KEEPING UP WITH THE TIMES: ARE MORE CONSERVATIVE CONTROL RULES NEEDED TO PROTECT INTERMIXING LAKE WHITEFISH POPULATIONS?

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ABSTRACT

KEEPING UP WITH THE TIMES: ARE MORE CONSERVATIVE CONTROL RULES NEEDED TO PROTECT INTERMIXING LAKE WHITEFISH POPULATIONS?

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The goals of this research were to: 1) investigate how intermixing of populations affected the performance of the 65% total mortality control rule that is currently used to manage lake whitefish (*Coregonus clupeaformis*) fisheries in the 1836 Treaty waters (TW) of the Great Lakes; and 2) explore the performance of alternative mortality rates for lake whitefish fisheries in the 1836 TW under different intermixing and productivity scenarios. The simulation framework that was developed modeled the dynamics of four intermixing, age-structured fish populations with varying levels of productivity. The framework also included a full age-structured assessment of the mixed fisheries, with abundance, mortality and recruitment estimates from these assessments used in combination with harvest control rules to set total allowable catches for stocks. In chapter 1, the 65% total mortality control rule was found to perform poorly in terms of protecting lower productivity populations. Yields from areas occupied by low productivity populations were often similar in magnitude to areas occupied by high productivity populations as a result of intermixing, which could result in managers thinking low productivity populations could be fished more intensively. In chapter 2, 45% and 55% total mortality control rules were found to perform better than the current control rule in ensuring population sustainability, maximizing yields, and increasing yield stability under certain productivity and intermixing levels. Alternative control rules resulted in mortality rates similar to what has been estimated for lake whitefish stocks in the 1836 TW, reducing the potential effects on commercial fishers if the control rule was indeed changed to this lower mortality rate.

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PREFACE

The chapters of this thesis were drafted as standalone papers that will be submitted for publication in peer-review journals. Chapter 1 is intended for submission to the *Journal of Great Lakes Research*; Chapter 2 is intended for submission to *Fisheries Research*. The bibliographic references in this thesis are therefore formatted according to the requisite reference style for those publications. When submitted, both manuscripts will include Drs. Travis Brenden and James Bence as co-authors. Consequently, both Chapters 1 and 2 are written with first person, plural narratives, even though I am listed as the sole author of the thesis.

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INTRODUCTION

Management of lake whitefish (*Coregonus clupeaformis*) fisheries in the 1836 Treaty waters (TW) of the Great Lakes uses a stock-based management approach, with assessments conducted on and total allowable catches set for individual stocks (Ebener et al., 2005; Woldt et al., 2007). A common assumption with stock-based management is that exploited fisheries are comprised of fish from a single spawning population. Recent evidence, however, suggests that lake whitefish populations in the 1836 TW intermix considerably during non-spawning periods and that many of the fish stocks exploited by commercial fishers consist of individuals from multiple spawning populations (Ebener et al., 2010). This intermixing is not accounted for in current assessment and management of lake whitefish fisheries, but nevertheless is a source of concern. Intermixing of populations can have implications on fishery yields and sustainability of individual populations depending on the degree of mixing, the underlying dynamics of the populations, and the harvest policies that are used to manage the fisheries (Heifetz et al., 1997; Quinn and Deriso, 1999; Punt et al., 2005; Dichmont et al., 2006; Punt, 2008; Kell et al,. 2009; Kerr et al., 2010). Despite a general consensus that intermixing of fish populations is important, a lack of understanding as to its effects makes it difficult to know if existing harvest policies for lake whitefish fisheries in the 1836 TW are appropriate. Alternate strategies have been proposed to account for population intermixing in some lake whitefish management units in the 1836 TW (Ebener et al., 2010), but, to date, no formal assessment has been conducted to compare performance of these different strategies.

Management of commercial and recreational fisheries often depends on harvest policies set by managers seeking specific ecological, economic, and social outcomes. Balance between conservation and economic objectives can be difficult to achieve due to conflicts between the objectives (Hall and Donovan, 2002). It has been recommended that harvest policies be chosen using computer-based simulations that consider uncertainties intrinsic to the system being managed, weighing the ability of different approaches to meet desired outcomes (Cooke, 1999; Smith et al., 1999; Punt et al., 2002; Kell et al., 2006; Deroba and Bence, 2008). Simulation-based evaluations have been used to investigate performance of different harvest policies for lake whitefish fisheries in the Great Lakes while accounting for factors such as stochasticity in life history attributes (Deroba, 2009). To date, simulation-based evaluations of the performance of different harvest policies that also account for intermixing among lake whitefish populations have not been conducted. Simulation modeling has shown considerable promise as a method to better understand the management implications of spatial structure of stocks (Kerr et al., 2010), but spatial structure has seldom been incorporated into actual evaluations. Notable exceptions include the evaluations conducted by Heifetz et al. (1997), Punt et al. (2005), Dichmont et al. (2006), Wilberg et al. (2008), and Kell et al. (2009). Two reasons why spatial structure or intermixing of fish populations is not commonly included in formal harvest policy evaluations are that there are limited methods for modeling intermixing of fish populations and also many systems lack reliable estimates of intermixing rates required for such an analysis (Quinn and Deriso, 1999).

The goal of this research was to determine the effectiveness of the current control rule and alternative variants of that rule for management of lake whitefish in the 1836 TW of the Great Lakes, taking into consideration recent evidence that some populations intermix considerably during the harvest season. In Chapter 1, I investigate how intermixing of populations affects the performance of the 65% total mortality control rule that is currently used to manage lake whitefish fisheries in the 1836 TW. In Chapter 2, I explore the performance of alternative control rules for lake whitefish populations under different scenarios of population intermixing and productivity levels. Each chapter was intended to provide valuable information regarding the management of lake whitefish fisheries in the Great Lakes, but also to be informative to broader audiences due to the commonness of population intermixing.

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CHAPTER 1

CONTROL RULE PERFORMANCE FOR INTERMIXING LAKE WHITEFISH POPULATIONS IN THE 1836 TREATY WATERS OF THE GREAT LAKES: A SIMULATION-BASED EVALUATION

Abstract

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 that of populations 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. Mean annual yield, inter-annual variation in yield, mean percentage of unfished spawning biomass ($SSB_{F=0}$), and percentage of years that spawning biomass declined to less than 20% $SSB_{F=0}$ were used to evaluate the performance of the 65% total annual mortality control rule to different population intermixing and productivity scenarios. Mean annual yield was the most sensitive metric to assumptions about intermixing and population productivity. Yields from areas occupied by low productivity populations were often similar to those occupied by high productivity populations when intermixing occurred, which could result in managers thinking low productivity populations could be fished more intensively. Large yields occurred despite spawning biomass

levels of low productivity populations generally being less than 20% of $SSB_{F=0}$, suggesting that the current control rule may not offer adequate protection to low productivity populations and that more conservative rules may be needed to ensure sustainability of intermixed populations.

Introduction

The 1836 Treaty waters (TW) of lakes Huron, Michigan and Superior is a region of the Laurentian Great Lakes comprising approximately 5.8 million ha that was ceded to the U.S. federal government by the Chippewa and Ottawa Nations of Native Americans as part of the Treaty of Washington. Although lands and waters within the treaty boundaries were ceded to the federal government, tribal members retained the right to subsistence hunt and fish free of state regulations. The right to subsistence fish in the 1836 TW was upheld in both a 1979 U.S. District Court ruling (United States v. Michigan, 1979) and a 1981 U.S. Court of Appeals ruling (United States v. Michigan, 1981). In addition to having the recognized right to fish free of state regulations, Native American tribes also are expected to participate in the management of 1836 TW fisheries to ensure protection and future sustainability of the resources (Brenden et al., in press). Two federal-ordered Consent Decrees that govern the management, allocation, and regulation of fishery resources within the 1836 TW have been enacted that have evolved through negotiations between representatives of the State of Michigan, the U.S. Department of Interior, and several Chippewa-Ottawa tribal governments (Ebener et al., 2008). The first Consent Decree was enacted in 1985; the second was enacted in 2000 and will expire in 2020. Management of lake whitefish (*Coregonus clupeaformis*) and lake trout (*Salvelinus namaycush*) stocks within the 1836 TW is the primary focus of the 1985 and 2000 Consent Decrees, although management of several other species is also addressed.

As part of the 2000 Consent Decree, a set of guidelines for managing lake whitefish fisheries in each of the 18 lake whitefish management units that lie within the 1836 TW was enacted. The guidelines define a maximum allowable annual mortality rate of 65%, which has been further refined to a harvest control rule of 65% total allowable annual mortality on the age class with the greatest fishing mortality. Additionally, it has been stipulated that spawning stock biomass per recruit (SSBR) in each of the management areas should not fall below 20% of what each stock would achieve without fishing (Mohr and Ebener, 2005). If a 65% mortality rate results in SSBR falling below this level, then the mortality rate is reduced until a 20% SSBR level is obtained. The 2000 Consent Decree specifies that harvest limits within each management unit will be calculated using appropriate statistical and mathematical modeling techniques. Presently for most management units, statistical catch-at-age (SCAA) models are used to annually estimate mortality rates and project lake whitefish abundances at age (Caroffino and Lenart, 2011). These projected abundances along with the 65% total annual mortality control rule are then used to generate total allowable catches (TAC) for each unit (Ebener et al., 2005; Mohr and Ebener, 2005). Apportionment of the TAC to state and tribal fishers differs by management unit with the exact apportionments specified in the 2000 Consent Decree.

Lake whitefish management units were originally delineated to represent the spatial distributions of reproductively isolated spawning populations and the dynamics of the fisheries that exploited the populations (Rybicki and Schneeberger, 1990; Ebener et al., 2005, 2008). This stock-based approach to management was proposed in the 1970s to protect spawning populations and thereby maintain genetic diversity of lake whitefish populations (Patriarche, 1977; Spangler et al., 1981; MacLean and Evans, 1981). The intensive management actions implemented in the 1836 TW and elsewhere in the Great Lakes, along with reductions in sea lamprey (*Petromyzon* *marinus*) densities, habitat restoration, and water quality improvements, have been credited with the phenomenal rebound of lake whitefish from the low abundance levels of the 1950s and 1960s (Ebener, 1997; Ebener et al., 2008). Recently, concerns have arisen that sustainability of lake whitefish populations may be at risk due to major changes in the Great Lakes benthic communities, 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, 2009a). One purported consequence of dreissenid mussel invasion has been a decrease in pelagic productivity in invaded lakes (Vanderploeg et al., 2002; Higgins et al., 2011). This decline in productivity coupled with increased lake whitefish abundance in the Great Lakes may be resulting in altered lake whitefish foraging behavior (Pothoven and Madenjian, 2008; Nalepa et al., 2009b) as well as reduced growth and body condition (Pothoven et al., 2001, Rennie et al., 2009), reduced egg production and egg quality (Kratzer et al., 2007), and shifts in depth distribution (Mohr and Ebener, 2005). Recent tagging and genetic studies conducted in northern lakes Huron and Michigan suggest that movement of lake whitefish has also increased considerably over the last 15 to 30 years with fish from various spawning populations now intermixing substantially during non-spawning periods (VanDeHey, 2009; Ebener et al., 2010; Stott et al., 2010). Although it is not known definitively what has led to increased movement of lake whitefish, one obvious hypothesis is that it is a consequence of reduced densities of *Diporeia*, which has resulted in fish expanding foraging areas to meet energetic needs (Ebener et al., 2010).

Stock-based management, such as that implemented for lake whitefish in the 1836 TW, has been a relatively common management approach both within the Great Lakes and more broadly (Stephenson, 1999). A common underlying assumption of stock-based management is that exploited stocks consist of fish from a single spawning population rather than consisting of fish from multiple spawning populations. When exploited stocks consist of intermixed fish populations, past research has found that stock-based management approaches can perform poorly (Heifetz et al., 1997; Quinn and Deriso, 1999; Punt et al., 2005; Dichmont et al., 2006; Punt, 2008). The sustainability of harvest and spawning populations under marine protected areas (MPA), a quasi-form of stock-based management with certain stocks closed to fishing, can be reduced when there is movement between populations, particularly when there are both source and sink populations (Crowder et al., 2000; Sanchirico et al., 2006; Armstrong, 2007). Wilberg et al. (2008) found that source-sink dynamics could affect harvest policy performance for yellow perch (*Perca flavescens*) in Lake Michigan beyond a protected area context. Fu and Fanning (2004) and Kell et al. (2009) each found that metapopulations of fish could be extirpated if intermixing of populations was not accounted for in a manner consistent with actual conditions. Perhaps the most well-known case of admixed fisheries negatively affecting individual spawning populations have occurred in the Pacific Northwest of North America, where entire spawning populations of Chinook (*Oncorhynchus tshawytscha*), coho (*O. kisutch*), pink (*O. gorbuscha*), chum (*O. keta*), sockeye (*O. nerka*), and steelhead salmon have been extirpated due in part to overfishing of low productivity populations in admixed stocks (Morishima and Henry, 1999).

Despite wide recognition that population intermixing can be important, spatially-explicit assessment models are rarely implemented, although recently this has begun to change (Cadrin and Secor, 2009; Goethel et al., 2011). Ultimately, the effect that intermixing has on fish populations depends on the mixing rates, the productivities of the populations, and the particular policies that are used to manage the stocks. Within the 1836 TW, lake whitefish fisheries continue to be managed primarily through a stock-based approach. It is not currently known how populations may be affected by intermixing under the current 65% total annual mortality control rule. Originally, this control rule was adopted based on research that indicated that this level of mortality was sustainable, and substantially higher mortality rates were not (Ebener et al., 2008). Deroba (2009), found the 65% control rule to perform reasonably even with changes in life history characteristics of lake whitefish in recent years, however the considerable ecosystem-level changes that have occurred in the Great Lakes, including greater rates of intermixing among populations with differing levels of productivity, still raise concern as to whether the current limit on mortality is sufficient to protect genetic diversity of populations in the 1836 TW.

The purpose of this research was to evaluate the performance of the 65% total annual mortality control rule that is currently in effect in the 1836 TW under different scenarios of population productivity and intermixing. The intent was to provide guidance to managers 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.

Methods

Definitions of Terms

Herein, “population” and “spawning population” are used interchangeably and refer to a group of fish that spawn in the same geographical area and exhibit natal philopatry. 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 harvest, and may contain fish from several different spawning populations if mixing occurs. This means that all aspects of the fishery (i.e.

harvest and assessment) occur in relation to stocks, while measures such as spawning biomass and recruitment are characteristics of populations.

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, this matched the overlap" assumption with reproductive isolation described by Porch (2003) and Cadrin and Secor (2009). The simulated populations had characteristics similar to those of lake whitefish populations in northern lakes Huron and Michigan, but were not meant to exactly replicate particular populations. 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 certain fractions of each population either staying within their natal areas or moving to areas where the other populations spawned. After movement occurred, each mixed stock was assumed to be commercially exploited during the remainder of the year. Surviving fish redistributed among the stocks each year, with mature fish spawning in their natal stocks after returning at the end of each year.

Four different levels of intermixing were assigned to spawning populations in this analysis. No mixing where all fish stayed in their natal area during the harvest season, low mixing where 10% of the fish moved from their natal area to the other areas, intermediate mixing where 40% of the fish moved from their natal area to the other areas, and high mixing where 80% of the fish moved from their natal area to the other areas. The levels of high, intermediate and low intermixing were based in part on the results of tagging studies conducted by Ebener et al. (2010), who found comparable levels of intermixing for lake whitefish populations in northern Lakes Huron and Michigan. We assumed that the proportion of the fish emigrating from an area would be equally divided among the other areas of the mixed stock system.

Abundances at age of each of the populations were simulated using an exponential population model, with total mortality partitioned into natural and fishing mortality components. Instantaneous natural mortality for all ages for each of the populations was set equal to 0.25, which is within the range of natural mortality rates reported for the 1836 TW (Caroffino and Lenart, 2011). Recruitment of the populations was modeled with a Ricker recruitment model using egg production of the spawning population as stock size (SSE) and with recruits defined as numbers of age-1 fish produced in the year following spawning (Table 1.1). Stochasticity was incorporated via a multiplicative lognormal process error. We chose the Ricker formulation for modeling recruitment because of strong evidence for over-compensation in lake whitefish populations at high abundances (Healey, 1978; Henderson et al., 1983; Kratzer et al., 2007) and because it is the assumed recruitment relationship for lake whitefish assessment models in the 1836 TW (Caroffino and Lenart, 2011).

Differences in productivity among the four spawning populations were incorporated via adjustments to the coefficients of the 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 for the spawning populations: high, medium-high, medium-low, and low productivities (Figure 1.1). High productivity populations were defined such that they had spawning potential ratios (the ratio of spawning stock biomass per recruit at MSY exploitation to unfished spawning stock biomass) of 20% (Table 1.2). Medium-high, medium-low, and low productivity populations were defined such that they had spawning potential ratios of 30, 40 and 50%, respectively (Table 1.2). Based on deterministic models sharing the same stock recruitment parameters and fishery characteristics used in this analysis, the estimated MSY 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 TW (Deroba, 2009).

Egg production of the spawning populations was calculated as the product of abundance at age, proportion mature at age, weight at age, proportion of females in the population, and the number of eggs per kilogram of fish (Table 1.1). 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 1.1). 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 1.1). Total SSE was calculated by summing age-specific SSE.

For simplicity, it was assumed that each stock was 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. Age-specific fishing mortalities 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 a given area (i) regardless of which area fish originated in. Fishery selectivity was modeled as a gamma function of age (Table 1.1), 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 TW. Selectivities were scaled such that the fully selected age class had a selectivity value of 1.0.

The fully-selected fishing mortality rates that fish experienced in the simulations were determined from how much harvest occurred in each year and area and the abundance at age of all fish in the particular area at the time of exploitation. Implementation error associated with the TAC was incorporated via an independent lognormal error

$$C_{i,y} = TAC_{i,y} \exp\left(\upsilon_{i,y} - 0.5\sigma_C^2\right); \quad \upsilon_{i,y} \sim N\left(0, \sigma_C^2\right),$$

where $C_{i,y}$ is the actual amount of commercial harvest for an area, $TAC_{i,y}$ is the assessed TAC for an area, and $\upsilon_{i,y}$ is a normally distributed random variable with expectation 0 and variance of σ_C^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 exploitation levels 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 as described in Deroba (2009).

Given the intermixing and population dynamics framework described above, abundance at age of a particular population depended on what fraction of the population moved to other areas and the amount of fishing mortality that each of these fractions experienced in the areas to which they moved. Using an exponential population model, abundances at age of a particular spawning population could be represented as

$$N_{i,y+1,a+1} = N_{i,y,a}\theta_{i\rightarrow i}\exp\left(-M - F_{i,y,a}\right) + \sum_{j} N_{i,y,a}\theta_{i\rightarrow j}\exp\left(-M - F_{j,y,a}\right),$$

where $N_{i,y,a}$ is the abundance of fish from spawning population *i* of age *a* in year *y*, θ is the fraction of each spawning population either located within their natal area ($\theta_{i\rightarrow i}$) or located in other areas after movement ($\theta_{i\rightarrow j}$), 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 of fish occurring in the natal area of spawning population *i*. 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 area once intermixing occurred ($\tilde{N}_{i,y,a}$) could be represented as

$$\tilde{N}_{i,y,a} = N_{i,y,a}\theta_{i\rightarrow i} + \sum_{j} N_{j,y,a}\theta_{j\rightarrow i}\ .$$

Observation Components

The data available for use in stock assessment models was assumed to consist of fishery harvest-at-age for each stock and year and a reported measure of the amount of fishing effort occurring in each area and year, which matches the data used in many of the lake whitefish assessments in the Great Lakes. Observed harvest for a given fished area differed from actual harvest as a result of observation error (Francis and Shotton, 1997; Butterworth and Punt, 1999), which like implementation error was modeled as an independent lognormal error

$$\tilde{C}_{i,y} = C_{i,y} \exp\left(\varpi_{i,y} - 0.5\sigma^2_{\tilde{C}}\right); \quad \varpi_{i,y} \sim N\left(0, \sigma^2_{\tilde{C}}\right),$$

where $\tilde{C}_{i,y}$ is observed commercial harvest and $\varpi_{i,y}$ is a normally distributed random variable with expectation 0 and variance of $\sigma^2_{\tilde{C}}$, which was assumed to equal 0.01. We modeled observed proportions at age in the harvest as though they arose from a multinomial distribution with probabilities equal to the actual age composition of harvest and an assumed sample size of 200 fish. Again, this was intended to mimic the real-world situation where harvest estimates arise from a harvest reporting system and the age composition of the harvest arise from a biological sampling program; consequently, there is some level of error associated with both observations.

The amount of fishing effort that occurred in each area and year was calculated by dividing the fully-selected fishing mortality rate for that area and year by a catchability of $1.50\times10\text{e}^{-6}$. Observation error in the effort measurements was again modeled as an independent lognormal error

$$\tilde{E}_{i,y} = \frac{F_{i,y}}{1.50\times10\text{e}^{-6}} \exp\left(\nu_{i,y} - 0.5\sigma^2_{\tilde{E}}\right); \quad \nu_{i,y} \sim N\left(0, \sigma^2_{\tilde{E}}\right),$$

where $\tilde{E}_{i,y}$ is observed effort, $F_{i,y}$ is the fully selected fishing mortality rate, and $\nu_{i,y}$ is a normally distributed random variable with expectation of 0 and variance of $\sigma^2_{\tilde{E}}$, which was assumed to equal 0.04.

Assessment Model

The assessment model that was used to estimate abundances and mortality rates for the purpose of determining the TACs for each simulated stock in each year consisted of a SCAA model similar to those currently used to assess lake whitefish stocks in the 1836 TW (Ebener et al., 2005; Caroffino and Lenart, 2011). 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 area. 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 the assumed effective sample size of 200.

In the 2000 Consent Decree, it is specified that lake whitefish harvest limits are to be set in the year preceding that in which the limits will take effect using data collected two years prior to the effective harvest year (Ebener et al., 2008); thus TACs set for 2011 are based on assessments conducted in 2010 using data collected through 2009. We incorporated a similar time lag in our simulations. 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 structure of the SCAA model that was used to assess the stocks was similar to that used to simulate the population dynamics (e.g., abundances were computed using the exponential population with fishing and natural mortality components). Abundance at age in the SCAA model were estimated for ages 3 to 12, with the last age class consisting of an aggregate group that included age-12 and older fish. For the SCAA model, it was assumed that biologists were unaware of or ignored population intermixing and thus did not attempt to incorporate fish movement in the assessment models. Natural mortality rates were not estimated in the SCAA models; rather, the natural mortality rates in the SCAA models were set equal to the values used to simulate dynamics of the populations (0.25). Fishing mortality for the fishery component included in the SCAA model was assumed to be separable into age and year effects (Doubleday, 1976; Quinn and Deriso, 1999). Specifically, instantaneous fishing mortality for each stock was estimated as

$$\hat{F}_{i,y,a} = \hat{s}_{i,a}\hat{q}_i\tilde{E}_{i,y}\varepsilon_{i,y}$$

where $\hat{F}_{i,y,a}$ was the estimated fishing mortality rate by stock, year, and age, $\hat{s}_{i,a}$ was the estimated selectivity at age for each stock, $\hat{q}_i$ was the estimated catchability for each stock, $\tilde{E}_{i,y}$ was the measured fishing effort in each stock and year, and $\varepsilon_{i,y}$ were stock and year multiplicative deviations from the direct proportionality between observed fishing effort and fishing mortality. The annual deviations in the fishing mortality-effort relationships were constrained to sum to zero and as suggested earlier were assumed to be distributed lognormally in terms of their contribution to the objective function used in fitting the model. As when simulating the stock dynamics, selectivities in the SCAA model were calculated as gamma functions of age with the parameters of the functions estimated as part of the model fitting process. Estimated selectivities at age were scaled relative to age-10 selectivities.

Initial abundances at age for age-4 to age-12 fish in the SCAA models were estimated as the product of a mean abundance value multiplied by an annual multiplicative deviation. Annual recruitment in the SCAA models (age-3 abundance) was also estimated as the product of a mean recruitment value multiplied by an annual multiplicative deviation. The deviations for both initial abundances and recruitments were constrained to sum to 0, but no distributions were assumed for the deviations so large differences in annual values from the means were not penalized. Age-specific harvest from each stock in the SCAA models was predicted using the Baranov catch equation. Total harvest was calculated by summing age-specific values, and age composition of the harvest for the stocks was calculated by dividing age-specific harvest by the total harvest. Both totals and composition contributed to the objective function via comparison with actual (simulated) values based on their assumed distributions.

Because of the considerable processing time needed to conduct the simulations for this research, the SCAA model assessments were conducted on the stocks 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 TW, there are some within the group responsible for conducting the assessments on the lake whitefish stocks 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 three years was farfetched; rather, we thought it would provide useful guidance to those who conduct the actual lake whitefish assessments as to the positive and negative aspects of switching when the assessments were conducted.

The search for the HPD SCAA model parameter estimates used the quasi-Newton optimization algorithm implemented in AD Model Builder (Fournier et al., in press). The SCAA models were considered to have converged on a solution when the maximum gradient of parameters with respect to the objective function was less than 0.001. Upper and lower bounds were specified for all parameters to help keep the optimization algorithm from flat parts of the likelihood surface. These bounds were chosen to represent values above or below which would be considered implausible. In rare cases where the assessment model failed to converge properly as defined above, the previous TAC generated for the stock was implemented until the next assessment was performed so faulty assessment outputs would not bias the analysis.

The performance of the SCAA model was assessed by calculating the mean relative error (MRE) and mean absolute relative error (MARE) between the estimated and true harvest for the

20 years of harvest data included each time an assessment was performed. We also calculated the MRE and MARE between the estimated and true abundances of the stocks (after mixing but prior to fishery harvest) in the last year of each assessment.

Abundance Projections and TAC Calculations

The SCAA model estimates of abundances at age, age-specific mortality rates, and recruitment levels were used to project future abundances at age and calculate TACs for each stock area. 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. It is not presently 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 within lake whitefish populations 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 1.3. 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 varied levels of productivity. For this grouping of scenarios, it was assumed each lake whitefish population had one of the four productivity levels developed for the analysis. The Shared Productivity grouping 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 were assumed to be different. The Correlated group consisted of just two scenarios in which movement of fish from spawning areas was either positively or negatively (inversely) correlated with population productivity levels. In the negatively correlated scenario, the population with the lowest rate of intermixing had the highest productivity level. In the positively correlated scenario, the population with the lowest rate of intermixing had the lowest productivity level.

Performance Metrics and Simulation Details

The performance of the 65% total annual mortality control rule to 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), inter-annual variability in fishery yields, mean percentage of unfished SSB ($SSB_{F=0}$), and the percentage of years the SSB declined to less than 20% of $SSB_{F=0}$. The 20% $SSB_{F=0}$ is a frequently used measure of risk of depletion (Beddington and Cooke, 1983; Francis, 1992; Punt, 1995, 1997), although as pointed out by Hilborn (1997) the 20% level is arbitrary.

Simulations were conducted in AD Model Builder (Fournier et al., in press). Each simulation involved the projection of stock dynamics under the assumed intermixing and productivity levels over a 100 year time span. 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 dispersion (range) of the simulation results.

Results

The SCAA assessments that were conducted on the stocks performed well. Non-convergence of the SCAA models was a rare occurrence with at most only two assessments failing to converge during any 100 year model run, which was unlikely to have any bearing on the overall results of this research. The harvest MRE and MARE were generally quite small with the median harvest MRE and MARE for all scenarios being less than 3.0% (Table 1.4). The abundance MRE and MARE were greater than those for harvest, with median abundance MRE as large as 19% in some scenarios, with median abundance MARE as large as 29% (Table 1.4).

All Shared Group

The highest mean annual yields were for the medium-high productivity scenarios, followed by the high and medium-low productivity scenarios (Figure 1.2). Not surprisingly, mean annual yield was the lowest for the scenarios with low productivity populations. The range of yields across the simulations was greater for the medium-low and low productivity scenarios than for the high and medium-high productivity scenarios (Figure 1.2). Overall, intermixing had little effect on fishery yields, which was to be expected for this scenario as all populations had the same productivities and thus intermixing led to nearly equal levels of movement to and from stocks areas. Cumulative mean annual yield results were similar to the mean annual yield results; that is, the greatest yields were found for the medium-high productivity scenarios with intermixing having very little effect on cumulative yields and the range of yields across the simulations being greatest for medium low and low productivity scenarios (Figure 1.3). As for inter-annual variability in yield, there was an inverse relationship between variability and intermixing for the different productivity scenarios, with inter-annual variability decreasing with higher rates of intermixing (Figure 1.4).

Both the mean percent of years that SSB declined to less than 20% of $SSB_{F=0}$ (Figure 1.5) and the mean percent of $SSB_{F=0}$ (Figure 1.6) were highly dependent on the productivity of the spawning population. The percentage of years that spawning stock biomass declined to less than 20% of $SSB_{F=0}$ was low (<10%) for high productivity populations, and high (>80%) for low productivity populations (Figure 1.5). Medium-high productivity populations performed similar to that of high productivity populations, having very low percentages of years below the threshold, while the medium-low productivity populations had a median value of around 50% of years below the threshold with at range covering near 0 to 100% (Figure 1.5). In terms of the mean percent of $SSB_{F=0}$, for high productivity populations median SSBs were approximately 50% of $SSB_{F=0}$. For medium-high, medium-low, and low productivity populations, mean percent of $SSB_{F=0}$ was on the order of 40%, 20%, and 5% respectively. As with the other performance metrics, intermixing appeared to have little overall effect on the mean percent of years that SSB declined to less than 20% of $SSB_{F=0}$ and mean percent of $SSB_{F=0}$ with perhaps a slight decrease in the mean percent of years that SSB declined to less than 20% of $SSB_{F=0}$ and a slight increases in mean percent of $SSB_{F=0}$ with higher rates of intermixing (Figures 1.5 and 1.6).

Shared Mixing Group

For the shared mixing group of scenarios, intermediate and high rates of intermixing led to decreases in mean annual yield for high and medium-high productivity areas. For medium-low productivity areas there was little change in yield with intermixing rate but the range about the yield decreased slightly with increased mixing (Figure 1.2). Conversely, for low productivity areas, mean annual yield increased considerably under intermediate rates of stock intermixing compared to low rates of intermixing, and increased even more profoundly under high rates of intermixing (Figure 1.2). The magnitude of increase in mean annual yield for the stock with low productivity levels under high rates of intermixing was such that yields were nearly comparable to those of areas with higher productivity levels under the All Shared group of scenarios. The cumulative mean annual yield was approximately 550 tonnes for all three scenarios, suggesting that overall yield from the mixture system was relatively unaffected by intermixing and it primarily resulted in reallocating harvest to different areas (Figure 1.3). Across all productivity levels, inter-annual variability in yield declined as intermixing rates increased, although the decline observed for the low and medium low productivity areas was slightly less than that observed for the high and medium high productivity areas (Figure 1.4).

The results for percentage of years that SSB declined to less than 20% $SSB_{F=0}$ and mean percentage of $SSB_{F=0}$ were similar to that observed for the All Shared grouping. That is, the percentage of years that SSB declined to less than 20% $SSB_{F=0}$ was less than 20% for high and medium high productivity populations, near 50% for medium-low productivity populations, and generally greater than 80% for low productivity populations (Figure 1.5). Additionally, for high productivity populations, mean percentage of $SSB_{F=0}$was generally around 50%, while lower productivity populations mean percentages were around 35, 20 and 5%, respectively (Figure 1.6).

Shared Productivity Group

The mean annual yield for simulations in the Shared Productivity group varied considerably with both rate of intermixing and productivity. When all populations had high productivity levels, the medians of the mean annual yields varied from over 200 tonnes in the area with no intermixing to nearly 75 tonnes in the area with high intermixing (Figure 1.2). Most notably, a high productivity population with high intermixing could have yields similar to that of low productivity populations in the all shared scenarios. Similar results were obtained when all populations had medium-high and medium-low productivity levels, although the range in values obtained from the simulations was somewhat greater for the medium-low productivity level than it was for the high productivity levels. When all populations had low productivity levels, mean annual yields for areas with no or low intermixing were near100 tonnes. Areas with high intermixing rates had mean annual yields ranging from 25 to 50 tonnes (Figure 1.2). Much like what was observed for the All Shared scenarios, the cumulative mean annual yield depended on the productivity of the populations in the scenario, with the cumulative yields obtained for the various productivity levels nearly equal to the corresponding All Shared scenarios (Figure 1.3), again suggesting that overall yield from the mixture system was relatively unaffected by intermixing. Inter-annual variability in yield was fairly similar across the areas regardless of the productivity levels assumed for the populations, although it did appear to decline with both lower productivity levels and higher intermixing rates (Figure 1.4).

The results for percentage of years that SSB was less than 20% $SSB_{F=0}$ (Figure 1.5) and mean percent of $SSB_{F=0}$ (Figure 1.6) were similar to the previous scenarios. The percentage of years that SSB was less than 20% $SSB_{F=0}$ level was generally less than 20% when populations had high or medium-high productivity levels, between 20 and 60 % when populations had medium-low productivity and greater than 80% when populations had low productivity levels (Figure 1.5). The mean percentage of $SSB_{F=0}$ when populations had high productivity levels was approximately 50%; and for low productivity levels the mean percentage of $SSB_{F=0}$ was around10%, with the medium-high and medium-low populations in between (Figure 1.6).

Correlated Group

When population productivity and intermixing levels were inversely correlated (i.e., lower productivity populations had higher intermixing rates), mean annual yields in high productivity populations increased to levels greater than those of medium-high productivity populations in the all shared scenarios. For medium-high and medium-low productivity populations, yields remained relatively stable, whereas yields for low productivity populations decreased considerably from those of low productivity populations in the all shared scenarios. When population productivity and intermixing levels were positively correlated (i.e., more productive populations had higher intermixing rates), mean annual yields of areas with high productivity populations declined to levels comparable to that of areas with low productivity populations in the all shared scenarios (Figure 1.2). Similarly, mean annual yields of stocks with less productive populations increased to levels comparable to that of stocks with high productivity populations in the all shared scenarios. For medium-high productivity populations, yields decreased to levels similar to medium-low productivity populations in the all shared scenarios, whereas yields for medium-low productivity populations increased to levels similar to medium-high productivity populations in the all shared scenarios. In terms of cumulative mean annual yield, yields were nearly equal to those in the shared mixing scenarios with the positively correlated mixing scenario slightly greater to that of the negatively correlated scenario (Figure 1.3). The inter-annual variability in yield (Figure 1.4), percentage of years that SSB was less than 20% $SSB_{F=0}$ (Figure 1.5), and mean percentage of $SSB_{F=0}$ (Figure 1.6) result were similar to those from other examined scenarios.

Discussion

The performance of harvest control rules for managing lake whitefish fisheries in the Laurentian Great Lakes has previously been evaluated by Jacobson and Taylor (1985) and Deroba (2009). In both cases, constant mortality control rules were found to perform adequately with respect to maximizing fishery yield (Jacobson and Taylor, 1985; Deroba, 2009), although Deroba (2009) found that biomass-based control rules 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 in the harvest evaluations that were performed, although Deroba (2009) did account for substantial complexity and uncertainty in various life-history characteristics of fish populations (e.g., growth and recruitment rates). Overall, we found intermixing to have little influence on inter-annual variability in fishery yields, at least at the population productivity levels considered in this research. Risk of depletion to fish populations as measured by the percentage of years that SSB declined to less than 20% $SSB_{F=0}$ also was not affected by stock intermixing, but was strongly linked to assumed productivity levels. Conversely, fishery yields in each stock area were clearly influenced by population intermixing and productivity levels, and our research demonstrated that under particular combinations a population can have a high risk of depletion even though the amount of harvest from the area near where the population spawns was high as a result of fish from other populations moving into the area. In essence, the productivities of the populations determined the yield from the system as a whole, as demonstrated by the relatively stable cumulative fishery yields in the shared mixing group of scenarios, but intermixing influenced the realizable yield from each area by redistributing harvest. In particular, when higher productivity populations mixed substantially into areas occupied by low productivity populations, the yield from the area approached that of areas associated with high productivity populations. Similarly, it was possible for areas where highly productive populations spawned to have yields similar in magnitude to that of areas where low productivity populations spawned.

Perhaps the most concerning result was that the 65% total annual mortality control rule may not be sufficiently conservative for low productivity populations, but it would be difficult for managers to determine this without knowledge as to the actual productivity levels of the populations. This is in contrast to Deroba (2009), who found that the 65% mortality control rule performed relatively well for lake whitefish stocks, even accounting for changes in life history characteristics that concern managers (minus intermixing). One potential reason for the mismatch in conclusions was that Deroba (2009) looked at the probability of outcomes for harvest policies, with stock recruitment (productivity) values drawn from a set of estimated values in each simulation. This meant the effects on low productivity populations were not investigated directly, but included in a distribution of outcomes with higher productivity populations. Another explanation for the mismatch is that the stock recruitment relationships in Deroba (2009) were estimated from stock assessments conducted on lake whitefish stocks in the TW, so intermixing may have led to overestimates of productivity in low productivity populations. Our analysis, in contrast, investigated a plausible range of productivity levels, without linking the productivities in our analysis to assessments performed on intermixing stocks.

Because allowable catches 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 populations spawning stock biomass (Belcher and

Jennings, 2009). This issue is often combated by including fishery independent data that targets the spawning population spatially or seasonally and is thus less biased into assessments (Mesnil et al., 2009; Harms et al., 2010). Consistent with the findings of Kell et al. (2009) who showed 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.

The modeling subcommittee, which is responsible for assessment modeling of lake trout and lake whitefish fisheries in the 1836 TW, has begun taking steps to account for the intermixing of some lake whitefish populations. In northern Lake Huron, four lake whitefish management units (WFH-01 to WFH-04) that 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). The impetus for this change was the extensive intermixing of lake whitefish populations from these management units based on the results of a tagging study conducted by Ebener et al. (2010). Although combining intermixing stocks into a single assessment and management system is one reasonable approach for dealing with stock intermixing, lumping the assessment can, depending on details, lead to biased estimates of abundance and mortality rates (Kell et al., 2009). Furthermore, how the combined TAC for a mixed stock is allocated spatially or to different fishery components can influence sustainability (Heifetz et al., 1997), making knowledge about productivity of individual populations important.

An alternative to pooling the assessment for management units with significant levels of intermixing would be to construct a tag-integrated assessment model, which would incorporate a tag-recapture component within an SCAA assessment model (Goethel el. al., 2011). Such an approach would certainly complicate the existing management system and require a long-term commitment to tagging lake whitefish throughout the 1836 TW, but ultimately may prove useful for lake whitefish management in the 1836 TW. Regardless, there still would remain the issue of whether the 65% total annual mortality control rule is appropriate given current productivity levels of lake whitefish stocks in the Great Lakes. Short of reducing allowable mortality, spatial closures, seasonal closures, and regional or temporal allocation of TAC may also be useful to account for intermixing. Another alternative to pooled or tag-integrated assessment models would be to incorporate in existing SCAA models a fishery independent assessment of the lake whitefish stocks during the spawning season in order to index spawning population size.

A simulation-based framework such as that used in this research is a relatively common approach for providing advice to fishery managers about performance of fishery harvest control rules and to explore how aspects of fish behavior and ecology or fishery dynamics can influence management (Cooke, 1999; Deroba and Bence, 2008; Ralston and O’Farrel, 2008; Kerr et al., 2010). Ebener et al. (2010) estimated that proportions of lake whitefish tagged at spawning sites in northern lakes Huron and Michigan and recaptured in other management areas ranged from 19 to 90%, although it is not presently known with certainty what factors govern lake whitefish movement. As previously indicated, one hypothesis is that movement rates are linked to food availability and that stocks with locally depleted food resources move more widely in search of areas with more abundant resources. Additional research to better understand intermixing in lake whitefish stocks and what factors lead to high rates of intermixing would be beneficial for providing more directed advice to fishery managers. Developing a better understanding of the productivity of the lake whitefish spawning populations in the Great Lakes would allow us to better determine how actual populations compare to the productivity levels we used in our analysis. Investigations that focus on the productivity of genetically and geographically distinct spawning aggregations may lead to a better understanding of the true productivity of lake whitefish populations in the upper Great Lakes than the current stock focused analyses. Managers should keep in mind that the productivity levels of spawning populations have important effects on the sustainability of the control rule used in the 1836 TW. If several populations with different productivity levels intermix considerably, the assessments used do not allow biologists and managers to develop a good understanding of the population responses to fishing, limiting the capacity to improve management of lake whitefish populations. Understanding the effects of productivity and intermixing on the performance of this control rule will help to better manage lake whitefish into the future. Caution is required for managing mixed stocks of lake whitefish as the lower productivity populations in the mixed stock may be put at considerable risk if the stock is managed to harvest at a rate more appropriate for higher productivity populations (Stephenson 1999).

APPENDIX

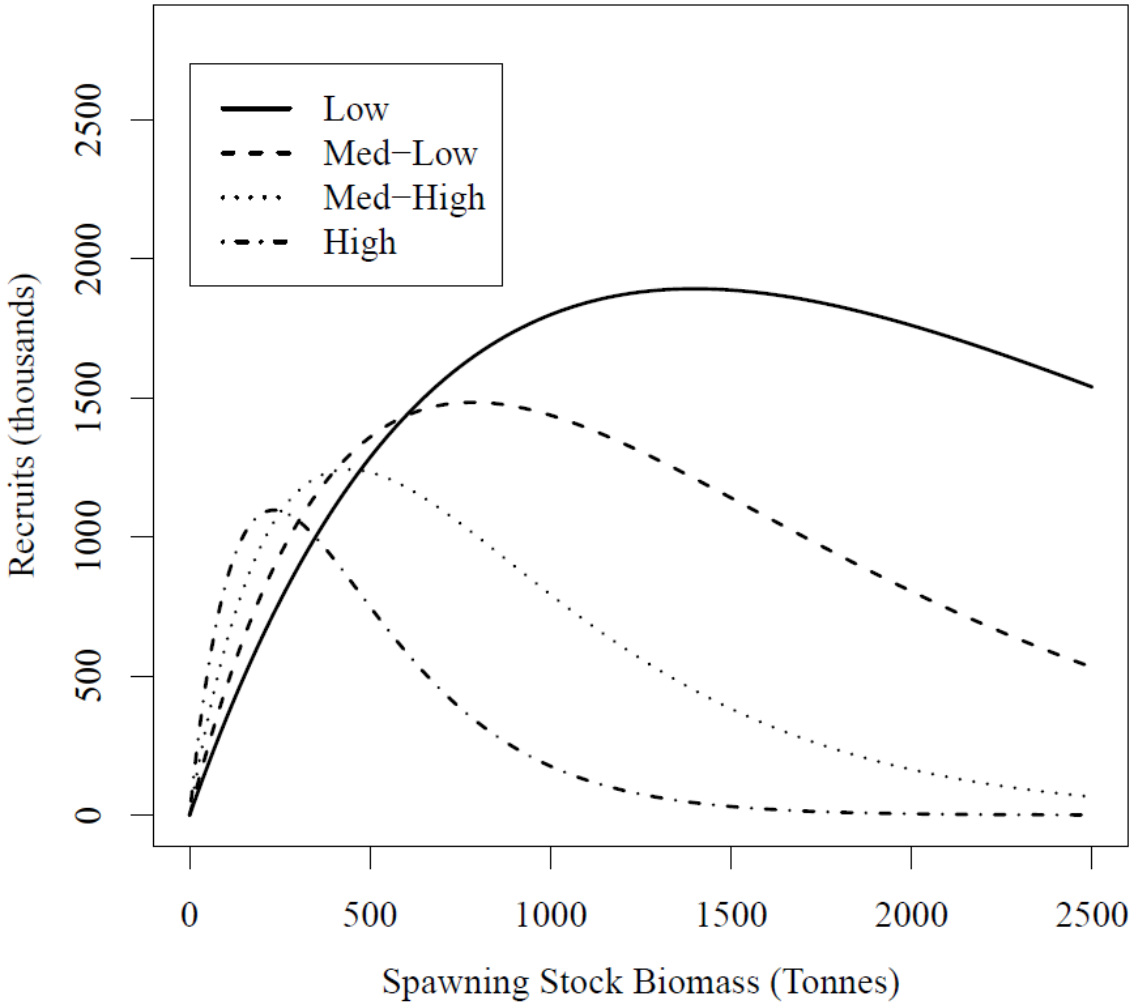

Figure 1.1. Ricker-stock recruitment relationships for the four levels of productivity used to investigate the effects of population intermixing on the 65% total annual mortality control rule used to manage lake whitefish fisheries in the 1836 Treaty waters of the Great Lakes.

Figure 1.2

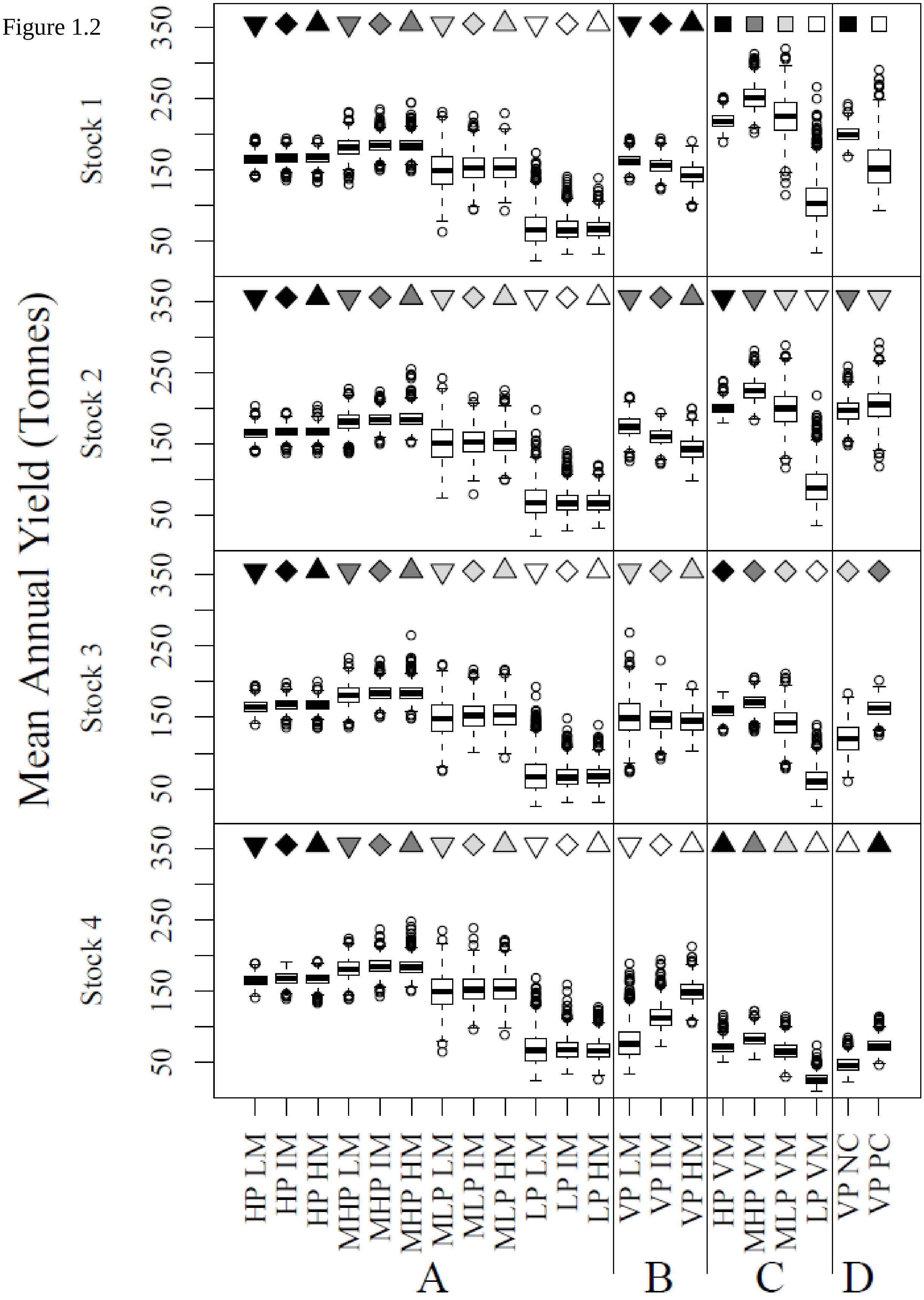
Mean Annual Yield (Tonnes)
Stock 1
Stock 2
Stock 3
Stock 4
50
150
250
350
HP LM
HP IM
HP HM
MHP LM
MHP IM
MHP HM
MLP LM
MLP IM
MLP HM
LP LM
LP IM
LP HM
VP LM
VP IM
VP HM
HP VM
MHP VM
MLP VM
LP VM
VP NC
VP PC
A
B
C
D

Figure 1.2 (cont'd)

Mean annual fishery yield for each unit stock for the investigated scenarios. Boxes indicate the 25th and 75th percentiles over the simulations, while whiskers indicate 1.5 times the interquartile range over simulations. Horizontal lines indicate the median of the yields for the simulations. The symbols appearing above the boxplots indicate the level of intermixing and productivities for the populations spawning in each stock region (square=no mixing, upside down triangle=low mixing, diamond=intermediate mixing, triangle= high mixing; black=high productivity, dark grey=medium high productivity, light grey=medium low productivity, white=low productivity). On the x-axis, vertically oriented labels correspond to specific scenarios. See Table 1.3 for a description of the investigated scenarios (A=all shared; B=shared mixing; C=shared productivity; D=correlated).

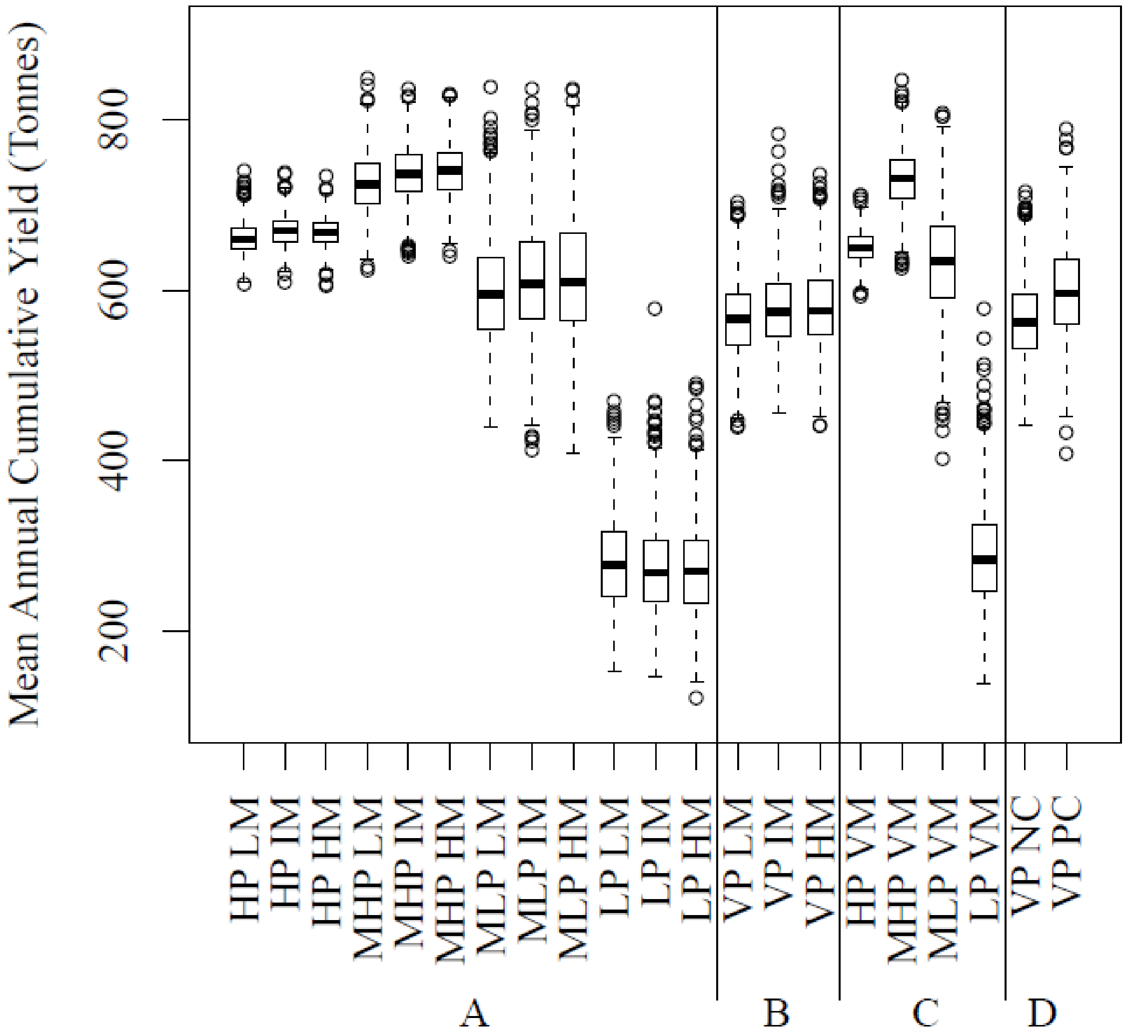

Figure 1.3. Mean annual cumulative fishery yield summed for each investigated scenario. Boxes indicate the 25th and 75th percentiles over the simulations, while whiskers indicate 1.5 times the interquartile range over simulations. Horizontal lines indicate the median of the yields for the simulations. On the x-axis, vertically oriented labels correspond to specific scenarios. See Table 1.3 for a description of the scenarios (A=all shared; B=shared mixing; C=shared productivity; D=correlated).

Figure 1.4

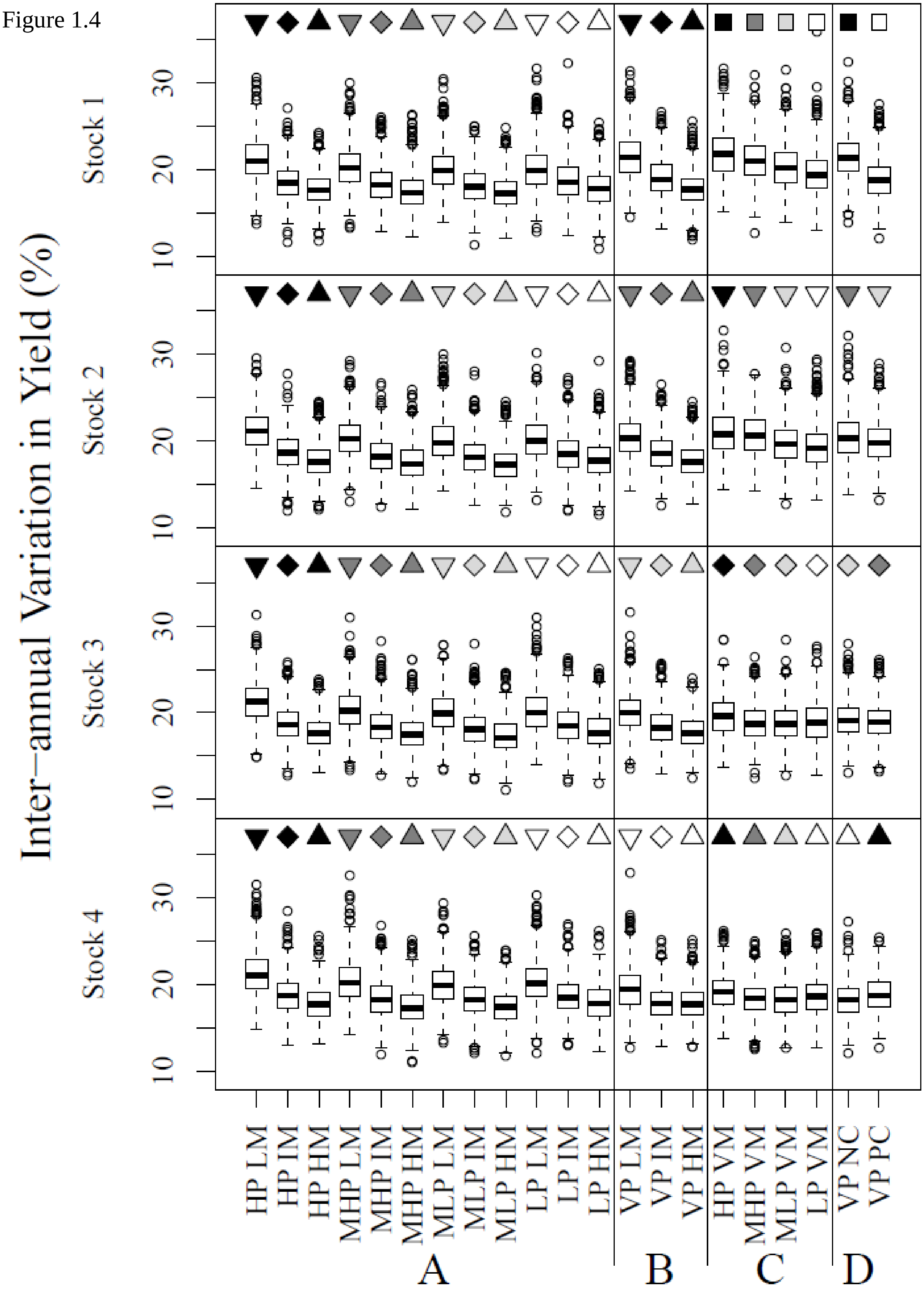
Inter−annual Variation in Yield (%)
Stock 1
Stock 2
Stock 3
Stock 4
10
20
30
HP LM
HP IM
HP HM
MHP LM
MHP IM
MHP HM
MLP LM
MLP IM
MLP HM
LP LM
LP IM
LP HM
VP LM
VP IM
VP HM
HP VM
MHP VM
MLP VM
LP VM
VP NC
VP PC
A
B
C
D

Figure 1.4 (cont'd)

As for Fig. 1.3, except y-axis is mean inter-annual percent variation in fishery yield.

Figure 1.5

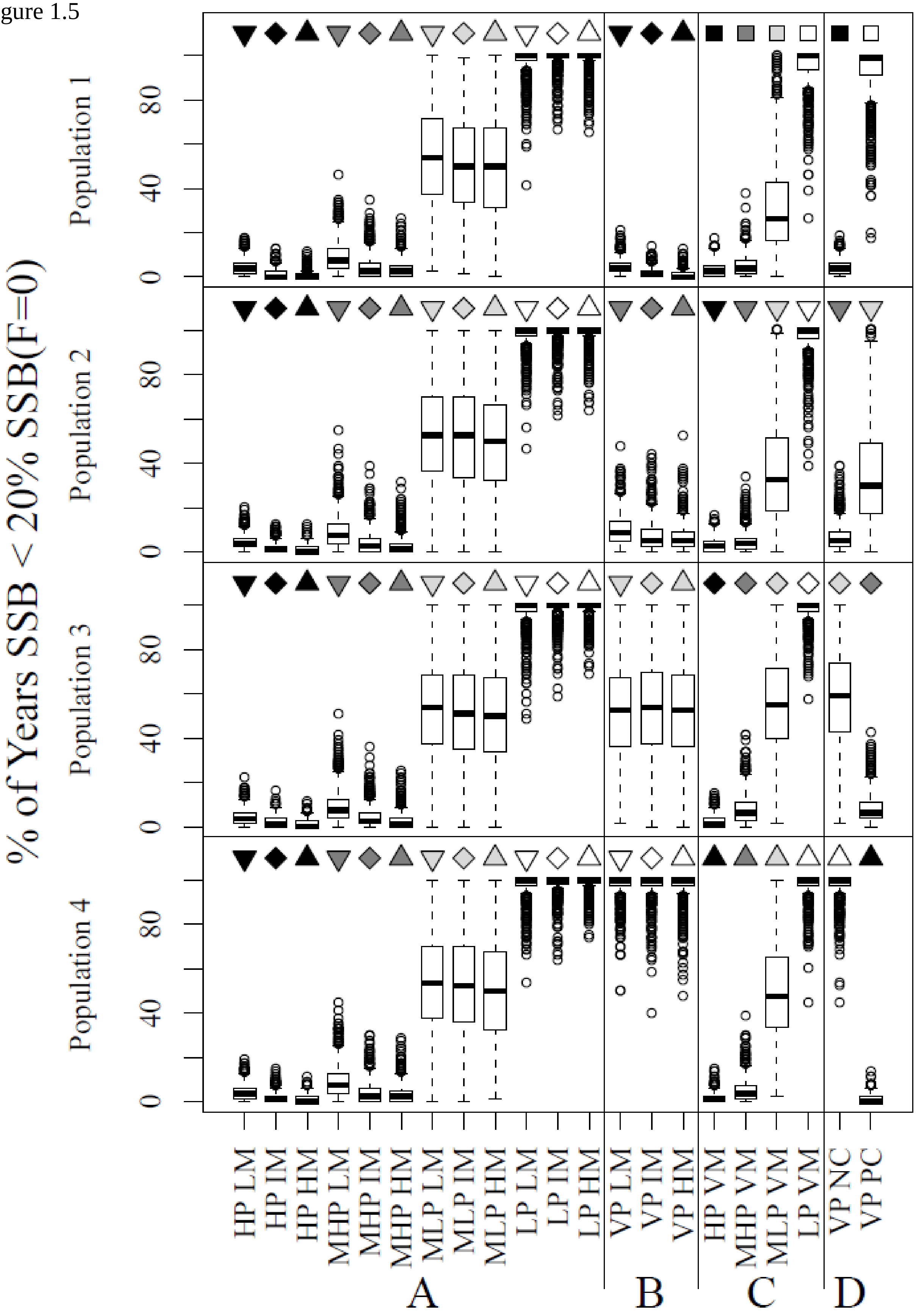
% of Years SSB < 20% SSB(F=0)
Population 1
Population 2
Population 3
Population 4
0
40
80
HP LM
HP IM
HP HM
MHP LM
MHP IM
MHP HM
MLP LM
MLP IM
MLP HM
LP LM
LP IM
LP HM
VP LM
VP IM
VP HM
HP VM
MHP VM
MLP VM
LP VM
VP NC
VP PC
A
B
C
D

Figure 1.5 (cont'd)

As in Fig. 1.3, except y-axis is the mean percentage of years in each simulation that the spawning stock biomass declined to less than 20 percent of the unfished spawning stock biomass ($SSB_{F=0}$).

Figure 1.6

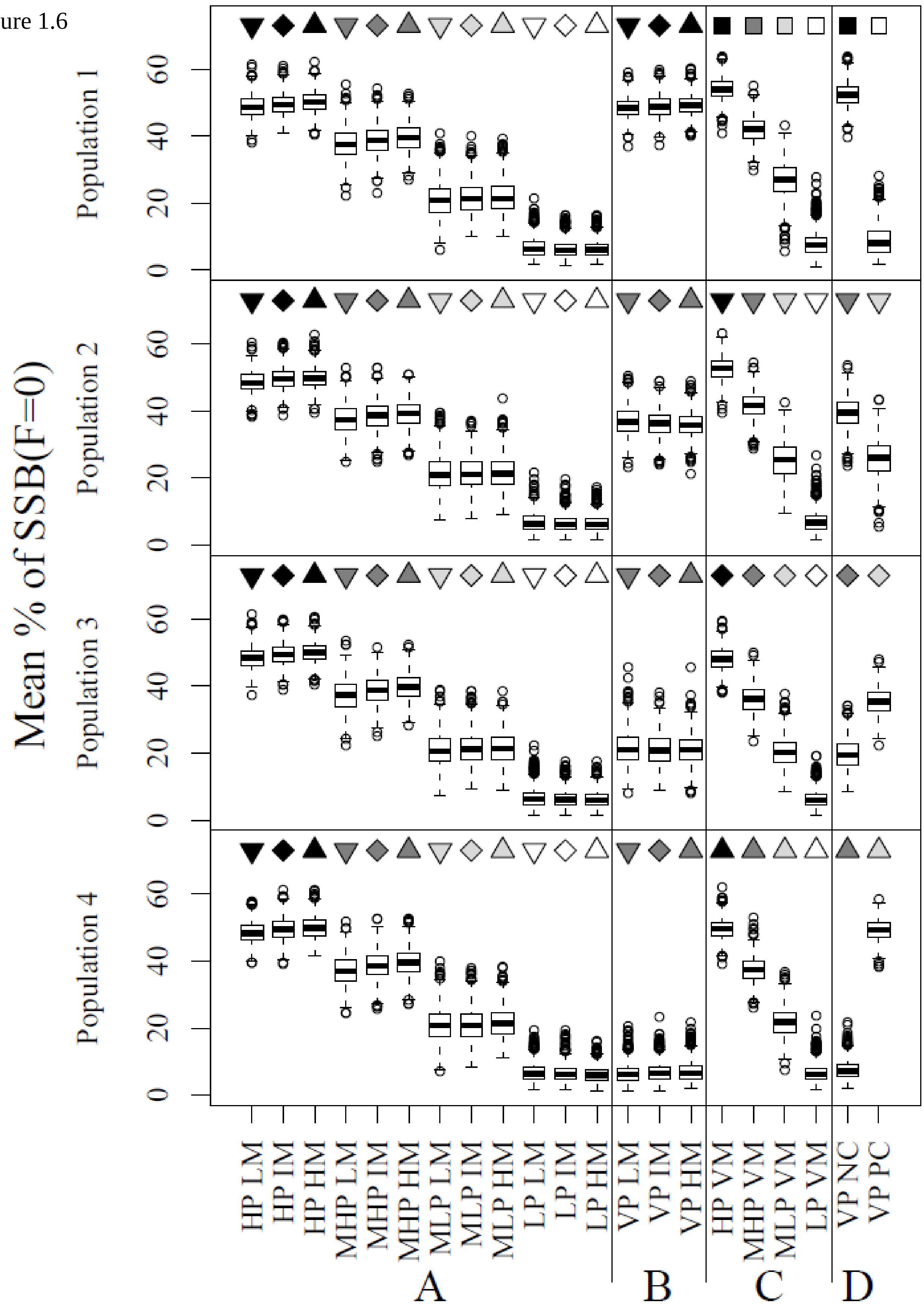
Mean % of SSB(F=0)
Population 1
Population 2
Population 3
Population 4
0
20
40
60
HP LM
HP IM
HP HM
MHP LM
MHP IM
MHP HM
MLP LM
MLP IM
MLP HM
LP LM
LP IM
LP HM
VP LM
VP IM
VP HM
HP VM
MHP VM
MLP VM
LP VM
VP NC
VP PC
A
B
C
D

Figure 1.6 (cont'd)

As in Fig 1.3, except y-axis is mean annual percentage of unfished spawning stock biomass ($SSB_{F=0}$) for the spawning populations

Table 1.1. Equations with descriptions and values for fixed variable inputs used in the simulation of lake whitefish populations and fisheries in this analysis.

Description of Equation	Equation	Parameter Coefficients
Abundance (*N*) at age of recruitment (age 1) by year (*y*)	$N_{y,1} = \alpha SSE_{y-1} \exp\left(-\beta \cdot SSE_{y-1}\right) \exp\left(\sigma_R^2\right)$	α = see Table 1.2 β = see Table 1.2 $\sigma_R^2 = 0.36$
Spawning Stock Biomass (*SSB*) by year (*y*)	$SSE_y = \sum_a N_{y,a} m_a w_a Fem \cdot Eggs$	$Fem = 0.5$ $Eggs = 19937$/kg
Length (*L*) at age (*a*)	$L_a = L_\infty \left(1 - \exp\left(-\kappa\left(a - t_0\right)\right)\right)$	$L_\infty = 60.9$ cm $\kappa = 0.1686$ $t_0 = 0.0$ years
Weight (*w*) at age (*a*)	$w_a = \gamma L_a^{\psi}$	$\gamma = 8.06\text{x}10^{-5}$ $\psi = 2.45$
Maturity (*m*) at age (*a*)	$m_a = \dfrac{m_\infty}{1 + \exp\left(-\vartheta\left(L_a - \delta\right)\right)}$	$m_\infty = 1.0$ $\vartheta = 0.315$ $\delta = 37.9$ cm
Selectivity (*s*) at age (*a*)	$s_a = \dfrac{a^{\eta} \exp\left(-\tau a\right)}{10^{\eta} \exp\left(-\tau 10\right)}$	$\eta = 13.074$ $\tau = 1.26$

Table 1.2. Ricker stock-recruitment coefficients (Table 1.1) 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.

Productivity Level	Alpha (α)	Beta (β)
Low	0.000369	$7.1708\text{x}10^{-11}$
Medium-Low	0.000516	$1.2780\text{x}10^{-10}$
Medium-High	0.0007687	$2.2758\text{x}10^{-10}$
High	0.001281	$4.2988\text{x}10^{-10}$

Table 1.3. 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 natal region during the harvest season. Productivity levels refer to high (H), medium-high (MH), medium-low (ML), or low (L) productivities as described in Table 1.2.

Group	Scenario	Pop. 1		Pop. 2		Pop. 3		Pop. 4	
		M	P	M	P	M	P	M	P
All Shared	HP LM (High Prod., Low Mix.)	10	H	10	H	10	H	10	H
	HP IM (High Prod., Int. Mix.)	40	H	40	H	40	H	40	H
	HP HM (High Prod., High Mix.)	80	H	80	H	80	H	80	H
	MHP LM (Med-High Prod., Low Mix.)	10	MH	10	MH	10	MH	10	MH
	MHP IM (Med-High Prod., Int. Mix.)	40	MH	40	MH	40	MH	40	MH
	MHP HM (Med-High Prod., High Mix.)	80	MH	80	MH	80	MH	80	MH
	MLP LM (Med-Low Prod., Low Mix.)	10	ML	10	ML	10	ML	10	ML
	MLP IM (Med-Low Prod., Int. Mix.)	40	ML	40	ML	40	ML	40	ML
	MLP HM (Med-Low Prod., High Mix.)	80	ML	80	ML	80	ML	80	ML
	LP LM (Low Prod., Low Mix.)	10	L	10	L	10	L	10	L
	LP IM (Low Prod., Int. Mix.)	40	L	40	L	40	L	40	L
	LP HM (Low Prod., High Mix.)	80	L	80	L	80	L	80	L
Shared Mix.	VP LM (Varied Prod., Low Mix.)	10	H	10	MH	10	ML	10	L
	VP IM (Varied Prod., Int. Mix.)	40	H	40	MH	40	ML	40	L
	VP HM (Varied Prod., High Mix.)	80	H	80	MH	80	ML	80	L
Shared Prod.	HP VM (High Prod., Varied Mix.)	0	H	10	H	40	H	80	H
	MHP VM (Med-High Prod., Varied Mix.)	0	MH	10	MH	40	MH	80	MH
	MLP VM (Med-Low Prod., Varied Mix.)	0	ML	10	ML	40	ML	80	ML
	LP VM (Low Prod., Varied Mix.)	0	L	10	L	40	L	80	L

Table 1.3 (cont'd)

Correlated	NEGC (Varied Prod., Negatively Correlated Mix.)	0	H	10	MH	40	ML	80	L
	POSC (Varied Prod., Positively Correlated Mix.)	0	L	10	ML	40	MH	80	H

Table 1.4. Median of the mean relative error (MRE) and the mean absolute relative error (MARE) for lake whitefish harvest and abundance estimates from the SCAA assessments across stocks and simulations. The values in parentheses are the ranges of the MREs and MAREs values. See Table 1.3 for a description of the Scenarios.

Group.	Scenario	Harvest MRE	Harvest MARE	Abundance MRE	Abundance MARE
All Shared	HP LM	0.0001 (-0.0360–0.0063)	0.0279 (0.0209–0.0636)	-0.0005 (-0.1347–0.1273)	0.1353 (0.0748–0.2071)
	HP IM	-0.0004 (-0.0071–0.0067)	0.0286 (0.0210–0.0385)	-0.0340 (-0.2016–0.1018)	0.1297 (0.0652–0.2239)
	HP HM	-0.0005 (-0.0079–0.0068)	0.0286 (0.0212–0.0390)	-0.0550 (-0.1874–0.0743)	0.1287 (0.0725–0.2152)
	MHP LM	-0.0005 (-0.0360–0.0051)	0.0278 (0.0203–0.0657)	-0.0791 (-0.3050–0.1344)	0.1611 (0.0719–0.3101)
	MHP IM	-0.0012 (-0.0100–0.0053)	0.0286 (0.0194–0.0392)	-0.1537 (-0.3508–0.0919)	0.1883 (0.0884–0.3543)
	MHP HM	-0.0013 (-0.0089–0.0062)	0.0286 (0.0215–0.0398)	-0.1902 (-0.3224–0.0153)	0.2084 (0.0907–0.3224)
	MLP LM	-0.0002 (-0.0069–0.0059)	0.0278 (0.0200–0.0379)	-0.0106 (-0.3190–0.1893)	0.1473 (0.0778–0.3190)
	MLP IM	-0.0004 (-0.0076–0.0065)	0.0286 (0.0214–0.0571)	-0.0296 (-0.3458–0.2370)	0.1491 (0.0768–0.3458)
	MLP HM	-0.0005 (-0.0068–0.0123)	0.0287 (0.0210–0.0459)	-0.0467 (-0.3311–0.2857)	0.1494 (0.0702–0.3350)
	LP LM	0.0000 (-0.0063–0.0062)	0.0279 (0.0205–0.0380)	0.0151 (-0.1769–0.4471)	0.1397 (0.0745–0.5197)
	LP IM	-0.0001 (-0.0078–0.0063)	0.0289 (0.0212–0.0387)	0.0217 (-0.1789–0.3273)	0.1434 (0.0758–0.3808)
	LP HM	-0.0001 (-0.0070–0.0063)	0.0290 (0.0212–0.0421)	0.0232 (-0.2376–0.3684)	0.1470 (0.0774–0.4187)
Shared Mix.	VP LM	-0.0002 (-0.0074–0.0058)	0.0280 (0.0201–0.0367)	-0.0034 (-0.2958–0.2736)	0.1440 (0.0767–0.3062)
	VP IM	-0.0002 (-0.0065–0.0060)	0.0287 (0.0214–0.0401)	-0.0076 (-0.2755–0.3230)	0.1419 (0.0765–0.3598)
	VP HM	-0.0002 (-0.0069–0.0067)	0.0289 (0.0210–0.0382)	-0.0143 (-0.2521–0.2459)	0.1437 (0.0754–0.2783)
Shared Prod.	HP VM	-0.0009 (-0.0342–0.0536)	0.0286 (0.0213–0.0819)	-0.1190 (-0.3897–0.7883)	0.2482 (0.0759–0.7883)
	MHP VM	-0.0011 (-0.0081–0.0073)	0.0286 (0.0201–0.0443)	-0.1768 (-0.4117–0.7651)	0.2901 (0.0790–0.7651)
	MLP VM	-0.0008 (-0.0071–0.0952)	0.0285 (0.0205–0.1271)	-0.0625 (-0.4149–0.6202)	0.2163 (0.0845–0.6506)
	LP VM	-0.0001 (-0.0369–0.0068)	0.0285 (0.0214–0.0670)	0.0056 (-0.3367–0.5842)	0.1480 (0.0757–0.5888)
Corr.	VP NC	-0.0007 (-0.0367–0.0146)	0.0285 (0.0208–0.0663)	-0.0689 (-0.3914–0.9644)	0.2041 (0.0827–0.9644)
	VP PC	-0.0006 (-0.0074–0.0563)	0.0286 (0.0209–0.0879)	-0.0294 (-0.4195–0.7538)	0.1792 (0.0778–0.7719)

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CHAPTER 2

HARVEST CONTROL RULES THAT CONSERVE SPAWNING BIOMASS MAY PROVIDE HIGHER AND MORE STABLE YIELDS FOR INTERMIXED FISHERIES

Abstract

We conducted a simulation-based evaluation of harvest control rule performance for four intermixing fish populations that were loosely patterned after lake whitefish (*Coregonus clupeaformis*) fisheries in northern lakes Michigan and Huron. The developed framework included an operating model that simulated the dynamics of each population, the harvests from fisheries exploiting the intermixed populations, and a full age-structured assessment of each exploited stock. The four harvest control rules that were evaluated included a 65% total mortality control rule that presently is used to manage lake whitefish fisheries in northern lakes Michigan and Huron and three more conservative control rules (35, 45, and 55% total mortality control rules). Mean annual yields varied considerably with control rule and rate of intermixing, while sustainability metrics depended primarily on productivity characteristics of the spawning populations. Under many scenarios, the current 65% total mortality control rule was found to have high risk of overexploitation of lower productivity spawning populations, which reduced overall harvest across stocks. More conservative control rules generally resulted in more sustainable fisheries and in some instances increased overall yield from the stocks. Our analysis suggests that control rules that conserve spawning biomass through lower mortality rates may provide multiple benefits including greater yields from mixture fisheries, reduced inter-annual variability in yields, and reduced risk of depleting low productivity spawning populations. We encourage the implementation of precautionary harvest control rules for fisheries that exploit

stocks consisting of intermixed spawning populations with differing productivity levels to help ensure sustainability of less productive stocks.

Introduction

Stock-based management of exploited fish populations has long been an important tool of fisheries managers. This management approach typically involves assigning spatial management units and assessing the dynamics of fish populations occurring within the boundaries of each management unit to set harvest levels. One of the perceived benefits of stock-based management is that it protects spawning populations by managing at spatial scales best suited for ensuring sustainability of individual populations thus promoting overall intra-species diversity (Patriarche, 1977; Spangler et al., 1981; MacLean and Evans, 1981; Stephenson, 1999). Although stock-based management is widely used, it is not infallible. For one, it is generally assumed that managed fisheries consist of fish from a single spawning population (Quinn and Deriso, 1999). However, management unit boundaries are often based on jurisdictional or management convenience and may not accurately reflect the dynamics of individual populations (Goethel et al., 2011). Recent research using tag-recovery and genetics data have in some fisheries found considerable discrepancy between management units and spawning population distributions (Reiss et al., 2009; Ebener et al., 2010). Further, movement and therefore intermixing may be a dynamic feature with changes in the environment or abundance leading to changes in the spatial distribution of populations (Perry et al., 2005; Ebener et al., 2010). As a result, appropriateness of management unit boundaries may wane over time.

Population intermixing during periods of fishery harvest is common in both freshwater and marine environments (Policansky and Magnuson, 1998; Stephenson, 1999). Despite its ubiquity, there is a general lack of understanding as to what effects intermixing may have on exploited populations because most harvest policy evaluations have ignored intermixing and spatial structure of fish populations (Deroba and Bence, 2008). The research that has been conducted has shown that effects can vary depending on the magnitude of mixing (Tuck and Possingham, 2000; Sanchirico et al., 2006) and the underlying dynamics of the populations (Heifetz et al., 1997; Kerr et al., 2010).

Lake whitefish (*Coregonus clupeaformis*) fisheries in the Laurentian Great Lakes of North America are examples of commercially exploited freshwater fisheries managed using a stock-based approach in which management unit boundaries do not align with the complex spatial structure exhibited by spawning components. Throughout large areas of lakes Michigan, Huron, and Superior, lake whitefish fisheries are managed with 65% total annual mortality controls, the basis of which is empirical observations that stocks with mortality exceeding this level perform poorly (Ebener et al., 2005). Over the last 15 to 30 years, intermixing of lake whitefish spawning populations has increased considerably (VanDeHey et al., 2009; Ebener et al., 2010). As well, the intrinsic productivity of lake whitefish spawning populations is believed to have declined as a result of massive ecosystem level changes that have occurred in the Great Lakes subsequent to the invasion of dreissenid mussels (Pothoven et al., 2001; Kratzer et al., 2007; Rennie et al., 2009). The combination of increased mixing rates and declining productivity calls into question whether some lake whitefish populations may be at risk of overexploitation under the existing 65% allowable annual mortality control rule.

The potential for mixture fisheries to negatively influence individual spawning populations, even to the point of extirpation, has been well documented. Frank and Brickman (2000) and Kell et al. (2009) each found that subpopulations could be extirpated in mixed stock fisheries even though conventional assessments suggested stocks were healthy. Ying et al. (2011) found that managing a metapopulation as several independent populations may lead to overexploitation, while managing metapopulations as single units may lead to depletion of components. Erosion of spawning components was documented in Atlantic cod (*Gadus morhua*) and Atlantic herring (*Clupea harengus*) stocks that subsequently collapsed (Sinclair et al., 1996; Cury et al., 2000), and has been implicated in the slow recovery of cod and herring stocks even after considerable reductions in fishing mortality (Smedbol and Stephenson, 2001; Ames, 2004; Lilly et al., 2008). From a biological standpoint, extirpation of spawning population is problematic as it can lead to a loss of genetic diversity, reducing the evolutionary potential of a species and possibly suppressing characteristics adapted for local environments (Stephenson and Kenchington, 2000).

The goal of this research was to conduct conducted a simulation-based evaluation of harvest control rule performance of four intermixing fish populations with characteristics similar to those of lake whitefish populations in northern lakes Huron and Michigan. Our intent was to provide fishery managers guidance as to whether the current management approach is adequate for ensuring the goals of maximizing harvest, increasing fishery yield stability, and ensuring long term protection of spawning populations.

Methods

For clarity, we define some of the common terms used herein. Population and spawning population are used interchangeably to refer to a group of fish that spawn in the same region and exhibit natal philopatry. Mixed stock and stock are also used interchangeably to refer to fish from multiple spawning populations residing in a particular region during periods of exploitation. This means that all aspects of the fishery, such as harvest and assessment, occur in relation to stocks, while measures such as spawning biomass and recruitment are characteristics of populations.

Operating Model

Abundances at age of the four fish populations were represented through an operating model in which the true dynamics of each population were specified. In the operating model, the four fish populations were assumed to intermix to varying degrees during the non-spawning season but maintained strict spawning site fidelity and were therefore unmixed during the spawning season. This matches the overlap with reproductive isolation assumption described in Porch (2003) and Cadrin and Secor (2009). Although the simulated populations had characteristics similar to lake whitefish populations in the upper Great Lakes, our simulations were not meant to replicate particular populations. Each population included fish ranging from age 1 (age of recruitment) to age 12, with the last age class an aggregate group including age-12 and older fish. Fish from each spawning population were assumed to intermix with other populations immediately after spawning, with a population specific proportion staying within their natal area and the remainder moving into the spawning areas of the other populations. The proportion that moved to areas occupied by other populations was assumed to equally distribute themselves among the other three areas. Each stock was assumed to be exploited commercially throughout the time fish were intermixed. All fish surviving the year were assumed to return to their natal regions at the end of the year, with only the sexually mature fraction spawning.

Parameter definitions and equations used in the description of the operating model and elsewhere in the text are presented in Tables 2.1 and 2.2. An exponential population model (Eq. T.2.2.1) was used to project abundances at age, with instantaneous total mortality partitioned into natural and fishing mortality components (Eq. T.2.2.2). Instantaneous natural mortality rates for all ages and populations were assumed to be constant (Table 2.1). Recruitment to each population was modeled using a Ricker recruitment function with stock size equal to the egg production potential of mature females (SSE) and recruits defined as the abundance of age-1 fish produced the year after spawning (Eq. T.2.2.3). Stochasticity was included in the stock recruitment relationship via a multiplicative lognormal error.

Total SSE was calculated as the sum of the product of abundance at age, proportion mature at age, weight at age, proportion of females in the population, and the eggs produced per kilogram of mature female (Eq. T.2.2.4). Length at age was modeled with a von Bertalanffy growth model (Eq. T.2.2.5) with weight at age predicted as a function of length through an allometric growth model (Eq. T.2.2.6). Maturity was modeled as a logistic function of length (Eq. T.2.2.7). The von Bertalanffy growth, allometric weight, and logistic maturity models were parameterized such that the simulated populations had characteristics similar to lake whitefish stocks in northern lakes Huron and Michigan (Table 2.1). The sex ratio in all populations was assumed to be 50:50, with the number of eggs produced per kg of mature female a constant across all scenarios (Table 2.1).

Each stock was assumed to be exploited by a single commercial fishery. Age-specific fishing mortality rates were modeled as the product of a fully-selected fishing mortality and age-specific selectivities (Eq. T.2.2.8). The fisheries operating in each stock were assumed to have common selectivity patterns. Fishery selectivity at age was modeled with a gamma function scaled such that the maximum selectivity at age had a value of one (Eq. T.2.2.9). Selectivities for age-2 and younger fish were set equal to 0 as these ages are rarely captured or retained in the lake whitefish fishery. The parameters of the selectivity function were chosen such that selectivity was dome-shaped with peak selectivity at age 10 (Table 2.1).

The fishing mortality rate that each stock experienced was dependent on the total allowable catch (TAC) that was set in each year and the abundance of fish that moved into a stock area during harvest. The actual amount of harvest that a stock experienced included an implementation error component to account for the fact that perfect control over a fishery can rarely be exerted. Implementation error was incorporated via an independent lognormal error (Eq. T.2.2.10). Fully-selected fishing mortality rates capable of producing the actual level of harvest were solved for numerically using a Newton-Raphson algorithm as described in Deroba (2009). Given this intermixing framework, abundance at age of each population depended on what fraction of the population moved to other stock areas and the level of exploitation that each of these fractions experienced in the other stock areas. Under an exponential population model, abundance at age of each spawning population could be represented with Eq. T.2.2.11, while the total abundance of fish found in any stock after intermixing occurred could be represented with Eq. T.2.2.12.

Observation components

The information available for use in the stock assessment models was assumed to consist of fishery harvest-at-age for the stocks and a reported measure of the amount of fishing effort occurring in each stock area. This matches the data currently used in most Great Lakes lake whitefish assessment models (Caroffino and Lenart, 2011). Observed harvest in the stock areas was assumed to differ from actual harvest as a result of observation error (Francis and Shotton, 1997; Butterworth and Punt, 1999), which like implementation error was modeled as an independent lognormal error (Eq. T.2.2.13). Observed age composition of the harvest was generated from a multinomial distribution with probabilities equal to the actual age composition of harvest and an assumed sample size of 200 fish (Eq. T.2.2.14). The amount of fishing effort that each stock experienced was calculated by dividing the fully-selected instantaneous fishing mortality rate in each stock and year by an assumed catchability value (Eq. T.2.2.15; Table 2.1). As with fishery harvest, observation error was incorporated in the fishery effort measurements.

Assessment Model and TAC Generation

A statistical catch-at-age (SCAA) model that was similar to the assessment models used to assess lake whitefish stocks in the upper Great Lakes was used to estimate abundance, mortality, and recruitment levels for the purpose of setting the TACs for the stocks based on the evaluated harvest control rules (Ebener et al., 2005; Caroffino and Lenart, 2011). The estimates from the assessment models used to set the TACs were the highest posterior density (HPD) estimates, which also are referred to as maximum penalized likelihood estimates (Schnute, 1994). The objective function of the assessment model consisted of the sum of three negative log-likelihood or negative log-prior components. Lognormal distributions were assumed for the log-likelihood component for the total fishery harvest (Eq. T.2.2.16) and for the log-prior component associated with the fishing mortality-effort relationship (Eq.T.2.2.17). The dispersion parameter for the negative log-likelihood component for total fishery harvest was estimated as part of the model fitting process, with the dispersion parameter for the negative log-prior component for the fishing mortality-effort relationship deviation set equal to four times the value of the estimated fishery harvest dispersion parameter. The age composition of the fishery harvest was assumed to have a multinomial distribution, and was weighted by an assumed effective sample size of 200 fish (Eq. T.2.2.18).

The current guidelines for setting lake whitefish harvest limits across much of lakes Huron, Michigan, and Superior is for them to be set in the year preceding that in which they will take effect using data collected two years prior to the effective harvest year (Ebener et al., 2008). We incorporated a similar time lag into our assessments. When fitting the assessment models only the 20 years of data prior to the year for which abundances, mortality rates, and recruitment levels were to be assessed were included. Although the operating model assumed selectivity, catchability, and natural mortality rates were constant, in a natural system factors like these are highly dynamic. Consequently, the use of a continually growing time series with assumed constant conditions would provide an unrealistic perception of certainty in the system. Because assessments were only conducted when 20 years or more of data were available, assessments were not conducted during the first 20 years of each simulation. During this “burn-in” period the TAC for each stock was calculated using the true abundance rather than estimated assessment-based abundance. The “burn-in” period was used to obtain an initial abundance at age at year 21, so that a model-based assessment of the stock could be conducted.

The SCAA model estimated abundance at age 3 to age 12, with the last age group an aggregate group similar to what was assumed in the operating model. Also like the operating model, abundances at age in the SCAA model calculated under an exponential population model with fishing and natural mortality components. We assumed that biologists did not realize intermixing was occurring and therefor it was not incorporated into the assessment models. We did not attempt to estimate natural mortality in the SCAA model, rather these rates were set equal to those assumed in the operating model. Fishing mortality was separated into both age and year effects (Eq. T.2.2.19) (Doubleday, 1976; Quinn and Deriso, 1999). Annual multiplicative deviations were included to relax the direct proportionality assumption for the fishing mortality-effort relationship (Eq. T.2.2.19). As in the operating model, selectivities were modeled as gamma functions of age, with parameters of the gamma model estimated as part of the SCAA model fitting process (Eq. T.2.2.20). Catchability was estimated as part of the SCAA model fitting process as well.

The SCAA model estimated initial abundances for ages 4 to 12 as the product of a mean abundance and an annual multiplicative deviation term (Eq. T.2.2.21). Recruitment in the assessment (annual age-3 abundance) was estimated similarly using the product of a mean recruitment value and a multiplicative annual deviation term (Eq. T.2.2.22). The deviations for initializing abundance and age-3 recruitment summed to 0, but no other distributional assumptions were made with regards to the deviations so large fluctuations in recruitment and initial abundances were not penalized. The Baranov catch equation was used to predict harvest at age (Eq. T.2.2.23). Age composition of the harvest was calculated by dividing age-specific harvest by total harvest (Eq. T.2.2.24). Total harvest was calculated by summing age-specific values, and age composition of the harvest for the stocks was calculated by dividing age-specific harvest by the total harvest.

In our simulations, assessments were conducted every third year with TACs in intervening years set to the level based on the most recent SCAA model assessment. The main reason for conducting assessments every third year was to reduce processing time of the simulations, although in reality avoiding annual assessments may be of interest to managers and stakeholders as complicated statistical assessment results are often controversial and can add to conflict or distrust in some management systems (Roel and De Oliveira, 2007; Cox and

Krunlund, 2008). Preliminary comparisons did not reveal major changes in performance metrics in annual versus triennial assessments in a limited group of explored scenarios.

The search for the HPD SCAA model parameter estimates used the quasi-Newton optimization algorithm implemented in AD Model Builder (Forunier et al., in press). Models were considered to have converged on a solution when the maximum gradient for the SCAA parameters was less than 0.001. To avoid implausible values and keep the optimization algorithm from flat regions of the likelihood surface, parameters were assigned upper and lower boundary values.

The SCAA model estimates of abundances at age, age-specific mortality rates, and recruitment levels were used to project future abundances at age and calculate TACs for each stock area. 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 fishing mortality at age was then calculated by subtracting the natural mortality rate from the instantaneous target mortality rate for the different control rules and multiplying the difference by the age-specific selectivity estimated in the last year of the SCAA model. The TAC for each stock was generated by inputting the target fishing mortality at age and the projected abundance at age into the Baranov catch equation.

Experimental Control Rules and Scenarios

The control rules explored in this research were total allowable annual mortality control rules, which, based on our assumption of constant natural mortality, were equivalent to constant fishing mortality control rules (Deroba, 2009). Each control rule was defined by the target total mortality rate on the fully selected age class. Target total annual mortality rates considered ranged from 35% to 65% in 10% increments. The range of mortality rates considered was based on consultation with Great Lakes fishery managers and biologists, with the upper limit corresponding to the existing target annual mortality for lake whitefish stocks in the upper Great Lakes.

Thirty-six scenarios grouped into four major categories were examined (Table 2.3). Scenarios consisted of different combinations of population intermixing and productivity levels combined with a particular control rule. Five levels of intermixing between populations were considered in this research; no mixing in which 0% of the spawning populations mixed with other populations, low in which 10% of the spawning populations mixed with other populations, medium-low in which 30% of the spawning population mixed with other populations, medium-high in which 60% of the spawning population mixed with other populations, and high in which 80% of the spawning population mixing with other populations. The rates of intermixing considered in this research roughly overlap the range of intermixing rates observed in tagging studies of lake whitefish in lakes Huron and Michigan (Ebener et al., 2010). Four productivity levels were considered: high, medium-high, medium-low, and low productivities (Figure 2.1). Differences in productivity levels between spawning populations were accounted for through adjustments to the coefficients of the Ricker recruitment functions. Specifically, coefficients were adjusted so that each population would sustain an identical maximum sustainable yield at a constant fishing mortality rate in the absence of intermixing, but at different levels of exploitation (Table 2.4). The stock-recruitment function coefficients used to represent the different productivity levels were similar to values estimated in past analyses concerning lake whitefish recruitment in the upper Great Lakes (Deroba, 2009).

The first category of scenarios, the “No Mixing” category, included four scenarios (Table 2.3). In each scenario, all populations shared the same level of productivity and no intermixing of the populations was assumed to occur. Each of the four stocks was assigned a different total allowable mortality control rule. The intent of these scenarios was to establish a baseline performance of each control rule for each of the productivity level to which results from scenarios with intermixing could be compared. Because the four populations had similar characteristics and no mixing occurred, their performance under the different harvest policies would be similar apart from random errors at a particular productivity level, which is why we felt it was sufficient to simply evaluate the response of a single population with a particular productivity level to each control rule.

The second category of scenarios, the “Correlated” category, included eight scenarios (Table 2.3). These scenarios were intended to investigate the performance of the different control roles in circumstances where there is a strong positive or negative relationship between the rate of intermixing and the productivity characteristics of a spawning population. In the case of the positively correlated scenarios, a population with a high rate of productivity was assigned a high rate of intermixing, while in the negatively correlated scenarios a population with a high rate of productivity was assigned a low rate of intermixing. In all scenarios, the intermixing and productivity levels varied among populations so that each was assigned a particular combination of levels.

The third category of scenarios, the “State Shift” category, included eight scenarios (Table 2.3). In the first four scenarios for this category, populations were assigned either medium-high or high productivity levels, and either medium-low or low intermixing rates. Each scenario was then assigned a different control rule for all stocks. The next four scenarios were set up identically, except that populations were assigned either medium-low or low productivity levels, and either medium-high or high intermixing rates. These scenarios were intended to compare the performance of each control rule between two alternative system states, one with strong productivity and low mixing and another with poor productivity and higher intermixing. Our reason for examining these two scenarios is that it is believed that such a shift has occurred in the Great Lakes subsequent to invasion of dreissenid mussels and we were interested in exploring how this might affect control rule performance. We also believed that this would be broadly informative for evaluating the effect of regime shifts and changes in migratory behavior of fish populations on control rule performance.

The final category of scenarios, the “Shared Mixing” category, included 16 scenarios (Table 2.3). Under each of these scenarios spawning populations were assigned a different productivity level so that all four levels of productivity were represented in each scenario. Each scenario was then assigned a level of intermixing that was shared between all populations in the scenario so that four scenarios shared each level of intermixing. Each scenario in each of these groups was then assigned a different harvest control rule that was applied to all stocks in the scenario. These scenarios were intended to investigate relative performance of the different harvest policies under circumstances where populations with different productivity characteristics intermixed at similar rates.

Performance Metrics

Metrics used to evaluate performance of the different control rules included those that measured attributes of the fisheries exploiting the stocks (fishery metrics) as well as those of the spawning populations (sustainability metrics). Fishery metrics included mean annual yield (both cumulative and for individual stocks) and the mean inter-annual variability in yield, while the sustainability metrics were related to spawning stock biomass (SSB) and included mean annual percentage of unfished SSB ($SSB_{F=0}$) and the percentage of years the SSB declined to less than 20% of $SSB_{F=0.}$ These performance metrics were chosen because in combination they measure the desirable properties of maximizing harvest, minimizing risk to the resource, and minimizing industry volatility (Butterworth and Punt, 1999).

Simulations were conducted in AD Model Builder (Fournier et al., in press). Each simulation involved the projected dynamics under the assumed intermixing rates, productivity levels, and harvest control rule over a 100 year timespan. Performance metrics were not calculated for the burn-in period. One thousand simulations were investigated for each of the scenarios described in Table 2.4. The distributions of results for the different performance metrics for each of the investigated scenarios were summarized using box plots.

Results

No Mixing Scenarios

Mean annual yield varied with both productivity level and control rule in the absence of intermixing (Figure 2.2). Hereafter, stocks will be referred to by the productivity of the population that spawns in that stock area so an area with a high productivity spawning population will be referred to as a high productivity stock keeping in mind the high productivity is really a characteristic of the spawning population. In the high productivity stocks, the greatest mean annual yield (median near 165 tonnes) occurred with a 65% total mortality control rule and decreased at lower allowable mortality rules, with the lowest mean annual yield (median near 75 tonnes) at the 35% control rule. In stocks with medium-high productivity, yields at the 65 and

55% control rules were similar (median near 180 tonnes), with slightly lower yields under the 55% control rule. For medium-low productivity stocks, both the 55 and 45% control rule had high mean annual yields (median near 190 tonnes), while the 35 and 65 % control rules had slightly lower annual yields (medians near 150 tonnes). In stocks with low productivity, the highest yield occurred under the 45% control rule (median near 190 tonnes) with the lowest yield under the 65% control rule (median near 75 tonnes).

Inter-annual variability in yield also varied with both control rule and productivity level (Figure 2.2). In all scenarios, the median inter-annual variation in yield was between 17 and 23 percent, with higher productivity stocks near the upper end of the range and lower productivity stocks near the lower end. Inter-annual variation in yield also decreased with more conservative harvest policies across the productivity levels although the differences were slight and there remained substantial overlap in the range of results across the scenarios.

Productivity level and control rule also influenced the percentage of years that the spawning population declined to less than 20% $SSB_{F=0}$ and the mean percentage of $SSB_{F=0}$ (Figure 2.2). For high productivity populations, the percentage of years that SSB declined to less than 20% $SSB_{F=0}$ was generally less than 10% with a mean percentage of $SSB_{F=0}$ in excess of 50% for all control rules. For medium-high productivity populations the percentage of years that SSB declined to less than 20% of $SSB_{F=0}$ was slightly higher than for the high productivity populations but still was generally less than 15% for each of the different target mortality rates. As well, the mean percentage of $SSB_{F=0}$ was generally in excess of 40% for medium-high productivity populations for each of the control rules. For medium-low productivity stocks, the percentage of years that SSB declined to less than 20% $SSB_{F=0}$ increased considerably (median near 50%) under the 65% total mortality rule relative to the other productivity levels, although it was generally comparable to the higher productivity levels for the 35% to 55% total mortality rules (<15%). Mean percentage of $SSB_{F=0}$ ranged from approximately 20% to 75% for the 35% to 65% target mortality control rules. For the low productivity populations, the 65% total mortality control rule resulted in a large percentage (median 100%) of years with SSB below 20% $SSB_{F=0}$ and a low mean percentage of $SSB_{F=0}$ (median 5%). The 55% total mortality rule also resulted in a large percentage (median 55%) of years with SSB less than 20% $SSB_{F=0}$, with a mean percentage of $SSB_{F=0}$ near 20%. Conversely, in less than 10% of years the SSB declined to less than 20% $SSB_{F=0}$ for low productivity populations under the 45% and 35% total mortality control rules. Mean percentage of $SSB_{F=0}$ exceeded 40% for these lower mortality control rules as well.

Correlated Scenarios

The mean annual yield for the stocks by productivity level was considerably different in cases where mixing and productivity were positively (Figure 2.3) and negatively correlated (Figure 2.4). In the case of positive correlations between mixing and productivity levels, high productivity stocks with high mixing had low yield (less than expected under baseline conditions) under each of the control rules, while low productivity stocks with low mixing had greater yields (Figure 2.3). The greatest yields in the case of a positive correlation occurred under the 45% total mortality control in the low productivity and low intermixing stock, which resulted from fish mixing into that stock from other populations. For inverse correlations between productivity and rate of intermixing, high productivity stocks with low mixing had the greatest yields under all control rules, while low productivity stocks with high mixing rates had the lowest yields under all rules (Figure 2.4). The greatest yields for the negative correlation scenarios occurred under the 55% total mortality control rule in the high productivity, low mixing stock, although the yields for the 65% and 45% control rule in the high productivity, low mixing stock were also quite large.

Mean annual cumulative yields exhibited a similar pattern in results to the individual stock yields. For both positively and negative correlated scenarios, the greatest cumulative yields occurred under 45 and 55% control rules (Figure 2.5). The yield under the 65% total mortality control rule was the next greatest, followed by yields under a 35% control rule (Figure 2.5). Overall yield levels were similar between positively and negative correlated scenarios under a particular control rule, with slightly larger yields obtained for the positively correlated scenarios.

The inter-annual variation in yield for the different control rules for the correlated scenarios was similar to those observed for the no mixing scenarios. That is inter-annual variation generally declined with more conservative control rules. Compared to the no mixing scenarios, inter-annual variation in yield declined slightly for the negative and positive correlation scenarios across all the control rules, however, the differences were generally less than 5%. The percentage of years the SSB declined to less than 20% $SSB_{F=0}$ and the mean percent of $SSB_{F=0}$ also had very similar responses to the no mixing group of scenarios without intermixing with risk of depletion depending both on the productivity of the populations and the evaluated control rule.

State Shift Scenarios

The mean annual yield in all stocks in the first state shift case (high productivity levels and low rates of intermixing) was greatest for all stocks under the 65% control rule (Figure 2.6). As control rules became more conservative, mean annual yield decreased with the greatest difference between the 45 and 35% control rules. In the second state shift case (low productivity and high rates of intermixing) mean annual yield was the greatest for all stocks under the 45% control rule and lowest under the 65% control rule (Figure 2.7). The mean cumulative yield of the scenarios reflected the findings for the yield from the individual stocks. Under the first state shift case, the greatest cumulative yield was obtained with the 65% control rule, while in the second case it was obtained with the 45% control rule (Figure 2.5).

As in earlier scenario categories, the inter-annual variation in yield decreased slightly with more conservative control rules although there was overlap in the distributions for the control rules (Figures 2.6 and 2.7). This was true for the scenario with higher productivity and lower intermixing and the scenario with lower productivity and higher intermixing. The variation in yield was slightly higher (3 to 5%) for the case with higher productivity and lower intermixing characteristics. The percentage of years that SSB declined to less than 20% $SSB_{F=0}$ and the mean percentage of $SSB_{F=0}$ had very similar responses to different control rules for the various levels of productivity when compared to the scenarios without intermixing.

Shared Intermixing, Varied Productivity Scenarios

The mean annual yields for stocks with low intermixing rates were largely indiscernible from those when stocks did not intermix (Figure 2.8). For high productivity stocks, the 65% mortality control rule resulted in the largest mean annual yields, while for the medium-low and low productivity stocks the 45% total mortality control rule resulted in the largest mean annual yield. When stocks intermixed at a medium-low rate, there were noticeable changes in mean annual yields from the baseline condition (Figure 2.9). Perhaps most notably, the 65% total mortality control rule no longer resulted in the largest yields from the most productive stock, rather the 55% mortality control rule resulted in the largest yields. Under medium-high rates of intermixing, the improved performance at the 55% mortality control rule compared to the 65% mortality control rule in terms of fishery yield became more apparent (Figure 2.10). However, the 45% mortality control rule began resulting in mean annual yields comparable to those under the 55% mortality control rule at higher productivities. Under high intermixing rates, the 45% total mortality control rule produced mean annual yields that were very similar to those produced by the 55% mortality control rule (Figure 2.11). Unlike the yield for the individual stocks, the mean annual cumulative yield showed an almost identical pattern across harvest policies regardless of the rate of intermixing, with the greatest cumulative yields at the 55% and 45% control rule. Considerably lower cumulative yields were observed under the 65% and 35% control rules (Figure 2.5).

As in earlier scenario categories, the inter-annual variation in yield decreased slightly with more conservative harvest policies, although there remained substantial overlap in the distributions under the examined control rules at each level of productivity. There were slight changes in variation in yield as intermixing rates increased. Inter-annual variation in yield under an assumption of high intermixing was approximately 5% lower than that observed under low intermixing rates. The percentage of years that SSB declined to less than 20% $SSB_{F=0}$ and the mean percentage of $SSB_{F=0}$ had very similar responses to different harvest policies for the various scenarios when compared to the scenarios without intermixing.

Discussion

Our research indicated that across a wide range of intermixing and productivity scenarios control rules for mixture fisheries that preserve spawning biomass of the lowest productivity spawning components can produce more desirable outcomes than those that seek simply to maximize harvest. Not only did more conservative control rules lower the risk of populations being overexploited, but in some cases they also produced greater yields than control rules that allowed greater exploitation of mixed stocks. In other words, more conservative control rules could produce outcomes that were desirable from both economic and biological standpoints. Thus, although “resource-oriented” and “user-oriented” management objectives are often seen as conflicting (Hall and Donovan, 2002), under the scenarios and policies investigated in our research these objectives were found to be in agreement regarding the best options for managing mixture fisheries.

In addition to producing greater yields and lowering risk of depletion, this research also demonstrated that inter-annual variation in yield could be lessened, albeit only somewhat, with more conservative harvest policies. This likely was a consequence of lower exploitation rates resulting in populations with an SSB closer to that of $SSB_{F=0}$, which resulted in more stable populations as a result of less variability in annual recruitment levels. Nevertheless, fishery managers will undoubtedly find this a beneficial result given that stable harvest levels are generally of interest to commercial fishers because it helps ensure a somewhat consistent livelihood from year to year. Our finding that inter-annual variation in yield was reduced with more conservative harvest policies supports the findings of Ricker (1958) and Anderson et al. (2008) who found that exploitation can lead to instability in the dynamics of fish populations.

In previous evaluations of constant fishing mortality control rules, it has been well established that control rule performance depends heavily on the productivities of the exploited populations, in particular the ability of populations to rebound from low stock sizes (Walters and Parma, 1996; Brodziak, 2002). The importance of population productivity levels on the results of all the performance metrics that we evaluated in this research confirms these earlier findings. However, our results also indicate that when intermixing of populations occurs, determining the appropriateness of a constant mortality control rule no longer simply is a function of the productivity of a single population. Rather, it depends on the productivity of all the components populations of that fishery as well as the mixing rates of the populations. This in turn can lead to considerable confusion regarding what level of exploitation a stock can support with high yields coming from areas where low productivity populations spawn (as demonstrated in Chapter 1 of this thesis), which could lead to managers thinking the population could support even greater exploitation rates. Recently, preservation of low productivity populations has focused on reducing harvest in regions where populations spawn, even when the rate of intermixing between populations may be significant (Stephenson, 1999). Our results suggest that rather than developing individualized harvest policies for each stock, a management approach of fishing at mortality rates that account for the underlying productivity over larger geographic regions can provide surprisingly desirable fishery outcomes. Similarly, Walters and Parma (1996) and DiNardo and Wetherall (1999) found that constant fishing mortality rules performed well in cases without intermixing when regime shifts or climate variation occurred if the rates chosen were conservative enough to not put populations at risk during low productivity periods. This is especially encouraging for systems with limited data or in situations where managers must take action before adequate studies can be completed on intermixing and productivity of population components.

In this research, we limited our evaluations to total mortality control rules because for Great Lakes lake whitefish stocks this is considered the most viable type of policy for making management decisions. Although prior simulation-based evaluations have found biomass-based control rules to perform well for lake whitefish fisheries (Deroba, 2009), such rules have not been adopted in the Great Lakes because of the perceived difficulty in identifying appropriate biomass reference points. Other researchers as well have pointed out the difficulty in specifying reference points for managing fisheries using biomass-based control rules (Cadrin and Pastoors, 2008; Dowling et al., 2008; Haltuch et al., 2008; Prince et al., 2008; Smith et al., 2008). Despite our not considering a wide array of control rules, we still believe our results to be broadly informative given the widespread use of constant fishing mortality control rules.

In terms of lake whitefish management, our research suggests that the 65% total allowable mortality control used to manage fisheries across much of the upper Great Lakes has the potentially to negatively influence sustainability of lower productivity populations and that fisheries could benefit from more conservative control rules. Our analysis suggests that if a single control rule is used to manage intermixing lake whitefish stocks, it should be sufficiently conservative to account for the sustainability of the lowest productivity component. Given the productivity levels used in the research, the 45% mortality control rule produced the best performance, with low risk of depletion, high yields, and low inter-annual variation in yield. The 55% mortality control rule, although not ranked as highly as the 45% rule, was found to have more desirable performance that the 65% rule for many metrics, especially sustainability metrics.

These findings are somewhat conflictive with those of Deroba (2009) who found that the 65% total mortality control rule performed well for lake whitefish fisheries in a simulation-based control rule evaluation for the upper Great Lakes. This discrepancy in results is likely related to differences in the approach and assumptions of these two analyses. Deroba (2009) accounted for uncertainty in future growth and recruitment as influenced by ecosystem level changes by assessing the probability of outcomes for lake whitefish stocks under control rules with recruitment drawn from assessment-based estimates of recruitment relationships in TW stocks. This approach included the lower and higher productivity groups in the outcome distribution, so the effect on low productivity populations was not directly measured. Additionally, since estimates of recruitment were based on assessments, and assessments can be biased by intermixing, the estimates of productivity may not have adequately captured the dynamics of lower productivity components. Our analysis focused instead on the control rule performance on individual populations, and included plausible productivity levels instead of assessment based recruitment. Given that our range of productivity levels was somewhat arbitrary, we cannot be certain to have more appropriately described the distribution of productivity of Great Lakes whitefish populations than did Deroba. However, we believe our choices were reasonable given the available information, and the lack of a comprehensive analysis reconsidering population productivity accounting for the effect of intermixing on stock assessment estimates of recruitment and spawning biomass.

Annual mortality rates for lake whitefish stocks in northern lakes Huron and Michigan are generally lower than the 65% currently allowed (Caroffino and Lenart, 2011; Figure 2.12), meaning that cutting TACs in many units to the 55% or even 45% control rule may not result in major reductions in harvest compared to that in recent years, strengthening the argument for reducing mortality. In some cases, the lower-than-allowed mortality rates in lake whitefish stocks may be allowing lower productivity spawning aggregations to persist under the existing policy even while filling TAC's may put them at considerable risk of depletion. It is important to keep in mind that the productivity levels used in this analysis were used to examine a plausible range of productivity levels for lake whitefish in the upper Great Lakes, not to reflect the productivity of any particular lake whitefish populations.

By comparing results between the state shift scenarios, we found that changes in the productivity and intermixing of spawning populations, as is believed to be the case for Great Lakes lake whitefish, could lead to changes in the performance of control rules. Despite the lower productivity and higher intermixing rates, it was still possible for overall yields to approach or even surpass those of the earlier state by matching control rules to the correct productivity levels. For the Great Lakes, this has important consequences given the current state of the system and it continuing to be threatened by invasion of additional exotic species. The threat of additional invasions, along with the threats of global climate change and other environmental changes, suggest that Great Lakes fishery managers need to continue to evaluate whether harvest control rules are appropriate for the stocks they manage (Roessig et al., 2004; Ficke et al., 2007).

APPENDIX

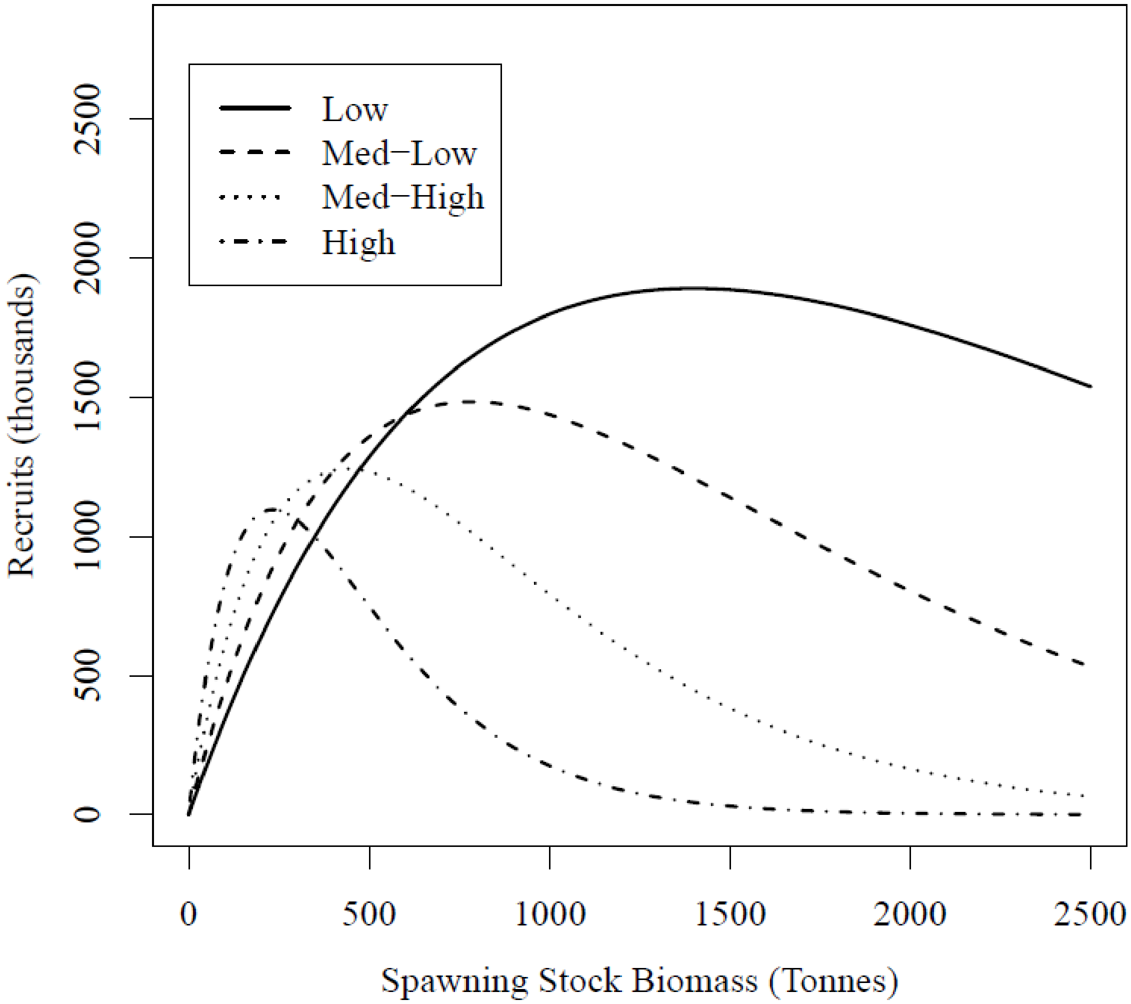
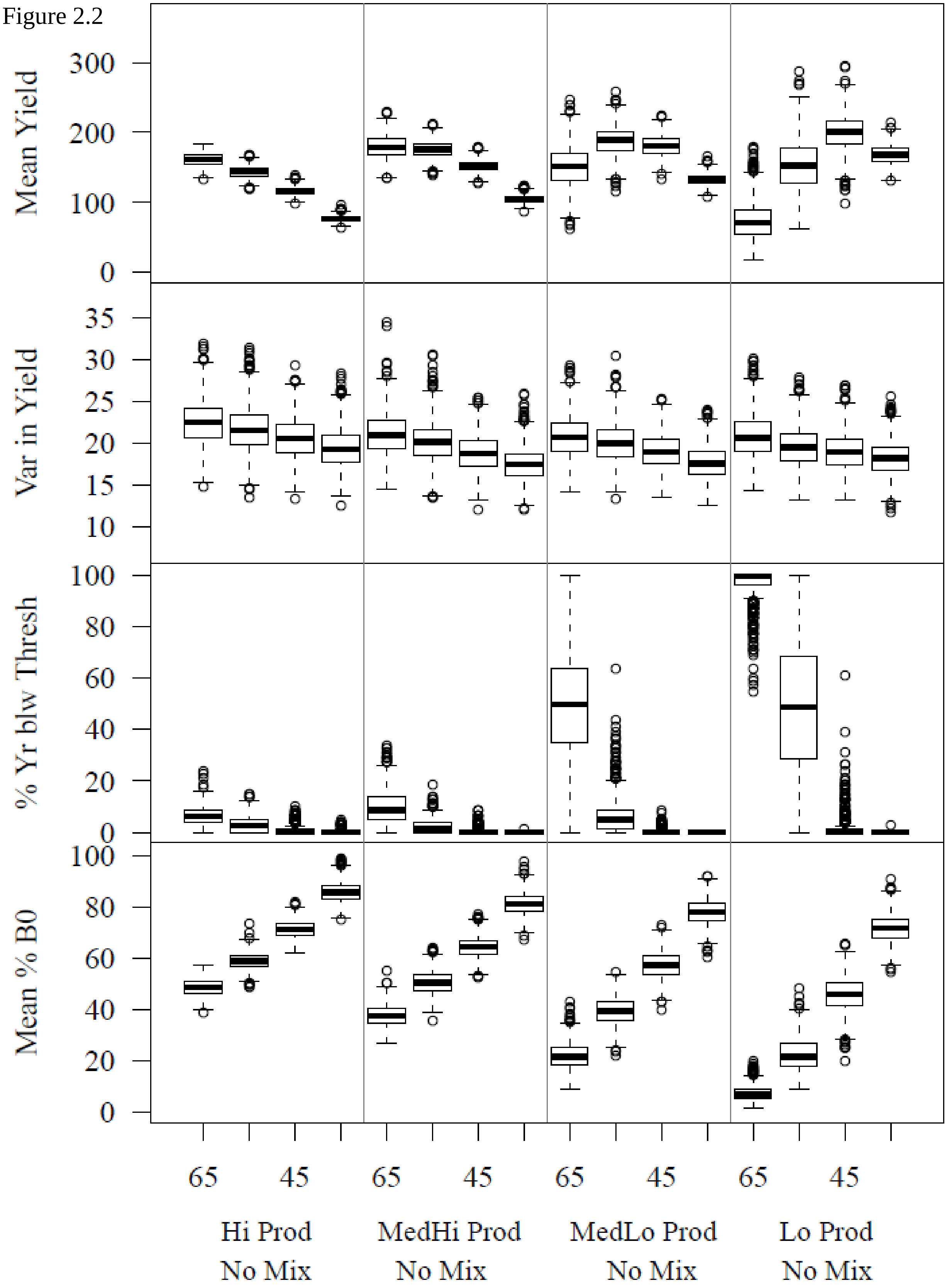


Figure 2.1. The four productivity levels used in this simulation analysis. The higher steepness at low SSB indicates higher capacity for the population to rebound from depletion and therefor higher productivity. Recruitment is defined as age-1 fish in the population the year following spawning.

Figure 2.2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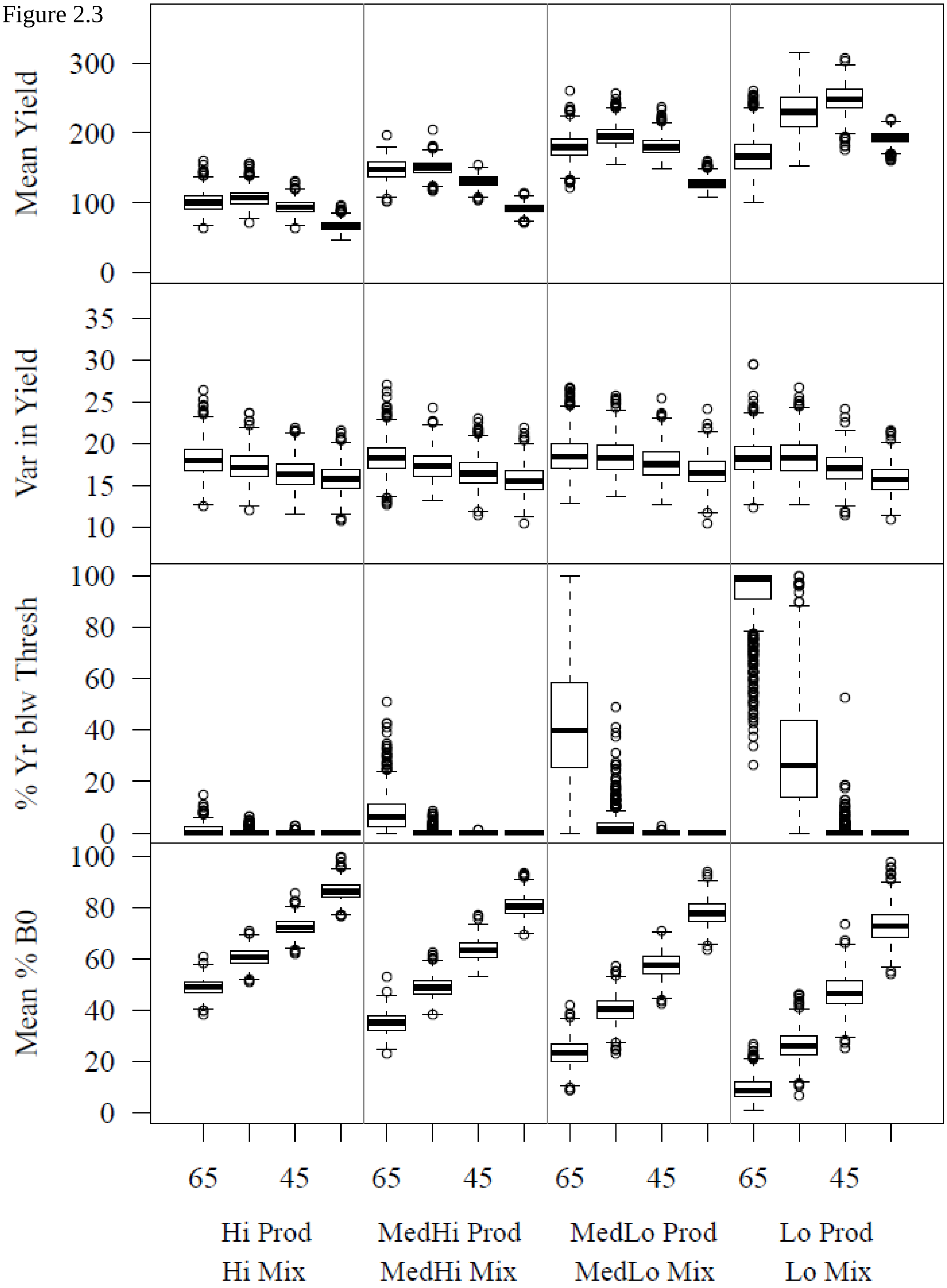
300
200
100
0
Var in Yield
35
30
25
20
15
10
% Yr blw Thresh
100
80
60
40
20
0
Mean % B0
100
80
60
40
20
0
65
45
65
45
65
45
65
45
Hi Prod
No Mix
MedHi Prod
No Mix
MedLo Prod
No Mix
Lo Prod
No Mix

Figure 2.2 (cont'd)

Performance metrics for scenarios without intermixing between stocks. Labels along the y-axis represent the different performance metrics used to compare harvest policies in this analysis. Mean annual yield is represented in tonnes. Inter-annual variation in yield, the percentage of years spawning stock biomass fell below 20% of unfished spawning stock biomass ($SSB_{F=0}$), and mean percentage of $SSB_{F=0}$ are all expressed in a percentage. The labels along the x-axis describe the productivity and intermixing level of the spawning population in each stock, while the numbers at the tick marks correspond to the allowable annual mortality rates investigated in this analysis.

Figure 2.3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Var in Yield
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% Yr blw Thresh
100
80
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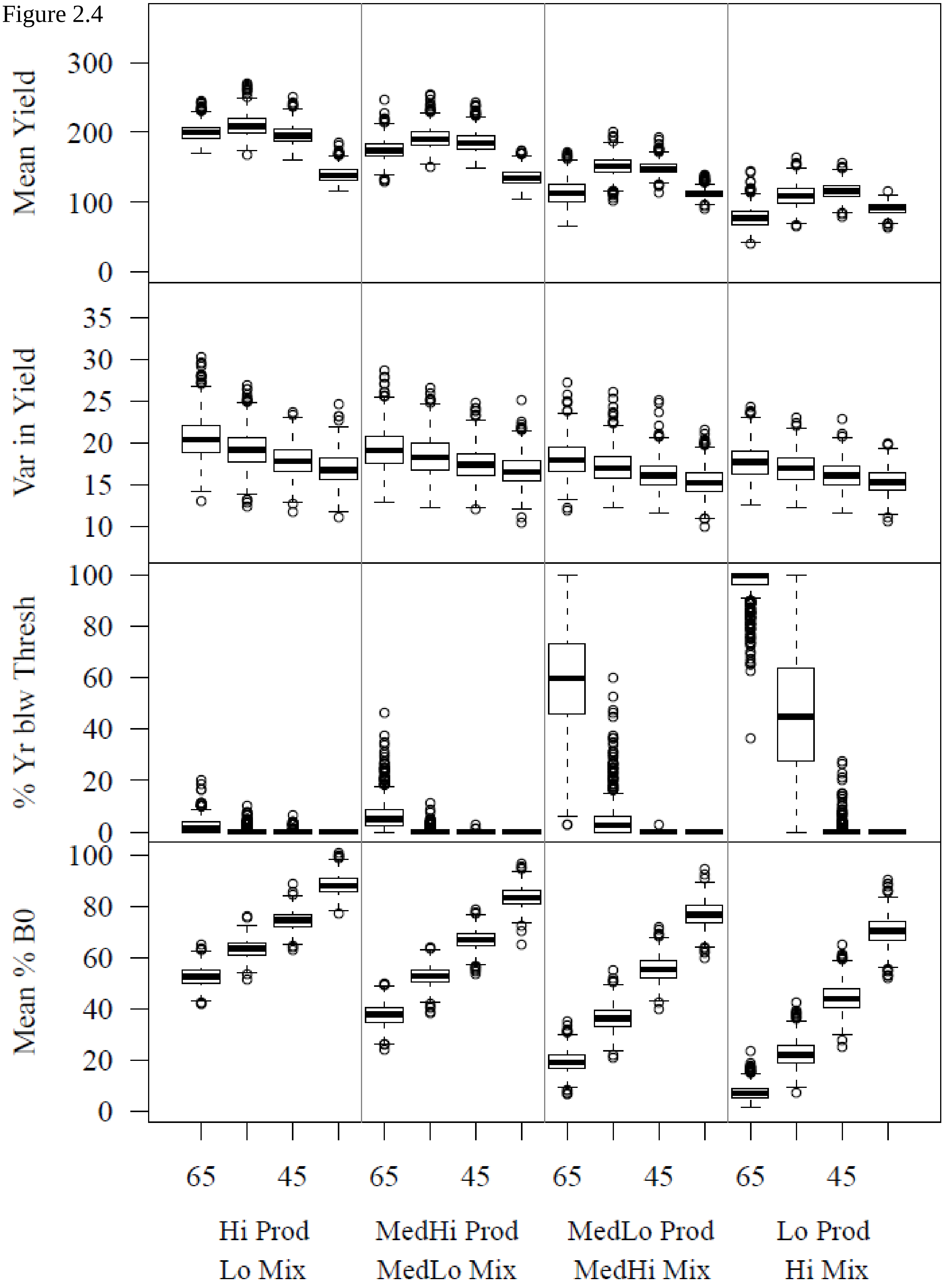
40
20
0
Mean % B0
100
80
60
40
20
0
65
45
65
45
65
45
65
45
Hi Prod
Hi Mix
MedHi Prod
MedHi Mix
MedLo Prod
MedLo Mix
Lo Prod
Lo Mix

Figure 2.3 (cont'd)

As in Figure 2.2, except for scenarios when productivity and intermixing are positively correlated.

Figure 2.4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Var in Yield
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% Yr blw Thresh
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20
0
Mean % B0
100
80
60
40
20
0
65
45
65
45
65
45
65
45
Hi Prod
Lo Mix
MedHi Prod
MedLo Mix
MedLo Prod
MedHi Mix
Lo Prod
Hi Mix

Figure 2.4 (cont’d)

As in Figure 2.2, except for scenarios when productivity and intermixing are negatively correlated

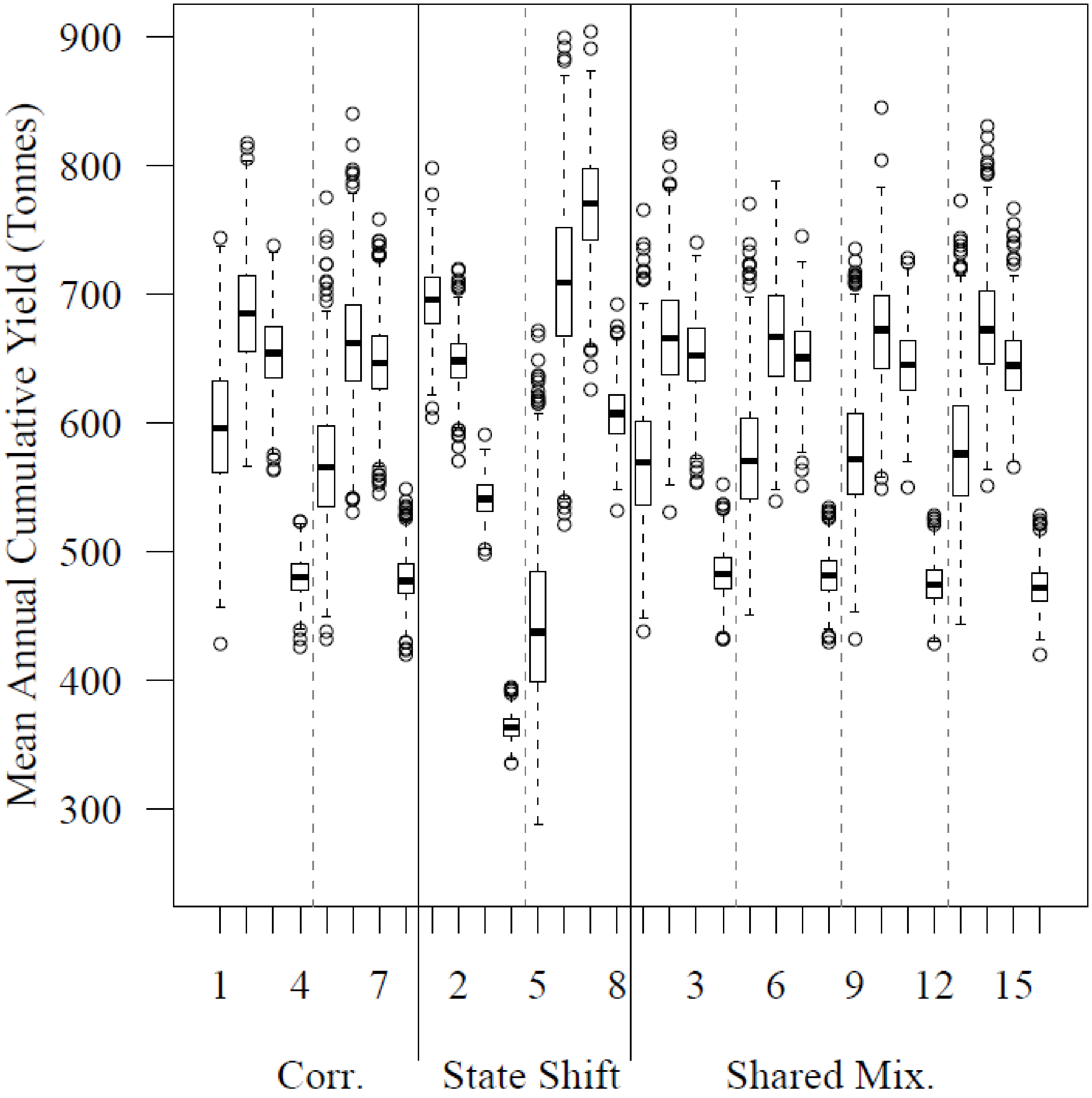
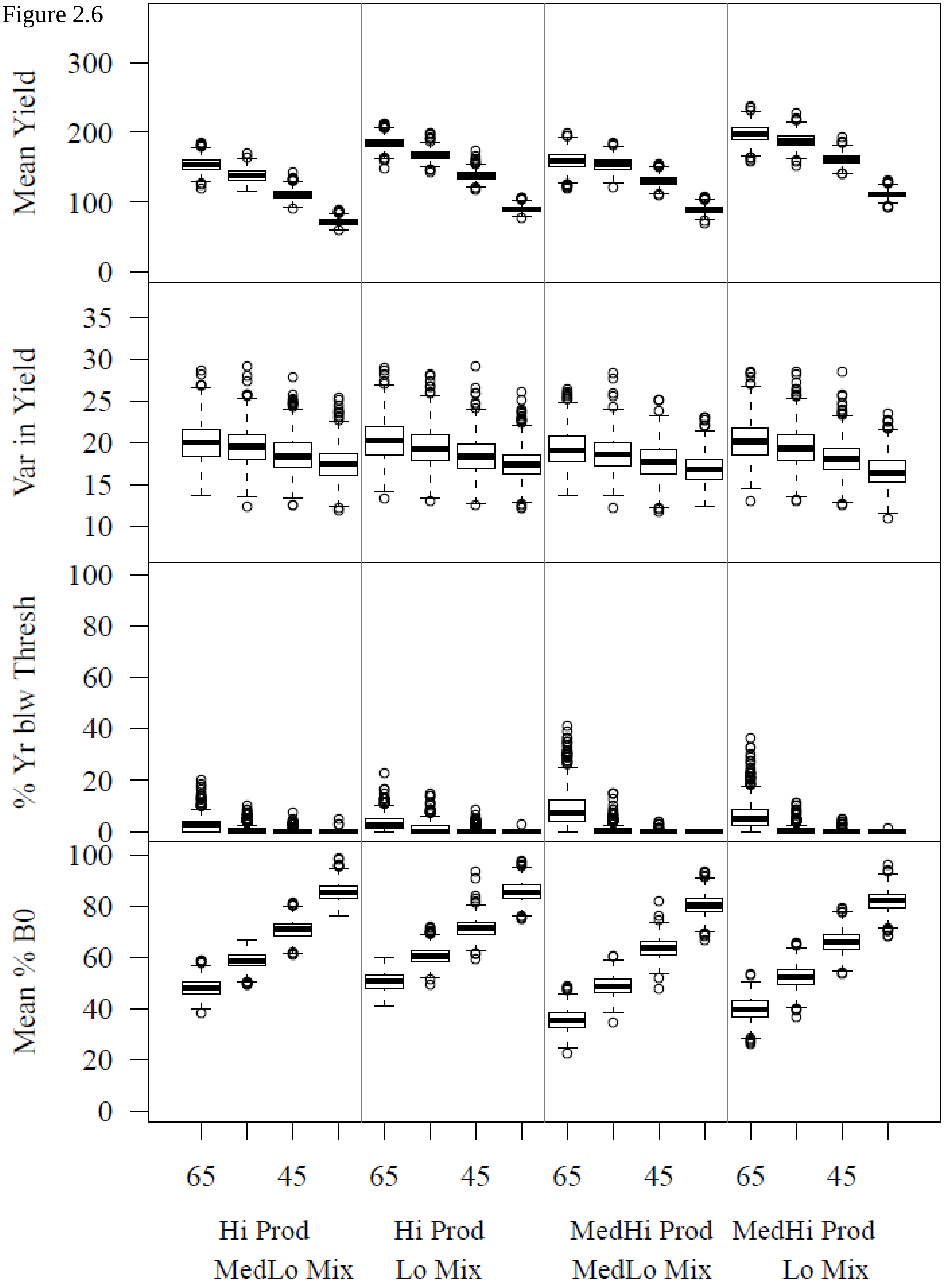


Figure 2.5. Mean annual cumulative fishery yield summed for each investigated scenario. Cumulative yields for the No Mixing group of scenarios are not presented as for these scenarios stocks differed in the harvest control rules so comparisons of yields with other scenarios would not be informative. Boxes indicate the 25th and 75th percentiles over the simulations, while whiskers indicate 1.5 times the interquartile range over simulations. Horizontal lines indicate the median of the yields for the simulations. On the x-axis, numbered labels correspond to specific scenarios within each category. See Table 2.3 for a description of the scenarios.

Figure 2.6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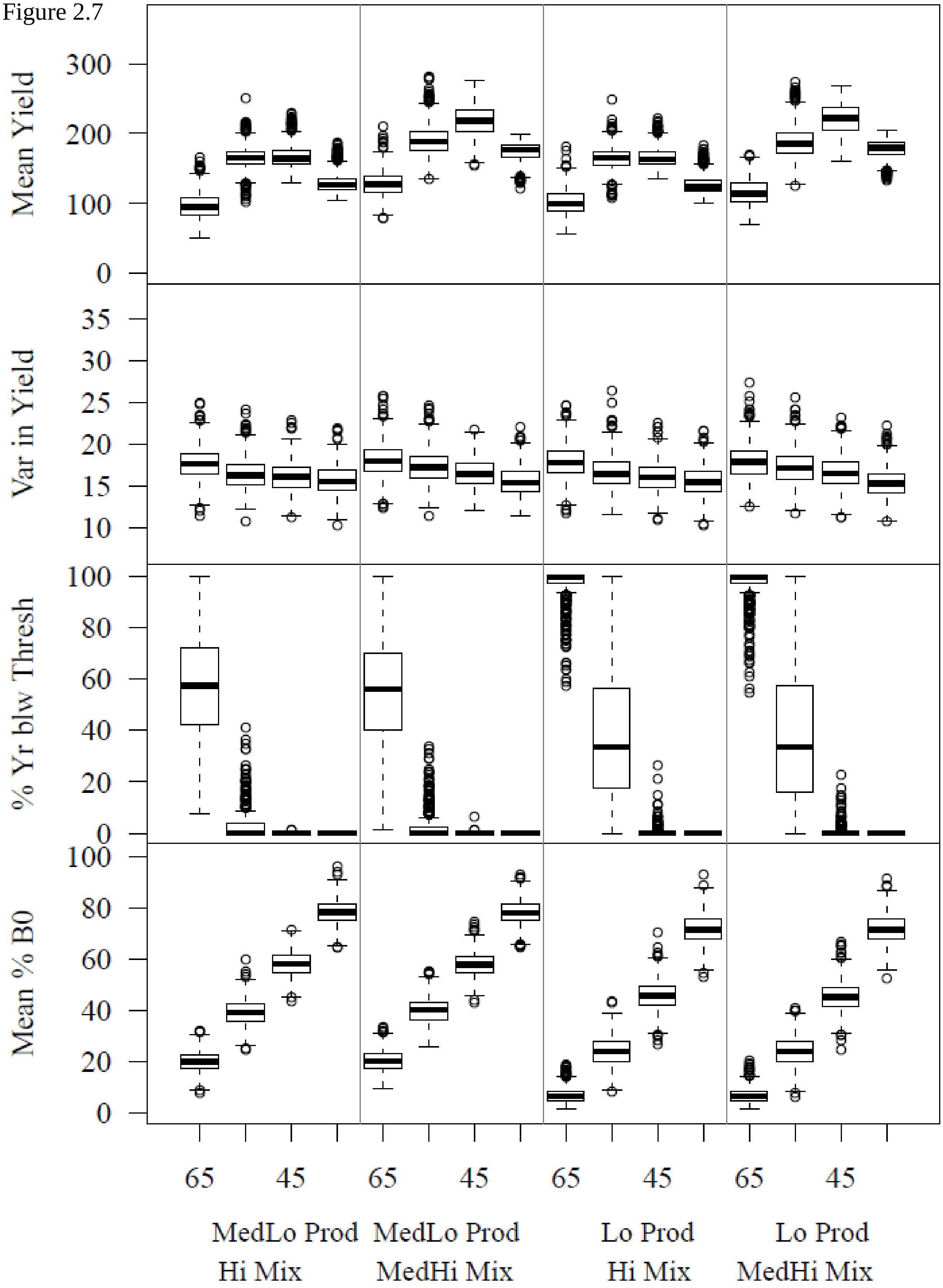
300
200
100
0
Var in Yield
35
30
25
20
15
10
% Yr blw Thresh
100
80
60
40
20
0
Mean % B0
100
80
60
40
20
0
65
45
65
45
65
45
65
45
Hi Prod
MedLo Mix
Hi Prod
Lo Mix
MedHi Prod
MedLo Mix
MedHi Prod
Lo Mix

Figure 2.6 (cont’d)

As in Figure 2.2, except for the state shift scenarios with relatively high productivity and relatively low intermixing.

Figure 2.7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100
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Var in Yield
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25
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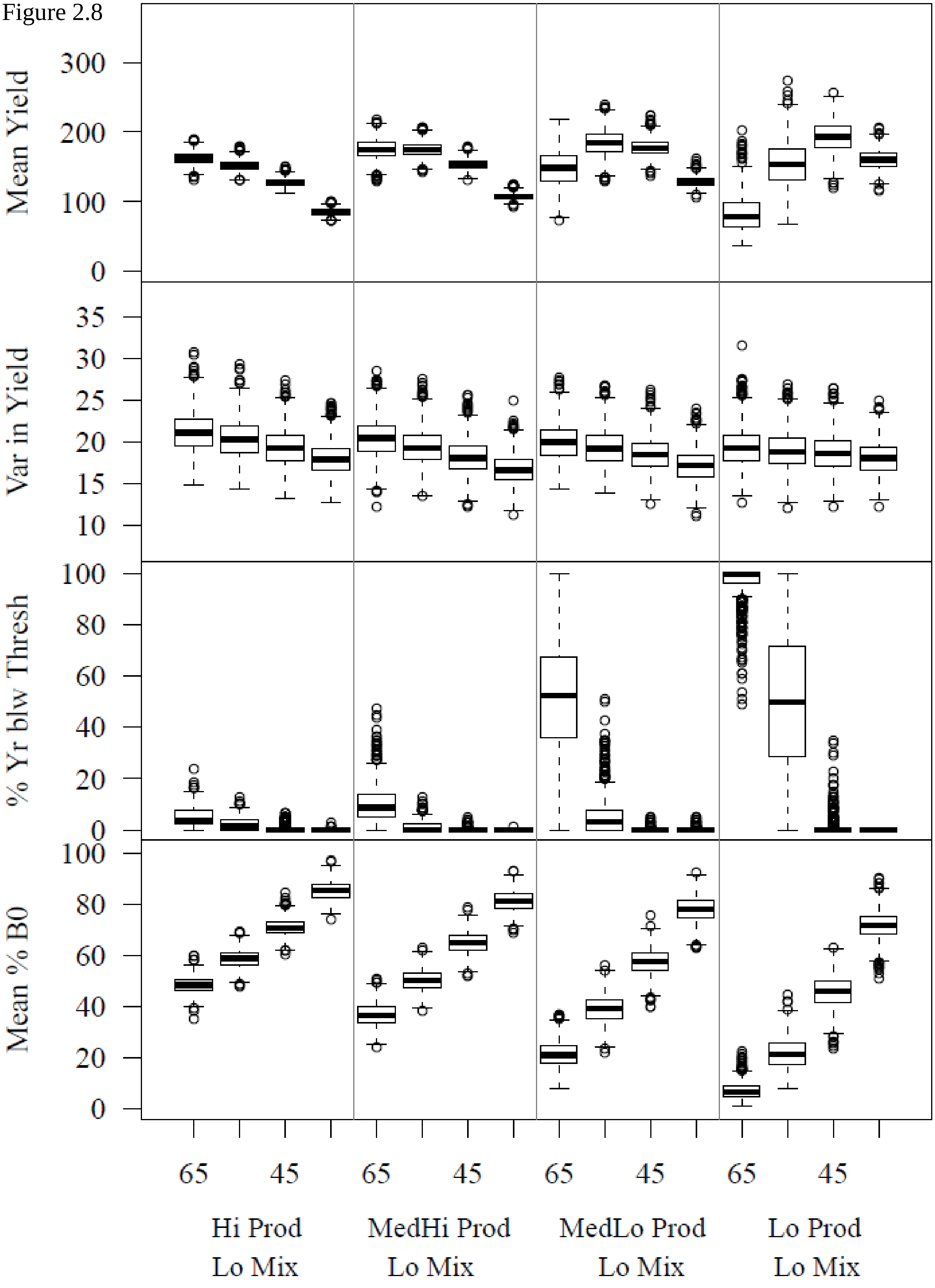
10
% Yr blw Thresh
100
80
60
40
20
0
Mean % B0
100
80
60
40
20
0
65
45
65
45
65
45
65
45
MedLo Prod
Hi Mix
MedLo Prod
MedHi Mix
Lo Prod
Hi Mix
Lo Prod
MedHi Mix

Figure 2.7 (cont’d)

As in Figure 2.2, except for the state shift scenarios with relatively low productivity and relatively high intermixing.

Figure 2.8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Var in Yield
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% Yr blw Thresh
100
80
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40
20
0
Mean % B0
100
80
60
40
20
0
65
45
65
45
65
45
65
45
Hi Prod
Lo Mix
MedHi Prod
Lo Mix
MedLo Prod
Lo Mix
Lo Prod
Lo Mix

Figure 2.8 (cont’d)

As in Figure 2.2, except for the shared mixing scenarios with varied productivity and low intermixing.

Figure 2.9

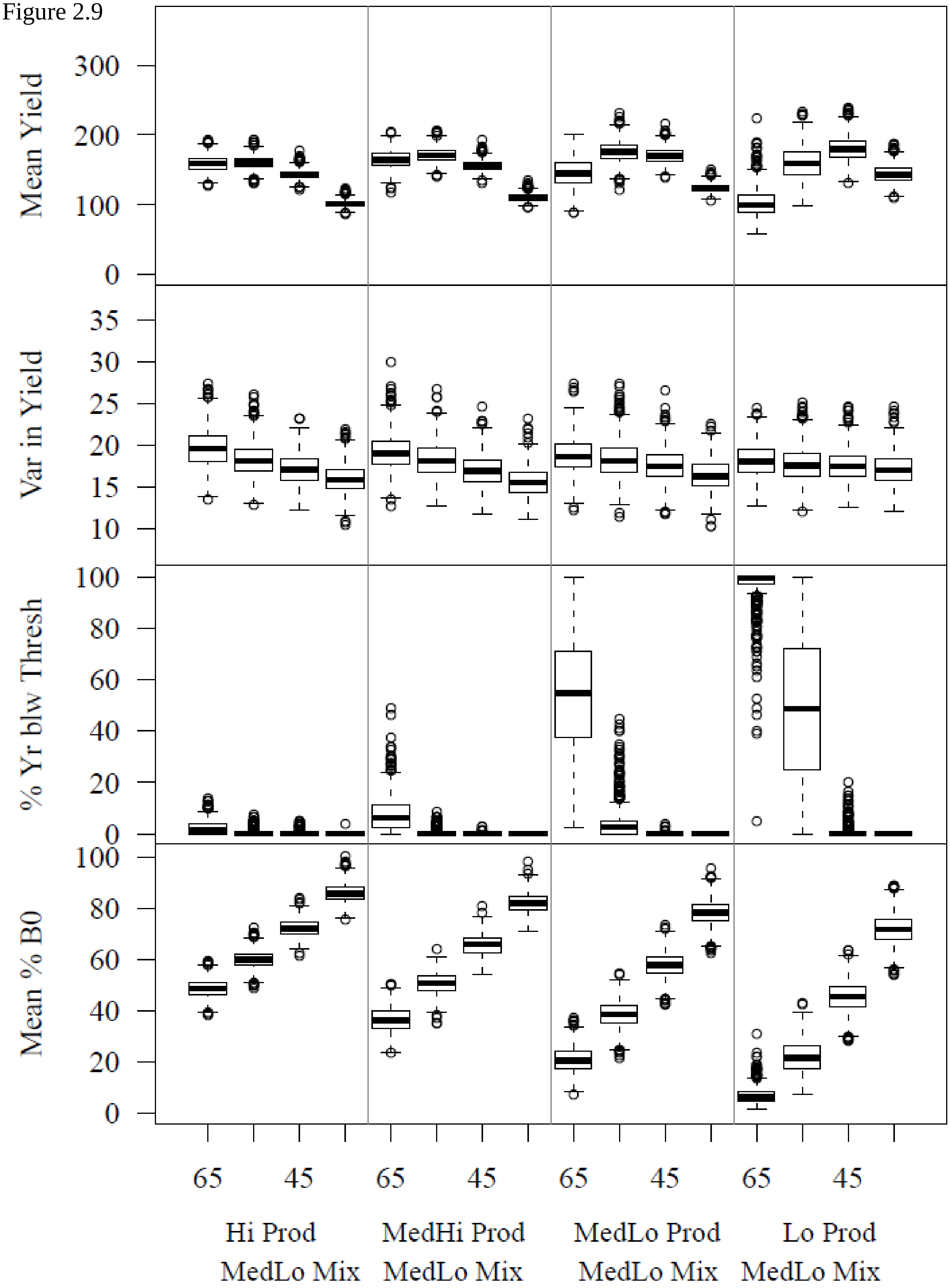
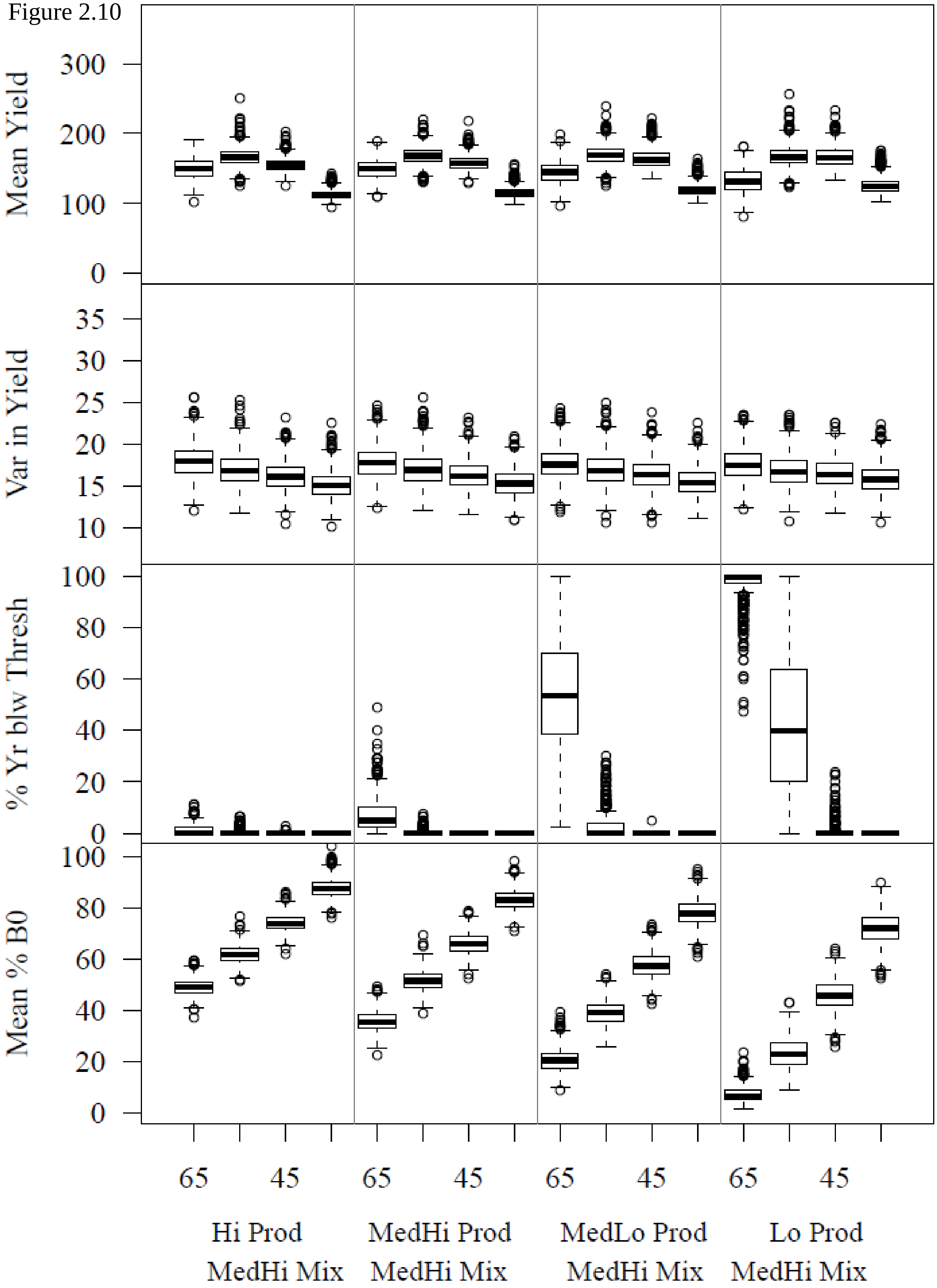

Mean Yield
0
100
200
300
Var in Yield
10
15
20
25
30
35
% Yr blw Thresh
0
20
40
60
80
100
Mean % B0
0
20
40
60
80
100
65
45
65
45
65
45
65
45
Hi Prod
MedLo Mix
MedHi Prod
MedLo Mix
MedLo Prod
MedLo Mix
Lo Prod
MedLo Mix

Figure 2.9 (cont’d)

As in Figure 2.2, except for the shared mixing scenarios with varied productivity and medium-low intermixing.

Figure 2.10



Mean Yield
300
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100
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Var in Yield
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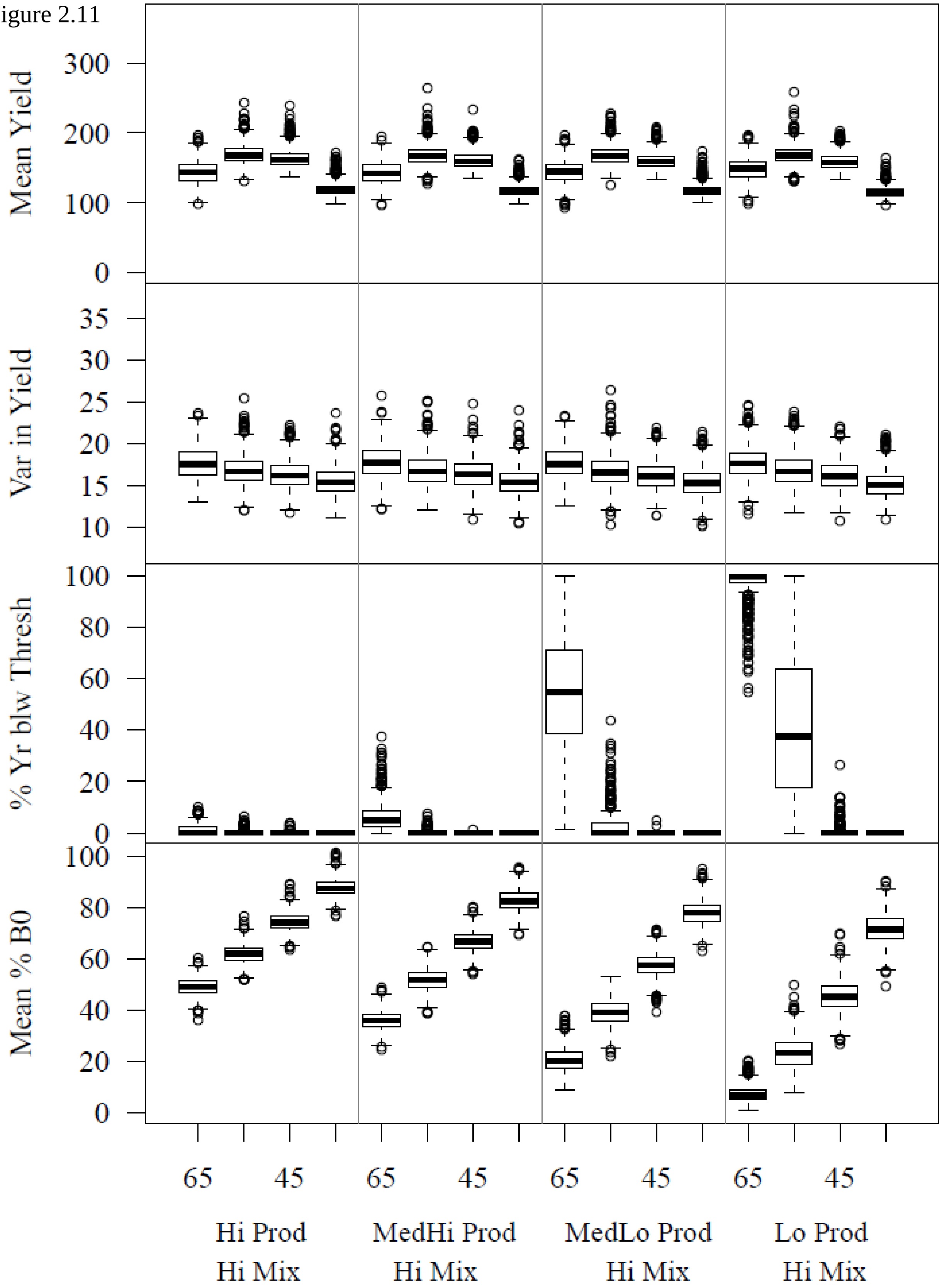
30
25
20
15
10
% Yr blw Thresh
100
80
60
40
20
0
Mean % B0
100
80
60
40
20
0
65
45
65
45
65
45
65
45
Hi Prod
MedHi Mix
MedHi Prod
MedHi Mix
MedLo Prod
MedHi Mix
Lo Prod
MedHi Mix

Figure 2.10 (cont'd)

As in Figure 2.2, except for the shared mixing scenarios with varied productivity and medium-high intermixing.

Figure 2.11


Mean Yield
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Var in Yield
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% Yr blw Thresh
100
80
60
40
20
0
Mean % B0
100
80
60
40
20
0
65
45
65
45
65
45
65
45
Hi Prod
Hi Mix
MedHi Prod
Hi Mix
MedLo Prod
Hi Mix
Lo Prod
Hi Mix

Figure 2.11 (cont’d)

As in Figure 2.2, except for the shared mixing scenarios with varied productivity and high intermixing.

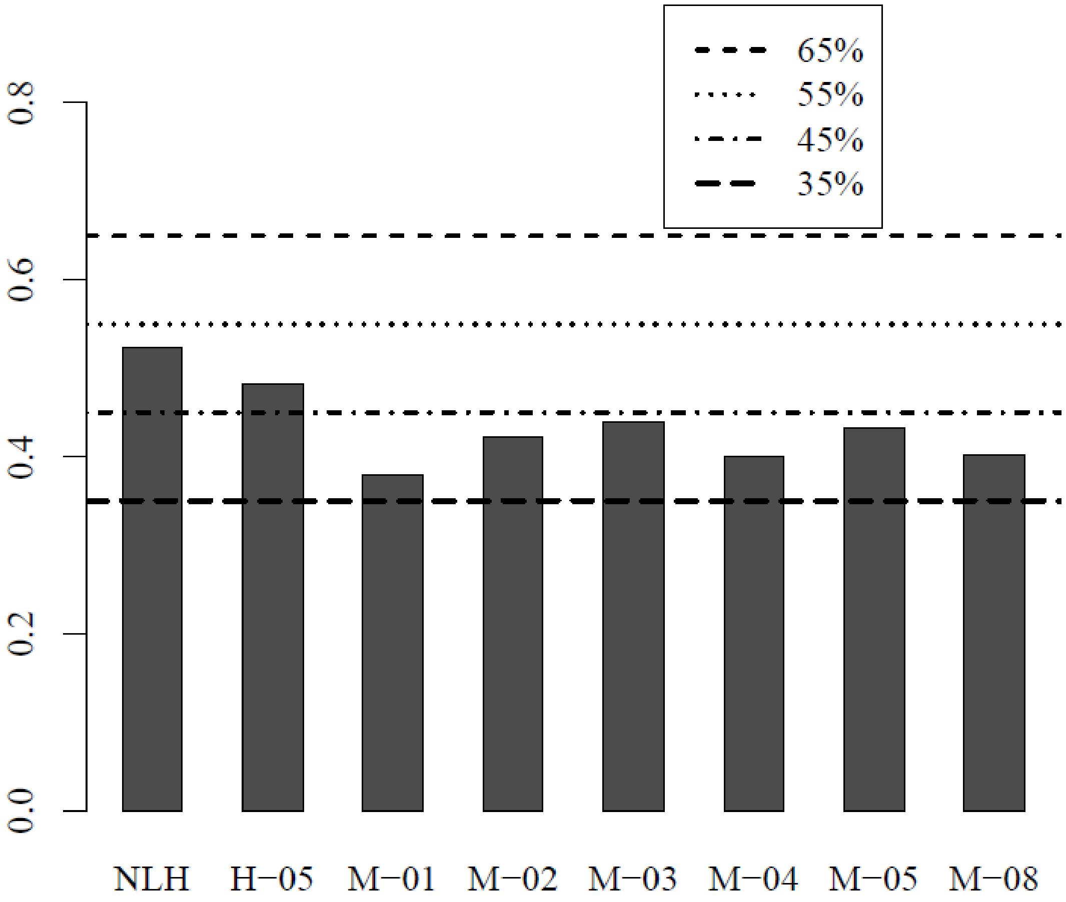

Figure 2.12. Total mortality estimates for the highest selected age class for selected lake whitefish stocks in northern Lakes Huron and Michigan according to the 2010 stock assessments (Carrofino and Lenart, 2011). These values are compared to the total annual mortality targets under the control rules investigated in this research study.

Table 2.1. Descriptions and values (if applicable) for index and state variables, structural parameters, stochastic deviation and error terms, and likelihood components used in the description of equations for models used in this analysis. Variables and parameters denoted with diacritical marks (i.e. ∧ or ¯) are identical to those describe in Table 2.1, but are used to denote either an estimated quantity (^) or the mean (¯) of a variable.

Variable	**Description**	**Value**
Index Variables		
i	Current population or stock	
j	Population or stock other than the current	
y	Year	
a	Age	
State Variables		
N	Abundance	
Z	Instantaneous total mortality	
SSE	Recruitment function stock size (in number of eggs produced)	
F	Instantaneous fishing mortality	
m	Maturity	
w	Weight	
L	Length	
s	Selectivity	
TAC	Total allowable harvest in a management unit	
$\tilde{N}$	Stock abundance after intermixing	
$\tilde{C}$	Observed stock harvest	
C	Actual stock harvest	
$\tilde{P}$	Observed age composition of harvest	
P	Actual age composition of harvest	
$\tilde{E}$	Observed effort	
Structural Parameters		
M	Instantaneous natural mortality	0.25
α	Recruitment function productivity coefficient	See Table 2.4
β	Recruitment function density dependence coefficient	See Table 2.4
σ_R^2	Recruitment function variance	0.36
ρ	Proportion of population female	0.5
$Eggs$	Eggs per kilogram mature female	19937
L_∞	Growth model theoretical maximum length	60.9
κ	Growth model growth coefficient	0.1686
t_0	Growth model time coefficient (age at length = 0)	0.0
γ	Allometric model condition factor	$8.06x10^{-5}$
ψ	Allometric model curvature parameter	2.45
m_∞	Asymptotic maturity for logistic maturity model	1.0

Table 2.1 (cont'd)

ϑ	Slope parameter for logistic maturity model	0.315
δ	Inflection point length for logistic maturity model	37.9
η	Parameter 1 of gamma selectivity function	13.074
τ	Parameter 2 of gamma selectivity function	1.26
σ_C^2	Implementation error variance	0.01
θ	Proportion of population mixing into another management unit	Varied with scenario and stock
$\sigma_{\tilde{C}}^2$	Harvest observation error variance	0.01
q	Catchability	$1.5\text{x}10^{-6}$
$\sigma_{\tilde{E}}^2$	Effort deviation variance	0.04
σ_F^2	Assessment fishing mortality deviation variance	0.01
Stochastic deviation and error terms		
ε_R	Recruitment stochastic error	
ε_C	TAC implementation error	
$\varepsilon_{\tilde{C}}$	Harvest observation error	
$\varepsilon_{\tilde{E}}$	Effort observation error	
ε_F	Assessment fishing mortality deviations	
$\varepsilon_{\bar{\tilde{N}}_{4-12}}$	Assessment initial abundance deviations	
$\varepsilon_{\bar{\tilde{N}}_3}$	Assessment recruitment deviations	
Likelihood components (assessment model)		
ℓ_C	Harvest likelihood component	
ℓ_{ε_F}	Fishing mortality deviation likelihood component	
ℓ_P	Proportion at age likelihood component	

Table 2.2. Operating and assessment model equations. Variables and parameters denoted with diacritical marks (i.e. ∧ or ¯) are identical to those describe in Table 2.1, but are used to denote either an estimated quantity (^) or the mean (¯) of a variable.

Equation	**Equation Number**
Operating Model	
$N_{y+1,a+1} = N_{y,a} \exp\left(-Z_{y,a}\right)$	T.2.2.1
$Z_{y,a} = M + F_{y,a}$	T.2.2.2
$N_{y,1} = \alpha \cdot SSE_{y-1} \exp\left(-\beta \cdot SSE_{y-1}\right) \exp\left(\varepsilon_R\right); \quad \varepsilon_R \sim N\left(0, \sigma_R^2\right)$	T.2.2.3
$SSE_y = \sum_a N_{y,a} m_a w_a \rho Eggs$	T.2.2.4
$L_a = L_\infty \left(1 - \exp\left(-\kappa\left(a - t_0\right)\right)\right)$	T.2.2.5
$w_a = \gamma L_a{}^{\psi}$	T.2.2.6
$m_a = \dfrac{m_\infty}{1 + \exp\left(-\vartheta\left(L_a - \delta\right)\right)}$	T.2.2.7
$F_{y,a} = s_a F_y$	T.2.2.8
$s_a = \dfrac{a^{\eta} \exp\left(-\tau a\right)}{10^{\eta} \exp\left(-\tau 10\right)}$	T.2.2.9
$C_y = TAC_y \exp\left(\varepsilon_C - 0.5\sigma_C^2\right); \quad \varepsilon_C \sim N\left(0, \sigma_C^2\right)$	T.2.2.10
$N_{i,y+1,a+1} = N_{i,y,a}\theta_{i \to i} \exp\left(-M - F_{i,y.a}\right) + \sum_j N_{i,y,a}\theta_{i \to j} \exp\left(-M - F_{j,y.a}\right)$	T.2.2.11
$\tilde{N}_{i,y,a} = N_{i,y,a}\theta_{i \to i} + \sum_j N_{j,y,a}\theta_{j \to i}$	T.2.2.12
Observed Data	
$\tilde{C}_y = C_y \exp\left(\varepsilon_{\tilde{C}} - 0.5\sigma_{\tilde{C}}^2\right); \quad \varepsilon_{\tilde{C}} \sim N\left(0, \sigma_{\tilde{C}}^2\right)$	T.2.2.13
$\tilde{P}_{y,a} \sim MN\left(200, P_{y,a}\right)$	T.2.2.14
$\tilde{E}_y = \dfrac{F_y}{1.50 \times 10\text{e}^{-6}} \exp\left(\varepsilon_{\tilde{E}} - 0.5\sigma_{\tilde{E}}^2\right); \quad \varepsilon_{\tilde{E}} \sim N\left(0, \sigma_{\tilde{E}}^2\right)$	T.2.2.15

Table 2.2 (cont'd)

Assessment Model

$$\ell_C = n_C \log_e\left(\hat{\sigma}_C\right) + \left(\frac{1}{2\hat{\sigma}_C^2}\right)\sum_y \log_e\left(\frac{\tilde{C}_y}{\hat{\tilde{C}}_y}\right)^2 \qquad \text{T.2.2.16}$$

$$\ell_{\varepsilon_F} = n_{\varepsilon_F} \log_e\left(\frac{\hat{\sigma}_C}{\sqrt{0.25}}\right) + \left(\frac{0.25}{2\hat{\sigma}_C^2}\right)\sum_y \log_e\left(\varepsilon_F\right)^2 \qquad \text{T.2.2.17}$$

$$\ell_P = -\sum_y 200 \sum_a \left(\tilde{P}_{y,a} \log_e \hat{\tilde{P}}_{y,a}\right) \qquad \text{T.2.2.18}$$

$$\hat{F}_{y,a} = \hat{q}\hat{s}_a \tilde{E}_y \exp\left(\varepsilon_F\right); \quad \varepsilon_F \sim N\left(0, \sigma_F^2\right) \qquad \text{T.2.2.19}$$

$$\hat{s}_a = \frac{a^{\hat{\eta}} \exp\left(-\hat{\tau}a\right)}{10^{\hat{\eta}} \exp\left(-\hat{\tau}10\right)} \qquad \text{T.2.2.20}$$

$$\hat{\tilde{N}}_{4-12} = \bar{\tilde{N}}_{4-12} \exp\left(\varepsilon_{\bar{\tilde{N}}_{4-12}}\right); \quad \sum \varepsilon_{\bar{\tilde{N}}_{4-12}} = 0 \qquad \text{T.2.2.21}$$

$$\hat{\tilde{N}}_{y,3} = \bar{\tilde{N}}_3 \exp\left(\varepsilon_{\bar{\tilde{N}}_3}\right); \quad \sum \varepsilon_{\bar{\tilde{N}}_3} = 0 \qquad \text{T.2.2.22}$$

$$\hat{\tilde{C}}_{y,a} = \frac{\hat{F}_{y,a}}{\hat{F}_{y,a} + M} \hat{\tilde{N}}_{y,a} \exp\left(-\hat{F}_{y,a} - M\right) \qquad \text{T.2.2.23}$$

$$\hat{\tilde{P}}_{y,a} = \frac{\hat{\tilde{C}}_{y,a}}{\sum_a \hat{\tilde{C}}_{y,a}} \qquad \text{T.2.2.24}$$

Table 2.3. Productivity levels, intermixing rates, and control rules used in each of the scenarios evaluated in this research. Varied productivity refers to cases where the 4 different spawning population were assigned unique stock recruitment relationship.

Category	Scenario	Mixing	Productivity	Control Rule
No Mixing	1	None	(All Stocks) Low	65,55,45,35 (1 stock with each)
	2	None	Med. Low	65,55,45,35
	3	None	Med. High	65,55,45,35
	4	None	High	65,55,45,35
Corr	1	Low, Med. Low, Med. High, High	Low, Med. Low, Med. High, High	65 (all stocks)
	2	Low, Med. Low, Med. High, High	Low, Med. Low, Med. High, High	55
	3	Low, Med. Low, Med. High, High	Low, Med. Low, Med. High, High	45
	4	Low, Med. Low, Med. High, High	Low, Med. Low, Med. High, High	35
	5	Low, Med. Low, Med. High, High	High, Med. High, Med. Low, Low	65
	6	Low, Med. Low, Med. High, High	High, Med. High, Med. Low, Low	55
	7	Low, Med. Low, Med. High, High	High, Med. High, Med. Low, Low	45
	8	Low, Med. Low, Med. High, High	High, Med. High, Med. Low, Low	35
State Shift	1	2 Low, 2 Med. Low	2 Med. High, 2 High	65 (all stocks)
	2	2 Low, 2 Med. Low	2 Med. High, 2 High	55
	3	2 Low, 2 Med. Low	2 Med. High, 2 High	45
	4	2 Low, 2 Med. Low	2 Med. High, 2 High	35
	5	2 Med. High, 2 High	2 Low, 2 Med. Low	65
	6	2 Med. High, 2 High	2 Low, 2 Med. Low	55
	7	2 Med. High, 2 High	2 Low, 2 Med. Low	45
	8	2 Med. High, 2 High	2 Low, 2 Med. Low	35
Shared Mixing	1	(All Stocks) Low	Low, Med. Low, Med. High, High	65 (all stocks)
	2	Low	Low, Med. Low, Med. High, High	55
	3	Low	Low, Med. Low, Med. High, High	45
	4	Low	Low, Med. Low, Med. High, High	35

Table 2.3 (cont'd)

5	Med. Low	Low, Med. Low, Med. High, High	65
6	Med. Low	Low, Med. Low, Med. High, High	55
7	Med. Low	Low, Med. Low, Med. High, High	45
8	Med. Low	Low, Med. Low, Med. High, High	35
9	Med. High	Low, Med. Low, Med. High, High	65
10	Med. High	Low, Med. Low, Med. High, High	55
11	Med. High	Low, Med. Low, Med. High, High	45
12	Med. High	Low, Med. Low, Med. High, High	35
13	High	Low, Med. Low, Med. High, High	65
14	High	Low, Med. Low, Med. High, High	55
15	High	Low, Med. Low, Med. High, High	45
16	High	Low, Med. Low, Med. High, High	35

Table 2.4. Recruitment parameters for the four productivity levels assigned to spawning populations in this analysis.

Productivity Level	α	β
Low	0.000369	$7.1708\text{x}10^{-11}$
Medium Low	0.000516	$1.2780\text{x}10^{-10}$
Medium High	0.000769	$2.2758\text{x}10^{-10}$
High	0.001281	$4.2988\text{x}10^{-10}$

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CONCLUSIONS

The results of the analyses included in this thesis have important implications for lake whitefish management in the upper Great Lakes, as well as being generally informative for fisheries management when stock intermixing occurs. In Chapter 1, the performance of the existing control rule for lake whitefish stocks in the 1836 Treaty waters was found to vary with the intermixing and productivity of the populations that made up mixed stocks. Harvest in a management unit was a poor indicator of the health of the underlying spawning population when there was considerable intermixing. Yield varied considerably between stocks under different scenarios. The sustainability and risk of depletion of spawning populations was dependent on their productivity level, with low productivity populations having a very high risk of depletion and maintaining a very small proportion of their unfished biomass. I conclude that intermixing of populations with varying levels of productivity can seriously affect management of lake whitefish fisheries in the 1836 Treaty waters and could foreseeably result in overharvest of some low productivity populations.

In Chapter 2, the performance of several control rules were compared across a wide spectrum of scenarios for intermixing and productivity of spawning populations. Control rules more conservative than the current 65% mortality policy were found to perform better at preserving spawning biomass and reducing the risk of depletion. The inter-annual variability in yield was also found to decrease slightly at more conservative control rules. Yield varied between stocks under each scenario, but in general control rules more conservative than the existing rule, but less conservative than the 35% mortality control rule, had the highest annual yields. I concluded that the 45% allowable mortality control rule provided very high sustainability regardless of productivity and high overall yield across the majority of scenarios, making it an excellent candidate for lake whitefish management. Additional research into the stock recruitment (productivity) relationships for spawning populations would better inform the selection of an appropriate harvest level for lake whitefish stocks in the 1836 Treaty waters.