J. Great Lakes Res. 33 (Special Issue 2):35–47
Internat. Assoc. Great Lakes Res., 2007

Toward Improved Assessment of Sea Lamprey Population Dynamics in Support of Cost-effective Sea Lamprey Management

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ABSTRACT. *Cost-effective integrated pest management of sea lampreys requires good assessment information. Assessment of sea lamprey populations is used to inform decisions about which control methods to use, as well as where and when to apply them. Additionally, assessment data are used to evaluate the performance of past management actions. This theme paper identifies key research questions that limit our understanding of sea lamprey population dynamics, as well as the quality of the assessment information currently used to inform management. The discussion is organized by dividing the sea lamprey life history into four stages—spawning, recruitment to age 1, larval, and parasitic—and examining the state of knowledge about population dynamics and assessment for each life stage. For spawning lamprey key research questions include migration timing, mating systems, and factors influencing spawning success. For recruitment to age 1, factors affecting recruitment variation and methods for age determination are critical needs. For larval lampreys, the primary target of control using lampricides, the key questions concern the accuracy of assessment methods used to guide lampricide treatment decisions and the effects of uncertainty on the utility of these methods. For parasitic lampreys, the main questions center on the nature of the host attack process and variation in survival during the parasitic phase. Finally, this review noted that the development of integrated models to evaluate control strategies remains a high priority for research. Because resources available for sea lamprey management are limited, high quality assessment information and good knowledge of sea lamprey population dynamics are key ingredients of a cost-effective control program.*

INDEX WORDS: *Sea lamprey, assessment, population dynamics, research priorities.*

INTRODUCTION

Sea lampreys (*Petromyzon marinus*) are an exotic pest fish that caused enormous ecological damage to the Laurentian Great Lakes in the twentieth century, and continue to be the object of an expensive control program. Why? Because it is widely believed that if lampreys were allowed to escape from control, they would once again do enormous damage to valued fish populations, especially top predators. More than $14 million a year are spent on the sea lamprey control program ($7.6—control; $4.0— assessment; $2.5—research: 2000–2004 averages) to protect a fishery that has been valued in excess of $1.5 billion, based on recreational fisheries alone (Bence and Smith 1999). The control program helps to maintain the health of one of the largest and most valuable freshwater ecosystems in the world.

Sea lamprey invaded the Great Lakes, except Lake Ontario, in the early part of the twentieth century (Smith and Tibbles 1980). Their origins in Lake Ontario are less certain (Waldman *et al.* 2004), but their detrimental impact on fish populations in all of the Great Lakes is not disputed. Lamprey abundance rose sharply soon after their arrival in each of the upper Great Lakes, followed by precipitous declines in host species, most notably lake trout *Salvelinus namaycush* (Smith and Tibbles 1980, Eshenroder *et al.* 1992).

Sea lamprey control is achieved through a program of integrated pest management that includes

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application of the lampricides TFM and Bayluscide to tributary streams (Brege *et al.* 2003), operation of low-head barrier dams (Lavis *et al*. 2003), trapping of adults, and release of sterile male sea lampreys Twohey *et al.* 2003). The control program is coordinated by the Great Lakes Fishery Commission and executed by the U.S. Fish and Wildlife Service in the United States and by the Department of Fisheries and Oceans in Canada (jointly known as "the agents"). Efficacious application of these controls requires good assessment information. In this paper assessment refers to the gathering of data on the status of sea lamprey populations or their effects on Great Lakes fishes for the purpose of informing stakeholders and to support management decisions. For example assessment helps to identify where to most efficiently apply lampricide treatments, whether existing barriers are effective and where to locate new barriers, and how many females should be removed from and sterile males released into a stream to achieve a target reduction in reproductive success. As well, assessment programs can provide information about both the status and the dynamics of sea lamprey populations and the damage they inflict on host fishes. This information makes it possible to develop and calibrate models used to plan control strategies, design management programs for optimal control, and determine whether management objectives are being met.

This theme paper will address two objectives. First a detailed overview is presented of the sea lamprey assessment program and its role in sea lamprey control. Second, critical information needs are summarized for sea lamprey assessment, thereby providing prospective investigators with useful insights into important areas for assessment-related research. Sea lamprey assessment is best thought of in the context of the population dynamics and ecology of the pest, so this theme paper is organized around its life-history. Existing assessment activities target all life stages of sea lamprey, to varying extents and for contrasting purposes. For each life stage: spawning, reproduction/recruitment (egg deposition to age 1), larval, metamorphosis, and parasitic (juvenile), the ecology, the relevance to control, current approaches to assessment, and research needs are discussed. The research theme paper concludes with a brief synthesis that highlights the role that integrative models need to play in bridging from assessment to management and focusing research attention on critical knowledge gaps.

SPAWNING

Ecology

Sea lampreys are semelparous spawners that deposit their eggs in coarse substrates (gravel, rubble) in streams in late spring or early summer. They have been observed to stage near or in the mouths of streams in late winter (Applegate 1950) until temperatures rise to levels that stimulate upstream migration (12–15°C)—(R.B. McDonald, Department of Fisheries and Oceans, Sault Ste, Marie, Ontario, Canada, personal communication; B. Young, Michigan State University, East Lansing, MI, unpublished data), at which time they become vulnerable to trapping. Sea lampreys do not home to natal streams in the Great Lakes (Bergstedt and Seelye 1995) but strong evidence exists that selection of streams for spawning is influenced by a migratory pheromone released by larval lamprey inhabiting suitable streams (Sorensen and Vrieze 2003). Within a stream, mature male sea lamprey select spawning sites and construct u-shaped nests. Females are attracted to spermiated males that release a second (mating) pheromone (Li *et al.* 2003). Observational data and recent microsatellite evidence suggest that the mating system is complex, with both polyandry and polygyny occurring in wild populations (Scribner and Jones 2002). Some evidence exists that not all adult lamprey entering streams in spring actually reproduce, possibly due to their poor condition (O'Connor 2001) and that lampreys sometimes emigrate from streams prior to spawning (Kelso 1998a).

Relevance to Control

Control of spawning-phase sea lampreys occurs by blocking access to spawning areas with barriers, by trapping, and by interfering with spawning through release of sterile males. Adult sea lampreys are not strong swimmers nor jumpers and their limited ability to ascend barriers to upstream migration that are easily passed by jumping fish such as salmonines has been effectively exploited. Various artificial barriers have been developed to prevent access of sea lampreys to spawning habitats (Lavis *et al.* 2003, McLaughlin *et al.* 2007). The current barrier program is moving toward (1) seasonally operable barriers that allow free movement of other fishes when sea lampreys are not migrating and (2) fish passage devices that allow upstream movement of teleosts but not sea lampreys. Trapping was historically a major component of control, but has recently been used primarily for assessment and for collection of male lamprey for sterilization, except in the St. Marys River where they are an important component of the integrated control program. However, with improvements in trap design and deployment, and the potential for using pheromones to increase trap capture rates (Li *et al.* 2007), trapping may become a key element of control in the future, even surpassing barriers as the primary alternative to lampricides. Sterilized adult male lamprey also have been used (currently only in the St. Marys River) to interfere with reproduction of wild, fertile lamprey (Twohey *et al.* 2003).

Assessment

Spawning lamprey populations are assessed primarily by capture in fixed and portable traps. The principal objective is to estimate spawning-run size in individual rivers and then combine these estimates to obtain a "whole-lake" adult population estimate. Whole-lake estimates are a primary indicator of the performance of the control program and are reported annually by the agents (e.g., Young and Klar 2004).

Spawning-run size in individual rivers is estimated using a mark-recapture technique. Sea lampreys are trapped, marked, and released downstream of traps. The observed rates of recapture are used to estimate the abundance of the spawning run in the river, using a Schaefer-type multiple recapture model (Ricker 1975: page 101, Mullett *et al.* 2003). Only a small proportion (20%) of all sea lamprey-producing rivers in each Great Lake is trapped, so whole-lake abundance estimates depend on a regression model that enables extrapolation to rivers without traps (Mullett *et al*. 2003). The model relates population estimates on trapped rivers to drainage area (larger rivers generally have larger runs) and the number of years since the last lampricide treatment (recently treated streams tend to have smaller spawning runs). The lakewide estimate is obtained by summing the mark-recapture estimates from river with traps together with the regression estimates from rivers without traps.

Monitoring spawning migrations of sea lampreys using traps also provides valuable information on the timing of the migration, which could potentially be used to aid deployment of traps and to operate seasonal barriers. Trapping data have been analyzed to determine whether environmental variables such as temperature and discharge consistently and predictably affect capture rates (B. Young, Michigan State University, East Lansing, MI, unpublished data). However these data have not yet been used to influence current practices. Some concern exists that these data represent seasonal changes in the propensity of lampreys to enter traps, rather than their actual migration patterns (Rod McDonald, DFO, personal communication).

Sea lampreys' movements have also been observed using radio-telemetry. These studies have sought to determine how and where lampreys move during their spawning migration, particularly when they encounter impediments to upstream movement, and to observe behavior and movements during the actual spawning period (Kelso 1998b). Data from telemetry studies can potentially aid in determining preferred locations for trapping and understanding factors influencing spawning success (e.g., can sea lampreys that encounter barriers simply emigrate from the blocked river and seek another site for spawning?).

Research Needs

Spawning-phase assessment data are used annually to determine the abundance of adult lamprey in each of the Great Lakes. An expert panel evaluated the adult assessment program in 1998, concluding that the regression-extrapolation method described above for adult assessment was appropriate, but that confidence in the estimates could be greatly improved if mark-recapture estimates could be obtained from more large rivers. They argued that the small number of large rivers from which trapping data were obtained leads to large uncertainty about the precision and accuracy of extrapolated lakewide estimates. They also recommended that the regression-extrapolation method be combined with other methods to estimate parasitic and adult lamprey abundance (see below—parasitic life stage) using an integrated assessment model (Young *et al.* 2003). Research should continue in this area.

Increased knowledge of the behavioral ecology of spawning-phase sea lampreys prior to and during spawning could enhance opportunities for deployment of alternative controls. For example, the mating system of sea lampreys is poorly understood, although recent research on the parentage of larvae using microsatellite loci suggests that both polyandry and polygyny are widespread (Scribner and Jones 2002). A better understanding of the mating system could prove valuable for implementation and refinement of sterile male and female release strategies (Bergstedt and Twohey 2007), as well as possibilities for control using mating pheromones (Li *et al*. 2007*)*. It would also be valuable to understand more about factors contributing to successful spawning, such as adult female condition and the amount of spawning habitat. Spawning habitat supply is assumed not to limit sea lamprey production in Great Lakes tributaries, but this assumption has never been evaluated and spawning habitat is generally not quantified in lamprey stream habitat assessments. Better information on the role of spawning habitat, adult condition, sex ratios, and other factors in determining spawning success would contribute important insights into the mechanisms affecting recruitment variation, a phenomenon recently shown to be critical to the efficacy of alternative control strategies (Jones *et al.* 2003). Finally, it would be valuable to have a better understanding of the factors influencing the movements of sea lampreys in to rivers and the timing of sea lamprey spawning runs, particularly the factors that determine the beginning and end of the run. This information could facilitate more efficient operation of seasonal barriers and traps.

REPRODUCTION/RECRUITMENT

Ecology

Sea lamprey reproduction occurs during mid-May through July, depending on the warming rate of spawning streams; typically spawning does not begins before temperatures reach 15°C (Manion and Hanson 1980). Adult male lamprey construct nests in coarse (gravel, rubble) substrates with flows of 0.5–1.5 m/s and attract females by releasing a potent pheromone Li *et al*. 2003). Fertilized eggs incubate for approximately two weeks before emerging from nests as prolarvae (Applegate 1950, Derosier 2001) and drifting downstream to burrow into suitable rearing habitat at development stage 17 (Piavis 1961), Development times depend on temperature (Piavis 1961, Derosier 2001). Prolarvae emerge from nests at night over several weeks, and range in size from 5 to 12 mm (Derosier 2001). Little is known about the fate of larval sea lamprey after emergence, although recent work suggests that some age-0 lamprey disperse hundreds of meters from nests soon after emergence (Derosier *et al.* 2007).

Larval sea lamprey burrow into soft sediments and feed by filtering suspended organic matter from stream water (Sutton and Bowen 1994, Yap and Bowen 2003). Little is known about how food quality and quantity, or environmental conditions, affect growth rates of age-0 sea lamprey.

Research has begun on factors that influence sea lamprey recruitment. Observations of recruitment (defined here as abundance of age-1 sea lamprey) in streams where the abundance of spawning lamprey was either known or estimated from mark-recapture surveys (Mullett *et al.* 2003) suggests that recruitment variation, independent of adult stock size, can be very large (Jones *et al*. 2003). Despite this large variation, however, the data reveal density-dependent compensation—lower survival from egg deposition to recruitment as spawning stock size increases. Factors such as weather conditions, stream productivity, and the abundance of other species of larval lamprey may explain some of the density-independent recruitment variation. Thus far, however, supporting evidence is either absent or equivocal. For example, some studies have shown that the growth and biomass of age-1 lamprey is lower when other age classes are present (Purvis 1979, Weise and Pajos 1998); other analyses have produced mixed results (Jones *et al*. 2003).

Relevance to Control

Stock-recruitment relationships play a critical role in determining the efficacy of alternative controls that target adult lamprey, such as trapping and sterile male releases (Jones *et al*. 2003). If density-dependent compensation is strong, or density-independent recruitment variation is large, reductions in spawning populations may not regularly lead to concomitant reductions in recruitment. Analyses of stock-recruitment relationships have been used to evaluate alternative control strategies on the St. Marys River (Haeseker *et al.* 2003), and will continue to be used for this purpose. However, our understanding of this relationship is still limited, which reduces our ability to make informed decisions about trade-offs between the use of alternative control and of lampricides (Jones *et al.* 2003).

Assessment

No regular assessment activities target early larval life stages. Nevertheless several techniques have been evaluated or used for research activities. Nest surveys have been used to estimate the number of actual spawning events that occurred in a stream. However, confidence in these methods is low because male lamprey will construct nests but not actually use them, nests can be difficult to distinguish only days after abandonment, and multiple spawning events can occur at the same location. Nest surveys have also been used successfully to assess the effectiveness of sterile male releases at reducing reproductive success (Kaye *et al.* 2003). Drift nets have been used to sample lamprey emerging from nests (Derosier 2001), but this method is labor intensive and gear efficiency is unknown. Recruitment has been defined for stock-recruitment analyses as abundance of age-1 larvae because this is the earliest life stage at which reliable, cost-effective quantitative assessment is currently possible. Age-0 sea lampreys are difficult to capture with conventional larval assessment electrofishing equipment (see below) because of their small size, so catches of age-0 larvae are not considered representative of population size. For research projects age-0 abundance can be quantified using a dredging technique, in which suitable substrate (the soft sediments using by burrowing larvae) is excavated from the stream and passed through sieves to separate larval lamprey from the substrate itself (Derosier 2001). The labor required to use this method limits its potential as a routine assessment tool.

Age-1 sea lampreys are captured effectively by larval assessment gear during routine quantitative surveys (see below). To estimate recruitment, however, age-1 larvae must be distinguished from older larvae. Usually the age 1 larvae form a distinct mode in the length-frequency distribution (Jones *et al.* 2003). However, considerable overlap can sometimes occur between the length distributions of age 1 and age 2 or older larvae. In these cases an alternative method is required to quantify recruitment, and statoliths have been suggested as a means to determine ages of larval lamprey (Beamish and Medland 1988).

Research Needs

The demographics of sea lamprey during their first year of life continue to be very poorly understood. In particular, little is known about the factors that might explain both density dependent and density independent variation in recruitment among years and streams. Further quantification of recruitment dynamics and mechanistic investigations of factors that influence recruitment variation would improve our ability to assess the efficacy of alternative control strategies. In particular, those factors that explain recruitment differences *among streams* must be distinguished from those that explain differences *among years*. In models used to evaluate strategies, "stream effects" need to be explicitly accounted for when specific streams are being considered for alternative control, whereas "year effects" can be treated as uncontrollable variation.

A reliable method for determining larval lamprey ages should also be developed. Ageing error is a serious problem for older larvae, where length-frequency data are unreliable, but even for young larvae it would be valuable to eliminate ageing error as a substantial source of uncertainty in recruitment studies. Statolith-based ageing techniques need to be refined and verified as reliable, by using known-age specimens from a wide range of age-classes and from streams with contrasting growth conditions.

LARVAL STAGE (AGE 1 THROUGH METAMORPHOSIS)

Ecology

Sea lamprey larvae spend several years as benthic filter feeders, burrowed in soft sediments in stream and sometimes lake habitats, before reaching a size at which they metamorphose and begin their parasitic life stage. Growth rates vary considerably among streams and among years within streams (Hansen *et al.* 2003). Larval lamprey appear to prefer depositional habitats with an abundance of fine particles and organic matter, these habitats provide a regular supply of the suspended organic matter upon which the larvae feed (Sutton and Bowen 1994, Yap and Bowen 2003). As larvae grow their preference appears to shift toward larger particle sizes (Sullivan 2003), but even large (> 120 mm) larvae are rarely found in coarse substrates such as gravel, cobble, or rubble.

Sea lamprey larvae probably redistribute frequently, either because of physical events such as bedload movement during high flows or dewatering at low flows, or simply to seek better habitats for feeding. Little evidence exists for upstream movements of larvae, however. Little is known about actual movements of individual larvae, except for very young (age-0) animals (Derosier *et al.* 2007). Larval populations have been observed to build up in lentic areas near the mouths of rivers in the years after a treatment, especially in those streams where spawning occurs fairly close to the mouth, and this provides evidence of downstream movements at the population level.

Considerable research has been completed on the factors that trigger metamorphosis (see review by Youson 2003). Briefly, for metamorphosis to occur larval lamprey need to reach a size in excess of approximately 120 mm and have accumulated sufficient lipid reserves to allow them to survive the protracted (10–11 month) non-trophic period associated with their metamorphosis. Laboratory studies have shown (Youson *et al.* 1993) that a combination of length (120 mm), weight (3 g) and condition factor (1.5) appears to be the minimum condition for larvae to undergo metamorphosis. Field observations of metamorphosis rates for tagged larvae in two streams suggested little difference between the performance of models that did or did not include weight in addition to length (either as weight or as condition factor) to predict metamorphosis (Henson *et al.* 2003). Evidence from laboratory studies suggests that a rapid rise in temperatures in spring is a strong stimulus for larvae to enter metamorphosis (Holmes and Youson 1997).

Relevance to Control

By far the largest component of the sea lamprey control program is the periodic treatment of streams with lampricides. This method of control targets lamprey during their larval stage. Because not all possible streams can be treated each year, it is necessary to choose among streams (Christie *et al.* 2003). The selection of streams is based on estimates of the abundance of larval lampreys and predictions of future rates of metamorphosis for those larvae (Slade *et al.* 2003). Streams are ranked for treatment based on the predicted abundance of future metamorphosing lamprey, relative to the cost of treatment of that stream. Thus, knowledge of the demographics of this life stage (abundance, distribution, survival, growth, and metamorphosis rates) is critical for cost effective sea lamprey control using lampricides.

Assessment

Because of the large allocation of funds to lampricide use it is not surprising that nearly 75% of the assessment budget is devoted to larval assessment, particularly assessment conducted in the interests of selecting streams for treatment. Larval assessment seeks quantitative information considered necessary to make an objective decision about which streams to treat. Streams are surveyed using specific protocols that are designed to obtain quantitative, unbiased estimates of (1) larval densities, (2) larval habitat abundance, and (3) the size distribution of larvae (Slade *et al.* 2003). Distinct protocols have been developed for wadable (Larval Assessment Work Group 2004) and non-wadable (Larval Assessment Work Group 1998) waters because sampling techniques differ between these two habitats. Briefly, larval densities are estimated from randomly selected plots of suitable habitat, habitat quantity (four habitat types, based on substrate attributes) is measured along randomly selected transects, and the size distribution is determined by collecting a haphazard sample of at least 100 larvae. These data are summarized in an integrated database and used to project the estimated number of sea lamprey that will likely undergo metamorphosis and leave the stream during the following year to become parasites in the lake.

Other assessment activities target larval and metamorphic life stages. Qualitative surveys are conducted regularly on a wider range of streams to detect the establishment of new populations, to determine whether quantitative surveys are needed, and to determine the upstream limit of the distribution of larvae in a stream that has been selected for treatment. In lentic areas past surveys have generally been qualitative in nature, as quantitative approaches have only recently been developed and applied (e.g., Fodale *et al.* 2003). Post-treatment surveys are sometimes conducted to determine the success of a lampricide treatment. Recently, mark-recapture surveys have been used to provide an independent assessment of survey accuracy. Larvae are collected, marked and released back into streams a few weeks prior to a scheduled treatment. Recapture occurs during the treatment (Steeves 2002). By comparing mark-recapture population estimates with the population estimates derived from survey data and used to rank the stream for treatment, the accuracy of the survey can be assessed.

Research Needs

Larval assessment is a critical ingredient of the control program, in that it provides the data necessary to make costly treatment decisions. Standardized, quantitative techniques have been used since 1995 to obtain larval population estimates (Slade *et al.* 2003). An important benefit of using a standardized quantitative method is that it has allowed us to assess the uncertainty associated with the estimates. A recent analysis of this uncertainty (Steeves 2002) led to the conclusion that current methods do not provide precise and accurate estimates, particularly of metamorphic sea lamprey. Steeves (2002) computed coefficients of variation (CVs) for sea lamprey abundance estimates from nine streams and found them to range 0.42–0.80 for larvae and 0.97–1.92 for juveniles (defined here as sea lamprey that have completed metamorphosis). CVs for juvenile lampreys were substantially larger than for larvae because of the large uncertainty associated with estimates of growth rates and of the dependence of metamorphosis on larval size (Hansen *et al.* 2003), both of which are needed to estimate juvenile production from the quantitative assessment data. This raises two key research needs. First, this uncertainty must be reduced, presumably by refining assessment techniques and/or developing alternative methods for interpreting the data. Second, there is a need to examine how this uncertainty influences the stream selection process. At present streams are ranked for treatment based on the implicit assumption that assessment data are precise and accurate (i.e., that we know the true abundance of juvenile lampreys in each stream). This ranking method ignores the risk associated with making choices based on inaccurate data. Decision theory suggests that when uncertainty is considered the best decision often differs from that which would be judged best when uncertainty is ignored (Clemen and Reilly 2001).

Hansen *et al.* (2003) examined several components of the larval assessment program, and concluded that research is critically needed to reduce uncertainty, particularly that associated with estimating larval growth rates and predicting metamorphosis rates from larval size. A recent expert panel review of the larval assessment program produced several recommendations, including (1) compare alternative methods for assessing larval abundance (i.e., intensive plot-level density estimates—current practice—versus less intensive reach-level catch-per-effort surveys), (2) evaluate the implicit assumption that larval densities are similar in wadable and non-wadable habitats in streams that contain both types of habitats (this assumption is implicit because non-wadable habitats are not presently surveyed in streams that contain both wadable and non-wadable areas), and (3) shift emphasis from allocating virtually all survey resources to pre-treatment assessment (count-then-kill) to a much greater emphasis on post-treatment assessment (kill-then-count). The panel noted, as discussed above, that current assessment techniques yield imprecise information, and we have very little information that allows us to assess the performance of decisions based on these techniques. Post-treatment assessments, such as the mark-recapture approach discussed above, would provide this information.

PARASITIC STAGE (JUVENILE)

Ecology

Juvenile sea lampreys emigrate from streams and enter the Great Lakes as parasites in fall or spring. They then spend 12 (spring migrants) to 18 (fall migrants) months feeding on teleost hosts before returning to rivers to spawn and die. As parasites, lampreys search for and attach to host species, use their rasping mouth parts to penetrate their host's skin and extract body fluids. In general, if attachment continues for long enough, and sufficient fluids are removed, lamprey attacks result either directly or indirectly (through a secondary infection) in the death of the host. Not all lamprey hosts are killed by attacks, however, as evidenced by the common observation of teleosts with lamprey wounds, particularly when lamprey abundances are believed to be high. Parasitic sea lamprey feeding and growth is not continuous; rather, a burst of feeding and consequently growth occurs in the fall prior to maturation (Bergstedt and Swink 1995). Because of this, host mortality due to sea lampreys is also greatest during this period (Bergstedt and Schneider 1988).

The parasitic life stage is when sea lampreys do their damage and obviously this damage is the motivation for the sea lamprey control program. Unfortunately surprisingly little is known about the dynamics of the sea lamprey host-parasite interaction Bence *et al.* 2003, Swink 2003). In contrast to spawning and larval life stages, field observations of the parasitic stage are very difficult to obtain; consequently inferences have been drawn largely from laboratory studies of lamprey feeding (Swink 2003) and indirect observations of attack dynamics from wounds observed on hosts that survive attacks (Ebener *et al.* 2003). The difficulty of directly observing lamprey parasite-host interactions in the Great Lakes has led to contrasting assessments of the actual damage caused by lampreys (range 0.66 to 10.1 lake trout deaths per spawner: Madenjian *et al.* 2003, p. 344). The differences arise from the methods use to estimate mortality (stock assessment models—Bence *et al.* 2003; individual-based bioenergetics models—Madenjian *et al.* 2003; laboratory extrapolations—Swink 2003), from whether deaths due to secondary infection as well as direct blood loss are included in the assessment, and from assumptions about the proportion of time lampreys spend searching for their hosts as opposed to feeding. This life stage is the subject of extensive discussion in the aforementioned reviews in the SLIS (Sea Lamprey International Symposium) II volume.

Relevance to Control

No sea lamprey control actions operate on the parasitic phase. Justification for control actions, however, depends on excellent assessment for this life stage. Sawyer (1980) argued for the implementation of an Economic Injury Level (EIL) criterion for determining an appropriate level of sea lamprey control for each Great Lake. The EIL for a lake was defined as the level of control at which the marginal cost of an additional unit of control exceeds the marginal benefit that results from that control. Because the benefits of control derive from reduced sea lamprey-induced mortality of teleost fishes, quantitative understanding of how lamprey abundance and host abundance interact to affect attack rates and subsequent host mortality is a critical ingredient of EIL-based control.

Decisions about the appropriate allocation of control resources among the Great Lakes also depend on assessment information regarding the parasitic life stage. Thus far, EILs have only been computed for the lower lakes (Sullivan *et al.* 2003, Larson *et al.* 2003), but in 2004 the GLFC elected to partially allocate control resources based on differences among lakes in wounding rates on lake trout hosts compared to a basin-wide standard of five wounds per 100 fish (Mark Ebener, Chippewa Ottawa Resource Authority and GLFC, personal communication).

Assessment

Parasitic sea lamprey populations and their effects on host fish populations are assessed in three ways in the Great Lakes. First, wounds (marks) that did not cause host mortality are used as a measure of damage (Ebener *et al.* 2003), based on inferences about the probability of a host fish surviving an attack (Bence *et al.* 2003). Marks are classified using the method of King (1980), with modifications suggested by Eshenroder and Koonce (1984). Ebener *et al.* (2003) evaluated the agreement among observers in classifying marks and found large discrepancies, suggesting the need for improved standardization. As well, some agencies collect marking data during fall surveys while others use spring collections. Uncertainty about healing times for lamprey wounds makes it difficult to determine the best time for collecting marking data.

Second, sea lamprey marking data are combined with host fishery stock assessments, particularly for lake trout, to estimate the actual mortality of host species attributable to lampreys (e.g., Sitar *et al.* 1999), and to compare lamprey-induced mortality to other sources. To infer mortality rates from marking rates it is necessary to make assumptions about the lethality of an attack.

Third, several attempts have been made in Lake Huron to estimate the abundance of parasitic sea lamprey by marking either recently metamorphosed lamprey captured during their lakeward migration or parasitic lamprey captured in sport or commercial fisheries in the lake and recapturing these lamprey as adults when they enter traps during their spawning migration (Bergstedt *et al.* 2003). Contrary to expectation, the population estimates from recently metamorphosed lamprey tended to be smaller than estimates from lampreys that were marked in the lake. Bergstedt *et al.* (2003) concluded that lake-marked lamprey must have suffered greater mortality than unmarked fish, leading to inflated estimates of abundance.

Research Needs

Bence *et al.* (2003), Ebener *et al.* (2003), and Stewart *et al.* (2003) all offer valuable recommendations for research on the parasitic phase of the sea lamprey life history, particularly as it relates to the assessment of damage due to lampreys and optimal allocation of control expenditures. Investigators interested in conducting research on the life stage should review these reports for a more thorough discussion of research needs. Here I note four key recommendations. First, better assessments are needed of the differences among lakes and source streams in survival of parasitic lamprey. At present the methods for allocating control resources assume that a recently metamorphosed lamprey will do the same amount of damage regardless of the lake it enters and the stream from which it came. Consequently, treatment resources may be inappropriately allocated to streams which produce large numbers of juveniles , but that experience low survival rates in the Great Lakes. Second, a better understanding is needed of how changes in the relative abundance of alternative hosts affect sea lamprey attack rates. As Great Lakes fish communities change it will be important to understand the implications for sea lamprey parasitism. For both of these first two rec-

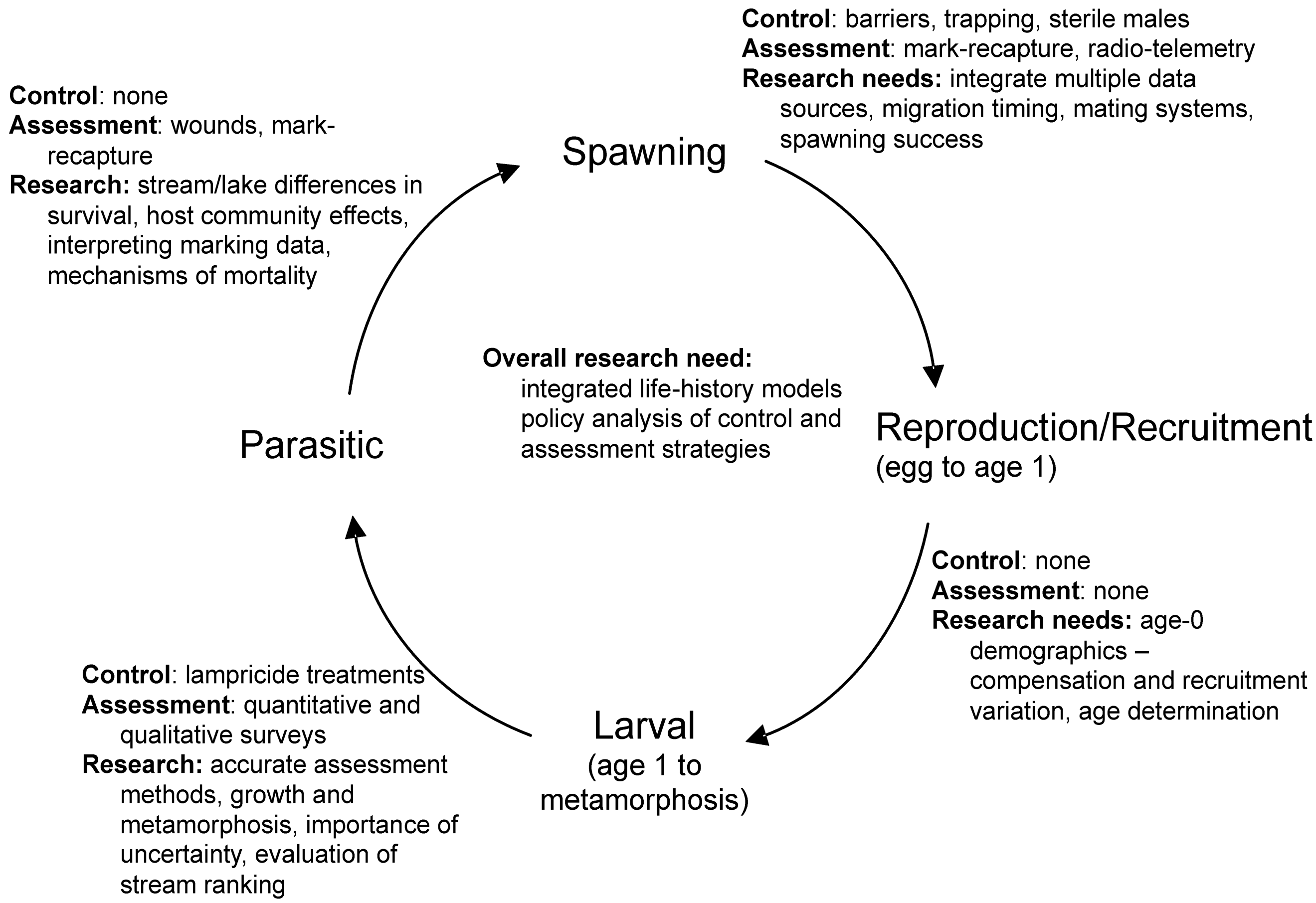

FIG. 1. Major control options, assessment tools, and research needs for the four life stages of Great Lakes sea lampreys.

ommendations our limited knowledge of the factors affecting the growth and survival of sea lampreys soon after they begin to feed in the lakes is undoubtedly a key uncertainty. Third, more repeatable methods need to be developed for assessing and interpreting marking data. These new methods should include the development of standardized classification criteria and an improved database of wound healing times and the dependence of healing times on temperature. Finally, a better understanding is needed about the mechanisms of sea lamprey-induced host mortality, including the relationship of mortality to blood loss and secondary infection.

SUMMARY OF RESEARCH QUESTIONS

This theme paper addresses the state of knowledge of sea lamprey population dynamics in the Great Lakes, and the role that assessment plays in gaining knowledge about populations in order to make good decisions and determine the success of past decisions. The discussion was organized around the life-cycle of the sea lamprey (Fig. 1), and has identified a number of particularly important research questions in the area of assessment and population dynamics. To summarize the key questions are:

1. Spawning-phase
   a) What is the optimal mixture of methods to provide the most accurate assessment of spawning-phase abundance at an acceptable cost?
   b) What factors affect the timing of sea lamprey spawning migrations?
   c) How do factors such as density and sex ratio affect the sea lamprey mating system?
   d) How do factors such as habitat supply and quality, adult condition, and sex ratios affect spawning success?

2. Reproduction/recruitment
   a) What factors, both density dependent and density independent, determine the survival and growth of sea lampreys during their first year of life?
   b) How can we reliably determine the age composition of sea lamprey populations?
3. Larval phase (age 1 through metamorphosis)
   a) How can we accurately assess larval population densities, especially in non-wadable waters?
   b) What factors influence larval growth and metamorphosis, and how can we incorporate these factors into improved models for assessment and forecasting?
   c) How does uncertainty in the assessment process affect the optimal selection of streams for lampricide treatment?
   d) How can we best assess the performance of alternative methods for ranking streams for lampricide treatment?
4. Parasitic
   a) How does parasitic lamprey survival vary among streams and lakes and what factors might explain this variation?
   b) How does host community composition affect the distribution of sea lamprey attacks among hosts?
   c) Can we develop a repeatable method for assessing and interpreting sea lamprey wounding observations?
   d) How do sea lamprey attacks kill their hosts?

In addition to research to address uncertainties about a particular life stage, there is a great need to develop and use models that integrate the entire lamprey life cycle. Ever since the adoption of an integrated pest management approach to sea lamprey control (Davis *et al.* 1982), following first Sea Lamprey International Symposium (c.f. Sawyer 1980), system models of sea lamprey control have been viewed as a key element of the program (Koonce *et al.* 1982, Spangler and Jacobson 1985, Koonce and Locci-Hernandez 1989, Greig *et al.* 1992, Koonce *et al.* 1993, Larson *et al.* 2003, Schleen *et al.* 2003). However, the models require updating and refinement, taking advantage of the abundance of new information about sea lamprey population dynamics that can be extracted from quantitative assessments. They also need to incorporate uncertainty and variability, aspects of system dynamics that are now widely recognized as being key to the use of systems models to evaluate policy (Haeseker *et al.* 2003, Jones *et al.* 2003). A final research question is thus:

5. Overall
   a) Can we develop improved models that integrate sea lamprey life history information and management and allow evaluation of a range of control and assessment strategies?

CONCLUSIONS

If the resources available for sea lamprey control were effectively unlimited, it might be reasonable to suggest that understanding population dynamics and having accurate assessment methods would be less important than figuring out how to quickly eliminate the pest from the Great Lakes basin. Obviously this is not the case, and so the GFLC and its agents are routinely faced with very difficult decisions about how and where to apply scarce control resources. We continue to be very uncertain about how manipulations of sea lamprey populations through control will affect their population dynamics, particularly at the whole-lake level, and thus the damage they will do to economically and socially important fishes in the Great Lakes. Research aimed at addressing the critical uncertainties described in this theme paper has the potential to profoundly affect the ability of the GLFC to achieve its goal of suppressing sea lamprey populations to economic-injury levels in a cost-effective manner.

ACKNOWLEDGMENTS

This theme paper was improved through comments by several members of the Task Force as well as Roy Stein, Chuck Krueger, Sara Adlerstein, and Trent Sutton. The author would also like to acknowledge the assistance of Sean Sisler in preparing the final draft. This is contribution number 2007-003 of the Quantitative Fisheries Center at Michigan State University.

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Submitted: 22 November 2006
Accepted: 15 February 2007
Editorial handling: J. Ellen Marsden