IMPROVING LARVAL SEA LAMPREY ASSESSMENT IN THE GREAT LAKES USING ADAPTIVE MANAGEMENT AND HISTORICAL RECORDS

By

Gretchen J. Anderson

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ABSTRACT

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Sea lampreys in the Great Lakes are managed by treating tributaries with lampricides that target the larval stage. A resource-intensive but imperfect larval assessment process (Quantitative Assessment Sampling, QAS) is currently used to determine which streams to treat annually. I developed an alternative assessment method (Rapid Assessment, RA) that requires fewer resources, and compared the costs and benefits of RA vs. QAS by conducting both methods on all wadeable streams requiring assessment in 2005 and 2006 and ranking streams for treatment priority. The use of RA resulted in more treated streams, and based on population estimates generated by QAS and by capture-recapture experiments, the use of RA would allow greater suppression of sea lampreys basin-wide. Assessment expenses could also be reduced through the incorporation of historical knowledge. Some tributaries are highly regular in their need for treatments, while others vary widely. I analyzed data collected from 1959 -2005 using mixed-effects models to test for differences in recruitment and growth to age-1 between regularly and irregularly treated streams. Recruitment was twice as large in regular streams than in irregular streams, indicating that year class strength is established early in the sea lamprey life cycle. I found no consistent differences in growth to age-1 among categories of streams; however, a variance components analysis showed that Lake Superior streams that are treated irregularly also exhibit more irregular size at age-1 than streams treated regularly.

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THESIS INTRODUCTION

The sea lamprey (*Petromyzon marinus*) is an invasive species in the Great Lakes and is the focus of an intensive control program. Sea lampreys are native to the Atlantic Ocean, and spawn both in North America and Europe (Beamish 1980). Sea lampreys were first documented in Lake Ontario in the early 1800s, although their impacts on other fish stocks in Lake Ontario appear to have been minimal until the 20th century (Christie and Kolenosky 1980). Sea lampreys invaded the other Great Lakes through the Welland canal beginning in the 1920s (Applegate 1950, Christie and Goddard 2003). Spawning runs of sea lampreys were confirmed in all of the upper Great Lakes by 1947 (Smith and Tibbles 1980).

Adult sea lampreys spawn in streams, where the non-parasitic larvae typically live for 3-7 years (Potter 1980), although they can remain in streams for as many as 18 years (Manion and Smith 1978). Upon completion of the larval phase, sea lampreys metamorphose and migrate downstream into large bodies of water, where they parasitize other fishes, often injuring or killing the host. An early life history study identified stream-dwelling larval sea lampreys as the life stage most vulnerable to control (Applegate 1950); in particular, managers were encouraged to focus control efforts on larvae undergoing metamorphosis (called transformers) to maximize efficiency (Smith and Tibbles 1980).

The ecological impacts of sea lampreys on native species of the Great Lakes have been well documented, including their contribution to the extirpation of lake trout in all lakes except Superior and Huron (Smith and Tibbles 1980, Pearce et al. 1980). By 1946, sea lampreys were recognized as a major threat to the fisheries of the Great Lakes

(Fetterolf 1980), stimulating the formation of the Great Lakes Fishery Commission (GLFC) in 1955 to coordinate the management of this species (Christie and Goddard 2003). After several years of limited and relatively unsuccessful attempts to control sea lampreys using mechanical and electrical barriers to block spawning adults, chemical control using 3-triflouromethyl-4-nitrophenol (TFM) was initiated in Lake Superior in 1958 (Christie and Goddard 2003). Use of chemical control in Lakes Michigan, Huron, and Ontario was initiated in the 1960's and 1970's, and Lake Erie did not start using chemical control until 1986 (Christie and Goddard 2003). Sea lamprey populations and wounding rates of lake trout declined drastically immediately following the initiation of chemical controls (Smith and Tibbles 1980). Chemical controls are now used in conjunction with alternative control methods, and adult sea lamprey populations are judged to be at around 10% of their former abundance (Smith and Tibbles 1980, GLFC 2001, Heinrich et al. 2003).

Although alternative control methods are currently used to supplement chemical control techniques, control is achieved mainly through the periodic treatment of sea lamprey-producing streams with TFM, which typically kills 95-100% of the larvae present (Smith and Swink 2003). Because larval sea lampreys remain in their natal streams for several years before becoming parasitic juveniles, it is neither necessary nor cost-effective to treat every stream each year. Rather, treatments should be applied on a cycle that matches the duration of the larval phase in a given stream. However, natural variation in recruitment, growth rates, and survival of larval sea lampreys makes it impossible to predict with certainty when each stream will require treatment to prevent the downstream migration of parasitic juveniles. Therefore, each year a group of candidate streams is assessed to determine which streams have the largest populations of transformers relative to their treatment cost and thus should be prioritized for treatment (Slade et al. 2003).

The current larval assessment methods are costly, yet still produce highly uncertain population estimates. Recent studies have identified and quantified sources of this uncertainty (Steeves 2002) and drawn attention to assumptions in the assessment and stream ranking process that are often violated (Steeves et al. 2003, Hansen et al. 2003). Using current assessment and control methods, suppression of sea lampreys to target levels has yet to be accomplished consistently throughout the Great Lakes (*Gavin Christie, Great Lakes Fishery Commission, personal communication*), indicating that the exploration of alternative methods is warranted. It seems reasonable to assume that an increase in resources allocated to assessment would result in a corresponding increase in the accuracy of larval population estimates, and therefore in the certainty of stream selection decisions. However, high levels of variability in larval growth and metamorphic rates, combined with the practical limitation that larval assessments must be conducted in the year prior to a stream treatment, preclude managers from ever being absolutely certain about which streams to treat, regardless of the level of assessment expenditures. Additionally, because the GLFC manages sea lampreys with a finite budget, any increase in assessment costs will result in a corresponding decrease in the resources available to actually treat streams. An alternative management strategy would be to allot minimal resources to assessment, accept a high level of uncertainty surrounding predictions of larval and transformer abundance, but make stream treatment decisions less sensitive to this uncertainty by using the resources saved on assessment to treat additional streams.

In Chapter 1 of this thesis I describe the development, implementation, and evaluation of an alternative assessment and stream selection protocol called Rapid Assessment (RA). RA requires fewer resources than the current assessment procedure (Quantitative Assessment Sampling, QAS), and the resources saved on assessment are used to treat additional streams. The objective of this research was to evaluate the effectiveness of RA relative to QAS by comparing their costs to the sea lamprey control program and their benefits in terms of sea lampreys killed. I evaluated the costs and benefits of RA compared to QAS by implementing both methods on a basin-wide scale and monitoring the consequences in terms of the streams selected for treatment and the predicted number of sea lampreys killed. I compared the predicted numbers of sea lampreys killed using population estimates predicted by QAS as well as population estimates generated from capture-recapture studies. I compared the two assessment methods using an adaptive management framework in the sense that the comparisons were conducted on the scale relevant to management, and involved the use of alternative management tactics to learn more about the best management strategy to employ in the future.

Another means through which assessment costs could be reduced is through the incorporation of historical knowledge into the stream selection process. Larval assessment surveys have been conducted in Great Lakes tributaries since the inception of the sea lamprey control program, but these data have never been formally analyzed for patterns in demographic rates such as recruitment and growth. In Chapter 2, I describe the analysis of historical survey data collected from 1959 – 2005. Sea lamprey managers have classified lamprey-producing streams in the Great Lakes into four categories based on their regularity of lampricide treatments. I used mixed-effects models to analyze differences in recruitment and growth to age-1 among stream categories. I also used variance components analyses to determine if differences existed between categories in the variability of recruitment or growth to age-1. The objectives of this research were to determine the usefulness of this stream categorization framework in directing assessment efforts, and to determine which demographic processes of larval sea lampreys have the greatest influence on the regularity of sea lamprey production and need for treatment in a stream. The results of these analyses are presented in a management context, and recommendations for assessment and future analyses based on my results are included.

CHAPTER ONE

DEVELOPMENT AND EVALUATION OF AN ALTERNATIVE ASSESSMENT PROCEDURE FOR LARVAL SEA LAMPREYS: A CASE STUDY IN ADAPTIVE MANAGEMENT

Introduction

The sea lamprey (*Petromyzon marinus*) is an invasive species in the Great Lakes and is the focus of an intensive control program. Sea lampreys were first documented in Lake Ontario in the early 1800s, and invaded the other Great Lakes through the Welland canal beginning in the 1920s (Applegate 1950, Christie and Goddard 2003). Their ecological impacts on native species of the Great Lakes have been well documented, including their contribution to the extirpation of lake trout in all lakes except Superior and Huron (Smith and Tibbles 1980, Pearce et al. 1980), prompting the formation of the Great Lakes Fishery Commission (GLFC) in 1955 to oversee sea lamprey management (Christie and Goddard 2003).

Adult sea lampreys spawn in streams, where the non-parasitic larvae live for an average of 3-7 years (Potter 1980), although they can remain in streams for as many as 18 years (Manion and Smith 1978). Upon completion of the larval phase, sea lampreys metamorphose and migrate downstream into large bodies of water, where they parasitize other fishes, often injuring or killing the host. An early life history study identified stream-dwelling larval sea lampreys as the life stage most vulnerable to control (Applegate 1950); in particular, managers were encouraged to focus control efforts on larvae undergoing metamorphosis (called transformers) to maximize efficiency (Smith and Tibbles 1980). Control is currently achieved mainly through the periodic treatment of streams with the lampricide 3-triflouromethyl-4-nitrophenol (TFM), which typically kills 95-100% of the larvae present (Smith and Swink 2003). Because larval sea lampreys remain in their natal streams for several years before becoming parasitic juveniles, it is neither necessary nor cost-effective to treat every stream each year. Rather, treatments should be applied on a cycle that matches the duration of the larval phase in a given stream. However, natural variation in recruitment, growth rates, and survival of larval sea lampreys makes it impossible to predict with certainty when each stream will require treatment to prevent the downstream migration of parasitic juveniles. Therefore, each year a group of candidate streams is assessed to determine which streams have the largest populations of transformers relative to their treatment cost and thus should be prioritized for treatment. The current larval assessment methods are costly, yet still produce highly uncertain population estimates (Steeves 2002). The GLFC has a finite budget for sea lamprey management, and resources allocated to assessment diminish those available to implement control strategies. The optimal balance between assessment and control expenditures has yet to be determined, and is the subject of this research.

Trade-offs between competing management actions are common to systems managed under a limited budget. The optimal allocation of resources among two or more valued activities is a common goal of economic modeling (i.e., Hoy et al. 2001, Varian 2003), but has been formally evaluated infrequently in natural resource management (but see Cochrane 1999, Shogren et al. 1999). In the case of sea lamprey control, a trade-off exists between resources allocated to larval assessment, used to determine which streams need to be chemically treated, and those allocated to the actual treatment of those streams. The optimal balance between these two management activities can be determined through testing alternative assessment protocols and monitoring their efficiency and effectiveness on the scale relevant to management. In this research, I have initiated an adaptive management experiment to develop, implement, and evaluate one such alternative assessment method that allocates fewer resources to assessment and more to treatment.

Before 1995, streams were selected for lampricide treatment based on unstandardized measures of larval abundance in streams, length-frequency distributions of larvae derived from non-random sampling, and personal judgments (Slade et al. 2003). In an effort to standardize assessment procedures so that selection criteria could be more objective, a method known as quantitative assessment sampling (QAS) was implemented in 1995 to estimate larval abundances in Great Lakes tributaries. QAS provides data on larval densities, larval size distributions, and available habitat through intensive, standardized, random sampling (Slade et al. 2003). These survey data are used in combination with the Empiric Stream Treatment Ranking (ESTR) model to predict the abundance of transformers in the year following assessment based on assumptions about stream-specific growth rates and models of length-based metamorphic probability (Christie et al. 2003). Streams are then ranked based on the predicted number of transformers relative to the cost of treating the stream. Streams with the highest predicted number of transformers killed per dollar of treatment cost are ranked highest, and streams are treated in rank order until the control budget is exhausted.

Despite the rigorous sampling protocol associated with QAS, it remains an imperfect assessment method. Larval population estimates obtained from QAS survey data and the models used in ESTR to predict transformation rates both introduce uncertainty into stream selection decisions. Recent studies have identified and quantified sources of this uncertainty (Steeves 2002) and drawn attention to assumptions in the assessment and stream ranking process that are often violated (Steeves et al. 2003, Hansen et al. 2003). Hansen et al. (2003) determined that larval growth rates vary substantially among streams as well as among years. This variation introduces uncertainty into larval length predictions generated by existing growth models, and this uncertainty is compounded when these predicted lengths are subsequently used to predict transformation rates. Therefore, Hansen et al. (2003) recommend investigating assessment methods that sample larvae near the end of the growing season to reduce the number of growing days that must be modeled to estimate end-of-year larval lengths. Reducing the reliance of stream selection decisions on growth models by conducting assessments later in the year could improve the accuracy of these decisions. However, given the large number of streams that must be sampled each year, assessment methods would have to be less time- and effort-intensive than current methods to complete all assessment surveys in a shorter period of time (i.e., within 60 days of the end of the growing season). Hansen et al. (2003) also observed high variability in metamorphic rates, and concluded that reliable prediction of metamorphosis is unlikely in the absence of stream- and year-specific models. Since the development of such models would be extremely difficult, they proposed eliminating the use of metamorphosis models altogether, making the stream treatment selection process independent of metamorphic rates. In another review of assessment techniques, Slade et al. (2003) called for the evaluation of alternative methods for estimating larval and transformer abundance that will constitute the "most prudent use of resources available to control sea lampreys." They proposed that assessment could be improved either by making assessment methods more accurate, or by developing a procedure for ranking and selecting streams for treatment that is more robust to the variability inherent in the processes that influence the number of sea lampreys migrating to the Great Lakes.

Any evaluation of alternative assessment techniques will require a consideration of the economics as well as the biology of sea lamprey control. It seems reasonable to assume that an increase in resources allocated to assessment would result in a corresponding increase in the accuracy of larval population estimates and in the certainty of stream selection decisions (Figure 1). Therefore, one option to reduce uncertainty about which streams to treat in a given year is to allocate more money to assessment. The implementation of QAS in 1995 represented an increase in assessment expenses to increase the reliability of stream selection decisions. In 2006, the GLFC allocated $3.1 million to larval assessment, constituting 16% of the total sea lamprey management budget (*Gavin Christie, Great Lakes Fishery Commission, personal communication*). Despite the current high investment in assessment, critical uncertainties in the stream selection process still exist (Hansen et al. 2003, Steeves 2002, Steeves et al. 2003). Further investments in assessment could serve to reduce these uncertainties; however, high levels of variability in larval growth and metamorphic rates could preclude managers from ever being absolutely certain about which streams to treat regardless of the level of assessment expenditures. Additionally, because of the time needed to plan chemical treatments, the set of streams treated in a given year must be chosen the year prior to treatment, and therefore the need to forecast future population structures is an inevitable component of sea lamprey management regardless of the resources spent on assessment. Any increase in assessment costs will result in a corresponding decrease in the resources available to actually treat streams. An alternative management strategy would be to allot minimal resources to assessment, accept a high level of uncertainty surrounding predictions of larval and transformer abundance, but make stream treatment decisions less sensitive to this uncertainty by using the resources saved on assessment to treat additional streams – in effect hedging bets against assessment uncertainty. Presently, the balance between assessment and control expenditures that will maximize the number of transformers killed is unclear; studies that explore alternative strategies of resource allocation are needed to evaluate the current balance and determine whether better strategies could be employed.

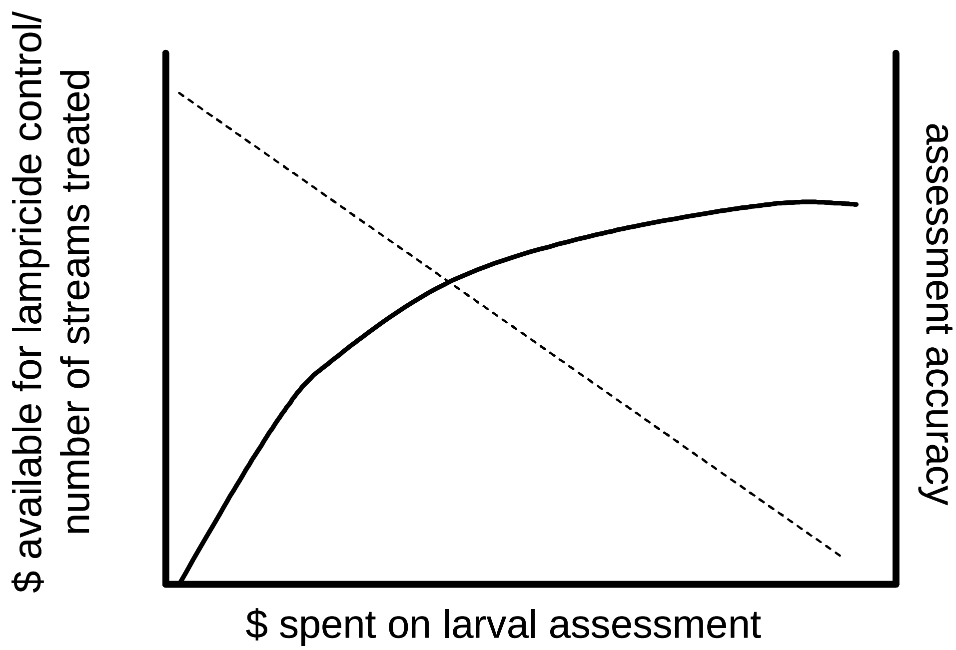

Figure 1. Illustration of the trade-off between expenditures on larval assessment versus lampricide application. As more resources are spent on assessment, fewer resources are available for lampricide control, as illustrated by the dotted line. On the other hand, as assessment expenditures increase, the accuracy of that assessment increases and the streams that are treated are selected with greater confidence, as illustrated by the solid line.

The conflict between resources available for assessment of a system and those available for other management activities is not unique to sea lamprey management.

Commercial fisheries managers expend abundant resources on complex stock assessment techniques and analyses to monitor the status of fisheries and to set future management targets. Cotter et al. (2004) argue that these stock assessment models are often too complicated to be useful, and rely on assumptions that are unjustified by available data. Despite the complexity of these models, critical uncertainties remain in the predictions they generate. Because stock assessments and the data collections that support them also preempt a great deal of effort that could be used to improve management in other ways, Cotter et al. (2004) advocate a shift to a simpler model of stock assessment when making policy recommendations. Cochrane (1999) also argues that activities in a management system should be assessed in terms of their cost-effectiveness, and that doing so could lead to the adoption of simpler but more effective management measures than are currently evolving. Additionally, budgetary constraints restrict resources for assessment for many natural resource managers, making the need for cost-effective assessment methods all the more urgent. Rapid assessment techniques that are less extensive than traditional quantitative sampling methods are effective in other systems and have been advocated as cost-effective means of achieving management goals (e.g., Jones and Stockwell 1995, Pido et al. 1997, Risk et al. 2001). For example, rapid assessment of macroinvertebrate species composition allows managers to detect critical changes in community structure while offering substantial savings in the cost and effort needed to obtain such information compared to traditional more resource-intensive sampling techniques (Metzeling et al. 2003). To effectively determine the usefulness of rapid assessment techniques in sea lamprey management, such techniques must be tested on a scale that is relevant to management decisions. Adaptive management is a tool that lends itself well to this type of experimentation.

The use of adaptive management in natural resource management has been widely advocated and adopted in several natural resource management systems (e.g., Walters and Hilborn 1978, Lee 1993, Cottingham et al. 2001). Adaptive management is based on the premise that the dynamics of managed ecosystems are complex and difficult to predict, and that meaningful understanding of these systems cannot be achieved by dividing systems into simple components that are easily researched using traditional methods of experimentation (Holling 1978, Walters 1986). Rather, adaptive management uses alternative management actions themselves as experimental tools to test hypotheses, decrease uncertainty about managed systems, and optimize management decisions. Alternative management actions are developed as the result of well-defined goals; they are then implemented, continuously monitored and evaluated for success in terms of ecological, economic, and social impacts, and are changed or “adapted” as necessary (Walters 1986).

The goal of sea lamprey management is to reduce the number of parasitic sea lampreys in the Great Lakes to levels that allow the realization of fish community objectives (GLFC 2001, Christie and Goddard 2003). Using current assessment and control methods, suppression of sea lampreys to target levels has yet to be accomplished consistently throughout the Great Lakes (*Gavin Christie, Great Lakes Fishery Commission, personal communication*), indicating that the exploration of alternative methods is warranted. QAS has been implemented basin-wide since 1995, but has never been formally evaluated in terms of its performance relative to other assessment techniques. Additionally, quantifying the impact of management decisions based on QAS on sea lamprey populations in the Great Lakes has proven difficult due to the simultaneous adoption of other large-scale changes in the sea lamprey control program (i.e., a reduction in the amount of lampricide used to treat streams, Brege et al. 2003). Given the high levels of uncertainty associated with QAS in spite of its high resource demand, and given that it is the basis for stream selection decisions that are of utmost importance to sea lamprey management, it seems prudent to investigate the effectiveness of this assessment method relative to that of an alternative method.

The management action of interest in this study is larval assessment of sea lampreys. To reduce uncertainty about the optimal allocation of resources between assessment and control activities, I have developed an alternative larval assessment method called Rapid Assessment (RA) that is less resource-intensive than QAS. I have implemented RA alongside QAS on a basin-wide scale for two years, and monitored the results in the form of the set of streams that would be selected for treatment based on the results of each assessment method and the predicted number of sea lampreys that would be killed if those streams were treated. I assumed that the RA method would be less accurate, but also less costly than QAS. I also assumed that any resources saved in using RA will be used to chemically treat additional streams.

I hypothesized that the use of Rapid Assessment would lead to greater suppression of sea lampreys than the use of QAS. To test this hypothesis, I applied two different "treatments" by conducting both assessment methods on the same set of streams. I estimated the effect of each treatment by comparing the costs (assessment plus control costs) and benefits (estimated number of sea lampreys killed) of each method.

This experiment is not a traditional example of adaptive management, because assessment options rather than control options are being compared. However, because I compared assessment methods that have a minimal effect on the system being observed, I was able to apply both treatments to the same set of streams in each year and directly compare the results. In this chapter, I describe the RA method and its implementation, evaluation, and implications for the sea lamprey control program in an adaptive management context.

Methods

Implementation of Rapid Assessment

Great Lakes tributaries are divided into "biological reaches", which were defined by sea lamprey managers in 1995 to facilitate larval assessment surveys. A reach is a section of stream that is relatively homogenous in terms of larval habitat, larval densities, and control strategies (i.e., above or below a sea lamprey barrier: Slade et al. 2003). Rapid Assessment (RA) and Quantitative Assessment Sampling (QAS) were both conducted on all wadeable Great Lakes reaches scheduled for quantitative assessment in 2005 and 2006, and the streams that would be selected for treatment based on the results of the two methods were compared. In each year of the experiment a small number of wadeable reaches lacked sufficient larval habitat to conduct both assessment methods without re-sampling the same habitat areas, and these streams were excluded from this analysis.

Quantitative Assessment Sampling

Larval Sampling

QAS surveys are conducted between April and October and are intended to provide an estimate of the abundance of larval sea lamprey age-1 and older (Slade et al. 2003). Six access points are randomly selected from all available access points on a reach. Larval habitat is qualitatively classified into three categories based on its suitability for supporting larval sea lampreys, and is measured along four randomly placed transects at each access point. Type-I habitat is considered optimal and consists of a mixture of sand and fine organic matter, Type-II habitat is acceptable but not preferred and primarily consists of sand, and Type-III habitat is uninhabitable and consists of hard packed gravel, bedrock, or other substrates into which larvae cannot burrow (Dustin et al. 1989, Slade et al. 2003). The proportion of each habitat type and the mean stream width measured at the habitat transects, along with the estimated infested length of the stream, are used to generate estimates of the available larval habitat in each stream.

Larval lampreys are collected at each access point by systematic sampling with an ABP-2 backpack electroshocker (University of Wisconsin, Engineering Technical Services, Madison, WI). Sampled plots are either 15 m^2 or 5 m^2, depending on available habitat area. The first habitat encountered of a given type is sampled at an access point, with no consideration given its quality relative to other areas of the same habitat type. Two plots of Type-I habitat are demarcated at each site, and sampled at the standardized rate of 0.67 m^2/min. Two plots of Type-II habitat are measured and sampled at the same rate at half of the access points for a reach.

Stream Treatment Ranking

Population estimates of larvae and transformers are generated from QAS data using the ESTR model (Christie et al. 2003). In the ESTR model, total larval catch for each stream is adjusted to account for the efficiency of the backpack electrofisher (Steeves et al. 2003). Larval density is calculated by dividing this adjusted catch by the total area sampled, and larval abundance is estimated by multiplying the larval density by the estimated habitat area of a reach. The projected size structure of the population at the end of the growing season is forecasted from the size structure of the sea lampreys collected in QAS surveys using estimates of average daily growth rates and the length of the growing season for each reach. The number of larvae that will metamorphose in the following year is estimated from the projected size structure at the end of the growing season and length-based equations describing the probability of metamorphosis (Slade et al. 2003, Christie et al. 2003). The number of metamorphosing sea lampreys predicted to be in a stream is multiplied by an estimate of treatment effectiveness for that stream to yield the predicted number of transformers that would be killed if that stream were treated in the following year (Christie et al. 2003). The cost of treating that stream is then divided by the predicted number of metamorphosing sea lampreys that would be killed, resulting in an estimate of cost per transformer killed. Streams are ranked according to this cost per kill estimate, with streams the lowest cost per kill estimate given the highest priority for treatment. Streams are then selected for treatment in order of treatment priority until the control budget is exhausted.

Rapid Assessment Sampling

Larval Sampling

RA surveys were conducted to provide an index of larval abundance for each stream to be used for comparisons among streams, not to provide actual larval population estimates. All RA surveys were conducted after August 15th. RA surveys were conducted at reference stations subjectively determined by the managing agents to be representative of the reach as a whole. The number of reference stations sampled in a reach was proportional to the weighted area of larval habitat in that reach. Weighted larval habitat area (A) was calculated using the equation:

$$A = L*W*(P_{T1}+\omega*P_{T2}) \qquad (1)$$

where L is the infested length of the reach, W is the average width of the reach, P_{T1} is the proportion of Type-I habitat, P_{T2} is the proportion of Type-II habitat, and ω is the lake-specific estimate of the ratio of larval density in Type-II to that in Type-I habitats. All estimates of reach-specific characteristics were based on QAS survey data collected from 1995 to 2004. Lake-specific density ratios were calculated from larval densities in Type-I and Type-II habitats collected in surveys during 1997-2004 and averaged across all reaches for a given lake (M. Jones, Michigan State University, East Lansing, MI, unpublished data). Reaches with less than 50,000 m^2 of weighted larval habitat were sampled at 2 reference stations, reaches with 50,000-200,000 m^2 of weighted larval habitat were sampled at 3 reference stations, and reaches with $\geq$200,000 m^2 of weighted larval habitat were sampled at 4 reference stations. Care was taken to avoid re-sampling areas that had already been surveyed using QAS. If a QAS survey at the same access point was also conducted after August 15th, both surveys were performed on the same day in different sampling plots adjacent to the same access point. If QAS had been conducted before August 15th, the sampled areas were marked by flagging tape and by recording the latitude and longitude coordinates, and these previously sampled areas were avoided when collecting RA samples.

RA surveys were conducted using an ABP-2 backpack electroshocker. Reference stations were sampled by a two-person crew; one crew member sampled upstream and the other downstream of the access point. Both crew members sampled for 15 min of shocker time at a rate of 1 m^2/min, resulting in a total of 30 m^2 of habitat sampled per reference station. The area sampled was not measured; rather, operators visually estimated area sampled based on estimated electrofishing rates and time spent shocking. The highest quality larval habitat available at each access site was sampled. All larvae observed while shocking were captured and identified to genus. Identification and measurement of larvae was carried out according to the protocol of the management agency conducting the assessment. Some larvae were anesthetized in the field using MS222 and measured immediately to the nearest 1 mm. Others were preserved in 10% formalin solution and measured $\geq$ 72 hours later. If larvae were measured in the field, live lengths (LL) were converted to preserved lengths (PL) using the equation

$$PL = (LL + 1.634)/1.602 \tag{2}$$

(*Michael Fodale, United States Fish and Wildlife Service, Marquette, MI, personal communication*).

Stream Treatment Ranking

Stream-specific estimates of larval growth rates and growing season length from the ESTR database were used to estimate the length that each larva collected in RA surveys would have attained by the end of the growing season. The total number of larvae projected to be $\geq$ 100 mm in length by the end of the growing season was summed for each reach. This number was divided by the area sampled to calculate an index of population density for the reach, and was then multiplied by the weighted habitat area of the reach to yield an index of abundance of larvae $\geq$100 mm. Weighted habitat area used for calculating the RA indices of abundance were calculated using equation 1; however, in the calculations of the indices of abundance a stream-specific estimate of ω was used if two or more estimates of densities in TI and TII habitats were available from the ESTR database. If fewer than two estimates of habitat-specific densities were available, the lake-specific estimate of ω was used. Indices of abundance for individual reaches were summed to arrive at a single index for each "treatment unit"; these units are composed of one or more reaches in a stream and are predetermined by managers to facilitate treatment decisions. The cost of treating a unit was divided by its index of abundance to give a cost/kill ratio for larvae $\geq$100 mm. Streams were prioritized for treatment based on this cost/kill ratio, where the unit with the lowest cost/kill was given the highest treatment priority.

Stream Treatment Selection

In each year of the study, I compared the two assessment methods by developing two lists of streams: one in which streams were ranked in order of treatment priority based on QAS survey data, and a second based on RA survey data. Only streams that were surveyed using both RA and QAS methods were included in this analysis. Streams that were selected for treatment on the basis of other criteria[1] were not included in the comparison. I then determined which streams would be treated based on the lists of treatment priority generated from the results of each assessment method and the budget available for control given the cost of conducting each assessment method.

[1] Each year, some streams are ranked for treatment based on criteria other than QAS, such as deep-water survey techniques, the expert opinion of managers, and survey data from past years. These streams were excluded from my comparison

The monetary unit for sea lamprey control is the staff day. To compare the streams that would be treated based on each method given an equal overall budget (i.e., assessment and control costs), I assumed that any resource savings gained from using RA would be applied directly to the chemical control budget, and would therefore allow for the treatment of additional streams. Sea lamprey assessment managers estimate that an average of 14 staff days are required to survey a reach using QAS, and an average of 4.3 staff days are required to survey a reach using RA (*Jeffrey Slade, United States Fish and Wildlife Service, Ludington, MI, personal communication*). These average staff day estimates were multiplied by the number of reaches surveyed in a given year to estimate the cost in staff days of conducting assessment basin-wide using each method. The difference between these two staff day requirements served as the estimate of the assessment staff days saved through the use of RA. The cost of an assessment staff day does not equal the cost of a treatment staff day, and treatment staff days are the monetary unit used in the selection of streams for treatment (*Gavin Christie, Great Lakes Fishery Commission, Ann Arbor, MI, personal communication*). Therefore, after calculating the number of assessment staff days saved through the use of RA, this staff day estimate was converted to treatment staff days using the cost of deploying a person to the field to do each type of work. The additional treatment staff days available through the use of RA were added to the number of staff days budgeted for the treatment of streams assessed by QAS to determine which streams could be treated if the RA method were employed. Because of concerns raised by sea lamprey managers regarding whether or not assessment savings generated from the use of RA would actually translate into additional resources to be used for treatment, comparisons were also made assuming that the RA savings would not be used to treat additional streams, and that an equal number of treatment staff days would be available to treat streams regardless of which assessment method was used.

Evaluation of Rapid Assessment

Comparison of rank lists

I used several methods to compare the two lists. The correlation of the RA and QAS ranks was calculated using Spearman's rank correlation for all surveyed streams, as well as for the subset of streams that would rank for treatment based on the RA results. Population estimates of transformers and larvae predicted by the ESTR model were summed for all streams that would be treated based on the QAS method and for all streams that would be treated based on the RA method. The RA population estimates were calculated both with and without the additional treatment staff days allocated for treatment based on savings from the RA surveys. The ratios of estimated transformers and larvae that would be killed in RA streams to those that would be killed in QAS streams were calculated to give an index of the performance of RA relative to QAS. The total labor costs (assessment + control) that would be incurred by treating each set of streams and the ratios of RA to QAS labor costs were also calculated. Assessment staff days were converted to treatment staff days when calculating total labor costs.

Capture-Recapture

Capture-recapture studies were conducted in 2006 on streams ranked for treatment in 2005 as an independent means of comparing the number of sea lampreys that would be killed as a result of making treatment decisions based on the two different assessment methods. Under ideal circumstances, population estimates of the number of sea lampreys present in a stream at the time of treatment would be obtained from capture-recapture studies on all streams that would have been selected based on one method but not the other; the sea lamprey populations in streams treated based on both lists are irrelevant to this comparison because they would have been treated regardless of which method had been used. However, some streams were not selected for capture-recapture despite ranking for treatment based on only one assessment method because agency personnel did not believe it was feasible to conduct a successful capture-recapture experiment, or because managers elected not to treat the stream in the year following assessment for practical reasons.

Metamorphosing sea lampreys do not reliably show physical characteristics of transformation until late July to early August of the year they begin to metamorphose (Manion and Stouffer 1970, Youson and Potter 1979). Due to the high number of streams requiring treatment and practical constraints of management agencies, some streams were chemically treated before the time when physical signs of metamorphosis were visible. Therefore, it was not possible to accurately determine the number of metamorphosing sea lampreys killed as a result of these treatments. In the absence of information on metamorphosing sea lampreys, comparisons were made of the number of larvae with a 50% or greater probability of metamorphosing based on their total length as determined by the ESTR model. For the upper lakes (Superior, Huron, and Michigan), larvae that were 144 mm had a 50% chance of metamorphosing, and for the lower lakes (Erie and Ontario) larvae that were 131 mm had a 50% chance of metamorphosing. The number of larvae that were greater than or equal to these size cutoffs was used as a surrogate for the number of metamorphosing sea lampreys in streams that were treated prior to July 15^{th}.

The ESTR model larval population estimates were used to develop targets of the number of larvae to mark and to collect during treatments in each stream. The target number of sea lampreys to mark and recapture was estimated using the appropriate nomograph for the desired precision of the population estimate from Figure 6 in Robson and Regier (1964). The +/- 10% level of accuracy was targeted when possible, although the +/-25% level of precision was considered acceptable if the effort needed to capture a sufficient number of sea lampreys to achieve the +/-10% accuracy level was prohibitively high.

The predetermined number of larval sea lampreys targeted for marking were collected using an ABP-2 backpack electroshocker, anesthetized using MS-222, measured (+/- 1 mm), marked by removing a portion of non-vascular tissue at the end of the caudal fin, and revived in an aerated cooler. Most samples were kept overnight to observe any post-marking mortality. Upon revival, marked larvae were released throughout the available habitat of the stream. Larvae used for marking were collected from the stream of interest whenever possible; however, low larval densities and poor collecting conditions in some streams necessitated collecting and marking animals from nearby source streams and importing them into the study stream. Streams were divided into sections of approximately equal length to facilitate the distribution of marking and recapture effort. When sea lampreys from outside streams were marked and imported, the projected size structure of the target stream based on ESTR estimates was matched, and marked larvae were distributed randomly throughout each stream section in proportion to its area. When larvae were collected and marked from within the source stream, they were released in proportion to the abundance of larvae captured in each stream section. Marking was completed two weeks or more in advance of anticipated lampricide treatment date to allow marked animals to redistribute evenly throughout the population.

The recapture event took place within 24 hours of lampricide treatment. During this time period, as many larval and metamorphosed lampreys as possible were collected by stationary fyke nets and by actively hand dipping with scap nets. Collection efforts were distributed throughout the infested area of the stream. All collected larvae were preserved in 10% formalin solution. Preserved lampreys were identified to genus, examined for marks, measured (+/- 1 mm), classified to the appropriate life stage (i.e. ammocete, transformer stage 1, transformer stage 2, etc: following Youson and Potter 1979) and counted.

The total sea lamprey population ($\hat{N}$) of a stream was calculated using the Chapman modification of the Petersen estimator (Seber 1982):

$$\hat{N} = \frac{(M+1)*(C+1)}{(R+1)} - 1 \tag{3}$$

where M=number of individuals marked, C= total number of individuals in treatment collection, and R=number of recaptured individuals in the treatment collection. The variance was estimated as:

$$V(\hat{N}) = \frac{(M+1)^2 * (C+1) * (C-R)}{(R+1)^2 * (R+2)} \quad . \tag{4}$$

In streams that were treated after July 15^{th}, the number of metamorphosed sea lampreys in each population was estimated as:

$$\hat{N}_T = \hat{N} * \frac{C_T}{C} \qquad (5)$$

where $\hat{N}_T$ = the estimated number of metamorphosed sea lampreys, $\hat{N}$ = the Petersen population estimate, C_T=the number of sea lampreys in the treatment collection exhibiting external signs of metamorphosis, and C= the total number of individuals in the treatment collection. Similarly, for streams in which the treatment occurred prior to July 15th, the number of sea lampreys over the size at which 50% or more would be expected to metamorphose (large larvae) was calculated as:

$$\hat{N}_{LL} = \hat{N} * \frac{C_{LL}}{C} \qquad (6)$$

where $\hat{N}_{LL}$ = the estimated number of large sea lampreys, $\hat{N}$ = the Petersen population estimate, C_{LL}=the number of sea lampreys in the treatment collection larger than the designated size, and C= the total number of individuals in the treatment collection. The variance of the estimators of population proportions was calculated as:

$$V(\hat{N}_x) = (\hat{N})^2 * V(\frac{C_x}{C}) + V(\hat{N}) * (\frac{C_x}{C})^2 \qquad (7)$$

where $V(\hat{N}_x)$ = the variance of the proportion of interest, either T or LL as appropriate; $\hat{N}$ = the Petersen population estimate; V($\hat{N}$)=the variance of the Petersen population estimate; $V(\frac{C_x}{C}) = \frac{\frac{C_x}{C} * (1 - \frac{C_x}{C})}{C}$, the variance of the proportion of interest based on the binomial distribution; C_x=the number of transformers (T) or large larvae (LL) in the treatment collection as appropriate; and C= the total number of individuals in the treatment collection. Confidence intervals for the estimates were calculated using the normal approximation:

$$(\hat{N}_x) \pm 1.96 * \sqrt{V(\hat{N}_x)} \tag{8}$$

I assumed that the capture-recapture estimate provided an unbiased population estimate at the time of treatment. The total number of sea lampreys, transformers, and large larvae estimated from the capture-recapture studies was summed for the streams that were treated based on RA only and for the streams that were treated based on QAS only. The variances of these population estimates were also summed, and 95% confidence intervals were calculated for the total populations present in each set of streams.

Results

Rank Lists and Streams Selected for Treatment

In 2005, 104 reaches in 56 streams were surveyed using both QAS and RA. Based on the average number of staff days required to conduct each type of assessment method, 1456 staff days were required to conduct QAS and 447 staff days were required to conduct RA on these reaches. Therefore, the use of RA resulted in a savings of 1009 assessment staff days. To convert these assessment staff day savings into staff days to be used to treat additional streams, a conversion factor of 1.00 assessment staff day per 0.65 treatment staff days was used based on the different costs of each activity (*Gavin Christie, Great Lakes Fishery Commission, Ann Arbor, MI, personal communication*). This conversion resulted in an estimated 656 additional treatment staff days that would be available to treat additional streams if the RA method were used for assessment. In 2006, 68 reaches in 46 streams were surveyed using both QAS and RA, with a cost of 952 assessment staff days to conduct QAS and 292 staff days to conduct RA. The use of RA resulted in a savings of 660 assessment staff days, or 429 treatment staff days to be used to treat additional streams.

The 16 top-ranked streams from the QAS treatment rank list were selected for treatment in 2005 using the baseline level of treatment effort of 1409 treatment staff days (Table 1). This baseline level of treatment effort reflects only the number of staff days needed to treat streams that ranked for treatment on the basis of QAS surveys; the actual treatment budget is much higher than 1409 treatment staff days, but includes the cost of treating streams that ranked based on assessment methods other than QAS. Given the same 1409 treatment staff days plus the 656 additional staff days available from the use of RA, 24 streams would be selected for treatment based on the RA rankings (Table 1). Of these 24 streams, 11 would be treated regardless of which assessment method was used. Thirteen streams would be treated only based on the RA method, and three streams would be treated only based on the QAS method (Table 2).

Table 1. Streams that would be selected for treatment based on either assessment method in 2005, the rank of treatment priority based on RA and QAS, whether or not the stream would be selected for treatment based on the different assessment methods, and the ESTR model population estimates for larvae (N_L) and transformers (N_T). Streams are placed in order of RA ranking and only streams that would be selected for treatment based on at least one method are listed.

			Treated				
Stream Name	**RA Rank**	**QAS Rank**	**QAS**	**RA (extra staff days)**	**RA (equal staff days)**	N_L	N_T
Garden River (entire)	1	11	X	X	X	641,883	1,281
Oshawa Creek (entire)	2	1	X	X	X	47,339	19,791
Millecoquins River (Furlong)	3	2	X	X	X	31,236	1,949
Cloud River (entire)	4	4	X	X	X	17,908	1,840
Chocolay River (entire)	5	6	X	X	X	407,574	1,933
Mindemoya River (entire)	6	10	X	X	X	31,215	280
Au Train River (upper)	7	13	X	X	X	58,059	737
Traverse River (entire)	8	18		X	X	137,697	491
Sucker River (entire)	9	14	X	X	X	40,167	1,463
Pere Marquette River (no Middle)	10	12	X	X	X	145,960	3,860
Betsie River (below barrier)	11	34		X	X	157,020	234
Carp River (entire)	12	9	X	X	X	23,265	403
Boyne River (mainstream)	13	45		X	X	114,767	59
Kaministiquia (entire)	14	20		X	X	748,191	1,671
Trail Creek (entire)	15	17		X	X	5,084	986
Platte River (middle)	16	27		X	X	50,281	158
Jordan River (entire)	17	26		X		139,858	665
Red Cliff Creek (entire)	18	30		X	X	2,205	43
Crow River (entire)	19	5	X	X		23,782	695
Whitefish River (entire)	20	16	X	X		218,965	2,479
Beaver Lake Creek (Lowney)	21	39		X		3,982	19
Trent River (Mayhew Creek)	22	3	X	X		27,796	910
Saginaw R. (Big Salt, Bluff, Home)	23	21		X		58,153	1,254
Lindsey Creek (entire)	26	19		X		7,306	323
Lincoln River (entire)	27	15	X			13,431	1,086
Little Munuscong River (entire)	32	8	X			49,137	1,018
Big Munuscong River (Taylor)	55	7	X			14,583	514

Table 2. Streams that would be treated based on the results of one assessment method but not the other in 2005 given the allocation of 659 additional staff days for treating streams ranked by RA. The top panel shows the streams that would rank for treatment based on RA, not QAS, and the bottom panel shows the streams that would rank for treatment based onQAS, not RA. The ESTR population estimate of transformers and larvae are shown for each stream, along with the sum of the number of transformers and larvae present in each set of streams.

RA only

QAS rank	RA rank	Name	ESTR Transformer estimate	ESTR larval estimate
18	8	Traverse River	491	137,697
34	11	Betsie River	234	157,020
45	13	Boyne River	59	114,767
20	14	Kaministiquia	1,671	748,191
17	15	Trail Creek	986	5,084
27	16	Platte River (middle)	158	50,281
26	17	Jordan River	665	139,858
30	18	Red Cliff Creek	43	2,205
39	21	Beaver Lake Ck	19	3,982
21	23	Saginaw River (Big Salt, Bluff, & Home Drain)	1,254	58,153
19	26	Lindsey Creek	323	7,306
		TOTALS	**5,902**	**1,424,543**

QAS only

QAS rank	RA rank	Name	ESTR Transformer estimate	ESTR larval estimate
7	55	Big Munuscong River (Taylor Ck)	514	14,583
8	32	Little Munuscong River	1,018	49,137
15	27	Lincoln River	1,086	13,431
		TOTALS	**2,619**	**77,152**

In 2006, the 21 top-ranked streams from the QAS treatment rank list were selected for treatment using the baseline treatment effort level of 1735 treatment staff days (Table 3). Again, this effort level reflects the cost of treating only the streams that were ranked based on current QAS transformer estimates; streams ranked through other methods were excluded from the calculation of treatment costs. Given the same 1735 treatment staff days plus the additional 429 additional staff days available through the use of RA, 29 streams would be selected for treatment based on the RA rankings (Table 3). Of these 29 streams, 19 would be treated based on the QAS results as well. Ten streams would only be selected for treatment based on RA results, and two streams would be selected for treatment only based on QAS results (Table 4).

Table 3. Streams that would be selected for treatment based on either assessment method in 2006, the rank of treatment priority based on RA and QAS, whether or not the stream would be selected for treatment based on the different assessment methods, and the ESTR model population estimates for larvae (N_L) and transformers (N_T). Streams are placed in order of RA ranking, and only streams that would be selected for treatment based on at least one method are listed.

			Treated				
Stream Name	**RA Rank**	**QAS Rank**	**QAS**	**RA (extra staff days)**	**RA (equal staff days)**	**N_L**	**N_T**
Bighead River (entire)	1	1	X	X	X	1,705,376	80,899
Bad River (fall-sturgeon)	2	3	X	X	X	1,795,270	18,713
Poplar River (entire)	3	23		X	X	56,502	228
Platte River (entire)	4	10	X	X	X	1,210,067	4,157
Fishdam River (entire)	5	34		X	X	26,352	26
Coldwater Creek (entire)	6	12	X	X	X	92,139	567
Augres River (entire)	7	11	X	X	X	272,453	3,015
Sturgeon River (entire)	8	7	X	X	X	12,602	4,933
White River (main and N. Branch)	9	6	X	X	X	30,642	10,611
Galloway Creek (entire)	10	41		X	X	226	1
Middle River (barrier down)	11	8	X	X	X	28,694	782
McKay Creek (entire)	12	4	X	X	X	24,522	2,943
Cypress (entire)	13	14	X	X	X	40,029	434
Cheboygan River (Maple)	14	17	X	X	X	46,112	637
Good Harbor Creek (main)	15	31		X	X	38,351	38
Wolf River	16	29		X	X	24,210	92
Long Lake Creek (lower)	17	5	X	X	X	30,571	1,286
Kalamazoo River (Mann)	18	19	X	X	X	1,387	93
Cheboygan River (Pigeon)	19	15	X	X	X	90,341	2,092
Martineau Creek (entire)	20	16	X	X	X	1,684	166
Neebing-McIntyre Floodway	21	28		X	X	28,269	148
Au Sable River (lower)	22	39		X		146,110	27
Boyne River (main)	23	32		X	X	274	25
Saginaw River (Carroll Creek)	24	24		X	X	621	141
Cedar River (main)	25	21	X	X		261,516	1,308
Swan River (entire)	26	20	X	X	X	148,364	601
Pentwater River (North, Cedar, Crystal)	27	2	X	X		77,418	8,491
Rouge River (entire)	28	25		X		334	154
Grand River (Norris, Rhymer, Sullivan)	30	9	X	X		1,195	744
Grand River (Sand)	41	18	X			1,279	521
Bark River (entire)	46	13	X			85,694	718

Table 4. Streams that would be treated based on the results of one assessment method but not the other in 2006 given the allocation of 416 additional treatment staff days for treating streams ranked by RA. The top panel shows the streams that would rank for treatment based on RA only, and the bottom panel shows the streams that would rank for treatment based on QAS only. The ESTR population estimate of transformers and larvae are shown for each stream, along with the sum of the number of transformers and larvae present in each set of streams.

RA not QAS

RA rank	QAS rank	Name	ESTR Transformer estimate	ESTR larval estimate
3	23	Poplar River (entire)	228	56,502
5	34	Fishdam River (entire)	26	26,352
10	41	Galloway Creek (entire)	148	28,269
15	31	Good Harbor Creek (main)	1	226
16	29	Wolf River	38	38,351
21	28	Neebing-McIntyre Floodway	92	24,210
22	39	Au Sable River (lower)	27	146,110
23	32	Boyne River (main)	25	274
24	24	Saginaw River (Carroll Creek)	141	621
28	25	Rouge River (entire)	154	334
		TOTALS	**878**	**321,248**

QAS not RA

RA rank	QAS rank	Name	ESTR Transformer estimate	ESTR larval estimate
41	18	Grand River (Sand)	521	1,279
46	13	Bark River (entire)	718	85,694
		TOTALS	**1,239**	**86,974**

For each year of the comparison, I also considered the treatment scenario with an equal number of treatment staff days budgeted to treat streams ranked by either method. Under this equal treatment staff day scenario, in 2005, 17 streams would be treated based on the RA rankings (Table 1). Ten of these 17 streams would be treated regardless of which assessment method was used. Seven streams would be treated only based on the RA results, and an additional six streams would be treated based on the QAS results only. In 2006, 24 streams would be treated based on the RA rankings, 16 of which would be treated regardless of which assessment method was used (Table 3). Eight streams would be treated based only on RA, and five streams would be treated based only on QAS.

The RA and QAS rankings of the full set of 56 streams surveyed in 2005 were significantly correlated (Spearman's rank correlation = 0.67, $p<0.001$, Figure 2). The RA and QAS ranks of the subset of 24 streams that would be treated based on the RA results with the allocation of 659 additional staff days in 2005 were also significantly correlated, although the correlation was not as strong (Spearman's rank correlation = 0.50, $p<0.02$, Figure 3).

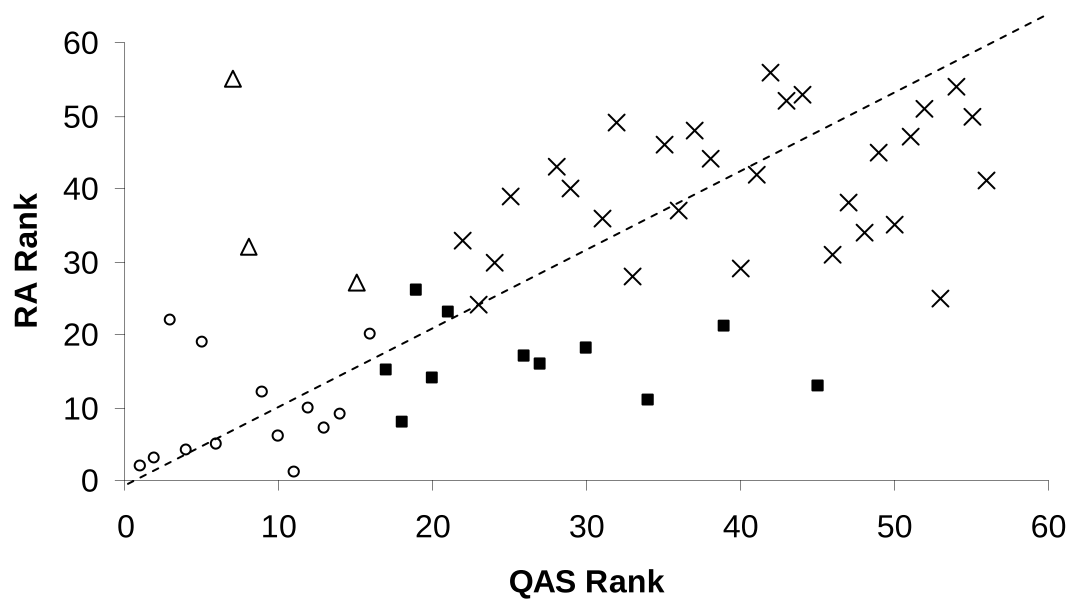

Figure 2. Correlation between QAS and RA rank for the 56 streams surveyed with both methods in 2005. Stream rankings were significantly correlated (Spearman's rank correlation = 0.67, $p<0.001$). Open circles represent streams treated based on both methods, dark squares represent streams treated based on the RA ranking only, open triangles represent streams treated based on the QAS list only, and X's represent streams not treated based on either method. The dashed line indicates perfect (1:1) correlation.

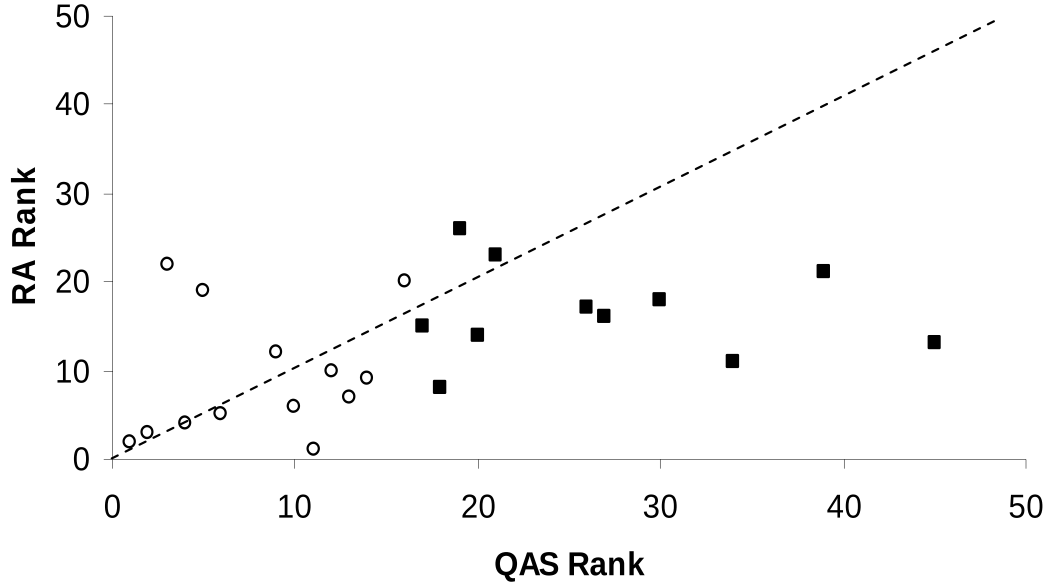

Figure 3. Correlation between QAS and RA rank for the 24 streams that ranked for treatment based on RA results in 2005 with additional staff days allocated to treat RA streams. Stream rankings were significantly correlated (Spearman's rank correlation = 0.50, p = 0.02). Open circles represent streams treated based on both methods, and dark squares represent streams treated based on the RA ranking only. The dashed line indicates perfect (1:1) correlation.

The RA and QAS rankings of the full set of 46 streams surveyed in 2006 were also significantly correlated (Spearman's rank correlation = 0.56, $p<0.001$, Figure 4). The rankings of the subset of 29 streams that would be treated based on RA given additional staff days for treatment were not significantly correlated (Spearman's rank correlation = 0.29, $p=0.13$) although the 24 streams that would be treated based on RA given equal staff days for treatment were significantly correlated (Spearman's rank correlation = 0.44, $p = 0.03$, Figure 5).

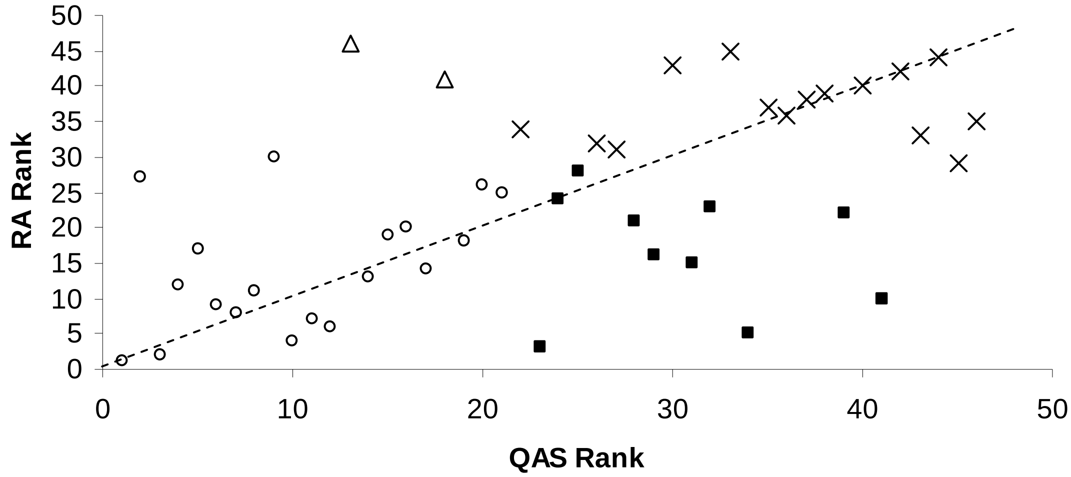

Figure 4. Correlation between QAS and RA rank for the 46 streams surveyed with both methods in 2006. Stream rankings were significantly correlated (Spearman's rank correlation = 0.56, $p<0.001$). Open circles represent streams treated based on both methods, dark squares represent streams treated based on the RA ranking only, open triangles represent streams treated based on the QAS list only, and X's represent streams not treated based on either method. The dashed line indicates perfect (1:1) correlation.

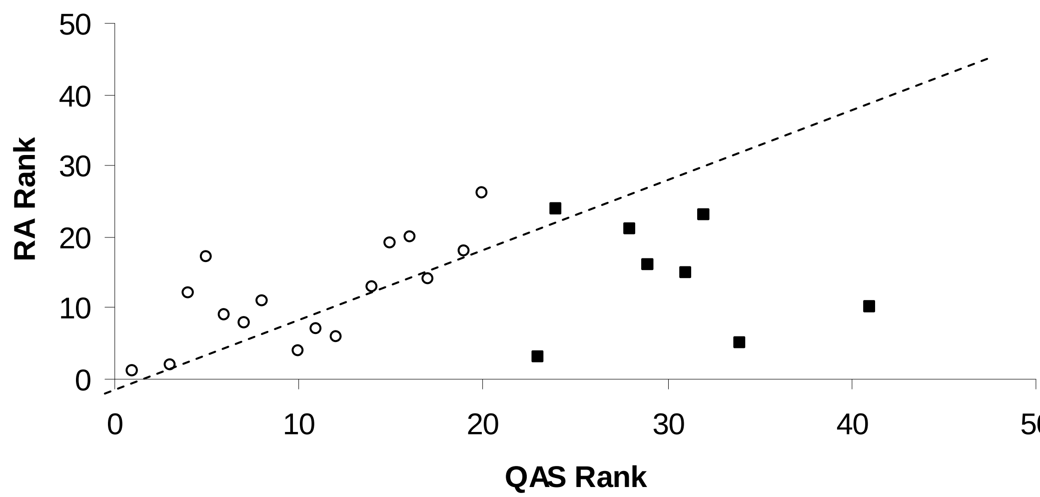

Figure 5. Correlation between QAS and RA rank for the 24 streams that ranked for treatment based on RA results in 2006 with equal staff days allocated for treatment of RA streams. Stream rankings were significantly correlated (Spearman's rank correlation = 0.44, $p = 0.03$). Open circles represent streams treated based on both methods, and dark squares represent streams treated based on the RA ranking only. The dashed line indicates perfect (1:1) correlation.

Comparison of ESTR Population Estimates

If the staff days saved by using RA were used to treat additional streams, the total labor costs (assessment + control costs) of using each method would be equal. Under this scenario, based on the ESTR model single-year population forecasts, in 2005 the use of RA would allow for 1.1 times as many transformers and 1.8 times as many larvae to be killed as compared to the QAS method (Figure 6). In 2006, under equal labor costs, the RA method would allow for the same amount of transformers and 4% more larvae to be killed as compared to the QAS method according to ESTR model predictions (Figure 6).

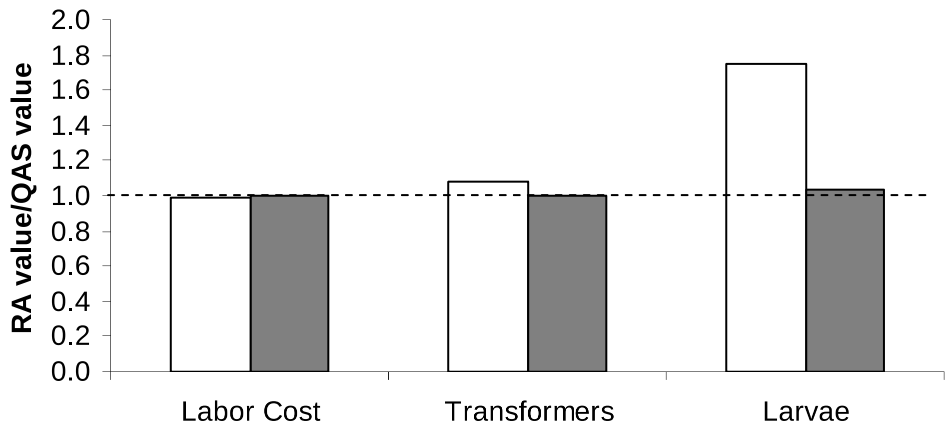

Figure 6. The ratio of RA values to QAS values for labor cost (assessment + control costs), total estimated number of transformers killed, and total estimated number of larvae killed when additional treatment staff days are allocated to treat streams ranked by RA. Light bars represent 2005 values, and dark bars represent 2006 values. Total transformer and larvae estimates were the sum of the population estimates generated by the ESTR model for all the streams that would be treated based on the results of each assessment method. Dashed line indicates where the RA and QAS values are equal; above this line, RA values are higher, below this line QAS values are higher.

If the staff days saved by using RA were not used to treat additional streams, the labor cost (assessment + control cost) of using RA would be approximately 30% less than that of using QAS in 2005. Under this scenario, based on the ESTR model single-year population forecasts, the use of RA would allow for 0.9 times as many transformers and 1.5 times as many larvae to be killed as compared to the QAS method (Figure 7). In 2006, if the staff day savings generated by RA were not used to treat more streams, the labor cost of assessment and treatment of RA would be approximately 20% less than that of QAS, resulting in 0.9 times as many transformers and approximately the same number of larvae killed as compared to the QAS method (Figure 7).

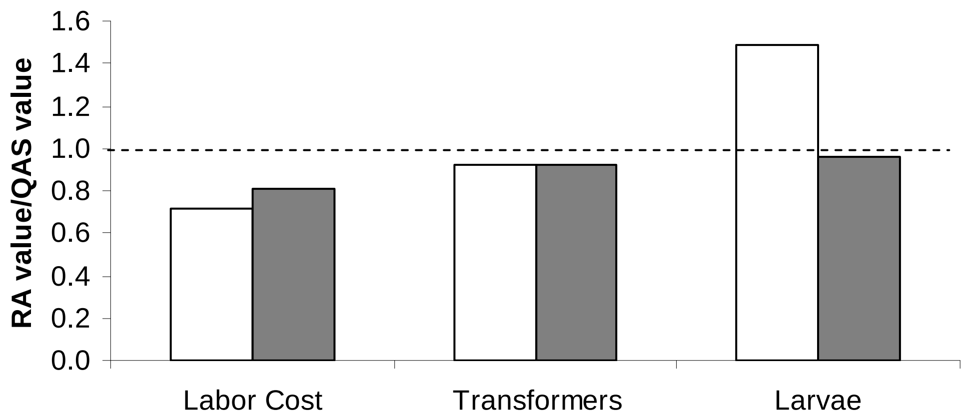

Figure 7. The ratio of RA values to QAS values for labor cost (assessment + control costs), total estimated number of transformers killed, and total estimated number of larvae killed when equal numbers of treatment staff days are allocated to treat streams ranked by RA and QAS. Light bars represent 2005 values, and dark bars represent 2006 values. Total transformer and larvae estimates were the sum of the population estimates generated by the ESTR model for the streams that would be treated based on the results of each assessment method. Dashed line indicates where the RA and QAS values are equal; above this line, RA values are higher, below this line QAS values are higher.

Capture-Recapture

Streams were selected for capture-recapture from the set of streams that ranked on the basis of one method of assessment, but not the other in 2005 (Table 2) to compare the difference in the number of sea lampreys that would be killed as a result of making treatment decisions based on RA or QAS. Because of logistical constraints preventing capture-recaptures on all of these streams, a subset of streams was chosen (Table 5). Three streams were chosen from the 11 that would rank for treatment based only on RA, given additional staff days for treatment, (RA streams), and 3 streams were chosen that would rank for treatment based only on QAS (QAS streams). The accuracy of the capture-recapture results for two streams (the Little Munuscong and the Big Munuscong) are suspect because neither the release of marked animals nor the recapture effort was distributed randomly throughout the stream, and the population estimates from these streams should be treated as a minimum estimate rather than an unbiased population estimate.

Table 5. Capture-recapture estimates of sea lamprey abundance (all life stages) for the 6 study streams. M is the number marked, C is the number collected in the recapture event, R is the number of recaptures, and N is the Petersen population estimate. (95% Confidence intervals on N are shown for each stream, and ESTR N represents the initial population estimate of all life stages of sea lampreys generated by the ESTR model from QAS data.

					95% CI		**ESTR**
RA streams	**M**	**C**	**R**	**N**	**Lower**	**Upper**	**estimate**
Boyne River	2,012	5,321	107	99,195	80,763	117,628	114,826
Trail Creek	888	1,394	23	59,821	36,546	83,097	6,070
Betsie River	2,892	5,439	34	449,654	303,240	596,068	157,254
QAS streams							
Lincoln River	1,458	1,730	30	81,468	53,494	109,441	14,517
Little Munuscong*	2,517	1,649	328	12,627	11,408	13,846	32,280
Big Munuscong*	1,488	299	125	3,544	3,075	4,014	15,097

*Streams for which population estimates are suspect due to non-random release and recapture of larvae

The initial ESTR model population estimate of the total stream population falls within the 95% confidence intervals of the capture-recapture population estimate in only one of the six streams (Table 5). The ESTR model population estimate for transformers or large larvae does not fall within the 95% confidence intervals of the capture-recapture population estimate for any of the six streams (Table 6). The summed capture-recapture population estimates show that when RA savings are used to treat additional streams, the

RA streams contain more sea lampreys and more large larvae/transformers than the QAS streams (Figure 8).

Table 6. Capture-recapture estimates for either transformers (T) or large larvae (larvae > 144 mm, LL) for the 6 streams on which capture-recapture was conducted in 2006. Transformer estimates were only generated for streams treated after July 15th, otherwise large larvae estimates were used. ESTR estimates are of transformer abundance if transformers were estimated in the capture-recapture study, otherwise the ESTR estimate is of large larvae abundance as predicted by the ESTR model.

RA streams	**Treatment Date**	**Life-stage**	**Proportion of N as T or LL**	**N_T or N_{LL}**	**95% CI lower**	**95% CI upper**	**ESTR estimate**
Boyne River	May 23, 2006	LL	0.002	224	91	357	0
Trail Creek	July 29-Aug 2, 2006	T	0.081	4,818	2,782	6,854	986
Betsie River	Sept 8, 2006	T	0.014	6,283	3,803	8,764	234
QAS streams							
Lincoln River	July 5-6, 2006	LL	0.010	801	333	1,268	1,519
Little Munuscong*	June 28-29, 2006	LL	0.050	636	489	782	396
Big Munuscong*	June 27-28, 2006	LL	0.067	237	132	342	448

Streams for which the population estimates are suspect due to non-random release and recapture of larvae

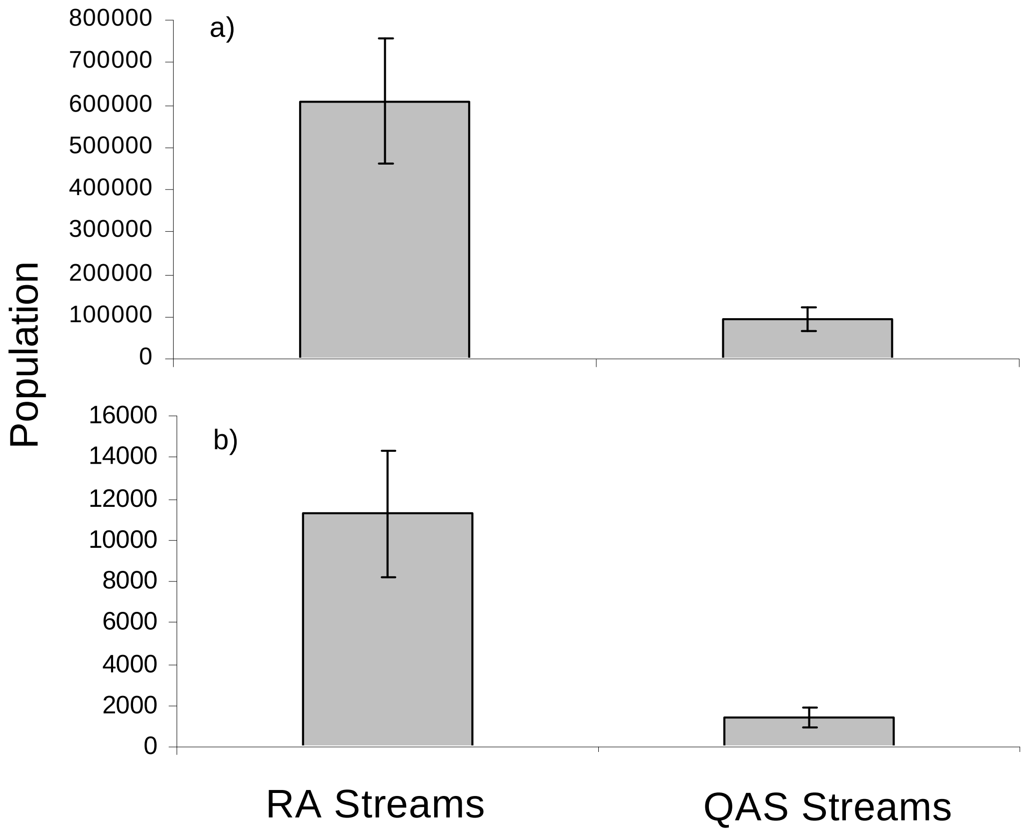

Figure 8. The sum and 95% confidence intervals of the capture-recapture population estimates for a) the total (larval + transformer) population estimates, and b) the large larvae/transformer population estimates for the streams that ranked on the basis of RA only (RA streams) and QAS only (QAS Streams) with additional treatment staff days allocated for the treatment of RA streams. The total RA population estimates include the populations of 3 RA streams out of the 11 that ranked based on this method and not based on QAS, and the total QAS population estimates include the populations of all 3 QAS streams that ranked based on this method and not based on RA. Confidence intervals are calculated from the summed variance estimates of the three streams used in each category. Population estimates in two of the three QAS streams are potentially underestimated due to non-random release of marked animals and non-random recapture events (see text for further explanation).

Discussion

The acquisition of knowledge to inform decision-makers about the optimal course of action is a common goal of scientific inquiry. Often it is assumed that the more knowledge acquired, the better the decisions will be. However, in situations of limited resources, that increased knowledge can come at the expense of the ability to carry out the very actions the increased knowledge was intended to inform. When resources are limited, it is important to analyze the trade-off between resources used to assess a system and resources used to carry out management actions. In the case of sea lamprey control, streams are chemically treated to kill larval sea lampreys to achieve management goals. Assessment is needed to inform managers which streams, if treated, would provide the greatest benefit to the lamprey program in terms of sea lampreys killed. Finding the optimal balance between resources spent on this assessment and resources reserved for treating streams requires testing alternative frameworks of resource allocation and monitoring the consequences. In this research, I have tested one such alternative method and observed the consequences in terms of the streams that would be selected for treatment and the estimated number of sea lampreys that would be killed. After two years of conducting RA and QAS concurrently, I have concluded that the use of RA to assess and select streams for treatment allows managers to kill more sea lampreys at equal or lesser costs to the GLFC. While finding the optimal balance of assessment and control resources will require further inquiry, the use of RA is an improvement over the current allocation of resources.

On average, RA surveys cost about 70% less than QAS surveys to conduct. I expected the RA surveys to be less accurate than the QAS surveys given the lower level of effort needed to conduct them, and the rationale behind conducting the RA surveys was that this loss of accuracy would be compensated for with additional resources available to treat streams. However, I found that the information obtained from the two types of surveys in terms of the ranking of stream treatment priority was similar despite the lower costs associated with RA. In 2005, basing treatment decisions on the RA data would result in the treatment of all but three of the streams that would be treated under QAS, with the addition of 11 more streams under the RA list. In 2006, the use of RA would result in the treatment of all but two of the streams that would be treated under QAS, and ten additional streams would be treated under RA. Qualitatively, RA is more cost effective in terms of the number of streams it allows managers to treat, and not much information is lost in using RA since the majority of streams that rank for treatment under QAS also rank under RA.

Using the ESTR model population estimates as a basis for comparison, under equal labor costs to the sea lamprey program, the use of RA results in at least as many, if not more transformers and more larvae to be killed than does the use of QAS (Figure 6). Even if the savings resulting from the use of RA were not used to treat more streams, the use of RA still results in almost as many transformers and larvae killed as compared to streams treated based on QAS (Figure 7). These ESTR-based estimates of the relative performance of RA are conservative, because they are generated from the QAS surveys on which the QAS rank list is based, and therefore will tend to favor the QAS surveys. In calculating the relative costs of the two assessment methods, chemical costs of treating streams were not included. Currently, the sea lamprey control program possesses a surplus of lampricide chemicals used to treat streams, and therefore chemical costs are not a limiting factor in selecting streams for treatment (*Gavin Christie, Great Lakes Fishery Commission, Ann Arbor, MI, personal communication*). However, if RA were to be adopted by the GLFC and on average more streams per year were to be treated, the cost of lampricide may become a limiting factor. If in the future RA is adopted, some of the savings generated through the use of RA may need to be used to purchase additional lampricides, reducing the number of additional streams treated.

The capture-recapture portion of this study was intended to provide an additional, independent means of comparing the benefits of making decisions based on the two assessment methods. By conducting capture-recapture on all of the streams that ranked for treatment on the basis of only QAS (QAS streams), I expected to be able to quantify the lower bound of the number of larvae or transformers that would have to be killed based on the RA method in order for it to outperform QAS. I also conducted capture-recapture studies on three of the eleven streams that ranked for treatment based only on RA (RA streams). If the capture-recapture population estimates were unbiased, I would simply sum the population estimates for all three QAS streams, sum the population estimates for the subset of three RA streams, and compare the two totals. If the total population for the RA streams were higher, I would be confident that making treatment decisions based on RA would allow managers to kill more sea lampreys, especially given that there are eight additional streams that would be treated based on only RA that would contribute to the total number of sea lampreys killed. If this method is followed, it is clear that at least in the first year of the study, more larvae and more transformers would be killed if streams were treated based on the results of RA rather than QAS (Figure 6).

Unfortunately, the estimates obtained from the capture-recapture studies on the Little Munuscong and Big Munuscong Rivers, two of the three streams that rank for treatment based on only QAS, were suspect because neither the release of marked animals nor the recapture effort was distributed randomly throughout the streams. The accuracy of a capture-recapture population estimate requires that either the marked animals or the recapture effort are randomly distributed throughout the population being sampled (Ricker 1975). In these two streams, the marked animals were highly concentrated in certain areas, and the subsequent recapture efforts were also generally concentrated in these same areas. Violating the assumption of equal distribution of marked animals amongst unmarked animals in a capture recapture experiment, particularly when the recapture effort is also unequal and focuses on these same concentrated areas, can result in a high proportion of marks collected on the second collection event and hence a low population estimate. For these two streams called into question because of the marking methods, the population estimate obtained from the capture-recapture experiment was significantly lower than that generated by ESTR (Table 6). Because one of the major assumptions of a capture-recapture experiment was violated for these two streams, their population estimates cannot be treated as unbiased.

In the absence of a reliable population estimate for these two streams, the comparison of the number of sea lampreys killed based on the two methods becomes more equivocal. However, assuming that the population estimates for the Little Munuscong and Big Munuscong rivers are uninformative, some level of comparison is still possible. The combined larval and transformer populations of these two streams would have to be approximately 528,000 (11 times larger than their combined ESTR model population estimates) for the total population of the 3 QAS streams to equal that of the 3 RA streams. While this seems unlikely, it is not impossible, especially given the capture-recapture results of this and another study (Steeves 2002), which showed that in some cases the capture-recapture population estimates were eight to nine times higher than the ESTR population predictions. However, there are eight additional streams that would be treated on the basis of RA and not QAS with sea lamprey populations that will also contribute to the total number killed in RA streams. Given the populations estimated from the capture-recapture studies and the existence of these eight additional RA streams, it seems reasonable to conclude that the use of RA surveys to rank streams for treatment and the subsequent treatment of those streams would result in higher total numbers of sea lampreys killed than the use of QAS.

A similar situation exists when comparing the number of large larvae/transformers that would be killed if treatment decisions were based on RA or QAS. The subset of three RA streams have almost seven times as many large larvae/transformers as the full set of three QAS streams, and there are still eight RA streams for which I have no capture-recapture population estimates. Assuming we know nothing about the number of transformers in the Little or Big Munuscong Rivers, they would need to contain over 10,000 transformers (approximately nine times the ESTR model transformer estimate for these streams) to equal those in the subset of RA streams for which we have data. Coupled with the fact that there are eight additional RA streams that would contribute to the total number of transformers killed as a result of treating streams based on RA, this seems highly unlikely. Therefore I conclude that making stream treatment decisions based on RA results would allow managers to kill more large larvae/transformers than would making stream treatment decisions based on QAS results.

In addition to providing a basis for comparison of the outcome of using an alternative assessment method, the capture-recapture population estimates also serve to illustrate the inaccuracies that exist in the QAS and ESTR population estimates despite their high resource demand. The capture-recapture population estimates ranged from 0.9-10 times the ESTR total population estimates, and from 0.5-27 times the ESTR large larvae/transformer estimates. These results could serve as a warning for managers against putting too much confidence in ESTR population estimates; however, there are reasons to approach these results with caution. In four of the six streams on which capture-recapture experiments were conducted, the marked sea lampreys were imported from an outside source stream. A major assumption of any recapture study involving the importation of marked subjects is that the behavior of the marked imports must be indistinguishable from that of unmarked members of the target population. Therefore, this methodology should only be applied when there are adequate grounds for believing that this assumption is a reasonable approximation of reality (Goudie 1995). This assumption has not been formally evaluated for sea lampreys. We have reason to believe that sea lampreys imported from other streams will behave the same as residents of that stream, given the high survival rate of marked sea lampreys even when kept in target stream water, and given the agencies' long history of keeping larvae alive in a variety of waters (*Jeffrey Slade, USFWS, Ludington, MI, personal communication*). However, this assumption has not been formally tested, and warrants further investigation.

In this study, I have implemented an alternative larval assessment and stream treatment selection method, observed the results in the form of the set of streams that would be selected for treatment, and compared the results to those obtained from the use of the current assessment method. In doing so, I have initiated an adaptive management experiment that can provide insight into how to improve the balance of resources allocated to sea lamprey larval assessment and those allocated to control activities. This experiment is not a traditional example of adaptive management, because the management action of interest in this case is the assessment of a system. However, the principles of adaptive management still apply (Walters 1986). An alternative management action (assessment) was implemented on a scale relevant to management decisions, and the consequences of implementing this action were monitored in the form of the streams that would be selected for treatment. Monitoring these consequences have shown that RA is a more efficient use of resources for sea lamprey control than QAS in that it allows for more streams to be treated resulting in more sea lampreys killed at equal program costs. The ESTR population estimates alone demonstrate that making stream treatment decisions based on RA results in just as many, if not more, larvae and transformers killed than making stream treatment decisions based on QAS results. While not a complete or perfect picture, the capture-recapture population estimates lend additional support to this idea. This study will continue for one more year of RA surveys and two more years of capture-recapture experiments. Following the acquisition of these additional data, it will be possible to more definitively determine the assessment method that best serves the goals of sea lamprey management, and the GLFC will be in a better position to rationalize the assessment program that they employ.

The balance between resources spent to learn more about a system and resources spent to actually manage that system are applicable to other natural resource situations. Rapid assessment techniques have also been shown to be effective in other systems (Jones and Stockwell 1995, Metzeling et al. 2003), and could potentially be applied even more broadly. Detailed stock assessments of commercial fisheries, evaluation of the status of an endangered species, and determining the ideal location for reserves and protected areas are a few examples of situations in which a conflict could exist between resources allocated to learn more about the system and resources allocated to the management, conservation, or protection of that system. Based on the results found in this study of sea lamprey management, it is not necessarily always the best strategy to allocate large amounts of resources to learn more before acting. Further research into the optimal allocation of limited resources in such situations and the development of strategies for determining the point at which additional information ceases to be valuable will lead to better management of natural resource systems. The use of adaptive management to test new methods of assessment and resource allocation is a means through which the optimal balance of resource demands can be determined, and should be applied to other systems.

CHAPTER TWO

DOES DEMOGRAPHIC VARIATION IN LARVAL SEA LAMPREYS DETERMINE THE REGULARITY OF CHEMICAL TREATMENTS IN GREAT LAKES STREMS?

Introduction

Variation in population abundance is widespread among fish species, and understanding how growth and recruitment affect fluctuations in population size is a common and important goal of fisheries science (Rothschild 1986, Houde 1987, Hilborn and Walters 1992, Myers 2001). Variation in life history parameters has been well studied, both among species (Pauly 1980, Roff 1984, Winemiller and Rose 1992), and among populations within species (e.g. Hutchings and Jones 1998, Shuter et al.1998, Berg and Pedersen 2001, Purchase et al. 2005). This research indicates that understanding variation in demographic rates such as growth and recruitment among populations can be used to improve management policies (Winemiller 2005). For most fisheries, knowledge of population variation is used to develop better harvest strategies; however, in the case of an undesirable fish species, accounting for differences in demographic rates among populations can also be used to aid suppression and allow for more effective use of resources in controlling that species. Variation in recruitment and other demographic rates is common among vertebrate pest species, and accounting for this variation and that of other demographic rates can influence the effectiveness of control efforts on these and other species (e.g. European rabbits, *Oryctolagus cuniculus*, Twigg and Williams 1999; great cormorants, *Phalacrocorax carbo sinensis*, Frederiksen et al. 2001, sea lampreys, *Petromyzon marinus* , Jones et al. 2003; carp, *Cyprinus carpio*

L., Brown et al. 2005; and brushtail possums, *Trichosurus velpecula*, Ramsey 2005) . However, as in desired fish populations, often times variation in recruitment that is essential for successful management is not well understood.

Sea lampreys (*Petromyzon marinus*) invaded the Great Lakes in the 1920's, and their negative impacts on the native fish community have been well documented (i.e. Smith and Tibbles 1980, Youngs 1980, Heinrich et al. 2003). Adult sea lampreys spawn in streams, where the non-parasitic larvae live for an average of 3-7 years (Potter 1980), although they can remain in streams for as many as 18 years (Manion and Smith 1978). Upon completion of the larval phase, sea lampreys metamorphose and migrate downstream into large bodies of water, where they parasitize other fishes, often injuring or killing the host. An early life history study identified stream-dwelling larval sea lampreys as the life stage most vulnerable to control (Applegate 1950); in particular, larvae undergoing metamorphosis (called transformers) are the life stage on which managers were encouraged to focus control efforts to maximize efficiency (Smith and Tibbles 1980).

Sea lampreys have been the focus of intensive control efforts since the early 1950's (Smith and Tibbles 1980). The majority of control efforts currently being used target the non-parasitic, stream-dwelling larval phase of sea lampreys through the periodic treatment of streams with the lampricide 3-triflouromethyl-4-nitrophenol (TFM). The application of TFM usually kills from 95-100% of larvae present in the stream at the time of treatment (Christie et al. 2003). Because larval sea lampreys remain in their natal streams for several years before becoming parasitic, it is neither necessary nor cost effective to treat every stream each year. Rather, treatments should ideally be applied on a cycle that matches the duration of the larval phase in a given stream. However, natural variability in recruitment, growth rates, and survival within each stream results in inconsistency in the length of time before streams require treatment to prevent the escapement of parasitic sea lampreys; therefore, subsets of streams are assessed annually to determine their need for treatment (Slade et al. 2003).

Assessment of larval, stream-dwelling lamprey populations is conducted to provide managers with estimates of sea lamprey numbers and size structure within streams in order to direct stream treatments. Larval assessment is a costly yet uncertain process, and resources allocated to assessment reduce those available to carry out control efforts and research new methods of control. Although some level of larval assessment is certainly needed to direct stream treatments, recent studies have drawn attention to the uncertainty inherent in the current assessment and stream selection process (Hansen et al. 2003, Steeves et al. 2003). The incorporation of historical data into assessment and stream selection procedures may provide a means for managers to make effective treatment decisions with minimal expenses on assessment, thereby freeing up resources to be used in other ways that could improve the overall effectiveness of the sea lamprey control program.

For the purposes of these analyses, I considered larval sea lampreys within different streams to be distinct populations, despite the fact that sea lampreys mix as one population within the lake environment and do not home to natal streams (Bergstedt and Seelye 1995). In spite of this mixing during juvenile and adult life stages, sea lampreys spend the duration of their larval phase in the same stream, and demographic rates such as growth and incidence of metamorphosis are known to differ among streams (Hansen et al. 2003). Because genetic differences among stream populations are unlikely to exist due to the absence of homing in sea lampreys, demographic variation among larval populations is likely to be a consequence of differences among stream environments.

Larval assessment surveys have been conducted since the late 1950's to estimate population levels and size structure, direct lampricide treatments to the appropriate streams, and evaluate treatment effectiveness (Slade et al. 2003). Despite the plethora of historical data available, these data have not yet been used to examine demographic patterns in stream-dwelling sea lamprey populations. Ideally, lampricide treatment cycles should match the cycles of recolonization, growth, and maturation of sea lampreys following treatment events (hereafter referred to as "lamprey production") in individual streams. Most lamprey-producing streams are treated on a 3-5 year cycle, but streams differ in the regularity with which large populations of transformers develop (Heinrich et al. 2003, Lavis et al. 2003, Morse et al. 2003). In other words, some streams are highly regular in their cycles of lamprey production and need for treatment, while others vary widely. Previous authors have suggested that differences in recruitment, growth, and survival following lampricide treatments contribute to differences in treatment regularity (Heinrich et al. 2003, Lavis et al. 2003); however, these assertions have never been formally tested. Through this research, I will test whether streams with irregular lamprey production and treatment cycles have more variable recruitment and/or growth rates than streams with naturally regular cycles of lamprey production. Understanding the population-level causes of variation in lamprey production could allow for better prediction of the need for treatment in irregularly producing streams, help to shape a more cost-effective and efficient assessment procedure, and increase general understanding of sea lamprey ecology.

Researchers and sea lamprey managers together have divided streams considered for chemical control into four categories based on their regularity of lamprey production inferred from the historic regularity of chemical treatments and from the expert opinion of assessment biologists who work on these streams. Category 1 streams are very predictable in their lamprey production cycle and their treatment schedule. These have also recently been referred to as “expert judgment” streams, because decisions regarding their treatment have been based on prior knowledge rather than on assessment data. Category 2 streams are somewhat variable in their lamprey production cycle and treatment schedule, but can be somewhat predictable. Category 3 streams are highly variable in their production of sea lampreys and treatment schedule. Category 4 streams are streams in which sea lampreys have been found in the past, but do not currently support sea lamprey populations and are no longer treated.

This categorization was created in part to direct assessment efforts to the streams that need them most. Category 1 streams are likely to require minimal or no assessment to effectively predict their need for treatment, and in the future managers could potentially rely heavily on historical patterns to make treatment decisions for these streams. Category 3 streams are likely to require the most assessment to determine their need for treatment. As useful as these categorizations could be to direct assessment activities, they were created in a subjective manner based on the expertise of sea lamprey biologists. Before directing assessment resources preferentially to certain stream categories, a formal evaluation of the demographic basis for differences in variability in sea lamprey populations seems appropriate. The two demographic processes that can be examined using historical surveys are growth to age-1 and recruitment to age-1 as measured by catch per unit effort (CPUE). I have analyzed data from historical surveys conducted between 1959 and 2005 to determine whether the stream categorization is supported empirically as demonstrated by the existence of measurable differences in growth and/or recruitment among stream categories. In particular, I have looked for differences in the variability of growth and recruitment rates, as well as differences in the mean growth and recruitment rates across stream categories.

This analysis of differences in growth and recruitment will i) assess the usefulness of the stream categorization developed by managers for directing assessment activities, ii) determine whether growth or recruitment is the more important driver of lamprey production, and iii) will help to shape an assessment protocol that targets the larval stage that is most influential in determining lamprey production. For example, if differences in lamprey production and treatment regularity are driven by differences in larval recruitment, larval assessment could focus on early life stages, and the detection of a re-established larval population of a certain threshold size within a stream could serve as the main treatment selection criterion. Alternatively, if differences in growth rates are associated with treatment regularity, treatment schedules based on recruitment will be less effective and larval assessment would more likely focus on later life stages. Further, if sea lampreys from different stream categories differ in these vital demographic rates, an understanding of these differences can allow for a more cost-effective and efficient assessment procedure by preferentially directing assessment resources to stream types exhibiting higher levels of variation and higher uncertainty in their need for treatment.

Finally, this type of analysis could serve as a precursor to the use of a more formal Bayesian approach to selecting streams for treatment, in which managers could calculate an expected larval population based on prior surveys and patterns to be used in combination with current assessment data.

Methods

Historical Survey Data

Over 30,000 larval sea lamprey assessment surveys were conducted between 1959 and 2005 by the United States Fish and Wildlife Service (USFWS) and the Department of Fisheries and Oceans, Canada (DFO). I obtained the results of subsets of these surveys determined by the timing criteria described below, and analyzed them separately for larval growth and recruitment. Several types of larval assessment surveys exist (i.e. index surveys, Quantitative Assessment Surveys, biocollection surveys), and all types were initially obtained from the USFWS and DFO. Only age-1 individuals were used for these analyses because it was difficult to distinguish reliably between older age-classes of larval sea lampreys based on length-frequency histograms; however, generally the first two age classes are more clearly separable (Potter 1980). To increase the likelihood of only age-1 and younger larvae being present in an assessment collection, only surveys that followed fall lampricide treatments were used in these analyses, since treatments that occur in the fall are more consistent than spring or summer treatments in their elimination of that year's recruits (*D. Cuddy, Department of Fisheries and Oceans, Sault Ste. Marie, Ontario, personal communication*). Surveys that took place two years after fall treatments were selected for analysis because the first opportunity for a year class to re-establish after a fall treatment is in the spring of the year following treatment, and two years after the treatment that year class would be age-1. At the time of these surveys, the streams should have contained a maximum of two year classes (age-0 and age-1). However, streams might have also contained residual sea lampreys that survived the lampricide treatment. I examined length-frequency histograms for each stream and year to determine which individuals were age-1 and should be included for further analysis. Streams with two or more years of survey data that fit the timing criteria were included in this analysis. No surveys from Lake Erie were included in any analyses due to the paucity of data from Lake Erie streams[2].

Recruitment Analysis

Recruitment was analyzed using a relative measurement of catch per unit effort (CPUE). To standardize for effort, I only used index surveys to calculate CPUE, resulting in a total of 900 surveys collected in 305 stream-years for this analysis. Index surveys have been conducted at the same access points for many years with a relatively consistent level of sampling effort. The CPUE value used as an index of recruitment for each stream-year was calculated using the total number of age-1 sea lampreys caught in all the surveys in a given stream-year divided by the total time (in hours) spent electrofishing to collect them (meter time). Some surveys reported effort as “collecting time”, which is a measure of total time spent at a site rather than time spent electrofishing. These measures of collecting time were converted to meter time using a conversion factor of 1.595 units of collecting time for every 1.0 unit of meter time, developed by USFWS-Marquette sea lamprey control (M. Fodale, USFWS, Marquette,

[2] Chemical treatments have only been used in Lake Erie tributaries since 1986, and only two Lake Erie streams had more than one year of data that fit the timing criteria required for this analysis. This paucity of data made the establishment of patterns in variation of population level processes among stream categories impossible.

MI, unpublished data). Summary statistics of the data used for the recruitment analysis are shown in Table 7.

Table 7. Summary of data used for recruitment analysis. For each category, the number of stream-years of data, the % of occasions in which zero recruitment was observed, and the mean and standard deviations of the non-zero catch per unit effort values are shown.

			CPUE (catch/hr)	
Category	**N**	**% zero recruitment**	**mean***	**SD***
1	158	10.13	50.7	61.7
2	43	16.28	35.1	38.6
3	76	14.47	30	40.8
4	28	57.14	10.5	9.7

* = mean and SD are calculated for only non-zero CPUE values.

The recruitment analysis was conducted as a two-step process using the delta approach (Maunder and Punt 2004). First, differences among stream categories in the probability of occurrence of an age-1 year class in the second year following a chemical treatment were analyzed using a binary response variable indicating whether any age-1 sea lampreys were caught in the surveys (yes = 1; no = 0). Then, non-zero CPUE values were examined for differences in mean CPUE as well as variation in CPUE among stream categories.

Probability of Successful Recruitment

The objective of this analysis was to determine if differences exist among stream categories in the establishment of a cohort following the chemical treatment of a stream. Streams with no age-1 sea lampreys collected two years following a fall treatment were assumed to have no recruitment, and recruitment was assumed to have occurred in streams with one or more age-1 sea lampreys collected. Recruitment events (no recruitment = 0, recruitment event=1) were modeled using generalized linear mixed effects models with a binary response variable and a logit link function (Schall 1991). In addition to stream category, the lake into which a stream flows was included as a potential fixed effect in the model. For this analysis, fixed effects were selected prior to random effects due to the inability of the model to converge with all fixed effects and random effects included. After the fixed effects structure was determined, the significance of stream and year as non-nested random effects was evaluated. After the model that best explained the data was selected, probability of successful recruitment and 95% confidence intervals were calculated from the parameter estimates using the logit link function (Faraway 2006).

<u>Analysis of Non-Zero Recruitment</u>

Analysis of mean CPUE

The objective of this analysis was to determine if significant differences existed in mean CPUE among stream categories. All CPUE values > zero were modeled using linear mixed effects models. Due to non-normality of error terms, CPUE was transformed prior to analysis. The data were heavily skewed, and error terms remained non-normally distributed after using either a square root or cubed root transformation; therefore, data were transformed using a quarter-root transformation, resulting in normally distributed residuals. To account for non-independence in recruitment data, stream and year were tested as potential non-nested random effects. Stream category and lake were included as potential fixed effects. The full model against which other models were tested was:

$$y_{jklmn} = \beta_0 + \beta_{1j} + \beta_{2k} + b_l + b_m + \varepsilon_{jklmn}, \tag{9}$$

$j = 1,\ldots,4;\ \ k = 1,\ldots,5;\ \ l = 1,\ldots,95;\ \ m = 1,\ldots, 44,\ \ n = 1,\ldots,255\ ;$

$$b_l \sim \mathrm{N}(0,\sigma_1^2),\quad b_m \sim \mathrm{N}(0,\sigma_2^2),\quad \varepsilon_{ijklm} \sim \mathrm{N}(0,\sigma^2),$$

where y_{jklmn} is the quarter-root transformed CPUE from stream year *n*, β_0 is the overall mean CPUE or intercept, β_{1j} is the fixed effect of stream category *j*, β_{2k} is the fixed effect of lake *k*, b_l is the random stream effect, b_m is the random year effect, and ε_{jklmn} is the unexplained residual error. All random effects and error terms were assumed to be normally distributed with a mean of zero and a variance estimated by the model.

Analysis of variation in CPUE

The objective of this analysis was to determine if stream categories differed significantly in recruitment variation. After selecting the best model to describe mean CPUE (above), differences in variation of CPUE among categories were tested by modeling standard deviation ratios of the within group errors using variance covariates (Pinheiro and Bates 2000). The same fixed and random effects selected in the analysis of mean CPUE described above were used in this model. The error structure in the variance components model was represented by:

$$\varepsilon_{jklmn} \sim \mathrm{N}(0,\sigma^2\delta_j^2\ ), \qquad (10)$$

where j =1,…,4. ε_j is the residual error for each sample from stream category *j*, and δ_j is the variance component estimated for stream category *j*. In order to achieve identifiably of all parameters, restrictions must be placed on δ. The variance component of the first category was held constant at one ($\delta_1 = 1$), and the estimates of the other variance components represent the ratio between their standard deviations and the standard deviation of the first stratum (Pinheiro and Bates 2000).

Categories were determined to have significantly different levels of variation in CPUE if the model allowing different levels of variance modeled for each category was a significantly better fit to the data than the model with a constant level of variance for all stream categories. The relative fit of the two models to the data was assessed using a likelihood ratio test (α=0.05).

Growth Analysis

A total of 2405 larval assessment surveys that collected 60,281 age-1 larvae were chosen that took place two years following fall treatments. All types of larval assessment surveys were used for the growth analysis, resulting in more surveys available for analysis than in the recruitment analyses. The streams and individual sea lampreys included in this analysis are summarized in Table 8. The preponderance of Category 1 streams in the dataset was due to the higher number of surveys that fit the timing criteria on these types of streams that are by definition treated more regularly than other categories of streams.

Table 8. Summary of data used for growth analysis. The number of streams falling in each category, number of individual sea lampreys collected from each category, the mean length, standard deviation of length, and mean DOY on which a survey was taken are shown.

			Length (mm)		
Category	**N streams**	**N individuals**	**Mean**	**SD**	**mean DOY**
1	57	46310	44.52	12.08	216.75
2	21	5158	44.50	13.88	208.16
3	30	6455	42.80	12.07	216.80
4	8	2226	50.96	10.01	223.21

Analysis of mean length at age-1

The aim of this statistical analysis was to determine if significant differences existed in mean length at age-1 among stream categories. I evaluated differences in mean length using linear mixed effects models. Length was log transformed to correct for non-normality and heteroscedasticity of residuals. When reporting results, estimates of back-transformed mean effect sizes were bias corrected (Beauchamp and Olsen 1973). The assessment surveys used for this analysis were conducted between May 1st and October 31st. The Julian day on which a survey was conducted (day of year, DOY) was included as a continuous fixed effect in all models to correct for differences in length due to different collection dates. DOY was centered around the mean survey DOY (mean=216.3, N=60,281, sd=45.5) to avoid correlation among estimates of random slopes and intercepts (Pinheiro and Bates 2000). Category was included as a potential fixed effect in the model to test for differences among stream categories in mean length at age-1. The lake into which a streams flows was also included as a potential fixed effect. Initially, all possible interactions among fixed effects were also included as fixed effects. However, the inclusion of category by lake and DOY by lake interactions caused models to not converge. Therefore, these interactions were not considered as potential fixed effects in model selection.

Multiple streams from each category were sampled, and within streams there are often many subsections (reaches). Each stream had at least two years of survey data, and in most cases more than one survey was conducted on a given reach in a given year. Multiple individuals were collected from each survey. Because of the hierarchical nature of the data, nested random effects were included in the model to account for the structure of the data and to correct for the lack of independence among individuals from the same stream, reach, year, and survey.

The full model against which other models were tested is shown below. The stream, reach, year, and survey ID in which a sample was collected were tested as potential random effects and all were nested within the next highest level. Random slopes (representing the effect on the relationship between length and DOY) and random intercepts were estimated for stream, year, and reach, and random intercepts were estimated for survey ID. The full model is represented by the equation:

$$y_{ijklmno} = \beta_0 + (\beta_1 + \beta_{2n} + b_{j,1} + b_{jk,1} + b_{jkl,1})x_i + \beta_{3n} + \beta_{4o} + b_{j,2} + b_{jk,2} + b_{jkl,2} + b_{jklm} + \varepsilon_{ijklmno}, \quad (11)$$

$$b_{j,1} \sim \mathrm{N}(0,\sigma_1^2),\ b_{j,2} \sim \mathrm{N}(0,\sigma_2^2),\ b_{jk,1} \sim \mathrm{N}(0,\sigma_3^2),\ b_{jk,2} \sim \mathrm{N}(0,\sigma_4^2),$$

$$b_{jkl,1} \sim \mathrm{N}(0,\sigma_5^2),\quad b_{jkl,2} \sim \mathrm{N}(0,\sigma_6^2), b_{jklm} \sim \mathrm{N}(0,\sigma_7^2), \varepsilon_{ijklmno} \sim \mathrm{N}(0,\sigma^2),$$

where $y_{ijklmno}$ is the log-transformed length of individual sea lamprey *i* (*i*=1,…,60281); β_0 is the overall mean length or intercept; β_1 is the fixed day of year effect for the day of year x_i for individual *i*, centered around the mean day of year; β_{2n} is the fixed interaction effect of category n (*n*=1,…,4) by day of year x; β_{3n} is the fixed effect of category ;, β_{4o} is the fixed effect of lake *o* (*o*=1,…,4); b_j is the random effect of stream *j* (*j*=1,…,118), where $b_{j,1}$ is the random slope and $b_{j,2}$ is the random intercept; b_{jk} is the random effect of year *k* within stream *j* (*k*=1,...,N_j), where $b_{jk,1}$ is the random slope and $b_{jk,2}$ is the random intercept; b_{jkl} is the random effect of reach *l* within year *k* and stream *j* (l=1,…,N_{jk}), where $b_{jkl,1}$ is the random slope and $b_{jkl,2}$ is the random intercept; b_{jklm} is the random effect of survey *m* nested within reach *l*, year *k*, and stream *j* (m=1,…,N_{jkl}); and $\varepsilon_{ijklmno}$ is the unexplained residual error. All random effects and error terms were assumed to be normally distributed with a mean of zero and a variance estimated by the model.

Analysis of variation in length at age-1

The aim of this statistical analysis was to test for different levels of variation in mean length at age-1 among stream categories and among lakes. Preliminary analysis showed that the relationship between stream category and variance in growth differed among lakes. In order to test for differences in variation, different residual variances were estimated for each level of a stratification variable (Pinheiro and Bates 2000). To determine if the within group variance in length at age-1 differed significantly among lakes, variance components ∂ were estimated for each lake using stream and reach as random effects. To determine if within group variance in length at age-1 also differed among stream categories within lakes, variance covariates were then estimated for each category and lake combination, again including stream and reach as random effects. The error structure of these models is represented by:

$$\varepsilon_{ijklmno} \sim \mathrm{N}(0, \sigma^2 \partial_p^2), \tag{12}$$

where p =1,…,N; and $\partial_1 = 1$. $\varepsilon_{ijklmno}$ is the residual error for each individual sea lamprey *i* from strata *p*, p is the stratification variable in which an individual was collected, either the lake or the stream category and lake combination, and ∂_p is the variance component estimate for variable *p*. The residual variance for each category and lake combination was calculated by multiplying the variance parameter estimate (∂^2) by the residual variance of the model.

I tested the significance of the separate variance components by testing the models with separate variance components against the simpler models using likelihood ratio tests. If likelihood ratio tests were significant, indicating a better model fit when separate variance components were estimated for different strata, I used 95% confidence intervals on the estimates of variance components for each stratum to determine which strata differed from one another in their variance component estimates. For these variance models, the same fixed effects selected in the analysis of mean growth from equation 11 were used, random slopes and intercepts were estimated for stream, and random intercepts were estimated for reach.

The variance component analysis that included stream and reach as random effects determined whether or not lakes, and categories within lakes, differed in their residual variances, composed of both within- and among-year variance. Both types of variance are important to sea lamprey managers, although the among-year variance is of most interest for this analysis. To determine the relative contribution of within- and among-year variance to the overall differences in variance observed among strata, an additional model was created that estimated random slopes and intercepts for each year in addition to the random effects estimated for stream and reach. Variance components were again estimated for each category and lake combination. Because of the inclusion of year as a random effect, the variance components estimated in this model encompassed within-year variance only. The ∂^2 estimated for each stratification factor was multiplied by the residual variance of the model to estimate the within year variance for each category and lake combination, and compared to the estimate of the total residual variance obtained from the model in which only stream and reach were included as random effects.

Model Selection

The significance of random and fixed terms were evaluated using Akaike's Information Criterion (AIC), and effects were considered significant if their inclusion resulted in a decrease in AIC value of $\geq$2 (Burnham and Anderson 1998). Random effects were modeled with all possible fixed effects included except when otherwise noted. Significance of individual random effects were evaluated using AIC values for individual models using the restricted maximum likelihood (REML) method of estimation of model fit (Pinheiro and Bates 2000). After determining the appropriate random effects structure for each model, significance of individual fixed effects were determined by sequentially removing fixed effects from the model and comparing AIC values. All tests for fixed effects were performed using the maximum likelihood (ML) method of estimation of model fit (Pinheiro and Bates 2000). Diagnostics of all selected models were examined to ensure no assumptions were violated. All modeling and statistical analyses were performed using R V.2.1.1 (R Core Development Team 2005).

Results

Recruitment Analysis

Probability of Successful Recruitment

The probability of a successful recruitment event was best explained by a model including only category as a fixed effect (Table 9). Including stream as a random effect did not improve model fit, and including year as a random effect only marginally improved model fit (ΔAIC=1.1), so neither random effect was included in the final model (Table 10). Models with both year and stream as random effects could not be fit to the data due to insufficient sample number. Category 4 streams were half as likely to have successful recruitment events as any other type of stream, and categories 1-3 did not differ in their probability of a successful recruitment event (Table 11, Figure 9).

Table 9. Candidate models with different fixed effects in the binary model of Recruitment success of age-1 sea lampreys. Fixed effects are shown with the estimated number of parameters (K), their AIC values, and the difference between the AIC value of a given model and that of the best model (ΔAIC).

Model	Fixed Effects	K	AIC	Δ AIC
1	Category	5	250.90	0
2	Category+Lake	8	253.43	2.53
3	(Intercept)	2	274.14	23.24
4	Lake	4	275.95	25.05

Table 10. Random effect selection for the binary model of recruitment success of age-1 sea lampreys. The number of estimated parameters (K), AIC value, and the difference between the AIC value of a model and that of the best model (ΔAIC) are shown. Random effects were modeled with a fixed category effect also included.

Model	Random effect	K	AIC	Δ AIC
1	Year	5	249.8	NA
2	None	4	250.9	1.1
3	Stream	5	254.9	5.1

Table 11. Fixed effects estimates, standard error, z-value, and p-values for the binary model of recruitment success of age-1 sea lampreys. The expected probability of successful recruitment for each category is also shown. In this model, the intercept refers to category 1, and the error DF=301.

Effect	Estimate	SE	z	p-value	Category	p(success)
Intercept	2.180	0.264	8.28	<.001	1	0.899
Category 2	-0.546	0.49	-1.11	0.266	2	0.837
Category 3	-0.407	0.419	-0.97	0.332	3	0.855
Category 4	-0.247	0.464	-0.532	<.001	4	0.429

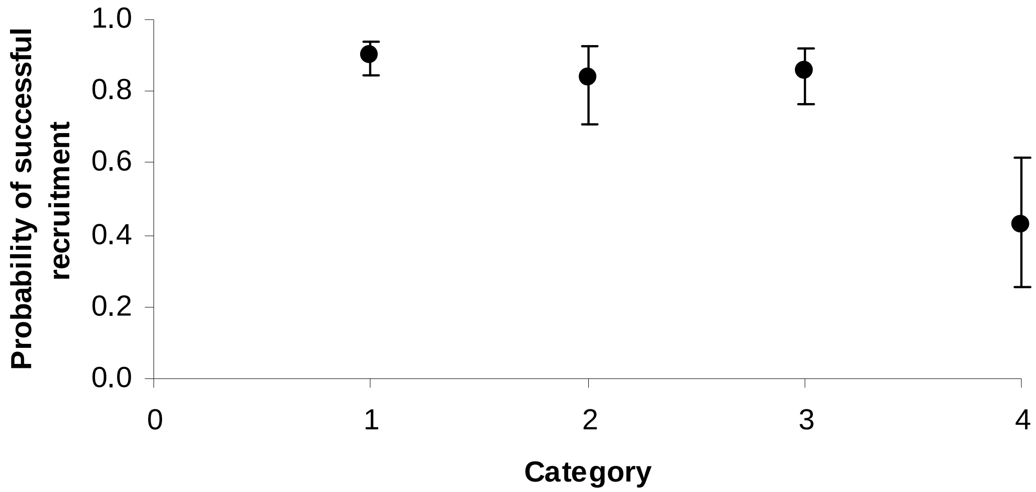

Figure 9. Probability of successful recruitment and 95% confidence intervals for each stream category as predicted by binomial model.

<u>Analysis of Non-Zero Recruitment</u>

Mean CPUE

The mean CPUE of a stream was influenced by the stream category and the lake into which a stream flows. The model that best explained mean CPUE included no random effects (Table 12) and category and lake as fixed effects (Table 13). Category 1 streams had the highest level of mean recruitment of any stream category, and Lake Ontario streams had the highest mean recruitment of any lake (Table 14). When held constant for lake, the mean recruitment level in category 1 streams was almost twice as large as that in category 3 streams, and nearly 5 times as high as that in category 4 streams (Figure 10). When held constant for category, the mean recruitment in Lake Ontario streams was more than twice that of streams in any other lake (Figure 11). While this model explained significant differences in mean recruitment, it did not explain the majority of recruitment variation (Multiple R^2=0.13).

Table 12. Random effect selection for the model of mean recruitment (CPUE^1/4)of age-1 sea lampreys. The number of estimated parameters (K), AIC value, and the difference between the AIC value of a model and that of the best model (ΔAIC) are shown. Random effects were modeled with fixed effects of category and lake also included.

Model	Random Effects	K	AIC	Δ AIC
1	None	9	499.3	0
2	Stream+Year	11	508.4	9.1
3	Stream	10	511.2	11.9
4	Year	10	516.6	17.3

Table 13. Candidate models with different fixed effects for the model of mean recruitment (CPUE^1/4) of age-1 sea lampreys. The number of estimated parameters (K), AIC value, and the difference between the AIC value of a model and that of the best model (ΔAIC) are shown.

Model	Fixed effects	K	AIC	Δ AIC
1	Category+Lake	8	497.72	0
2	Category	5	500.54	2.82
3	Lake	5	518.74	21.02
4	(Intercept)	1	520.74	23.02

Table 14. Fixed effects estimates, standard errors, t-values, and p-values for each parameter included in the model of mean recruitment (CPUE^1/4) of age-1 sea lampreys. In this model, the intercept accounts for the effects of both category 1 and Lake Superior, and the error DF=248.

Parameter	Estimate	St. Error	t value	p value
Intercept	2.410	0.069	35.07	<0.001
Category 2	-0.283	0.121	-2.35	0.020
Category 3	-0.380	0.095	-3.99	<0.001
Category 4	-0.732	0.191	-3.83	<0.001
Lake Michigan	-0.026	0.093	-0.28	0.780
Lake Huron	0.049	0.111	0.44	0.661
Lake Ontario	0.599	0.210	2.84	0.005

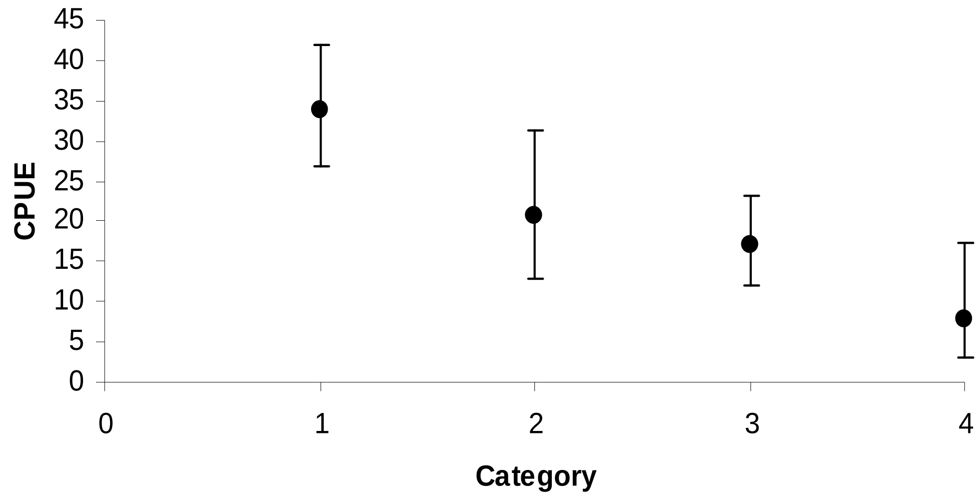

Figure 10. Mean CPUE (catch per hour) and 95% confidence intervals for each stream category as predicted by the linear model when holding lake constant (values shown are for Lake Superior streams).

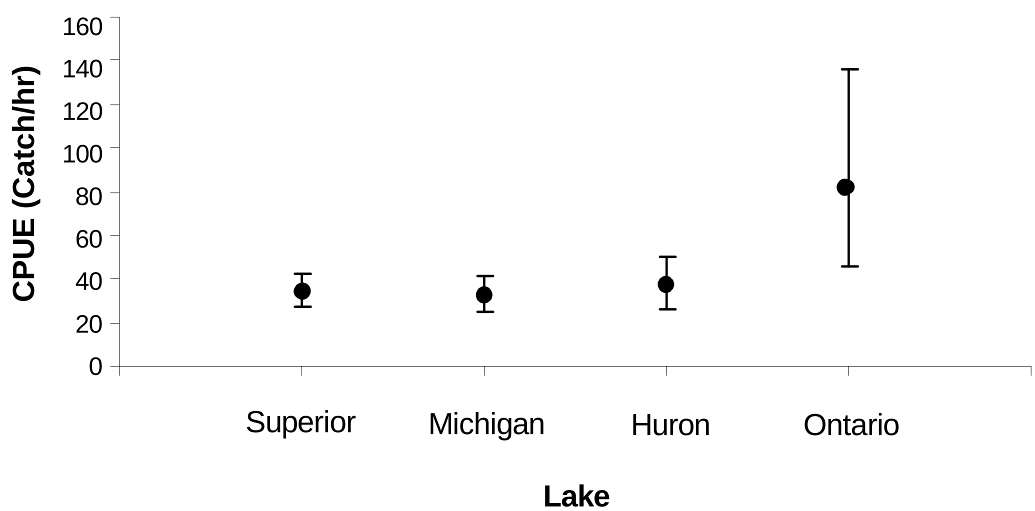

Figure 11. Mean CPUE and 95% confidence intervals for each lake as predicted by the linear model when holding category constant (values shown are for category 1 streams).

Variation in CPUE

Stream categories did not differ significantly in their variation in CPUE; the model allowing for different levels of variation for each category did not have greater support than the model with constant variance (Likelihood ratio=3.3, DF=3, p=0.35).

Growth Analysis

<u>Analysis of mean length at age-1</u>

Mean length at age-1 was best explained by a model including stream, year, reach, and survey ID as random effects (Table 15). Random slopes and intercepts were estimated for stream and year, and random intercepts were estimated for reach and survey ID. DOY and lake were included in the model as fixed effects (Table 16). The standard deviation of log(length) at age-1 explained by each random effect is shown in Table 17.

Table 15. Random effects for the model of log(length)of age-1 sea lampreys. Random effects were estimated for the slope (S) and intercept (I) of each level except survey ID, which only occurred on one day of year (DOY). Candidate models are shown along with the number of estimated parameters (K), AIC value, and the difference between the AIC value of a model and that of the best model (ΔAIC) are shown. Random effects were modeled with all possible fixed effects also included (DOY, Category, Lake, and a Category*Lake interaction).

Model	Random effects	K	AIC	ΔAIC
1	Stream(I)+Stream(S)+Year(I)+Year(S)+Reach(I) +ID(I)	17	-79316.0	0.0
2	Stream(I)+Stream(S)+Year(I)+Year(S)+Reach(S)+ Reach(I)+ID(I)	18	-79313.0	3.0
3	Stream(I)+Stream(S)+Year(I)+Year(S)+Reach(I)+ Reach(S)	17	-72875.3	6440.7
4	Stream(I)+Stream(S)+Year(I)+Year(S)+Reach(I)	16	-72592.2	6723.7
5	Stream(I)+Stream(S)+Year(I)+Year(S)	15	-68616.5	10699.5
6	Stream(I)+Stream(S)+Year(I)	14	-63624.3	15691.7
7	Stream(I)+Stream(S)	13	-47047.5	32268.5
8	Stream(I)	12	-39910.6	39405.4
9	None	11	-7883.1	71432.9

Table 16. Candidate models with different fixed effects for the model of log(length) at age-1, the number of parameters estimated (K), their AIC values and the difference between each model's AIC and that of the best fit model (ΔAIC). All fixed effects were modeled with random effects included. Random intercepts for stream, year, reach, and ID, and random slopes for stream and year were included in each model.

Model	Fixed Effects	K	AIC	ΔAIC
1	DOY+Lake	11	-79412.6	0
2	DOY+Category+Lake	14	-79408.1	4.5
3	DOY	8	-79403.7	8.9
4	DOY+Category+Lake+Category*DOY	17	-79403.4	9.3
5	DOY+Category	11	-79401.1	11.5
6	DOY+Category+Category*DOY	14	-79396.2	16.4

Table 17. Standard deviation estimates and 95% confidence intervals for all random effects included in the final model of log(length) at age-1. Fixed effects of DOY and Lake were also included in this model.

Random effects			95% CI	
Level	**Term**	**SD**	**lower**	**upper**
Stream	Intercept	0.1414	0.1164	0.1717
	Slope	0.0009	0.0006	0.0015
Year	Intercept	0.1160	0.0998	0.1340
	Slope	0.0015	0.0012	0.0019
Reach	Intercept	0.0730	0.0623	0.0857
ID	Intercept	0.0787	0.0749	0.0826
	Residual	0.1190	0.1183	0.1197

Sea lampreys from Lake Ontario were on average 30% larger than those from Lake Superior (Table 18, Figure 12). Sea lampreys from Lakes Michigan and Huron did not differ significantly in their mean length at age-1 from Lake Superior sea lampreys (Table 18, Figure 12). The day that a survey was conducted positively influenced mean length at age-1 (Table 18).

Table 18. Fixed effects estimates, standard errors, residual degrees of freedom, t-values, and p-values for each parameter in the model of log (length) at age-1 of sea lampreys. In this model, the intercept accounts for the effect of Lake Superior. Random intercepts for stream, year, reach, and survey, and random slopes for stream and year were also estimated in this model.

Parameter	Estimate	St. Error	DF	t-value	p-value
Intercept	3.740	0.0229	57743	163.06	<0.001
DOY-216.3	0.004	0.0002	57743	22.71	<0.001
Lake Michigan	0.004	0.0368	112	0.12	0.91
Lake Huron	0.042	0.0427	112	0.98	0.33
Lake Ontario	0.260	0.0676	112	3.85	<0.001

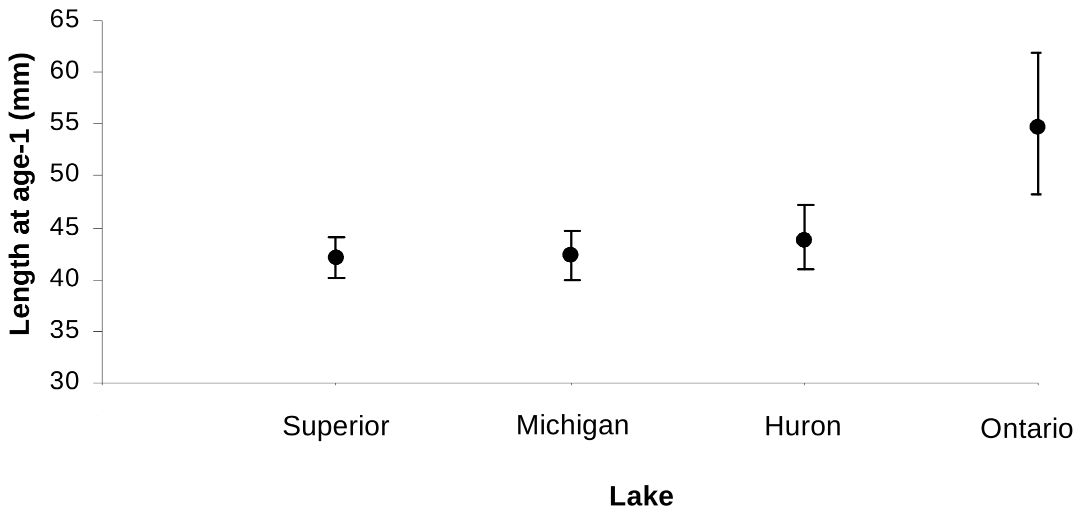

Figure 12. Mean length at age-1 (bias-corrected) and 95% confidence intervals for each lake as predicted by the mixed effects growth model.

<u>Analysis of variation in length at age-1</u>

Length at age-1 was better explained by the model with separate variance components for each lake than the model with no variance covariates (Likelihood ratio=65.5, df=3, p<0.001). Likewise, modeling separate variance components for category/lake combinations better explained variation in length at age-1 than modeling variance components for lake only (Likelihood ratio=487.8, df=10, p<0.001), indicating that variation in length at age-1 differed significantly among lakes and among categories within lakes. Sea lampreys from Lake Huron and Lake Ontario were 94% and 90% as variable in length at age-1 (on the log scale) as sea lampreys from Lake Superior, respectively (Figure 13). Sea lampreys from Lake Michigan did not differ significantly from those from Lake Superior in their variability in length at age-1. The relative variability in length at age-1 observed in sea lampreys from different stream categories differed among lakes, and all but one lake exhibited significant differences in variability of length at age-1 among categories. In Lake Superior, sea lampreys from category 3 exhibited higher levels of variability in mean length at age-1 than sea lampreys from other types of streams (Figure 14a). The majority of this variation was due to within year variance, although among-year variance was also highest in category 3 streams (Figure 15a). In Lake Michigan and Lake Ontario, sea lampreys from category 1 streams were significantly more variable in length at age-1 than individuals from any other stream category (Figures 14b and 14c). In these two lakes, category 1 sea lampreys had the highest levels of both within- and among-year variance in length at age-1 (Figures 15b and 15c). Lake Huron sea lampreys showed no evidence of differences in overall variation in length at age-1 among stream categories (Figure 14d), although sea lampreys from category 3 streams did have higher among-year variance than any other category of streams in Lake Huron (Figure 15d).

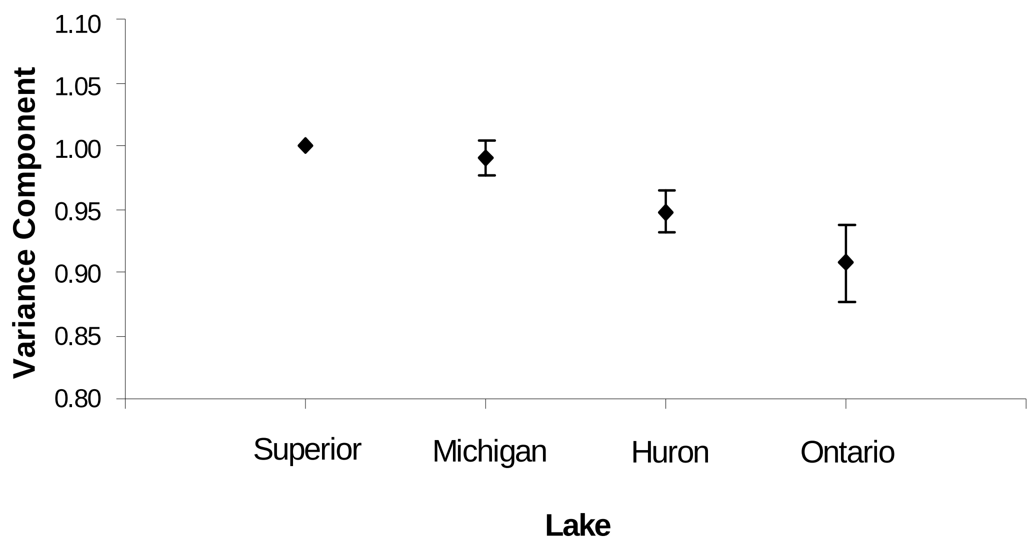

Figure 13. Estimates of relative variation and 95% confidence intervals for each lake except Erie. To estimate variance components, the variance component for Lake Superior was held constant at 1, and the relative variance components for the other lakes are estimated.

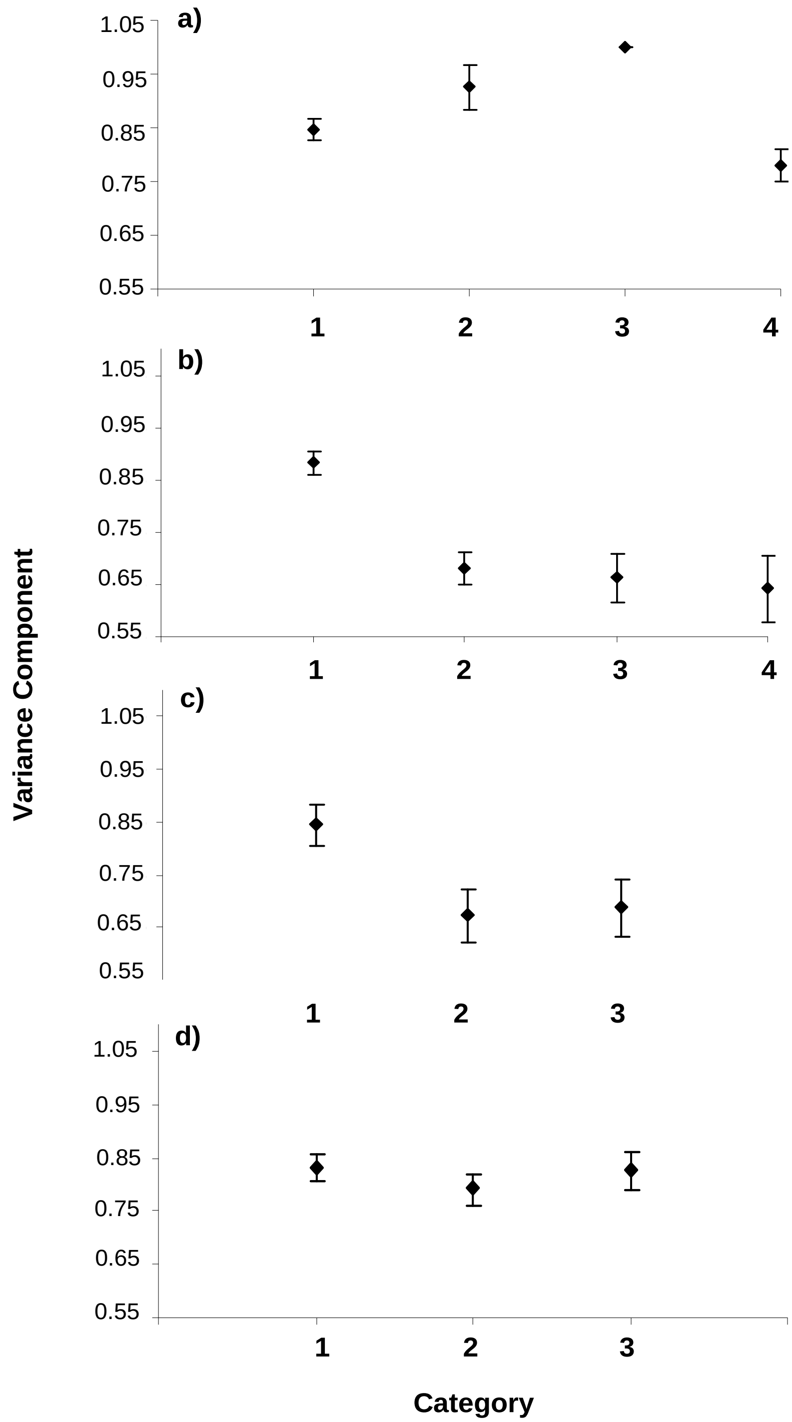

Figure 14. Estimates of variance components and 95% confidence intervals for different stream categories in a) Lake Superior, b) Lake Michigan, c) Lake Ontario, and d) Lake Huron. The variance component of category 3 in Lake Superior was held constant at 1, and others estimated relative to it.

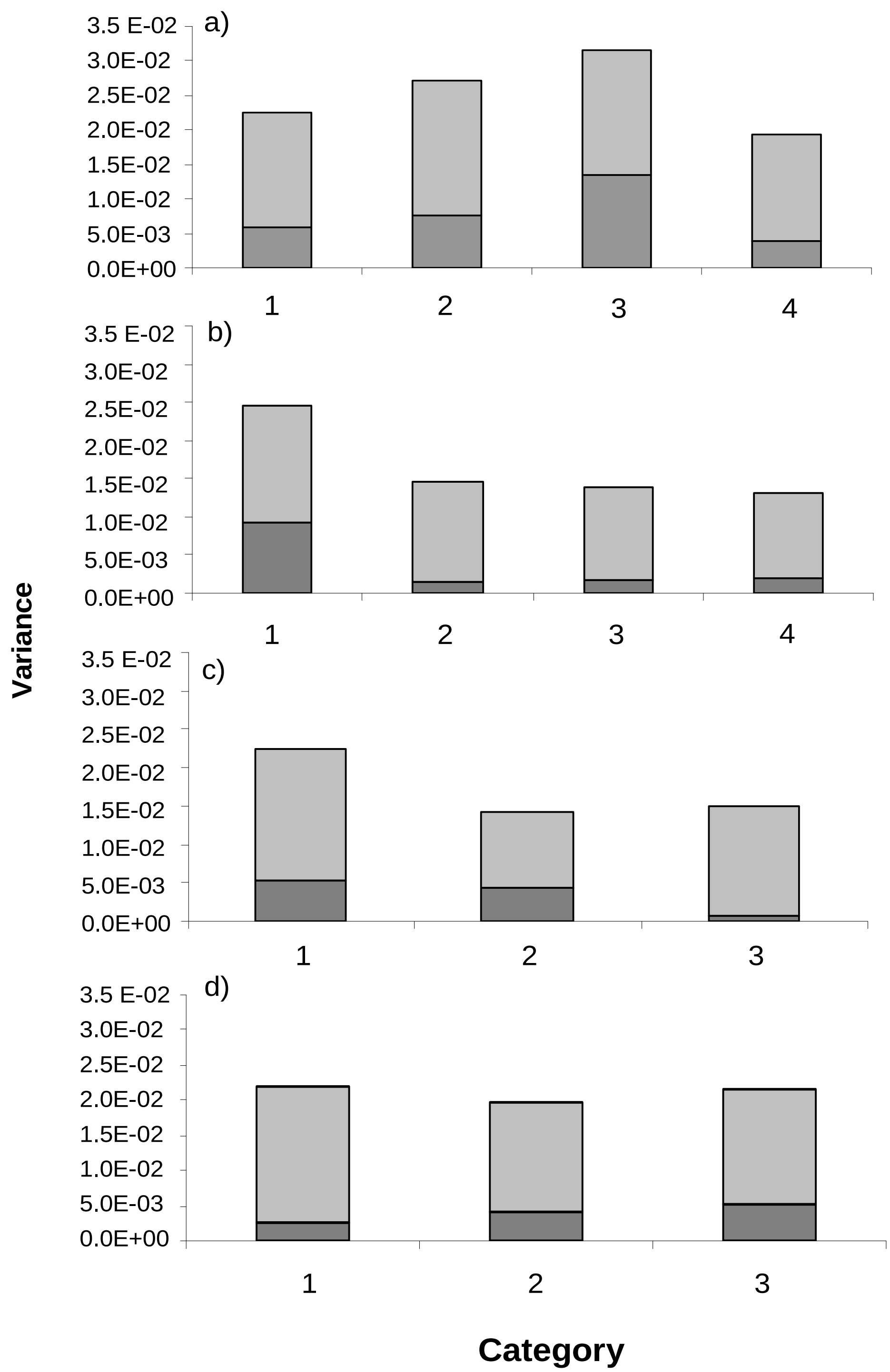

Figure 15. Residual variance attributable to within-year variance (light grey bars) and among-year variance (dark grey bars) for each stream category in a) Lake Superior, b) Lake Michigan, c) Lake Ontario, and d) Lake Huron.

Discussion

Variation in recruitment can influence the success or failure of management strategies, whether the management goal is to sustain a population or to suppress it. In the case of sea lampreys, variation in recruitment can determine the effectiveness of alternative control techniques (Jones et al. 2003). Additionally, I have demonstrated that differences in recruitment to age-1 influence the regularity of lamprey production and the need for chemical treatments by showing that streams with highly regular treatment cycles (category 1 streams) also tend to have higher levels of recruitment. The regularity of stream treatments appears to also be associated with the regularity of larval growth in Lake Superior streams, although not in other lakes. Overall, successful recruitment above a certain threshold level is more important than early larval growth in determining the regularity of lamprey production.

Category 4 streams (those that in the past have required treatment, but no longer support sea lamprey populations) were more likely to have no recruitment following a lampricide treatment than any other category of stream. Category 4 streams also had the lowest mean recruitment of any type of stream. This propensity for failed recruitment years could explain why these streams no longer need to be treated. Sea lamprey numbers throughout the Great Lakes have been reduced dramatically in the past 45 years (Smith and Tibbles 1980, Larson et al. 2003, Sullivan et al. 2003), and streams with lower average densities of age-1 larvae and higher probability of failed recruitment than other types of streams could likely no longer support viable sea lamprey populations once the lake-wide density of sea lampreys was reduced past a certain point. It is possible that these category 4 streams have some common environmental characteristics that make them less hospitable to sea lamprey larvae (i.e. habitat types, temperature regimes, Young et al. 1990), and only under high density conditions are these types of streams used by sea lampreys. Further research into the environmental characteristics of these types of streams and what makes them relatively inhospitable to sea lampreys could be useful in developing strategies to eliminate sea lamprey populations from other types of rivers.

Categories 1-3 did not differ in their probability of successful recruitment; these types of streams had approximately an 85% chance of successful recruitment of an age-1 year class following the chemical treatment of the stream. However, stream categories did differ in their mean recruitment as measured by CPUE. The mean CPUE in category 1 streams was almost twice as large as that in category 3 streams, and almost 5 times as large as that in category 4 streams. However, much variation in CPUE remained unexplained even by the best model, indicating that even within stream categories recruitment varies widely. This variation could be due to actual variation in sea lamprey recruitment; sea lamprey recruitment can vary up to three orders of magnitude even with a constant number of spawning females (Jones et al. 2003). The high levels of unexplained variation could also be due to the imprecision of CPUE as an index of recruitment. Although CPUE provides a rather imprecise index of recruitment and provides little information regarding the actual size of the age-1 year class, it is useful for comparative purposes, and CPUE has been widely used as an index of population size in fisheries (Ney 1993). The identification of a clear pattern in recruitment among stream categories in spite of the high levels of variation that would tend to obscure any patterns, due to both natural fluctuations and the imprecise metric used to measure recruitment, indicates that differences in recruitment among stream categories are indeed quite pronounced. Observed differences in recruitment to age-1 could potentially be used in management to make stream treatment decisions.

The association of the regularity of lamprey production with my index of recruitment suggests that variations in the size of a year class at age-1 persists in subsequent years, a pattern that has been demonstrated in other fish populations (e.g. Helle et al. 2000, Smith et al. 2005). Other researchers have emphasized the utility of sampling juvenile fishes in an attempt to index year-class strength of a cohort before they reach the age of management interest due to the importance of the larval stage in the determination of year-class strength (Rijnsdorp et al. 1985, Uphoff 1989, Sammons and Bettoli 1998). In the case of sea lampreys, the correlation between age-1 year-class strength and the regularity of chemical treatment indicates that larval assessment could be conducted several years before a stream might need to be treated, and the relative abundance of young larvae could serve as an indicator of the future transformer abundance on which managers could base treatment decisions.

The variability in CPUE of age-1 sea lampreys did not differ among stream categories. The most regularly treated streams (category 1) did not have more consistent recruitment, but they did have higher mean recruitment. A threshold cohort size may be necessary for a year class to persist in sufficient numbers to warrant treatment as the cohort approaches metamorphosis. Below this threshold size normal variations in cohort survival and growth may result in an inconsistent need for treatment. Category 2-4 streams may achieve this threshold level of recruitment less consistently than Category 1 streams. The strong pattern observed of higher CPUE in regularly treated streams could allow for the identification of this threshold CPUE value to be used for management purposes. If such a threshold could be identified, streams could be surveyed one or two years following treatment to quantify recruitment to age-1, and if the threshold catch rate was observed, managers would schedule the stream for treatment some number of years later. The number of years between survey and treatment would be determined by the historical growth and metamorphosis cycle of the stream. Identification of this threshold CPUE value will require an analysis of the observed CPUE of age-1 larvae vs. selection for treatment in subsequent years, and should be the subject of future investigation.

Sea lampreys from different stream categories did not differ in their mean length at age-1, although sea lampreys from the Lake Ontario were significantly larger at age-1 than those from the upper lakes (Superior, Michigan, and Huron). Lower lakes sea lampreys are known to achieve larger sizes more quickly than upper lakes sea lampreys (Potter 1980, Hansen et al. 2003, Slade et al. 2003), so the existence of larger sea lampreys in Lake Ontario was not surprising. I used mean size at age-1 as a surrogate for early larval growth, under the assumption that larger individuals must have grown faster in order to achieve that larger size. This assumption may not be correct, as larvae could hatch out at larger sizes or experience longer growing seasons in certain types of streams or in tributaries to certain lakes, allowing them to achieve larger sizes despite equivalent or even slower growth rates. Within-year growth of age-1 larvae was measured in my analysis through the relationship between the Julian day of sampling and the mean length of the larvae collected; however, this measure of growth was fairly crude, as collections from different streams and years were combined, and the range of dates sampled within a given stream and year were often too small to reliably predict growth rates. I found no significant interaction between stream category and the day of sampling, indicating that, at least with this crude measure of growth, within-year growth did not differ among stream categories. Within-year growth did differ among streams and years, as indicated by the random effects of stream and year on the relationship between day of sampling and length (random slope), as would be expected as a result of different growing conditions.

The relationship between variability in length at age-1 and stream category differed among lakes. In Lake Superior, sea lampreys from category 3 streams exhibited the most variability in length at age-1. In other lakes, either no relationship existed between category and variability in length at age-1 (Lake Huron), or sea lampreys from category 1 streams were the most variable in length at age-1 (Lakes Michigan and Ontario). Lake Superior streams have been treated for the longest time period of any lake (Heinrich et al. 2003), and Lake Superior contains more streams included in this analysis than any other lake. It is possible that streams from other lakes will exhibit similar growth patterns given more treatment cycles or the inclusion of more streams that fit the timing criteria required for this analysis. Alternatively, it is possible that because of their longer treatment history, Lake Superior streams exhibit more clear distinctions in treatment regularity and lamprey production, lending them more readily to a useful categorization.

In all lakes and all categories, the majority of variation in growth was a result of within-year variation. Larvae of the same age in the same stream at the same time show considerable variation in length, indicating the need for large sample sizes when conducting assessment surveys if a precise estimate of the size-structure of the stream population is desired. Despite accounting for the majority of residual variation, the relative contribution of within-year variation to overall variation was fairly consistent among categories within a lake. Most of the differences among categories in variation in length at age-1 resulted from differences in variation among years. Variation among years in length at age-1 was highest in category 3 streams in Lakes Superior, but highest in category 1 streams in Lakes Michigan and Ontario, indicating no consistent growth pattern within stream categories across all lakes. Therefore, the stream categorization framework is not supported by growth differences in any lake except Superior. Again, Lake Superior streams could be easier to categorize due to their longer treatment history. Alternatively, growth differences could be less important than recruitment differences in determining treatment regularity in the Great Lakes other than Lake Superior.

The stream categorization system developed by sea lamprey managers is consistent with demographic patterns in recruitment, and could be useful for directing assessment needs. The relationship between categories and growth varies by lake, and may not be consistent enough to be useful for assessment purposes. My results suggest that growth to age-1 of sea lampreys in category 3 streams are more variable in Lake Superior, which implies a greater need for assessment to focus on later life stages in these streams. Of more use for sea lamprey managers is the observation that category 1 streams have higher levels of recruitment across all lakes. Category 1 streams could likely be selected for treatment with little to no assessment, allowing more resources to be targeted to Category 2 and 3 streams, which could be assessed using a method designed to detect the presence or absence of a year class of a certain threshold size in order to determine a stream’s need for treatment.

Recruitment and growth are two of the three primary factors that determine fish population dynamics (mortality is the other). Understanding growth and recruitment and their variability are vital to managing fisheries (Houde 1987, Quinn and Deriso 1999, Myers 2001). Stable recruitment can reduce the complexity of fisheries management, but many fish populations have highly variable recruitment (Ricker 1954, Hilborn and Walters 1992, Myers 1998, MacKenzie et al. 2003). If not properly accounted for, this variability can cause high inter-annual variation in yield or catch rates in the case of desired fisheries, and high annual variation in control success in pest species such as sea lampreys. Variation in growth can also contribute to variable success of fisheries management strategies (e.g. Houde 1987, Campana 1996, Van den Avyle and Hayward 1999, Scharf 2000). By improving our understanding of the variability in recruitment and growth within and among economically important fish populations, it should be possible to design policies for exploitation and control that more effectively account for this variation. The analyses presented in this chapter provide an example of how such knowledge can be used to improve management.

This study represents the utility of historical data in understanding the dynamics of a managed population, and could be extended within the field of sea lamprey management. Based on this analysis, historical sea lamprey assessment data exhibit patterns across years that can inform future assessment activities and resource allocation. In the future, historical surveys could be used in a more rigorous manner to direct stream treatment decisions. A threshold level of recruitment could be identified above which chemical treatments would be applied, directing assessment efforts to early (age-1) life stages of sea lampreys and providing an additional objective metric on which to base treatment decisions. Alternatively, a Bayesian approach in which historical data are used to create informative prior probabilities of a stream's need for treatment could be employed, and combined with less-intensive data collection to make stream treatment decisions. This type of Bayesian assessment would be less costly than current assessment since it would rely less heavily on conducting surveys and more heavily on the wealth of data that have already been collected. Continued research into the use of historical survey data to make present-day decisions is warranted within sea lamprey management and in other systems for which informative historical records are available.

THESIS DISCUSSION

The acquisition of knowledge to determine the optimal course of action is a common goal of scientific inquiry. Often it is assumed that the more knowledge acquired, the better the decisions will be. However, in situations of limited resources, the gathering of information to increase knowledge can come at the expense of the ability to carry out the very actions the increased knowledge was intended to inform. When resources are limited, it is important to analyze the trade-off between resources used to assess a system and resources used to carry out management actions. Testing alternative strategies of resource allocation on the scale relevant to management and monitoring their consequences is a way to determine the optimal balance between competing management goals. Additionally, one means of reducing reliance on present-day assessment and information gathering is to use historical knowledge to inform decision making. In many managed systems, data have been collected for various purposes throughout the history of management, which can be used to direct management decisions or to better understand population dynamics, reducing the reliance on information gathered from present-day formal assessments (Myers et al. 1995, Patton et al. 1997, Swetnam et al. 1999).

In the case of sea lamprey control, streams are chemically treated to kill larval sea lampreys to achieve management goals. Assessment is needed to inform managers which streams, if treated, would provide the greatest benefit to the sea lamprey program in terms of sea lampreys killed. Finding the optimal balance between resources spent on this assessment and resources reserved for treating streams requires testing alternative frameworks of resource allocation and monitoring the consequences. Based on the results presented in chapter one, sea lamprey managers could allocate fewer resources to assessment and more to control and achieve greater suppression of sea lampreys. The rapid assessment procedure described in this chapter is one of a potentially infinite number of alternative assessment methods. RA may not represent the optimal balance between assessment and control, but it appears to be at least an improvement over the current allocation of resources in that it allows for greater numbers of sea lampreys to be killed than the current assessment method. The use of adaptive management to test alternative means of resource allocation and assessment will allow for the direct application of the results of this experiment to sea lamprey management decisions. Adaptive management is a tool that should be used more often to test alternative management actions and their results in real world systems, allowing for the continuous refinement of management actions in order to approach the optimal course of action.

Larval assessment surveys have been conducted to direct sea lamprey management since the inception of sea lamprey management. Based on the results presented chapter two, historical data can be useful in identifying demographic patterns in larval sea lamprey populations, and potentially in improving management, even if the data were originally collected for other purposes. The categories describing the regularity of lamprey production and treatment cycles developed by managers are supported by differences in recruitment to age-1, even when recruitment is measured on a very crude scale. Differences in growth rates are significantly related to treatment regularity only in Lake Superior streams, where irregularly treated streams exhibit the highest variation in mean length at age-1. Chemical treatments have been occurring longest in Lake Superior tributaries, and therefore these streams may be more easily categorized, or different population dynamics may be driving differences in treatments in Lake Superior streams than in tributaries to other lakes.

Further refinements to the Rapid Assessment method could be achieved by incorporating historical information. For example, category 1 streams may require an even less resource-intensive assessment method, aimed simply at identifying the presence or absence of a year class. Because differences in recruitment to age-1 appear to be driving differences in lamprey production across stream categories, it may be possible to identify a threshold level of recruitment above which a stream will require treatment, and develop an assessment procedure that identifies whether or not this threshold level has been achieved in category 2 and 3 streams. Alternatively, historical data could be used in a Bayesian framework, in which prior probabilities of a stream's need for treatment are formed using historical data, and combined with data collected from a rapid assessment procedure to determine which streams require treatment.

Understanding how best to balance resources used to gather information and those used to manage is important in many natural resource systems. Stock assessments of commercial fisheries, evaluations of the status of endangered species, and the determination of the optimal location for reserves and protected areas are examples of situations in which a conflict could arise between resources allocated to learn more about a system and those allocated to the management, conservation, or protection of that system. The use of historical data to identify demographic patterns in populations and/or to improve management may be a means through which managers could spend fewer resources on assessment, thereby freeing up resources to be used for other purposes. Studies that examine the tradeoff between assessment and management will assist managers in making critical decisions in situations of limited resources, and should be initiated in other systems in which competing management goals exist and in which historical records are available.

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