## Final Report

# Finding Appropriate Harvest Policies for Intermixed Fisheries to Ensure Long Term Population Sustainability of Native Great Lakes Fishes 

Project number: 2012.1250

## PROJECT ABSTRACT

## Finding Appropriate Harvest Policies for Admixed Fisheries to Ensure Long Term Population Sustainability of Native Great Lakes Fishes

Many Great Lake fisheries exploit intermixed fish stocks in which individuals from several different spawning populations overlap in habitat occupancy during periods of exploitation by commercial and/or recreational fisheries. Examples of economically and ecologically important Great Lakes fishes that are exploited as admixed fisheries include lake whitefish (Coregonus clupeaformis), walleye (Sander vitreus), lake trout (Salvelinus namaycush), lake sturgeon (Acipenser fulvescens), cisco (Coregonus artedi), Chinook salmon (Oncorhynchus tshawytscha), yellow perch (Perca flavescens) and steelhead (Oncorhynchus mykiss). Our overall research goal was to provide fishery managers insight into pragmatic techniques for assessment and management of intermixed fisheries that exploit multiple spawning populations. Our ultimate aim was to promote management that would cost-effectively help ensure sustainable commercial/ recreational harvest of lake whitefish, lake trout, and walleye in the Great Lakes region. The 6 objectives for our research project were the following: Objective 1) evaluate the relative performance of different fishing mortality control rules and three stock assessment approaches for dealing with intermixing (separate assessment models, combined model, treating movement as known) and how these harvest policies perform under various mixing and productivity scenarios; Objective 2 ) address how the spatial scale at which target fishing is applied affects performance by comparing case where target fishing mortality is applied to each population versus jointly across populations; Objective 3) address how harvest policy performance is affected by the frequency that stock assessments are conducted; Objective 4) determine how inaccuracies in mixing rates affect harvest policy performance; Objective 5) evaluate the estimability of model parameters within a release-conditioned tag-integrated catch-at-age assessment model under a range of conditions, and Objective 6) develop a model framework based on Bayesian variable selection for analyzing how factors influence net movement distances in a large water body based on conventional tag-recovery results. Based on our results, a pooled assessment approach was the most consistent performing method for assessing intermixed fish stocks. A total annual mortality control rule based on $50 \%$ of the fishing mortality that resulted in the maximum sustainable yield for the least productive population did the best job of protecting spawning populations across the range of explore simulation scenarios. There was little to no benefit of attempting to establish fishing harvest policies for individual regions based on catch data from mixture fisheries. If such an approach was attempted, conservative control rules would still be necessary to have a low risk of overharvesting spawning populations. For single populations, relative yields were reduced and risk of stock depletion and interannual variability in yield increased when assessments were multiannual. Conversely for intermixed populations, inter-annual variability in yield actually
decreased when assessments became multiannual, which may be related to data-quality issues with respect to assessment models. Accuracy and precision of ITCAAN model estimates generally decreased with greater model complexity, but estimates were generally more precise and less biased versus when natural mortality or reporting rate was misspecified. Overall, ITCAAN models were robust for estimating movement rates. At high movement rates, recruitment for the smallest stocks was overestimated, whereas the largest stocks' recruitment was underestimated. When stocks had identical Ricker stock-recruitment parameters, ITCAAN model recruitment estimates were unbiased even with the highest movement scenario. Based on Bayesian variable selection, Lake Huron lake whitefish movement distances were found to be related to total length and tagging site. Further, shorter movement distances were predicted if the relative density of the benthic amphipod Diporeia spp. was high near the tagging site during the recovery year.

## Final Narrative Report

Project Title: Finding Appropriate Harvest Policies for Intermixed Fisheries to Ensure Long Term Population Sustainability of Native Great Lakes Fishes

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## Background/Overview

1. Briefly summarize the project description as outlined in the original proposal.

Many Great Lake fisheries exploit intermixed fish stocks in which individuals from several different spawning populations overlap in habitat occupancy during periods of exploitation by commercial and/or recreational fisheries. Examples of economically and ecologically important Great Lakes fishes that are exploited as admixed fisheries include lake whitefish (Coregonus clupeaformis), walleye (Sander vitreus), lake trout (Salvelinus namaycush), lake sturgeon (Acipenser fulvescens), cisco (Coregonus artedi), Chinook salmon (Oncorhynchus tshawytscha), yellow perch (Perca flavescens) and steelhead (Oncorhynchus mykiss). For several of these species, both genetic and tag-recovery studies have shown substantial population intermixing. For example, Ebener et al. (2010a) through tagging found that more than half of tagged lake whitefish from some spawning populations in northern lakes Huron and Michigan moved to other areas in the lakes, which matches observations from genetic studies conducted in this same area (Stott et al. 2010). With intermixed fisheries, there often is a danger that less-productive populations may be overharvested, even to the point of extirpation, if harvest limits do not take intermixing into consideration (Hilborn and Walters 1992). Perhaps the most well-known cases of admixed fisheries negatively affecting individual spawning populations have occurred in the Pacific Northwest of North America, where entire spawning populations of Chinook, coho ( $O$. kisutch), pink (O. gorbuscha), chum (O. keta), sockeye ( $O$. nerka), and steelhead salmon have been extirpated (Morishima and Henry 1999). From a management standpoint, preservation of even low productivity populations is important so that genetic diversity of the species within a given region is maintained, which helps ensure viability and evolutionary potential of the species.

Despite recognition that many fisheries in the Great Lakes exploit mixtures of populations, stocks continue to be largely treated as discrete, independent units for management purposes. For example, most of the statistical catch-at-age (SCAA) assessment models that are used to estimate abundances and mortality rates for lake whitefish and lake trout in the 1836

Treaty waters of Lakes Huron, Michigan, and Superior make no accommodations for fish movement. The only exception to this is that in northern Lake Huron four formerly distinct assessment areas into one larger area and estimating a pooled total allowable catch (TAC) for lake whitefish (Caroffino and Lenart, 2011). Similarly, the SCAA models that are used to manage percids in Lake Erie do not account for movement of fish between the western and eastern basins or for fish moving into the Huron-Erie corridor or beyond. In both cases, this unaccounted movement could be impacting the accuracy of the SCAA model predictions, as well as the appropriateness of harvest limits that are set based on the different harvest control rules used to manage the respective fisheries.

The spatial issues being faced in Great Lakes fishery management are neither unique to the system nor surprising given general understanding of ecological processes. MacCall (1990) called for wider consideration in fishery management of how fish geographic distributions change in response to changes in density and habitat quality. There is a growing recognition that many managed populations actually consist of meta-populations (sensu Levins 1970), with processes occurring at spatial scales differing from those at which assessment or management occur. Despite this, in general, there is poor understanding of how fishery managers should pragmatically deal with population intermixing as attempts to incorporate movement into stock assessments or harvest policy evaluations is not frequently undertaken (Butterworth and Punt 1999; Quinn and Deriso 1999). In some cases, admixed fisheries are analyzed using a single set of population and management parameters with catch limits then apportioned to specific regions based on a particular policy, such as equal apportionment or apportionment based on a weighted average of relative biomass (Quinn et al. 1982, 1985; Deriso and Quinn 1983; Heifetz et al. 1997). Evaluations of these various apportionment policies, as well as other assessment and harvest policy approaches, with regards to their performance under different mixing and productivity scenarios have not been conducted.

Our immediate goal for this research project was to provide fishery managers insight into pragmatic techniques for dealing with admixture fisheries that exploit multiple spawning populations, both from the stock assessment and harvest policy perspectives. For example, during assessment phases, some practical approaches for dealing with intermixed fisheries are to assess fishery stocks as independent units, aggregate the data and conduct an assessment on a pooled stock, or to assess the fishery stocks treating movement between the stocks as known rates. None of these assessment approaches would be difficult to implement or require survey modification, but it is unclear whether one approach would perform better than the other approaches. Other pragmatic techniques that we envision could be used for managing admixed fisheries are discussed below in the experimental design section of this proposal. Ultimately, our aim is to promote management that will cost-effectively help ensure sustainable commercial/ recreational harvest of lake whitefish, lake trout, and walleye in the Great Lakes region.

The 4 objectives for this project as outlined in the original proposal were as follows: Objective 1) evaluate the relative performance of different fishing mortality control rules and three stock assessment approaches for dealing with intermixing (separate assessment models, combined model, treating movement as known) and how these harvest policies perform under various mixing and productivity scenarios; Objective 2) address how the spatial scale at which target fishing is applied affects performance by comparing case where target fishing mortality is applied to each population versus jointly across populations; Objective 3) address how harvest policy performance is affected by the frequency that stock assessments are conducted; and Objective 4) determine how mismatch in mixing rates between true and perceived systems
affected harvest policy performance. Two other objectives were added to the project based on interactions with Great Lakes fishery biologists as to methodologies that would be beneficial for the management of intermixing fish stocks: Objective 5) evaluate the estimability of model parameters within a release-conditioned tag-integrated catch-at-age assessment model under a range of conditions, and Objective 6) develop a model framework based on Bayesian variable selection for analyzing how factors influence net movement distances in a large water body based on conventional tag-recovery results
2. Briefly summarize any significant changes to the work performed in comparison to the plan of work originally proposed and funded. If changes were made, describe how they affected your ability to achieve the intended outcomes for the work.
The only change to the plan of work was Objectives 5 and 6 were added to the study concerning the assessment of intermixed fish stocks and degree of actual mixing in lake whitefish stocks in Lake Huron. Objective 5 was added to evaluate the estimability of model parameters within a release-conditioned tag-integrated catch-at-age assessment model. In our proposal we indicated that our immediate goal was to provide fishery managers insight into pragmatic techniques for dealing with intermixed fisheries that exploit multiple spawning populations, both from the stock assessment and harvest policy perspectives. As we worked through this project, Great Lakes fishery management agency biologists indicated their interest in using tag-integrated assessment models as part of quota-setting procedures, but they were unsure as to performance of tag-integrated assessment models. Thus, we conducted research into factors that can influence how well tag-integrated assessment models perform. Objective 6 was added to develop a model framework based on Bayesian variable selection for analyzing how factors influence net movement distances in fish populations. The purpose of this final objective was to develop a cohesive framework for understanding what factors contribute to population intermixing, which could assist in determining the anticipated degree of intermixing in other systems. The addition of these two objectives did not affect achievement of the intended outcomes of the project, although it did influence the timeline of the project.

## Outcomes

3. To what extent and how (if at all) did this research project advance scientific knowledge of the issue?
This research has shown that methods for managing intermixed fish stocks to a certain extent depend on characteristics of the species being managed. As far as assessment approaches to consider for intermixed fish stocks, the pooled approach was the most consistent method across the simulations conducted.
4. To what extent and how (if at all) did this project contribute to the education and advancement of graduate or undergraduate students focused on Great Lakes fishery issues?
Two Ph.D. graduate students, Ms. Yang Li and Mr. Matthew Vincent, were partly funded through this research project. Ms. Li and Mr. Vincent worked collaboratively with project PIs, Drs. Travis Brenden and Jim Bence, to conduct the simulation experiments laid out in the original proposal. Ms. Li and Mr. Vincent are presently Ph.D. candidates in the Department of Fisheries and Wildlife at Michigan State University and are expected to graduate sometime in 2017.
5. To what extent and how (if at all) did this work help you or others on your team build new relationships with others in the research or management communities?
As part of this project, we interacted with management and research biologists affiliated with the Great Lakes Indian Fish and Wildlife Commission, Michigan Department of Natural Resources, Minnesota Department of Natural Resources, Ohio Department of Natural Resources, Ontario Ministry of Natural Resources, Ontario Commercial Fisheries Association, and U.S. Fish and Wildlife Service. Although this was not the first opportunity that we had to interact with these biologists, this project nevertheless served to strengthen and enhance existing relationships.
6. To what extent and how (if at all) do the findings have action implications for fishery managers? If the research has direct management implications, do you have any knowledge of use of the finding by managers? If the research does not have direct management implications at this stage, to what extent did the research advance the process of identifying management responses to critical issues?
This research project was designed specifically to aid fishery managers with the assessment and management of Great Lakes fish stocks, so it has many action implications. We do not have any knowledge of our results already being used by fishery managers, nor would we expect immediate use because in some cases assessment approaches and harvest policies are specified as part of consent decrees or have been in use for a number of years and fishery management agencies are unlikely to quickly change approaches as it may have drastic implications on enacted quotas. However, in the future when management agencies are ready to consider revising the quota-management system for the fisheries for which they are responsible, we believe the results of this research project will provide valuable information for changes to consider.
7. Considering the above or other factors not listed, what do you consider to be the most important benefits or outcomes of the project?
The most important outcome from this project is that it provides information of direct relevance to Great Lakes fishery managers. As previously mentioned, many Great Lake fisheries exploit intermixed fish stocks even though the management framework largely used in the region is based on the unit-stock concept. The results from this project provide a reference of sorts for managers to consider as to management updates that could be considered for a particular species. Additionally, our research into tag-integrated catch-at-age models and Bayesian variable selection of factors affecting fish movement distance provides information to fishery managers both in the Great Lakes region and beyond as to the expected performance of these modeling approaches.

## Related Efforts

8. Was this project a stand-alone effort, or was there a broader effort beyond the part funded by the GLFT? Have other funders been involved, either during the time of your GLFT grant or subsequently?
At the time that we were notified that the Great Lakes Fishery Trust (GLFT) would be funding this project, we were notified by the Great Lakes Fishery Commission (GLFC) that we were receiving funding $(\$ 134,650)$ on a project relating to the assessment and management of intermixing fish populations. The GLFT and GLFC projects are different in the scope of work, but are quite complementary. The GLFT research focuses on general recommendations for how
best to manage intermixed fisheries, while the GLFC research project focuses on recommendations for specific cases. Because of the number of populations we will be modeling for the GLFC project, we anticipate simplifying how assessments are performed in the simulation model, while the GLFT project will still entail realistic assessment models. When we were notified by the GLFC that we would be receiving funding, we alerted the GLFC Science Director to the fact that we were receiving funding from the GLFT and described how the work differed but was still complementary. The GLFC Science Director was sufficiently comfortable with the distinctiveness of the project to approve the GLFC project for funding. We also previously notified Jonathan Beard about the GLFC project in earlier progress reports for this project.
9. Has there been any spin-off work or follow-up work related to this project? Did the work inspire subsequent, related research involving you or others?
There has not been any spin-off work from this project, although assessment and management of intermixed fish stocks remains a research interest of both Drs. Brenden and Bence so we anticipate future spin-off work is likely.

## Communication/Publication of Findings

10. List publications, presentations, websites, and other forms of formal dissemination of the project deliverables, tools, or results, including those that are planned or in process.

## Publications

Li, Y., J.R. Bence, and T.O. Brenden. 2015. An evaluation of alternative assessment approaches for intermixing fish populations: a case study with Great Lakes lake whitefish. ICES Journal of Marine Science 72:70-81.
Li, Y., J.R. Bence, and T.O. Brenden. 2016. The influence of stock assessment frequency on achievement of fishery management objectives. North American Journal of Fisheries Management 36:793-812.
Vincent, M.T., T.O. Brenden, and J.R. Bence. In preparation. Accuracy and precision of parameter estimates of a multi-region tag-integrated catch-at-age assessment model evaluated through simulation analysis. Target Journal: Canadian Journal of Fisheries and Aquatic Sciences
Li, Y., J.R. Bence, Z. Zhang, and M.P. Ebener. In preparation. Bayesian variable selection for the determination of factors related to Lake Huon lake whitefish net movement distance. Target Journal: Fisheries Research

## Presentations (* indicates presenter)

Li, Y., J.R. Bence, T. O. Brenden, and M.T. Vincent*. 2016. Simulation-based evaluation of assessment approaches for intermixing fish populations. Invited Presentation: 2016 AFS Annual Meeting, Kansas City, Missouri.
Vincent*, M., T.O. Brenden, and J.R. Bence. 2015. Simulation analysis of tag-integrated catch-at-age models. Oral Presentation: 2015 AFS Annual Meeting, Portland, Oregon.
Vincent*, M., T. Brenden, and J.R. Bence. 2015. Assessment of tag-integrated catch-at-age models through simulation and application to Lake Erie walleye. Oral Presentation: 2015 Department of Fisheries and Wildlife Graduate Student Organization Research Symposium, East Lansing, Michigan.

Li*, Y., J.R. Bence, and T.O. Brenden. 2014. Sensitivity of fishery management performance to alternative frequencies of stock assessments. Oral Presentation: 2014 AFS Annual Meeting, Quebec City, Quebec.
Li*, Y., J.R. Bence, and T.O. Brenden. 2013. Modeling intermixing lake whitefish populations: a simulation study to evaluate alternative stock assessment methods. Oral Presentation: World Conference on Stock Assessment Methods, Boston, Massachusetts.
Li, Y., J.R. Bence*, and T.O. Brenden. 2013. Relative influence on assessment frequency and assessment model structure of fishery management performance. Oral Presentation: World Conference on Stock Assessment Methods, Boston, Massachusetts.
Li*, Y., J.R. Bence, and T.O. Brenden. 2013. Evaluating fishery assessment approaches for intermixing lake whitefish populations. Oral Presentation: 2013 Department of Fisheries and Wildlife Graduate Student Organization Research Symposium, East Lansing, Michigan.
Li*, Y., J.R. Bence, and T.O. Brenden. 2013. Addressing intermixing of lake whitefish populations comparing fishery management and assessment performance based on alternative assessment approaches. Oral Presentation: 2013 Canadian Conference for Fisheries Research, Windsor, Ontario.
11. Please characterize your efforts to share the findings of this research with state, federal, Tribal, and interjurisdictional (e.g., Great Lakes Fishery Commission) agencies charged with management responsibilities for the Great Lakes fishery, If other audiences were priority for this research, please characterize your outreach efforts to the audiences as well. (Please note: You may wish to consult midterm reports in which specific audiences for the findings, and means of outreach to these audiences, were identified.)

Mr. Matt Vincent regularly attended Lake Erie Walleye Task Group meetings to discuss his dissertation research and to engage Task Group Members for data, information, and suggestions regarding parameterization of simulation models for his dissertation research and this research project. Similarly, Ms. Yang Li regularly attended Modeling Subcommittee Meetings for the 1836 Treaty-Ceded Waters to obtain data and suggestions from MSC members on Lake Huron lake whitefish. Additionally, the management and assessment of intermixed fish stocks is of research interest at both national and international scales and thus we Mr. Vincent and Ms. Li presented their research at several American Fisheries Society Annual Meeting and at a World Conference on Stock Assessment Methods.
12. Please identify technical reports and materials attached to this report by name and indicate for each whether you are requesting that GLFT restrict access to the materials while you seek publication. (Please note that the maximum amount of time during which GLFT will restrict access to the results of funded research is six months, unless notified that more time is needed.)
We request that access be restricted for Attachments 2, 3, 5, 6, 7, and 8. Attachment 7 (Vincent et al. Accuracy and bias of parameter estimates of a multi-region tag-integrated catch-at-age assessment model evaluated through simulation analysis) is presently being considered for publication in Canadian Journal of Fisheries and Aquatic Sciences. Attachment 8 (Li et al. Bayesian variable selection for the determination of factors related to Lake Huon lake whitefish net movement distance) is being finalized for submission for possible publication in Fisheries

Research. We are requesting restricted access on Attachments 2, 3, 5, and 6 as we finalize plans for attempting to publish results from these objectives.
> 13. Manuscripts: Grantees submitting one or more publications or pending publications in lieu of a stand-alone technical report must submit a cover memo that confirms that all aspects of the funded research are incorporated in the published work, and in cases of multiple publications, identifies or crosswalks the grant-funded objectives to the published article containing results.

See attached cover memo.
14. Compilation reports. Grantees working on several related sub-projects under a single grant may submit a series of sub-project reports rather than a single, integrated report. However, grantees must submit a cover sheet or introduction that outlines and crosswalks grant objectives with the location of the results in the compilation document.
See attached cover memo.

## Discussion

Objective 1) evaluate the relative performance of different fishing mortality control rules and three stock assessment approaches for dealing with intermixing (separate assessment models, combined model, treating movement as known) and how these harvest policies perform under various mixing and productivity scenarios;

We found that performance of different fishing mortality control rules and assessment approaches varied by species, which means that fishery managers should be cautious in simply adopting approaches that others have used elsewhere. We are a little suspect of the results from lake trout given how different they were from the other species. We consider these results to be preliminary and will be conducting follow-up work to explore whether the results for lake trout were indeed accurate or were perhaps a consequence of problems in computer code or estimation of stock-recruitment parameters based on the study of Nieland et al. (2008). However, even apart from the suspect results for lake trout, there were differences observed between the simulations based on Lake Huron lake whitefish and Lake Erie walleye. In particular, for simulations based on Lake Erie walleye the overlap assessment approach had estimation issues whereas for Lake Huron lake whitefish the separate assessment approach had estimation issues. Across all 3 sets of simulations as well as the additional research by Li et al. (2015), the pooled approach provided the most consistent results. Thus, based on our research, the pooled approach might be an initial approach to consider when managing intermixed fish stocks, although in some situations other assessment approaches could perform better. A clear advantage of using the pooled approach to managing fish stocks is that it does not depend on having estimates of fish movement rates. However, one added complexity from a pooled assessment approach is then deciding how to allocate allowable harvest levels to different fisheries. In the research for our objective, we allocated harvest based on the annual area-specific catch per unit effort observed from the regions. Other approaches could be considered and we encourage further research into this topic. Recently, in the 1836 Treaty-ceded waters of Lake Huron, several lake whitefish management units were pooled together for assessment and management purposes. Based on the results from this objective, this was an appropriate choice for that circumstance.

Based on the results from the lake whitefish and walleye simulations, the best harvest policy to adopt was the lowest total annual mortality control rule, which was based on $50 \%$ of the fishing mortality that produced the maximum sustainable yield for the least productive stockrecruitment relationship. Any higher total mortality control rule engendered some risk to at least some populations in some of the scenarios examined. Although the lowest total annual mortality control rule reduced the amount of yield that could be taken from the regions, at least in the case of lake whitefish it also resulted in the lowest inter-annual variability in yield. The simulations based on lake trout suggest in some situations higher mortality control rules could be adopted without endangering spawning populations; however, we again are suspect of these results and will be investigating further. A variety of simulation studies have shown that low productivity spawning populations can be at risk of overharvest when fisheries exploit mixtures of fish populations. The results from this objective further supports this as an area of concern for fishery managers.

Objective 2) address how the spatial scale at which target fishing is applied affects performance by comparing case where target fishing mortality is applied to each population versus jointly across populations

From a management standpoint, we found little benefit to targeting total annual mortality control rules to individual fishing regions in situations of intermixing fish populations. If such an approach is being considered, the results from this objective suggests that control rules would need to be conservative (e.g., based on $25 \%$ of the $F_{M S Y}$ calculated from the fitted stockrecruitment relationship to the estimated stock recruitment data from the mixture). It is possible other approaches to setting target fishing mortalities for fishery regions perhaps could prove more beneficial for this purpose. Absent of finding such a method, our recommendation would be to consider adding a fishery independent survey at time periods when populations are not intermixed to determine the productivity level of individual spawning populations or to consider genetic or other data sources for determining what spawning populations are contributing to mixtures.

## Objective 3) address how harvest policy performance is affected by the frequency that stock assessments are conducted

Li et al. (2016) baseline research - Based on the baseline research conducted by Li et al. (2016) addressing this objective for a single population, we found that decreasing assessment frequency across most of the conditions considered herein resulted in greater risk of stock depletion, lower relative yields, and greater realized $F$. Multiannual assessments also resulted in greater IAV in yield, but unlike the other performance metrics, IAV in yield did not necessarily get progressively worse when moving from triennial to quinquennial assessments.

If there were no costs to conducting assessments of fish stocks, the results of Li et al. (2016) would generally be supportive of annual assessments without a lag between data collection and assessment. However, it is unrealistic to not consider those results in light of assessment costs. The trade-offs between the costs of conducting more frequent assessment versus the benefits of obtaining higher yields and avoiding risk of depletion will need to be considered on a system- and stock-specific basis. Based on the results of Li et al. (2016), the obvious candidates for less frequent assessments are those where target fishing mortality rates are low and/or productivity is high. In such situations, the risks of substantial depletion are generally low, and the costs in terms of forgone yield are lower than when productivity is lower
or target fishing rates are higher. The conclusions of Li et al. (2016) correspond to some extent with those from ICES (2012), where it was concluded that stocks under modest exploitation should be considered as potential candidates for less frequent than annual assessments. ICES (2012) added the additional condition that stocks should be stable, which is similar in vein to our recommendation that low productivity stocks are less viable candidates for multiannual assessments.

Most published studies that have considered stock assessment frequency have focused on the consequences of management delays after major shifts in population dynamics and/or ecosystem characteristics (Shertzer and Prager 2007; De Leeuw et al. 2008; Brown et al. 2012). Shertzer and Prager (2007) and De Leeuw et al (2008) found that delays in management responses could result in long-term losses and longer recovery times. However, those studies both focused on stocks that were substantially depleted, and the delays that resulted in the greatest loss were on the order of 10 or more years. Brown et al. (2012) found that if environmental change caused population declines, delays greater than 5 years increased the chance of population collapse. Unlike these previous studies, our study was designed to explore the long-term consequences of assessment frequency under steady-state conditions, rather than an ability to respond to a one-time major change. Nevertheless, the longest assessment frequency we considered (quinquennial) was found by these other studies to be sufficient for detecting and responding to one-time changes.

The one-year lag between data collection and incorporation in the stock assessment model of Li et al. (2016) matches the process that has been used for Lake Whitefish stocks in 1836-Tready ceded water since 2000. The study of Li et al. (2016) is the first evaluation of the long-term influence of such a lag as far as we are aware. Management agencies oftentimes expend considerable efforts to avoid lags of this nature so that harvest recommendations can be made based on the most recent collected data. The results of Li et al. (2016) suggest that, at least for fish with life histories similar to Lake Whitefish, removing the one-year lag may slightly reduce risk of stock depletion, and moderately decrease inter-annual variation (IAV) in yield, but is not expected to have any major effect on typical yield levels. The higher IAV in yield when there was a lag reflects somewhat poorer quality assessments and thus more variable realized fishing mortality, which outweighs any added constancy resulting from assuming that the most recent recruitment was equal to a historical average. Thus, for stable stocks that are not in danger of being overfished, and where constancy in yield is not of overriding importance, avoiding the one-year lag may not be worth the associated costs, which might include conducting assessments with data that have not been properly vetted.

The consequences of a one-year lag became more pronounced as recruitment variation and mortality targets increased. We attributed this result to the process used to forward project population conditions through the lag [i.e., mean recruitment and fishing mortality rates estimated as part of the stock assessment for the last 10 (recruitment) or 3 (fishing mortality) years]. Mean recruitment generally exceeded typical values due to the right skewness of recruitment distributions and the average fishing mortality tended to be lower than typical values also due to skewed distributions of values. This mechanism also contributed to the performance of the multiannual assessments. Understanding what may be causing some of the costs of lags and infrequent assessments suggests that these could be ameliorated by changes in how projections are done when calculating harvest limits. In particular, future analyses may want to consider potential benefits of using different projections of recruitment and fishing mortality
(e.g., using median rather than mean recruitment levels or mortality rates so that values were less sensitive to outliers).

While data quality did not influence the main conclusions of Li et al. (2016) regarding when to implement less frequent assessments, clearly there are limits to the applicability of this conclusion. Higher quality than what were considered in our study or different types of data (e.g., annual surveys providing absolute measures of population abundance) might lead to greater benefits for annual assessments. As evidenced by the sensitivity analysis of Li et al. (2016), one consequence of very low quality data is that more frequent assessments can result in greater IAV in yield thus there may be benefits to adopting a more conservative and constant strategy (i.e., less frequent assessments) in such situations. Given the range of data quality that is reflective of important fish stocks in the Great Lakes and elsewhere, the results of Li et al. (2016) appear robust to data quality.

One of the consequences of multiannual assessments was that the realized fishing mortality rate (i.e., the true fishing mortality that stocks experience) was greater than when assessments were conducted annually. When Li et al. (2016) checked the trajectory of realized fishing mortality for individual simulations under the multiannual stock assessment scenario, it was found that the trend of realized fishing mortalities during non-assessment years depended on the realized fishing mortality in the starting year in each assessment period. If the realized fishing mortality was greater than the target fishing mortality at the start, the realized fishing mortality continued to increase and result in larger-and-larger discrepancies from the target fishing mortality. Conversely, if it started from a value lower than target fishing mortality, true fishing tended to become even lower in later years. These two situations, however, have asymmetrical consequences. Severe overfishing could occur between assessments, leading to cascading increases in realized fishing mortalities as the stock was depleted. In contrast the effect of more conservative than intended fishing led to more modest increases in stock size and decreases in true fishing mortality.

The results of Li et al. (2016) indicated that the manner in which harvest targets are set between full assessment years overall was less important than assessment frequency. The approach was most important in influencing interannual variation of yield. The two forward projection approaches to set harvest targets between full assessment years resulted in higher interannual variation of yield than using the same target from the last full assessment. Although the difference in other management performance was modest, using the same target among nonassessment years had lower risk of stock depletion and higher yield than the other two when productivity was not high and mortality target was not low, especially for quinquennial assessments. The failure of the two forward projection rules in those cases was largely due to the assessment error. The assessment error would be amplified in the forward projection years, given the target harvest in those years were always estimated based on the biased-estimated stock. Regardless of the interannual variation of yield, calculating harvest targets during the years between assessments based on updating TACs to match observed harvest from previous lag years (AH) generally was among the better performing rules, especially when target mortality rates was low. This may due to the annual adjustment and early detecting mechanism for the AH rule, in which overfishing could be detected earlier than other rules.

The basic premise of the Li et al. (2016) study was that annual harvest targets would be set on the basis of a fitted stock assessment model and that when the model was not fit every year, target harvests between assessment years would either remain unchanged or be based on model projections since the last stock assessment. Alternatively, one could view the periodic
assessments as providing a calibration between some empiric quantity (such as catch per effort) and an appropriate harvest level (Cox and Kronlund 2008; Holland 2010). One version of this simply might be to treat periodic assessments as a way to update catchability estimates to translate catch per effort to abundance. Alternatively, one could revise the view of assessments by Li et al. (2016) to be primarily about gaining an understanding about how population dynamics work, for use in evaluating alternative strategies (McDonald et al. 1997; Punt 2008). In the study of Li et al. (2016), the only use of data that was considered for the period between assessments was in making projections consistent with observed yield. The higher variability Li et al. (2016) observed in this case likely reflects, in part, the fact that this procedure does not smooth out any of the measurement error, as fitting a dynamic model does. While empiric procedures also can experience higher variation for the same reason, survey or fishery catch per effort might be more informative and potentially could extend the period between assessments if they were used as indicators to either adjust model-based target harvest or as a signal to do a new assessment earlier than planned. ICES (2012) also discussed the value of using key indicators as a guide to management between times of full assessments, and there is still much to be learned in the optimal approach to applying assessment efforts. Although Li et al. (2016) only considered the constant mortality rate harvest strategies, given the strong preference of managers of Lake Whitefish stocks for this strategy, it is possible that a state-dependent mortality rate, for example one that declines when biomass is low (Wilberg et al. 2008), could be more sensitive to changes in assessment frequency. Additional studies are needed to evaluate the influence of assessment frequency for fisheries that use such management strategies.

Intermixing conditions - In the case of the consequences of multiannual assessments in intermixed fisheries, the most noticeable affect was that IAV in yield decreased when moving from annual to multiannual assessments. From the Li et al. (2016) research, greater IAV in yield with more frequent assessments occurred in situations of low quality data. As evidenced by the sensitivity analysis of Li et al. (2016), one consequence of very low quality data is that more frequent assessments can result in greater IAV in yield thus there may be benefits to adopting a more conservative and constant strategy (i.e., less frequent assessments) in such situations. Based on these results, it seems reasonable to conclude that from an assessment perspective the occurrence of intermixing imparts a data quality issue on measured data perhaps as a consequence of propagating variances of individual spawning populations via process error in recruitments. This in the case of intermixing fisheries, there may be benefits to not conducting assessments annually.

## Objective 4) determine how mismatch in mixing rates between true and perceived systems

 affected harvest policy performanceMismatch in mixing rates between the true and perceived systems were not found to have a large effect on total annual mortality control rules. Randomly varying rates in either the true system or perceived system increased the variability among the simulations within a particular scenario, but did not affect how individual populations responded to different total annual mortality control rules. Trending mixing rates in either positive or negative directions in the true system when rates were fixed in the perceived system had the largest effect on simulation results, suggesting that systematic variation in mixing rates may be a larger problem for the assessment of intermixed fish stocks. However, even then the mismatch in movement rates did not really impact overall conclusions on control rule performance.

Objective 5) evaluate the estimability of model parameters within a release-conditioned tagintegrated catch-at-age assessment model under a range of conditions

Part of our motivations for investigating the performance of release-conditioned tagintegrated catch-at-age assessment (ITCAAN) was that we envisioned there could be confounding among parameters that fishery scientists might be interested in estimating. In particular, we envisioned there could be complications that could arise when estimating movement rates, reporting rates, and/or natural mortality along with other parameters that are routinely estimated in assessment models. One of the main parameters of interest in an ITCAAN model is the estimation of movement rates among the stocks. Goethel et al. (2015b) demonstrated that spatially explicit catch-at-age models without tagging data and high variance in catch-at-age data can result in poor movement estimates. Accordingly, some form of tagging is likely necessary for movement rates to be estimated in spatial assessment models. Across the range of scenarios considered in this research, movement rates were accurately and precisely estimated even at the lowest tagging level. Previous simulations of ITCAAN models under different movement dynamics also found that movement rate estimates were accurate even when movement varied as a function of environmental variables (Hulson et al. 2013) or as a function of regional population density (Goethel et al. 2015b). Our findings from this objective in combination with these other studies suggest that unbiased and precise estimation of movement is a robust feature of ITCAAN models. However, this conclusion may depend on the simplistic movement models in the operating models used to generate the tagging data. The methods employed in this objecitive, as well as those of Hulson et al. (2013) and Goethel et al. (2015b), assumed that movement occurred instantaneously and that after movement fish became sedentary. In actuality, movement will not be instantaneous and may vary seasonally or across even shorter time periods. Future evaluations of ITCAAN models would benefit from including more complex movement scenarios to determine whether the apparent robustness of ITCAAN models for estimating movement is a general feature of the models or an artifact of the simplified movement characteristics assumed in previous simulations.

We found that both natural mortality and reporting rates can be accurately and precisely estimated in an ITCAAN model assuming natal homing, although both accuracy and precision diminished when the parameters were estimated together and movement rate increased. Accuracy and precision of natural mortality and reporting rates were largely unaffected by the degree of measurement error assumed in fishery effort, harvest, and survey indices of abundance data and effective sample size of age composition data, but they were affected by tagged cohort sample size. This suggests that the tag-recovery data primarily inform the estimation of natural mortality and reporting rates in ITCAAN models. Bias and precision in reporting rates and natural mortality were also affected by the degree of spatial complexity assumed in reporting rates and natural mortalities in the ITCAAN model. This has important implications because with fish populations exhibiting complex spatial structuring, both fishery dynamics and stock population dynamics are likely to vary spatially. For example, natural mortality can vary because of differences in temperature, water quality, and/or prey availability (Vetter 1988); conversely, reporting rate can vary because of the type of fisheries operating in a region (Vandergoot et al. 2012) or how well a tagging study is advertised. In some cases, it might be possible to estimate spatially-varying parameters by modeling rates as a function of some measured quantity, such as modeling natural mortality as a function of temperature. Prior to this being attempted, careful consideration will be needed to determine whether parameters should be modeled as a spatial feature or an innate feature of the originating stock. Regardless, our findings illustrate that
caution should be used when considering expanded parameterization within ITCAAN models as greater model complexity may lead to greater variability in parameter estimates. One approach to consider would be using a model selection criteria, such as deviance information criteria, to determine how spatially complex of an ITCAAN model may be supported by observed data (Wilberg and Bence 2008; Linton and Bence 2011).

The estimation of reporting rates within an ITCAAN model is a recent proposal (Goethel et al. 2015a,b). Our findings from this objective found that reporting rates could be estimated with some bias and moderate precision when the natural mortality rate was correctly specified or estimated. These findings align with the reproductive mixing ITCAAN model of Goethel et al. (2015b). However, our results showed that misspecification of natural mortalities in the ITCAAN model can result in biased estimates of reporting rates and total abundance of the stocks. The study by Goethel et al. (2015b) assumed natural mortality was correctly specified, and did not assess the estimation of natural mortality with reporting rate. Though the difference in how movement is modeled between our research for this objective and Goethel et al. (2015b) makes extrapolation uncertain, we hypothesize that the low reporting rates estimated for the three regions individually in the reproductive mixing ITCAAN model of Goethel et al. (2015b) were much lower than the estimated reporting rate for all areas combined from the high reward tagging study (Cadrin 2006) due to misspecification of natural mortality in the ITCAAN model. Accordingly, we caution that estimation of reporting rates in ITCAAN models when fixing natural mortalities at assumed values should be undertaken with caution and only when there is a high degree of confidence in natural mortality estimates. Alternatively, the estimation of reporting rates and natural mortalities could be improved by incorporating methods that normally are factored into tagging studies when attempting to estimate reporting rate; for example, the release of high-reward tags, using observers, or planted tags (Polacheck et al. 2006; Eveson et al. 2007) could be incorporated into the likelihood of the ITCAAN model.

Given the consequences on ITCAAN model parameter estimates from misspecifying reporting rates and natural mortalities, we advocate initially attempting to estimate these parameters simultaneously rather than fixing them at assumed values. Admittedly, the ability to estimate reporting rates and natural mortalities simultaneously might be more challenging than what we encountered because data generated in simulation studies under-represents the degree of uncertainty likely encountered in actual data. Our simulation scenarios that explored the consequences of data quality showed that greater levels of bias and imprecision in parameter estimates resulted with lower quality data; however, the amount of bias in parameter estimates were generally greater when reporting rates or natural mortalities were misspecified. Our simulations did not include errors in model structure, which may affect the ability to estimate reporting rates and natural mortalities. However, such model errors would also affect parameter estimates when reporting rates or natural mortalities were fixed at assumed values. Therefore, it is difficult to determine whether under such conditions it indeed would be better to fix natural mortalities or reporting rates at possibly incorrect quantities.

One of the key findings from this objective was that under conditions of high movement and large differences in spawning population size, ITCAAN models were biased and imprecise estimators of individual stock annual recruitment. However, overall total abundance estimates were relatively unbiased and precise, though precision decreased as movement rates increased. Higher movement rates also affected precision of most other parameters that were considered, but estimates remained unbiased. Very small biases in movement estimates may have been exacerbated by the large differences in stock size that resulted in the large biases in individual
stock recruitment estimates. However, biases in stock recruitment estimates become more pronounced when reporting rates were estimated, which may indicate that the estimation of reporting rates within an ITCAAN model could lead to biased estimates if large differences in stock size are present. These biases in recruitments and reporting rate dissipate when parity in stock-recruitment relationships was assumed for the spawning stocks. One of the major motivators for incorporating spatially-explicit dynamics in assessment models is the concern that less productive stocks may be overexploited or even extirpated if spatially-varying dynamics are not incorporated in the management process $\backslash$ citep $\{$ Molton13,Li14\}. Although in our simulations we assumed fairly large differences in stock size among the spawning stocks, such differences arguably may be more reflective of actual conditions for many species than an assumption of equality in stock-recruitment relationships. Consequently, the potential for overestimating recruitment of smaller stocks and underestimating recruitment of larger stocks under conditions of high movement and large differences in relative size of spawning stocks is an important issue to consider for fishery scientists looking to implement ITCAAN models.

Objective 6) develop a model framework based on Bayesian variable selection for analyzing how factors influence net movement distances in a large water body based on conventional tagrecovery results

The goal of this objectives was to evaluate which physical and environmental factors most likely influenced lake whitefish net movement distance in Lake Huron using a data-driven Bayesian variable selection method. Variables that examined for Lake Huron lake whitefish net movement distances included total length and sex of a tagged fish, tag and release year, recovery year, recovery month, years between tagging and recovery, Diporeia spp. density near the spawning locations relative to the lake-wide Diporeia spp. density, relative difference between the tagging site and lake-wide growing degree days (GDDs), and the interaction term between lake-wide growing degree days and recovery month. Some of above hypotheses were well supported by the results presented.

There was a significant positive relationship between lake whitefish net movement distance and fish total length at the time of tagging. This is consistent with conclusions from previous studies of stream-dwelling fish, in which longer movement and home range was observed for larger fish (Gunning and Shoop, 1963; Gatz and Adams, 1994). This greater movement may be due to the increasing mass-specific bioenergetic costs of mobility with decreasing body size (Roff, 1991). Minns (1995) also found that the home range is related to body size in freshwater fish and is consistently larger in lakes than in rivers.

Because of the spawning site fidelity of lake whitefish, recovery months were expected to have significant effects on net movement distance. Ebener et al. (2010b) demonstrated that season of recapture played an important role in the distance moved by lake whitefish. In our study, net movement distance was negatively related to recovery month September, October and November, and positively related to December. This suggested that the spawning migration movement for lake whitefish generally occurred within months from September to November, and after that, fish left their spawning site in December.

Past research has documented that some life history events such as reproduction can be accelerated with warmer water temperatures (Forseth et al., 1999). For example, the spawning of walleye in Minnesota occurred earlier with earlier ice-out related to warmer temperature (Schneider et al., 2010). Similar patterns were found from the research conducted for this objective. When lake average GDD was higher, lake whitefish tend to move or stay closer to
their spawning sites from September to November, and to be further away from their spawning sites in December. This suggests that fish may start their annual spawning migration runs earlier in warmer years after acquiring and processing energy needed for spawning. The underlying mechanism could be that fish have to either achieve a critical condition before the cost of migration/spawning can be offset (Forseth et al., 1999), or to accumulate enough energy to survive a winter starvation period before spawning.

Although the decline of Diporeia spp. density in the Laurentian Great Lakes due to the establishment of dreissenid mussels has been argued as the main reason of lake whitefish expanding their movement range (Ebener et al., 2010b; Rennie et al., 2012), we know of no other direct evaluation of an effect of Diporeia density on movement. The research for this objective evaluated this hypothesis by including relative Diporeia spp. density as a predictor for modeling lake whitefish net movement distance, and we found that when relative Diporeia spp. density was high near the spawning grounds, lake whitefish tended to stay closer to the spawning sites. This implies that lake whitefish might expand their foraging area when Diporeia density was low near their preferred habitat. Our analysis focused on the effect of the relative density of Diporeia within a year, and thus our results suggests a pattern related to the density of this prey, other than a general change in movement over time throughout the lake as Diporeia declined.

Lake whitefish tagged and released from the spawning locations at Cheboygan and Alpena had significantly greater net movement distance than those released from other areas. Such finding is consistent with Ebener et al. (2010b), in which stock was found to be the dominant feature influencing lake whitefish movement. Although we are not sure about the underlying reasons why lake whitefish stocks spawning near Cheboygan and Alpena had greater spatial distribution than other stocks, we thought this may related to the amount of spawning and nursery habitats closed to their spawning habitat. The more/better spawning and nursery habitats nearby, more opportunities fish stocks become distinct in those areas. Bathymetry in combination with shoreline can also have impact on fish movement (Ebener et al., 2010b).

