Control rule performance for intermixing lake whitefish populations in the 1836 Treaty waters of the Great Lakes: A simulation-based evaluation

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A B S T R A C T

We conducted a simulation-based evaluation exploring the effects of population intermixing on the current 65% total annual mortality control rule used to manage lake whitefish (Coregonus clupeaformis) fisheries in the 1836 Treaty waters of the Laurentian Great Lakes. The simulations incorporated intermixing among four populations with characteristics similar to those of lake whitefish in northern lakes Huron and Michigan. Dynamics of each population were simulated for 100 years with each stock exploited by a single fishery. An age-structured assessment of each stock was conducted every third year, with the abundance, mortality, and recruitment estimates used with the current control rule to set future harvest limits. Overall aggregate yield of the modeled system was generally not affected by intermixing, but did depend on assumed productivity levels. Mean annual yields for individual fisheries were sensitive to mixing levels, with yields from fisheries coinciding with low productivity spawning populations often similar to those coinciding with high productivity populations when intermixing occurred. Variability in yield tended to decrease slightly as mixing rates increased. Intermixing did not have a large influence on measures of spawning population sustainability, but detection of declining population sizes in low productivity populations may be difficult when intermixing occurs because of fishery yields remaining high due to immigration of fish from other spawning areas. This raises concern about the current control rule given that low productivity populations had spawning population sizes less than 20% of the unfished level in most years.

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Introduction

Stock-based management of exploited fish populations has long been an important tool of fishery managers (Stephenson, 1999). This management approach typically involves assigning spatial management units and assessing the dynamics of fish populations occurring within the boundaries of each unit to set harvest levels. A common underlying assumption of stock-based management is that an exploited stock consists of fish from a single spawning population rather than multiple spawning populations (Fig. 1). When an exploited stock actually consists of intermixed fish from multiple spawning populations (Fig. 1), past research has found that stock-based management approaches can perform poorly (Dichmont et al., 2006; Heifetz et al., 1997; Punt, 2008; Punt et al., 2005; Quinn and Deriso, 1999). In extreme cases, severe reductions in abundances or complete extirpation of spawning populations can result if intermixing of populations is not accounted for in a manner consistent with actual conditions. Perhaps the most well-known case of intermixed fisheries negatively affecting individual spawning populations is the salmon fisheries of the Pacific Northwest of North America where low productivity spawning populations of Chinook salmon (Oncorhynchus tshawytscha), coho salmon (Oncorhynchus kisutch), pink salmon (Oncorhynchus gorbuscha), chum salmon (Oncorhynchus keta), sockeye salmon (Oncorhynchus nerka), and steelhead (Oncorhynchus mykiss) have been extirpated due in part to overfishing in mixture fisheries (Morishima and Henry, 1999). Overharvest of spawning components is also believed to have contributed to collapse and delayed recovery of Atlantic cod (Gadus morhua) and Atlantic herring (Clupea harengus) stocks in northeastern North America (Anes, 2004; Fu and Fanning, 2004; Lilly et al., 2008; Sinclair et al., 1996; Smedbol and Stephenson, 2001).

Lake whitefish (Coregonus clupeaformis) fisheries in the 1836 Treaty waters of lakes Huron, Michigan, and Superior are one example of a species in the Laurentian Great Lakes that are managed using a stock-based approach. The 1836 Treaty waters have a surface area of approximately 5.8 million ha and were ceded to the U.S. federal government by the Chippewa and Ottawa Nations of Native Americans as part of the Treaty of Washington. Management, allocation, and regulation of the fishery resources in the 1836 Treaty waters are governed through a consent decree that was entered into by the State of Michigan, the U.S. Department of Interior, and several Chippewa–Ottawa tribal governments (Ebener et al., 2008). The consent decree specifies that
the 18 lake whitefish management units lying within the 1836 Treaty
water boundaries are to be managed with a 65% total annual mortality
control rule, which has been interpreted operationally to mean 65%
total allowable annual mortality on the age class with the greatest
fishing mortality. The consent decree additionally specifies that harvest
limits or targets within the management units are to be determined
using appropriate statistical and mathematical modeling techniques.
Presently, statistical catch-at-age (SCAA) models are used to annually
estimate mortality rates and project lake whitefish abundances at
age for most management units (Caroffino and Lenart, 2011). These
projected abundances along with the 65% total annual mortality control
rule are then used to generate recommended harvests, which form
the basis for setting total allowable catches (TAC) or other fishery
regulations for the management units (Ebener et al., 2005; Mohr and
Ebener, 2005).

Lake whitefish management units in the Great Lakes were origi-
nally delineated to protect spawning populations and maintain gen-
etic diversity of the populations in the region (MacLean and Evans,
1981; Patriarche, 1977; Spangler et al., 1981). Recently, however,
benthic communities in the Great Lakes have undergone considerable
restructuring, including the collapse of the preferred prey of lake
whitefish, Diporeia spp., and increased abundance of non-native
dreissenid mussels (Nalepa et al., 1998, 2007, 2009b). This benthic
community restructuring along with major increases in lake
whitefish abundances (Ebener et al., 2008) is believed to have altered
lake whitefish foraging behavior (Nalepa et al., 2009a; Pothoven and
Madenjian, 2008). Indeed, a recent tagging study conducted in north-
ern lakes Huron and Michigan suggested that lake whitefish dispersal
after spawning has increased considerably over the last 15 to
30 years, possibly as a result of fish expanding foraging areas to
meet energetic and nutritional needs (Ebener et al., 2010). Conse-
quently, spawning populations of lake whitefish now intermix sub-
stantially during non-spawning periods. Multiple genetic studies
have confirmed this intermixing of lake whitefish spawning popu-
lations during periods of exploitation (Stott et al., 2010, 2012;
VanDeHey et al., 2009).

Ultimately, the effect of harvest on an intermixed group of inde-
pendent spawning populations depends on the degree of mixing,
the productivities of the spawning populations, and the policies that
are used to regulate the fisheries. Within the 1836 Treaty waters, it is
not clear how sustainability of individual fish populations may be affect-
ed by intermixing under the current control rule. Originally, the 65%
total annual mortality control rule was adopted based on research
that indicated that this level of mortality was sustainable, and substan-
tially higher mortality rates were not (Ebener et al., 2008, Deroba and
Bence (2012) found that the 65% total annual mortality control rule
allowed significant harvest without high risk of overexploitation even
with changes in life history characteristics of lake whitefish in recent
years. However, intermixing among populations was not evaluated by
Deroba and Bence (2012). Furthermore, their focus was on the overall
distribution of performance metrics, and not on the fate of individual
spawning populations. Thus, concerns remain as to whether the current
limit on mortality is sufficient to ensure sustainability of lake whitefish
populations in the 1836 Treaty waters given that intermixed spawning
populations may differ in productivity.

The purpose of this research was to conduct a simulation-based
evaluation of the sensitivity of the 65% total annual mortality control
rule that is currently used to manage lake whitefish fisheries in the
1836 Treaty waters of the Great Lakes to different levels of population
productivity and intermixing. The goal was to provide guidance to man-
ger as to what effect different intermixing and productivity scenarios
could have on commercial fishery harvest and sustainability of lake
whitefish populations if they continued to be managed under the existing
control rule.

Materials and methods

Definitions of terms

Herein, population and spawning population are used interchange-
ably and refer to a group of fish that spawn in the same geographical
area and exhibit natal philopatry. The area where these fish spawn is
called either a fishing area or a spawning ground. Similarly, stock and
mixed stock are also used interchangeably and refer to fish that
reside in a particular geographic area during the period of fishery har-
vest, and may contain fish from several different spawning populations
if mixing occurs. The area where a stock is exploited is called either
a fishing area or a fishing ground. This means that all aspects of the
fishery (i.e. harvest and assessment) occur in relation to stocks, while
measures such as spawning population size and recruitment are charac-
teristics of populations. We assumed that the areas where spawning oc-
curred were each contained within an area targeted by a single fishery
(its fishing grounds), but members of spawning population during the
fishing season were allowed to move to fishing areas coinciding with
different spawning areas. Thus, with mixing, portions of the i-th popu-
lation could be part of the i-th stock, but the remainder of the popu-
lation would be parts of other stocks. In equations presented below,
when referring to the i-th population and its associated spawning
area/ground or the i-th stock and its associated fishing area/ground,
we refer to related locations, in the sense that the i-th spawning

Fig. 1. Illustration of non-mixed fisheries in which fisheries exploit individuals from a
single spawning population (top panel), which is a common underlying assumption
for a stock-based management approach, and intermixed fisheries in which fisheries
exploit individuals from potentially many different spawning populations (bottom
panel). The arrows in the intermixed fisheries case depict fish from the various spawning
populations dispersing to other fishing areas. In the present research, mixing rates and
spawning population productivity levels differ depending on the investigated scenarios.
population reproduces in an area contained within the i-th stock’s fishing grounds.

**Model of lake whitefish dynamics**

We simulated the dynamics of four fish populations that were assumed to intermix to varying degrees during large portions of the year but which maintained strong spawning site fidelity and thus did not intermix during spawning. Conceptually, our simulated dynamics matched the assumption of overlapping groups with reproductive isolation as described by Porch (2003) and Cadrin and Secor (2009). The simulated populations had characteristics similar to those of lake whitefish in northern lakes Huron and Michigan, but were not meant to exactly replicate particular populations. This was a constraint driven by limited knowledge about population productivity and actual rates of intermixing, but also by our desire to understand the general influences of these factors. The composition of each population was represented by fish ages 1 (age of recruitment) through 11, and an aggregated group of all fish ages 12 and older. Fish were assumed to intermix immediately after spawning, with fractions of each population either staying within the fishing grounds surrounding their natal areas, or moving to other fishing grounds of the system. After movement occurred, each mixed stock was commercially exploited during the remainder of the year. Surviving fish were redistributed among the stocks each year. That is, mature fish spawned in their natal area after returning at the end of each year, and then all fish in each population were distributed among the stocks again.

Four different levels of mixing were assigned to spawning populations in this analysis: no mixing where all fish stayed in their natal area during the harvest season (resulting in stocks matching the spawning populations perfectly), low mixing where 10% of the fish moved from the fishing grounds surrounding their natal area to the other fishing grounds, intermediate mixing where 40% of the fish moved from the fishing grounds surrounding their natal area to the other fishing grounds, and high mixing where 80% of the fish moved from the fishing grounds surrounding their natal area to other fishing grounds. The levels of mixing assumed in this study were based in part on the results of tagging studies conducted by Ebener et al. (2010), as well as through consultation with lake whitefish managers in the upper Great Lakes. We assumed that the proportion of the fish emigrating from the fishing grounds surrounding their natal area would be equally divided among the other fishing grounds of the mixed stock system to both simplify model development and interpretation of results.

After recruitment, abundances at age of each cohort of the populations were simulated using an exponential population model, with total mortality partitioned into natural (M) and fishing (F) mortality components. Instantaneous natural mortality for all ages was set equal to 0.25, which is within the range of natural mortality rates reported for the lake whitefish populations in the 1836 Treaty waters (Caroffino and Lenart, 2011). Recruitment of the populations was modeled with a Ricker recruitment model relating the recruitment to the spawning population size in terms of egg production (SE), with recruits defined as numbers of age-1 fish produced in the year following spawning (Table 1). Stochasticity in recruitment was incorporated via a multiplicative lognormal process error.

Differences in productivity among spawning populations were incorporated via adjustments to the coefficients of their recruitment functions. Specifically, the coefficients were adjusted so that each population in the absence of intermixing had equal maximum sustainable yields (MSY) but at differing levels of exploitation. For our evaluations, we considered four productivity levels: high, medium–high, medium–low, and low productivities. High productivity populations were defined such that they had spawning potential ratios of 30, 40, and 50%, respectively (Table 2). These levels are largely defined by how steep the stock-recruitment function is near the origin, which depends upon the Ricker parameter α, and this range roughly corresponds to a four-fold difference in the number of recruits per egg at low spawning population sizes. The Ricker parameter simultaneously had to be adjusted to keep the MSY constant. Based on deterministic models sharing the same stock-recruitment parameters and fishery characteristics used in this analysis, the estimated maximum sustainable yield instantaneous fishing mortality rate on the most selected age class for each productivity level was 0.258 (low productivity), 0.393 (medium–low productivity), 0.631 (medium–high productivity), and 1.15 (high productivity). The range of the recruitment parameter coefficients used to characterize the different productivity levels was similar to what has been estimated for lake whitefish fisheries in the 1836 Treaty waters (Deroba and Bence, 2012), indicating that the values selected were reasonable for lake whitefish in the Great Lakes.

Spawning population size was calculated as the product of abundance at age in each population, proportion mature at age, weight at age, proportion of females, and the number of eggs per kilogram of fish (Table 1). Lengths at age were predicted with a von Bertalanffy growth model, weight at age was predicted using an allometric growth model, and maturity was modeled as a logistic function (Table 1). The ratio of males to females at all ages was assumed to be equal and the number of eggs produced per kg of fish was constant (Table 1).

For simplicity, each stock was assumed to be exploited independently by a single commercial fishery, and that the age-specific vulnerability (i.e., selectivity) patterns were the same for each stock, although the level of exploitation for the stocks varied according to the allotted TAC. In this study, TACs were set in terms of numbers, rather than biomass. For the actual lake whitefish fisheries in the 1836 Treaty waters, TACs or harvest targets are set in terms of biomass because allocation is done in some areas among components which select for different sizes of fish. Age-specific fishing mortalities

**Table 1**

Equations with descriptions and values for fixed variable inputs used in the simulation of lake whitefish populations and fisheries in this analysis.

<table>
<thead>
<tr>
<th>Description of equation</th>
<th>Equation</th>
<th>Parameter coefficients</th>
</tr>
</thead>
<tbody>
<tr>
<td>Abundance (Ny) at age of recruitment (year y) by year y</td>
<td>( Ny_y = \alpha \sum_{i=1}^{y} \exp(-\beta \sum_{y=1}^{i} \exp(\gamma i)) )</td>
<td>( \alpha = \text{see Table 2} )</td>
</tr>
<tr>
<td>Spawning population egg production (SE) by year y</td>
<td>( SE_y = \sum \left(N_y, u_e, u_a, \text{Fem Eggs} = \text{Fem} \times 0.5 \times \text{Eggs} = 19.937 \text{kg} \right) )</td>
<td>( \beta = \text{see Table 2} )</td>
</tr>
<tr>
<td>Length (L) at age (a)</td>
<td>( L_a = L_0(1 - \exp(-\kappa (a - \theta))) )</td>
<td>( \gamma = 60.9 \text{ cm} )</td>
</tr>
<tr>
<td>Weight (w) at age (a)</td>
<td>( w_a = \gamma L_a^b )</td>
<td>( \beta = 0.1686 )</td>
</tr>
<tr>
<td>Maturity (m) at age (a)</td>
<td>( m_a = \frac{\exp(-\gamma (a - \theta))}{\exp(-\gamma (a - \theta)) + \delta} )</td>
<td>( \theta = 0.09 \text{ years} )</td>
</tr>
<tr>
<td>Selectivity (s) at age (a)</td>
<td>( s_a = \frac{\exp(-\gamma (a - \theta))}{\exp(-\gamma (a - \theta)) + \delta} )</td>
<td>( \delta = 37.9 \text{ cm} )</td>
</tr>
</tbody>
</table>

**Table 2**

Ricker stock-recruitment coefficients (Table 1) that were assumed for the different productivity levels for lake whitefish spawning populations for assessing the effects of stock intermixing on the current 65% total annual mortality control rule used to manage lake whitefish fisheries in the 1836 Treaty waters of the Great Lakes.

<table>
<thead>
<tr>
<th>Productivity level</th>
<th>Alpha (( \alpha ))</th>
<th>Beta (( \beta ))</th>
</tr>
</thead>
<tbody>
<tr>
<td>Low</td>
<td>0.0000369</td>
<td>7.1708 \times 10^{-11}</td>
</tr>
<tr>
<td>Medium–low</td>
<td>0.0000516</td>
<td>1.2780 \times 10^{-10}</td>
</tr>
<tr>
<td>Medium–high</td>
<td>0.00007687</td>
<td>2.2758 \times 10^{-10}</td>
</tr>
<tr>
<td>High</td>
<td>0.0001281</td>
<td>4.2988 \times 10^{-10}</td>
</tr>
</tbody>
</table>
were modeled as the product of a fully-selected fishing rate and the age-specific selectivities

\[ F_{i,y,a} = s_a F_{i,y} \]

where \( s_a \) indicates selectivity at age \( a \), and \( F_{i,y} \) represents the fully-selected fishing mortality rate in year \( y \) for the fishery surrounding spawning area \( i \) regardless of where the fish originated. Fishery selectivity was modeled as a gamma function of age (Table 1), which permitted a dome-shaped relationship between selectivity and age. Selectivity was set equal to 0 for age-2 and younger fish as these ages of fish are rarely harvested in the 1836 Treaty waters. Selectivities were scaled such that the fully selected age class had a selectivity value of 1.0.

The fully-selected fishing mortality rates in the simulations were determined from harvest occurring in each year and fishing area (i.e., fishing grounds surrounding a spawning area) and the abundance at age of all fish in a particular fishing area at the time of exploitation. Implementation error associated with the TAC was incorporated via an independent lognormal error

\[ C_{i,y} = TAC_{i,y} \exp \left( v_{i,y} - 0.5 \sigma^2 \right); \quad v_{i,y} \sim N(0, \sigma^2). \]

where \( C_{i,y} \) is the actual amount of commercial harvest for fishing area \( i \), \( C_{i,y} \) is the assessed TAC for the fishing area, and \( v_{i,y} \) is a normally distributed random variable with expectation 0 and variance \( \sigma^2 \), which was set equal to 0.01. A correction factor was included so that the expectation of actual harvest was equal to the target TAC. The intent of the implementation error was to mimic management actions that alter harvest, but do so imperfectly as a consequence of managers not having complete control over a fishery. Because the fishery was assumed to occur throughout the year with age-specific vulnerabilities, the fishing mortality rate that produced the correct amount of harvest in each area and year was solved for numerically using a Newton–Raphson algorithm.

Abundance at age of a particular population depended on what fraction of the population moved to become part of each fished stock, and the amount of fishing mortality experienced by those stocks. Using an exponential population model, abundance at age of a particular spawning population was represented as

\[ N_{y-1,a+1} = \sum_j N_{i,y,a} \theta_j \exp \left( -M - F_{i,y,a} \right). \]

where \( N_{i,y,a} \) is the abundance of fish from spawning population \( i \) of age \( a \) in year \( y \), \( \theta_j \) is the fraction of the population spawning in area \( i \) that is located within the fishing grounds surrounding spawning area \( j \) during the fishing season (\( j \) can be equal to 1), \( M \) is the natural mortality rate that is assumed for this research to be constant across populations, years, and ages, and \( F_{i,y,a} \) is the year- and age-specific instantaneous fishing mortality rate for the fishing grounds that surround spawning area \( j \) during the fishing season of year \( y \). This specification of abundances at age for the spawning populations matched the discrete-time format of the Beverton and Holt (1957) box-transfer model for describing changes in abundance as a result of movement across a region boundary (Goethel et al., 2011). The total abundance of fish in a particular fishing ground once intermixing occurred (\( \bar{N}_{i,y,a} \)) was represented as

\[ \bar{N}_{i,y,a} = \sum_j N_{i,y,a} \theta_j. \]

Abundance projections and TAC calculations

The assessment model that was used to estimate abundances and fishing mortality rates for the purpose of determining the TACs for each simulated stock in each year consisted of a SCAA model (see Supplementary information 1 for a description of the SCAA model) similar to those currently used to assess lake whitefish stocks in the 1836 Treaty waters (Caroffino and Lenart, 2011; Ebener et al., 2005). The estimates from the assessment model used to implement the harvest control rule each year were based on the highest posterior density estimates (sometimes referred to as maximum penalized likelihood estimates). The data used in fitting the SCAA models included observed harvest, observed age composition of the harvest, and observed fishing effort for each fish stock, which matches the data used to fit the actual SCAA assessments for lake whitefish in the 1836 Treaty water (see Supplementary information 1 for a description of how observations for the assessment models were generated). The objective function for the SCAA model consisted of the sum of three components being either negative log-likelihood components or negative log-prior (penalty) components. Lognormal distributions were assumed for the total annual harvest from the fishery and for the log-prior (penalty) component associated with the fishing mortality–effort relationships as explained below. The proportions at age of the harvest in each year were assumed to have arisen from a multinomial sample. When fitting the SCAA model, the dispersion parameter for the negative log-likelihood for the fishery harvest data component was included as one of the estimated parameters. The dispersion parameter for the negative log-prior (penalty) component for the fishing mortality–effort relationship deviation was set equal to four-times the value of the estimated fishery harvest dispersion parameter. The negative log-likelihood component for the fishery harvest age composition was weighted by an assumed effective sample size of 200.

Because of the considerable processing time needed to conduct the simulations, the SCAA model assessments were conducted every third year rather than annually. In the intervening years, TACs for the stocks remained at the levels set from when the SCAA model assessments were last conducted. Although this diverges from how the assessments have been conducted for lake whitefish stocks in the 1836 Treaty waters, there are some within the group responsible for conducting the lake whitefish assessments suggesting a move from conducting annual assessments in favor of every other or every third year assessments (M. P. Ebener, Chippewa–Ottawa Resource Authority, personal communication). Based on this, we did not believe that designing our simulations such that assessments were conducted every third year was unreasonable.

We incorporated a time lag in our assessments similar to that used in actual management of lake whitefish fisheries in the 1836 Treaty waters (Ebener et al., 2008). Specifically, TACs for a particular year were set based on assessments conducted the prior year using data collected two years previously. When fitting the assessment models, only the 20 years of data prior to the year for which current abundances and mortality rates were assessed were included. Because assessments were only conducted when 20 years or more of data were available, no assessments were conducted during the first 20 years of the simulation period. During this “burn-in” period, the TAC for each area and year was set based on actual abundances rather than the unavailable assessed abundances. This “burn-in” period was simply a method to obtain an initial abundance at age for year 21, at which point a full fishery harvest policy analysis, including actual assessment of the stocks, could be implemented.

The SCAA model estimates of abundances at age, age-specific fishing mortality rates, and recruitment levels were used to project future abundances at age and calculate TACs for each stock. The projections used the abundance-at-age estimates from the beginning of the last year of the stock assessment model, along with the mean recruitment levels and mortality rates from the previous five years to project abundances. The target age-specific fishing mortality rates were then calculated by subtracting the natural mortality rates from a 65% total annual mortality rate control rule (converted to an instantaneous scale) and multiplying this difference by the age-specific selectivities that were
estimated in the last year of the SCAA model. These target age-specific fishing mortality rates were then included in the Baranov catch equation along with the projected abundance at age estimates to determine what the allowable TAC would be for each stock.

Experimental design

A total of 21 scenarios consisting of different combinations of population intermixing rates and productivity levels were examined to assess the performance of the 65% total annual mortality control rule. Presently, it is not known what factors contribute to intermixing of lake whitefish populations or why some populations in northern lakes Huron and Michigan appear to move little while others disperse widely. Thus, we examined a broad range of scenarios so as to provide managers with the most information possible in the event that intermixing–productivity relationships are better clarified. The examined scenarios were categorized into four groups: All Shared, Shared Mixing, Shared Productivity, and Correlated. The exact intermixing rates and productivity levels that were assumed for the populations under each investigated scenario are listed in Table 3. In the All Shared grouping, productivity and intermixing levels were set at the same values for all populations. The intent of these scenarios was to test the performance of the control rule when all populations experienced the same intermixing and productivity levels. The Shared Mixing group consisted of three scenarios in which all populations intermixed at the same rate but had different productivities. For this grouping of scenarios, it was assumed that each lake whitefish population had one of the four productivity levels developed for the analysis. The Shared Productivity group of scenarios was in the same vein as the Shared Mixing group except that productivity levels of the populations were the same and the mixing rates differed among the populations. The Correlated group consisted of just two scenarios in which movement of fish from fishing grounds surrounding their spawning areas was either positively or negatively (inversely) correlated with population productivity levels for those spawning areas. In the negatively correlated scenario, the population with the lowest rate of intermixing was the most productive. In the positively correlated scenario, the population with the lowest rate of intermixing was the least productive.

Performance metrics and simulation details

The performance of the 65% total annual mortality control rule for each examined scenario was evaluated based on the assumption that the management objectives for the fisheries were to have high and stable yields and for populations to be sustainable over long time periods. Based on these objectives, metrics that were used to evaluate performance included mean fishery yield for each area, the mean aggregate fishery yield (sum of the yields across the areas), interannual variation in fishery yields, mean percent of SEF = 0 for each population, and the percent of years the SE declined to less than 20% of SEF = 0. The performance of the SCAA model was assessed by calculating the mean relative error and mean absolute relative error in harvest estimates for the 20 years of harvest data included each time an assessment was performed. Relative error was calculated as the relative difference between the estimated and true values, while absolute relative error was calculated as the absolute of the relative difference between the estimated and true values. We also calculated the mean relative error and mean absolute relative error in estimated abundances of the stocks (after mixing but prior to fishery harvest) in the last year of each assessment.

Simulations were conducted in AD Model Builder (Fournier et al., 2012). Each simulation involved the projection of stock dynamics under the assumed intermixing and productivity levels for 100 years. Abundance at age at the start of each simulation was set equal to the stable age distribution expected at the target fishing mortality level for the various productivity levels considered in that simulation. Performance metrics were only calculated based on the data from the last 80 years of the simulations (i.e., the burn-in period was not included in the calculations). One thousand simulations were conducted for each investigated scenario, with comparisons among scenarios based on both the central tendency (median) and variability (range) of the simulation results.

Results

The SCAA models generally converged and produced estimates of harvest that closely agreed with observed values. At most, two assessments failed to converge during any 100-year model run, which was unlikely to have much influence on the overall results of this research. The harvest mean relative error had medians for the simulations ranging between −0.13 and 0.01% for mean relative error and 2.78 and 2.90% for mean absolute relative error (Supplementary information 2). Errors in abundance estimates were substantially larger than those of harvest. The abundance mean relative error was as low as −19.02% and as large as 2.32% for some of the investigated scenarios, while the mean absolute error ranged from 13 to 29% (Supplementary information 2). The magnitude of absolute errors in abundance was generally similar to those reported or assumed for SCAA assessments in other simulation studies (Linton and Bence, 2011; Punt et al., 2008; Wilberg and Bence, 2006). The highest levels occurred when some or all populations had high mixing rates suggesting model misspecification was having some influence on assessment accuracy. The mean relative errors for abundance also tended to be further below zero for scenarios

Table 3 Assumed intermixing (M) and productivity (P) levels of individual spawning populations for each of the scenarios investigated in this research. Intermixing values indicate the percent of lake whitefish that move from the target region during the harvest season. Intermixing levels correspond to 0% (N), 10% (L), 40% (I), and 80% (H) of spawning populations moving from natal areas to other areas of the simulated system. Mixing productivity levels refer to high (H), medium–high (MH), medium–low (ML), or low (L) productivities as described in Table 2.

<table>
<thead>
<tr>
<th>Group</th>
<th>Scenario</th>
<th>Pop. 1</th>
<th>Pop. 2</th>
<th>Pop. 3</th>
<th>Pop. 4</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>M</td>
<td>P</td>
<td>M</td>
<td>P</td>
<td>M</td>
</tr>
<tr>
<td>All Shared</td>
<td>HP LM (high prod., low mix.)</td>
<td>L</td>
<td>H</td>
<td>L</td>
<td>H</td>
</tr>
<tr>
<td></td>
<td>HP IM (high prod., int. mix.)</td>
<td>I</td>
<td>H</td>
<td>I</td>
<td>H</td>
</tr>
<tr>
<td></td>
<td>HP HM (high prod., high mix.)</td>
<td>L</td>
<td>H</td>
<td>H</td>
<td>H</td>
</tr>
<tr>
<td></td>
<td>MHP LM (med−high prod., low mix.)</td>
<td>L</td>
<td>MH</td>
<td>L</td>
<td>MH</td>
</tr>
<tr>
<td></td>
<td>MHP IM (med−high prod., int. mix.)</td>
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where one or more populations had high levels of mixing, suggesting that model misspecification (ignoring mixing) was causing bias.

Mean aggregate annual yields were the greatest for those scenarios where all populations had medium–high productivity levels, followed by those where all populations had high productivity, medium–low productivity, and finally low productivity levels (Fig. 2). For medium–high productivity populations, the medians of the aggregate yields across the simulations were on the order of 730 tonnes, while for high, medium–low, and low productivity populations the medians were 660, 590, and 200 tonnes. Under deterministic conditions (no recruitment stochasticity, implementation error, process error, or observation error), the MSY for the simulated system was on the order of 620 tonnes. Variability in the mean aggregate annual yields across the simulations was the greatest for those scenarios where all populations had medium–low and low productivity levels. For those scenarios in which the spawning populations had varying levels of productivity levels, the mean aggregate annual yields that resulted from the 65% total annual mortality control rule were most similar to the yields for the medium–low productivity populations (Fig. 2).

The effects of higher mixing rates differed depending on the productivity level of the spawning populations. For scenarios where all spawning populations had high productivity levels, the medians and variability across all the simulations were similar for the different mixing levels. For scenarios with medium–high productivity levels, the medians of the mean aggregate annual yields across all the simulations increased slightly with higher mixing rates, although variability across the simulations decreased somewhat (Fig. 2). For the scenarios with medium–low productivity levels, the medians and variability across all the simulations increased with higher mixing rates (Fig. 2). For the scenarios with low productivity levels, the medians of the mean aggregate annual yields across all the simulations decreased with higher mixing rates, although variability across the simulations increased (Fig. 2).

High productivity populations and associated fisheries

Under the All Shared group of scenarios, intermixing had little effect on mean annual yields for fisheries coinciding with high productivity population spawning areas (Fig. 3), which was to be expected since all populations had the same productivities and thus intermixing led to nearly equal levels of movement to and from regions. Under all mixing levels, mean annual yields were approximately 160 tonnes, which was just slightly greater than the deterministic MSY of 155 tonnes. There was an inverse relationship between the interannual variation in yield for a fishery and the intermixing rate of the population that spawned in that area, with variability decreasing somewhat with higher rates of intermixing (Fig. 3). The percent of years that SE declined to less than 20% of SEF=0 was low, being generally <15% for high productivity populations regardless of mixing rates. As with the mean interannual percent variation in yield, there was a slight inverse relationship between the percent of years that SE declined to less than 20% of SEF=0 and mixing rates (Fig. 3). The mean percent of SEF=0 across the simulations for the All Shared groups of scenarios ranged between 40 and 60%, with mean percent of SEF=0 slightly increasing with higher mixing rates (Fig. 3).

The results of the Shared Mixing group of scenarios for high productivity populations were very similar to the results under the All Shared group of scenarios. Interaannual variation in yield and the percent of years that SE declined to less than 20% of SEF=0 decreased with higher rates of mixing and the mean percent of SEF=0 increasing slightly with higher mixing (Fig. 3). The one difference between the scenarios was that higher rates of mixing led to slight decreases in mean annual yields for the fisheries coinciding with high productivity spawning population areas (Fig. 3), which was a consequence of fishing grounds experiencing net emigration between the spawning and harvest seasons.

Under the Shared Productivity group of scenarios, mean annual yields varied substantially among fisheries, with yields surpassing 200 tonnes for the fishery coinciding with the spawning population that did not mix, to less than 75 tonnes for the fishery coinciding with the spawning population that had a high rate of mixing (Fig. 3). This was not unexpected given that there was net emigration after spawning from the fishing grounds around the area where the population with a high rate of mixing spawned, with net immigration into the fishing grounds around the area where the spawning population stayed in those fishing grounds during the harvest period. Interaannual variation in yield ranged from 15 to 30% across most scenarios and declined for fisheries coinciding with spawning populations with higher rates of mixing. In addition, the percent of years that SE declined to less than 20% of SEF=0 declined with increasing mixing rate. Both these results were similar to the results from the All Shared and Shared Mixing groups of scenarios (Fig. 3). The mean percent of SEF=0 was the greatest for the no mixing and low mixing levels. The lowest mean percent of SEF=0 occurred under the intermediate mixing level, with the high mixing level having a slightly greater mean percent of SEF=0 (Fig. 3).

When population productivity and intermixing levels were negatively correlated (i.e., high productivity populations had lower mixing rates), mean annual yields from fisheries coinciding with high productivity spawning populations increased again to as much as 200 tonnes (Fig. 3). When population productivity and intermixing levels were positively correlated (i.e., more productive populations had higher intermixing rates), mean annual yields were again as low as 75 tonnes (Fig. 3). Interaannual variation in yield, percent of years that SE declined to less than 20% of SEF=0 and mean percent of SEF=0 for high productivity populations (or fishing grounds surrounding the spawning grounds for those populations) were all greater in the negatively correlated scenario than in the positively correlated scenario, but as a whole the results for these performance statistics were very similar to the levels obtained in the other examined scenarios.
Medium–high productivity populations and associated fisheries

Qualitatively, the patterns in the results for the medium–high productivity populations were similar to those for the high productivity populations. Some of the similarities that were observed were decreases in mean annual yields with higher mixing levels under the Shared Mixing and Shared Productivity scenarios, similar levels of interannual variation in yield combined with decreases in interannual variation in yield with higher mixing rates across the All Shared, Shared Mixing, and Shared Productivity scenarios, and decreases in the percent of years that SE declined to less than 20% of SEF=0 with higher mixing rates for the All Shared and Shared Mixing scenarios (Fig. 4). In addition, the mean percent of SEF=0 increased slightly with higher mixing rates for the All Productivity scenarios, and was the lowest for the intermediate mixing rate and the greatest for the no mixing rate level for the Shared Productivity scenarios, which was similar to what was found for the high productivity populations (Fig. 4).

Among the differences between the medium–high and high productivity levels that were observed, mean annual yields under the All Shared, Shared Mixing, and Shared Productivity scenarios were modestly greater than that of the high productivity level (Fig. 4). The medians of the yields across the simulations for the All Shared group of scenarios were on the order of 180 tonnes, which was about 16% greater than the deterministic MSY. The percent of years that SE declined to less than 20% of SEF=0 was greater for the medium–high productivity levels than it was for the high productivity levels; likewise, the mean percent of SEF=0 was smaller for the medium–high productivity levels than it was for the high productivity levels (Fig. 4).
Whereas in the high productivity populations there was a negative relationship between mixing rates and the percent of years that SE declined to less than 20% of SEF=0, under the Shared Productivity scenarios, for medium–high productivity populations the intermediate mixing rates had the largest percent of years where SE was less than 20% of SEF=0 (Fig. 4). An additional difference between the productivity levels was that the mean percent of SEF=0 decreased slightly with higher mixing rates for the Shared Mixing group of scenarios (Fig. 4). Furthermore, whereas the fisheries coinciding with high productivity spawning populations had large differences in mean annual yields between the negatively and positively correlated scenarios, for the medium–high productivity levels the differences in fishery yields were much smaller between the scenarios (Fig. 4).

Medium–low productivity populations and associated fisheries

For the medium–low productivity populations, mean-annual yields were approximately 150 tonnes for the All Shared group of scenarios, with variability in the simulation results decreasing as mixing rates increased (Fig. 5). The interannual variation in yield for the fisheries coinciding with medium–low productivity populations was similar to that of the medium–high and high productivity levels, ranging from 15 to 30% across most scenarios (Fig. 5). Within an examined scenario, there was substantial variability in the percent of years that SE was less than 20% of SEF=0, with ranges of 0 and 100% for most scenarios (Fig. 5). For the All Shared group of scenarios, the median of the simulations for the mean percent of SEF=0 was approximately 20%, with ranges of between 10 and 40% (Fig. 5).

Under the Shared Productivity group of scenarios, mean annual yields for the fisheries coinciding with the spawning populations that did not mix with other regions were on the order of 200 tonnes (Fig. 5). Despite this higher mean yield, the sustainability performance metrics for the spawning populations suggested that each populations were at risk from this level of harvest, as indicated by the relatively high percent of years that SE was less than 20% of SEF=0 and a low mean percent of SEF=0.

Many of the qualitative patterns in terms of how the performance statistics were affected by increasing levels of mixing for the medium–
Low productivity populations were similar to that observed for the high and medium–high productivity populations. For example, interannual variation in yield generally declined with higher mixing rates as did the percent of years that SE was less than 20% of $SE_{F=0}$ (Fig. 5). One noticeable difference in the results for the areas within which the medium–low populations spawned, in contrast to higher productivity levels, was that in the Correlated group of scenarios the mean annual yields for the negatively correlated scenario was lower than that of the positively correlated scenario (Fig. 5). In the case of the positively correlated scenario, mean annual yields in some simulations exceeded 200 tonnes, which was similar to the yields obtained from the scenario where all populations had medium–high productivity levels.

Low productivity populations and associated fisheries

The medians of the mean annual yields across the simulations for the fisheries coinciding with low productivity spawning populations under the All Shared group of scenarios was approximately 65 tonnes, or about 42% of the deterministic MSY (Fig. 6). As was found for the other productivity levels, interannual variation in yield generally ranged from 15 to 30% across the investigated scenarios (Fig. 6). For the low productivity populations, the percent of years that SE was less than 20% of $SE_{F=0}$ was quite large with inter-quartile ranges generally greater than 90% (Fig. 6). Likewise, the mean percent of $SE_{F=0}$ was generally low, with the medians from the simulations being less than 10% for all the investigated scenarios (Fig. 6).

Under the Shared Mixing grouping of scenarios, mean annual yields for the fisheries coinciding with low productivity spawning populations increased along with increases in mixing rates (Fig. 6), which was a different pattern than that observed for the other productivity populations. This was a consequence of fishing grounds surrounding low productivity areas receiving more immigrants from other populations than what was lost to emigration. Under high mixing levels, the mean annual yields for the fisheries coinciding with low productivity spawning populations were close to 150 tonnes, reflecting net immigration into an area during the harvest season of fish from higher productivity populations (Fig. 6). For the Shared Productivity scenarios, mean yields decreased with higher rates of mixing, which matched the results for

Fig. 5. As in Fig. 3, except for medium–low productivity populations.
the other productivity levels; however, the difference in yields among the various mixing levels was not as extreme as in the other productivity levels (Fig. 6). Like the medium–low productivity levels, mean annual yields were lower for the negatively correlated scenario than they were for the positively correlated scenario, with the yields from the positively correlated scenarios again approaching the yields observed for the higher productivity levels in some of the examined scenarios (Fig. 6).

Discussion

The performance of harvest control rules for managing lake whitefish fisheries in the Laurentian Great Lakes was previously evaluated by Jacobson and Taylor (1985) and Deroba and Bence (2012). In both cases, constant mortality control rules were found to perform adequately with respect to producing near maximum fishery yield (Deroba and Bence, 2012; Jacobson and Taylor, 1985), although Deroba and Bence (2012) found that biomass-based control rules produced larger yields and were better at minimizing risk of depletion if stock-specific levels of unfished biomass were known. Neither of these previous research studies accounted for population intermixing when conducting their harvest evaluations, although Deroba and Bence (2012) did account for substantial complexity and uncertainty in lake whitefish life-history characteristics.

In this study, we found risk of depletion to fish populations, as measured by the percent of years that $SE$ declined to less than 20\% $SE_{F=0}$, and also mean percent of $SE_{F=0}$, was not strongly affected by differing levels of intermixing, but was strongly linked to assumed productivity levels. Conversely, intermixing had some influence on interannual variation in fishery yields, with interannual variation generally decreasing as mixing levels increased, at least at the population productivity levels considered in this research. Mean annual yields were clearly influenced by both mixing and productivity levels, and our research demonstrated that under particular combinations of mixing and productivity levels a population could have a high risk of depletion even though the amount of harvest for a fishery operating in the vicinity of the spawning population was large. This was a consequence of the fishery benefitting from immigration of fish from other spawning populations during periods of exploitation. In essence, the productivities of the populations determined the

![Performance Statistics for Low Productivity Populations](image)

Fig. 6. As in Fig. 3, except for low productivity populations.
yield from the system as a whole, as demonstrated by the relatively stable mean aggregate annual fishery yields in the Shared Mixing group of scenarios, but mixing influenced the realizable yields of the fisheries through redistribution of harvest. In particular, when higher productivity populations mixed substantially into the areas where low productivity populations spawned, the yield from the fisheries coinciding with the low productivity spawning population approached that of fisheries coinciding with high productivity spawning populations.

Mixing among populations influenced assessment results, and when there was substantial intermixing, errors in estimated abundance tended to be larger and these estimates tended to be biased. However, we believe that this, and assessment error per se, played a second-order effect on the metrics by which we evaluated harvest policies. For example, when mixing and productivity were the same for all populations, high levels of mixing led to larger errors in abundance estimates and bias, but in this case mixing had little influence on measures of depletion or yield. In addition, for scenarios where mixing was low or not important, our results are consistent with results reported by Deroba and Bence (2012) who did not incorporate mixing. Deroba and Bence (2012) incorporated levels of assessment error into their study similar to that which arose in our study, and did a sensitivity analysis showing that results were not particularly sensitive to the magnitude of assessment error.

Perhaps the most concerning result of our research was that the 65% total annual mortality control rule may not be sufficiently conservative for low productivity populations, but it would be difficult to determine that this was an issue for a particular population without knowledge of the actual population productivities. This was in contrast to Deroba and Bence (2012), who found that the 65% total annual mortality control rule performed relatively well for lake whitefish, even accounting for changes in life history characteristics that concern managers (minus intermixing). An important difference between the study of Deroba and Bence (2012) and ours is that in their study they looked at the probability of outcomes for harvest policies across simulations, with stock recruitment (productivity) values drawn from a set of estimated values in each simulation. This meant that the effects on low productivity populations were not investigated directly. The conclusion of Deroba and Bence (2012) that the current 65% total annual mortality control rule performed relatively well apparently depended on what they considered low productivity populations being infrequently selected in their simulations, although we selected our low productivity level because it was considered plausible for lake whitefish based on the analysis of Deroba and Bence (2012).

Because allowable catches in our simulations (and in actual management of lake whitefish stocks in the Great Lakes) were based on assessments that only made use of fishery harvest and effort data, TACs were entirely based on the number of fish in a stock area during the harvest season rather than the size of the spawning population. This discrepancy between the spatial management approach and the data used in the assessment led to estimates of biomass that were not reflective of the resident population’s spawning biomass (Belcher and Jennings, 2009). These results were consistent with the findings of Kell et al. (2009), who found that when catches from two simulated fish metapopulations were mixed in a virtual population analysis assessment, it was possible for the collapse of one population to go entirely undetected, raising concern that assessment mismatch may put some populations at risk. Furthermore, productivity at the low end of the range of productivities could be overestimated based on the stock assessments that ignore mixing because the harvest and apparent health of these populations would be partially supported by fish emigrating from more productive areas. This likely applies to the productivity levels we assumed for lake whitefish spawning populations. These were based on Deroba and Bence’s (2012) estimated Ricker stock–recruitment relationships for some lake whitefish populations in the 1836 Treaty waters; these recruitment relationships were fit to SCAA model estimates of stock and recruitment abundances.

While these are the best available productivity estimates for lake whitefish in the Great Lakes, they are based on assessments that relied on fishery dependent data and did not account for mixing among the spawning populations during the fishing season. Fishery independent determination of spawner–recruit relationships at appropriate times of year (i.e., when populations are unmixed) for distinct spawning aggregations may lead to a better understanding of the true productivity of lake whitefish populations in the Great Lakes and give a better sense of what populations may be at risk from overharvest.

As in any simulation study, we made a number of simplifying assumptions, including the assumptions that emigrating fish from spawning populations dispersed equally to other areas, that the proportions of fish emigrating to other areas did not change over time, that there was no gene flow among the different spawning populations, and that life-history characteristics of the spawning populations did not vary. We believe that our major qualitative conclusions are robust to these simplifications. For example, Deroba and Bence (2012) previously explored the effects of variable life history characteristics and found that the sustainable level of annual mortality was not strongly influenced by allowing for such variation. Nevertheless, we readily acknowledge that simplifying assumptions did have some bearing on our results. For example, if fish were more prone to move to particular areas because of the conditions within those areas, then yields for those areas would have been greater than what was found in this research.

Recently, some steps have been taken to account for intermixing of lake whitefish populations in the 1836 Treaty waters of the Great Lakes. In northern Lake Huron, four lake whitefish management units (WFH-01 to WFH-04), which were previously assessed and managed separately, are now being assessed with a single SCAA model that includes biological and commercial fishery data from each management unit (Caroffino and Lenart, 2011). Although combining intermixing stocks into a single assessment and management system is a reasonable approach for dealing with stock intermixing, pooling the assessment can, depending on details of the fishery and how the pooled TAC is allocated, lead to biased abundance and mortality rate estimates and influence sustainability of spawning components (Heifetz et al., 1997; Kell et al., 2009). In addition, there are alternative assessment approaches other than pooling, such as building assessments that account for movement among areas, although they would likely require additional data as might arise from ongoing tagging studies (e.g., Goethel et al., 2011) or fishery independent assessments during the spawning season. The types of simulations we used in this study could also be used to evaluate such alternative combinations of assessment and management for dealing with whitefish movement.

Presently, there is considerable uncertainty regarding factors that govern lake whitefish dispersal after spawning and productivity levels of individual spawning components. Ebener et al. (2010) estimated dispersal ranges from 19 to 90% for lake whitefish spawning populations in northern lakes Huron and Michigan that in some cases were separated by less than 50 km. As previously indicated, one hypothesis is that lake whitefish dispersal is linked to food availability and that stocks with locally depleted food resources move more widely in search of areas with more abundant resources. Such a movement strategy would seemingly be in line with ideal free distribution theory (Fretwell, 1972; Fretwell and Lucas, 1970), which has been confirmed for species such as northern pike (Esox lucius) (Haugen et al., 2006). Continued investigation of lake whitefish dispersal through genetic and/or tag-recapture studies on larger spatial (i.e., involving more spawning population) and temporal (i.e., over longer time periods) scales would be beneficial for identifying factors influencing movement after spawning.

Besides lake whitefish, there are many other examples in the Great Lakes of fisheries exploiting stocks of fish that consist of mixtures of multiple spawning populations. Other examples include walleye (Sander vitreus) in lakes Erie and Huron (Wang et al., 2007) and
cisco (Coregonus arteri) in Lake Superior (Stockwell et al., 2009). As well, extensive movements of stocked fishes, including Chinook salmon and lake trout (Salvelinus namaycush), have been documented (Adlerstein et al., 2007a, 2007b, 2008) suggesting that fisheries that exploit these species also are exploiting mixtures of individuals. Although it may be difficult to generalize the results from this study to management of other species given likely differences, our findings suggest caution when managing such fisheries that exploit mixtures of spawning populations. A similar simulation framework to that employed in the current study could potentially be extended to explore the consequences of spawning population intermixing on these other species.

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