GREAT LAKES FISHERY COMMISSION

Project Completion Report[1]

# ASSESSMENT OF ALTERNATIVE SEA LAMPREY CONTROL RESEARCH PRIORITIES

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# Assessment of Alternative Sea Lamprey Control Research Priorities

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# ABSTRACT

A review and synthesis of existing methods, published concepts, and hypothetical concepts was conducted to identify key research needs leading to the development and implementation of practical alternatives to the control of sea lamprey (Petromyzon marinus) abundance in the Great Lakes using lampricides. The review considered lampricides, barriers, trapping, sex-ratio manipulation, attractants and repellants, genetic manipulation, developmental blockers, natural controls, and habitat manipulation, and identified three key research needs within each category. Although some reductions in lampricide use can be attained through improved application methods, the largest gains will be made by the application of other control methods. Improvements to existing alternatives (barriers, trapping, and experimental sterile-male releases) probably can be made sooner than new alternatives can be brought on line. Among new alternatives, research into attractants and repellants and developmental blockers (ways to delay, alter, or induce metamorphosis) are promising but cost will likely be high. The development of migratory cues for use in attracting adult sea lamprey appears to be closer to implementation than practical ways to interfere with metamorphosis. Research into genetic manipulation to alter gene expression during critical life-history events (e.g., metamorphosis, reproduction) has just begun and must be considered a long-term strategy. The development and implementation of natural controls (competition, predation, parasites, pathogens, and host tolerance and resistance) cannot be assessed at present because there is a lack of knowledge concerning sea lamprey population regulation in the absence of human control efforts. Better definition of relationships between key habitat variables (e.g., substrate type, temperature) and larval abundance is needed before the scope for habitat manipulation can be examined. The use of alternative controls and knowledge of the joint impacts of these methods are of critical importance to the successful implementation of an integrated pest management program to control sea lamprey in the Great Lakes.

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# 1.0 INTRODUCTION

The Great Lakes Fishery Commission (GLFC) is responsible for formulating and implementing a program to eradicate or minimize sea lamprey (Petromyzon marinus) populations in the Great Lakes. The success of this program since the 1950s is based on the use of selective toxicants, primarily 3-trifluoromethyl-4-nitrophenol (TFM), to kill nonparasitic larvae in their natal streams before they metamorphose and migrate into the lakes. Effective control of sea lamprey abundance combined with wide-scale fish stocking, exploitation controls, habitat rehabilitation, water quality improvements, and other programs have produced an impressive recovery of fisheries resources in the Great Lakes (Koonce et al. 1993). These ongoing fisheries management programs are predicated on the continuing suppression of sea lamprey since the goal of eradicating sea lamprey from the Great Lakes is not practical. Thus, the emphasis in sea lamprey control has shifted towards minimizing populations to some level of abundance which exerts an acceptable level of mortality on desired fish stocks.

The development of effective supplementary and alternative sea lamprey control techniques is essential to the control program (Lamsa et al. 1980). Larval populations in lentic areas and in the large connecting channels between the lakes, particularly the St. Marys River, may be beyond the reach of a control program using chemicals. Improved water quality achieved at great expense in watersheds such as the Saginaw and Fox Rivers, has opened up new habitat for spawning and larval sea lamprey and will require increased control effort. Concerns about the effects of lampricides on non-target organisms (NRCC 1985) and the socio-economic acceptability of continued pesticide use are such that it is increasingly difficult to justify budgets necessary to achieve an acceptable level of control based on the use of chemicals (Koonce et al. 1993).

The GLFC and its control experts have been committed to the application of integrated pest management (IPM) concepts to control sea lamprey abundance since 1982. The fundamental concepts of IPM as applied in terrestrial insect and plant-pathogen managment include (1) an ecological orientation, (2) an economic foundation, and (3) the use of a variety of control methods consisting of pesticides combined with biological controls, pest resistant hosts, and cultural controls (Sawyer 1980). The GLFC reaffirmed the commitment to IPM recently in its vision statement (GLFC 1992):

> *The Commission will provide an integrated sea lamprey management program that supports the Fish Community Objectives for each of the Great Lakes and that is ecologically and socially acceptable.*

Two goals were established for sea lamprey management: (1) establish target levels of sea lamprey abundance to maximize the net benefits of management, and (2) suppress sea lamprey populations to target levels. The latter goal is characterized by four implementation steps including

> *... development and use of alternate control techniques to reduce reliance on lampricides to 50% of current levels....*

An optimistic target date of the year 2000 was set for meeting the lampricide-use guideline.

The GLFC commitment to IPM concepts and to the goals and milestones for judging implementation clearly place added emphasis on research to improve the efficiency and efficacy of existing control technologies and to develop and implement alternative control methods. A process for soliciting, reviewing, and funding alternative control research was initiated in 1991 to hasten progress and 12 projects were funded. Although these efforts have been productive, a recently adopted research strategy expressed some concern that progress toward the development and implementation of practical alternative control methods was not fast enough (Sawyer and Gillman 1994) to allow the GLFC to meet its stated commitments. The adoption of this strategy in an era of budget constraints requires the development of a research plan with explicit priorization of research needs to ensure that funds are spent prudently and that progress towards developing and implementing practical alternatives to chemical control occurs. The objective of this report is to identify research priorities which will aid the GLFC and its cooperators in the development and implementation of practical alternative control measures. To identify these priorities, a review and synthesis of existing methods, published concepts, and envisioned concepts was conducted.

This report is organized into nine technological areas: lampricide formulations and applications, barriers, trapping, sex-ratio manipulation (including sterile-male release), attractants/repellants, genetic manipulation, developmental blockers (including manipulation of growth or metamorphosis), natural controls (including competitive displacement, pathology, predators, and host tolerance/resistance), and habitat manipulation. Some areas are further divided into existing (barriers and sterile-male-release technique; SMRT) and new areas, where existing areas are those that are currently implemented or in the field-testing stage of development and new areas are at earlier stages in their development. This organization approximates the budget structure of the GLFC's sea lamprey program which consists of lampricide control, alternative controls, and ecology and integrated management. Although ecology and integrated management is an important subject area for research, it is not directly addressed in the results section of this report. Instead, research priorities that are relevant to more than one of the nine technological areas and that fall into a discipline such as physiology, ethology, or ecology, are identified in the discussion as being important to the ecology and integrated management area.

Lampreys have two life-history patterns: parasitic and non-parasitic. The parasitic life-cycle exemplifed by sea lamprey in the Great Lakes consists of a benign larval period lasting 3-7 yr followed by a metamorphosis which results in the development of a juvenile capable of parasitizing teleost fish (Applegate 1950, Potter 1980). Metamorphosis is a non-trophic period which begins in mid-July and is finished by late October. Newly metamorphosed parasites (juveniles) may emerge from the substrate and migrate into the Great Lakes in the fall or overwinter and migrate the following spring. After a parasitic period lasting 18-24 mo, the animals begin maturing and in the spring adults migrate upstream to complete maturation, spawn, and die. The non-parasitic life-history is the same as the parasitic type up to the end of metamorphosis. Following metamorphosis, non-parasitic species such as American brook lamprey (Lampetra appendix) immediately begin maturing sexually, foregoing the extended feeding period of parasitic species. Spawning and death occur the following spring. In this report, parasites and adults will be used when referring to juvenile animals feeding on teleosts and animals that are migrating upstream or spawning, respectively.

## 2.0 METHODS

Information for this review of research priorities was gathered primarily from published and in-house (grey) literature (Table 1). On-line reference databases were also searched. In addition, individuals involved in sea lamprey and fisheries management programs in the Great Lakes, experts in specific areas of alternative control, and IPM experts in terrestrial insect and plant-pathogen management, were interviewed (Appendix 1). The aim of the interviews was to check the information in the published literature, to identify additional sources of unpublished or soon-to-be published information, and to identify additional research or research approaches. A comprehensive list of all research needs was compiled (Appendix 2) and from this a first-draft report without the concluding section on research needs was prepared. Relevant sections of the draft were circulated to experts for comment. A final draft was then produced which identified research priorities within each

Table 1. Primary literature from GLFC-sponsored symposia, workshops, and meetings reviewed for research recommendations.

| Technology Area[A] | Reference |
|---|---|
| 1,2,3,4,5,6,7,8,9 | Lamsa et al. (1980) |
| 8,9 | Walters et al. (1980) |
| 1,2,3 | Johnson (1987) |
| 2 | Biette and Griswold (1988) |
| 1,2,4,5,8 | BOTE (1993) |
| 1,4,5,7,8 | Beamish and Eshenroder (1988) |
| 1,2,3 | Christie (1991) |
| 2,4,5,6,7,8 | Meyer (1990) |
| 1,2,3,4,5,6,7,8,9 | Bergstedt and Seelye (1992) |
| 1,4 | St. Mary's River Control Task Group (1992) |
| 1,2,3,4,5,6,7,8,9 | Seelye and Hanson (1992) |
| 4 | Sower and Hanson (1992) |
| 5 | Sorensen and Hanson (1994) |
| 4,7 | Youson and Holmes (1993) |
| 2 | Katopodis et al. (1994) |
| 1 | Koonce et al. (1993) |
| 5 | Sorensen and Gallaher (1994) |
| 7 | Youson et al. (1994c) |
| 5,7 | Zielinski (1994) |
| 4 | Sterile Male Release Technique Task Force (1994) |

[A] Numbers refer to technology areas as follows: 1--lampricide formulations and applications; 2--barriers; 3--trapping; 4--sex-ratio manipulation; 5--attractants and repellants; 6--genetic manipulation; 7--developmental blockers; 8--natural controls; and 9--habitat manipulation.

technological area. Four critieria were used to assess whether a particular research need in any of the nine technological areas was a priority: (1) potential impact, (2) feasibility of implementation, (3) cost, and (4) environmental impacts (Table 2).

Key research needs within each technology area are identified but not priorized in this report. These needs represent a synthesis of opinion. By distilling and reporting these research needs in this report, the process of establishing funding priorities should be enhanced considerably.

## 3.0 SEA LAMPREY RESEARCH PROGRAM

### 3.1 Lampricide Formulations/Applications

Lampricides have been used to kill larval sea lamprey and reduce the abundance of parasitic animals in the Great Lakes for more than 35 years. TFM is the principal lampricide and is used in liquid and slow-release bar formulations during treatments of natal streams. A second lampricide, Bayer 73, may be added in powdered form as a supplement to reduce TFM use and cost while retaining selective toxicity to lampreys. A granular form of Bayer 73 is used as a bottom toxicant to survey lotic and lentic areas. Unlike research into other areas of alternative control, most of the lampricide research is contracted with the U.S. Fish and Wildlife Service. The development of new lampricides has been suggested in the past, but the commitment of the GLFC to IPM, the recommendation by advisory committes that

Table 2. Criteria for assessing sea lamprey research needs. Modified from the GLFC's research strategy document.

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**1. Potential Impact**

- geographic scope (stream, lake, region)
- biological impact (sea lamprey populations, fish stocks)
- economic impact (sea lamprey control program, fishery)
- social impact (fishery)

**2. Feasibility of Implementation**

- technical feasibility in light of current knowledge
- research completed to date
- logistical uncertainties
- projected time line

**3. Cost**

- estimated research costs
- estimated cost to develop and implement practical management tool in relation to existing control methods

**4. Environmental Impacts**

- lampricide use
- non-target species
- water quality
- land-use
- other environmental attributes

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such research not be pursued, and the substantial costs of developing and registering new toxicants, essentially forecloses this option. Thus, the development of new lampricides is not considered in this review.

### *3.1.1 TFM Formulations*

Field formulations of TFM contain on average 38% active ingredient (TFM), 22% isopropanol, 38% water, and sodium fluoride (T. Bills, U.S. Fish and Wildlife Service, LaCrosse, Wisconsin, pers. comm.). Munkittrick et al. (1994) demonstrated that an unidentified contaminant in the carrier portion of the field formulation was a potent inducer of hepatic mixed function oxygenase (MFO) enzyme activity in fish in both field and laboratory conditions; induction was not associated with exposure to purified TFM nor was it associated with exposure to powdered Bayer 73 (Munkittrick et al. 1994). Limited testing of four batches of field-formulation TFM produced by Hoechst between 1990 and 1992 indicated that induction of MFO activity in fish varied between batches (Munkittrick et al. 1994). The extent of MFO induction also varies between formulations produced by Hoechst and Kinetic Industries (KI) (M. Servos, Department of Fisheries and Oceans, Burlington, Ontario, pers. comm.). Two different chemicals with MFO-inducing properties are contained in Hoechst formulations and three different chemicals with MFO inducing abilities are in KI formulations (Servos et al. 1994). Whether the same two chemicals in the Hoechst formulations are also found in KI formulations or if as many as five different chemicals are responsible for MFO induction in TFM formulations is not known.

The induction of MFO activity in aquatic organisms is believed to be a relatively sensitive but non-specific indicator of exposure to planar chemicals such as dioxins, polynuclear aromatic hydrocarbons (PAHs), and PCBs (Luxon et al. 1987). The relationship between MFO induction and other biological responses, including measures of fish health, are not clear. Munkittrick et al. (1994) reported that exposure to field-formulations of TFM induced MFO enzyme activity in goldfish (Carrasius auratus) and they observed a transient alteration of plasma steroid-hormone levels, principally testosterone, lasting at least 4 days post exposure. Similar findings have been reported in white sucker (Catostomus commersoni) and lake whitefish (Coregonus clupeaformis) exposed to pulp mill effluent in the Great Lakes (Munkittrick et al. 1991, 1992) but in these cases the induction of hepatic MFOs was long-term. No plausible causal mechanism linking steroid disruption and MFO induction has been established nor have adverse reproductive effects (e.g., reduced fecundity, lower hatching success, lower year-class strength) been reported in wild or feral populations as a result of disturbances to plasma steroid-hormone profiles.

MFO induction is a regulatory issue in Canada but not the United States at present. Despite the absence of strong causal connections, the principal concern associated with MFO induction in fish exposed to field-formulations of TFM is the potential for reproductive or teratogenic effects, particularly if the causal chemicals from past usage of TFM are persistent. The chemicals associated with MFO induction in TFM formulations used in the field should be identified. Preliminary work reported by Munkittrick et al. (1994) indicated that dioxins, furans, and PCBs were unlikely to be the inducing agents. The U.S. Environmental Protection Agency (EPA) was notified of the MFO induction and the agency indicated that the induction would not affect the re-registration process for TFM and Bayer 73 (T. Bills, U.S. Fish and Wildlife Service, LaCrosse, Wisconsin, pers. comm.).

Resistance to pesticides is common among insect pest populations and concern has been expressed periodically that larval sea lamprey may develop increased resistance to TFM (Lamsa et al. 1980). This concern is based on the long history of TFM use and the fact that some larvae (residuals) may survive TFM treatments (Purvis 1979). Scholefield and Seelye (1990) concluded that resistance to TFM had not developed in sea lamprey larvae because $LC_{50}$s for comparable bioassays conducted at the Lake Huron Biological Station (LHBS) in the 1960s and 1980s were not significantly different. More recent data from the 1990s are not available or have not been analyzed. The conclusion that larval sea lamprey have not developed resistance to lampricide refers only to the physiological expression of resistance under laboratory conditions; behavioral means of resistance are well known in insect management programs (Lockwood et al. 1984, Roush and Daly 1990) but have not been considered with respect to lampricide use. Even when physiological resistance develops, experience with insects shows that $LC_{50}$s change little until the frequency of resistance is high in the population (Roush and Miller 1986).

Physiological and behavioral expressions of resistance to pesticides in arthropods usually have a simple genetic basis, consisting of changes in loci on one or two genes. Most modern pesticides usually have a specific mode of action, which predisposes them to potentially high magnitudes of resistance by mutations of a single gene that either alters the target site or increases the metabolism of the pesticide (Roush and Daly 1990). These mutations are usually rare, but even frequencies of less than $10^{-6}$ may be sufficient to provide adequate mutations for resistance in fecund organisms. The modes of action and selectivity of TFM and Bayer 73 for sea lamprey are not definitively known, but if they are comparable to insecticides, then the potential for resistance should be taken more seriously.

Proof of behavioral resistance to lampricides in sea lamprey involves more than simply demonstrating that larvae avoid lampricides; it also requires proof that the trait (behavior) is heritable, i.e., that there are genetic differences between resistant and susceptible individuals or populations. Behavioral resistance in sea lamprey larvae might be expressed as an increased tendency to drift downstream, an increase in colonization of lentic areas, or movement into springs or backwater areas in which lampricide application (including secondary application) is not effective. Some data collected by the control agents may be useful for assessing these potential mechanisms. For example, an increasing number of residual larvae after lampricide treatments may suggest that treatments are selecting for individuals that are not killed by lampricide because they avoid the treatment. Whether residuals are resistant to lampricides or if they represent a measure of the effectiveness of a lampricide treatment is not known because lampricide resistance has not been investigated thoroughly in sea lamprey.

Given the importance of lampricides to the sea lamprey control program, research into the potential for development of lampricide resistance in larval sea lamprey is warranted. This research should consider both behavioral and physiological mechanisms of resistance and should include analysis of possible genetic differences in support of behavioral and physiological data. Resistance management programs are common place in insect control operations using pesticides and include an extensive monitoring program using diagnostic doses (a fixed dose of pesticide which kills susceptible individuals but not resistant individuals) rather than a range of doses to detect the presence of physiologically resistant individuals (ffrench-Constant and Roush 1990).

A granular formulation of TFM for use as a bottom toxicant has been developed but never used extensively. The principal problem is that contact time was too long (the time required to release the active ingredient) which caused too much dilution in deepwater areas for this formulation to be a practical tool (T. Bills, U.S. Fish and Wildlife Service, LaCrosse, Wisconsin, pers. comm.). At present there does not appear to be any solution to the dilution problem so research into this formulation has not continued.

### *3.1.2 Bayer 73 Formulations*

Bayer 73 is currently used as a wettable powder to supplement TFM and in granular formulation as a bottom toxicant. There are few published environmental concerns about Bayer 73 but the control agents are concerned with safety and handling during application. Bayer 73 is practically insoluble in water and the powder is difficult to handle when used to supplement TFM during lampricide treatments.

The impetus for the development of a liquid Bayer 73 formulation is to overcome the problem of the wettable powder settling out of solution prior to delivery with TFM during stream treatments. The concept is to produce a liquid Bayer 73 formulation that is soluble in water and would be added to TFM formulations at the application site. The two chemicals would not be mixed prior to application. The development and implementation of a liquid formulation is expected to require 3-4 years and is dependent on successful re-registration of Bayer 73 as a lampricide with the EPA and finding a suitable solvent, i.e., one meeting all environmental regulations (T. Bills, U.S. Fish and Wildlife Service, LaCrosse, Wisconsin, pers. comm.).

The current formulation of granular Bayer consists of 5% active ingredient (niclosamide) and is not an effective sampling tool, particularly in deep water, because of variable release rates. A new formulation using 3.3% active ingredient and a different coating method has been developed and awaits implementation (T. Bills, U.S. Fish and Wildlife Service, LaCrosse, Wisconsin, pers comm.). Regulatory approval is expected in 1995 and tests may be conducted on areas in the St. Marys River at the same rate (100 lb/acre) used for the current formulation.

### *3.1.3 Application*

TFM is applied to tributary streams at rates that provide a concentration in the water between the minimum required to kill 100% of the larval sea lamprey (minimum lethal concentration) and the maximum concentration that will not cause mortality to fish such as brown trout (Salmo trutta) or white suckers (Catostomus commersoni). The objective of conventional treatments is to maximize the number of sea lamprey killed while minimizing non-target mortality. The ability to meet this goal has improved steadily over the years as a result of studies demonstrating that the toxicity of TFM to sea lampreys and other organisms is influenced by alkalinity, dissolved oxygen, temperature, the presence of other toxic substances, and, in particular, pH (Marking and Bills 1985, Seelye et al. 1988, Bills et al. 1988, Seelye and Scholefield 1990). Research along these lines is continuing, particularly attempts to look at interactions between water chemistry variables, e.g., pH and alkalinity (D. Johnson, U.S. Fish and Wildlife Service, Marquette, Michigan, pers. comm.). When a pH-alkalinity model was implemented in 1992, the one-year reduction in TFM use was as high as 19.8% on individual streams and 8-10% annually.

Decisions on which stream systems to treat can greatly affect the number of lampreys killed per unit of TFM (effectiveness) and hence the amount of chemical used and annual cost (Koonce et al. 1993). Koonce et al. (1993) cite a modelling study of Lake Ontario by Jones et al. (1987) which suggests that decisions to treat only the largest streams in a field season consistently resulted in higher levels of parasite abundance in Lake Ontario than if a broader spectrum of stream sizes were treated. Further modelling work to define decision rules on a lake-wide basis may lead to reductions in lampricide use and hence cost, recognizing that unforeseen circumstances may change treatment schedules and that the mix of control options employed may contribute to the level of treatment needed on a lake.

Improvements in the application of TFM also might be possible by investigating tactical decisions at the stream level. For example, U.S. control experts recently tested a treatment on the Brule River in which TFM concentration was held nearer to the minimum lethal than normal but maintained for 24 hours rather than the usual 12-16 hours. The objective was to minimize the concentration and non-target mortality but still maximize the number of larval sea lamprey killed by lengthening the exposure period (D. Johnson, U.S. Fish and Wildlife Service, Marquette, Michigan, pers. comm.). The largest benefits from extended treatments are expected to occur in alkaline waters because of the interactive effects of pH and alkalinity. However, while this tactic effectively met both objectives in the Brule River, extended treatments will use more TFM, resulting in higher costs.

Relatively little is known concerning the toxicity of granular Bayer (GB) in relation to water chemistry variables such as alkalinity, pH, dissolved oxygen, and temperature, in contrast to the situation for TFM. Similar studies to those completed for TFM at the LHBS would help to fine-tune the use of GB, maximizing lamprey kill and minimize non-target mortality. These types of studies are relatively inexpensive and will add to the existing information base.

Research is underway to develop treatment guidelines for the use of TFM-Bayer 73 mixtures (T. Bills, U.S. Fish and Wildife Service, LaCrosse, Wisconsin, pers. comm.). This research is focusing on the effects of alkalinity and pH on the toxicity of the mixture. Preliminary results show that in streams with certain water qualities, the addition of 1% Bayluscide can reduce TFM use by up to 40%. The applicability of this approach will have to be evaluated on a stream-by-stream basis.

## 3.2 Barriers

Prior to the development and implementation of TFM in the 1960s, sea lamprey control in the Great Lakes relied on mechanical weirs and electrical barriers to block the upstream migration of adults (Smith and Tibbles 1980). Although providing partial control, these devices were expensive to build and operate, hazardous to migrating teleost fish, and their effectiveness was hampered by ice-breakup and flooding in the spring (Smith and Tibbles 1980). As the use of selective toxicants increased, electrical barriers were gradually phased out or used to assess adult sea lamprey abundance.

### *3.2.1 Existing Approaches*

New research in the 1970s led to the development of low-head barrier dams and improved electrical-barrier designs. These barriers maintain their effectiveness over a wide range of flows, are safer from an operational viewpoint, and have lower impacts on fish and on recreational and aesthetic values (Katopodis et al. 1994). Barriers reduce the stream area requiring treatment, reduce the amount of lampricide used (and cost of treatment) and reduce exposure of non-target organisms to TFM. Both types of barrier also provide important trapping capabilities for removal of adults, which can be used for the sterile-male release-technique (SMRT) program (see Section 3.4.1). A total of 39 low-head barriers and 4 electrical barriers are currently installed on small and moderately sized Great Lakes tributaries to block adult sea lampreys. Despite the long history of barrier use in the control program, the effects of low-head barriers on larval and parasite recruitment have not been investigated. This information will be needed if barriers are to be considered more than simply convenient sites for assessment traps in an IPM program.

Low-head barriers are designed to block migrating adult sea lamprey and pass jumping fish (mostly salmonines) over the structure. However, design criteria for constructing and operating a minimum-sized structure with minimal environmental disruption have not been established (Biette and Griswold 1988). For example, in Canada low-head barriers are currently designed to maintain a head of 50-90 cm during mean annual discharge or a 46-75 cm drop, depending on hydrologic conditions and site characteristics (T. McAuley, Canada Department of Fisheries and Oceans, Sault Ste. Marie, Ontario, pers. comm.). These criteria are partially based on the results of studies on spawning migrations of Cayuga Lake sea lamprey which demonstrated that these lampreys were unable to pass a vertical barrier of 30 cm or more in height (Hunn and Youngs 1980). The 30-cm height reflects only the physical ability of lampreys to get over a barrier. Extra height is added in the design to account for stream-specific hydrological conditions. A barrier design task force recommended that a head of 45 cm should be maintained during the period of active lamprey migration (Hunn and Youngs 1980). This recommendation is presumably to ensure the blocking ability of the barrier under a wide range of conditions and is followed on barriers in Michigan. Additional blocking is provided by a lip to keep the vertical face of the dam dry, preventing lampreys from attaching with their oral disc and working their way over the structure. At present, there are no standardized criteria for lip design. Current experience in barrier design on large rivers is limited, and yet these may be where the benefits of using barriers are greatest.

The passage of non-target fish species blocked by low-head barriers and electrical barriers is also a key issue for the barrier program (E. Koon, U.S. Fish and Wildlife Service, Ludington, Michigan, pers. comm.). Kelso and Noltie (1990) provide the only published assessment of the effects of a lamprey barrier on fish passage. Based on abundance estimates derived from mark-recapture studies between 1983 and 1987, Kelso and Noltie (1990) reported that pink salmon (Oncorhynchus gorbuscha) were blocked by a barrier on the Carp River while the upstream movements of coho (O. kisutch) and chinook (O. tshawytscha) salmon were not impeded by the barrier. The blocking of pink salmon by the barrier was attributed by Kelso and Noltie (1990) to the fact that this species is a poorer swimmer/jumper compared with the other Pacific salmon species. The Carp River barrier may have been a contributing factor in a decline of pink salmon either by reducing the availability of spawning habitat or through restrictions on the size of the spawning run.

Fish passage facilities with lamprey barriers have been constructed on some streams in which the drop is too large for fish to negotiate, e.g., the Beaver River (Crook 1991) and the Brule River (Holloway 1991). These structures are successful at blocking sea lampreys moving upstream but they only pass jumping fish. Research on the design and use of fishways to facilitate the movements of non-jumping fish (i.e., non-salmonines) around dams and other instream obstructions is extensive (see Schwalme et al. 1985; Katopodis et al. 1991). These studies indicate that species ranging from cyprinids to esocids will ascend fishways (such as the Denil or vertical-slot) and that there are often preferences for different types of structures based on the swimming performance of each species.

The practical difficulty with using conventional fishways designed for non-jumping teleost species is that these structures would also allow migrating lamprey to ascend above the barrier. Perforated metal baffles in Denil fishways have apparently been used to block the ascent of Pacific lamprey (Lampetra tridentata) up the Columbia River (D. Smith, Smith-Root Inc., Vancouver, Washington, pers. comm.) and could be tried in some Great Lakes tributaries. The effectiveness of these baffles at stopping the ascent of migrating lampreys is not known since data were not available for assessment. A second approach to stopping migrating sea lampreys in fishways may be to separate sea lamprey from teleosts on the basis of behavioral or performance differences in lotic waters. However, studies of sensory cues used by migrating lamprey are generally lacking (except see Sections 3.2.2 and 3.5 below). If fishways have to be used at barrier sites because of the need for fish passage, there may be no way of overcoming the labor-intensive solution of manually separating ascending teleosts from sea lamprey collected in traps. Designing and constructing fishways at barrier sites retroactively likely would be an expensive and site-specific approach to providing fish passage in part because the purchase of additional land or access rights for these structures may be necessary. The benefit-cost ratio for this approach may be most favorable on rivers supporting important stocks of nonjumping species, e.g., walleye Stizostedion vitreum. On other rivers or streams, some other approach to fish passage may be more appropriate (see below).

The current generation of electrical barriers from Smith-Root employ an array of bottom-mounted electrodes to produced a graduated electrical field (D. Smith 1994). Advantages include the gradual entry and halting of migrating fish before they are injured or killed, flush mounted electrodes on the bottom that do not collect debris and are less susceptible to ice damage, no impoundment upstream of the barrier, and, except during the period of sea lamprey migration, the movements of nonjumping fish and invertebrates are not blocked. The disadvantages of the four electrical barriers currently installed on Great Lakes tributaries is that they block all migrating fish, including sea lamprey and some lamprey passage may occur during power outages unless backup generators are installed. Three of the four barriers installed on Great Lakes tributaries were not operated for the last two years because they also blocked migrating steelhead (Oncorhynchus mykiss).

One approach for providing fish passage at electrical barriers is to modify the barrier through the addition of sloping decks along the banks and a nonattachable surface to prevent lamprey from pulling themselves over the structure (D. Smith cited in Katopodis et al. 1994). This suggestion is based on the observation at facilities in the western United States that fish with their backs and lateral line out of the water are not affected by the electrical field and so can move upstream past the barrier (D. Smith cited in Katopodis et al. 1994). However, no data were presented supporting these observations, particularly data on the proportion of blocked salmonines that used this method to continue upstream. Furthermore, migratory sea lamprey are capable of swimming in water as shallow as 2 cm (T. McAuley, Canada Department of Fisheries and Oceans, Sault Ste. Marie, Ontario, pers. comm.) and may be able to pass electrical barriers in the same way. The behavior of lamprey and teleosts in electrical fields has not been investigated but will be relevant to the problem of fish passage. The sensitivity of lamprey to electrical fields is comparable to that of cartilagenous sharks and electroreceptive teleosts (Bodznick and Northcutt 1981).

An another approach to permitting fish passage at electrical barriers is to use conventional fishways. These devices would have the same problems as described previously and, in addition, pumps would have to be used to create flow through the fishway and to create attractant flow at the entrance since electrical barriers do not create any hydraulic head. This would be an expensive solution and is unlikely to be used widely. For example, the cost of designing and installing a pumped fishway around the electrical barrier on the Pere Marquette River is approximately $140,000 (T. McAuley, Canada Department of Fisheries and Oceans, Sault Ste. Marie, Ontario, pers. comm.). Barriers would still have to be installed in the fishway to trap lamprey so the labor-intensive approach of sorting lamprey and teleosts in traps remains.

Knowledge of the behavior of migrating sea lamprey when they encounter a barrier, either electrical or physical, is lacking. This information is important because most barriers are inundated by flooding occasionally, allowing sea lamprey to get past the structure and spawn upstream. Presumably the animals search for ways around the structure but except for anecdotal reports the search pattern used is unknown (E. Koon, U.S. Fish and Wildlife Service, Ludington, Michigan, pers comm.). For example, if sea lamprey use their oral disk to attach to the structure and slowly creep over in strong currents, then the use of non-attachable surfaces on the dam might be warranted. Radio-telemetry studies in the field combined with video observations through glass-sided laboratory flumes plus tagging are obvious approaches to obtain the needed knowledge of behavior.

Most low-head dams and electrical barriers have traps in them which remove some portion of the migrating sea lamprey that encounter the structure (either for destruction or the SMRT program) but the fate of the untrapped animals is not known. The fact that sea lamprey do not home to their natal streams (Johnson 1987, Bergstedt and Seelye 1994) is important because there may be potential for movement and dispersal to alternative spawning streams. For example, sea lamprey from a blocked spawning migration in the Cheboygan River were major contributors (in terms of numbers) to migrations in streams up to 64 km away and made minor contributions to streams as far as 241 km distant (Applegate and Smith 1951). Escapement has not been a major concern in the 30 years since TFM has been used because nearby streams were also likely to be treated with lampricide. Because escapement is not desirable in the control program, knowledge of the dispersal of blocked sea lamprey may be useful in siting barriers. Whether all animals in a blocked run disperse to alternative sites, how far they move in their search for alternate sites, and in particular, how blocking affects the reproductive fitness of blocked females compared with females that are not blocked, require further research. Tagging blocked adult sea lampreys using sequential coded wire tags (CWTs) would be a useful approach to obtain information on dispersal of blocked animals to nearby streams.

The environmental effects of impoundments behind large hydro-electric, flood control, and irrigation dams have been studied but formal assessment of the environmental effects of impoundments typical of barriers used in the sea lamprey control program is lacking. Impoundments created behind barrier dams may alter water quality downstream (e.g., increase temperature, altered nutrient levels) and retain a large portion of the suspended sediment load moving downstream. The latter possibility will change habitat in the vicinity of the barrier, lead to infilling behind the barrier, and may eventually compromise its integrity. Barriers also may have direct impacts on aquatic communities, including invertebrates and fish. Invertebrate recolonization of downstream areas through drift is an important component of stream ecology. This drift contributes to the rapid recovery of defaunated streams after lampricide treatments and may be impeded below sea lamprey control barriers. Construction of the barrier will alter habitat locally, which could affect the success of some species depending on the importance of the modified habitat and the availability of other habitat upstream or downstream of the barrier site (e.g., see Kelso and Noltie 1990).

Monitoring of fish migratory patterns in Wilmot Creek and to a lesser extent the Credit River (both Lake Ontario streams) indicates that there are seasonal and diurnal patterns of movement for a variety of fish species and age-classes (L. Stanfield, Ontario Ministry of Natural Resources, Glenora, Ontario, pers. comm.). Species observed moving up- and downstream include rainbow trout (O. mykiss), coho salmon (O. kisutch), Atlantic salmon (S. salar), brown trout (S. trutta), white (C. commersoni) and longnose suckers (C. catostomus), longnose dace (Rhinichthys cataractae), creek chub (Semotilus atromaculatus), rock bass (Ambloplites rupestris), and adult sea lampreys and newly metamorphosed parasites. Some of these movements are related to physiological processes and flow conditions -- for example, seasonal outmigrations of juvenile rainbow trout and white suckers in mid-May (L. Stanfield cited in Katopodis et al. 1994). Up- and downstream movements of other species such as longnose dace, rock bass, and in some seasons coho salmon are believed to be related to habitat selection, particularly temperature. Allowing for these types of movements is the challenge facing the use of velocity barriers and other structures designed to facilitate the passage of non-jumping fish.

The movements of migrating fish were often delayed by the Wilmot Creek weir for several days. Even a temporary delay at barriers may be important to spawning non-target species because maturation is predicated on arrival at spawning sites at certain times and this may vary within a waterbody from year-to-year, influencing recruitment. Fleming and Reynolds (1991) found that delaying the upstream spawning migrations of Arctic grayling, Thymallus arcticus, in Fish Creek, Alaska, by 3, 6, or 12 d resulted in a reduction in the distances travelled by both sexes. This in turn lead to the use of nonpreferred or suboptimal spawning habitats and decreased recruitment. Similar effects could occur in non-target fish species delayed at barriers in the Great Lakes, but no data are available.

### *3.2.2 New Approaches*

Incorporating velocity barriers into low-head dams may be a practical way of providing passage to non-jumping fish. This approach is based on the hypothesis that migrating sea lamprey have poorer swimming capabilities than non-jumping teleosts provided they are not allowed to attach to the barrier (T. McAuley cited in Katopodis et al. 1994). Thus, there should be some maximum velocity and distance which prevents adult sea lampreys from navigating a chute. Previous research and more recent research at several temperatures points to a velocity of approximately 1.7 m/s as the maximum velocity against which sea lamprey can move if they cannot attach to a surface (T. McAuley cited in Katopodis et al. 1994).

A prototype structure consisting of a low-head dam and a velocity barrier (chute) lined with non-attachable surface material was constructed and operated in the Neebing-McIntyre River, Lake Superior, in 1994. The design, which was based on 14 years of discharge data during the sea lamprey migration period, accommodates flows ranging from 0.5 to 2 times the mean annual discharge (T. McAuley, Canada Department of Fisheries and Oceans, Sault Ste. Marie, Ontario, pers. comm.). Based on nest observations upstream of the site, the dam and velocity barrier were able to block migrating adult sea lampreys and allow migrating white suckers to move upstream until late June when the structure was inundated by a large flood, allowing some lampreys (three nests were found) to move upstream and spawn (T. McAuley, Canada Department of Fisheries and Oceans, Sault Ste. Marie, Ontario, pers. comm.).

The velocity barrier is a promising concept but several issues require attention before implementation on a wider scale can be considered. First, as discharge changes so will water velocity in the chute. Approaches to overcome this problem include using an inflatable crest to maintain a constant hydraulic head or using a velocity tube so that water velocity remains constant (T. McAuley, Canada Department of Fisheries and Oceans, Sault Ste. Marie, Ontario, pers. comm.). Second, the velocity chute is designed to pass most common, adult migratory species as long as individuals are about 30-cm long or larger (T. McAuley, Canada Department of Fisheries and Oceans, Sault Ste. Marie, Ontario, pers. comm.). Detailed information on species and their migratory habits and swimming abilities will be needed at the design stage to ensure passage is accommodated on some streams. Smaller-bodied native species such as rock bass and cyprinids (minnows), which may undergo migrations, will be blocked by velocity barriers at most flows.

Inflatable barriers have been used to collect Pacific salmon broodstock (Oncorhynchus spp.) in the state of Washington (Katopodis et al. 1994) and may have some merit for sea lamprey control. These barriers deflate and lie on the bottom of a stream most of the year. During the migratory period they are inflated with water. Height from the top crest to tailwater can be adjusted automatically as water levels fall. Assessments of the advantages and disadvantages of inflatable barriers are lacking at present. Inflatable barriers in the sea lamprey control program could virtually eliminate upstream and downstream environmental effects due to impoundment and they should be effective over a wider range of flows than permanent barriers. Potential difficulties with implementing this approach are that some permanent anchor structures are required and they block non-jumping teleosts unless fishways are built. Consideration should be given to the possibility that inflatable barriers (and electrical barriers) which can be turned on and off could alter the spawning season of sea lamprey. For example, deflating a barrier too early and allowing some late spawning individuals to reproduce may select for late spawning individuals, if spawning time is a heritable trait in sea lamprey. Since adult sea lamprey do not home to their natal streams, several inflatable barriers would be needed around one of the Lakes to create this situation. Therefore, better information on when sea lamprey enter streams will be required than is now available so that the barrier is erected throughout the entire spawning migration, but no longer than necessary.

A prototype inflatable barrier will be constructed during the winter of 1995 and operated the following spring by Canadian sea lamprey control experts (T. McAuley, Canada Department of Fisheries and Oceans, Sault Ste. Marie, Ontario, pers. comm.). The structure consists of a concrete slab on the stream bottom, abutments, the inflatable dam with deck plating for a lip, and a fish channel to one side. The dam will be inflated to automatically retain a 20-cm drop between crest and tailwater. This configuration may cost 20-30% more to design and construct than a more conventional dam, in part because of the inclusion of the fishway.

The use of low-head barriers, velocity barriers, and inflatable barriers will be site-specific and based to some extent on a trial-and-error approach. Proper design requires good information on discharge throughout the year and data on migratory species during the sea lamprey migration period. Fish-passage facilities can be built but the need must be carefully assessed since these structures may cost as much as the barrier. Furthermore, there is no practical way to stop sea lamprey from ascending Denil and vertical slot fishways at present except to trap them. This will require manual sorting of teleosts and lamprey unless some automatic method can be found.

Behavioral measures relying on responses to light, sound, and bubble curtains have been proposed as possible alternatives to dams for blocking migrating sea lamprey or as leading mechanisms to improve the efficiency of trapping devices (Lamsa et al. 1980, Katopodis et al. 1994). These systems rely on the voluntary responses of fish to a controlled stimulus and have been the focus of numerous fish-protection studies at power plants (Hocutt 1980). Behavioral measures are particularly attractive because they cost less and have limited potential for fouling (collecting debris, algal buildup, sediments) compared with physical structures (Haymes and Patrick 1986, Patrick et al. 1988). Approaches that rely on eliciting predictable behaviors in fish, clearly do not provide a barrier in the conventional sense, i.e., they do not completely block or exclude fish from an area, particularly if that area is a preferred route of movement (Patrick et al. 1982, Smith and Anderson 1984, Haymes and Patrick 1986, Nestler et al. 1992, Kynard and O'Leary 1993). In the context of sea lamprey control, behavioral responses to stimuli such as light, sound, and air bubbles might be employed to guide migrating adults away from fish passage structures or into traps at barrier sites.

**Light.** Numerous studies have demonstrated that fish may be either attracted or repelled by light, depending on whether the light is of constant intensity or flashing. All species tested have consistently been repelled or exhibited an avoidance behavior to strobe lights (e.g., Patrick et al. 1982, Nemeth and Anderson 1992) whereas fish may exhibit a mixture of attraction and avoidance behaviors in response to constant lighting (Wickham 1973, Nemeth and Anderson 1992). The greatest changes in fish behavior associated with a light stimulus tend to occur at night when most of the studied species migrate. High intensity, constant light generally elicits an avoidance response in fish but low intensities may be attractive to some species (Nemeth and Anderson 1992). Light intensities associated with these different behaviors tend to be species specific. Strobe flash frequency tends to have little influence on the avoidance response (Patrick et al. 1982).

The quality of light differentially influences the behavior of some fish in predictable ways. Patrick et al. (1982) tested the response of American eel (Anguilla rostrata) to red (600 to >700 nm) and white (highest energy in the blue-green region, 400-570 nm) strobe lights and found that eels showed no avoidance of the red strobe while strongly avoiding the white strobe. As pointed out by Patrick et al. (1982), these responses are opposite to those observed by Ben-Yami (1976) in several pelagic fish species, which tended to be attracted to blue-green light and avoid light of longer wavelengths. These findings indicate that fish guidance devices might be constructed for certain species on the basis of differences in response to the quality of light used.

Migratory adult sea lampreys move almost exclusively at night and are known to respond to light stimuli, although their sensitivity to differing intensities and qualities of light is unknown. Upstream migrant sea lamprey exhibit a pronounced photokinetic response to sudden illumination, detaching from the sides of tanks and swimming about (McCauley et al. 1978) and locomotory activity exhibits a diurnal periodicity, peaking after midnight and near dawn (Kleerekoper et al. 1961). Bodznick and Northcutt (1981) recorded large electrophysiological potentials in the midbrain of adult Lampetra tridentata in response to 10 $\mu$s light flashes.

Attempts to increase the effectiveness of sea lamprey trapping using lights were inconclusive. Low-intensity lights placed in traps on the Cheboygan River significantly increased the catch of migrating lamprey (Purvis et al. 1985) but this success was not duplicated in the nearby Ocqueoc River nor in streams without a barrier (W. Swink in Katopodis et al. 1994). Swink also reported that researchers from Hammond Bay tested a bank of overhead lights ($\approx$ 500 W each) but were not able to block or guide migrating sea lamprey into traps in May. These studies used constant illumination so contradictory results are not surprising given the background information on fish protection at power plants. However, the only successful application used low-intensity light, which is known to attract other fish. The eye of migrant sea lamprey has only one visual pigment, rhodopsin (Kleerekoper 1972). This may be useful for control because the maximum absorption peak of rhodopsin occurs at a wavelength of about 500 nm (Kleerekoper 1972), which is within the blue-green portion of the visual spectrum. Also, the skin of larval lamprey is sensitive to light, with the greatest response in the blue-green region of the spectrum (Kleerekoper 1972). One inference drawn from these studies is that upstream-migrating sea lamprey could be more sensitive to blue-green wavelengths than other migrating species. If evidence can be found to support this hypothesis, then it may be possible to develop a behavioral system using light stimuli.

One approach that may be useful is to investigate the use of strobe lights as a behavioral avoidance measure in migrating adult sea lamprey. Light intensity, wavelength, and flashing frequency are variables that should be examined for their influence on lamprey behavior. The possibility of habituation to light should also be investigated at the same time. Initially these studies could be conducted in laboratory raceways in which the sides and bottoms are covered with a non-attachable surface so that the animals will move in response to the light stimulus. Experimental design could consist of control runs (lights off) prior to experimental (lights on) runs, looking for changes in position and locomotory activity. The best-candidate lighting conditions determined in the first phase can then be evaluated at night on unconfined sea lampreys in a stream with a barrier under ambient water quality and meterological conditions. The second phase could employ the same design as the laboratory studies, using animals trapped at the dam as the response variable.

Because of the limited time period during which spawning phase animals are available, the initial laboratory studies would likely require 1-2 years with an additional 2 years of field testing. Implementation on a wider scale, presumably at existing barrier sites would require approximately 5 years as some design work to accommodate the light equipment would be required. This time-line assumes that some useful results are produced in the laboratory studies. Light equipment is relatively inexpensive compared with physical structures.

Implementation of light guidance systems at barrier dams would have to overcome two practical problems. First, the effectiveness of lights as an attracting or repelling stimulus is dependent on water clarity. Turbid water, which often occurs during spring runoff and the upstream migration period, will reduce the distance over which light may be used effectively. Second, the most appropriate position for the lights will need to be determined. Studies by Ontario Hydro suggest that light position depends on the approach behavior of the animal, i.e., whether it swims on the surface or along the bottom (S. McKinley, Ontario Hydro, Toronto, Ontario, pers. comm.). The behavior of migratory sea lamprey as they approach a barrier is not known.

**Sound.** The application of acoustics has been extensively investigated as a way of reducing fish losses at power plants. Clupeid species have been repelled from generating station structures using low-frequency (50-60 Hz, Haymes and Patrick 1986) and high-frequency (110-140 kHz, Nestler et al. 1992) sounds. Haymes and Patrick (1986) used low-frequency sound from mechanical devices (modified seismic devices called pneumatic poppers) to frighten alewives (Alosa pseudoharengus) away from the Pickering Nuclear Generating Station (NGS) intake, reducing alewives entering the intake by up to 99% when the sound devices were on. Nestler et al. (1992) demonstrated that blueback herring (Alosa aestivalis) in a cage strongly avoided high-frequency sounds between 110 and 140 kHz at sound-pressure levels (SPLs) above 180 dB (at 1 m from the transducer). Alewives in a cage suspended in a flooded quarry strongly avoided high-frequency sounds between 117 and 133 kHz at or above SPLs of 157 dB (Dunning et al. 1992) and habituation did not occur at SPLs above 163 dB. At night the response weakened and avoidance did not occur. In testing a full-scale system to exclude alewives at a New York NGS on Lake Ontario near Oswego, Ross et al. (1993) found that high-frequency broadband sound (122-128 kHz) at an SPL of 190 dB decreased fish density near the intake by as much as 96% and that the impingement of alewives on the intake screens decreased by up to 87%. This system was effective day and night, and had an effective range of more than 80 m.

The potential for the application of sound in the sea lamprey control program cannot be easily assessed at present. Sound is most useful for eliciting predictable behaviors in fish that are "hearing specialists", e.g., clupeids (S. McKinley, Ontario Hydro, Toronto, Ontario, pers. comm.) and in species such as goldfish (Carassius auratus) which have a chain of bones connecting the swim bladder to the inner ear (Hawkins 1981). Sound may be less useful in species such as the sea lamprey, that do not have a bony skeleton. However, nothing is known about the hearing abilities of lampreys, although the general morphology of the ear, particularly the vestibular labyrinths, has been well reviewed (see Kleerekoper 1972, Rovainen 1980). There are anecdotal reports that adult lampreys probably respond to sound (T. McAuley, Canada Department of Fisheries and Oceans, Sault Ste. Marie, Ontario, pers. comm.), but more systematic laboratory studies of sound stimuli would be worthwhile. These studies should investigate both low- and high-frequency sounds and could be conducted in raceways in which the sides and bottom are covered with non-attachable surfaces, using an experimental design similar to that suggested for light investigations. Although this design is unnatural, it rules out the strong confounding influence of lamprey attachment and subsequent immobility. These studies will likely require 1-2 years and should determine if sea lamprey are more sensitive to particular frequencies than other freshwater fish. If no differences are found in responses to sound, particularly with respect to frequency, then sound will not provide a practical behavioral system for sea lamprey control.

Implementation of sound systems for sea lamprey control would have to overcome several practical problems. Swimming speed, water velocity, positioning in the water column, bathymetry, bottom morphology, and locality hydraulics are important parameters in the positioning of an acoustic system (Loeffelman cited in Katopodis et al. 1994). In addition, because of background noise created by water flowing over a barrier, sound levels would have to increase with flow to be effective. However, high sound-pressure levels will stun and damage fish close to the sound source (within 1-3 m) if used to guide or repel fish in confined areas (Menin cited in Nestler et al. 1992); the damage to fish and area affected would increase as sound levels (dB) increase. There are contradictory reports concerning the potential for habituation to sound, even among tests of the same species. The behavior of sea lampreys at barriers is not known but if considerable time is spent searching then habituation could become a problem. Loeffelman (cited in Katopodis et al. 1994) suggests adjusting the amplitude and pulse rate of the sound generating system as one approach to overcoming habituation.

Both low- and high-frequency sound systems are effective at eliciting avoidance responses in fish over a distance of at least 30 m in the open waters of lakes (Haymes and Patrick 1986, Nestler et al. 1992, Ross et al. 1993). Mechanical devices used to produce low-frequency sounds such as the poppers used at Pickering are thought to have limited application in most cases because their reliability is poor and maintenance requirements are extensive and expensive (SWEC 1986 cited in Ross et al. 1993). High-frequency sound systems are smaller and less expensive to construct and operate than low-frequency systems (Dunning et al. 1992). Also, high-frequency sound is less costly to produce electronically at high amplitudes compared with low-frequency sounds (Dunning et al. 1992).

**Bubble Curtains.** Bubble curtains have also been investigated as barriers to reduce fish entrainment at power plants. Akiyama et al. (1991) demonstrated that Japanese parrotfish (Oplegnathus fasciatus), jack mackerel (Tracharus japanicus), and threeline grunt (Parapristipoma trilineatum) could be herded to varying degrees in laboratory troughs using air curtains at flow rates of 3-12 L/min. However, all species rapidly habituated to the barrier (< 1 hr) and gradually lost the herding effect. Field applications of bubble curtains by Ontario Hydro have not been successful because the effectiveness of the barrier is lost in the presence of currents or wave action (S. McKinley, Ontario Hydro, Toronto, Ontario, pers. comm.; and cited in Katopodis et al. 1994). The difficulty of maintaining the integrity of a bubble curtain would be even greater in running water environments compared to lake habitats. Thus the potential for using air bubble curtains as a behavioral device against migrating adult sea lamprey is low.

Research into the use of barriers for sea lamprey management will focus on improving existing methods and on the development of new concepts that block sea lamprey but allow the ascent of non-jumping fish. One promising concept is the velocity barrier, which in preliminary testing was relatively successful at blocking sea lamprey while allowing white sucker passage. Denil or vertical slot fishways could be modified with perforated internal baffles so that lamprey cannot attach and creep through the structure. However, such fishways have high costs in terms of design, construction, operation, and maintenance and likely would be unsuitable on all except the largest rivers in the Great Lakes. Other concepts with potential that merit preliminary laboratory studies are the use of light or sound stimuli to elicit behaviors that deflect sea lamprey from the entrance to fish passage structures or enhance trapping devices. At present, the use of traps and manual sorting of desirable fish from sea lamprey probably cannot be avoided at barrier sites.

## 3.3 Trapping

Migrating adult sea lampreys are trapped at low-head barriers and at migratory obstacles in streams without lamprey control barriers. The traps prevent blocked sea lamprey from moving to adjacent systems to spawn, reduce the number of adults spawning below the dam, provide assessment data on the relative abundance of parasitic animals, and, since 1991, have provided males for the SMRT program (Katopodis et al. 1994). Improving the effectiveness of trapping either through better positioning with respect to attractant cues in streams or integration with chemical attractants or repellants could allow mass trapping to reduce the population or increase the collection of males for the SMRT program.

Mass-trapping is an effective nonchemical method of controlling insect and mammalian pests. The boll weevil control program in the southeastern United States has employed trapping in combination with other methods to suppress abundance to tolerable levels (J. Smith cited in Seelye and Hanson 1992). A program to eradicate coypu in Great Britain, a small semi-aquatic rodent imported for its fur, employed baited traps as the primary control technique and by 1987 had effectively eradicated coypu (Gosling 1989). In both situations, trapping has been successful because the outcome of this strategy on the population was, within limits, predicatable and because the factors affecting trapping effectiveness were known.

Factors influencing the effectiveness of existing traps in barriers and portable traps used in the sea lamprey control program have not been evaluated. Sea lamprey control experts believe that permanent traps built into low-head barriers are more effective than portable traps and estimate that permanent traps capture 45-80% of the migratory sea lamprey compared with 10-40% captured by portable traps (R. McDonald, Canada Department of Fisheries and Oceans, Sault Ste. Marie, Ontario, pers. comm.). Portable traps on the Cheboygan and Manistique Rivers in Michigan are believed to capture an estimated 60% of the migrating sea lamprey (J. Heinrich, U.S. Fish and Wildlife Service, Marquette, Michigan, pers. comm.). The effectiveness of permanent and portable traps should be investigated with respect to trap design (e.g., portable traps do not have one-way entrances so some escapement may occur), positioning of the trap relative to migratory cues, and the behavior of migrating animals when they encounter a trap or other barriers to migration. The use of radio-telemetry and underwater video will facilitate these studies. Underwater video has limited range so some of these studies might be best suited to laboratory raceways lined with non-attachable surfaces. Improved trapping ability may reduce the abundance of sea lamprey further, but the effort require to obtain detectable reductions due to trapping is not known because the effects of trapping on larval and parasite recruitment have not been investigated.

Although expansion of the existing trapping network into larger streams is desirable, information on the factors affecting the effectiveness of traps in large rivers is lacking. Most of the existing information is from small and moderately sized streams and may not be useful in larger streams. Sea lamprey control experts indicate that water currents and possibly darkness associated with permanent traps are cues which attract migrating adults but the effects of these factors have not been investigated systematically with the objective of improving the efficiency of trapping. Both types of information will be needed if the existing trapping network is expanded into large streams.

Improved and more wide spread trapping effort may mean more non-target species are captured. Studies to determine the effects of trapping and release on non-target species are needed. These studies should consider mortality and behavior of fish released upstream and downstream of the barrier in an attempt to devise the optimal strategy for checking and sorting fish (Katopodis et al. 1994).

Development work to improve trapping, particularly portable traps, is inexpensive relative to the expected benefits. Studies to assess the level of stress on non-target species and the best release strategy are probably moderate in cost and should combine the efforts of physiologists and behavioral scientists.

## 3.4 Sex-ratio Manipulation

### *3.4.1 Sterile-Male-Release Technique (SMRT)*

Laboratory and field studies beginning in 1971 culminated with the implementation of an experimental program of sterile-male sea lamprey releases in Great Lakes tributaries in 1991. These studies demonstrated that bisazir caused complete sterility in both males and females with no serious adverse effects on mating behavior and competitiveness of sterilized males and that the resulting reductions in reproductive potential should be predictable on the basis of the ratio of sterile-to-normal males in a target stream (Hanson and Manion 1978, 1980). Gamma radiation is also an effective sterilant if the gonads are in advanced stages of development, but it suppresses the immune system, leading to high levels of mortality from disease (Manion et al. 1988, Hanson 1990).

The SMRT program was initiated on Lake Superior in 1991. Twenty-seven streams were identified as candidate sites because they were difficult to treat effectively with lampricides. Post-treatment surveys have consistently found residual larvae in these streams which are assumed to be the major source of parasitic sea lamprey in Lake Superior (Bergstedt and Seelye 1992). The St. Marys River became a target site in 1992. Between 1991 and 1993, 87,392 sterile males were released, with 68,069 distributed among the tributaries and 19,523 in the St. Marys River (Sterile Male Release Technique Task Force 1994).

Initially, an objective of a 2:1 ratio of sterile-to-normal males, which represented a theoretical reduction of 65% in the production of larvae from nests in the target streams, was employed for the SMRT program. This estimate was based on assessment data which indicated that approximately 20,000 male sea lampreys were available for sterilization and release in Lake Superior per year compared with total spawning runs of approximately 10,000 normal males per year in the target streams (Sterile Male Release Technique Task Force 1994). The calculations assume that the population is at a stage where recruitment to the parasitic-phase is linearly related to the number of spawning animals. Preliminary assessment data indicate that the predicted ratio of sterile to normal males has been achieved only once in the St. Marys River in 1993 (Sterile Male Release Technique Task Force 1994). The reasons for this failure are not clear but could be related to inaccurate assessments of spawning numbers in target streams, failure of released males to migrate to spawning areas in target streams, or reduced health and sexual competitiveness of sterilized males compared with normal males. As fecundity declines, compensatory mechanisms such as an increase in larval survival or growth due to reduced density may become important. These mechanisms have not been investigated in sea lamprey.

Implementation of the SMRT program is continuing in Lake Superior but its application to other lakes is problematical. The GLFC established a task force in 1992 and charged it with developing a long-range plan to implement and assess SMRT as an alternative technology for sea lamprey control (Sterile Male Release Technique Task Force 1994). The task force developed a list of research needs summarized in Table 3. These information needs focus on three primary points: (1) optimizing the efficiency of the sterilization process, including implementing quality control procedures for bisazir sterilization; (2) finding alternative sources of male sea lamprey to supplement existing sources; and (3) determining the effect of reductions in spawning success on recruitment of larvae to the parasitic stage of the life-cycle. Implementation on other lakes will require additional sources of males and

Table 3. Summary of research needs identified as impediments to implementation and assessment of SMRT by the Sterile Male Release Technique Task Force (1994).

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## Sterilization Process

1. Determine the lowest effective sterilizing dose of bisazir.

2. Determine the proportion of males actually sterilized by the existing procedure.

3. Investigate the reasons for the delivery of an inadequate bisazir dosage for sterilizing some males.

4. Identify the elements of the process that may affect distribution and performance of males in streams after release.

5. Assess the health and sexual competitiveness of sterilized males relative to normal males.

6. Determine the feasibility of mating anadromous lampreys with landlocked lampreys to supplement present sources of males.

7. Assess the feasibility of culturing males to supplement present sources of males for sterilization.

## Assessment

1. Determine the number of normal males spawning in target streams.

2. Determine the ratio of sterilized to normal males in areas of implementation.

3. Determine the fate of sterilized males that do not appear in spawning areas of target streams after release.

4. Determine the extent of reductions in prolarval production achieved in target streams, i.e., do sterile males affect reproductive success in a stream?

5. Determine if reproductive success is proportional to number of sterilized males released into target streams.

6. Determine the relationship, if any, between larval production and spawning stock size.

7. Determine if larval survival is density-dependent and investigate potential compensatory mechanisms.

8. Determine if growth and age at metamorphosis are density-dependent and compensatory mechanisms that may affect performance of the SMRT program.

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changes in the sterilization process to increase the output of sterilized males. Expansion of the SMRT program to other lakes will require improvements in the ability to predict the effects of SMRT on the reproductive potential of fertile sea lamprey, i.e., an understanding of the stock-recruitment relationship in landlocked sea lamprey.

The possibility of compensatory effects in adult sea lamprey should be given consideration. Oscillations in the sex-ratio of adult sea lamprey in the upper Great Lakes have been related to prey and predator abundances (Heinrich et al. 1980, Houston and Kelso 1991). Increased prey abundance has resulted in an increase in the proportion of males in the upper Great Lakes and Lake Ontario since 1980 and an increase in the size (length and weight) of males in Lakes Huron and Ontario (Houston and Kelso 1991). Fecundity is known to be related to size in many teleosts and this relationship has been demonstrated in southern brook lamprey, Ichthyomyzon gagei (Beamish et al. 1994). If sea lamprey fecundity is also related to size, a compensatory increase in fecundity may occur as numbers decline with improved control.

Long-term research for the SMRT program should focus on compensatory mechanisms. Short-term solutions to increase the number of males available for sterilization include more effective trapping, possibly culturing, particularly all-male lines (see below), and the importation of anadromous male sea lampreys from the Atlantic coast of North America. Better assessments of the abundance of migratory animals in target streams is also needed as is research on the health and reproductive behavior of sterilized males when released (i.e., do they stay in the stream or leave).

### *3.4.2 New Approaches*

The primary determinant of sex in teleost fish is usually genetic and first manifests itself in the primary sex organs which in turn secrete steroids and non-steroidal substances after differentiation and control phenotypic sex (Chan and Young 1983). The translation of genotypic sex to phenotypic sex is accomplished by biochemical processes which are susceptible to environmental influences (Chan and Young 1983). Sex determination models among teleosts are diverse and include species with male and female homogamety (i.e., XX), species with environmental or behavioral sex determination, and self-fertilizing hermaphrodites (Davis et al. 1991). A variety of experimental methods have been developed to control sex both genetically and phenotypically.

#### 3.4.2.1 Sterilization

At present, male sea lamprey are sterilized using intraperitoneal injections of bisazir in a specially constructed facility at the LHBS. This facility can process the present number of males (about 29,000 annually) plus about 10,000 more annually without expansion (J. Heinrich, U.S. Fish and Wildlife Service, Marquette, Michigan, pers. comm.). Bisazir is a potent mammalian mutagen so a less hazardous method of sterilization is desirable (Sower and Hanson 1992). Although the current facility is adequate for the number of males available, as more males become available through supplemental methods (more trapped, imported from the Atlantic coast, cultured) a less labor-intensive method of sterilization would be a benefit to the SMRT program. New sterilization methods should increase the number of animals processed and improve the health and performance of sterilized males as a result of less handling during the sterilization process before they can be considered beneficial to the SMRT program.

Aside from chemically neutering fish, other methods to induce sterility include hormonal treatments of embryos or larvae, treatments of maturing fish with hormonal agonists or antagonists, the creation of polyploid fish (usually triploid), and hybrid crosses. Use of any of these sterilization methods must not affect the spawning behavior or mating competitiveness of sterilized males.

The ability to sterilize male salmonids using relatively high doses of androgens is well known and varies with the method of treatment (oral, immersion, or both), the concentration of steroids used, and species. Jalabert et al. (1975) found that after feeding rainbow trout 15, 30, or 60 mg methyltestosterone/kg diet from 1 month after hatching to 5 months post-hatch 11.7% of 2-yr old fish were sterile. Methyltestosterone or estradiol fed to adult trout at a rate of 0.5 mg/kg diet during spermatogenesis completely inhibited gonadal development. In a study aimed at controlling sex differentiation to produce sterile fish, Goetz et al. (1979) immersed eyed eggs and alevins of coho salmon in 25-400 ug methyltestosterone/L and fed fry a 20 mg methyltestosterone/kg diet for 10 weeks. After 3 months all groups of eggs and alevins receiving immersion and feeding treatments combined were sterile. Only 52% of the fish receiving the dietary treatment alone were sterile. Immersion of coho eggs and alevins in 400 ug/L methyltestosterone followed by feeding a 10 mg/kg diet resulted in almost all sterile fish after 3 months (G.A. Hunter et al., unpublished data cited in Donaldson and Hunter 1982). None of these studies considered the spawning behavior of sterile fish because in an aquaculture setting, sterilization is usually used to improve food conversion efficiency and growth. In contrast, appropriate spawning behavior in sterilized male sea lamprey is critical to the success of the SMRT program.

The precise mechanism by which high hormone doses produce sterile fish is not clear. Sterilization may be attributable to feedback inhibition in the hypothalamic-hypophyseal-gonadal axis or direct action on the gonads (Hunter and Donaldson 1983). The advantage of hormonal sterilization, at least from an aquaculture viewpoint, is that effective treatment can be achieved using genetic males and females (Hunter and Donaldson 1983). The major disadvantage is that relatively high levels of steroids must be applied for extended periods of time at an early stage of development to effect sterilization.

Hormonal sterilization of lampreys has not been attempted. Docker (1992) administered hormones during the period of sexual differentiation of larval sea lamprey but was largely unsuccessful in redirecting sex differentiation. Studies would have to be conducted to determine the timing (embryos, larvae) and duration of treatment, dosages, and appropriate hormones. Even if it is possible to hormonally sterilize male sea lamprey, there are several practical problems. For example, gonadal differentiation in sea lamprey begins at lengths of about 60 mm and is not usually complete below lengths of 90 mm or until about 3 years of age (Docker 1992). If treatments have to be applied at the time of sexual differentiation, animals would have to be cultured for at least 2-3 years. Secondly, large quantities of expensive synthetic sex steroids would have to be applied for lengthy periods. Given the variable response of male salmonids to hormonal sterilization and the lack of information on lampreys, this approach does not seem to hold much promise as an alternative to bisazir sterilization.

Teleost reproduction is controlled by the hypothalamic-pituitary-gonadal axis (Donaldson and Hunter 1983). This mechanism is sequential with a number of hormonal feedback loops which allow for human intervention at several levels to manipulate reproduction. Years of research on mammals has lead to the use of gonadotropin-releasing hormone (GnRH) analogues for sterilization and other clinical applications (Sower and Hanson 1992).

Two forms of lamprey GnRH have been identified, -I and -III. The lamprey GnRH-I molecule is structurally distinct from other known vertebrate GnRH molecules (Sower et al. 1987) which may mean that manipulation is relatively straightforward. Administration of agonist and antagonist analogues of GnRH demonstrated that the hypothalamus controls pituitary and gonadal function in sea lamprey through the release of GnRH (Sower et al. 1983). These studies also showed that GnRH receptors in the sea lamprey adenohypophysis and gonad are specific and can distinguish between molecular variants of this peptide. This specificity plus more recent evidence indicating that lamprey GnRH is found in the brain (Sherwood et al. 1986) and evidence that lamprey GnRH stimulates reproductive processes in sea lamprey (Sower et al. 1987) implies that there is neuroendocrine control over reproduction in lampreys (Sower 1990). Based on this evidence studies are currently underway to determine the effects of GnRH-I and -III analogues on steroidogenesis and spermatogenesis in male sea lamprey and to determine the effects of antagonistic GnRH analogues on the spawning behavior and mating competitiveness of males and the development of eggs fertilized by treated males. The hypothesis underlying these studies is that the analogues bind non-competitively to receptor sites for normal GnRH molecules, resulting in effective sterilization of males. The level of sterilization will depend on the dose of GnRH antagonist used and metabolism of GnRH and analogues.

Several features of sterilization using GnRH analogues are useful from a control standpoint. This method would provide a cost effective and efficient method (one injection) of sterilization (Sower and Hanson 1992). GnRH antagonists are peptides and are easily degraded and would be non-toxic to humans. A major advantage relative to other methods of sterilization or sex control is that sterilization using GnRH analogues will not require the culture of large numbers of male sea lampreys. The feasibility of this method on a large scale can be better assessed once current studies are completed. Assuming these studies are positive, then appropriate antagonistic analogues and dosages must be chosen. Also field studies of mating behavior and competitiveness will be necessary.

Hybridization has been suggested as a method for sterilizing sea lampreys because some hybrid crosses produce sterile males among their progeny (Sower and Hanson 1992). Although comparative embryological studies demonstrated gross similarities in both the secondary sex characteristics and stages of embryological development (Smith et al. 1968) of sea lamprey and four native lamprey species in the Great Lakes, experimental hybridizations between sea lamprey and native species were unsuccessful (Piavis et al. 1970). A few hybrid sea lamprey embryos survived to stage 16, but most were dead by stage 9 or 10 in development and none survived to stage 17 (burrowing). In contrast, hybrid crosses among the four native species had survival rates to stage 17 ranging from 0 to 88%. Survival was highest among crosses of closely related species, i.e., Ichthyomyzon spp., and lower for Lampetra appendix and Ichthyomyzon spp. crosses. Based on these data, the hypothesis that sterilization of sea lamprey can be achieved through hybridization with other lamprey species is not supported and further research is not warranted.

Induced triploidy is a simple method of creating sterile fish with demonstrated success in salmonids (Thorgaard 1992). The technique consists of applying a thermal, pressure, or chemical shock to the egg shortly after fertilization (Thorgaard 1983). The shock causes retention of the second polar body and individuals develop a third set of chromosomes. Triploid fish are nearly always sterile because of disturbances in gonadal development from having an odd number of chromosome sets pairing in meiosis during gametogenesis (Thorgaard 1983). In salmonines, triploid males develop secondary sexual characteristics during the spawning season (Sower and Hanson 1992). Tetraploid fish (four sets of chromosome) may be useful in the production of triploids, if they are viable and fertile and can be successfully crossed with normal diploids (Purdom 1983). This strategy has been attempted experimentally on a few occasions but it is not used widely at present.

The best known case of triploidy in biocontrol of an aquatic pest is the use of triploid grass carp (Ctenopharyngodon idella) for aquatic vegetation control in large, open-lake systems in many of the southern states in the U.S.A. (Clapp et al. 1993). Although all individuals released were triploid and believed to be sterile, substantial numbers of young-of-the-year and yearling grass carp have been captured during surveys far from known release sites (e.g., Brown and Coon 1991), indicating that natural reproduction is occurring.

The induction of triploid in sea lamprey has not been attempted. Considerable experimental research has been required to determine an appropriate protocol for teleosts (e.g., heat shock, cold shock, pressure, or chemicals such as cytochalsin B -- see Purdom 1983) and to obtain satisfactory yields of triploid individuals. Sea lamprey possess the greatest number and smallest size of chromosomes of any known vertebrate (Potter and Robinson 1971). The disadvantages of triploidy are that large numbers of animals must be cultured, yields of viable triploid individuals are not high, and some method is needed to detect triploid individuals early and ensure that they are sterile so that fertile animals are not released.

Use of methods other than bisazir to sterilize sea lamprey will have some negative environmental effects. Releasing sterilized larvae into streams would allow them to grow, become parasites, and kill fish prior to spawning. Furthermore, the potential for releasing unsterilized males must be investigated. Also, if culturing is undertaken, concerns about waste effluents and disease from a culture facility will have to be addressed.

The costs of developing and implementing GnRH antagonist sterilization may be moderate compared with bisazir sterilization. The feasibility of inducing triploidy is unknown, but costs would be high for development and implementation since this procedure requires culturing of large numbers of larval sea lamprey. Similar high costs could be expected if hormonal sterilization proves to be effective.

#### 3.4.2.2 Other Methods of Sex Control

Other methods of sex control in fish involve hormonal or genetic sex inversion or reversal and environmental-sex determination. With the exception of environmental determination, which has been investigated empirically and experimentally, hormonal and genetic-sex reversal have been used to create monosex cultures for production purposes in aquaculture and experimental settings. If some of these methods of sex control are effective against sea lamprey, they could be used to create monosex cultures of males for sterilization. If sex reversal followed by sterilization does not affect the health and competitiveness of these animals, they could be released into target streams to compete with normal animals, boosting the sterile:normal male ratio.

Hormonal sex control has been achieved in coho salmon (Goetz et al. 1979), chinook salmon (Hunter et al. 1986, Baker et al. 1988), channel catfish (Ictalurus punctatus -- Davis et al. 1990), carp (Cyprinus carpio -- Komen et al. 1989), and largemouth bass (Micropterus salmoides -- Garrett 1989). These investigations have produce sex-ratios ranging from 100% males (Baker et al. 1988) to 100% females (Hunter et al. 1986). Hormonal sex control in teleosts is usually achieved by treating embryos, larvae, or juveniles with hormones prior to or during sex differentiation. In this manner the course of primary-sex differentiation is altered, although genotypic sex is unaffected. Methyltestosterone or estradiol are most commonly used to masculinize or feminize teleosts respectively. Effective sex reversal requires that the appropriate hormones, dosages, and treatment timing and duration be used (Hunter and Donaldson 1983). Hormonal sex control differs from hormonal sterilization in that much lower doses of androgens or estrogens are used to redirect sexual development.

Experimental attempts at hormonal sex control of lamprey have been unsuccessful. Docker (1992) treated larval sea lamprey to twice-weekly immersions in estradiol-17β, testosterone, or 17α-methyltestosterone at concentrations of 0.01, 0.1, or 1.0 mg/L for 21 weeks and found that these treatments were ineffective in altering the sex ratio of previously undifferentiated larvae (<60 mm) and larvae 60-90 mm in length. The results among larvae already showing sex differentiation, i.e., >90 mm long, were inconclusive. Significantly more females were noted in the 0.1 mg/L estradiol-treated groups and at the 0.01 and 0.1 mg/L doses of methyltestosterone than in control groups. However, many of these larger larvae exhibited gonadal abnormalities and mortality was high, particularly in the 0.1 and 1.0 mg/L methyltestosterone treatments.

The results of Docker's (1992) studies suggest that sex differentiation in sea lamprey cannot be readily controlled by exogenous steroids. Before accepting this conclusion, Docker (1992) recommended refining the treatment protocol with respect to the time and duration of treatment, the choice of steroids, and their doses. These refinements include lengthening the treatment period to cover the period of sexual differentiation completely and the use of different steroids and doses in future studies. Docker (1992) chose to use estradiol, testosterone, and methyltestosterone because these steroids have been used to alter phenotypic sex of teleosts. However, responses in sea lamprey differed from those typically observed in teleosts and growth and survival were also somewhat lower. Other candidate steroids for testing were not identified by Docker.

Chromosome-set manipulation has been widely used to create monosex cultures of teleosts. Induced gynogenesis (all maternal inheritance) can be achieved by inactivating paternal chromosomes in the sperm before fertilization, and induced androgenesis (all paternal inheritance) is the result of inactivation of maternal chromosomes in the egg before or shortly after fertilization (Thorgaard 1983). Chromosome inactivation is usually achieved by irradiation, chemical, or physical treatments. The resulting embryos are haploid and abnormal at hatching and usually do not survive. Diploid gynogens or androgens are created by applying cold or heat shocks to newly "fertilized" eggs so that mitosis is disrupted (Purdom 1983). Although these methods have proven to be reliable and relatively quick for generating monosex lines, the resulting offspring are inbred and likely to have poorer survival and growth rates than normal fish (inbreeding depression) (Thorgaard 1983). Furthermore, the use of gynogens or androgens depends on the appropriate sex being homogametic (e.g., XX for females). The homogametic sex can only be determined through examination of the sex-ratio of progeny produced by crossing a suspected gynogen or androgen with a normal fish of the opposite sex. Highly skewed sex ratios in the resulting progeny would indicate homogamety for that sex.

Androgenesis may be useful for creating an all-male line of sea lamprey for sterilization. However, considerable research would be required to develop and implement this approach. These studies would have to determine how to create androgens and most importantly, determine if genetic-sex determination is homogametic for males in sea lamprey.

These studies would also have to determine whether androgens go through metamorphosis properly, that they develop secondary sexual characteristics, and that mating competitiveness and behavior are not inferior to normal (unsterilized) males. The androgen approach is only useful in a culture situation to create a large pool of male sea lampreys for sterilization.

The expression of sex in lower vertebrates is variable, often labile, and subject to environmental influence. Docker (1992) and Beamish (1993) suggested that sex determination in the least brook lamprey (L. aepyptera) and southern brook lamprey (I. gagei), respectively, is density-dependent. Sex ratios of least brook lamprey in 12 streams varied from 24 to 71% male, with the proportion of males increasing significantly with density, which ranged from 0.003 to 0.462 larvae/m$^2$ (Docker 1992). Similarly, sex ratios of southern brook lamprey in 20 populations varied from 9 to 49% males; in rapid-growth conditions the proportion of males varied directly with density and inversely with temperature whereas in slow-growth conditions the density relationship was inverse (Beamish 1993). In both cases the skewed sex ratios were unrelated to differential mortality because the sex ratios were consistent among age groups within a population. Although pH, temperature, and growth were significant influences on the sex ratio of southern brook lamprey, none of these factors were important determinants of the sex ratio of least brook lamprey populations. However, these findings clearly indicate that larval sex ratios respond to changes in environmental quality. The adaptive significance of environmental sex determination is unclear nor is it clear how adverse conditions affect sex differentiation (Docker 1992, Beamish 1993).

Some empirical evidence supports the hypothesis that sea lamprey sex ratios in the Great Lakes are affected by population density. Prior to the initiation of effective control, sex ratios were variable with females predominating in some streams and males in other streams (Torblaa and Westman 1980). Reductions in abundance due to lampricide treatments brought about a concomitant shift in sex ratios in favor of female larvae (Purvis 1979, Torblaa and Westman 1980). How environmental sex determination could be used in the control program is uncertain. The available evidence suggests that a decrease in abundance (and density) will eventually result in a decrease in the proportion of males in natural populations which would enhance the effectiveness of the SMRT program (Sower and Hanson 1992).

### 3.4.3 Culturing

Large-scale culturing has been suggested as a potential solution to supplement present sources of males for the SMRT program (Sterile Male Release Technique Task Force 1994). The potential of this approach relates to releasing large numbers of sterilized animals which would subsequently compete with normal males for females. However, the cost of culturing and public attitude to culturing are not likely to be favorable for sea lamprey (Meyer 1990). Sea lamprey would have to be cultured through the parasitic feeding period to the spawning phase of the life cycle, i.e., at least 5-6 years before release. The economic costs per adult are not known but would probably be high. Information on annual mortality, rates of metamorphosis, and the cost of feeding live fish to parasites for 18-24 months is not available but will be necessary for assessing the technical feasibility of this approach.

Many researchers routinely collect and hold embryos and larvae in the laboratory for varying periods. After a few months in captivity these animals are usually thin, often have visibly enlarged gall bladders (filled with bile), and appear to be in poorer health than wild larvae. A variety of culture practices are used but most resemble the guidelines published by Hanson et al. (1974). The largest differences relate to feeding. Yeast is most often fed to larvae, but the quantities and number of feedings per week have varied. Mallatt (1983) attempted to supplement yeast with vitamins but found that they had no effect on growth. More recently, fry feeds developed for intensive teleost culture have been tested at Hammond Bay and were found to significantly enhance growth (W. Swink, National Biological Service, Lake Huron Biological Station, Millersburg, Michigan, pers. comm.). However, this supplement is expensive and cleaning and tank maintenance demands are more frequent. Good sea lamprey-husbandry practices suitable for large-scale culturing have not been investigated. Information on water and substrate quality and quantity, nutrition, and disease control is lacking but would be necessary for culturing larval sea lamprey.

Alternatively, sea lamprey could be cultured until the males can be sterilized and then released into a nursery stream for subsequent growth and metamorphosis (Sower and Hanson 1992). Two types of streams could be considered for seeding as nursery streams: (1) a stream in which a barrier is constructed to prevent reestablishment of normal males and resident animals are removed by lampricide treatment immediately prior to seeding; or (2) a stream with abundant habitat above an existing barrier such as a large hydro-electric dam. The nursery stream option, especially a stream with an existing barrier, may be less expensive than undertaking research on husbandry practices and construction of a facility large enough to culture large numbers of larvae. However, sterile parasites would be released into the Great Lakes where they would damage and kill fish.

### 3.4.4 Anadromous Male Sea Lamprey

Importing male sea lamprey from the east coast of North America has also been suggested as a means of supplementing the current supply of sterile males (Sterile Male Release Technique Task Force 1994) but is problematical for several reasons. First, information on the size and timing of anadromous sea lamprey spawning runs is lacking (see Beamish 1980) except in streams of interest to particular researchers (e.g., the St. John River in New Brunswick, Canada). Second, the effect of increased handling during capture and transport to the sterilization facility at the LHBS on the health and competitiveness of males needs to be assessed. Third, adult anadromous sea lamprey are generally larger in size compared with landlocked sea lamprey. This difference in lengths may present a mechanical barrier to successful spawning since the urogenital openings of both sexes are usually in close proximity during spawning. Fourth, there may be differences in terms of cues or spawning behavior that could be detrimental to the use of anadromous sea lampreys. Fifth, bringing in anadromous animals raises the possibility of importing new diseases or pathogens currently unknown in the Great Lakes basin. Appropriate prophylactic and other measures would have to be routinely applied, increasing costs. Sixth, imported sea lampreys could bring unknown genetic alleles (heritable mutations of a gene resulting in different phenotypic expressions of a trait) into the Great Lakes that may influence the effectiveness of sea lamprey control (e.g., an allele that increases genetic resistance to lampricides). Seventh, the long transportation distance may present difficulties in coordinating the release of imported males with the appearance of landlocked males in streams and on nests. Lastly, the cost-effectiveness of importing anadromous sea lampreys relative to other solutions, e.g., enhanced trapping using attractants, seems questionable. A suitable location for trapping would have to be found and crews would be needed to trap, load, and transport the animals. A study exploring the benefits and dangers of using bisazir-sterilized male sea lamprey from the Atlantic coast in the SMRT program should be conducted before a decision to proceed is made (Meyer 1990).

## 3.5 Attractants and Repellants

The role of olfaction and olfactory cues in the biology of sea lamprey has attracted interest concerning potential applications in the sea lamprey control program. This interest is based on the fact that lampreys have large functional olfactory organs from early in the larval stage to late in the migratory adult stage and the demonstrated importance of olfaction and olfactory cues in the reproductive biology of many teleost fish (Sorensen and Hanson 1994). Research is focusing on chemical signals used as migratory cues by upstream migrating adult sea lamprey, especially bile acids produced and excreted into the water by larvae (Sorensen and Gallaher 1994). Mature sea lampreys are known to produce sex pheromones, but the precise substances have not been identified at present. Given the potency of sex pheromones in teleosts, this line of research has been suggested as a important adjunct to the work on migratory attractants and as a possible compliment for the SMRT program (Sorensen and Hanson 1994).

### *3.5.1 Attractants*

Better knowledge of what attracts migratory sea lamprey to certain streams for spawning will be useful in several areas of the control program. Migratory cues could be used to enhance the effectiveness of trapping (see Section 3.3), guide migratory sea lamprey away from fishway entrances, or attract lamprey to streams with poor habitat or streams that are easily treated with lampricide thereby increasing the number of lampreys killed per unit of lampricide applied. Sex pheromones (and perhaps migratory cues) could be added to the aquatic environment to create a state of confusion, disrupting reproduction.

Research into attractants and repellants of upstream migratory sea lamprey began in the late 1970s. Teeter (1980) showed that mature males and females exhibited a preference for water in which conspecifics of the opposite sex were held and that immature males, early in the spawning migration, exhibit a preference for water in which larval sea lamprey were held. Teeter (1980) did not identify specific substances that may have been acting as attractants but he inferred that pheromones were providing chemical cues for mate selection and the selection of suitable spawning streams.

Research into lamprey attractants has recently focused on the finding that larval sea lamprey seem to provide a migratory cue and guide stream selection in upstream migrating adults. Based on research into teleost migratory cues, particularly the cues used by Arctic charr, Salvelinus alpinus (see Sorensen and Gallaher 1994), the hypothesis that bile acids produced and released by larval sea lamprey act as a cue for stream selection by upstream migrants is being investigated (Sorensen and Gallaher 1994). At present three pieces of evidence from these studies support the bile-acid hypothesis.

First, a bile acid unique to larval sea lamprey, petromyzonol sulfate, has been chemically characterized and synthesized, confirming the original report of Haslewood and Tökés (1969). Relatively large quantities of allocholic acid and petromyzonol sulfate are produced by larval lamprey (e.g., up to 100 $\mu$g per animal) and are found in the liver and intestines, but adult intestines appear to lack these bile acids. Bile acid concentrations in water from the St. Marys River in July were estimated to be about $5 \times 10^{-10}$ M. These concentrations are biologically significant given the sensitivity of the olfactory epithelium to these substances. Research is underway to confirm the concentrations of larval bile acids in stream waters.

Second, physiological studies using electroolfactograms (EOGs) demonstrated that the olfactory epithelium of migratory sea lamprey is very sensitive to allocholic acid and petromyzonol sulfate, with detection limits of $10^{-12}$ to $10^{-13}$ M (Sorensen and Gallaher 1994). These compounds appear to be recognized by different receptor mechanisms, which could mean that either substance alone may not elicit any response while a mixture of the two may be biologically potent in natural conditions (P. Sorensen, University of Minnesota, Minneapolis, Minnesota, pers. comm.). The response to these bile acids is strongly seasonal. Sea lamprey captured early in the migration period exhibit a strong physiological response compared with those captured late in the migration (late June) which do not respond to either bile acid. Taurolithocholic acid sulfate, a mammalian bile acid, is also detected by the olfactory epithelium of adult sea lampreys, but with less sensitivity compared with the bile acids. Tests of 35 other bile acids did not find any to be highly stimulatory to sea lamprey (Sorensen and Gallaher 1994). The physiological data provide strong evidence that upstream migrants have the ability to respond to species-specific substances that may be migratory cues. Although the olfactory specificity of adult sea lampreys is different from that of teleosts, other lamprey species have not been examined so the issue of species-specificity should be addressed.

Third, recent evidence indicates that petromyzonol sulfate can elicit a behavioral response in migratory sea lamprey under controlled laboratory conditions and that this response is strongly seasonal (P. Sorensen, University of Minnesota, Minneapolis, Minnesota, pers. comm.). The behavioral response consisted of changes in the distribution and locomotory activity of animals in tanks present with a choice of control water (alcohol mixture) and water with petromyzonol sulfate. The finding that behavioral responsiveness to larval washes declines late in the season confirms the EOG recording data. Preliminary behavioral tests in the field during 1993 were hampered by poor conditions but the data obtained were consistent with Teeter (1980) in that odors from larvae appeared to produced a response in migratory sea lamprey. These behavioral studies provide evidence that petromyzonol sulfate released by larval sea lamprey is detected by migratory adults and produces changes in their behavior. How this behavioral response is accomplished is not known.

An explanation for the seasonality of the physiological response of adult sea lampreys to the larval bile acids is lacking. Preliminary research in 1993 raised the possibility that the density of olfactory receptor cells (ORCs) might be lower in late migrants compared with early migrants and so account for the reduction in olfactory ability (Zielinski 1994). However, the relationship between ORC density and olfaction is not known and the differences in density observed between late and early migrants were not significant. An interesting finding is that there may be population differences in ORC density, with animals from the St. Marys River having a significantly lower ORC density than animals from the Ocqueoc River (Zielinski 1994). If olfaction is related to ORC density, then the delayed migration in the St. Marys River could be related to the reduced olfactory abilities of spawning sea lamprey. Why sea lamprey from the St. Marys River would have reduced olfactory capabilities compared with adults from other streams has not been addressed. Recent collaborative research points to biochemical changes in cells over time as a possible explanation for the degradation in olfactory sensitivity to bile acids of adults as the migration period progresses (B. Zielinski, University of Windsor, Windsor, Ontario, pers. comm.; P. Sorensen, University of Minnesota, Minneapolis, Minnesota, pers. comm.). These findings warrant further research to determine the mechanism by which the responsiveness of the olfactory epithelium in migratory sea lamprey declines during the spawning migration.

Several pieces of information are needed to fully assess the feasibility of using bile acids as attractants in the sea lamprey control program. Although the physiological response to bile acids is clear, the precise behavioral function(s) of these pheromones in migratory sea lamprey needs to be determined and the possibility that other cues might be involved in the behavioral responses should be examined. Distinguishing between the response of migratory animals to water currents (rheotaxis) and their response to the proposed attractants in behavioral testing will be important. These tests should be conducted using concentrations of bile acids found in water from streams supporting larval populations. A comparison of the response of sea lamprey in which the olfactory organ is blocked with the response of normal lampreys to a choice of control water and water with bile acids may be a useful approach. If bile acids are an important cue, then ablated lampreys should not respond to these treatments. Other lamprey species which produce and respond to bile acids should be identified and the identity of teleosts that detect and respond to these substance also should be determined.

Physiological and ecological factors influencing bile-acid production and release into stream water (and hence concentration) need to be clarified. This need is critical since the behavioral and physiological responses are both strongly seasonal. Where and when migratory sea lamprey use a cue such as bile acids (lake, river mouth, instream) is important information for the practical use of these substances. For example, if these substances are only used as cues to select streams and not used instream, then their utility as a trapping enhancement would be lessened. A time line of about 4-7 yr may be appropriate for the completion of these studies and initial field trials. Conducting a field trial will be difficult and expensive because no facility for this work exists. Also, a method to produce the compounds has to be determined, although this apparently is a tractable problem (P. Sorensen, University of Minnesota, Minneapolis, Minnesota, pers. comm.).

Use of substances produced and released naturally by sea lamprey should have few adverse environmental impacts, particularly since petromyzonol sulfate and allocholic acid mixtures may be specific to sea lamprey. If native lamprey species are also attracted by these substances, then adverse environmental effects may occur. These effects may not be great compared with the effects of lampricides on native lamprey species. However, more dramatic adverse effects on native lampreys are likely if attractants are used in streams that have not received lampricide treatments or in streams that have been recolonized after lampricide treatments were discontinued. Some reduction in TFM use and in the area of a stream exposed to lampricide and non-target mortality may be possible if efficiency is increased by using attractants to guide sea lamprey into easily treated areas. If odors specific for lampreys are used as attractants, non-target effects should be minimal.

Research necessary to determine the usefulness of bile acids as migratory cues is likely to be expensive because it involves considerable field verification of laboratory results using purified allocholic acid and petromyzonol sulfate. The cost of making large quantities of petromyzonol sulfate will be high initially because this substance is relatively exotic and because of difficulties in the synthesis protocol (Sorensen and Gallaher 1994). Presumably cost will decline as production continues and market incentives to produce the chemical are provided (P. Sorensen, pers. comm.). The cost of registering a pheromone for use as a pest control agent appears to be low (about $100,000) relative to the costs for conventional pesticides (e.g., Staten et al. 1994). Application costs may be comparable to application costs associated with conventional lampricide treatments.

Adult sea lampreys may also be vulnerable to artificially released sex pheromones that are utilized by spawning lamprey to attract reproductive partners or to evoke other reproductive barriers (Stacey 1994). This suggestion is based on the fact that teleosts make widespread use of released hormones or their metabolites as sex pheromones (Stacey 1994).

Most of the research on teleost sex pheromones has focused on the role of prostaglandins (PGs) and C21 and C19 steroids as sex pheromones, with F2-series prostaglandins (PGF) the most widely used behavioral sex pheromones (Stacey and Goetz 1982).

The greatest potential for using sea lamprey sex pheromones in the control program is in combination with migratory cues, particularly if the migratory cues are only important for stream selection, rather than moving upstream. Sex pheromones could be used to confuse reproductive pairing or to enhance trapping. Sex pheromones also might be used to increase the mating competitiveness of sterile males used in the SMRT program (i.e., hyper-aggressive or super males) if an implantable formulation can be devised.

Similar behavioral responses to odors have been consistently identified in spawning-phase sea lamprey (Teeter 1980; Sorensen and Gallaher 1994) and consist of male attraction to the odor of ovulated eggs and female attraction to male urogenital fluid. Li et al. (1994) used EOGs and reported that sulphated C21 compounds were most stimulatory to the olfactory system of adult sea lamprey while C19 compounds and testosterone did not stimulate the olfactory epithelium. Physiological and behavioral evidence that mature male sea lamprey release sex pheromones was recently obtained (P. Sorensen, University of Minnesota, Minneapolis, Minnesota, pers. comm.). The identity of these compounds has not been established, but they are known to be conjugated and their activity is high. Preliminary chemical characterization suggests a sulfated steroid.

If sea lamprey have evolved pheromonal responses to sex hormones, the nature of the response needs to be determined before the feasibility of manipulating it can be assessed. In teleost fish two types of responses are observed to sex pheromones: (1) primers, which appear to act on the endocrine systems of conspecific fish rather than on their behavior through a continuous release of the pheromone, and (2) releasers, in which exposure to the pheromone triggers immediate behavioral responses without necessarily triggering endocrine changes (Stacey 1994). Although both types of pheromone response may be useful, the releaser response may be more amenable to human manipulation because it is simpler to dispense and because concentration gradients are unlikely to be important. The sex pheromone of mature male sea lampreys appears to be a releaser type pheromone.

The above evidence provides support for continuing studies to determine the nature of the pheromone(s) involved, the physiological response and their potency, whether a behavioral response is elicited, and the distance over which these messengers are operative as attractants. The EOG results suggest that C21 compounds should be a starting point for investigation. A useful approach to characterizing spawning pheromones could involve reverse-phase HPLC purification and behavioral bioassays of urogenital fluids and egg washes (which are known to be pheromone sources) as was done to characterize a male spawning pheromone in Pacific herring, Clupea harengus pallasi (Sherwood et al. 1991). Care must be taken to avoid urine contamination when collecting milt for pheromone studies because fish urine is a rich source of conjugated steroids, the most probable pheromones in teleosts (Scott et al. 1991).

The use of sex pheromones at levels normally occurring in stream water should not pose many adverse environmental impacts on non-target organisms. This may not be true with respect to native lamprey species which have sympatric distributions with sea lamprey (Stacey 1994).

Studies following up progress already achieved should be relatively low cost. The costliest aspect of this approach may be the development of a delivery system, particularly an implantable formulation to improve the attractiveness of sterilized males used in SMRT. Current experience with other pheromonal biocontrols (Staten et al. 1994) suggests that the licensing costs of sex pheromones is not overly expensive.

A third approach to using attractants in the lamprey control program is to develop and implement larval sea lamprey attractants. The usefulness of this approach depends on whether larvae use olfaction, whether larvae will respond physiologically and behaviorally to specific odors, whether this response can be manipulated easily and cost-effectively, and whether there are negative environmental effects associated with either the chemical nature of the substance or its use.

Larval attractants could be used to improve the efficacy of lampricide treatments by drawing larvae from habitats that are difficult to treat with conventional practices or by aggregating larvae in predefined locations prior to treatment. On some lakes where residuals are believed to be major contributors of newly recruited parasites, measures to suppress the abundance of residuals are desirable. Alternatively, larval attractants could be used to stimulate larvae to move from their habitats at vulnerable points in their life cycle (e.g., after hatching but before abandoning nests to move downstream or during metamorphosis) and reduce survival at these times.

Prolarval and larval sea lamprey possess mature olfactory receptor cells (ORCs), which are functional in larvae and may be functional in prolarvae (Zielinski 1994). Electrophysiological experiments demonstrate that larvae can detect L-arginine (Zielinski 1994) and the bile acids, petromyzonol sulfate and allocholic acid (P. Sorensen, University of Minnesota, Minneapolis, Minnesota, pers. comm.). D-arginine is less chemostimulatory than its stereo isomer and L-serine is not chemostimulatory in sea lamprey (Zielinski 1994). Approximately 60% of larvae tested showed a preference for L-arginine in preference/avoidance tests and this amino acid also resulted in an increase in the motility of prolarvae (Zielinski 1994). Unfortunately attraction to L-arginine and other amino acids is common in teleost fish as they are often found in mucous secretions on the skin (Caprio 1994). Other than inferences that olfaction may be important for larval habitat selection and individual spacing (e.g., Thomas 1963, Mallatt 1983) and anecdotal observations that larvae seem to be attracted to salmon carcasses (Sorensen and Hanson 1994), there is no information on olfaction and larval attractants in sea lamprey.

Although there is no direct evidence that larval sea lamprey use olfaction to select habitat, the fact that larvae are blind and that their olfactory organ is functional and may be functional in prolarvae, and the demonstration that larvae and prolarvae respond to L-arginine all suggest that attempts to identify the role of olfaction and larval olfactory attractants should continue. Research should focus on identifying other substances that elicit physiological responses and whether these responses will direct behavior in predictable ways.

Larval attractants could reduce stream area exposed to lampricides and non-target effects. The major environmental concern may be the potential for interference with native lamprey species. In those streams where native species are abundant, use of attractants could be avoided.

If studies on the role of bile acids are pursued, the costs are likely to be low as these experiments can be combined with ongoing studies.

### *3.5.2 Repellants*

Natural repellants, including odors from predators and alarm substances, are well known among teleosts and are useful in redirecting fish movements (R. Smith 1994). Alarm substances (Schreckstoff) seem to be characteristic of teleost species in the superorder Ostariophysi which includes minnows, suckers, catfish, characins, and loaches (R. Smith 1994). Species that possess alarm substances tend to school or form large aggregations and use alarm substances to respond in a coordinated fashion to the presence of predators. These substances are produced and stored in epidermal club cells which sea lamprey lack (Pfeiffer and Pletcher 1964). Habituation to alarm substances can occur if release is persistent, reducing the effectiveness of the signal.

Some predators produce chemical stimuli that elicit behavioral responses in fish. For example, coho salmon will stop migrating and drop downstream when L-serine is detected in the water (Rehnberg and Schreck 1987). L-serine is commonly found on mammalian skin and presumably is interpreted as a signal that predators are nearby. The practical problem with attempting to manipulate this response is that habituation may occur and other motivating factors such as spawning, may override the avoidance response (R. Smith 1994).

Research into lamprey repellants is not extensive so the feasibility of developing and implementing repellants into the control program cannot be assessed. Teeter (1980) found that odors from mature males repelled other males and these findings were recently reconfirmed (Sorensen and Gallaher 1994). The preponderance of evidence from teleost fish appears to suggest that there would be several practical difficulties in using repellants to direct lamprey behavior because of the potential for habituation and overriding by other motivating factors. The practical value of using repellant substances in sea lamprey control is minimal unless the fate of repelled animals is known, i.e., do they disperse to nearby streams?

## 3.6 Genetic Manipulation

This section considers genetic manipulations other than alterations of the sex chromosomes (see Section 3.4) and includes gene regulation and transgenic approaches. Gene transfer experiments in teleost fish have focused on growth enhancement using growth-hormone genes, usually of mammalian origin (Kapuscinski and Hallerman 1990). Several research groups have successfully introduced foreign growth-hormone genes into teleosts but few have noted significant increases in somatic growth of transgenic individuals compared with normal animals (e.g., Chourrout et al. 1986, Dunham et al. 1987, Gross et al. 1992). At present, the idea of inserting novel genetic constructs from conspecifics or unrelated species that encode for a specific protein that causes death or severely retards development has not received any attention. However, much work in molecular biology has focused on isolating, cloning, and sequencing genes for important proteins in an attempt to determine factors regulating gene expression at critical points in the life cycle. The following section will focus on manipulating gene expression in sea lamprey.

Genetic manipulation could provide a sophisticated method of controlling sea lamprey abundance in the Great Lakes. One way to effect such control is to mutate either the coding or the regulatory region of genes coding for important proteins so that the resulting protein is not functional or its functionality is compromised. If sufficient numbers of larvae can be cultured with these altered genes they could be released to grow and breed with normal animals and so pass on the altered genes. This approach to control will work best if dominant alleles are altered and if population abundance is already low. Thus, continued use of other control options is essential. Because sea lamprey do not home to natal streams this method should be useful for attacking populations on a lake-wide basis, using releases from several well-chosen sites, and gene regulation should be able to bring some control to lentic populations and populations in large connecting channels such as the St. Marys River.

One difficulty with genetic manipulation is the fitness of altered individuals. If the alteration adversely affects the survival of individuals or fecundity, then this approach is unlikely to be successful. Because this approach requires several generations before it may be possible to detect some effect, there will be some damage to fish by released animals that metamorphose and feed as parasites. Approaches to control that involve the culture and release of bioengineered animals, regardless of the reason, may receive more public scrutiny than other options not involving genetic manipulations.

Genes that are strongly up- or down-regulated (i.e., turning transcription and subsequent production of the protein encoded by the gene on or off respectively) at critical points in the lamprey life-cycle would be most amenable to manipulation for control purposes. The gene for lamprin, the principle protein of the extracellular matrix of lamprey cartilage supporting the oral disk and piston in parasitic and adult sea lampreys, is strongly upregulated during metamorphosis (Wright et al. 1983). This protein is unique to lampreys, and it's synthesis is essential to the acquisition of parasitic behavior in sea lamprey. A soluble form of lamprin was cloned, sequenced and partially characterized recently (Robson et al. 1993). Lamprin consists of two soluble precursor forms of 10 and 12 kDa molecular weight which are essentially identical except for the insertion of 19 amino acids into the larger protein through what appears to be an alternative splicing event. Two lamprin mRNAs of 0.9 and 1.8 kb (kilobases) were also identified, differing only in the 3' untranslated region of the mRNA, which may imply differential regulation of the expression of these two messages. Based on protein polymorphisms and restriction digests of genomic DNA, Robson et al. (1993) inferred that lamprin is coded for by at least two genes.

Research is underway to characterize the structure and sequence of the lamprin gene, with emphasis on the 5' promoter region (F. Keeley, Hospital for Sick Children, Toronto, Ontario, pers. comm.). Once sequenced, the 5' region of the gene can be searched for homologies to known enhancers and suppressors of transcriptional activity, including glucocorticoids, thyroid hormones, cAMP, and others. Sequences for known thyroid hormone responsive elements (TREs) should be examined because of the recent evidence that thyroid hormones are involved in regulating metamorphosis in sea lamprey (see Section 3.7.1). The functional importance of these 5' regulatory sequences in driving the lamprin gene can be assessed by transfecting cultured lamprey cartilage using constructs of these sequences linked to a CAT (chloramphenicol acetyl transferase) reporter gene. This research has the potential of providing a clue to the hormones controlling the events of the entire metamorphic process.

A parallel line of research is also underway to clone and sequence lamprey pituitary hormones (F. Keeley, Hospital for Sick Children, Toronto, Ontario, pers. comm.) At present a pituitary pro-hormone cDNA clone (complimentary DNA produced from mRNA) analogous to the POMC (corticotropin/melanotropin/lipotropin/b-endorphin) family of composite pro-hormones has been sequenced. Expression studies indicate this POMC cDNA is strongly expressed in spawning and parasitic animals, relatively weakly expressed in larvae, but not expressed by stage 3 of metamorphosis (F. Keeley, Hospital for Sick Children, Toronto, Ontario, pers. comm.). The implication drawn from these findings is that because this gene codes for a precursor to many pituitary hormones and because it is strongly down-regulated at metamorphosis, the POMC gene could be an important area for targeting gene manipulation.

Genetic manipulation must be considered over the long-term in sea lamprey control. At present two genes believed to be strongly regulated at metamorphosis have been partially sequenced. Comparison of the 5' regulatory regions of these genes may reveal common sequence elements important for metamorphosis. Research aimed at sequencing the 5'-untranslated promoter regions is expected to be completed in 1995 (F. Keeley, Hospital for Sick Children, Toronto, Ontario, pers. comm.) Once the promoter region is sequenced, then work on regulatory sequences can begin in an effort to determine hormones involved in regulation of gene expression at metamorphosis and the effects of alterations in the promoter sequences on subsequent gene expression. A conservative estimate is that 4-5 years of research is needed before a proper assessment of the feasibility of manipulating these genes can be made. This assessment would also have to determine how such manipulation could be accomplished.

## 3.7 Developmental Blockers

### *3.7.1 Metamorphosis*

Metamorphosis has long been identified as a potential point for alternative control (Lamsa et al. 1980) because it is an essential event for the acquisition of parasitic behavior in sea lamprey. Methods to induce, delay, or alter metamorphosis have obvious potential as control techniques. Metamorphosis is a vulnerable point in the life cycle because it is a non-trophic period and the animals are undergoing immense internal and external changes. Retardation of the process or elimination of parasitic feeding through premature stimulation of the reproductive system will lead to starvation and death (Youson 1994). Although altering the outcome of metamorphosis would be a potentially useful approach throughout the Great Lakes, initial research might focus on streams in specific areas where fish stocks are heavily attacked, e.g., northern Lake Huron, and lampricides are impractical.

Metamorphosis in sea lamprey occurs when physiological preparation coincides with environmental and hormonal cues involved in triggering metamorphosis. Landlocked sea lamprey must be at least 120-mm long, weigh at least 3.0 g, and have a condition factor of 1.50 or greater ($CF = weight/length^3 \times 10^6$) before entering metamorphosis in laboratory conditions (Youson et al. 1993, Holmes et al. 1994, Holmes and Youson 1994). The weight and CF criteria reflect lipid reserves while the length criterion identifies larvae at the end of an arrested growth phase, during which lipid is accumulated prior to entering the non-trophism of metamorphosis. Throughout larval life there is a gradual accumulation of thyroid hormones (thyroxine -- $T_4$ and triiodothyronine -- $T_3$) in the blood (Youson et al. 1994a). When lipid levels reach approximately 14% of the body weight (Lowe et al. 1973, O'Boyle and Beamish 1977) and thyroid hormone levels in the blood peak (Youson et al. 1994a), the normal rise in water temperature during the spring will trigger metamorphosis in animals of the appropriate size (Purvis 1980, Youson et al. 1993, Holmes and Youson 1994, Holmes et al. 1994). Larvae in the arrested-growth phase and accumulating lipid body reserves, appear to require a winter-chill period to prepare physiologically for metamorphosis followed by rising temperature in the spring to initiate the event (Holmes et al. 1994, Holmes and Youson 1994). The absence of either component of the seasonal temperature cycle will significantly reduce the number of animals that enter metamorphosis in laboratory conditions (Holmes et al. 1994, Holmes and Youson 1994, J. Holmes and J. Youson, unpubl. data). The upper and lower limits of temperature at which metamorphosis will occur are not known.

The effects of other environmental variables such as photoperiod, food availability, and density on metamorphosis are mixed but clearly not as strong as water temperature. Photoperiod and food availability had no short-term (1 month prior to metamorphosis) or long-term (9-11 months prior to metamorphosis) influence on metamorphosis (Cole and Youson 1981, Youson et al. 1993, Holmes et al. 1994), although the experimental periods in these studies may have been too short for these variables to exert detectable effects. In contrast, high density appears to inhibit metamorphosis. Morman (1987) reported that after 5 years in cages in five Michigan streams animals kept at a density of 28 larvae/m$^2$ metamorphosed but no metamorphosis was observed among animals kept at a density of 85 larvae/m$^2$. Experimental studies at the LHBS during the summer of 1993 also found that the incidence of metamorphosis tended to be higher among animals kept at a density of 66 larvae/m$^2$ compared with animals kept at a density of 164 larvae/m$^2$ (Youson et al. 1994c), although difficulties maintaining temperature and in obtaining a sufficient sample of animals of the appropriate size hampered this study.

The initiation and the outcome of metamorphosis in sea lamprey can be manipulated by the application of goitrogens. Holmes and Youson (1993) induced metamorphosis using $KClO_4$ in three size-classes of larval sea lamprey at a time (winter) when spontaneous metamorphosis does not occur. Although the degree of induction varied among size-classes (22%, 65-95 mm; 52% 110-119 mm; 98% > 130 mm), these results show that the physiological requirements and environmental cues of spontaneous metamorphosis can be overridden. Holmes and Youson (1993) also reported that animals in which metamorphosis was induced did not appear to follow the normal developmental pattern of synchronized internal and external changes that characterize spontaneous metamorphosis (see Youson and Potter 1979 for descriptions). Misshapen oral disks and small emaciated sizes suggested that metamorphosis was induced in these animals before adequate physiological preparation had occurred (i.e., lipid accumulation) and that these animals either would not survive metamorphosis or would not be capable of feeding parasitically afterwards. These findings are significant in the context of controlling sea lamprey because, once initiated, metamorphosis is irreversible so the animals cannot revert back to the larval form if conditions are inappropriate for metamorphosis or if conditions for downstream migration and feeding as parasites are poor.

Thyroid hormones ($T_4$ and $T_3$) are clearly important in triggering metamorphosis in sea lamprey and other vertebrates. Both $T_4$ and $T_3$ remain at low levels during the larval phase and increase through metamorphosis in amphibians, and in teleosts such as American eel (<u>Anguilla</u> <u>rostrata</u>) and flounders. In contrast, there are high concentrations of both thyroid hormones in the blood of larval lamprey which peak at metamorphic climax and decline as metamorphosis progresses (Wright and Youson 1977, Lintlop and Youson 1983, Youson et al. 1994a). Induction of metamorphosis with $KClO_4$ produced a significant decline in $T_3$ but not $T_4$ (Youson et al. 1994b), indicating that monodeiodination of $T_4$ to $T_3$ is an important biochemical event of metamorphosis. The hormonal differences between spontaneous metamorphosis in lamprey and other vertebrates provide some evidence that factors triggering metamorphosis are likely to be relatively specific for lamprey. Thus, any potential manipulation of sea lamprey metamorphosis in the Great Lakes may not necessarily affect metamorphosis in other cohabiting vertebrates (e.g., amphibians).

One of the primary stimuli for metamorphosis in lamprey is believed to be delivered through the hypothalamic-hypophyseal-gonadal axis (Sower and Hanson 1992; Youson and

Holmes 1993). Joss (1985) demonstrated that pituitary hormones played a significant role in the metamorphosis of Geotria australis. Cole and Youson (1981) found that pinealectomized sea lamprey did not enter metamorphosis whereas some control and sham-operated animals commenced normal metamorphosis in their studies. In nonparasitic species, the intestine begins to atrophy and the gonads mature at the end of metamorphosis, culminating in spawning and death (Youson 1988). This process differs from metamorphosis in parasitic species where intestinal atrophy and gonadal maturation are delayed 12-18 months during the feeding period. Recent evidence of a lamprey population with both life-history types (Beamish 1987) supports the inference that delaying gonadal maturation is important to the parasitic life history. A large portion of a population of Lampetra richardsoni are nonparasitic but a small number of animals are parasitic and feed when presented to host fish. The parasitic animals are genetically identical to nonparasitic animals from the same population, but they are males in which gonadal maturation had not begun and the intestine had not atrophied (Youson and Beamish 1991).

The reproductive system of sea lamprey apparently receives a stimulus during metamorphosis as a result of increased levels of gonadotropin-releasing hormone (GnRH) in the brain (Youson and Sower 1991). There are two lamprey GnRH molecules, I and III; lamprey GnRH-I is distinctly different structurally from other known vertebrate GnRHs and has no biological activity in chickens, rats, and sheep, although the function of stimulating the reproductive system is conserved in sea lamprey (Sower et al. 1987). Lamprey GnRH-III levels are highest early in metamorphosis and decline to low levels by the latter stages and remain relatively constant through the feeding phase while lamprey GnRH-I levels rise to their highest values after metamorphosis (Sower et al. 1993). Other hormones which may be involved and their modes of action are not known but under certain circumstances the balance between stimulation and inhibition can be altered to produce an alternate life-history type (e.g., L. richardsoni).

Knowledge of environmental and hormonal factors influencing metamorphosis has expanded greatly in the past 3 yr but is not yet sufficient for the development and implementation of practical tools to control sea lamprey. The evidence that environmental temperature and thyroid hormones are important cues, the demonstration that the mode of action of thyroid hormones in lampreys differs from metamorphosis in other vertebrates, the alternate (non-parasitic) life history model, the demonstration that differences between life history pattern are related to gonadal maturation and intestinal atrophy following metamorphosis, and the evidence that the timing of metamorphosis can be manipulated in the laboratory, overriding physiological preparation and other stimuli, all demonstrate the potential of this research area yielding a practical method of control. Fruitful approaches include a comparative endocrinological study of the hypothalamic-hypophyseal-gonadal axis in paired (satellite) species of parasitic and non-parasitic life-history types to determine factors stimulating and inhibiting intestinal atrophy and gonadal maturation, studies of temperature, density, and other environmental factors to determine environmental limits of metamorphosis so that the productive potential of streams can be estimated, and studies of methods to prevent or induce early metamorphosis including the effects of hormones, hypophysectomy, heat-shock proteins, temperature, condition factor, sex, and goitrogens on metamorphosis. Approximately 5 years of field and laboratory research may be required before consideration can be given to implementing some of these findings for control purposes. Because of the long life cycle of sea lamprey, use of an alternative species with a shorter life cycle or the culture of large numbers of sea lamprey known to metamorphose at 2-3 years of age have been suggested as alternate sources of experimental animals (Sower and Hanson 1992). The latter approach would require the development of better culture techniques and facilities than are currently available (see Section 3.5).

Interference with metamorphosis could lead to reductions in lampricide use either because the interval between treatments increases or because the need for treatment is lessened as the production of newly-metamorphosed parasites is reduced. The environmental effects will depend on the approach used to prevent or induce early metamorphosis or force animals to bypass feeding and mature early. Using goitrogens such as $KClO_4$ to induce metamorphosis would be relatively unselective and is likely to have adverse effects on other fish and aquatic organisms. Field applications of goitrogens are unlikely to be permitted because of the potential impacts on other aquatic species. Stimulatory or inhibitory hormones, particularly unique hormones such as lamprey GnRH-I or GnRH-III may not have widespread effects on other organisms except other sympatric lamprey species if delivered into streams. The alternative is to culture large numbers of sea lamprey, block metamorphosis by some means either at the embryo stage or early in the larval period, and release them into streams to grow and compete with normal animals. If this approach can only be implemented through competition, several years will be required (at least one generation) before effects on normal animals may be detectable. This approach may have fewer adverse impacts than instream treatment but great caution would have to be used to ensure that metamorphosis was blocked in released embryos or larvae.

The cost of developing and implementing control of sea lamprey through induction or blocking of metamorphosis or altering the outcome of metamorphosis will be relatively high, probably comparable to the costs of developing attractants since endocrinological studies are time consuming. At present, goitrogen-induced metamorphosis provides an experimental model that is useful for investigating the hormonal basis of metamorphosis in the laboratory even though the event is not identical to spontaneous metamorphosis (J. Youson, Divison of Life Sciences, Scarborough College, University of Toronto, Toronto, Ontario, pers. comm.).

### *3.7.2 Growth*

Although environmental factors influencing growth of sea lamprey are relatively well known (see Potter 1980, Holmes 1990, Young et al. 1990), knowledge of chemical factors regulating growth is lacking. If a chemical factor could be identified, then growth regulation might be possible (Bergstedt and Seelye 1992). Such regulation could lengthen the period between lampricide treatments since metamorphosis is size-specific.

Mallatt (1983) inferred from the results of his feeding studies that at high densities larval Lampetra tridentata may release a chemical into the substrate surrounding their burrows which inhibits or reduces the growth of neighbors. He did not identify a specific compound at the time and so far his hypothesis has not been tested experimentally or in the field. Mallatt is probably referring to some factor such as an attractant or repellant which regulates spacing, affecting growth indirectly rather than acting directly on growth rate. One practical approach is to investigate the potential of the bile acids petromyzonol sulfate and allocholic acid (see Section 3.5.1) as growth regulators. Both chemicals are produced by larvae and are found in biologically significant amounts in stream water, at least to upstream migratory sea lamprey (Sorensen and Gallaher 1994), and the olfactory epithelium of larvae is sensitive to both bile acids (P. Sorensen, University of Minnesota, Minneapolis, Minnesota, pers. comm.) Whether these bile acids are persistent substances, remaining adsorbed to substrate particles is not known but would be critical to the feasibility of chemical regulation since continuous (chronic) exposure would probably be required. If there is a chemical growth regulator, then research would be required to determine the mode of action and whether olfaction played a role in the detection and subsequent biological response.

Given the lack of evidence concerning the existence of chemicals regulating growth, concerns about the potential effects on sympatric lamprey species, and the fact that it is unlikely to have a significant impact on lampricide use, research to identify and characterize such substances does not seem to be warranted at this time.

## 3.8 Natural Controls

A variety of factors including species interactions which may involve predation or competition for space and other resources, parasites, pathogens, and environmental factors have been cited as natural controls on the abundance of wild fish populations. Where one or more of these factors have been implicated as a control agent, convincing evidence is elusive as there is no formal proof for mortality induced by these factors. Nonetheless, there remains considerable interest in the role of natural controls on population abundance.

Several researchers have suggested that natural controls on sea lamprey abundance should be investigated by the sea lamprey control program. Most of these suggestions have focused on competitive displacement, parasites and pathogens, predators, and more recently, host tolerance and resistance. The later mechanism differs from the other suggestions in that it does not directly affect sea lamprey abundance, rather it seeks to limit prey mortality induced by parasitic sea lamprey. The effects of environmental variation will be discussed in Section 3.9.

In order to use natural controls to suppress sea lamprey abundance effectively, information on when lamprey are vulnerable to these controls is needed. Knowledge of the role of biotic factors (competition, predation, parasites, pathogens) in regulating sea lamprey abundance is lacking. This information cannot be obtained from studies of landlocked sea lamprey populations because the control program is a significant confounding factor. Thus, studies of natural controls in uncontrolled lamprey populations are needed (i.e., anadromous sea lampreys along the east coast of North America or the west coast of Europe).

### *3.8.1 Competitive Displacement*

The displacement hypothesis postulates that indigenous species are displaced by invading non-native species, usually as a result of competition, although predation and hybridization resulting in genetic contamination and swamping of indigenous species, also have been invoked in biogeographic studies of fish distributions (Douglas et al. 1994). Native fishes are usually perceived in this scenario as being actively outcompeted by more efficient, non-native invaders. However, in the context of sea lamprey control, the suggestion is that native nonparasitic species in the Great Lakes might outcompete sea lamprey and be used to flood parasitic populations, slowing growth and possibly affecting abundance.

The growth rate of larval sea lamprey reestablished following chemical treatment is greater compared with growth rates prior to treatment (Purvis 1979) so a natural means of effecting a compensatory decrease in growth would help to reduce the frequency of lampricide treatments (Murdoch et al. 1991). The effect on sea lamprey is likely to be stream specific so savings in terms of lampricide use and costs are difficult to estimate. Fishery effects would also vary among regions because of the possibility of other compensatory mechanisms regulating sea lamprey populations. For example, growth reductions in some streams might lead to smaller size at metamorphosis in those streams so that the production of parasitic animals is unaffected. These smaller parasitic animals may have less impact on fish populations and be less fecund compared with larger animals. However, relationships between parasite size and impact on fish or fecundity have not been established.

Anecdotal field observations do not support the concept of competitive displacement as applied to sea lamprey. The spread of sea lamprey through the upper Great Lakes was not hindered by competition from native nonparasitic species, indicating that the larvae were able to outcompete native larvae, presumably for habitat space since food is not usually considered limiting. One possible explanation for the rapid spread of sea lamprey is that native species were not abundant enough to exert any detectable competitive effect given the fecundity of sea lamprey. In contrast, the importance of interspecific competition between sea lamprey and native lamprey species in Lake Ontario and the Finger Lakes of New York prior to the invasion of the upper Great Lakes and the beginning of control efforts is not clear and has not been investigated. Chemical control makes the concept of competitive displacement less viable since native species are also greatly reduced by lampricide treatments (Schuldt and Goold 1980).

Experimental studies of growth and interspecific competition did not demonstrate competitive superiority in either sea lamprey or least brook lamprey Lampetra aepyptera larvae relative to the other species (Murdoch et al. 1991). Interspecific competition seemed to have the same effect as intraspecific competition (density) on individuals from both species, i.e., a reduction in growth rate as density increases. This finding is potentially exploitable since larval lamprey growth rates are known to be inversely related to density in the laboratory and field (Mallatt 1983, Morman 1987, Murdoch et al. 1992). Whether growth can be slowed sufficiently to affect the frequency of lampricide application in a particular stream is unknown. Current control practices may keep larval populations in a state in which density is not a significant influence on population dynamics (Holmes 1990).

The concept of competitive displacement as a useful biological control in the sea lamprey management program cannot be properly assessed until factors regulating lamprey populations not subject to human control are investigated. Sea lamprey are indigenous to the east coast of North America and the west coast of Europe and in these areas they do not pose a known threat to fish stocks. Some unknown factors regulate abundance and may be easier to ascertain in these areas because of the absence of human efforts to control abundance. A second approach that may merit some attention is to investigate factors controlling populations of nonparasitic lamprey species above barriers or in untreated tributaries to the Great Lakes.

Theoretically, the use of nonparasitic native species for competition with sea lamprey should have few adverse environmental impacts since they do not pose a threat to fish stocks and are native to the region. The recommendation of Murdoch et al. (1991) to maintain these species in the wild because their effect on sea lamprey growth may be equal to that of conspecific sea lamprey in a population is reasonable in this context.

### *3.8.2 Parasites and Pathogens*

The pathological consequences of parasites and pathogens are well known and support the view that they may be major mortality agents in some fish populations. However, direct evidence of parasite- or pathogen-induced mortality of fishes is rare (Szalai et al. 1992). For example, studies in which parasite induced mortality is believed to be a major factor controlling abundance (e.g., Fisher and Kelso 1988, Szalai and Dick 1991) have seldom been free of the confounding effects of stress due to poor water quality, population demographics, or predation from other species.

A variety of insect pests have been subjected to successful control through the use of relatively host-specific parasites or pathogens (see comments in Seelye and Hanson 1992), but so far this form of biological control has not received much attention as a means of controlling pest-fish populations (Bergstedt and Seelye 1992). Because sea lamprey are so distantly related to teleosts it is possible that their natural parasites and pathogens would pose little threat to teleosts, although native lamprey species may be adversely affected. However, most teleost parasites and pathogens do not exhibit host-specificity so contamination of culture facilities drawing water from the Great Lakes (Bergstedt and Seelye 1992) and infection of wild and feral populations are objections that would be raised to the deliberate use of parasites or pathogens to control sea lamprey.

Sixty-eight species of parasites have been reported from larval and adult sea lamprey (Appy and Anderson 1981). Most of these parasites are also found in teleosts and are believed to be incidental acquisitions during feeding by parasitic sea lamprey (McLain 1951, Wilson and Ronald 1967, Appy and Anderson 1981). However, two metazoans appear to exhibit host-specificity in lampreys: Diplostomulum petromyzifluviatilis and Truttaedacnitis stelmioides (Appy and Anderson 1981). The former has been reported in four species from Great Britain and Russia while the latter is found in five species, including sea lamprey in Europe, Asia, and North America (Appy and Anderson 1981). Beverly-Burton and Margolis (1982) have also described a digenean worm Ophioxenos lampetrae sp. nov. that appears to be specific to western brook lamprey (Lampetra richardsoni). Pybus et al. (1978) described the life cycle of T. stelmioides in L. lamottenii and Eng and Youson (1992) reported that larval lamprey are able to survive heavy infestations of T. stelmioides in the liver for many years before entering metamorphosis.

Low levels of infection by T. stelmioides have been reported in sea lamprey from the Great Lakes. McLain (1951) found that 2.3% of recently transformed animals (N=215) and 10.3% of parasitic-phase animals (N=29) were infected with the nematode Camallanus sp. (probably T. stelmioides according to Appy and Anderson 1981). Wilson and Ronald (1967) sampled in the same area as McLain (Lake Huron) and found that 2.8% of the parasitic (N=431) and 0.4% of the spawning (N=284) sea lamprey were infected by Cucullanus stelmioides. Wilson and Ronald (1967) also reported that this was the only parasite which appeared capable of causing serious damage to the host and suggested that the difference in the incidence of infection shown above is an indication that this nematode may cause some mortality in sea lamprey.

Parasites do not seem likely to provide a useful approach to the development of a practical tool for biological control of sea lamprey. The available data appear to indicate that mortality induced by T. stelmioides occurs after the animal has had a chance to inflict some damage on fish stocks. Also, larval lamprey are able to cope with heavy infestations with few if any negative effects. A more useful approach to parasite-induced mortality is to find an organism that causes mortality in the larval phase of the life cycle or during metamorphosis. A method of increasing the rate of infection or virulence of infection would have to be developed in order to exert control (Bergstedt and Seelye 1992).

Knowledge of bacterial, fungal, or viral pathogens in lampreys and their effects on population abundance is lacking. The pathogenic organisms which have been reported from lampreys are capable of infecting a wide variety of unrelated teleosts (Appy and Anderson 1981). For example, red lesions due to an Aeromonas sp. infection (Horner cited in Bergstedt and Seelye 1992) have been observed on parasitic-phase sea lamprey captured in northern Lake

Huron (W. Swink, National Biological Service, Lake Huron Biological Station, Millersburg, Michigan, pers. comm.). The potential for using bacterial, fungal, or viral pathogens in sea lamprey control cannot be assessed properly at present. If sea lamprey are only infected by general fish pathogens, then the usefulness of these organisms to sea lamprey control will be marginal.

A successful strategy in developing biological controls of insect pests has been to examine natural controls of the species in its geographic origin. Similar work should be undertaken with respect to host-parasite and pathogen relationships in anadromous sea lamprey populations along the east coast of North America. Sea lamprey do not appear to have negative effects on fish stocks in the Atlantic Ocean so factors such as parasites or pathogens may be exerting some control on population abundance in these areas and may offer some approach that proves useful to sea lamprey control in the Great Lakes.

The potential effects of parasite or pathogen infection on sea lamprey abundance in the Great Lakes cannot be determined because of information relating sea lamprey mortality to such pathological conditions is not available. The potential for negative parasite or pathogenic effects on desirable fish stocks is not negligible since most of the parasites found on or in landlocked sea lamprey are not host-specific and because T. stelmioides, although specific to lamprey, probably doesn't influence mortality until after some damage to fish has occurred.

The cost of investigating natural controls in anadromous sea lamprey populations along the east coast of North America is probably low to moderate, depending on the availability of a suitable researcher in the area.

### *3.8.3 Predators*

Predation is a significant mortality factor on some invertebrate and fish populations (e.g., Pacific salmon in the Great Lakes feeding on alewife) and has been suggested as a potential mechanism for suppressing sea lamprey abundance. Predation on the eggs or larvae of sea lamprey has obvious value from a control standpoint because it suppresses abundance without the use of costly chemical control and it could be self-sustaining and continuous. Predation on parasitic sea lamprey has less value in a control context because these individuals have likely attacked some fish. The difficulty with predation as a method of control is that the effects on other fish species cannot be reliably predicted (Bergstedt and Seelye 1992).

Teleost predation of larval or adult sea lamprey is not well documented and in those studies where predation was observed, lamprey rarely comprised a significant portion of the diet. Logperch (Percina caprodes) and small rainbow trout (Oncorhynchus mykiss) have been observed consuming eggs during sea lamprey spawning and young larvae when nests were disturbed for sampling (Manion 1968). Perlmutter (1951) reported that American eels fed on larvae but this was observed in small aquaria in the laboratory and may not reflect stream conditions. The only report quantifying the dietary contribution of lampreys is that of Thomas

(1962) who noted that larval Lampetra planeri comprised 1.1-2.2% of the food items in the stomachs of European eel (A. anguilla) between June and September.

Feeding experiments conducted by Pfeiffer and Pletcher (1964) demonstrated that coho salmon (O. kisutch) fry and adults, redside shiners (Richardsonius balteatus), threespine stickleback (Gasterosteus aculeatus), prickly sculpin (Cottus asper), and adult rainbow trout would not consume larval L. tridentata unless the carcass was skinned. Distasteful secretions from granular cells in the skin of L. tridentata may have provided protection from predacious fish. This suggestion is in contrast with anecdotal observations that stream resident fishes will eat larvae during TFM treatments (Bergstedt and Seelye 1992) and that fish-eating birds such as herring and ring-billed gulls (Larus argentatus and L. delawarensis respectively) readily consume larvae during granular Bayer surveys (J. Holmes, Division of Life Sciences, Scarborough Collgeg, University of Toronto, Toronto, Ontario, pers. obs.). Larval lamprey normally remain burrowed in the sediment and thus are relatively unavailable to stream predators in the water column. The most vulnerable period for predation occurs when sea lamprey move between habitat patches, usually at night or during flooding (Thomas 1963). Predation on larval lampreys by species relying more on tactile stimuli such as brown bullhead, Ictalurus nebulosus, and white sucker, Catostomus commersoni, has not been observed or studied experimentally.

Information with which to assess the potential for predation-induced mortality as a method for controlling sea lamprey abundance is lacking. The impact of predation will depend on the point in the life cycle at which it is applied. While efforts to reduce the abundance of spawning animals (e.g., the SMRT program) could be hindered by compensatory effects on the production of newly-metamorphosed parasites, lampricide treatments aimed at larvae have reduced the production of parasitic animals. Predation on eggs or larvae could have the same effect but an examination of the role of predation in structuring anadromous populations along the east coast of North America is needed because the control program in the Great Lakes is a large confounding factor.

The possibility of negative predation effects on other desirable fish species exists. Good information on the abundance of sea lampreys, predators, and other prey species will be necessary to use predation as a control method. A new predator from elsewhere that feeds preferentially on sea lamprey may be better than native species but such an organism is not known at present and the ecological consequences of a new introduction are not entirely predictable.

### *3.8.4 Host Tolerance and Resistance*

Stocking by fisheries management agencies combined with sea lamprey control has provided fishable populations of introduced salmonines such as Pacific salmon, Oncorhynchus spp., brown trout, Salmo trutta, and rainbow trout, O. mykiss, plus native lake trout, Salvelinus namaycush, in the Great Lakes. Although these programs are successful, assessment data indicate that large numbers of salmonines are killed by sea lamprey. Several researchers have suggested that the negative impact of sea lamprey on salmonines, particularly lake trout, might be reduced or minimized through stocking of fish tolerant of or resistant to attacks. In this context tolerance and resistance refer to characteristics (genetic or phenotypic) in a species or strain that reduce vulnerability to attack and enhance survival, particularly in the older reproductive age-groups. Because of the emphasis on rehabilitation of lake trout stocks, the focus of this section will be on lake trout.

The number of sea lamprey attacks on preferred prey is the result of interactions between lampreys, prey, and other species, involving searching, the probability of encountering prey, interactions between individual lamprey and prey, and other relationships. Little is known concerning how lamprey locate prey so the effect of greater host tolerance or resistance on sea lamprey abundance is not clear. However, effects such as a reduction in the number of lamprey attacks on species of interest, reductions in lamprey feeding duration and opportunities, and reductions in growth, fecundity, and survival can be supposed. Negative effects on other fish species may occur if sea lamprey compensate for reduced availability of preferred prey (salmonines) by switching to less preferred species (e.g., walleye, Stizostedion vitreum).

Three approaches have been suggested as possibilities for employing host tolerance and resistance. The first approach is based on the observation that lampreys and lake trout have coexisted in the Finger Lakes of New York and therefore lake trout from these lakes may have some adaption which can be exploited on a larger scale in the Great Lakes. Second, following the model of splake (Salvelinus namaycush x S. fontinalis), strains that reach sexual maturity faster and reproduce at a smaller size may have greater reproductive success because they are less vulnerable to sea lamprey attacks and mortality prior to sexual maturation. The third approach is to develop host fish with blood characteristics that are offensive to sea lampreys and that would adversely affect feeding.

Comparison of the performance of the different strains of lake trout stocked into Lake Ontario since 1973 (Clearwater Lake, Green Lake, Lake Manitou, Lake Michigan, Marquette, and Seneca Lake) showed that the Seneca Lake strain performed better than the other strains in the presence of large numbers of sea lamprey. The average survival of the Seneca Lake lake trout in Lake Ontario was double the survival of other strains and Seneca strain fish age 9 and older were abundant whereas few individuals of the other strains were older than age 6 (Schneider 1985 cited in Swink and Hanson 1986). The superior performance of Seneca fish was interpreted as an indication that they were less vulnerable or more resistant to sea lamprey attacks. A test of this hypothesis in the laboratory did not reveal a significant difference in the mortality of Marquette and Seneca Lake strains subjected to single lamprey attacks (Swink and Hanson 1986), leading to the conclusion that differences in behavior or environmental preferences reduce the vulnerability of Seneca Lake strain fish to sea lamprey attack. In support of this hypothesis, wounding data were provided that show Seneca Lake fish had significantly fewer sea lamprey wounds than did individuals of other strains. Studies of the bathythermal distribution of juvenile lake trout in Lake Ontario (Elrod and Schneider 1987) and the dispersal of lake trout from stocking sites (Elrod 1987) did not reveal any differences between Seneca Lake fish and other strains that might account for the lower wounding rates, although the sample of Seneca Lake fish in both studies was small. Analysis of other behavioral or environmental differences between strains that may account for differences in vulnerability to sea lamprey is needed.

If the characteristics which seem to reduce the vulnerability of Seneca Lake strain lake trout to sea lamprey attack are heritable traits, then a selective breeding program is likely to succeed. Historical evidence indicates there were important differences in life-history traits of lake trout stocks such as the time and location of spawning, depth distribution, and food preferences (Brown et al. 1981, Goodier 1981) and that these differences may have a genetic basis (Krueger et al. 1989). The perceived improvement in performance of Seneca Lake strain fish compared with other strains stocked in Lake Ontario has lead to a debate in Ontario over the merits of switching some lake trout hatchery production to this strain (P. Ihssen, Ontario Ministry of Natural Resources, Maple, Ontario, pers. comm.) in an attempt to reduce losses from sea lamprey attack and to hasten the reestablishment of naturally reproducing lake trout stocks.

A second approach to the issue of reducing vulnerability to sea lamprey attack follows the rationale behind the development and implementation of the splake (S. namaycush x S. fontinalis) program by Ontario. Sea lamprey attacks are size-selective, with larger fish attacked more often than smaller individuals, and survival of large fish to maturity is generally poor (Cochran 1985; Swink 1991). Splake were introduced as a surrogate for lake trout in Georgian Bay prior to effective sea lamprey control because it was believed that the hybrid would mature faster and at a smaller size compared with lake trout and so reduce the number of years of vulnerability to sea lamprey prior to reproducing (P. Ihssen, Ontario Ministry of Natural Resources, Maple, Ontario, pers. comm.). The program had some success as limited natural reproduction was inferred from fry catches around spawning shoals, but splake stocking was eventually discontinued because of evidence that some lake trout were surviving to maturity and because of a commitment to continue effective sea lamprey control (P. Ihssen, Ontario Ministry of Natural Resources, Maple, Ontario, pers. comm.).

Despite the limited success of the splake program, the concept of using early maturing strains of lake trout may be exploitable for reducing sea lamprey predation on fish stocks. For example, some lake trout strains from inland lakes in Ontario may reach sexual maturity at an age of 4-5 years (P. Ihssen, Ontario Ministry of Natural Resources, Maple, Ontario, pers. comm.) compared with 6-7 years normally observed (Scott and Crossman 1973). A preliminary study on one such strain of lake trout is underway in Ontario. If it can be demonstrated that this strain matures earlier than other lake trout strains stocked in the Great Lakes, several years of research would be required to determine its performance in the Great Lakes and reproductive success in the presence of large numbers of sea lamprey, a species to which these strains do not have prior experience.

A third alternative for sea lamprey control is to stock the lakes with host fish that have blood characteristics that adversely affect the feeding of parasitic sea lampreys. Specific suggestions include inducing the production of antibodies in host-fish blood (Bergstedt and Seelye 1992) or inducing an offensive taste to lampreys in host-fish blood. The former concept was based on observations at the LHBS that more sea lampreys were dying when fed rainbow trout compare with those fed lake trout (Bergstedt and Seelye 1992), but this differential mortality hypothesis is not supported by the results of sea lamprey attack experiments using these species as host fish (Swink and Hanson 1989). Convincing evidence that taste plays a role in the feeding of sea lamprey is lacking. Farmer and Beamish (1973) found that sea lamprey would feed on most teleosts offered if their preferred prey (salmonines and coregonines) were not available. The lack of corroborating evidence for taste or antibody approaches makes it impossible to assess the potential for these approaches to lead to a practical means of reducing lamprey feeding and subsequent mortality of host species.

Stocking fish that are less vulnerable to sea lamprey attack either because they mature faster than other species or because behavioral or environmental preferences reduce range overlaps with sea lamprey, could result in better survival and natural reproduction of lake trout. This strategy is predicated on continuing sea lamprey control at current levels at least until feral populations of lake trout are firmly established. One potentially adverse effect is a reduction in genetic diversity. Historical evidence suggests that the lakes are able to support larger numbers of lake trout if they consist of discrete stocks (Goodier 1981). Thus, attempts to improve survival through stocking of Seneca Lake strain fish or early maturing strains should be cognizant of the potential for reduced genetic diversity.

Because hatchery programs are costly, strategies which reduce losses due to sea lamprey predation after release and support the establishment of natural reproduction will be useful. The costs of such a program would not be borne directly by the sea lamprey management program, but by management agencies engaged in stocking. Some costs may be involved in supporting studies to determine the reasons for the apparent performance superiority of Seneca Lake fish and to determine if early maturing lake trout have better survival and reproductive success than other strains that have coexisted with sea lamprey.

### 3.9 Habitat Manipulation

Larval sea lamprey have been found in less than 10% of the streams that drain into the Great Lakes (Morman et al. 1980), which implies that their habitat requirements are restrictive and potentially exploitable as a means of control. Streams can be classified on the basis of differences in substrate characteristics: those streams supporting larval sea lamprey have higher proportions of sand and lower proportions of bedrock and clay compared with streams that do not support larvae (Young et al. 1990). Temperature may limit the present range of larval sea lamprey in the northern (A.H. Lawrie cited in Christie and Kolenosky 1980) and southern regions (Holmes 1992) of the Great Lakes. Within a stream, the distribution of larvae is influenced by water quality, physical barriers to spawning, temperature, substrate, and flow (Morman et al. 1980). Temperature, substrate, and flow are probably the habitat variables most amenable to modification for the purpose of sea lamprey control.

### *3.9.1 Substrate and Flow*

Relationships between the quantity of suitable substrate and larval growth or abundance or other measures of performance have not been established so the potential effects of substrate manipulation are difficult to predict. Modifying substrate and flow to control sea lamprey is probably restricted to specific streams or problem sections within streams where habitat parameters are well defined. Substrate manipulation for controlling sea lamprey could consist of altering habitat that is difficult to treat with lampricides and reducing problems associated with residual larvae in these areas, or substrate may be modified to reduce the amount of suitable habitat for larvae resulting in reduced growth or abundance because of increased density. Ecosystem management considerations probably preclude widespread use because the objectives of such management normally do not focus on single species.

Larval sea lamprey occur most frequently in the soft bottoms of streams and lentic areas containing mixtures of sand and silt (Applegate 1950, Thomas 1963, Potter 1980). However, some larvae can be found in nearly all habitats including small pockets of soft sediments among rocks and boulders, inside discarded tires, under wood, and in debris piles (Applegate 1950, Thomas 1963). Lamprey larvae will avoid unstable shifting substrates. Streams with no soft substrates do not support larval lampreys but may have populations in the delta off of the mouth because this is the main depositional area (Morman et al. 1980). Experimental studies of larval lamprey habitat selection in lentic areas indicate that mean grain diameter and permeability are both determinants of suitable habitat (Lee 1989). Areas characterized by sand fractions of less than 10% were rarely inhabited compared with areas where sand fractions comprise more that 35% of the substrate. Mean grain diameter appears to set an upper limit with particles > 1.0 mm in diameter rejected in all tests while permeability sets the lower limit, probably as a result of its influence on burrow depth (Lee 1989). These preferences are consistent with Malmqvist's (1980) observation that substrates with a relatively large fraction of fine sand particles (0.125-0.25 mm in diameter) had higher densities of L. planeri larvae than other locations in a Swedish stream. Young et al. (1990) demonstrated that a general relationship existed between substrate quality (i.e., proportion of sand-silt) and the relative abundance of larvae using catch-per-unit-effort (CPUE) data. Young et al. (1990) suggest developing relationships for larval populations using variables such as gradient profile as surrogate measures of the suite of variables normally used to describe lamprey habitat. The preference for sand-silt substrates clearly indicates that larval habitat tends to be located in depositional areas of streams where particles of the appropriate size settle because current velocity is relatively low. Changes in the location of erosion and deposition zones (i.e., flow pattern) may change substrate characteristics enough to result in active avoidance of certain areas by larval sea lamprey.

Habitat modification to remedy specific limiting conditions in streams for native trout species, particularly brook trout, has been practiced for over 60 years (White 1975). Instream channel modifications and changes in riparian habitat are the most common categories of habitat alteration and are usually used experimentally rather than on the basis of theoretical considerations. Log and current deflectors placed in an alternating pattern on the stream banks or large boulders placed in the stream bed will narrow the channel, increasing water velocity, scouring pools, and removing silt and sediment deposited on spawning and food production areas important to trout (White and Brynildson 1967). Reconstructing or adding overhanging banks provides permanent cover for trout and stabilizes banks, reducing erosion and downstream sediment deposition (Hunt 1971, White 1975). Evaluations of habitat enhancement projects have reported positive short- and long-term effects on trout abundance and biomass (Hunt 1971, 1976, White 1975).

The evidence that fish populations will respond to simple but well-planned modifications of their habitat and the inference that substrate size is an important component of larval sea lamprey habitat selection suggest that substrate modification through alteration of stream-flow patterns may warrant further attention as an option to control sea lamprey abundance. The objective of this approach would be to create limiting habitat conditions for sea lamprey in small localized areas rather than correcting a limiting condition or enhancing existing habitat. The difficulty in applying this approach is that currently there is no way of predicting the effects of changes in substrate on larval abundance. Substrate modifications would have to be applied on an experimental basis initially with an intensive monitoring program to determine the most appropriate modifications. This approach to control is not quick, it cannot be applied to large areas of habitat, and it probably cannot be used in more than a few streams.

Some alterations in substrate as a result of modified streamflow may occur as a consequence of future global warming. Climatic warming will be accompanied by changes in regional and global precipitation patterns, with the mid-latitudes, including the Great Lakes region, expected to become drier as a result of higher evapotranspiration over land, increased evaporation from lakes, and reduced runoff into lakes (Kellog and Zhao 1988). Decreases in precipitation will affect flow regimes which in turn influences erosion and deposition patterns and the location and quantity of preferred substrate (Holmes 1992). Although there is uncertainty, the best available models estimate that reduced water supplies to the Great Lakes will reduce water levels by 0.23 m in Lake Superior, 1.6 m in Lakes Michigan and Huron, 1.4 m in Lake Erie, and 1.3 m in Lake Ontario (Levels Reference Study Board 1993).

Changes in flow pattern of the type necessary to affect sea lamprey would probably tend to favor teleost species that swim well, e.g., salmonines. In addition, changes in the invertebrate community may also occur. The possibility that habitat modifications could lead to the development of lentic sea lamprey populations off of stream mouths, if conditions are suitable, should be considered.

The cost of building instream structures to change flow patterns should be low since native materials nearby can be used. Monitoring will be necessary to ensure the integrity of the structures.

### 3.9.2 Stream Temperature

S.H. Smith (cited in Lamsa et al. 1980) hypothesized that well-shaded streams with steady discharges were too cold throughout the year to support sea lamprey production. He related this hypothesis to historical conditions characteristic of pristine watersheds in the Great Lakes. Restoration of similar conditions in appropriate locales through judicious reforestation and protection of in-stream cover could reduce sea lamprey growth and production. This suggestion has not been formally acted upon, although it has been discussed on several occasions.

Reduction of larval sea lamprey growth rates may provide some level of control by reducing the number of metamorphosing animals produced by streams, allowing less frequent lampricide treatments (Bergstedt and Seelye 1992). This approach to control is most likely to be useful in the lower Great Lakes because clearing of these watersheds has been more widespread. The potential benefits in terms of control are uncertain, but are expected to be restricted to specific streams.

The feasibility of using temperature to reduce growth and ultimately the production of parasitic sea lampreys in the control program depends on the relationships between temperature and growth and production of metamorphosed animals and on whether these relationships have sufficient scope to permit biologically meaningful manipulations of temperature.

Both larval growth and the incidence of metamorphosis in sea lamprey are influenced by temperature. Growth is faster in streams with moderately warm temperatures than in streams with cold temperatures (Holmes 1990, Young et al. 1990), and more larvae enter metamorphosis in warm water compared to cold water streams (Purvis 1980, Youson et al. 1993). Water temperature is the strongest environmental influence on metamorphosis and laboratory and field evidence indicates that the number of animals entering metamorphosis can be altered by varying environmental temperature in spring (Youson et al. 1993, Holmes et al. 1994). Habitat partitioning in streams among lamprey species appears to occur along temperature gradients (other factors being equal) in a manner consistent with the thermal preferences of different species (Applegate 1950, Morman 1979, Morman et al. 1980). These data and observations demonstrate that temperature is an important variable influencing the performance (growth, incidence of metamorphosis) of larval populations.

The biological effects of temperature are mediated by its influence on the bioenergetics of sea lamprey. The preferred temperature of larvae in summer is approximately 21°C and is similar to the temperature at which the maximum scope for activity (i.e., energy available for growth, locomotion, reproduction, and other functions except maintenance requirements) occurs, which is 19°C (Holmes and Lin 1994). The relationship between scope for activity and temperature can be approximated as a unimodal curve, with a peak near the preferred temperature and declining as temperature becomes cooler or warmer. Fish select habitat temperatures that provide maximum ability to do work (i.e., maximum scope for activity) if these temperatures are available in their environment (Magnuson et al. 1979). Magnuson et al. (1979) pointed out that population processes such as survival, growth, and reproductive success were predictable on the basis of the spatial and temporal availability of optimal temperatures in their environment. Christie and Regier (1988) used this generalization to characterize the thermal environment available to four commercially important fish species in 21 large North American lakes and developed time-integrated measures of thermal-habitat area and volume.

Although the precise relationship between temperature and larval growth is not known, the evidence that temperature influences growth and habitat selection, the demonstration of the bioenergetic effects of temperature in lamprey, and the many well-known relationships describing the thermal responses of ectothermic organisms (e.g., Fry 1947; Cossins and Bowler 1987) all suggest that attempts to define the relationship between temperature and measures of larval population performance are tractable. One useful approach could be to develop simple time-integrated measures of optimal thermal habitat for streams, as was done for lakes by Christie and Regier (1988), based on a preferred temperature for larval sea lamprey of about 21°C (Holmes and Lin 1994). These measures could be derived from comparative analyses of published temperature and discharge data combined with growth data and then used within a stream to forecast changes in the availability of optimal thermal habitat as a result of temperature changes. Coupling this relationship with stream temperature models based on a variety of variables including solar radiation and shading (e.g., Delay and Seaders 1966) could provide a useful predictive tool. Approximately two years would be needed to develop and begin applying optimal thermal-habitat measures.

Reforestation of watersheds or restoration of riparian vegetation and recovery of some ecological attributes associated with pristine conditions is generally considered desirable in many degraded streams. These types of landscape alterations will change community structure, since most species have specific temperature preferences and tolerance ranges. Changes in community structure are to some degree predictable on the basis of published temperature preference data, but some surprises may occur. In general, cooling streams should produce more favorable conditions for salmonines and sculpins (Cottus spp.) and other species that prefer cold water. The precise effects on larval sea lamprey are not known but they may be sufficient to reduce the frequency of lampricide treatments in some streams. This strategy will not have detectable impacts until vegetation provides sufficient shading of streams.

The possibility of altering stream temperature has been discussed previously and usually dismissed because it was believed to be too expensive (see Seelye and Hanson 1992). Presumably the cost-effectiveness of this proposal compared with conventional methods of control was not considered favorable. This assumption is probably true in the short-term if relatively quick results are desired. However, a longer-term payout is acceptable, then this approach may prove to be cost effective in some watersheds, particularly if volunteers are used to revegetate the watershed. At the very least, the studies to assess the relationship between temperature and growth should not be expensive (about $35,000 per year) and may provide information that will be useful in unforeseen ways.

## 4.0 DISCUSSION

The continued reliance on chemical control of sea lamprey in the Great Lakes is generally regarded as being undesirable both socially and ecologically. Since lampricides are unlikely to eradicate sea lamprey the emphasis has shifted to minimizing abundance to some acceptable level. Treatment frequencies and dose rates may be reduced as better information on larval development and the age and production of metamorphosing animals becomes available. Some reductions in lampricide use are possible using better data on variations in toxicity due to water chemistry, particularly interactions among pH and alkalinity. Critical treatments could be conducted in the fall, if feasible (Walters et al. 1980), because then young-of-the-year will be killed and because nontarget effects are likely to be lessened compared with spring treatments. Codification of decision rules for stream selection and linking these rules to specific targets for abundance of parasitic sea lampreys in a given lake may provide for more efficient use of lampricides (Koonce et al. 1993).

The GLFC and its cooperators are committed to the development and implementation of an integrated pest management program (IPM) which deemphasizes the use of selective toxicants in favour of a combination of biological and cultural controls. A thorough understanding of the fish community, the biology and ecology of sea lamprey, and potential alternative control methods is a prerequisite of IPM (Sawyer 1980). Much knowledge was available by the time of Sea Lamprey International Symposium (SLIS) in 1979 and more has been obtained in the interim, particularly since the alternative control research program was expanded in 1991. New approaches to control that can be simply tested should be tested as soon as practically possible using carefully designed, statistically sound, laboratory and field experiments before implementation decisions are made. Although this may cost more initially, it will be less costly than widely applying an approach with no real or detectable effects (Walters et al. 1980).

Research on new sea lamprey control techniques is actively pursuing the development of migratory cues and sex pheromones (attractants) (Sorensen and Gallaher 1994; Sorensen and Hanson 1994; Zielinski 1994) and ways to induce, delay, or alter the outcome of metamorphosis (Youson and Holmes 1993; Youson et al. 1994c). The attractant research shows the most promise for the near future while the metamorphosis work will take longer to develop practical tools for control. Over the long-term, the inherent natural differences in lamprey and teleost physiology, ecology, and behavior may be points at which sea lamprey are vulnerable to human intervention and should be researched to assess the potential as new control methods (Lamsa et al. 1980).

The goal of integrated management of sea lamprey (IMSL) is the integration of a variety of control options into a comprehensive program to control sea lamprey. In order to achieve this goal, information on the effects of different control options on sea lamprey is needed. Knowledge of the effects of lampricides on larval abundance and parasite recruitment is relatively good. In contrast, the effects on sea lamprey of existing alternatives to lampricides (barriers, traps, the SMRT program) have not been investigated, despite a long history of their use in the control program (barriers and traps). Questions such as how many traps, barriers, or sterile-males would be needed to cause a given reduction in parasite recruitment cannot be answered at present. This information gap will hinder IMSL because explicit evaluations of the tradeoffs among different control options is needed to optimize the suppression of sea lamprey in a given lake. There is no point in spending money on a particular control technique if the option would make little or no effect on the sea lamprey population.

Successful insect (e.g., boll weevil control program -- J. Smith cited in Seelye and Hanson 1992) and mammalian (e.g., coypu eradication in Great Britain -- Gosling 1989) pest management programs have been based on sound knowledge of the biology and population dynamics of the pest species. Although the control program is one of the main factors that affects sea lamprey numbers in the Great Lakes, the relative importance of other factors such as predation, competition, parasites and pathogens, and environmental variation has not been assessed. Considerable knowledge of the biology of sea lamprey during most periods of its life cycle is available, with the exception of parasitic animals, but estimates of natural mortality and other population variables are lacking. This type of information will be needed when evaluating the effects of different control options on sea lamprey.

Koonce et al. (1993) established the potential of an economic injury level approach for evaluating the tradeoffs among different control options on a lake, but they focused on chemical control and existing barriers in Lake Ontario. How methods such as attractants, sterile males, or interference with metamorphosis would be operationally implemented is not known because deployment rules have not been developed for any control techniques with the exception of lampricides, and to some extent barriers. Research on the integration of control methods and the joint effects of this program on sea lamprey in the Great Lakes is needed before implementation begins because the cost of using methods with no real impacts on sea lamprey is too high given funding uncertainties.

The biological differences between sea lamprey and teleost fish may be important for the development and implementation of new control methods (Lamsa et al. 1980). Sea lamprey do not have many of the specializations of higher vertebrates but they do have some unique characteristics which may make them vulnerable to specific control techniques. The following is an attempt to summarize common needs on the basis of research discipline --

ethology, ecology, physiology, endocrinology, genetics -- in the belief that one of the main sources of ideas for new control methods is a thorough understanding of sea lamprey biology and ecology. Although a disciplinary approach is followed in this discussion, significant progress towards implementation of practical alternative control methods will require interdisciplinary research teams. For example, research to improve barriers as blocking devices will require the talents of hydrologists, engineers, behavioral scientists, and biologists.

Research on the behavioral response of sea lamprey to a variety of stimuli including light, sound, chemicals, and pheromones was identified several times as important to many alternative control approaches. Whether these stimuli will elicit predictable behaviors in sea lamprey and whether these behaviors are exploitable for control purposes needs to be determined. Much of this behavioral research is directed at migratory adult sea lampreys since these animals by virtue of their migration are amenable to behavioral control. The behavior of migrating sea lamprey when they encounter portable traps or barriers is not known but may be helpful in improving the effectiveness of both methods as control techniques. For example, sea lamprey are able to surmount low-head barriers when the structure is inundated by unusually large flooding. How this is accomplished has not been observed but should be amenable to experimentation in laboratory raceways. Two hypotheses (there may be others) that should be considered are that the animals pull themselves over using the oral disk to attach to the barrier or that sudden powerful swimming for short periods at the point of lowest velocity propels individuals over the barrier. The latter hypothesis involves extensive searching behavior to find the lowest water velocity at the structure. Behavioral responses to lampricides (TFM and Bayer 73) also should be examined as they may lead to genetic resistance. Measures of these responses could be the abundance of residuals in streams after lampricide treatment or the abundance of lentic populations at the mouth of regularly treated streams.

Behavioral research is aimed at finding new methods of predictably directing the behavior of migrating sea lamprey in response to specific stimuli or cues. Bile acids (allocholic acid and petromyzonol sulfate), reproductive pheromones, light, and sound may be good candidates in the search for stimuli eliciting behaviors useful to IMSL. Some or all of these cues, alone or in combination, may provide new ways of conducting existing control practices or entirely novel methods of controlling abundance. Migratory and sexual cues have the most promise as attractants because of the relative vulnerability to disruption of adult sea lampreys during migration and spawning (Sorensen and Hanson 1994, Sorensen and Gallaher 1994). Light and sound may be useful for attracting or guiding migrating sea lampreys into portable and permanent traps, depending on the intensity and frequency of the stimulus used. Good progress has been made recently in migratory and reproductive cues and a critical mass of information and researchers are in place to continue this progress. In contrast, little research has been conducted to date on other behavioral cues (light, sound) even though they may be as useful as migratory and sex cues and less expensive to implement. An important aspect of behavioral research is an understanding of the physiological mechanisms linking specific cues to specific behaviors.

Some aspects of sea lamprey physiology may also prove to be useful to the development of new control methods. The role of taste receptors and taste in prey selection and attack by parasitic sea lampreys, and whether sea lamprey taste differs from that of other aquatic predators have not been investigated. If taste is important to feeding, then it may be possible to bioengineer prey (salmonines) that are offensive to sea lamprey but not to other aquatic organisms. Farmer and Beamish (1973) observed that sea lamprey will feed on any teleost offered, provided that they do not have access to preferred prey species, which suggests that taste may not be important to parasitic feeding. However, these experiments were not specifically designed to test a taste hypothesis. Similarly, several researchers have suggested that water chemistry may influence the survival of prey after a sea lamprey attack through effects on healing rates of wounds (e.g., see Beamish and Eshenroder 1988). Research addressing this hypothesis could lead to bioengineering of prey species better able to survive sea lamprey attacks in certain water chemistry conditions. An understanding of the physiological responses of sea lamprey to stimuli such as migratory cues, light, and sound is important to successful implementation of these approaches. For example, allocholic acid and petromyzonol sulfate are recognized by different receptor mechanisms in migratory sea lamprey (Sorensen and Gallaher 1994). This may mean that while both chemicals can be detected independently at low concentrations, one or the other or a mixture of the two substances is needed to elicit a behavioral response. Migratory adult sea lampreys have functional eyes but how vision is used during migration has not been investigated, especially the possibility that specific portions of the light spectrum may be attractive or repellant to sea lamprey but not to other species migrating at the same time. Physiology may also help to explain the differences in toxicity of TFM to sea lamprey and non-target fish. After 30 years of use, the mode of action of TFM remains largely unknown (NRCC 1985). Definition of the reasons for these differences between target and non-target effects of lampricide may lead to other selective mortality agents.

Knowledge of sea lamprey genetics consists of the number of chromosomes and the karyotype. Information on the nature of genotypic sex determination (i.e., X,Y or WZ models as in birds) and which sex is homogametic would be useful in the search for alternative methods of manipulating sex-ratios. Traits that are sex-linked could be useful as a means of enhancing differential mortality through selective breeding. Research is underway to sequence two genes that are strongly up- and down-regulated during metamorphosis in an effort to understand and ultimately manipulate metamorphosis. Gene manipulation is a sophisticated approach to control and does not offer any possibility of practical tools in the near future, although it provides a way of determining the hormones and other endogenous substances regulating important life-history events, such as metamorphosis, that may ultimately provide practical alternative control methods.

Significant progress will result from endocrine studies of growth, reproduction, and metamorphosis. Many vertebrate hormones have been found in lampreys including thyroxine ($T_4$), triiodothyronine ($T_3$), gonadotropin-releasing hormone (GnRH), insulin, adrenaline, noradrenaline, testosterone, estradiol, serotonin, melatonin, and dopamine (Lamsa et al.

1980). Other vertebrate hormones such as prolactin, oxytocin, growth hormone, thyrotropin, and parathyroid hormone, have not been reported in any lamprey species (Lamsa et al. 1980). Comparison of lamprey species with parasitic and nonparasitic life histories demonstrates a linkage between metamorphosis and subsequent sexual maturation, but the hormones involved and their roles (inhibitory or stimulatory) on these events are not clear. Such information would be useful to research on safer ways of sterilizing males, research on ways of inducing, delaying, or altering metamorphosis, and research on ways of altering or manipulating the time of gene expression at critical points in the life cycle. Hormonal regulation of growth has not been investigated but it is hypothesized that the presence of hormones such as growth hormone or prolactin in larvae may prevent metamorphosis until the animal is physiologically prepared (Youson 1994) in a situation analogous to the role of juvenile hormone in arthropods. The release of sex pheromones by mature male sea lamprey has been demonstrated (see Section 3.5), but the role of pheromones in mate selection and reproduction is not known. This research should be pursued because of the demonstrated potency of sex pheromones in teleosts and the fact that these substances are usually species specific. It will complement research on migratory cues and it will provide a more complete picture of communication among adult sea lampreys during migration and spawning.

Much is known of the ecology of sea lamprey, particularly during the larval period, but better knowledge will be needed to implement natural controls. The possibilities for natural control cannot be assessed until the ecology and natural enemies of sea lamprey in its native habitat (the Atlantic coasts of North American and Europe) have been investigated. Successful use of parasites, predators, pathogens, and competition from other species may involve importing these enemies from their native range and/or the enhancement by some means of natural enemies and competition already present in the Great Lakes environment (Lamsa et al. 1980). Presumably larval populations in the Great Lakes are regulated to some extent by natural controls (e.g., competition for space) but the extent of such regulation is unknown because it has not been investigated and because of the confounding influence of the control program. The history of intentional and unintentional invasions and introductions of new aquatic and terrestrial species and subsequent biotic crises in the Great Lakes is long (Mills et al. 1993) so the ethical implications of deliberating importing new species for sea lamprey control, regardless of the reasoning and assurances, may preclude this approach. Also, large-scale ecosystemic factors such as severe flooding or drought may cause substantial mortality of eggs or larval sea lamprey and reduce year-class strength. Some of the necessary data for testing these hypotheses may be available from control experts.

The manner in which parasitic sea lamprey detect, track, and attack prey has been identified as a key research need several times. Parasites have lesser swimming capabilities in terms of endurance and velocity compared with their preferred prey (salmonines) which may mean odors, sound, electrophysiological, or mechanical stimuli produced by prey and detected by parasitic sea lamprey are important. Limiting sea lamprey-prey interactions is an important component of IMSL and knowledge of the cues used by sea lamprey would be helpful in developing host species that are either tolerant or resistant to attacks by sea lamprey.

Furthermore, information on the seasonal distribution and movements of parasitic sea lamprey may be important to the use of attractants and/or repellants in the control program. Mark-recapture studies using coded-wire tags and measurement of downstream and upstream migrants are likely to be an important part of this research.

Natural population regulation of sea lamprey may occur through habitat limits on the production of newly metamorphosed animals in streams. This hypothesis has implications for existing alternative control measures (the SMRT program, trapping, and barriers) since these measures will be ineffective if larval survival and growth are enhanced by further in larval density (Walters et al. 1980). Larval density regulation might be accomplished by the release of chemical repellants around the burrow of established larvae (see Section 3.7.2) competition for food or space leading to reduced growth, later metamorphosis, and lower overall survival. Unfortunately, even general observations have not been assembled to test these hypotheses. This information gap should not be left much longer, since an accurate technique (statoliths) exists for aging larvae and metamorphosing animals. More quantitative information is needed to assess the potential scope for manipulating habitat variables and probable effects on abundance. Classifying streams on the basis of their potential to produce metamorphosed animals will help to assess the contribution to the total parasite population pool in a lake and in determining control options and the level of control for different streams. All aspects of the population dynamics of sea lamprey including survival rates, mortality rates, and density-dependent effects require attention in order to make use of the economic-injury-level concept (see Koonce et al. 1993). This information is particularly relevant to long-term assessment efforts to investigate the stock-recruitment relationship for the SMRT program.

Key research needs within each of the alternative control technology areas are identified in Table 4. This list represents a synthesis of opinion of the highest priorities identified by relevant experts at various workshops, in previous reports and documents, by interview, and based on the review documented here. These key research needs are **not** listed in any order of priority. The difficult task will be to priorize research needs across all nine categories because this exercise will require knowledge of what it would take to address these needs in terms of resources and subsequent tradeoffs in one area with that in another area. A paraphrased listing of documented recommendations in each technology area is found in Appendix 2.

Table 4. Key alternative sea lamprey control research needs identified in this review. A + means the criterion was judged to be favorable, a -- means the criterion was unfavorable and a 0 indicates information was insufficient to make a judgement.

| Research | Assessment Criterion<br>Potential Impact | Feasibility | Environmental Impact | Cost |
|---|---|---|---|---|
| **Lampricides** | | | | |
| 1. Investigate different tactics for TFM application, e.g., pH-alkalinity model. | + | + | + | 0 |
| 2. Investigate the potential for development of behavioral expressions of genetic resistance to lampricides. | 0 | + | 0 | 0 |
| 3. Identify and remove MFO inducing chemicals in lampricide formulations. | + | + | + | 0 |
| **Barriers** | | | | |
| 4. Investigate the behavior of migratory sea lamprey at barriers. | 0 | + | + | + |
| 5. Investigate behavioral responses of migratory animals to light and sound. | 0 | + | 0 | + |
| 6. Investigate measures to provide reliable passage for nonjumping fish at barriers. | + | + | + | -- |
| **Trapping** | | | | |
| 7. Determine factors affecting trap effectiveness, including design, cues, and behavior of migratory animals. | + | + | + | + |

Table 4. Key alternative sea lamprey control research needs identified in this review. A + means the criterion was judged to be favorable, a -- means the criterion was unfavorable and a 0 indicates information was insufficient to make a judgement.

| | Assessment Criterion | | | |
|---|---|---|---|---|
| Research | Potential Impact | Feasibility | Environmental Impact | Cost |
| 8. Determine the effect of trapping and release on non-target species. | + | + | + | 0 |
| 9. Investigate the effect of trapping on larval and parasitic recruitment. | + | 0 | + | 0 |
| **Sex-ratio Manipulation** | | | | |
| 10. Investigate alternate sources of males, including culture and importing east coast males. | 0 | + | 0 | -- |
| 11. Investigate behavior of sterilized males when released in target streams. | + | + | + | -- |
| 12. Determine effect of sterile males on larval and parasitic recruitment, i.e, stock-recruitment relationship. | + | 0 | + | -- |
| **Attractants and Repellants** | | | | |
| 13. Investigate behavioral response of migratory sea lamprey to larval bile acids. | + | + | 0 | + |
| 14. Determine where and when migratory cues are used by sea lamprey. | + | + | 0 | -- |
| 15. Identify physiological and ecological factors influencing larval bile acid production and release. | + | + | + | 0 |

Table 4. Key alternative sea lamprey control research needs identified in this review. A + means the criterion was judged to be favorable, a -- means the criterion was unfavorable and a 0 indicates information was insufficient to make a judgement.

| | Assessment Criterion | | | |
|---|---|---|---|---|
| Research | Potential Impact | Feasibility | Environmental Impact | Cost |
| **Genetic Manipulation** | | | | |
| 16. Isolate and sequence strongly regulated genes at critical points in the life history. | + | + | 0 | -- |
| 17. Investigate gene mutations to compromise functionality of important proteins. | 0 | 0 | 0 | 0 |
| 18. Determine hormones and other endogenous factors regulating gene expression | + | + | 0 | -- |
| **Developmental Blockers** | | | | |
| 19. Compare hormone profiles during metamorphosis in parasitic and nonparasitic species. | + | + | 0 | + |
| 20. Investigate methods to prevent or induce early metamorphosis. | + | + | 0 | -- |
| 21. Determine the environmental limits of metamorphosis. | 0 | + | 0 | + |
| **Natural Controls** | | | | |
| 22. Assess relative importance of competition, pathogens, and predators on lamprey numbers. | 0 | + | 0 | 0 |
| 23. Investigate population dynamics, including natural mortality, survival, and density-dependent effects. | 0 | + | 0 | 0 |

Table 4. Key alternative sea lamprey control research needs identified in this review. A + means the criterion was judged to be favorable, a -- means the criterion was unfavorable and a 0 indicates information was insufficient to make a judgement.

| | Assessment Criterion | | | |
|---|---|---|---|---|
| Research | Potential Impact | Feasibility | Environmental Impact | Cost |
| 24. Investigate behavioral and physiological mechanisms affecting prey susceptibility to lamprey attack and injury. | + | + | 0 | 0 |
| **Habitat Manipulation** | | | | |
| 25. Derive quantitative relationships between habitat variables and larval abundance. | + | + | 0 | 0 |
| 26. Investigate the relationship between water temperature and larval growth rate and habitat selection. | 0 | 0 | + | + |
| 27. Investigate methods of altering habitat to improve lampricide effectiveness. | 0 | + | 0 | + |

# 5.0 LITERATURE CITED

Akiyama, S., T. Arimoto, and M. Inoue. 1991. Fish herding effect by air bubble curtain in small scale experimental tank. Jap. Soc. Sci. Fish. Bull. 57:1301-1306.

Applegate, V.C. 1950. Natural history of the sea lamprey, Petromyzon marinus, in Michigan. U.S. Fish Wildl. Serv., Fish. 55:1-237.

Applegate, V.C., and B.R. Smith. 1951. Movement and dispersion of a blocked spawning run of sea lampreys in the Great Lakes. Trans. 16th N. Am. Wildl. Conf., 243-251.

Appy, R.G., and R.C. Anderson. 1981. The parasites of lampreys, p. 1-42. In M. W. Hardisty and I.C. Potter [ed.] The biology of lampreys, volume 3. Academic Press, London, U.K.

Baker, I.J., I.I. Solar, and E.M. Donaldson. 1988. Masculinization of chinook salmon (Oncorhynchus tshawaytscha) by immersion treatments using 17α-methyltestosterone around the time of hatching. Aquaculture 72:359-367.

Beamish, F.W.H. 1980. Biology of North American anadromous sea lamprey, Petromyzon marinus. Can. J. Fish. Aquat. Sci. 37:1924-1943.

Beamish, F.W.H. 1993. Environmental sex determination in southern brook lamprey, Ichthyomyzon gagei. Can. J. Fish. Aquat. Sci. 50:1299-1307.

Beamish, F.W.H., and R.L. Eshenroder. 1988. Review of recommendations made to the Great Lakes Fishery Commission on sea lamprey control and research, 1975-1987. Great Lakes Fish. Comm., Ann Arbor, MI, 21 p.

Beamish, F.W.H., P.K. Ott, and S.L. Roe. 1994. Interpopulational variation in fecundity and egg size in southern brook lamprey, Ichthyomyzon gagei. Copeia 1994:718-725.

Beamish, R.J. 1987. Evidence that parasitic and nonparasitic life history types are produced by one population of lamprey. Can. J. Fish. Aquat. Sci. 44:1779-1782.

Bergstedt, R.A., and J.G. Seelye. 1994. Evidence for lack of homing by sea lampreys. Trans. Am. Fish. Soc. (In press).

Bergstedt, R.A., and J.G. Seelye. 1992. Current and proposed alternative methods for the control of sea lampreys. U.S. Fish and Wildlife Service, Hammond Bay Biological Station, Millersburg, MI, 14 p.

Beverly-Burton, M., and L. Margolis. 1982. Ophioxenos lampetrae sp. nov. (Digenea: Paramphistomidae) from ammocoetes of the western brook lamprey (Lampetra richardsoni Vladykov and Follett) in British Columbia, with comments on lamprey host-parasite relationships. Can. J. Zool. 60:2514-2520.

Biette, R., and B.G. Griswold. 1988. Report of the evaluation of the Great Lakes Fishery Commission's program of sea lamprey barrier dams. Great Lakes Fish. Comm., Ann Arbor, MI.

Bills, T.D., L.L. Marking, G.E. Howe, and J.J. Rach. 1988. Relation of pH to toxicity of lampricide TFM in the laboratory. Great Lakes Fish. Comm. Tech. Rep. 56:6-113.

Board of Technical Experts (BOTE). 1993. Research priorities for the 1990s. Great Lakes Fish. Comm., Ann Arbor, MI, 14 p.

Bodznick, D., and R.G. Northcutt. 1981. Electroreception in lampreys: evidence that the earliest vertebrates were electroreceptive. Science 212:465-467.

Brown, E.H., Jr., G.W. Eck, N.R. Foster, R.M. Horrall, and C.E. Coberly. 1981. Historical evidence for discrete stocks of lake trout (Salvelinus namaycush) in Lake Michigan. Can. J. Fish. Aquat. Sci. 38:1747-1758.

Caprio, J. 1994. Identity, function, and application of feeding attractants, p. 74-75. In P.W. Sorensen and L.H. Hanson [ed.] Luring lampreys: assessing the feasibility of using odorants to control sea lamprey in the Great Lakes. Alternative Control Research Workshop Report, Great Lakes Fish. Comm., Ann Arbor, MI.

Chan, S.T.H., and W.S.B. Young. 1983. Sex control and sex reversal in fish under natural conditions, p. 171-222. In W.S. Hoar, D.J. Randall, and E.M. Donaldson [ed.] Fish physiology, Volume IXB. Academic Press, Toronto.

Chourrout, D., R. Guyomard, and L. Houdebine. 1986. High efficiency gene transfer in rainbow trout (Salmo gairdneri Rich.) by microinjection into egg cytoplasm. Aquaculture 51:143-150.

Christie, G.C. 1991. Integrated management of sea lamprey research needs: Draft October 1991. Great Lakes Fish. Comm., Ann Arbor, MI, 19 p.

Christie, G.C., and H.A. Regier. 1988. Measures of optimal thermal habitat and their relationship to yields for four commercial fish species. Can. J. Fish. Aquat. Sci. 45:301-314.

Christie, W.J., and D.P. Kolenosky. 1980. Parasitic phase of the sea lamprey (Petromyzon marinus) in Lake Ontario. Can. J. Fish. Aquat. Sci. 37:2021-2038.

Clapp, D.F., R.S. Hestand III, B.Z. Thompson, and L.L. Connor. 1993. Movement of grass carp in large Florida lakes. N. Am. J. Fish. Manage. 13:746-756.

Cochran, P.A. 1985. Size-selective attack by parasitic lampreys: consideration of alternate null hypotheses. Oecologia (Berlin) 67:137-141.

Cole, W.C., and J.H. Youson. 1981. The effect of pinealectomy, continuous light, and continuous darkness on metamorphosis of anadromous sea lampreys, Petromyzon marinus L. J. Exp. Zool. 218:397-404.

Cossins, A.R., and K. Bowler. 1987. Temperature biology of animals. Chapman and Hall, London, U.K. ix + 339 p.

Crook, P.H. 1991. Design of low-cost fishways. Am. Fish. Soc. Symp. 10:256-263.

Davis, K.B., B.A. Simco, C. A. Goudie, N.C. Parker, W. Cauldwell, and R. Snellgrove. 1990. Hormonal sex manipulation and evidence for female heterogamety in channel catfish. Gen. Comp. Endocrinol. 78:218-223.

Delay, W.H., and J. Seaders. 1966. Predicting temperatures in rivers and reservoirs. J. Am. Soc. Civ. Eng., Sanit. Eng. Div. 92:115-134.

Docker, M.F. 1992. Labile sex determination in lampreys: the effect of larval density and sex steroids on gonadal differentiation. Ph.D. thesis, Department of Zoology, University of Guelph, Guelph, Ontario, x + 269 p.

Donaldson, E.M., and G.A. Hunter. 1982. Sex control in fish with particular reference to salmonids. Can. J. Fish. Aquat. Sci. 39:99-110.

Douglas, M.E., P.C. Marsh, and W.L. Minckley. 1994. Indigenous fishes of western North America and the hypothesis of competitive displacement: Meda fulgida (Cyprinidae) as a case study. Copeia 1994:9-19.

Dunham, R.A., J. Eash, and J. Askins. 1987. Transfer of the metallothionein-human growth hormone fusion gene into channel catfish. Trans. Am. Fish. Soc. 116:87-91.

Dunning, D.J., Q.E. Ross, P. Geoghegan, J.J. Reichle, J.K. Menezes, and J.K. Watson. 1992. Alewives avoid high-frequency sound. N. Am. J. Fish. Manage. 12:407-416.

Elrod, J.H. 1987. Dispersal of three strains of hatchery-reared lake trout in Lake Ontario. J. Great Lakes Res. 13:157-167.

Elrod, J.H., and C.P. Schneider. 1987. Seasonal bathythermal distribution of juvenile lake trout in Lake Ontario. J. Great Lakes Res. 13:121-134.

Eng, F., and J.H. Youson. 1992. Morphology of the liver of the brook lamprey, Lampetra lamottenii, before and during infection with the nematode, Truttaedacnitis stelmioides, hepatocytes, sinusoids, and perisinusoidal cells. Tissue and Cell 24:575-592.

Farmer, G.J., and F.W.H. Beamish. 1973. Sea lamprey (Petromyzon marinus) predation on freshwater teleosts. J. Fish. Res. Board Can. 30:601-605.

ffrench-Constant, R.H., and R.T. Roush. 1990. Resistance detection and documentation: the relative roles of pesticidal and biochemical assays, p. 4-38. In R.T. Roush and B.E. Tabashnik [ed.] Pesticide resistance in arthropods. Chapman and Hall, New York.

Fischer, S.A., and W.E. Kelso. 1988. Potential parasite-induced mortality in age-0 bluegills in a floodplain pond of the Lower Mississippi River. Trans. Am. Fish. Soc. 117:565-573.

Fleming, D.F., and J.B. Reynolds. 1991. Effects of spawning-run delay on spawning migration of Arctic grayling. Am. Fish. Soc. Symp. 10:299-305.

Fry, F.E.J. 1947. Effects of the environment on animal activity. Univ. Toronto Stud., Biol. Ser. 55, Publ. Ont. Fish. Res. Lab. 68:1-62.

Garrett, G.P. 1989. Hormonal sex control of largemouth bass. Prog. Fish-Cult. 51:146-148.

Goetz, F.W., E.M. Donaldson, G.A. Hunter, and H.M. Dye. 1979. Effects of estradiol-17β and 17α-methyltestosterone on gonadal differentiation in the coho salmon, Oncorhynchus kisutch. Aquaculture 17:267-278.

Goodier, J.L. 1981. Native lake trout (Salvelinus namaycush) stocks in the Canadian waters of Lake Superior prior to 1955. Can. J. Fish. Aquat. Sci. 38:1724-1737.

Gosling, M. 1989. Extinction to order. New Scientist 121(1654):44-49.

Great Lakes Fishery Commission. 1992. Strategic vision of the Great Lakes Fishery Commission for the decade of the 1990s. Great Lakes Fish. Comm., Ann Arbor, MI, 38 p.

Gross, M.L., J.F. Schneider, N. Moav, B. Moav, C. Alvarez, S.H. Myster, Z. Liu, E.M. Hallerman, P.B. Hackett, K.S. Guise, A.J. Faras, and A.R. Kapuscinski. 1992. Molecular analysis and growth evaluation of northern pike (Esox lucius) microinjected with growth hormone genes. Aquaculture 103:253-273.

Hanson, L.H. 1990. Sterilizing effects of cobalt-60 and cesium-137 radiation on male sea lampreys. N. Am. J. Fish. Manage. 10:352-361.

Hanson, L.H., and P.J. Manion. 1978. Chemosterilization of the sea lamprey, Petromyzon marinus. Great Lakes Fish. Comm. Tech. Rep. 16, 35 p.

Hanson, L.H., and P.J. Manion. 1980. Sterility method of pest control and its potential role in an integrated sea lamprey (Petromyzon marinus) control program. Can. J. Fish. Aquat. Sci. 37:2108-2117.

Hanson, L.H., E.L. King, Jr., J.H. Howell, and A.J. Smith. 1974. A culture method for sea lamprey larvae. Prog. Fish-Cult. 36:122-128.

Haslewood, G.A.D., and L. Tökés. 1969. Comparative studies of bile salts. Bile salts of the lamprey Petromyzon marinus L. Biochem. J. 114:179-184.

Hawkins, A.D. 1981. The hearing abilities of fish, p. 109-138. In W.N. Tovolga, A.N. Popper, and R.R. Fay [ed.] Hearing and sound communication in fishes, Springer-Verlag, New York.

Haymes, G.T., and P.H. Patrick. 1986. Exclusion of adult alewive, Alosa pseudoharengus, using low-frequency sound for application at water intakes. Can. J. Fish. Aquat. Sci. 43:855-862.

Heinrich, J.W., J.G. Weise, and B.R. Smith. 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.

Hocutt, C.H. 1980. Behavioral barriers and guidance systems, p. 183-205. In C.H. Hocutt, J.R. Stauffer, Jr., J.E. Edinger, L.W. Hall, and R.P. Morgan, II [ed.] Power plants: effects on fish and shellfish. Academic Press, New York.

Holloway, G.A. 1991. The Brule River sea lamprey barrier and fish ladder, Wisconsin. Am. Fish. Soc. Symp. 10:264-267.

Holmes, J.A. 1990. Sea lamprey as an early responder to climate change in the Great Lakes basin. Trans. Am. Fish. Soc. 119:292-300.

Holmes, J.A. 1992. The thermal ecology of larval sea lamprey, Petromyzon marinus, in the Great Lakes basin. Ph.D. thesis, Department of Zoology, University of Toronto, Toronto, Ontario.

Holmes, J.A., and P. Lin. 1994. Thermal niche of larval sea lamprey, Petromyzon marinus. Can. J. Fish. Aquat. Sci. 51:253-262.

Holmes, J.A., and J.H. Youson. 1994. Fall condition factor and temperature influence the incidence of metamorphosis in sea lampreys, Petromyzon marinus. Can. J. Zool. 72:1134-1140.

Holmes, J.A., and J.H. Youson. 1993. Induction of metamorphosis in landlocked sea lampreys, Petromyzon marinus. J. Exp. Zool. 267:598-604.

Holmes, J.A., F.W.H. Beamish, J.G. Seelye, S.A. Sower, and J.H. Youson. 1994. Long-term influence of water temperature, photoperiod, and food deprivation on metamorphosis of sea lamprey, Petromyzon marinus. Can. J. Fish. Aquat. Sci. 51 (In press).

Houston, K.A., and J.R.M. Kelso. 1991. Relation of sea lamprey size and sex ratio to salmonid availability in three Great Lakes. J. Great Lakes Res. 17:270-280.

Hunn, J.B., and W.D. Youngs. 1980. Role of physical barriers in the control of sea lamprey (Petromyzon marinus). Can. J. Fish. Aquat. Sci. 37:1780-1801.

Hunt, R.L. 1971. Responses of a brook trout population to habitat development in Lawrence Creek. Wisc. Dept. Nat. Res. Tech. Bull. 48: 35 p.

Hunt, R.L. 1976. A long-term evaluation of trout habitat development and its relation to improving management-related research. Trans. Am. Fish. Soc. 105:361-364.

Hunter, G.A., and E.M. Donaldson. 1983. Hormonal sex control and its application to fish culture, p. 223-303. In W.S. Hoar, D.J. Randall, and E.M. Donaldson [ed.] Fish physiology, Volume IXB. Academic Press, Orlando, FL.

Hunter, G.A., I.I. Solar, I.J. Baker, and E.M. Donaldson. 1986. Feminization of coho salmon (Oncorhynchus kisutch) and chinook salmon (Oncorhynchus tshawaytscha) by immersion of alevins in a solution of estradiol-17β. Aquaculture 53:295-302.

Jalabert, B., R. Billard, and B. Chevassus. 1975. Preliminary experiments on sex control in trout: production of sterile fishes and simultaneous self-fertilizing hermaphrodites. Ann. Biol. Anim. Biochem. Biophys. 15:19-28.

Johnson, B.G.H. [ed.] 1987. Evaluation of sea lamprey populations in the Great Lakes: Background papers and Proceedings of the August 1985 workshop. Great Lakes Fish. Comm. Spec. Publ. 87-2.

Joss, J.M.P. 1985. Pituitary control of metamorphosis in the southern hemisphere lamprey, Geotria australis. Gen. Comp. Endocrinol. 60:58-62.

Kapuscinski, A.R., and E.M. Hallerman. 1990. Transgenic fish and public policy. I. Anticipating environmental impacts of transgenic fish. Fisheries 15(1):2-11.

Katopodis, C., A.J. Derksen, and B.L. Christensen. 1991. Assessment of two Denil fishways for passage of freshwater species. Am. Fish. Soc. Symp. 10:306-324.

Katopodis, C., E.M. Koon, and L.H. Hanson. 1994. Sea lamprey barrier workshop. Draft 4. Alternative Control Resarch Workshop Report, Great Lakes Fish. Comm., Ann Arbor, MI, 76 p.

Kellog, W.M., and Z. Zhao. 1988. Sensitivity of soil moisture to doubling of carbon dioxide in climate model experiments. J. Climatol. 111:348-366.

Kelso, J.R.M., and D.B. Noltie. 1990. Abundance of spawning pink salmon in two Lake Superior streams, 1981-1987. J. Great Lakes Res. 16:209-215.

King, J.C., S.A. Sower, and E.L.P. Anthony. 1988. Lamprey gonadotropin-releasing hormone neurons in the brain of the sea lamprey, Petromyzon marinus. Cell Tiss. Res. 253:1-8.

Kleerekoper, H. 1972. The sense organs, p. 373-404. In M.W. Hardisty and I.C. Potter [ed.] The biology of lampreys, volume 2. Academic Press, London.

Kleerekoper, H., G. Taylor, and R. Wilton. 1961. Diurnal periodicity in the activity of Petromyzon marinus and the effects of chemical stimulation. Trans. Am. Fish. Soc. 90:73-78.

Komen, J., P.A.J. Lodder, F. Huskens, C.J.J. Richter, and E.A. Huisman. 1989. Effects of oral administration of 17$\alpha$-methyltestosterone and 17$\beta$-estradiol on gonadal development in common carp, Cyprinus carpio L. Aquaculture 78:349-363.

Koonce, J.F., R.L. Eshenroder, and G.C. Christie. 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.

Krueger, C.C., J.E. Marsden, H.L. Kincaid, and B. May. 1989. Genetic differentiation among lake trout strains stocked into Lake Ontario. Trans. Am. Fish. Soc. 118:317-330.

Kynard, B., and J. O'Leary. 1993. Evaluation of a bypass system for spent American shad at Holyoke Dam, Massachusetts. N. Am. J. Fish. Manage. 13:782-789.

Lamsa, A.K., C.M. Rovainen, D.P. Kolenosky, and L.H. Hanson. 1980. Sea lamprey (Petromyzon marinus) control -- Where to from here? Report of the SLIS Control Theory Task Force. Can. J. Fish. Aquat. Sci. 37:2175-2192.

Lee, D.S. 1989. Proximate determinants of larval lamprey habitat selection. Ph.D. thesis, Department of Zoology, Michigan State University, Lansing, MI.

Lee, R.F. 1988. Possible linkages between mixed function oxygenase systems, steroid metabolism, reproduction, molting, and pollution in aquatic animals, p.201-213. In M.S. Evans [ed.] Toxic contaminants and ecosystem health: a Great Lakes focus. John Wiley and Sons, Toronto.

Levels Reference Study Board. 1993. Levels reference study. Great Lakes-St. Lawrence River Basin. International Joint Commission, Windsor, Ontario, xviii + 155 p.

Li, W., P. Sorensen, and D. Gallaher. 1994. Olfactory sensitivity of migratory adult sea lamprey (Petromyzon marinus) to bile acids, amino acids, and sex hormones: recent developments and future directions, p. 90-99. In P.W. Sorensen and L.H. Hanson [ed.] Luring lampreys: assessing the feasibility of using odorants to control sea lamprey in the Great Lakes. Alternative Control Research Workshop Report, Great Lakes Fish. Comm., Ann Arbor, MI.

Lintlop, S.P., and J.H. Youson. 1983. Concentration of triiodothyronine in the sera of the sea lamprey, Petromyzon marinus, and the brook lamprey, Lampetra lamottenii, at various phases of the life cycle. Gen. Comp. Endocrinol. 49:187-194.

Lockwood, J.A., T.C. Sparks, and R.N. Story. 1984. Evolution of insect resistance to insecticides: a reevaluation of the roles of physiology and behavior. Bull. Entomol. Soc. Am. 30(4):41-51.

Lowe, D.R., F.W.H. Beamish, and I.C. Potter. 1973. Changes in the proximate body composition of the landlocked sea lamprey, Petromyzon marinus (L.) during larval life and metamorphosis. J. Fish. Biol. 5:673-682.

Luxon, L., P.V. Hodson, and U. Borgmann. 1987. Hepatic aryl hydrocarbon hydroxylase activity of lake trout (Salvelinus namaycush) as an indicator of organic pollution. Environ. Toxicol. Chem. 6:649-657.

Magnuson, J.J., L.B. Crowder, and P.A. Medvick. 1979. Temperature as an ecological resource. Am. Zool. 19:331-343.

Mallatt, J. 1983. Laboratory growth of larval lampreys (*Lampetra* (*Entosphenus*) *tridentata* Richardson) at different food concentrations and animal densities. J. Fish. Biol. 22:293-301.

Malmqvist, B. 1980. Habitat selection of larval brook lampreys (*Lampetra* *planeri* Bloch) in a south Swedish stream. Oecologia 45:35-38.

Manion, P.J. 1968. Production of sea lamprey larvae from nests in two Lake Superior streams. Trans. Am. Fish. Soc. 97:484-486.

Manion, P.J., L.H. Hanson, and M.F. Fodale. 1988. Sterilizing effect of cesium-137 irradiation on male sea lampreys released in the Big Garlic River, Michigan. Great Lakes Fish. Comm. Tech. Rep. 53:1-7.

Marking, L.L., and T.D. Bills. 1985. Effects of contaminants on toxicity of the lampricide TFM and Bayer 73 to three species of fish. J. Great Lakes Res. 11:171-178.

McCauley, R.W., W.W. Reynolds, and N.H. Huggins. 1978. Photokinesis and behavioral thermoregulation in adult sea lampreys (*Petromyzon* *marinus*). J. Exp. Zool. 202:431-437.

McLain, A.L. 1951. Diseases and parasites of the sea lamprey, *Petromyzon* *marinus*, in the Lake Huron basin. Trans. Am. Fish. Soc. 81:94-100.

Meyer, F.P. 1990. Research perspectives for the future. Report to the Great Lakes Fishery Commission, Ann Arbor, MI, 14 p.

Mills, E.L., J.H. Leach, J.T. Carlton, and C.L. Secor. 1993. Exotic species in the Great Lakes: a history of biotic crises and anthropogenic introductions. J. Great Lakes Res. 19:1-54.

Morman, R.H. 1979. Distribution and ecology of lampreys in the lower peninsula of Michigan, 1957-75. Great Lakes Fish. Comm. Tech. Rep. 33: 59 p.

Morman, R.H. 1987. Relationship of density to growth and metamorphosis of caged larval sea lampreys, *Petromyzon* *marinus* Linnaeus, in Michigan streams. J. Fish. Biol. 30:173-181.

Morman, R.H., D.W. Cuddy, and P.C. Rugen. 1980. Factors influencing the distribution of sea lamprey (*Petromyzon* *marinus*) in the Great Lakes. Can. J. Fish. Aquat. Sci. 37:1811-1826.

Munkittrick, K.R., M.E. McMaster, C.B. Portt, G.J. Van Der Kraak, I.R. Smith, and D.G. Dixon. 1992. Changes in maturity, plasma sex steroid levels, hepatic MFO activity and the presence of external lesions in lake whitefish exposed to bleached kraft mill effluent. Can. J. Fish. Aquat. Sci. 49:1560-1569.

Munkittrick, K.R., C.B. Portt, G.J. Van Der Kraak, I.R. Smith, and D.A. Rokosh. 1991. Impact of bleached kraft mill effluent on population characteristics, liver MFO activity and serum steroid levels of a Lake Superior white sucker (Catostomus commersoni) population. Can. J. Fish. Aquat. Sci. 48:1371-1380.

Munkittrick, K.R., M.R. Servos, J.L. Parrott, V. Martin, J.H. Carey, P.A. Flett, and G.J. Van Der Kraak. 1994. Identification of lampricide formulations as a potent inducer of MFO activity in fish. J. Great Lakes Res. 20:355-365.

Murdoch, S.P., F.W.H. Beamish, and M.F. Docker. 1991. Laboratory study of growth and interspecific competition in larval lampreys. Trans. Am. Fish. Soc. 120:653-656.

Murdoch, S.P., M.F. Docker, and F.W.H. Beamish. 1992. Effect of density an individual variation on growth of sea lamprey (Petromyzon marinus) larvae in the laboratory. Can. J. Zool. 70:184-188.

National Research Council of Canada (NRCC). 1985. TFM and Bayer 73: lampricides in the aquatic environment. Associate Committee on Scientific Criteria for Environmental Quality, Ottawa, NRCC No. 22488, 184 p.

Nemeth, R.S., and J.J. Anderson. 1992. Response of juvenile coho and chinook salmon to strobe and mercury vapor lights. N. Am. J. Fish. Manage. 12:684-692.

Nestler, J.M., G.R. Ploskey, J. Pickens, J. Menezes, and C. Schilt. 1992. Responses of blueback herring to high-frequency sound and implications for reducing entrainment at hydropower plants. N. Am. J. Fish. Manage. 12:667-683.

O'Boyle, R.N., and F.W.H. Beamish. 1977. Growth and intermediary metabolism of larval and metamorphosing stages of the landlocked sea lamprey, Petromyzon marinus L. Environ. Biol. Fishes 2:103-120.

Patrick, P.H., R.S. McKinley, A.E. Christie, and J.G. Holsapple. 1988. Fish protection: sonic deterrents. In W.C. Micheletti [ed.] Proceedings of the Electric Power Research Institute conference on fish protection at steam and hydro plants. Electric Power Research Institute Report CS/EA/AP-5663-S-R, Palo Alto, California.

Patrick, P.H., R.W. Sheehan, and B. Sim. 1982. Effectiveness of a strobe light eel exclusion scheme. Hydrobiologia 94:269-277.

Perlmutter, A. 1951. An aquarium experiment on the American eel as a predator of larval lampreys. Copeia 1951:173-174.

Pfeiffer, W., and T.F. Pletcher. 1964. Club cells and granular cells in the skin of lamprey. J. Fish. Res. Board Can. 21:1083-1088.

Piavis, G.W., J.H. Howell, and A.J. Smith. 1970. Experimental hybridization among five species of lampreys from the Great Lakes. Copeia 1970:29-37.

Potter, I.C. 1980. Ecology of larval and metamorphosing lampreys. Can. J. Fish. Aquat. Sci. 37:1641-1657.

Potter, I.C., and E.S. Robinson. 1971. The chromosomes, p. 279-293. In M.W. Hardisty and I.C. Potter [ed.] The biology of lampreys, Volume 1. Academic Press, London, U.K.

Purdom, C.E. 1983. Genetic engineering by the manipulation of chromosomes. Aquaculture 33:287-300.

Purvis, H.A. 1980. Effects of temperature on metamorphosis and the age and length at metamorphosis in sea lamprey (Petromyzon marinus) in the Great Lakes. Can. J. Fish. Aquat. Sci. 37:1827-1834.

Purvis, H.A. 1979. Variations in growth, age at transformation, and sex ratio of sea lampreys reestablished in chemically treated tributaries of the upper Great Lakes. Great Lakes Fish. Comm. Tech. Rep. 35, 36 p.

Purvis, H.A., C.L. Chudy, E.L. King, Jr., and V.K. Dawson. 1985. Response of spawning-phase sea lampreys (Petromyzon marinus) to a lighted trap. Great Lakes Fish. Comm. Tech. Rep. 42:15-25.

Pybus, M.J., L.S. Uhazy, and R.C. Anderson. 1978. Life cycle of Truttaedacnitis stelmioides (Vessichelli, 1910) (Nematoda: Cucullanidae) in American brook lamprey (Lampetra lamottenii). Can. J. Zool. 56:1420-1429.

Rehnberg, B.G., and C.B. Schreck. 1987. Chemosensory detection of predators by coho salmon (Oncorhynchus kisutch): behavioral reaction and the physiological stress response. Can. J. Zool. 65:481-485.

Robson, P., G.M. Wright, E. Sitarz, A. Maiti, M. Rawat, J.H. Youson, and F.W. Keeley. 1993. Characterization of lamprin, an unusual matrix protein from lamprey cartilage. J. Biol. Chem. 268:1440-1447.

Ross, Q.E., D.J. Dunning, R. Thorne, J.K. Menezes, G.W. Tiller, and J.K. Watson. 1993. Response of alewives to high-frequency sound at a power plant intake on Lake Ontario. N. Am. J. Fish. Manage. 13:291-303.

Roush, R.T., and J.C. Daly. 1990. The role of population genetics in resistance research and management, p. 97-152. In R.T. Roush and B.E. Tabashnik [ed.] Pesticide resistance in arthropods. Chapman and Hall, New York.

Roush, R.T., and G.L. Miller. 1986. Considerations for design of insecticide resistance monitoring programs. J. Econ. Entomol. 79:293-298.

Rovainen, C.M. 1980. Neurophysiology of lampreys. Can. J. Fish. Aquat. Sci. 37:1723-1738.

St. Mary's River Control Task Group. 1994. St. Mary's River control strategy. Great Lakes Fish. Comm., Executive Meeting Agenda Item 4.c., 9 p.

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

Sawyer, A.J., and D.V. Gillman. 1994. Sea lamprey research strategy. Great Lakes Fishery Commission, Research and Alternative Technology Task Group, 19 p.

Scholefield, R.J., and J.G. Seelye. 1990. Resistance to 3-trifluoromethyl-4-nitrophenol (TFM) in sea lamprey. Great Lakes Fish. Comm. Tech. Rep. 56:1-5.

Schwalme, K., W.C. Mackay, and D. Lindner. 1985. Suitability of vertical slot and Denil fishways for passing north-temperate, nonsalmonid fish. Can. J. Fish. Aquat. Sci. 42:1815-1822.

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

Scott, A.P., A.V.M. Canario, N.M. Sherwood, and C.M. Warby. 1991. Levels of steroids, including cortisol and 17α, 20β-dihydroxy-4-pregnen-3-one, in plasma, seminal fluid, and urine of Pacific herring (Clupea harengus pallasi) and North Sea plaice (Pleuronectes platessa L.). Can. J. Zool. 69:111-116.

Scott, W.B., and E.J. Crossman. 1973. Freshwater fishes of Canada. Bull. Fish. Res. Board Can. 184, 966 p.

Seelye, J.G., and L.H. Hanson. [ed.] 1992. Current pest control techniques -- potential adaptations for sea lamprey control. Alternative Control Research Workshop Report, Great Lakes Fish. Comm., Ann Arbor, MI, 49 p.

Seelye, J.G., and R.J. Scholefield. 1990. Effects of changes in dissolved oxygen on the toxicity of 3-trifluoromethyl-4-nitrophenol (TFM) to sea lamprey and rainbow trout. Great Lakes Fish. Comm. Tech. Rep. 56:6-13.

Seelye, J.G., D.A. Johnson, J.G. Weise, and E.L. King, Jr. 1988. Guide for determining application rates of lampricides for control of sea lamprey ammocetes. Great Lakes Fish. Comm. Tech. Rep. 52, 23 p.

Servos, M.R., K.R. Munkittrick, M.L. Hewitt, and I. Scott. 1994. Isolation of bioactive components of commercial TFM formulations. Research Completion Report, Great Lakes Fish. Comm., Ann Arbor, MI, 52 p.

Sherwood, N.M., A.L. Kyle, H. Kreiberg, C.M. Warby, T.H. Magnus, J. Carolsfeld, and W.S. Price. 1991. Partial characterization of a spawning pheromone in the herring Clupea harengus pallasi. Can. J. Zool. 69:91-103.

Sherwood, N.M., S.A. Sower, D.R. Marshak, B.A. Fraser, and M.J. Brownstein. 1986. Primary structure of gonadotropin-releasing hormone from lamprey brain. J. Biol. Chem. 261:4812-4819.

Smith, A.J., J.H. Howell, and G.W. Piavis. 1968. Comparative embryology of five species of lampreys of the upper Great Lakes. Copeia 1968:461-469.

Smith, B.R., and J.J. Tibbles. 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.

Smith, D.V. 1994. Graduated electric field barriers to control sea lamprey, 6 p. Presented at the Second Annual Sea Lamprey Research Workshop, Rogers City, MI, June 23, 1994.

Smith, E.J., and J.K. Anderson. 1989. Attempts to alleviate fish losses from Allegheny Reservoir, Pennsylvania and New York, using acoustics. N. Am. J. Fish. Manage. 4:300-307.

Smith, R.J.F. 1994. Responses of teleost fishes to alarm pheromones and to chemical stimuli from predators, p. 71-74. In P.W. Sorensen and L.H. Hanson [ed.] Luring lampreys: assessing the feasibility of using odorants to control sea lamprey in the Great Lakes. Alternative Control Research Workshop Rep., Great Lakes Fish. Comm., Ann Arbor, MI.

Sorensen, P.W., and D.D. Gallaher. 1994. Determining why the sea lamprey olfactory system is extremely sensitive to bile acids: Are bile acids pheromones? Research Completion Report, Great Lakes Fish. Comm., Ann Arbor, MI, 31 p.

Sorensen, P.W., and L.H. Hanson. [ed.] 1994. Luring lampreys: assessing the feasibility of using odorants to control sea lamprey in the Great Lakes. Alternative Control Research Workshop Report, Great Lakes Fish. Comm., Ann Arbor, MI, 110 p.

Sower, S.A. 1990. Neuroendocrine control of reproduction in lampreys. Fish Physiol. Biochem. 8:365-374.

Sower, S.A., and L.H. Hanson. [ed.] 1992. Vertebrate sex determination/differentiation workshop. Alternative Control Research Workshop Report, Great Lakes Fish. Comm., Ann Arbor, MI, 36 p.

Sower, S.A., Y.-C. Chiang, S. Lovas, and J.M. Conlon. 1993. Primary structure and biological activity of a third gonadotropin-releasing hormone from lamprey brain. Endocrinology 132:1125-1131.

Sower, S.A., W.W. Dickhoff, A. Gorbman, J.E. Rivier, and W.W. Vale. 1983. Ovulatory and steroidal responses in the lamprey following administration of salmon gonadotropin and agonistic and antagonistic analogues of gonadotropin-releasing hormone. Can. J. Zool. 61:2653-2659.

Sower, S.A., J.A. King, R.P. Millar, N.M. Sherwood, and D.R. Marshak. 1987. Comparative biological properties of lamprey gonadotropin-releasing hormones in vertebrates. Endocrinology 120:773-779.

Stacey, N. 1994. Identity, function, and application of sex pheromones, p. 76-84. In P.W. Sorensen and L.H. Hanson [ed.] Luring lampreys: assessing the feasibility of using odorants to control sea lamprey in the Great Lakes. Alternative Control Research Workshop Report, Great Lakes Fish. Comm., Ann Arbor, MI.

Stacey, N.E., and F.W. Goetz. 1982. Role of prostaglandins in fish reproduction. Can. J. Fish. Aquat. Sci. 39:92-98.

Staten, R., L. Antilla, and O. El Lissy. 1994. Using sex pheromones to disrupt insect population development through mating disruption, p. 57-69. In P.W. Sorensen and L.H. Hanson [ed.] Luring lampreys: assessing the feasibility of using odorants to control sea lamprey in the Great Lakes. Alternative Control Research Workshop Report, Great Lakes Fish. Comm., Ann Arbor, MI.

Sterile Male Release Technique Task Force. 1994. Long-range plan for implementation and assessment of sterile male release technique in sea lamprey control 1994-99. Presented at Sea Lamprey Integration Committee Meeting, Detroit, MI, October 26-28, 1994. 24 p.

Swink, W.D. 1991. Host-size selection by parasitic sea lampreys. Trans. Am. Fish. Soc. 120:637-643.

Swink, W.D., and L.H. Hanson. 1989. Survival of rainbow trout and lake trout after sea lamprey attack. N. Am. J. Fish. Manage. 9:35-40.

Swink, W.D., and L.H. Hanson. 1986. Survival from sea lamprey (Petromyzon marinus) predation by two strains of lake trout (Salvelinus namaycush). Can. J. Fish. Aquat. Sci. 43:2528-2531.

Szalai, A.J., and T.A. Dick. 1991. Role of predation and parasitism in growth and mortality of yellow perch in Dauphin Lake, Manitoba. Trans. Am. Fish. Soc. 120:739-751.

Szalai, A.J., W. Lysack, and T.A. Dick. 1992. Use of confidence ellipses to detect effects of parasites on the growth of yellow perch, Perca flavescens. J. Parasitol. 78:64-69.

Teeter, J. 1980. Pheromone communication in sea lampreys (Petromyzon marinus): implications for population management. Can. J. Fish. Aquat. Sci. 37:2123-2132.

Thomas, J.D. 1962. The food and growth of brown trout (Salmo trutta L.) and its feeding relationship with the salmon parr (Salmo salar L.) and the eel (Anguilla anguilla L.) in the River Teify, West Wales. J. Anim. Ecol. 31:175-205.

Thomas, M.L.H. 1963. Studies on the biology of ammocoetes in streams. Fish. Res. Board Can., Manu. Rep. Ser. (Biol.), No 742, vii + 143 p.

Thorgaard, G.H. 1992. Application of genetic technologies to rainbow trout. Aquaculture 100:85-97.

Thorgaard, G.H. 1983. Chromosome set manipulation and sex control in fish, p. 405-434. In W.S. Hoar, D.J. Randall and E.M. Donaldson [ed.] Fish physiology, Volume IXB. Academic Press, Orlando, FL.

Torblaa, R.L., and R.W. Westman. 1980. Ecological impacts of lampricide treatments on sea lamprey (Petromyzon marinus) ammocoetes and metamorphosed individuals. Can. J. Fish. Aquat. Sci. 37:1835-1850.

Walters, C.J., G. Spangler, W.J. Christie, P.J. Manion, and J.F. Kitchell. 1980. A synthesis of knowns, unknowns, and policy recommendations from the Sea Lamprey International Symposium. Can. J. Fish. Aquat. Sci. 37:2202-2208.

White, R.J. 1975. Trout population responses to streamflow fluctuation and habitat management in Big Roche-a-Cri Creek, Wisconsin. Verh. Internat. Verein. Limnol. 19:2469-2477.

White, R.J., and O.M. Brynildson. 1967. Guidelines for the management of trout stream habitat in Wisconsin. Wisc. Dept. Nat. Res. Tech. Bull. 39: 65 p.

Wickham, D.A. 1973. Attracting and controlling coastal pelagic fish with night lights. Trans. Am. Fish. Soc. 102:816-825.

Wilson, K.A., and K. Ronald. 1967. Parasite fauna of the sea lamprey (*Petromyzon marinus* von Linné) in the Great Lakes region. Can. J. Zool. 45:1083-1092.

Wright, G.M., and J.H. Youson. 1977. Serum thyroxine concentrations in larval and metamorphosing anadromous sea lamprey, *Petromyzon marinus* L. J. Exp. Zool. 202:27-32.

Wright, G.M., F.W. Keeley, and J.H. Youson. 1983. Lamprin: a new vertebrate protein comprising the major structural protein of adult lamprey cartilage. Experientia 39:495-497.

Young, R.J., J.R.M. Kelso, and J.G. Weise. 1990. Occurrence, relative abundance, and size of landlocked sea lamprey (*Petromyzon marinus*) ammocoetes in relation to stream characteristics in the Great Lakes. Can. J. Fish. Aquat. Sci. 47:1773-1778.

Youson, J.H. 1994. Environmental and hormonal cues and endocrine glands during lamprey metamorphosis, p. 400-407. *In* K. Davey, R. Peter, and S. Tobe [ed.] Perspectives in comparative endocrinology. Nat. Res. Coun. Can., Ottawa.

Youson, J.H. 1988. First metamorphosis, p. 135-196. *In* W.S. Hoar and D.J. Randall [ed.] Fish physiology, Volume XIB. Academic Press, New York, N.Y.

Youson, J.H. and R.J. Beamish. 1991. Comparison of the internal morphology of adults of a population of lampreys that contains a non-parasitic life-history type, *Lampetra richardsoni*, and a potentially parasitic form, *L. richardsoni* var. *marifuga*. Can. J. Zool. 69:628-637.

Youson, J.H., and J.A. Holmes. 1993. Metamorphosis: Biological control for sea lampreys. Alternative Control Research Workshop Report, Great Lakes Fish. Comm., Ann Arbor, MI, 13 p.

Youson, J.H., and I.C. Potter. 1979. A description of the stages in the metamorphosis of the anadromous sea lamprey, Petromyzon marinus L. Can. J. Zool. 57:1808-1817.

Youson, J.H., and S.A. Sower. 1991. Concentration of gonadotropin-releasing hormone in the brain during metamorphosis in the lamprey, Petromyzon marinus. J. Exp. Zool. 259:399-404.

Youson, J.H., E.M. Plisetskaya, and J.F. Leatherland. 1994a. Concentrations of insulin and thyroid hormones in the serum of landlocked sea lampreys (Petromyzon marinus) of three larval year classes, in larvae exposed to two temperature regimes, and in individuals during and after metamorphosis. Gen. Comp. Endocrinol. 94:294-304.

Youson, J.H., J.A. Holmes, and J.F. Leatherland. 1994b. Serum concentrations of thyroid hormones in $KClO_4$-treated larval sea lampreys (Petromyzon marinus L.). Comp. Biochem. Physiol. (Accepted upon revision).

Youson, J.H., S.A. Sower, J.G. Seelye, F.W.H. Beamish, and J.A. Holmes. 1994c. Hormonal and environmental cues of metamorphosis in Petromyzon marinus. Research Completion Report, Great Lakes Fish. Comm., Ann Arbor, MI, 13 p.

Youson, J.H., J.A. Holmes, J.A. Guchardi, J.G. Seelye, R.E. Beaver, J.E. Gersmehl, S.A. Sower, and F.W.H. Beamish. 1993. Importance of condition factor and the influence of water temperature and photoperiod on metamorphosis of sea lamprey, Petromyzon marinus. Can. J. Fish. Aquat. Sci. 50:2448-2456.

Zielinski, B. 1994. Interaction of olfactory and endocrine systems in sea lamprey development: toward an integrated bio-chemical control: morphological development. Research Completion Report, Great Lakes Fish. Comm., Ann Arbor, MI.

Appendix 1. Experts interviewed during review of alternative sea lamprey control research priority assessment.

| Person | Agency | Technology Category |
|---|---|---|
| B. Beamish | University of Guelph, Guelph | Sex-ratio manipulation, natural controls |
| T. Bills | U.S. Fish and Wildlife Service, LaCrosse, WI | Lampricides |
| S. Bowen | University of Northern Michigan, Houghton, MI | Culturing, habitat manipulation |
| J. Heinrich | U.S. Fish and Wildlife Service, Marquette, MI | Sex-ratio manipulation |
| P. Ihssen | Ont. Min. of Natural Resources, Maple, Ont. | Natural controls, genetic manipulation |
| D. Johnson | U.S. Fish and Wildlife Service, Marquette, MI | Lampricides |
| F. Keeley | Hospital for Sick Children, Toronto, Ont. | Genetic manipulation |
| G. Klar | U.S. Fish and Wildlife Service, Marquette, MI | Lampricides |
| E. Koon | U.S. Fish and Wildlife Service, Ludington, MI | Barriers |
| T. McAuley | Department of Fisheries and Oceans, Sault Ste. Marie, Ont. | Barriers |
| R. McDonald | Department of Fisheries and Oceans, Sault Ste. Marie, Ont. | Trapping |
| R. McKinley | Ontario Hydro, Etobicoke, Ont. | Barriers |
| L. Schleen | Department of Fisheries and Oceans, Sault Ste. Marie, Ont. | Lampricides |
| J. Seelye | National Biological Survey, Hammond Bay, MI | Lampricides |
| M. Servos | Department of Fisheries and Oceans, Burlington, Ont. | Lampricides |

Appendix 1. Experts interviewed during review of alternative sea lamprey control research priority assessment.

| Person | Agency | Technology Category |
|---|---|---|
| B. Shuter | Ont. Min. of Natural Resources, Maple, Ont. | Sex-ratio manipulation, natural controls |
| D. Smith | Smith-Root, Inc., Vancouver, WA | Barriers |
| P. Sorensen | Univ. of Minnesota, Minneapolis, MN | Attractants and repellants |
| L. Stanfield | Ont. Min. of Natural Resources, Picton, Ont. | Barriers |
| W. Swink | National Biological Survey, Hammond Bay, MI | Barriers, natural controls |
| J. Youson | University of Toronto, Scarborough, Ont. | Developmental blockers, genetic manipulation |
| B. Zielinski | University of Windsor, Windsor, Ont. | Attractants and repellants |

Appendix 2. Research recommendations since 1980. Recommendations are paraphrased from original sources. References listed identify document in which the recommendation is recorded, not necessarily the author of that recommendation.

## Lampricides

Research on methods to improve delivery systems and site-specific treatments or formulations should continue (Meyer 1990)

Composition of TFM and Bayer 73 formulations need to be elucidated and impurities identified (NRCC 1985)

Mode of action of lampricides and biotransformation abilities of non-target taxa should be investigated (NRCC 1985)

Factors influencing treatment efficiency should be identified (Christie 1991)

Determine extent of larval dislocation from streams and colonization of lentic areas due to lampricide application (Christie 1991)

Improve application efficiency and reduce amounts of lampricide used (Seelye and Hanson 1992)

Develop and implement use of an effective bottom formulation to attack lentic populations (Seelye and Hanson 1992)

Maintain the integrity of lampricide control (Seelye and Hanson 1992)

Larval sea lamprey resistance to TFM and Bayer 73, plus mixtures, should be examined (NRCC 1985)

Persistence and toxicity of TFM and Bayer 73 and their metabolites to non-target species should be investigated (NRCC 1985)

Improve assessment of treatment effectiveness/efficiency at killing larvae (Christie 1991)

Investigate treatment efficiency in deepwater areas (Christie 1991)

Investigate impacts of lampricide treatments on non-target organisms (Seelye and Hanson 1992)

Refine TFM use to minimize social and environmental concerns, including improved formulations, stream selection, dose-determination, and scheduling and application methods (Seelye and Hanson 1992)

Define cost vs. kill of lamprey for conventional lampricide treatments (Seelye and Hanson 1992)

Minimize environmental impacts of lampricides (Seelye and Hanson 1992)

## Barriers

Investigate light or sound stimuli as alternatives to dams or leading devices (Lamsa et al. 1980)

Design dams to accomodate traps (Lamsa et al. 1980)

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Primary potential of electricity is to block access to spawning streams or direct migratory animals to traps (Meyer 1990)

Effects of blocked spawning runs on population estimates in adjacent streams should be investigated (Johnson 1987)

Determine how to pass nonjumping and jumping fish around or over barriers (Christie 1991)

Passage of nonjumping fish over barriers should be investigated (Biette and Griswold 1988)

Experience building barriers on moderate and large rivers needed (Biette and Griswold 1988)

Investigate impact of barrier dams on lentic populations of larvae (Biette and Griswold 1988)

Development of reliable fish passage critical to use of electrical and low-head dams (Bergstedt and Seelye 1992)

Continue development and deployment of electrical barriers (Seelye and Hanson 1992)

Investigate lamprey-specific physical and behavioral controls for use in conjunction with barriers (Seelye and Hanson 1992)

Design a lip that prevents lamprey passage when submerged by creating some hydraulic phenomenon (Katopodis et al. 1994)

Determine the limits of lamprey abilities to negotiate past flow, vertical barriers, and other hydraulic features (Meyer 1990)

Effectiveness of various designs in relation to stream, lamprey and fish movement characteristics should be investigated (Christie 1991)

Need information on effects of delaying and blocking nontarget fish at lamprey (Biette and Griswold 1988)

Evaluate various designs for building minimum sized structure for blocking and trapping lampreys with minimal environmental disruption (Biette and Griswold 1988)

Investigate environmental impacts of dams on fish passage, stream biota, and water quality (Biette and Griswold 1988)

Develop experimental facility for testing improved barrier dam designs and more efficient traps (Bergstedt and Seelye 1992)

Increase deployment of cost-effective low-head barrier dams (Seelye and Hanson 1992)

Develop barriers as effective non-chemical technique (Seelye and Hanson 1992)

Evaluate effectiveness of low-head barrier heights and lip design under variable flow and temperature regimes (Katopodis et al. 1994)

Test feasibility of using non-attachable surfaces on low-head dams to improve effectiveness (Katopodis et al. 1994)

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Study effects of small impoundments behind physical barriers on water quality, temperature, invertebrates, siltation, etc. (Katopodis et al. 1994)

Investigate feasibility of using portable or temporary barriers such as inflatable rubber dams (Katopodis et al. 1994)

Determine physiological effects on fish of moving through electric fields (Katopodis et al. 1994)

Determine most effective (for stopping lamprey) pulse characteristics of the electrical field (Katopodis et al. 1994)

Determine most efficient placement of electrical field in stream and its relation to orientation of fish as they move through it (Katopodis et al. 1994)

Design barriers that eliminate occurrence of downstream boils that are a danger to boaters, fishermen, and others (Katopodis et al. 1994)

Modify existing man-made and natural barriers to make them effective against sea lamprey (Katopodis et al. 1994)

Investigate ways to separate lamprey and large fish at electrical barriers based on performance (Katopodis et al. 1994)

Describe behavior of lamprey and other fish to graduated electrical field more precisely (Katopodis et al. 1994)

Design improvements for portable electrical barriers (Katopodis et al. 1994)

## Trapping

Design criteria for traps (portable) and nets needed that maximize capturing effectiveness (Johnson 1987)

Determine capture efficiency of permanent traps in barriers and if required design more efficient traps (Biette and Griswold 1988)

Improve trapping at barrier dams (Seelye and Hanson 1992)

Develop and test physical and chemical cues that might enhance traps (Katopodis et al. 1994)

Determine effects of trapping and release on non-target fish (Katopodis et al. 1994)

Efficiency of trap designs and factors affecting efficiency should be investigated systematically (Christie 1991)

Develop a technique for effective trapping in streams that do not have a barrier (Bergstedt and Seelye 1992)

Develop more effective trapping techniques (Seelye and Hanson 1992)

Test new designs to improve efficiency and selectivity of traps (Katopodis et al. 1994)

Determine effect of electricity, light, sound, and water velocity on lamprey behavior and the efficiency of traps (Katopodis et al. 1994)

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Optimize size, configuration, and positioning of traps in relation to barrier site (Katopodis et al. 1994)

Investigate use of olfactory attractants to increase trap efficiency (Katopodis et al. 1994)

Test trap designs using attraction water at electrical barriers (Katopodis et al. 1994)

Determine optimal use of attractant water flow (Katopodis et al. 1994)

Design traps that are self-unloading (Katopodis et al. 1994)

## Sex-Ratio Manipulation

Develop safe sterilants and methods of using them (Lamsa et al. 1980)

Thorough study of biology, behavior, and population dynamics is needed to implement sterilization successfully (Lamsa et al. 1980)

Gynogenesis and sex-reversal may have little effect on natural populations (Meyer 1990)

Study to explore benefits and dangers of using sterilized Atlantic coast or Lake Champlain sea lamprey in SMRT should be conducted before any decision is made (Meyer 1990)

Validation of nest counts as an approach to estimating populations of spawners is needed (Johnson 1987)

Ratios of sterile:fertile males required for reduction of larval populations (Christie 1991)

Determine if location and timing of release affect effectiveness of sterile males (Christie 1991)

Investigate factors controlling se-ratios in lamprey populations (Lamsa et al. 1980)

Develop monosex cultures (all male) for use in sterile male releases (Lamsa et al. 1980)

Artificial culture of lamprey numbers of animals unlikely to be accepted because of cost and public attitude (Meyer 1990)

Relationship between use of spawning habitat and total number of spawning adults should be determined (Johnson 1987)

Define relationships between spawning run size and production of larval year-classes and subsequent transformer production are needed (Christie 1991)

Determine if timing of spawning run, nest production, and spawning related to effectiveness of released sterile males (Christie 1991)

Develop alternative sterilant that is safer and environmentally friendly (Christie 1991)

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Investigate alternate sources of males for SMRT (Christie 1991)

Identify and develop alternate sources of males for sterilization (Seelye and Hanson 1992)

Refine SMRT so that it can be routinely implemented (Seelye and Hanson 1992)

Thoroughly test SMRT and support with data on safety of material used (Seelye and Hanson 1992)

Determine minimum dose of bisazir needed for safety reasons (Sower and Hanson 1992)

Investigate if possible to create female lamprey that will produce sterile males (Sower and Hanson 1992)

Determine if hormones can be used to sterilize lamprey as embryos, prolarvae or YOY (Sower and Hanson 1992)

Determine if sterilization can be accomplished by immersing embryos, prolarvae or larvae in bisazir (Sower and Hanson 1992)

More information on sex recognition and determination of heterogametic sex is needed (Sower and Hanson 1992)

Examine steroids, androgenesis, and steroid synthesis inhibitors for sterilization abilities (Sower and Hanson 1992)

Investigate ways of obtaining differential mortality, killing only females and produces all male culture (Sower and Hanson 1992)

Identify the most effective GnRH antagonist for use as a sterilant (Bergstedt and Seelye 1992)

Investigate biological sterilization (genetic, hormonal) (Seelye and Hanson 1992)

Alternate sources of males for sterilization must be secured (Seelye and Hanson 1992)

Continue to improve SMRT and develop methods to evaluate its effectiveness (Seelye and Hanson 1992)

Investigate use of GnRH antagonists as sterilant (Sower and Hanson 1992)

Determine if hybrid crosses produce sterile male sea lamprey among their progeny (Sower and Hanson 1992)

Assess induced triploidy as sterilization method (Sower and Hanson 1992)

Investigate whether selective carbohydrates can be used to alter GnRH neuron migration during embryonic development resulting in sterilization (Sower and Hanson 1992)

Better information on effects of density on sex-ratio of treated and untreated animals is needed (Sower and Hanson 1992)

Investigate environmental factors that determine sex in larval sea lamprey (Sower and Hanson 1992)

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## Attractants and Repellants

Investigate patterned vision in lamprey, responses to water currents and sound, proprioception, and chemosensitivity in larvae (Lamsa et al. 1980)

Determine if sea lamprey have alarm substances (Seelye and Hanson 1992)

Determine if self-generated repellants such as overcrowding factors or fecal factors are of use (Seelye and Hanson 1992)

Attractants and repellants should receive research attention (Meyer 1990)

Light, sound, and electrical stimuli should be investigated as attractants or repellants (Bergstedt and Seelye 1992)

Sex pheromones might be useful in trapping or selecting males (Seelye and Hanson 1992)

Self-generated repellants, over-crowding factors or fecal factors may be of no use because other motivating factors override them (Seelye and Hanson 1992)

Investigate application of attractants and repellants (Seelye and Hanson 1992)

Investigate use of chemical attractants and repellants (Seelye and Hanson 1992)

Investigate bile acids as possible larval aggregants (Sorensen and Hanson 1994)

Determine if secreted/excreted sex pheromones useful for trapping males (Seelye and Hanson 1992)

Better information on parasite distribution needed to implement attractants (Meyer 1990)

Identify hormones associated with reproductive behavior in male and female lamprey and test for ability to disrupt spawning (Bergstedt and Seelye 1992)

Knowledge of the presence of alarm substances in sea lamprey would be useful (Seelye and Hanson 1992)

Determine if sea lamprey use odors and/or electrical stimuli to detect/track fish (Seelye and Hanson 1992)

Emetics (polyphenolics), or cardiac glycosides which cause vomiting in birds, might be useful if they worked on sea lamprey and could be introduced via fish blood (Seelye and Hanson 1992)

Develop attractants for spawners (Seelye and Hanson 1992)

Determine if olfactory cues are important to larvae for aggregation (Sorensen and Hanson 1994)

Manipulation of feeding in parasites does not seem feasible (Sorensen and Hanson 1994)

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Nothing is known concerning repellants in sea lamprey (Sorensen and Hanson 1994)

Information on basic response of lamprey to predators and low dissolved oxygen is needed (Sorensen and Hanson 1994)

Development of good behavioral bioassay for testing migration cues, etc., is needed (Sorensen and Hanson 1994)

Determine if responsiveness to bile acids is seasonal (Sorensen and Hanson 1994)

Determine steroidal pathways in lamprey (Sorensen and Hanson 1994)

Investigate behavior response of sea lamprey to attractants under controlled conditions (Sorensen and Gallaher 1994)

Determine if other fish species detect and respond to bile acids (Sorensen and Gallaher 1994)

Identify sex pheromones based on studies of steroids, prostaglandins, gonadal products, and peptides (Sorensen and Hanson 1994)

Reports of responses to human saliva, dead lamprey, or dead salmon may be starting point in search for repellant or alarm substance (Sorensen and Hanson 1994)

Using migratory cues, especially bile acids, to manipulate lamprey behavior is promising (Sorensen and Hanson 1994)

Need to determine factors controlling lamprey bile acid production (Sorensen and Hanson 1994)

Determine if sex pheromones are used and their potency (Sorensen and Hanson 1994)

Determine if olfaction is involved in use of sex pheromones and release patterns of sex pheromones (Sorensen and Hanson 1994)

Determine if bile acids produced by larvae of other lamprey species (Sorensen and Gallaher 1994)

Determine if olfactory and behavioral sensitivity to bile acids is influenced by season and/or gonadal maturity (Sorensen and Gallaher 1994)

Investigate other possible attractants (bile, iron, etc.), repellants (spit, etc.), and fright reactions in lamprey (Sorensen and Hanson 1994)

## Genetic Manipulation

Investigate possibility of identifying dominant lethal gene and introducing it into wild populations. Mass producing carrier animals to introduce gene into wild animals is problem (Meyer 1990)

Appendix 2. Research recommendations since 1980. Recommendations are paraphrased from original sources. References listed identify document in which the recommendation is recorded, not necessarily the author of that recommendation.

## Developmental Blockers

Investigate ways to upset the timing (delay or prevent) of metamorphosis (Lamsa et al. 1980)

Investigate endocrinological controls of metamorphosis (Seelye and Hanson 1992)

Investigate physiology and control of metamorphosis to identify biological control (Beamish and Eshenroder 1988)

Determine role of pituitary hormones in controlling metamorphosis (Youson and Holmes 1993)

Conduct a comparative immunological study to determine changes during metamorphosis (Youson and Holmes 1993)

Investigate use of genetic engineering or hormonal intervention to interfere with metamorphosis (Seelye and Hanson 1992)

Determine factors that affect metamorphosis (Sower and Hanson 1992)

Investigate effects of hormones, hypophysectomy, heat shock proteins, temperature, condition factor, sex, etc. on metamorphosis (Sower and Hanson 1992)

Investigate factors controlling metamorphosis, particularly hormones, temperature, pituitary and pineal glands (Lamsa et al. 1980)

Research into triggers controlling metamorphosis has good potential for control (Meyer 1990)

Comparative endocrinological profile of parasitic and non-parasitic species or sea lamprey with markedly different larval periods (Youson and Holmes 1993)

Follow up condition factor work on factors initiating metamorphosis (Youson and Holmes 1993)

Thorough understanding of the endocrinology of metamorphosis will be valuable (Seelye and Hanson 1992)

Investigate physiological controls interfering with growth, development, metamorphosis or reproduction (Seelye and Hanson 1992)

Investigate role of environmental factors in controlling and setting limits to metamorphosis (Sower and Hanson 1992)

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## Natural Controls

Investigate possibility of genetically engineering fish to be repellant to parasitic sea lamprey (Seelye and Hanson 1992)

Conduct wounding and healing studies on host fish at relevant temperatures (Beamish and Eshenroder 1988)

Study population ecology of sea lamprey and related parasitic lamprey species in native habitats to determine natural regulatory factors (Seelye and Hanson 1992)

Investigate genetic variation among fish populations in their susceptibility to lamprey attack and injuring (Seelye and Hanson 1992)

Research on natural pathogens or parasites is a remote possibility for producing useful results (Meyer 1990)

Investigate role of water chemistry, especially ionic strength, in prey survival (Beamish and Eshenroder 1988)

Search for biological control agents, particularly lamprey-specific pathogens (Seelye and Hanson 1992)

Studies of the biology of natural populations on the Atlantic coast and Great Lakes streams not invaded should be conducted (Lamsa et al. 1980)

## Habitat Manipulation

Alterations of stream temperature through increased shading likely to be expensive and slow (Seelye and Hanson 1992)

Determine conditions which promote larval movement from one site to another (Lamsa et al. 1980)