.* 1994). The probability of survival for a sea lamprey attack was 0.35 for lake trout 43–53 cm long, 0.45 for lake trout 53–63 cm long, and 0.55 for lake trout longer than 63 cm (Swink 2003). However, Koonce and Pycha (1985) estimated the probability of survival from sea lamprey attacks as low as 0.14, which would result in higher estimates of lake trout deaths.

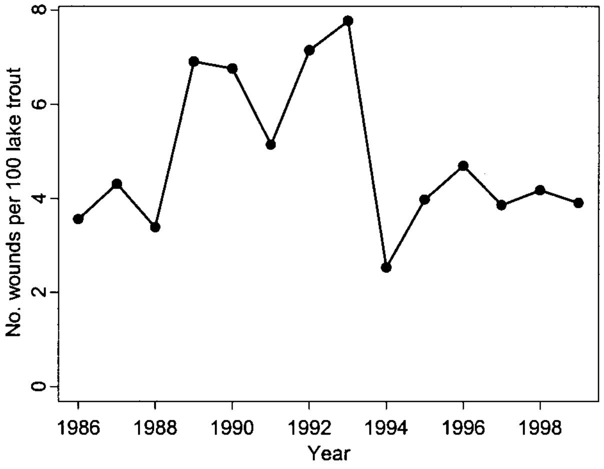


FIG. 5. Average sea lamprey wounding rates on lake trout captured in Lake Superior during spring 1986–1999.

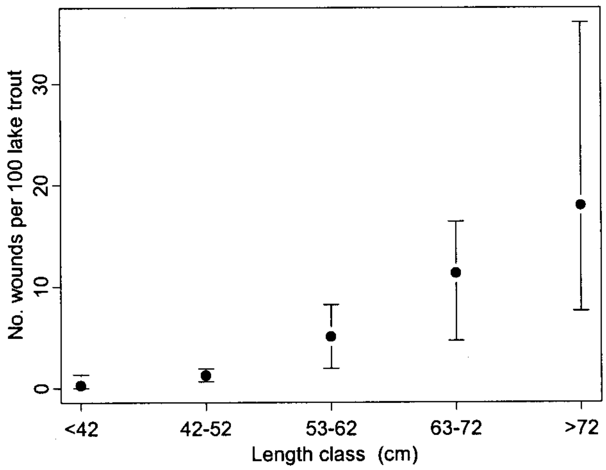


FIG. 6. Average sea lamprey wounding rates (± minimum and maximum) on five length-classes of lake trout captured in Lake Superior during spring 1986–1999. The wounds for lake trout < 42 cm do not include information from Michigan waters of Lake Superior.

Fish Community Objective

The fish community objective for lake trout in Lake Superior was to achieve a sustained annual yield (human harvest) of 2,000 t from naturally reproducing stocks (Busiahn 1990, Hansen 1996). This objective was based on the historic average annual harvest during 1929–1943, comprising all lake trout morphotypes. The average annual harvest of lake trout from all Lake Superior fisheries during 1995–1999 was 350 t, only 18% of the fishery objective and historic average annual harvest.

The average number of spawning-phase sea lampreys in Lake Superior was 74,000 during 1995–1999. Each sea lamprey was estimated to kill an average of 6.75 kg of lake trout annually based on a study in the eastern Wisconsin waters of Lake Superior (Hansen 1994). From this information, we estimated that 500 t of lake trout were killed by sea lampreys annually during 1995–1999. So, sea lampreys accounted for 59% and harvest by humans for 41% of the total annual extraction of lake trout from Lake Superior during those years.

RECOMMENDATIONS

Although sea lamprey abundance in Lake Superior has not been reduced to the level specified in the fish community objectives, it is important to maintain a basin-wide perspective when setting goals for sea lamprey control. The fish community objective for Lake Superior may not be realistic in light of sea lamprey population trends in the other Great Lakes. As part of the GLFC's strategic vision, economic injury levels for damage to fish populations by sea lampreys are being developed for each of the Great Lakes (GLFC 1992a). An economic injury level (EIL) is the sea lamprey population level at which additional money spent on suppression does not result in commensurate economic returns (Sawyer 1980, Koonce *et al.* 1993). These levels can be used to distribute sea lamprey control resources among the Great Lakes.

We make the following recommendations for the continued suppression and potential reduction of the sea lamprey population in Lake Superior: (1) increase the frequency of lampricide treatments on those streams that consistently produce large numbers of sea lamprey larvae; (2) determine how larvae survive TFM treatments; (3) develop EIL's and other procedures that select streams for treatment based on long-term costs, benefits, and risks; and, (4) where feasible, construct sea lamprey barriers in streams that have large amounts of Type I habitat.

We believe sea lamprey larvae that survive lampricide treatments are a major source of the parasitics in Lake Superior. Survival of a TFM treatment ranged from 1 to 7% 1 year after treatment for larval sea lampreys. In streams with large larval populations, this small fraction of survivors comprises a large number of sea lampreys, which can contribute parasitics to the lake annually until the next stream treatment. Increasing the frequency of lampricide treatments on those streams with consistently large numbers of sea lamprey larvae will probably reduce the contribution that these streams make to the parasitic population. This approach is based on the assumption that larvae that survive a lampricide treatment 1 year will be susceptible to treatment in the following years. More research is needed to confirm or refute this assumption. Throughout the decades of lampricide use in the sea lamprey control program, speculation has been that larvae survive treatments because they reside in areas protected from the lampricide application, e.g., backwaters or other freshwater influences. Shifts in pH levels have also been thought to influence toxic effects of TFM on sea lampreys (Bills and Johnson 1992). Determining the mechanism or mode by which sea lamprey larvae survive treatments may allow us to better target larval populations for treatment.

We believe the application of lampricide treatments should be optimized over a several-year window of time, because of the fluctuations in the annual abundance of sea lampreys in Lake Superior and the occasional occurrence of years with very large populations. Simply put, more effort should be spent in those years with large larval populations than in those years with low populations. Developing procedures that select streams for treatment based on multiple-year costs, benefits, and risks will increase our efficiency at suppressing sea lamprey populations.

Effective barriers limit the amount of available habitat for sea lamprey larvae and reduce or eliminate the production of larvae upstream of the barrier. Barriers also cut costs of sea lamprey control in the long run by eliminating the need for future lampricide treatments (Lavis et al. 2003). Selective placement of barriers in streams with large areas of Type I habitat is an efficient way to limit sea lamprey production. We recommend that barriers be constructed in the Pic, Goulais, and Nipigon rivers, which have 57, 41, and 24 ha of Type I habitat. We also recommend that barriers on the Misery, Neebing-McIntyre, and Big Carp rivers be improved or removed, as they have been ineffective in blocking sea lamprey production in 22 out of 25 stream-years of operation.

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REFERENCES

Applegate, V.C., Howell, J.H., Moffett, J.W., Johnson, B.G.H., and Smith, M.A. 1961. *Use of 3-trifluoromethyl-4-nitrophenol as a selective sea lamprey larvicide*. Great Lakes Fish. Comm. Tech. Rep. No. 1.

Armour, C.L., Burnham, K.P., and Platts, W.S. 1983. *Field methods and statistical analyses for monitoring small salmonid streams*. U.S. Dept. Int., Fish Wildl. Serv. FWS/OBS-83/33.

Auer, N.A. 1996. Response of spawning lake sturgeons to change in hydroelectric facility operation. *Trans. Am. Fish. Soc.* 125:66–77.

Baldwin, N.S., Saalfeld, R.W., Ross, M.A., and Buettner, H.J. 1979. *Commercial fish production in the Great Lakes 1867–1977*. Great Lakes Fish. Comm. Tech. Rep. No. 3.

Bergstedt, R.A., and Genovese, J.H. 1994. New technique for sampling sea lamprey larvae in deepwater habitats. *N. Am. J. Fish. Manage.* 14:449–452.

Bills, T.D., and Johnson, D.A. 1992. *Effect of pH on the toxicity of TFM to sea lamprey larvae and nontarget species during a stream treatment*. Great Lakes Fish. Comm. Tech. Rep. No. 57:7–19.

_____, Boogaard, M.A., Johnson, D.A., Brege, D.A., Scholefield, R.J., Westman, R.W., and Stephens, B.E. 2003. Development of a pH/alkalinity treatment model for applications of the lampricide TFM to streams tributary to the Great Lakes. *J. Great Lakes Res.* 29 (Suppl. 1):510–520.

Boogaard, M.A., Bills, T.D., and Johnson, D.A. 2003. Acute toxicity of TFM and a TFM/Niclosamide mixture to selected species of fish, including lake sturgeon *(Acipenser fulvescens)* and mudpuppies *(Necturus maculosus)*, in laboratory and field exposures. *J. Great Lakes Res.* 29 (Suppl. 1):529–541.

Bowen, A.K., Weisser, J.W., Bergstedt, R.A., and Famoye, F. 2003. Response of larval sea lampreys (*Petromyzon marinus*) to pulsed DC electrical stimuli in laboratory experiments. *J. Great Lakes Res.* 29 (Suppl. 1):174–182.

Brege, D.C., Davis, D.M., Genovese, J.H., McAuley, T.C., Stephens, B.E., and Westman, R.W. 2003. Factors responsible for the reduction in quantity of the lampricide, TFM, applied annually in streams tributary to the Great Lakes from 1979 to 1999. *J. Great Lakes Res.* 29 (Suppl. 1):500–509.

Bronte, C.R., Ebener, M.P., Schreiner, D.R., DeVault, S.S., Petzold, M.M., Jensen, D.A., Richards, C., and Lozano, S.J. *in review.* A case history of the fish community of Lake Superior, 1970–2000: a restoration in progress. *Can. J. Fish. Aquat. Sci.*

Busiahn, T.R. (ed.). 1990. *Fish Community Objectives for Lake Superior*. Great Lakes Fishery Commission, Ann Arbor, MI. Spec. Pub. 90-1.

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

_____, Adams, J.V., Steeves, T.B., Slade, J.W., Cuddy, D.W., Fodale, M.F., Young, R.J., Kuc, M., and Jones, M.L. 2003. Selecting Great Lakes streams for lampricide treatment based on larval sea lamprey surveys. *J. Great Lakes Res.* 29 (Suppl. 1):152–160.

Dahl, F.H., and McDonald, R.B. 1980. Effects of control of the sea lamprey (*Petromyzon marinus*) on migratory and resident fish populations. *Can. J. Fish. Aquat. Sci.* 37:1886–1894.

Dawson, V.K. 2003. Environmental fate and effects of the lampricide Bayluscide: a review *J. Great Lakes Res.* 29 (Suppl. 1):475–492.

Dochoda, M.R. (ed.). 1988. *Committee of the whole workshop on implementation of the Joint Strategic Plan for Management of Great Lakes Fisheries (reports and recommendations from the 18–20 February 1986 and 5–6 May 1986 meetings)*. Great Lakes Fishery Commission, Ann Arbor, MI. Spec. Pub. 88-1.

Dodd, H.R., Hayes, D.B., Baylis, J.R., Carl, L.M., Goldstein, J.D., McLaughlin, R.L., Noakes, D.L.G., Porto, L.M., and Jones, M.L. 2003. Low-head sea lamprey barrier effects on stream habitat and fish communities in the Great Lakes basin. *J. Great Lakes Res.* 29 (Suppl. 1):386–402.

Doemel, J.M. 2000. Dynamics of lake trout recruitment in Michigan waters of Lake Superior. M.S. thesis, University of Wisconsin, Stevens Point WI.

Garton, R.R. 1980. A simple continuous-flow toxicant delivery system. *Water Res.* 14:227–230.

Gilderhus, P.A. 1985. *Solid bars of 3-trifluoromethyl-4-nitrophenol: a simplified method of applying lampri-*

cide to small streams. Great Lakes Fish. Comm. Tech. Rep. No. 47: 6–12.

_____, and Johnson, B.G.H. 1980. Effects of sea lamprey (*Petromyzon marinus*) control in the Great Lakes on aquatic plants, invertebrates, and amphibians. *Can. J. Fish. Aquat. Sci.* 37:1895–1905.

Great Lakes Fishery Commission (GLFC). 1956. *Annual report of the Great Lakes Fishery Commission for 1956*, Ann Arbor, MI.

_____. 1967. *Annual report of the Great Lakes Fishery Commission for 1965*, Ann Arbor, MI.

_____. 1982. *Minutes of Annual Meeting of Lake Superior Committee, March, 1982*. Great Lakes Fish. Comm., Ann Arbor, MI. Appendix XXVIII, pp. 255–256.

_____. 1983a. *Minutes of Annual Meeting of Lake Superior Committee, March, 1983*. Great Lakes Fish. Comm., Ann Arbor, MI. Appendix XXII, pp. 187–188.

_____. 1983b. *Minutes of Sea Lamprey Committee, April 1983*. Great Lakes Fish. Comm., Ann Arbor, MI. Appendix X, pp. 87–97.

_____. 1984. *Annual report of the Great Lakes Fishery Commission for 1982*, Ann Arbor, MI.

_____. 1986. *Minutes of Annual Meeting of Lake Superior Committee, March, 1986*. Great Lakes Fish. Comm., Ann Arbor, MI. Appendix XXV, pp. 203–204.

_____. 1992a. *Strategic vision of the Great Lakes Fishery Commission for the decade of the 1990s*. Great Lakes Fishery Commission, Ann Arbor, MI.

_____. 1992b. *Minutes of the Annual Meeting of the Great Lakes Fishery Commission*, Ann Arbor, MI. Appendix VI, pp. 35–101.

_____. 1993. *Minutes of the Annual Meeting of the Great Lakes Fishery Commission*, Ann Arbor, MI. Appendix III, pp. 11–74.

_____. 1996. *Minutes of the Annual Meeting of the Great Lakes Fishery Commission*, Ann Arbor, MI. Appendix VI, pp. 45–180.

Hansen, M.J. (ed.). 1990. *Lake Superior: The state of the lake in 1989*. Great Lakes Fishery Commission, Ann Arbor, MI. Spec. Pub. 90-3.

_____. (ed.). 1994. *The state of Lake Superior in 1992*. Great Lakes Fishery Commission, Ann Arbor, MI. Spec. Pub. 94-1.

_____. (ed.). 1996. *A lake trout restoration plan for Lake Superior*. Great Lakes Fishery Commission, Ann Arbor, MI.

_____, Ebener, M.P., Shively, J.D., and Swanson, B.L. 1994. Lake trout. In *The state of Lake Superior in 1992*, ed. M.J. Hansen, pp. 13–34. Great Lakes Fishery Commission, Ann Arbor, MI. Spec. Pub. 94-1.

_____, Peck, J.W., Schorfhaar, R.G., Selgeby, J.H., Schreiner, D.R., Schram, S.T., Swanson, B.L., MacCallum, W.R., Burnham-Curtis, M.K., Curtis, G.L., Heinrich, J.W., and Young, R.J. 1995a. Lake trout (*Salvelinus namaycush*) populations in Lake Superior and their restoration in 1959–1993. *J. Great Lakes Res.* 21:152–175.

_____, Schorfhaar, R.G., Peck, J W., Selgeby, J.H., and Taylor, W.W. 1995b. Abundance indices for determining the status of lake trout restoration in Michigan waters of Lake Superior. *N. Am. J. Fish. Manage.* 15: 830–837.

_____, Ebener, M.P., Schorfhaar, R.G., Schram, S.T., Schreiner, D.R., Selgeby, J.H., and Taylor, W.W. 1996. Causes of declining survival of lake trout stocked in U.S. waters of Lake Superior in 1963–1986. *Trans. Am. Fish. Soc.* 125:831–843.

_____, Bence, J.R., Peck, J.W., and Taylor, W.W. 1997. Evaluation of the relative importance of hatchery-reared and wild fish in the restoration of Lake Superior lake trout. In *Developing and sustaining world fisheries resources: the state of science and management*, eds. D.A. Hancock, D.C. Smith, A. Grant, and J.P. Beumer, pp. 492–497. 2nd World Fisheries Congress proceedings. CSIRO Publishing. Collingwood, Australia.

_____, Adams, J.V., Cuddy, D.W., Richards, J.M., Fodale, M.F., Larson, G.L., Ollila, D.J., Slade, J.W., Steeves, T.B., Young, R.J., and Zerrenner, A. 2003. Optimizing larval assessment to support sea lamprey control in the Great Lakes. *J. Great Lakes Res.* 29 (Suppl. 1):766–782.

Hanson, L.H. 1990. Integration of the sterile-male-release technique in the sea lamprey control program in Lake Superior. Paper presented at Lake Superior Technical Committee 9 February 1990 meeting. Thunder Bay, Ontario.

Heinrich, J.W., Weise, J.G., and Smith, B.R. 1980. Changes in biological characteristics of the sea lamprey (*Petromyzon marinus*) as related to lamprey abundance, prey abundance, and sea lamprey control. *Can. J. Fish. Aquat. Sci.* 37:1861–1871.

_____, Seelye, J.G., and Johnson, B.G.H. 1987. Proceedings of the workshop to evaluate sea lamprey populations (WESLP) in the Great Lakes, August 1985. In *Evaluation of sea lamprey populations in the Great Lakes: background papers and proceedings of the August 1985 workshop*, ed. B.G.H. Johnson, pp. 1–32. Great Lakes Fishery Commission, Ann Arbor, MI. Spec. Pub. 87-2 (D).

Hintz, A.K. 1993. Electrofishing burrowed larval sea lamprey (*Petromyzon marinus*), the effect of slow pulsed direct current variables on emergence at varying water temperatures. M.S. thesis, Central Michigan University, Mount Pleasant MI.

Howell, J.H., King, E.L., Jr., Smith, A.J., and Hanson, L.H. 1964. *Synergism of 5, 2′-dichloro-4′-nitrosalicylanilide and 3-trifluoromethyl-4-nitrophenol in a selective lamprey larvicide*. Great Lakes Fish. Comm. Tech. Rep. No. 8.

Hubert, T.D. 2003. Environmental fate and effects of the lampricide TFM: a review. *J. Great Lakes Res.* 29 (Suppl. 1):456–474.

Johnson, D.A., and Stephens, B.E. 2003. Historical perspective on the development of procedures for conducting on-site toxicity tests and for measuring concentrations of lampricides in the sea lamprey control program during 1957 to 1999. *J. Great Lakes Res.* 29 (Suppl. 1):521–528.

_____, Weisser, J.W., and Bills, T.D. 1999. *Sensitivity of lake sturgeon (Asipenser fulvescens) to the lampricide 3-trifluoromethyl-4-nitrophenol (TFM) in field and laboratory exposures*. Great Lakes Fish. Comm. Tech. Rep. No. 62: 1–23.

King, E.L., and Edsall, T.A. 1979. *Illustrated field guide for the classification of sea lamprey attack marks on Great Lakes lake trout*. Great Lakes Fishery Commission, Ann Arbor, MI. Spec. Pub. 791.

Koonce, J.F., and Pycha, R.L. 1985. *Observability of lake trout mortality due to attacks of sea lamprey*. Research Completion Report. Great Lakes Fishery Commission, Ann Arbor, MI.

_____, Eshenroder, R.L., and Christie, G.C. 1993. An economic injury level approach to establishing the intensity of sea lamprey control in the Great Lakes. *N. Am. J. Fish. Manage.* 13:1–14.

Lavis, D.S., Hallett, A.G., Koon, E.M., and McAuley, T.C. 2003. History of and advances in barriers as an alternative method to suppress sea lampreys in the Great Lakes. *J. Great Lakes Res.* 29 (Suppl. 1): 362–372.

Lawrie, A.H. 1954. *Annual Report of the Great Lakes Research Committee*, Univ. of Toronto, Ont. Appendix 7, pp. 1–6.

_____. 1978. The fish community of Lake Superior. *J. Great Lakes Res.* 4:513–549.

_____, and Rahrer, J.F. 1972. Lake Superior: effects of exploitation and introductions and introductions on the salmonid community. *J. Fish. Res. Board Can.* 29: 765–776.

_____, and Rahrer, J.F. 1973. *Lake Superior: a case history of the lake and its fisheries*. Great Lakes Fish. Comm. Tech. Rep. No. 19.

Loeb, H.A. 1953. *Sea lamprey spawning: Wisconsin and Minnesota streams of Lake Superior*. U.S. Fish Wildl. Serv., Spec. Sci. Rep. Fish. 97.

_____, and Hall, A.E. Jr. 1952. *Sea lamprey spawning: Michigan streams of Lake Superior*. U.S. Fish Wildl. Serv., Spec. Sci. Rep. Fish. 70.

Maitland, P.S. 1980. Assessment of lamprey and fish stocks in the Great Lakes in relation to control of the sea lamprey (*Petromyzon marinus*): report from the SLIS assessment measurements task force. *Can. J. Fish. Aquat. Sci.* 37:2197–2201.

McLain, A.L., Smith, B.R., and Moore, H.H. 1965. *Experimental control of sea lampreys with electricity on the south shore of Lake Superior, 1953–60*. Great Lakes Fish. Comm. Tech. Rep. 10.

Mullett, K.M. 1997. Agreement of observers classifying larval sea lamprey (*Petromyzon marinus*) habitat. M.S. thesis, Northern Michigan University, Marquette MI.

_____, and Bergstedt, R.A. 2003. Agreement among observers in classifying larval sea lamprey (*Petromyzon marinus*) habitat. *J. Great Lakes Res.* 29 (Suppl. 1):183–189.

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

Purvis, H.A., and McDonald, R.B. 1987. Summary of evaluation methods and population studies of spawning phase sea lamprey. In *Evaluation of sea lamprey populations in the Great Lakes: background papers and proceedings of the August 1985 workshop*, ed. B.G.H. Johnson. Great Lakes Fishery Commission, Spec. Pub. 87-2 (C):1–112.

Pycha, R.L. 1980. Changes in mortality of lake trout (*Salvelinus namaycush*) in Michigan waters of Lake Superior in relation to sea lamprey (*Petromyzon marinus*) predation, 1968–78. *Can. J. Fish. Aquat. Sci.* 37: 2063–2073.

_____, and King, G.R. 1975. *Changes in the lake trout population of southern Lake Superior in relation to the fishery, the sea lamprey, and stocking, 1950–70*. Great Lakes Fish. Comm. Tech. Rep. No. 28.

Sawyer, A.J. 1980. Prospects for integrated pest management of the sea lamprey (*Petromyzon marinus*). *Can. J. Fish. Aquat. Sci.* 37:2081–2092.

Schaefer, M.B. 1951. Estimation of size of animal populations by marking experiments. *U.S. Dept. Int. Fish Wildl. Serv. Bull.* 69:187–203.

Schleen, L.P., Christie, G.C., Heinrich, J.W., Bergstedt, R.A., Young, R.J., Morse, T.J., Lavis, D.S., Bills, T.D., Johnson, J.E., and Ebener, M.P. 2003. Development and implementation of an integrated program for control of sea lampreys in the St. Marys River. *J. Great Lakes Res.* 29 (Suppl. 1):677–693.

Schuldt, R.J., and Goold, R. 1980. Changes in the distribution of native lampreys in Lake Superior in response to sea lamprey (*Petromyzon marinus*) control, 1953–77. *Can. J. Fish. Aquat. Sci.* 37: 1872–1885.

_____, and Heinrich, J.W. 1982. Portable trap for collecting adult sea lampreys. *Prog. Fish-Cult.* 44: 220–221.

Slade, J.W., Adams, J.V., Christie, G.C., Cuddy, D.W., Fodale, M.F., Heinrich, J.W., Quinlan, H.R., Weise, J.G., Weisser, J.W., and Young, R.J. 2003. Techniques and methods for estimating abundance of larval and metamorphosed sea lampreys in Great Lakes tributaries, 1995 to 2002. *J. Great Lakes Res.* 29 (Suppl. 1):137–151.

Smith, B.R., and Tibbles, J.J. 1980. Sea lamprey (*Petromyzon marinus*) in Lakes Huron, Michigan, and Superior: history of invasion and control, 1936–78. *Can. J. Fish. Aquat. Sci.* 37:1780–1801.

_____, Tibbles, J.J., and Johnson, B.G.H. 1974. *Control of the sea lamprey,* Petromyzon marinus*, in Lake Superior, 1953–70*. Gt. Lakes Fish. Comm. Tech. Rep. No. 26.

Swanson, B.L., and Swedberg, D.V. 1980. Decline and recovery of the Lake Superior Gull Island Reef lake trout (*Salvelinus namaycush*) population and the role of sea lamprey (*Petromyzon marinus*). *Can. J. Fish. Aquat. Sci.* 37:2074–2080.

Swink, W.D. 2003. Host selection and lethality of attacks by sea lampreys (*Petromyzon marinus*) in laboratory studies. *J. Great Lakes Res.* 29 (Suppl. 1): 307–319.

Torblaa, R.L. 1968. *Effects of lamprey larvicides on invertebrates in streams*. U.S. Fish Wildl. Serv. Spec. Sci. Rep. Fish. 572.

Twohey, M.B., Heinrich, J.W., Seelye, J.G., Fredricks, K.T., Bergstedt, R.A., Kaye, C.A., Schloefield, R.J., McDonald, R.B., and Christie, G.C. 2003. The sterile-male-release technique in Great Lakes sea lamprey management. *J. Great Lakes Res.* 29 (Suppl. 1): 410–423.

Weisser, J.W. 1994. Response of larval sea lamprey (*Petromyzon marinus*) to electrical stimulus. M.S. thesis, Northern Michigan University, Marquette MI.

_____, Adams, J.V., Schuldt, R.J., Baldwin, G.A., Lavis, D.S., Slade, J.W., and Heinrich, J.W. 2003. Effects of repeated TFM applications on riffle macroinvertebrate communities in four Great Lakes tributaries. *J. Great Lakes Res.* 29 (Suppl. 1):552–565.

Wilberg, M. 2000. Historic and modern lake trout abundance, effects of fishing on lake trout, and dynamics of the commercial lake trout fishery in Michigan waters of Lake Superior. M.S. thesis, University of Wisconsin, Stevens Point WI.

Young, R.J., Christie, G.C., McDonald, R.B., Cuddy, D.W., Morse, T.J., and Payne, N.R. 1996. Effects of habitat change in the St. Marys River and northern Lake Huron on sea lamprey (*Petromyzon marinus*) populations. *Can. J. Fish. Aquat. Sci.* 53:99–104.

Zippin, C. 1958. The removal method of population estimation. *J. Wildlife Manage.* 22:82–90.

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