ECO-EVOLUTIONARY DYNAMICS IN A COMMERCIALLY EXPLOITED FRESHWATER FISH

A Thesis Submitted to the Committee on Graduate Studies
in Partial Fulfillment of the Requirements for the Degree of Doctor of Philosophy
in the Faculty of Arts and Science

TRENT UNIVERSITY

Peterborough, Ontario, Canada

Environmental and Life Sciences Ph.D. Graduate Program

January 2019

ABSTRACT

Eco-evolutionary dynamics in a commercially exploited freshwater fish

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Fisheries assessment and management approaches have historically focused on individual species over relatively short timeframes. These approaches are being improved upon by considering the potential effects of both broader ecological and evolutionary processes. However, only recently has the question been raised of how ecological and evolutionary processes might interact to further influence fisheries yield and sustainability. My dissertation addresses this gap in our knowledge by investigating the role of eco-evolutionary dynamics in a commercially important lake whitefish fishery in the Laurentian Great Lakes, a system that has undergone substantial ecosystem change. First, I link the timing of large-scale ecological change associated with a species invasion with shifts in key density-dependent relationships that likely reflect declines in the population carrying capacity using a model selection approach. Then, using an individual-based model developed for lake whitefish in the southern main basin of Lake Huron, I demonstrate how ecosystem changes that lower growth and recruitment potential are predicted to reduce population productivity and sustainable harvest rates through demographic and plastic mechanisms. By further incorporating an evolutionary component within an eco-genetic model, I show that ecological conditions also affect evolutionary responses in maturation to harvest by altering selective pressures. Finally, using the same eco-genetic model, I provide a much-needed validation of the robustness of the probabilistic maturation reaction norm (PMRN) approach, an approach that is widely used to assess maturation and infer its evolution, to ecological and evolutionary processes experienced by exploited stocks in the wild. These findings together highlight the important role that ecological conditions play, not only in determining fishery yield and sustainability, but also in shaping evolutionary responses to harvest. Future studies evaluating the relative effects of ecological and evolutionary change and how these processes interact in harvested populations, especially with respect to freshwater versus marine ecosystems, could be especially valuable.

Keywords: *Coregonus clupeaformis*, density-dependent growth, dreissenid mussels, fisheries-induced evolution, individual-based eco-genetic model, Lake Huron, regime shift, stock-recruitment

ACKNOWLEDGEMENTS

I would like to acknowledge all the people who supported me over the course of completing my PhD and this dissertation. First, I acknowledge my entire thesis supervisory committee for sharing with me their time and expertise, without which my thesis would not have been a success. I thank my supervisor Dr. Erin Dunlop for the wonderful opportunity to do this research, sharing her models with me, her patience, financial support, and the opportunity to present this research at numerous conferences. I thank my co-supervisor Dr. Michael Fox for being a true mentor; his unwavering confidence and support, including me as part of his lab, and presenting me with every opportunity that he possibly could have helped me succeed in ways that extend beyond producing this thesis. He has also played a central role in my development as a teacher and mentor for others, for which I am incredibly grateful. I thank my committee member Dr. Nigel Lester for sharing his invaluable knowledge, experience, and insight; and for his ability to make complex concepts always appear simple and easy to understand. I thank my fellow PhD candidates Anna Rooke and Marisha Lamond. Anna is the one friend who was right there with me, every step of the way, from the beginning to the end, and I couldn't imagine having done this without her. In addition to being morally supportive, Marisha gave me her time and energy, when she had none of either to spare, which allowed me to work on campus following my injury this past year. I thank my significant other, Dave Priester, for standing by me not only through the challenges of completing my PhD and this dissertation, but everything else that life has thrown our way; and for reassuring me that we would always get through - together. I thank Gwen Little for being a mentor that helped spark passion in me during a difficult time, when I was most discouraged and had lost all motivation, and for helping me support myself financially by putting me on the path to developing my own business. Finally, I thank my family for their unconditional love, patience and support.

DECLARATION OF PREVIOUS PUBLICATION

Three of the thesis chapters included in this dissertation comprise original papers that have been accepted for publication or previously published in peer-review journals:

Chapter 1 - Gobin, J., N. P. Lester, A. Cottrill, M. G. Fox, and E. S. Dunlop. 2015. Trends in growth and recruitment of Lake Huron lake whitefish during a period of ecosystem change, 1985 to 2012. Journal of Great Lakes Research 14:405–414.

Chapter 2 - Gobin, J., N. P. Lester, M. G. Fox, and E. S. Dunlop. 2016. Effects of changes in density-dependent growth and recruitment on sustainable harvest of lake whitefish. Journal of Great Lakes Research 42: 871-882.

Chapter 3 – Gobin, J., N.P. Lester, M.G. Fox, and E.S. Dunlop. *In press*. Ecological change alters the evolutionary response to harvest in a freshwater fish. Ecological Applications. https://doi.org/10.1002/eap.1805.

These chapters may have been slightly modified from the original publications to maintain a consistent format throughout this dissertation.

I hereby declare that this dissertation incorporates published and unpublished materials resulting from joint research, as follows:

In all cases, Jenilee Gobin contributed to the main ideas presented and study design; developed the individual-based and eco-genetic models employed and conducted model simulations; compiled, analyzed and interpreted the data; and led the writing process. Adam Cottrill provided details regarding OMNRF survey data, advised on the estimation of standardized catch-per-unit-effort values, and provided feedback in the preparation of the manuscript for Chapter 1. As a key member of my supervisory committee, Dr. Nigel P. Lester provided guidance and feedback at all stages during the development of Chapters 1-4 relating to the main ideas presented, study design, the development of simulation models, data analysis and interpretation, and in the preparation of manuscripts. My co-supervisor, Dr. Michael G. Fox also provided guidance and feedback at all stages of the previously published research contained in Chapters 1-4. My primary supervisor, Dr. Erin S. Dunlop, in addition to providing guidance and feedback at all stages of the above research, also provided the original code used in the development of simulation models and contributed written work during the revision of manuscripts based on comments provided during the peer-review process.

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GENERAL INTRODUCTION

Standard evolutionary theory has long recognized that natural selection in the environment drives evolution (Laland et al. 2015, Svensson 2018). The idea that reciprocal feedbacks between organisms and their environment influence evolutionary processes, while also not new, has historically been less well-recognized among evolutionary biologists (Svensson 2018). However, the field of eco-evolutionary dynamics has recently gained in popularity, providing new views on how ecological and evolutionary processes interact. While it was previously thought that evolutionary processes occurred over much longer timescales (e.g. hundreds, thousands or millions of years) compared to ecological processes, it is becoming increasingly apparent that both processes can in fact occur and interact over relatively short timescales (e.g. decades) (Hendry 2016).

These new insights are helping us better understand natural populations and the impact that we as humans have on both ecological and evolutionary processes (Hendry et al. 2017, Palkovacs et al. 2018). An example of this is how considering eco-evolutionary dynamics is changing the way that we manage and exploit wild populations. Fisheries assessment and management approaches have historically focused more narrowly on individual species and their ecology, over relatively short time periods. However, mounting evidence strongly suggests that the selective harvesting practices associated with fisheries can induce rapid evolution in the populations we exploit, which in turn, can impact population productivity and fishery sustainability (Dunlop et al. 2015, Heino et al. 2015, Zimmermann and Jørgensen 2017). Recent research has also highlighted the benefits of ecosystem-based management that accounts for broader ecological processes (e.g. interactions among species and various trophic levels; see also Szuwalski et al. 2017). Only recently have studies begun to examine how these ecological and evolutionary processes might interact (e.g. Kindsvater and Palkovacs 2017, Morbey and Mema 2018), or how such interactions could impact harvest and sustainability (e.g. Wood et al. 2018).

In this dissertation, I investigate the interactions between ecological and evolutionary processes affecting a commercially exploited fish stock in a large freshwater lake that has undergone substantial ecological change stemming from species invasions. I focus on maturation-related traits that have previously been shown to evolve readily in response to harvest (Heino et al. 2015) and influence population productivity (Morgan 2018). I also investigate how ecological and evolutionary processes might affect our ability to assess age and size at maturation and to detect evolution of maturation in wild populations.

Ecological change is ubiquitous in natural systems. It can occur gradually (e.g. climate change) or rather abruptly (e.g. natural disasters). Humans have been identified as a “hyperkeystone” species, having unprecedented impacts on natural ecosystems by aggressively harvesting wild populations (Essington et al. 2006, Worm et al. 2009), as well as altering habitat and behavior (Worm and Paine 2016). In fisheries, the depletion of species through harvest, as well as the introduction of new species, can shift food webs and impact species composition, diversity, and overall ecosystem function (Essington et al. 2006). Such impacts are only expected to increase with future human disturbance and climate change (Meyer et al. 1999, Britten et al. 2016); with a central challenge of the 21st century being our ability to predict ecosystem responses to human activity (Kendall 2015, Worm and Paine 2016).

Species invasions, which are often facilitated by human movement and transportation, are a primary example of human impacts on natural ecosystems and a major cause of large-scale ecosystem change (Mack et al. 2000). Successful invaders can impart detrimental impacts on native species and alter entire communities in the ecosystems they invade (Mack et al. 2000). Over a decade ago now, the estimated cost of losses and environmental degradation associated with species invasions in the United States of America alone was estimated at almost $120 billion dollars (Pimentel et al. 2005). Technological advances have facilitated transportation around the world, leading to significant increases in species invasions that are likely to continue to occur in the foreseeable future, despite our best efforts to prevent them. Therefore, understanding how ecosystem changes, such as those arising from species invasions, could affect the dynamics of fish stocks that comprise a globally important aquatic resource and how they respond to exploitation will be vital to the future of sustainable fisheries management.

Density-dependent feedbacks, such as density-dependent somatic growth and density-dependent recruitment are key processes that may be impacted by large-scale ecosystem change. Historically, the importance of density-dependent processes in population regulation has been widely recognized (Lorenzen and Enberg 2002, Walters and Martell 2004). However, the non-stationarity of these relationships in response to changing environments has been underappreciated (Walters and Martell 2004, Britten et al. 2017). Once considered long term steady states, ecosystems and ecological processes are now becoming recognized as dynamic (Britten et al. 2017). Although density-dependent growth and stock recruitment relationships, such as the classically used Ricker and Beverton-Holt models, are often included in fishery stock assessment models, characterizing these relationships and accounting for how they might be changing over time is challenging and often not accounted for (Szuwalski et al. 2015). Data needed to estimate density-dependent relationships for specific populations are frequently limited, restricting our ability to measure variation in these important mechanisms of population regulation over time (Walters and Martell 2004). Nonetheless, density-dependent feedbacks do have the potential to change temporally and spatially in response to environmental factors that influence population carrying capacity (Walters and Martell 2004, Minto et al. 2014, Zhang et al. 2018). Furthermore, changes in density-dependent relationships could significantly alter productivity, harvest, and resilience to harvest in exploited stocks (Gobin et al. 2016).

The potential for stocks to exhibit evolutionary responses to exploitation and ecological change is also becoming more widely recognized. Fisheries-induced evolution has been a controversial and highly debated topic as challenges currently limit the collection of genetic evidence demonstrating evolutionary responses in wild populations that are clearly associated with harvest and the phenotypic traits undergoing selection (Heino et al. 2015). However, more than sufficient evidence exists from phenotypic and modelling studies to argue that the high rates of selective mortality associated with harvest can induce evolution of traits in the wild (Heino et al. 2015). Further debate surrounds how exploited stocks might evolve in response to harvest, in terms of the direction and magnitude of evolutionary trajectories, rates of evolution, and the implications for sustainable harvest and management. In some cases, fisheries-induced evolution appears to have contributed to declines in productivity, leading to population collapse in heavily exploited stocks (Olsen et al. 2004, Swain et al. 2007) and slowed recovery (Dunlop et al. 2009, 2015). However, studies have also shown that under certain conditions, harvest-induced evolution can increase productivity and resilience (Eikeset et al. 2013, Dunlop et al. 2015, Zimmermann and Jørgensen 2017). Harvest rates and the selectivity of fishing gear used have been found to play an especially important role in shaping trajectories and rates of fisheries-evolution (Zimmermann and Jørgensen 2017). However, few studies have considered the role of the ecological setting in fisheries-induced evolution, or how ecological and evolutionary processes might interact to influence a stock's response to harvest.

Traits related to maturation appear to be especially susceptible to fisheries-induced evolution (Dunlop et al. 2009, Heino et al. 2015). The probabilistic maturation reaction norm approach (PMRN) (Barot et al. 2004) is widely used to estimate age and size at maturation and infer its evolution in wild stocks (Heino et al. 2015). By describing maturation in terms of both an individual's age and size, PMRNs theoretically account for plasticity in maturation due to variation in somatic growth rates (Heino et al. 2002, Barot et al. 2004). The PMRN approach also allows us to account for stochasticity in the maturation process and estimate maturation probabilities at various ages and sizes when maturation events cannot be observed directly (Barot et al. 2004). Given that maturation can also respond plastically to environmental and ecological factors independently of growth (Dhillon and Fox 2004, Kuparinen et al. 2011, Tobin and Wright 2011), a concern with the PMRN approach is whether it captures all the plasticity in maturation exhibited by wild stocks. However, such growth-independent plasticity in maturation can be accounted for in the PMRN estimation process when data are available (Dieckmann and Heino 2007). What remains unknown is how the PMRN estimation process itself might be affected by natural conditions (i.e. ecological and evolutionary processes) experienced by populations in the wild.

Further advancement of sustainable fisheries management requires an understanding of how ecological and evolutionary processes interact in exploited stocks. Recent research has highlighted the advantages of going beyond single-species management over short timescales to account for broader ecological (Szuwalski et al. 2017) and evolutionary (Laugen et al. 2014) processes. Studies have only begun to consider how these processes might interact (e.g. Kindsvater and Palkovacs 2017, Morbey and Mema 2018) and their potential impacts on fishery yield and sustainability (e.g. Wood et al. 2018).

In this dissertation, I examine eco-evolutionary dynamics and their potential impact on fishery productivity, resilience, and sustainability, in a commercially-exploited freshwater fish. Lake whitefish (*Coregonus* clupeaformis) support valuable, large-scale commercial and subsistence fisheries in the Laurentian Great Lakes (Ebener et al. 2008, Brenden et al. 2010, Ebener 2013). The establishment of invasive dreissenids (zebra and quagga mussels) has been accompanied by substantial ecosystem change in several of the Laurentian Great Lakes (Higgins and Vander Zanden 2010). As ecosystem engineers, dreissenid mussels substantially alter aquatic food webs and the distribution and flow of energy between pelagic-profundal and benthic-littoral zones in the ecosystems they invade (Crooks 2002, Higgins and Vander Zanden 2010). In the Laurentian Great Lakes, they are thought to be the main cause of declines in the native amphipod, *Diporeia* spp. (Higgins and Vander Zanden 2010), and to have contributed to declines in primary productivity and shifts in food webs (Strayer 2009, Cha et al. 2011, Pilcher et al. 2017). Following the invasion of dreissenid mussels in several of the Great Lakes, lake whitefish exhibited dramatic declines in growth (Fera et al. 2015, Gobin et al. 2015), condition (Pothoven et al. 2001), and recruitment (Gobin et al. 2015) that are likely to impact population productivity and resilience.

I hypothesize that ecosystem changes associated with the establishment of dreissenid mussels have altered key density-dependent growth and recruitment relationships in lake whitefish, impacting productivity and sustainable harvest through plastic and demographic mechanisms. I further hypothesize that these ecosystem changes could alter evolutionary responses to harvest in lake whitefish and our ability to detect evolution of maturation using a probabilistic maturation reaction norm approach. In the first chapter of this thesis, I test whether density-dependent relationships have been altered by ecosystem changes using a model selection approach. In the second chapter, I go on to develop an individual-based model for lake whitefish to investigate how ecological changes affecting density-dependent feedbacks could impact harvest and the sustainability of the fishery. In the third chapter, I incorporate an eco-genetic component to the individual-based model to examine how ecosystem changes could influence the potential for harvest-induced evolution in these stocks. In the fourth chapter, I use the same eco-genetic model from chapter 3 to assess whether ecological and evolutionary processes could impact our ability to estimate age and size at maturation and detect its evolution using probabilistic maturation reaction norms. Finally, in the general discussion, I summarize the main findings of each chapter and discuss the implications of conclusions drawn in relation to my overall objective of investigating the role of eco-evolutionary dynamics in exploited fish stocks.

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CHAPTER 1: TRENDS IN GROWTH AND RECRUITMENT OF LAKE HURON LAKE WHITEFISH DURING A PERIOD OF ECOSYSTEM CHANGE, 1985 TO 2012

This chapter has been published in the Journal of Great Lakes Research. Volume 41(2):405-414

Authors: J. Gobin, N.P. Lester, M.G. Fox, and E.S. Dunlop

ABSTRACT

We use fishery-independent survey data to describe trends in growth and recruitment for lake whitefish (*Coregonus clupeaformis*) in the southern main basin of Lake Huron. We also used a model selection approach to evaluate the potential contribution of key variables (population biomass, temperature, dreissenid mussel establishment in 1993, and the regime shift in 2003) to trends in growth and recruitment. Overall, mean growth of juvenile whitefish (i.e. back-calculated growth occurring between ages 1 and 2 years) has been reduced to approximately half of what it was before dreissenids invaded. The number of recruits per kg spawner biomass averaged 36.1 before dreissenids were established, 2.48 between dreissenid establishment and the regime shift, and 4.61 thereafter. Accounting for the timing of dreissenid establishment and the regime shift greatly improved the ability of both density-dependent growth and stock-recruitment relationships to explain the variation in growth and relative recruitment over time, providing evidence that both of these relationships have been altered by recent ecosystem changes. Current rates of growth and recruitment are much lower than before dreissenids became established, likely reducing the productivity of these populations, and in turn affecting sustainable harvest levels.

KEYWORDS

Density-dependent growth, Ricker stock-recruitment, dreissenids, regime shift, food web

INTRODUCTION

The Laurentian Great Lakes have undergone large-scale ecosystem changes over the last century. Invasion by sea lamprey (*Petromyzon marinus*), overharvesting, and habitat degradation impacted the Great Lakes, leading to declines and collapses of several native fish species during the 1950s and 60s (Bunnell et al. 2014). More recently, the establishment of several Ponto-Caspian invasive species has spurred further ecosystem change in several of the lakes (Vanderploeg 2002, Bunnell et al. 2014). Most notably, dreissenid mussels (*Dreissena* sp.) considerably changed the benthic invertebrate community (Pothoven et al. 2001, McNickle et al. 2006, Nalepa, Fanslow et al. 2009, Barbiero, Lesht et al. 2011), consequently altering the distribution of nutrients and energy in the lakes (Hecky et al. 2004, Nalepa, Fanslow et al. 2009, Higgins and vander Zanden 2010).

Lake Huron in particular has experienced significant change over the last decade. In 1993, dreissenid mussels invaded the lake; after which, nearshore benthic invertebrate communities became dominated by dreissenids while open-water zooplankton exhibited declines without precedent (Barbiero et al. 2009). Round goby (*Neogobius melanostomus*) invaded Lake Huron in 1997 and spread farther into the offshore as their densities increased (Schaeffer et al. 2005). In 2003, the alewife (*Alosa pseudoharengus*) population, once among the most abundant species in offshore benthic trawl catches, collapsed and has yet to recover (Riley et al. 2008, Dunlop and Riley 2013). At about the same time as the expansion of dreissenids, *Diporeia*, an important food source for fishes such as lake whitefish (*Coregonus clupeaformis*) declined in abundance (Barbiero, Balcer et al. 2011). Other fishes including lake whitefish, lake trout (*Salvelinus namaycush*), burbot (*Lota lota*) and bloater (*Coregonus hoyi*), showed declines in bottom trawl catches (Riley et al. 2008), and the numbers and characteristics of fish schools were also significantly altered (Dunlop et al. 2010). Fish distributions have also changed (Riley and

Adams 2010, Rennie et al. 2009a), signaling a spatial component to the ecosystem changes. Together, these recent changes suggest that a regime shift has occurred in Lake Huron (Riley and Adams 2010, Ridgway 2010), with potential implications for commercially important fishes.

Lake whitefish (herein referred to as whitefish) support the largest and most valuable commercial fishery in the Laurentian Great Lakes (Kinnunen 2003, Ebener et al. 2008). Most whitefish are harvested from Lake Huron where they comprise 97% of the coregonine harvest, with yields that averaged 3.2 million kg annually between 2005 and 2010 (Ebener 2013). Declines in whitefish growth have been reported for various areas of Lake Huron and for other Great Lakes' populations following reductions in their main prey, *Diporeia* (Lumb et al. 2007, Rennie et al. 2009b, Ebener 2013, Fera 2014). At the same time, trends in growth have varied widely across lakes and populations (Fera 2014). In some locations, declines in whitefish growth appear to have preceded the loss of *Diporeia* (Fera, 2014), which has been attributed to density-dependence (Kratzer et al. 2005). Following the near disappearance of *Diporeia*, whitefish switched to consuming an energetically inferior diet comprised mainly of *Dreissena* and other molluscs (Pothoven et al. 2001, McNickle et al. 2006, Pothoven and Madenjian 2008, Nalepa, Pothoven et al. 2009, Rennie et al. 2009a). It is now clear that the invasion of dreissenid mussels has had some effect on the somatic growth of whitefish in several Great Lakes, with the main mechanism likely being alterations in whitefish diets (Fera 2014). However, few studies have considered how a broad range of factors that influence growth may have changed with the loss of *Diporeia* (but see Rennie et al. 2009b).

Trends in whitefish growth and recruitment are of concern because these processes are important determinants of a fishery's productivity, and therefore influence sustainable harvest levels. Much uncertainty surrounds the future of this fishery given the substantial ecosystem changes that have taken place in Lake Huron. Our study adds to the current understanding of changes occurring in Great Lakes whitefish populations by examining how more recent ecosystem change (i.e. the regime shift) has further affected growth and recruitment for one of the most important whitefish populations in the Great Lakes. We assess the degree to which shifts in growth or recruitment coincide with two key events: the establishment of dreissenid mussels in 1993, and the regime shift that was signaled by the collapse of alewife in 2003. We also explore how ecosystem changes associated with these events may have altered density-dependence of growth and recruitment, in the southern main basin of Lake Huron.

MATERIAL AND METHODS

Data and study area

For this study we used whitefish data collected by the Ontario Ministry of Natural Resources and Forestry (OMNRF) as part of their offshore index netting survey (Speers 2013) for the QMA 4-5 management area of Lake Huron (Fig. 1). We focused on whitefish collected in this region because of the large amount of data available from the offshore index netting survey and because it supports an important commercial fishery. This offshore index netting program employs standardized monofilament gill nets consisting of a 15 m panel of 32-mm mesh (added in 2002), a 25 m panel of 38-mm mesh, and 50 m panels of 51-mm, 76-mm, 89-mm, 102-mm, 114-mm, and 127-mm mesh (stretch-measure). Typically, nets were set for 20-24 hours and are configured parallel to one another 400-600 m apart, and perpendicular to depth contours. Surveys were conducted in the spring and fall of every year from 1984-2012, with the exception of 1996 in which no surveys were conducted. The program provides a fishery-independent source of information on biological attributes of whitefish, including fork length (mm), total length (mm), round weight (g), sex, maturity status, and age.

Growth

We measured growth as the length increment between the ages of 1 and 2 years for 663 whitefish collected between the years 1985 to 2009. We chose to measure growth between these ages to avoid the bias associated with the growth cost of maturation, and some whitefish were mature by age 3 (therefore allocating energy to maturation in the year prior), particularly in earlier years of the survey. As whitefish are not fully recruited to the survey gear until after age 2, we back-calculated lengths at age from scale samples collected through the survey, using the log-log method: $L_a=L_c(S_a/S_c)^\beta$, where L_c is the fork length at capture, S_a is the scale radius at age a, S_c is the scale radius at capture, and β is the slope of the relationship between log fork length and log scale radius (Francis 1990, Dunlop and Shuter 2006). We estimated β from a linear regression of log fork length and log scale radius at capture, which included both very small and large fish (Fig. A1).

Scales were used instead of otoliths, because the latter were not available. Estimating age of whitefish using scales has been found to yield lower age estimates and higher mean back-calculated lengths at age compared to otoliths, most notably for older fish (Muir et al. 2008). Another concern when back-calculating length at age is Lee's Phenomenon, whereby older individuals consistently exhibit less growth at younger ages (Bagenal and Tesch 1978) due to the differential survival of slower growing individuals that is generally thought to be associated with a trade-off between growth and mortality (Mangel and Stamps 2001). However, others have failed to detect evidence of Lee's Phenomenon in whitefish (e.g. Kennedy, W.A. 1943, Ayles, H.A. 1976, Morin et al. 1982). To minimize these potential biases, while avoiding bias associated with the size selectivity of fishing gear used in the survey, we aimed as much as possible to use age 5 whitefish for estimating back-calculated length increments. Using younger fish would have introduced bias associated with gear selectivity, while older fish would have resulted in increasingly biased age and growth estimates from scales.

We also developed mean growth curves for whitefish ages 1-10 years for the time period before dreissenids became established, after dreissenids became established but before the regime shift, and following the regime shift in the lake. Mean lengths at age were based on back-calculated lengths at age for ages 1-5 years and on observed fork lengths for ages 6-10 years.

Recruitment, mature biomass, and total biomass

As an index of recruitment, we estimated the mean catch-per-unit-effort (CPUE) of age 4 whitefish. Mature biomass was indexed as the CPUE of the biomass of all mature fish age 4 and older, and an index of total biomass was estimated as the CPUE of the biomass of all whitefish age 4 and older. Because maturity status and weights were not available for all fish sampled through the survey, year-specific mean weights at age were used to convert abundance to biomass, and annual age-specific proportions of mature fish were used to estimate mature biomass for each net set. These biomass estimates were then summed for ages 4 and older prior to carrying out CPUE calculations. We selected age 4 as our cutoff for CPUE and biomass estimates because we were confident that fish of this age were fully recruited to the survey gear over the entire time series, whereas this may not have been true for younger whitefish (Fig. A2). CPUE was estimated as the geometric mean catch for nets set in depths between 20 m and 45 m and standardized to a 24 hour period. We excluded mesh sizes not used for the entire study period (32 mm and 140 mm panels). To account for the gear change from multi-filament to monofilament nets that occurred in 1993-1994, we applied a correction factor by multiplying the CPUE of multifilament nets by 1.8 (Collins 1979, Rennie et al. 2009b). To normalize catch data and reduce the influence of nets that caught no whitefish on CPUE estimates, we $\log_e(x+1)$-transformed whitefish abundance and biomass per net prior to taking the geometric mean.

Growing degree days (GDD)

We estimated cumulative annual growing degree days as the difference between mean daily air temperature and 5°C, summed across all days for which the mean daily temperature was at least 5°C. Mean daily temperature data were obtained from Environment Canada's National Climate Data & Information Archive (http://climate.weather.gc.ca/) for the Sarnia Airport (latitude: 42°59'32" N; longitude: 82°18'17" W). Mean daily temperatures missing from this dataset were supplemented with data from the nearest Sarnia weather station (latitude: 42°59'58" N; longitude: 82°18'32" W and latitude: 43°00'00" N; longitude: 82°18'00" W) as necessary. The weather stations selected are the closest to the areas of southern Lake Huron where the offshore surveys were conducted. We chose the base temperature of 5°C to be consistent with previous studies examining effects of temperature on whitefish (e.g. Rennie et al. 2009b).

Statistical analysis

We used a model selection approach to examine whether including temperature or accounting for the timing of two key events (dreissenid mussel establishment in 1993 and the regime shift marked by the collapse of alewife in 2003), improved our ability to explain trends in density-dependent growth and stock-recruitment relationships. Growth and recruitment models were ranked using corrected Akaike's Information Criterion (AICc). Models with the lowest AICc values were identified as the highest ranked models. Models within ΔAICc ≤ 2 were considered to be strong models and comparable to the highest ranked model, whereas those with ΔAICc between 2 and 4 of the highest ranked model were considered to have moderate support (Burnham and Anderson 2002).

The basic growth model took the form of $h = a - b * \ln(total\_biomass)$, where h is length increment, *total_biomass* is the CPUE of the biomass of whitefish ages 4 and older, and a and b

are parameters. This model was chosen to allow growth to decrease as a function of biomass. Time series data available for the basic growth model spanned from 1985 to 2009. We compared this model with four alternative models: a model that (1) included *time_period* as a factor with three levels (before dreissenid establishment and before the regime shift [1985-1992], after dreissenid establishment and before the regime shift [1993-2002], and after dreissenid establishment and after the regime shift [2003-2009]), (2) included *time_period* and an interaction term *total_biomass*time_period*, (3) included temperature (cumulative *GDD* in the year of growth), and (4) included *GDD* and the interaction term *total_biomass*GDD*.

We selected these alternative models, to compare with the basic growth model, based on their potential biological relevance and the data available. The time period model was fitted to test the hypothesis that ecosystem changes associated with the establishment of dreissenids and the 2003 regime shift may have affected the availability of resources for whitefish and in turn altered the relationship between population density and growth. We also fit the time period model with an interaction term between biomass and time period in case ecosystem changes not only affected maximum potential growth in the density-dependent growth relationship (i.e. the intercept), but also the way in which growth varies with density (i.e. the slope). We included temperature models because of the large role temperature plays in the growth of ectotherms and because annual data were readily available. In the models we used cumulative annual GDD based on air temperatures because GDD is more biologically relevant to fish growth than other metrics such as mean daily temperature (Neuheimer and Taggart 2007, Venturelli et al. 2010), and because water temperature data were not available. Because effects of temperature on growth can also be influenced by changes in resource availability due to differences in population density (Baerum et al. 2013), we also fit a temperature model with a biomass*GDD interaction term. Alternative models were limited to 3 predictor variables or less due to the length of the time series for which data were available.

The recruitment model took the form of a linearized Ricker model (Hillborn and Walters 1992). We used a Ricker model because density-dependent recruitment has been demonstrated in whitefish (e.g. Bidgood 1973, Brown et al. 1993, Mills et al. 1995, Kratzer et al. 2007), and this stock-recruitment relationship has been used when modeling whitefish populations dynamics in stock assessment models (Ebener et al. 2005). The Ricker equation, $R = aSe^{-\beta S}$, predicts density-dependent recruitment (R) resulting in reduced recruitment at high spawner biomass (S). Here we use the linear form of this equation: $\ln(R/S) = \ln(\alpha)-\beta S$, which predicts a linear decline in the natural log of relative recruitment (recruits per unit spawner biomass) with increasing spawner biomass. Using this form of the equation simplified the model selection analysis by allowing us to fit and compare linear models instead of non-linear models. Recruits were measured as the CPUE of the abundance of age 4 whitefish. Because whitefish spawn and lay eggs in the fall that hatch the following spring, we offset spawning biomass by 5 years to match recruits with the spawning stock that would have produced them. Once data were offset, the years of recruitment data represented in the models were from 1990 to 2012. We also compared this model to models that included a *time_period* factor, a *time_period* factor with a *mature_biomass*time_period* interaction term, cumulative *GDD* in the year eggs were laid, and GDD with a *mature_biomass*GDD* interaction term.

A potential limitation of our analyses was that we used different ages to characterize growth (ages 1-2 years) versus biomass (ages 4 years plus). Ideally, we would have preferred to use similar ages because growth is likely to be influenced by the biomass of whitefish that are of similar size and age and therefore feeding on similar prey. This wasn't possible because whitefish were not fully recruited to the gear prior to age 4, whereas growth could be biased for ages above 3 because of maturation. To determine if the choice of ages considered had an effect, we also repeated our growth analyses with weight increment measured between ages 2 and 3 years old and total biomass represented by the CPUE of the biomass of whitefish ages 3 and older. Similarly, for our recruitment model, we also repeated our model selection analysis with recruitment measured as the abundance of age 3 whitefish and mature biomass represented by the CPUE of mature fish ages 3 and older. These results are included in the Appendix.

RESULTS

Growth

Growth of whitefish between ages 1 and 2 increased between 1985 and 1987, and fluctuated with a general decline from 1987 to 2004 (Fig. 2). During the latter period, the average growth increment decreased from approximately 110 mm to 50 mm, but since 2004, has remained relatively stable or increased slightly.

Mean lengths at age were highest across all ages during the earliest time period (before dreissenids established) and were generally lowest during the most recent time period (after the regime shift). Mean lengths at age differed most for whitefish ages 2 to 8, whereas mean lengths at ages 1, 9, and 10 were fairly similar across the three time periods (Fig. 3).

Of the density-dependent growth models compared, the highest ranked model was that which included *ln(total_biomass)* and *time_period* as predictor variables (Table 1) and explained 77% of the variation in growth. The addition of the *ln(total_biomass)*time_period* interaction term to this model explained only slightly more variation (79%), resulting in a model with moderate support. In comparison, the basic density-dependent model and those including *GDD* were very poorly supported and explained little variation in growth (<10%). When we repeated this analysis using back-calculated growth increment between the ages of 2 and 3 years, we obtained similar results (Table A1).

When considered across the entire time period, no relationship between total biomass and growth is apparent (Fig. 4). This also appears to be the case when we examine the pre-dreissenid and post-regime shift time periods individually, whereas the post-dreissenid and pre-regime shift time periods together actually appear to show a positive relationship between total biomass and growth (slope = 6.96, $F_{1,7} = 25.58$, $R^2 = 0.75$, $P < 0.002$). It is apparent that any relationship between growth and biomass appears to have changed, with the overall height of the relationship shifting downwards with each subsequent time period (Fig. 4).

Recruitment

Recruitment peaked and fluctuated greatly during the early to mid-1990s (Fig. 5a). After 1996, recruitment declined and remained relatively low, perhaps increasing slightly from the early 2000s until 2012. Trends in recruitment appear to reflect trends in relative recruitment (i.e. recruits per kg of spawner biomass) (Fig. 5b). Relative recruitment was highest during the pre-dreissenid period, lowest during the time period after dreissenids became established and before the regime shift, and increased after the regime shift.

The highest ranked Ricker stock-recruitment model included a *time_period* factor (Table 2) and explained 40% of the variation in relative recruitment. This model explained twice as much variation as the basic Ricker model, which was also strongly supported. The model that also included *GDD* and the *mature_biomass*GDD* interaction was moderately supported. The remaining two models were poorly supported, although the model with *time_period* and the *mature_biomass*time_period* interaction explained the most variation (45%) of all models compared (Table 2). Repeating the recruitment model analyses and including age 3 whitefish yielded results consistent with those above (Table A2). The model with time period remained the highest ranked model but explained slightly more of the variation in relative recruitment. In this case, the model that also included *GDD* and the *mature_biomass*GDD* interaction term was also strongly supported whereas the basic Ricker model and that which included *time_period* and the *mature_biomass*time_period* interaction term were moderately supported.

As was the case with density-dependent growth, the pattern of relative recruitment also changed over time. Although distinct linear relationships between ln(relative recruitment) and spawner biomass are not apparent, relative recruitment at low spawner biomass is highest during the pre-dreissenid period, lowest after dreissenids became established but before the regime shift, and slightly higher following the regime shift (Fig. 6).

DISCUSSION

Lake whitefish in the southern main basin of Lake Huron exhibited substantial changes through time with respect to both growth and recruitment. Overall, mean growth of juvenile whitefish declined over time, and in recent years has been reduced to approximately half of what it was during the mid to late 1980s when at its highest (Fig. 2). Similarly, recruitment has been consistently low over the last ten to fifteen years compared to during the first half of the 1990s, when recruitment of whitefish peaked (Fig. 5). The number of recruits per kilogram of spawner biomass averaged 36.1 before dreissenids were established, 2.48 between dreissenid establishment and the regime shift, and 4.61 thereafter. Signs of recovery in whitefish growth and recruitment are apparent in the most recent years of the time series, albeit to lower levels than before dreissenids invaded.

Density-dependent growth and stock-recruitment relationships can change temporally. This is contrary to the assumption often made when estimating a single set of parameters for these relationships over extended periods of time (Walters 1987, Walters and Martell 2004). For stock-recruitment relationships, environmental factors that change over time and affect recruitment independently of spawning stock size may also correlate with subsequent stock sizes. As a result, large deviations from the stock-recruitment relationship due to environmental effects can lead to biased parameter estimates that often overestimate productivity at low stock sizes and underestimate productivity at high stock sizes, when based on historical data for natural populations (Walters 1985). We can also expect that density-dependent relationships could similarly be affected by ecosystem change that alters the availability of resources, thus changing how stock size impacts growth or recruitment. Ecosystem changes such as those that occurred in Lake Huron can be complex; furthermore, annual estimates of the variables that might affect growth or recruitment could be unavailable, making them difficult to include in statistical models. Certain variables might also become more or less important through time as ecosystem conditions change, thus altering the shape or strength of density-dependence.

While we detected only weak density-dependence in growth at best before dreissenids became established, this relationship clearly changed following dreissenid establishment (Fig. 4). Following declines in *Diporeia* abundance, whitefish switched to feeding on dreissenids, a lower energy food source (Pothoven et al. 2001, McNickle et al. 2006, Pothoven and Madenjian 2008, Nalepa, Pothoven et al. 2009, Rennie et al. 2009a). Whitefish were consuming prey that are energetically inferior, with lower conversion efficiencies and at a higher cost due to increased foraging activity (Rennie et al. 2012). Declines in whitefish growth that occurred in other locations have therefore been attributed to decreases in the availability and consumption of high energy prey (Lumb et al. 2007, Lumb and Johnson 2008, Pothoven and Madenjian 2008, Herbst et al. 2013). Previous studies in the upper Great Lakes suggested that declines in whitefish growth due to increases in whitefish densities that already began prior to the dreissenid invasion, were then exacerbated by declines in *Diporeia* after dreissenids became established (Kratzer et al. 2005, Wright and Ebener 2005). Our data suggest a different interpretation, namely that high whitefish density possibly exacerbated the effect of dreissenids on whitefish, given the weak effect of density on both growth and recruitment prior to the establishment of dreissenids. Following the establishment of dreissenids and the loss of *Diporeia*, the ecosystem appears to have changed so as to alter the carrying capacity for whitefish and the resulting relationship between growth and population density.

As was the case with growth, density-dependent recruitment also appears to have changed across the various time periods. The *mature_biomass* + *time_period* model predicted a negative relationship between relative recruitment and spawner biomass as would be expected from a Ricker stock-recruitment relationship (Table 2). Density-dependent recruitment in whitefish has previously been demonstrated for populations within and outside of the Great Lakes (e.g. Bidgood 1973, Brown et al. 1993, Mills et al. 1995, Kratzer et al. 2007, reviewed in Muir 2008). Several studies have hypothesized that food web changes since the establishment of dreissenids in the Great Lakes have negatively impacted whitefish reproduction and survival (Mills et al. 1993, Hoyle et al. 2003, Pothoven et al. 2001, Hoyle et al. 2005, reviewed in Muir 2008, but see Kratzer et al. 2007). Decreased consumption of high energy food sources could affect the condition of whitefish, and negatively impact whitefish fecundity or the quality of offspring produced. However, Fagan et al. (2012) found no consistent evidence to suggest that changes in the quality of prey consumed influenced whitefish condition in Lake Michigan. Furthermore, Muir et al. (2014) found that female whitefish in poorer condition generally produced eggs of similar quality to those in better condition, by making larger tradeoffs among egg size and fecundity, lipids, and fatty acids provisioned to their eggs. Claramunt et al. (2010) similarly concluded that declines in whitefish condition are unlikely to impact recruitment, which could be due to total reproductive investment being more highly associated with adult size than condition (Muir et al. 2014). Our growth curves show that whitefish experiencing the largest decreases in size at age are those of ages that are maturing or would have recently matured, and which typically comprise the bulk of the spawning stock biomass in a population (Fig. 3).

Alternatively, dreissenids could also affect recruitment through direct effects on the prey of very young whitefish. Prey availability affected larval survival in Lake Michigan whitefish (Freeberg et al. 1990), as well as larval whitefish growth in Lake Ontario (Hoyle et al 2011), and in both cases these affected recruitment. Interestingly however, back-calculated mean length of age 1 whitefish in the southern main basin of Lake Huron does not appear to have changed suggesting that either growth of young-of-year whitefish has not been affected by recent ecosystem changes or that obtaining some minimum size is essential to survival past the first year of life (Fig. 3). The collapse of alewife could also have implications for the survival of now slower growing younger age classes of whitefish, which are vulnerable to predation by recovering walleye and lake trout populations due to a lack of alternative prey (He et al. 2015).

Although we lack sufficient data for the pre-dreissenid period to directly compare the stock-recruitment relationship before dreissenids invaded with that after dreissenids became established, the lower intercept for post-dreissenid time periods in the *mature biomass* + *time period* model suggests that either the number of offspring being produced or juvenile survival could have decreased after dreissenids became established. Prey availability could also play a role in the movement and distribution of whitefish in the lake, which could influence growth or estimates of recruitment. However, data collected from a mark-recapture study conducted in the early 2000s suggest that whitefish in Lake Huron are essentially divided into northern and southern meta-populations separated by the Amberly-Alpena Ridge (Ebener, M., personal communication). In that study, tags recovered in the southern main basin were mainly deployed in the south (Sarnia), with some originating from the western shore of the main basin (Alpena and Saginaw Bay) (Ebener, M., personal communication). Whether whitefish movement and distribution within Lake Huron shifted with changes in the densities of whitefish, *Diporeia*, and round goby, are also unclear.

Initial declines in growth and recruitment coincided with dreissenid establishment, but there have been signs of stabilization or even slight recovery of both of these variables in recent years (Figs. 2 and 5). These most recent changes in whitefish have also occurred despite further ecosystem changes that might be expected to negatively impact whitefish, namely further declines in primary productivity and changes in zooplankton communities towards a greater resemblance to those in Lake Superior (Barbiero et al. 2012). With reductions in the magnitude of the spring phytoplankton bloom in Lake Huron that began in 2003, cladoceran and cyclopoid copepod populations have declined (Barbiero, Lesht et al. 2011); both of which likely constitute important prey sources for age-0 whitefish (Pothoven et al. 2014).

In various parts of Lake Huron, adult whitefish are consuming fewer dreissenid mussels and more round gobies in recent years, which could constitute a higher energy prey item for whitefish (Pothoven and Madenjian 2013). The round goby became established in Lake Huron in 1997 and increased in abundance in the nearshore until about 2001. In the offshore, round goby abundance continues to increase (Schaeffer et al. 2005), although variability in catches can be high (Riley et al. 2014). Offshore, round gobies prey on native invertebrates such as *Mysis relicta*, deepwater amphipods, and fingernail clams (Sphaeriidae) (Schaeffer et al. 2005); these invertebrates are also preyed upon by whitefish (Pothoven et al. 2001, Nalepa, Pothoven et al. 2009). More recently however, distributional overlap between whitefish and round goby, particularly in winter, has been proposed to facilitate piscivory on round goby (Lehrer-Brey and

Kornis, 2014). Increased consumption of round goby by whitefish in southern Lake Huron is not as extensive as in the central part of the lake, and only occurs seasonally during the winter and spring (Pothoven and Madenjian 2013). Furthermore, these changes have yet to influence whitefish condition (Pothoven and Madenjian 2013). As piscivory in whitefish is also limited to those large enough to consume fish (> 400 mm – 450 mm) (Pothoven and Madenjian 2013, He et al. 2015), it is not clear whether it could explain any of the recent signs of recovery in juvenile growth and recruitment.

Generally, temperature did not add much explanatory power to growth and recruitment models. Other studies have found diet and prey availability better explain growth of Great Lakes whitefish than temperature. In their bioenergetics modeling of growth of whitefish from Lakes Erie and Ontario, Lumb and Johnson (2012) found that growth was 6 to 10 times more sensitive to diet composition than temperature. Similarly, Rennie (2009b) found that only in the absence of *Diporeia* did environmental variables best explain growth of whitefish. In our study, effects of temperature on growth could have been masked by the effects of the other ecosystem changes taking place. Interestingly, our recruitment model selection results suggest that temperature might have influenced recruitment, but that its effect may have changed with spawner biomass. The model with the *GDD*mature biomass* interaction term consistently ranked higher and explained over 10% more of the variation in relative recruitment than the *mature biomass* + *GDD* model without the interaction term (Tables 2 and A2). Temperature and climatic factors can influence recruitment of young whitefish. For example, air temperatures in May and the number of days of ice cover positively influenced recruitment of whitefish in Lake Michigan (Brown et al. 1993). Muir (2008) also found a thermal regime model in which density-dependent mortality was compensated for in favorable years but compounded in unfavourable years, to best fit larval and juvenile whitefish pre-recruit data for Lakes Michigan and Superior. Conversely, Claramunt et al. (2010) found neither length nor density of larval lake whitefish in Lake Michigan were regulated by temperature.

Our study was limited by the length of the time series, particularly for pre-dreissenid years. We could therefore only reasonably compare models with a limited number of parameters (i.e. ≤ 3 predictor variables). We took precautions to ensure as much as possible that CPUE estimates were comparable across years for the duration of the time series (e.g. excluding mesh sizes not used in all years and omitting fish of ages that may not have been fully recruited to the gear over the entire time series). However, other factors affecting catchability of whitefish in the index nets could affect CPUE estimates. For example, clogging of nets by *Cladophora* spp. (Ebener 2013), changes in water clarity, or changes in whitefish distribution beyond where nets are set could alter the relationship between CPUE and population abundance.

The declines in growth and recruitment we observed could impact fishery yields for whitefish in Lake Huron. Reductions in growth and recruitment signal possible declines in the carrying capacity of whitefish and are likely to reduce the harvest that can be sustainably fished from Lake Huron. There is no doubt that the ecosystem of Lake Huron is much different than it was even 10 or 20 years ago, and it should be expected that the fisheries resources that inhabit that system will be impacted. Additionally, the proportion of the whitefish population vulnerable to harvest is lower based on the reduced growth rates. Notably, whitefish that are 43-45 cm in length are already difficult to market, leading to an ad-hoc increase in the minimum size limit for commercial trap net fisheries in many areas (Ebener 2008). Systemic reductions in recruitment are expected to alter stock sizes, which could eventually translate into reduced catches. While whitefish yields in Lake Huron still averaged 3.2 million kg/year from 2005-2010, this is down from over 4 million kg/year during the late 1990s (Ebener 2013). Ebener (2013) notes, however, that these yields have also been affected by factors that are unrelated to whitefish abundance such as reduced fishing effort.

He et al. (2015) highlight the importance of whitefish as a new major piscivore and the primary consumer of round goby in Lake Huron. As they note however, strong year classes of whitefish that occurred during the 1990s are partly responsible for current high levels of predation of whitefish on round goby (He et al. 2015). Without further recovery of whitefish recruitment to levels observed in the past, the predation pressure by whitefish on gobies may subside somewhat and have implications for the effect of round goby on the Lake Huron food web.

The observed variability in whitefish dynamics and harvest among the Great Lakes could be due to a variety of factors such as lake size or the extent and time course of ecosystem changes. Complex interactions among factors such as nutritional status, disease dynamics, and natural mortality could also contribute to both spatial and temporal trends in whitefish populations (Wagner et al. 2010). Whitefish yields in Lake Ontario declined significantly following the dreissenid invasion (Hoyle et al. 2008) whereas in Lake Michigan, yields actually increased by 13% to an average of 2.3 million kg between 2005 and 2010 when compared to the previous reporting period (Clapp et al. 2012). In Lake Huron, where the recent ecosystem changes have been profound, the commercial yields that were possible in the past might not be possible today. This is similar to the conclusions drawn by Hoyle et al. (2008) for Lake Ontario. The fish community objective for coregonine harvest in Lake Huron was set at 3.8 million kg in the 1990s when whitefish yields were at historical highs (DesJardine et al. 1995). Given the changes to system carrying capacity and the recent dynamics of Lake Huron whitefish, these yield objectives may no longer be achievable.

ACKNOWLEDGMENTS

Funding for this work was provided by the Canada-Ontario Agreement Respecting the Great Lakes Basin Ecosystem, the Great Lakes Fishery Commission, and the Invasive Species Centre. We also thank Jim Johnson and several anonymous reviewers; whose suggestions greatly improved our paper.

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Table 1.1. Comparison of density-dependent growth models describing trends in the back-calculated length increment of Lake Huron lake whitefish between ages 1 and 2 years old using Akaike's Information Criterion corrected for small-sample bias (AICc). Growth model parameters include: natural log-transformed CPUE of the biomass of whitefish ages 4 years and older (ln(total biomass)); a time period factor for years before dreissenids invaded (pre), after dreissenids became established but before the regime shift signaled by the alewife collapse (post/pre), and after the regime shift (post); and cumulative growing degree days in the year of growth (GDD).

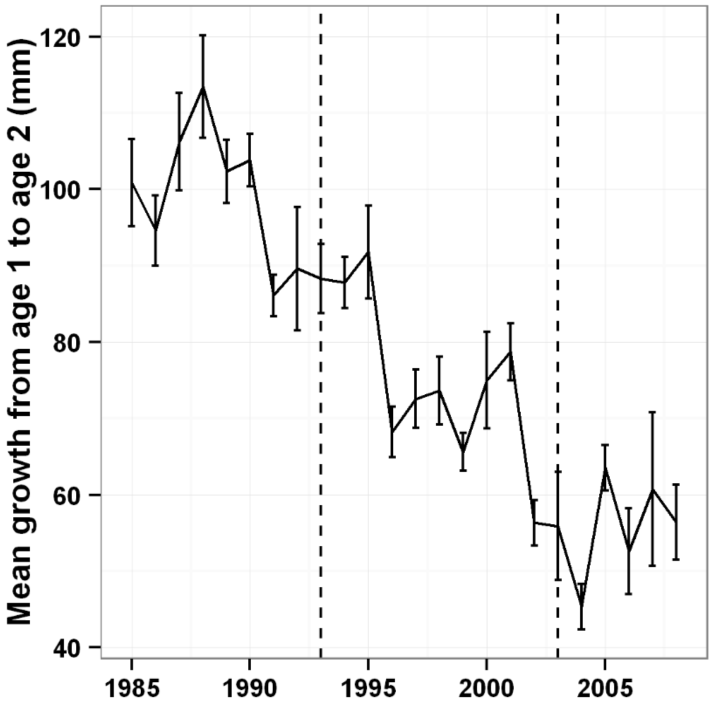
Rank	Growth Model	Variable	Coefficient	df	logLik	AICc	delta	Adj. R2
1	*ln(total biomass) + time period*	*ln(total biomass)*	0.16	3	-82.30	178.12	0	0.77
		time period (pre)	97.75					
		time period (post/pre)	75.23					
		time period (post)	55.45					
2	*ln(total biomass) + time period + ln(total biomass)* time period*	*ln(total biomass) (pre)*	-0.14	5	-79.63	180.73	2.61	0.79
		ln(total biomass) (post/pre)	0.54					
		ln(total biomass) (post)	0.19					
		time period (pre)	99.79					
		time period (post/pre)	70.69					
		time period (post)	55.16					
3	*ln(total biomass)*	*intercept*	75.26	1	-99.18	205.62	27.50	0.08
		ln(total biomass)	0.48					
4	*ln(total biomass) + GDD*	*intercept*	114.84	2	-98.87	207.95	29.83	0.06
		ln(total biomass)	0.45					
		GDD	-0.02					
5	*ln(total biomass) + GDD + ln(total biomass)*GDD*	*intercept*	111.72	3	-99.94	213.42	35.3	-0.08
		ln(total biomass)	18.34					
		GDD	-0.01					
		*GDD*ln(total biomass)*	-0.01					

Table 1.2. Comparison of linear Ricker stock-recruitment models describing trends in natural log-transformed relative recruitment (ln(R/S)) of age 4 Lake Huron lake whitefish using Akaike's Information Criterion corrected for small-sample bias (AICc). Relative recruitment model parameters include: CPUE of the biomass of mature whitefish ages 4 years and older (*mature biomass*); a *time period* factor for years before dreissenids invaded (pre), after dreissenids became established but before the regime shift signaled by the alewife collapse (post/pre), and after the regime shift (post); and cumulative growing degree days in the year eggs were laid (*GDD*).

Rank	**Recruitment Model**	**Variable**	**Coefficient**	**df**	**logLik**	**AICc**	**delta**	**Adj. R2**
1	*mature biomass +*	*mature biomass*	-0.07	3	-37.25	88.50	0	0.40
	time period	*time period (pre)*	2.80					
		time period (post/pre)	-0.50					
		time period (post)	0.81					
2	*mature biomass*	*intercept*	0.79	1	-41.45	90.31	1.81	0.20
		mature biomass	-0.13					
3	*mature biomass +*	*intercept*	11.44	3	-38.92	91.85	3.35	0.30
	GDD +	*mature biomass*	-2.15					
	*mature biomass*GDD*	*GDD*	-0.005					
		mature biomass	0.0008					
4	*mature biomass + time period +*	*mature biomass (pre)*	-1.69	5	-35.09	92.80	4.30	0.45
	*mature biomass*time period*	*mature biomass (post/pre)*	-0.06					
		mature biomass (post)	-0.47					
		time period (pre)	3.70					
		time period (post/pre)	-0.61					
		time period (post)	1.22					
5	*mature biomass +*	*intercept*	4.34	2	-41.28	93.08	4.58	0.17
	GDD	*mature biomass*	-0.12					
		GDD	-0.002					

Figure 1.1. Map of Lake Huron management areas, highlighting the source of data used for this study. Quota management areas (QMAs) are shown, with QMA 4-5, the source of data for the current study, highlighted in grey.

Figure 1.2. Temporal trends in juvenile growth of lake whitefish for 1985 to 2007. Juvenile growth here is represented by the back-calculated mean length increment of whitefish between 1 and 2 years of age. Standard error bars are shown. Dotted lines at 1993 and 2003 mark the timing of dreissenid establishment and the regime shift in southern Lake Huron, respectively.



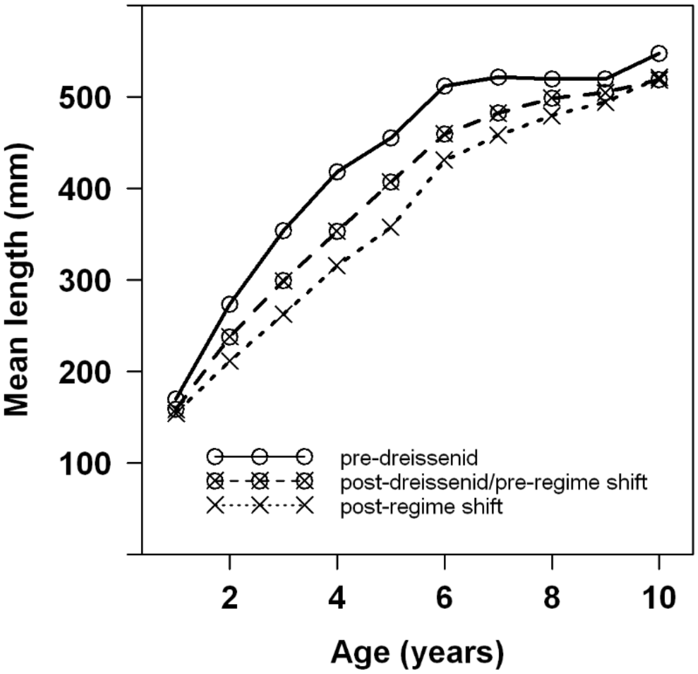


Figure 1.3. Mean growth curves of lake whitefish for three time periods: before dreissenids became established (1984-1992), after dreissenids became established but before the regime shift (1993-2002), and following the regime shift (2003-2009). Mean lengths are based on back-calculated lengths at age for ages 1-5 years and on observed fork lengths for ages 6-10 years.

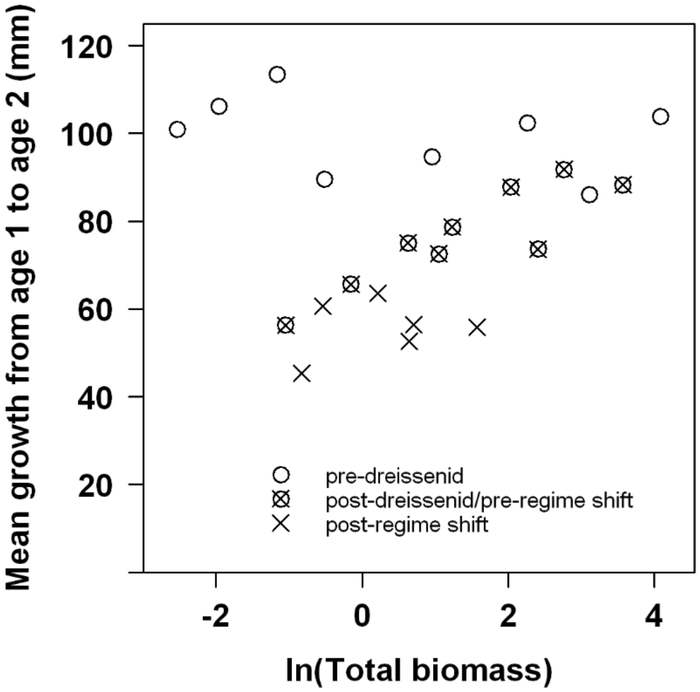
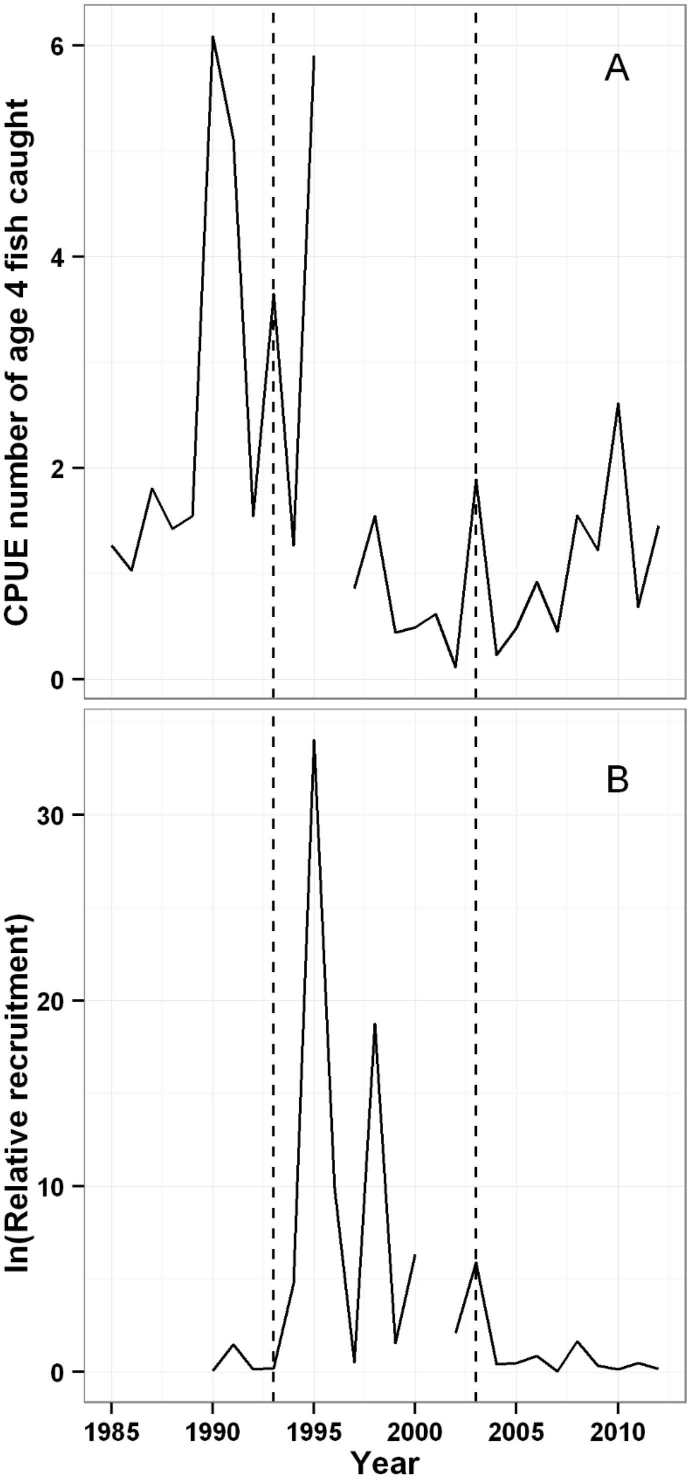


Figure 1.4. The relationship between growth and mean catch per unit effort of total biomass for three time periods: before dreissenids became established (1985-1992), after dreissenids became established but before the regime shift (1993-2002), and following the regime shift (2003-2008). Note that no data were available for 1996.

Figure 1.5. Temporal trends in a) recruitment of age 4 whitefish from 1985-2012 and b) relative recruitment (ln(*R*/*S*)) from 1990-2012. CPUE is catch-per–unit-effort. Relative recruitment is measured as (ln(*R*/*S*)), where *R* is recruitment indexed as the CPUE of age 4 whitefish and *S* is spawner biomass indexed as the CPUE of the biomass of mature whitefish ages 4 and older. Dotted lines at 1993 and 2003 mark the timing of dreissenid establishment and the regime shift, respectively.



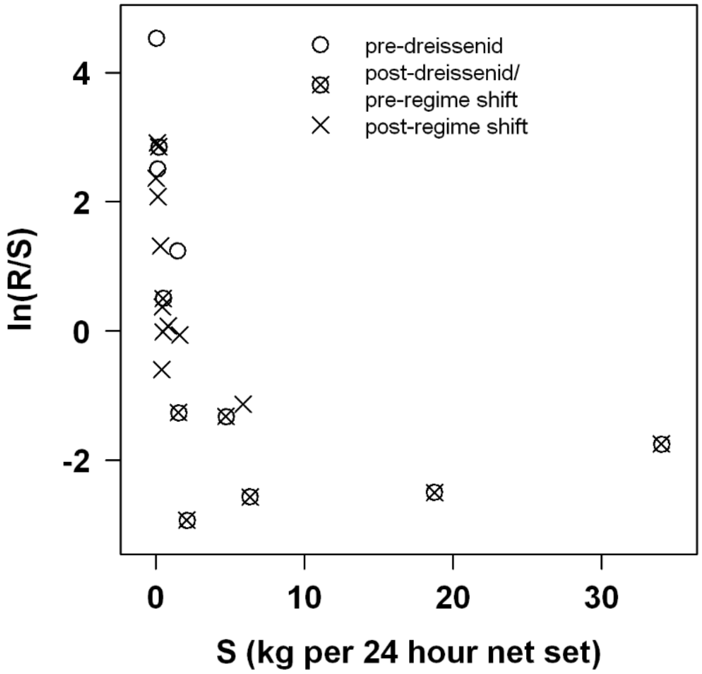


Figure 1.6. The relationship between relative recruitment (ln(*R*/*S*)) and spawner biomass (*S*). *R* is recruitment indexed as the mean catch-per-unit-effort (CPUE) of age 4 whitefish. Spawner biomass (*S*) is indexed as the CPUE of the biomass of mature whitefish ages 4 and older. Three time periods are shown: before dreissenids became established (1990-1992), after dreissenids became established but before the regime shift (1993-2002), and following the regime shift (2003-2012). Note that indices of either *R* or *S* were unavailable for 1996 or 2001.

APPENDIX 1.1. SUPPLEMENTARY TABLES AND FIGURES

Table. A1 Comparison of density-dependent growth models describing trends in the back-calculated length increment of Lake Huron lake whitefish between ages 2 and 3 years old using Akaike's Information Criterion corrected for small-sample bias (AICc). Growth model parameters include: natural log-transformed CPUE of the biomass of whitefish ages 4 years and older (*ln(total biomass)*); a *time period* factor for years before dreissenids invaded (pre), after dreissenids became established but before the regime shift signaled by the alewife collapse (post/pre), and after the regime shift (post); and cumulative growing degree days in the year of growth (*GDD*).

Rank	**Growth Model**	**Variable**	**Coefficient**	**df**	**logLik**	**AICc**	**delta**	**Adj. R2**
1	*ln(total biomass) + time period*	*ln(total biomass)*	0.16	3	-72.54	158.84	0	0.76
		time period (pre)	74.81					
		time period (post/pre)	55.82					
		time period (post)	44.00					
2	*ln(total biomass) + time period + ln(total biomass)* time period*	*ln(total biomass) (pre)*	0.06	5	-70.33	162.66	3.82	0.78
		ln(total biomass) (post/pre)	0.45					
		ln(total biomass) (post)	2.22					
		time period (pre)	76.07					
		time period (post/pre)	53.27					
		time period (post)	40.30					
3	*ln(total biomass)*	*Intercept*	58.25	1	-88.27	183.88	25.04	0.09
		ln(total biomass)	0.37					
4	*ln(total biomass) + GDD*	*Intercept*	80.93	2	-88.09	186.53	27.69	0.06
		ln(total biomass)	0.36					
		GDD	-0.01					
5	*ln(total biomass) + GDD + ln(total biomass)*GDD*	*Intercept*	101.74	3	-87.73	189.21	30.37	0.04
		ln(total biomass)	-2.84					
		GDD	-0.02					
		*GDD*ln(total biomass)*	0.001					

Table A2. Comparison of linear Ricker stock-recruitment models describing trends in natural log-transformed relative recruitment (ln(R/S)) of age 3 Lake Huron lake whitefish using Akaike's Information Criterion corrected for small-sample bias (AICc). Relative recruitment model parameters include: CPUE of the biomass of mature whitefish ages 3 years and older (*mature biomass*); a *time period* factor for years before dreissenids invaded (pre), after dreissenids became established but before the regime shift signaled by the alewife collapse (post/pre), and after the regime shift (post); and cumulative growing degree days in the year eggs were laid (*GDD*).

Rank	**Recruitment Model**	**Variable**	**Coefficient**	**Df**	**logLik**	**AICc**	**delta**	**Adj. R2**
1	*mature biomass +*	*mature biomass*	-0.09	3	-39.11	91.98	0	0.50
	time period	*time period (pre)*	3.28					
		time period (post/pre)	0.25					
		time period (post)	1.5					
2	*mature biomass +*	*Intercept*	11.27	3	-40.01	93.78	1.80	0.46
	GDD +	*mature biomass*	-1.43					
	*mature biomass*GDD*	*GDD*	-0.004					
		*GDD*mature biomass*	0.0005					
3	*mature biomass*	*Intercept*	1.57	1	-43.50	94.32	2.34	0.33
		mature biomass	-0.12					
4	*mature biomass +*	*mature biomass (pre)*	-0.31	5	-36.23	94.46	2.48	0.57
	time period +	*mature biomass (post/pre)*	-0.07					
	*mature biomass*time period*	*mature biomass (post)*	-1.45					
		time period (pre)	4.44					
		time period (post/pre)	0.01					
		time period (post)	2.37					
5	*mature biomass +*	*Intercept*	-2.35	2	-43.20	96.75	4.77	0.31
	GDD	*mature biomass*	-0.12					
		GDD	0.002					

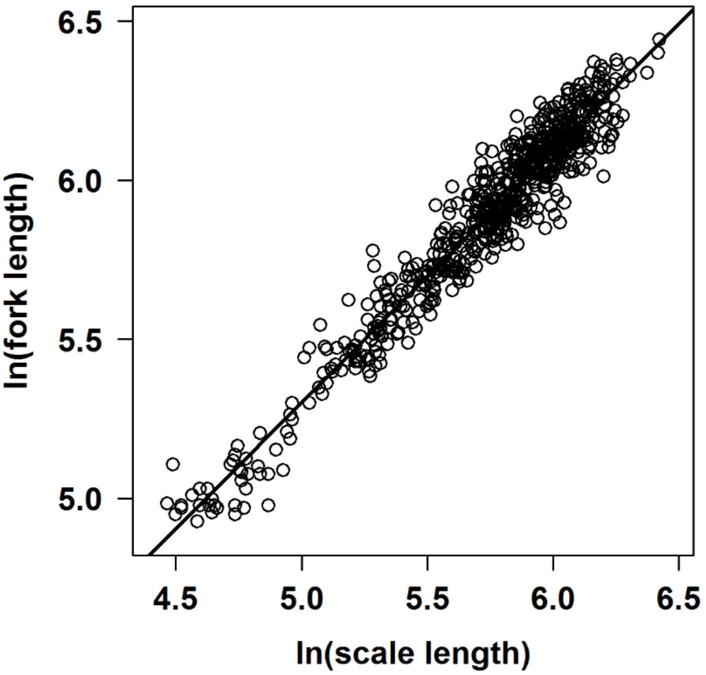
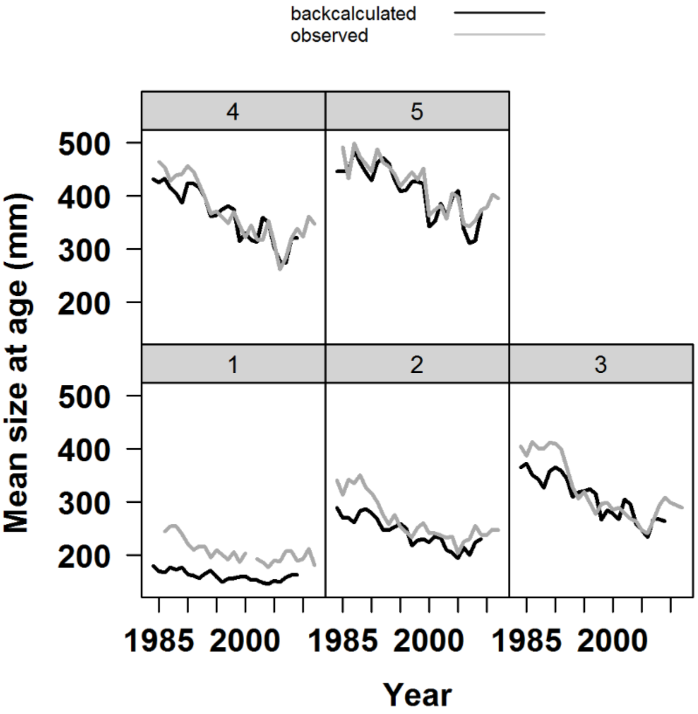


Figure A1. Relationship between fork length (mm) and scale length (pixels) (slope = 0.79, $F_{1, 657}$ = 9848, R^2= 0.94, $P<0.0001$) used for back-calculating length at age from scales using the log-log allometric method.

Figure A2. Annual catch curves for age 1 to 10+ whitefish collected through the offshore index netting survey. Dotted line marks age 4 whitefish in each panel.



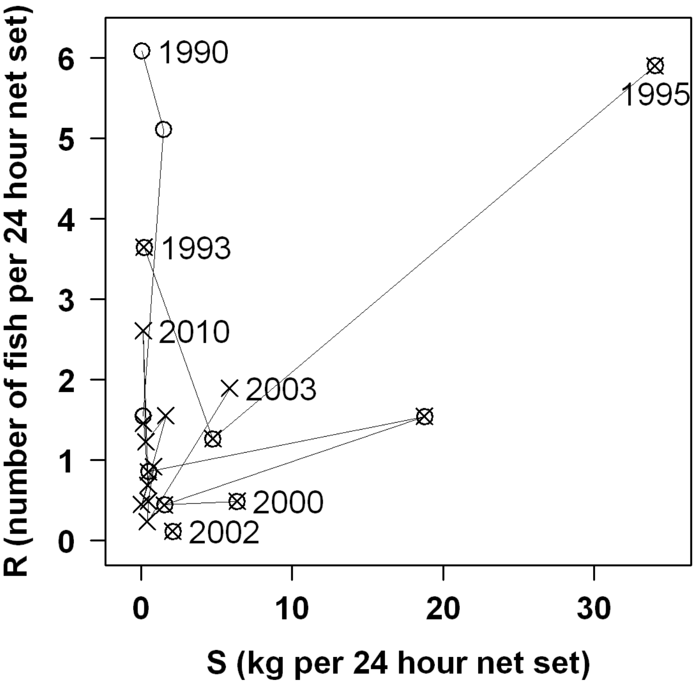


Figure A3. The relationship between recruitment (*R*) and mean catch-per-unit-effort of mature biomass (*S*) for three time periods: before dreissenids became established (1990-1992), after dreissenids became established but before the regime shift (1993-2002), and following the regime shift (2003-2012). Note that indices of either *R* or *S* were unavailable for 1996 or 2001. Line connects consecutive years in the time series.

CHAPTER 2: EFFECTS OF CHANGES IN DENSITY-DEPENDENT GROWTH AND RECRUITMENT ON SUSTAINABLE HARVEST OF LAKE WHITEFISH

This chapter has been published in the Journal of Great Lakes Research. Volume 42(4):871-882

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ABSTRACT

Substantial declines in growth and recruitment of lake whitefish (*Coregonus clupeaformis*) and changes in key density-dependent relationships since the 1990s have raised concerns about the effects of these changes on valuable commercial fisheries in Lake Huron. There is evidence that for lake whitefish in the southern main basin of Lake Huron, growth and recruitment rates have been reduced by up to 50%. Using a life history model parameterized from fishery-independent survey data for lake whitefish, we investigated the effects of declines in growth and recruitment rates on population dynamics and sustainable harvest. We evaluated a baseline scenario characterized by high growth and recruitment rates, an alternative scenario with a reduced growth rate, and another alternative scenario in which both growth and recruitment rates were reduced. Yield consistently declined by at least 71% in both alternative scenarios compared to the baseline scenario. Harvest also became unsustainable when both growth and recruitment rates were reduced, and the maximum instantaneous fishing mortality rate exceeded 0.5. Our results suggest that the recent reductions in growth and recruitment observed in Lake Huron are of sufficient magnitude to alter productivity and reduce how much can be sustainability harvested from these stocks.

KEYWORDS

Lake Huron, regime shift, dreissenids, fisheries yield, life history, individual-based model

INTRODUCTION

Density-dependence plays an important role in regulating populations by acting on key processes such as growth and recruitment. Density-dependent growth is a common process regulating fish populations and occurs when individuals compete for limited food resources (Lorenzen and Enberg, 2002). Density-dependence in recruitment can result from increased competition among larval fish, increased competition for spawning opportunities, or cannibalism of juveniles by adults (Wootton, 1998). Density-dependent growth and recruitment processes also interact (Lester et al., 2014). Recruitment influences growth through its effect on population density (Brodin and Johansson, 2002). At the same time, growth can affect the survival of recruits via size-dependent predation (Craig et al., 2006). Furthermore, somatic growth influences not only spawning stock biomass, but also individual reproductive output through the size-dependent nature of maturation and fecundity (Enberg et al., 2012).

The availability of resources in an environment (e.g. food, habitat, etc.) determines a populations' carrying capacity, and has direct implications for density dependence. As a population approaches its carrying capacity, growth and recruitment decline. Ecosystem changes that affect resource availability can alter the carrying capacity of a population, in turn affecting density-dependent relationships (Lorenzen and Enberg, 2002; Walters and Martell, 2004). Altered growth and recruitment rates associated with changing density-dependent relationships affect the productivity of a stock, including how much yield can be sustainably harvested (Lester et al., 2014).

The Laurentian Great Lakes, and Lake Huron in particular, have undergone large-scale ecosystem change since the dreissenid mussel invasion (Bunnell et al., 2014; Vanderploeg et al., 2002). In Lake Huron, primary productivity has declined (Barbiero et al., 2012, 2011a) and the once abundant benthic amphipod *Diporeia* spp., a food source for many fishes such as lake whitefish (*Coregonus clupeaformis*), has almost disappeared (Barbiero et al., 2011b). The predaceous invasive spiny water flea (*Bythotrephes longimanus*) has also affected the abundance and distribution of zooplankton, altering their availability to larval fish (Bunnell et al. 2011). Both nearshore and offshore fish communities have changed (McNickle et al., 2006; Riley et al., 2008), and a regime shift appears to have taken place in the lake (Ridgway, 2010; Riley and Adams, 2010).

Lake whitefish support valuable commercial fisheries within the Great Lakes (Ebener, 2013; Kinnunen, 2003). Historically, the cumulative effects of habitat degradation, overharvesting, and the establishment of invasive species, led to declines of several lake whitefish populations in the middle of the 20th century (Ebener et al., 2008). These populations began to recover around the 1970s and 1980s owing to management actions aimed at rehabilitating Great Lakes habitats, its fisheries, and controlling invasive sea lamprey (*Petromyzon marinus*) (Ebener et al., 2008). Lake whitefish have since come to support one of the Great Lakes largest commercial fisheries (Ebener et al., 2008). However, in the 1990s-2000s, growth and condition in many lake whitefish populations showed notable downward trends (Fera et al., 2015; Lumb et al., 2007; Rennie et al., 2009a). In several locations, declines in growth and condition prior to the invasion of dreissenid mussels coincided with high lake whitefish population densities, providing evidence that density-dependence contributed to the trends (Fera et al., 2015; Kratzer et al., 2007a; Wright and Ebener, 2005). Analyses of time series data also revealed that dreissenid mussel establishment was associated with the growth declines (Fera et al. 2015, Gobin et al., 2015), likely because lake whitefish switched to a diet more reliant on lower calorie prey items including dreissenids themselves (McNickle et al. 2006; Nalepa et al., 2009; Pothoven et al., 2001; Pothoven and Madenjian, 2008). Declines in lake whitefish recruitment were observed in Lake Huron (Ebener, 2013; Gobin et al., 2015), and lake whitefish in Lake Ontario also exhibited poor reproductive success after dreissenids invaded (Hoyle, 2005; Lumb et al., 2007). By 2010, lake whitefish harvest in Lake Huron declined by 35% since its peak at 4.2 million kg in 1999 (Ebener, 2013), but the extent to which these declines can be attributed to reduced abundance and recent ecosystem change remains unclear (Ebener et al., 2008; Gobin et al., 2015).

Reductions in lake whitefish growth and recruitment rates of up to 50% have been observed in the southern main basin of Lake Huron that could be associated with changes in density-dependent relationships following ecosystem change (Gobin et al., 2015). After dreissenids became established, both somatic growth and population density in the southern main basin of Lake Huron declined concurrently, suggesting that the inverse relationship between density and growth changed over time (Gobin et al., 2015). Although it is less clear how density-dependent recruitment has been affected, relative recruitment rates have varied through time, over a similar range of spawner biomass (Gobin et al., 2015). The ways in which lake whitefish growth, and possibly recruitment rates, respond to population density appear to have been altered. It is possible that recent ecosystem changes have lowered population carrying capacity, reducing growth and recruitment rates independently of changes in population density (Gobin et al. 2015).

In this study, we investigate the effects of reduced growth rate, as well as reduced growth rate combined with reduced recruitment rates, on lake whitefish population densities, sustainable harvest rates, and yield using an empirically grounded, individual-based life history model. This type of model links processes such as growth and maturation at the individual level, with population-level responses in abundance and recruitment (DeAngelis and Mooij, 2005). Feedbacks between fisheries, individual-level processes and populations can be built into the structure of an individual-based life history model in a mechanistic way that mimics natural processes (Dunlop et al. 2009). Therefore, this type of model is well-suited for predicting the effects of changes in density-dependent relationships on fish populations and their fisheries, while also providing a mechanistic context for interpreting those predictions. The model was parameterized with fishery-independent survey data collected in the southern main basin of Lake Huron. We consider scenarios in which growth and recruitment rates are reduced, reflecting recent changes in Lake Huron lake whitefish. We aim to shed light on whether the recent reductions in growth and recruitment sufficiently alter population productivity to affect sustainable harvest rates and yield.

METHODS

For this study, we developed an individual-based model for lake whitefish in the southern main basin of Lake Huron. This model was based on the eco-genetic model developed by Dunlop et al. (2007) for smallmouth bass (*Microperus dolomieu*) and had previously been adapted for Atlantic cod (*Gadus morhua*) (Dunlop et al., 2009) and Great Lakes populations of yellow perch (*Perca flavescens*) and lake whitefish (Dunlop et al. 2015). These previous versions of the model were used to investigate evolutionary change in life history traits; however, in the current study we set the genetic variance in the model to zero to constrain the evolution of genetic traits and focus solely on ecological dynamics (e.g. see Eikeset et al., 2013a). Individuals in the model undergo growth, maturation, reproduction, and mortality with annual time steps (Fig. 1). Being individual-based, the model tracks body size, age, maturation status, and the fates of individuals through time as the stock experiences commercial fishing. Population-level metrics, such as population abundance and total fishing harvest, are emergent properties that can also be tracked through time and can readily be compared to empirical data collected for the stock (Dunlop et al., 2007, 2009; Eikeset et al., 2013b).

We parameterized the individual-based model for lake whitefish in the QMA 4-5 management area of Lake Huron because of the data available and because this area supports an important commercial fishery. We estimated model parameters for lake whitefish from this area using (1) fishery-independent data collected by the Ontario Ministry of Natural Resources and Forestry (OMNRF) from 1984-2012 as part of their standardized offshore gill netting survey (survey methods are described in Speers, 2013 and Gobin et al., 2015), (2) output from the

OMNRF statistical catch-at-age stock assessment model for this region (based on Ebener et al., 2005), and (3) published literature for parameters that could not be estimated from survey data. A complete list of parameter values and their sources are provided in Table 1.

Growth

Growth was modeled using the bi-phasic growth model developed by Lester et al. (2004), in which prior to maturation all available energy is allocated to growth, and after maturation a proportion of available energy is invested in reproduction (Fig. 1A). Prior to maturation, an individual's length at age t years (L_t) is modeled as a linear function of its annual growth rate h:

$$L_t = h*t. \tag{1}$$

After maturation, allocation of energy to reproduction leads to a trade off with growth:

$$L_{t+1} = (3/3 + g)) * (L_t + h), \tag{2}$$

where an individual's body length is influenced by reproductive effort (g) via the gonado-somatic index (GSI) multiplied a conversion factor b to account for the difference in energetic content between gonads and somatic tissue (Lester et al., 2004):

$$g = b*\text{GSI}. \tag{3}$$

This investment is limited by the individual's body length and growth rate such that $g \leq (3*h)/L_t$ (Lester et al., 2004). An individual's annual growth was described by a density-dependent model (Walters and Post, 1993) (Fig. 1B):

$$h = h_{max} / (m + a*B), \tag{4}$$

where B is population biomass, a describes the loss of food resources due to intraspecific competition, m describes the loss of food resources due to other natural causes (e.g. consumption by other fish species, death not due to fish predation), and h_{max} describes the maximum growth rate when $B = 0$ and m=1. Parameters for the density-dependent growth relationship were estimated from growth data reflecting the mean length increment achieved by lake whitefish between the ages of 1 and 2 years old that were back-calculated from scales collected through the OMNRF survey (Gobin et al. 2015), and population biomass estimates from the statistical catch-at-age stock assessment model. Parameter estimates for this relationship are described in more detail below (see Model Scenarios). For computational reasons, abundance and biomass estimates from the stock were scaled (at a ratio of 1: 1,000 individuals or kg) when implementing the individual-based model (as in Eikeset et al. 2013b); results were then scaled up and presented as the stock-level values.

For the purposes of calculating biomass measures in the model, an individual's length (L_t) was converted to body mass W_t assuming a simple relationship,

$$W_t = c * L_t^d, \tag{5}$$

where c and d are parameters (Wootton, 1998). When estimating parameters for the length-weight relationship, we used OMNRF survey data for years before the invasion of dreissenid mussels (1984-1992) because of changes in lake whitefish condition that occurred since that time.

Maturation

Maturation was modeled using a probabilistic maturation reaction norm (PMRN), which describes how variation in growth affects the probability of maturing at a given age and size (Heino et al., 2002) (Fig. 1C). Following previously published models (e.g. Dunlop et al., 2007; Eikeset et al., 2013b; Enberg et al., 2009), we assumed a linear PMRN that is characterized by a slope and intercept. The midpoint of the PMRN describes the ages and sizes at which an individual has a 50% probability of becoming mature. The width of the PMRN defines the range of sizes over which individuals of a given age may become mature (often depicted as a lower bound of 25% maturation probability and an upper bound of 75% maturation probability). Individual PMRN trait values (their PMRN intercept and slope) were equal to population mean trait values based on empirical data. Each year in the model, the probability of maturation for a given individual was calculated according to their age and size, and a random number drawn above or below this probability determined whether or not that individual matured in that year (Dunlop et al., 2009). Because the timing of maturation is dependent on the age and size of the individual, the mean age and size at maturation of the population are therefore free to change through time as growing conditions change (e.g. with changes in population biomass through density-dependent feedback).

We estimated the slope, intercept, and width of the population mean PMRN using OMNRF survey data from the QMA 4-5 region and the method described by Barot et al. (2004). Logistic regressions of fish length with maturity status (i.e. mature/immature) were fit for consecutive age classes and cohorts with data available for >100 individuals, as this method is not robust with smaller sample sizes (Barot et al., 2004). The PMRN slope and intercept were then estimated from a linear regression of age with midpoints from these logistic regressions. The PMRN width, describing the body length difference between two set probabilities of maturing, was estimated as the average length between 25% and 75% maturation probabilities for these ages and cohorts.

Recruitment

An individual's fecundity was based on its body length (L_t):

$$f = a * L_t^j , \tag{6}$$

where *j* and *k* are parameters (Fig. 1D). This relationship is used to assign parents to offspring; therefore, larger fish in the model contribute disproportionately larger proportions of offspring to the newly recruited population, as is observed for lake whitefish (Kratzer et al., 2007b). Parameters for the fecundity-length relationship were estimated by Kratzer et al. (2007b) for lake whitefish collected at their Alpena study site from 1986-1987, as these differed from those estimated for the years after dreissenid mussels became established.

Early survival rates are applied to fecundity through the stock-recruitment relationship. Recruitment is density-dependent, with the rate of recruitment (*R/S*) in a given year described with a Ricker-type stock-recruitment model (Fig. 1E):

$$R/S = R_{max} * \exp(-\beta * S) \tag{7}$$

(Hillborn and Walters, 1992), where S is the biomass of the spawning stock, R_{max} is a parameter describing maximum recruitment per unit spawner biomass (i.e. the product of fecundity f and early survival when spawning biomass is very low), and β is a parameter describing the strength of density-dependence in recruitment. Parameters for the stock-recruitment relationship were based on spawner biomass and recruitment estimates from the statistical catch-at-age stock assessment model (based on Ebener et al., 2005), and are described below (see Model Scenarios).

Mortality

Individuals in the model were subject to natural mortality, comprised of background mortality (M_B) and lamprey predation (M_L), and fishing mortality (F); the sum of these equaling the instantaneous total mortality rate (Z):

$$Z = M_B + M_L + F. \tag{8}$$

In the individual-based model, these sources of mortality are implemented sequentially as individual probabilities based on annual proportions. We assumed a constant background mortality through time (Fig. 1F), set to the value used in the statistical catch-at-age stock assessment model for the QMA 4-5 management area (based on Ebener et al., 2005), which is estimated from the relationship between temperature and von Bertalanffy growth parameters (Pauly 1980). We calculated the annual probability of natural mortality (N) from the equation:

$$N = 1 - \exp(-M_B). \tag{9}$$

Sea lamprey predation was size-dependent and determined by the probability of a fish being attacked and the probability of an attack being fatal (Fig. 1F). The probability of being attacked by sea lamprey (L_{attack}) was calculated from a logistic model of wounding probabilities for lake whitefish in the southern main basin of Lake Huron developed by McLeod et al. (2011):

$$L_{attack} = 1/(1 + \exp(p - n * L)), \tag{10}$$

where L is the individual's length, and m and n are parameters. Lamprey wounding rate relationship parameters used were estimated by McLeod et al. (2011) for the year 2000, the earliest year in that time series. Given an attack, we then implemented a 75% probability of the attack being fatal, as this was the approximate percentage of attacks that were found to be fatal for whitefish in northern Lake Huron (Spangler et al., 1980). This 75% probability of an attack being fatal was assumed to be constant through time, as were parameters p and n. However, wounding rate probabilities vary over time in our model with changes in individual growth rates.

A commercial gillnet fishery was implemented in the model by scaling a size-selectivity curve developed for Lake Huron lake whitefish to the peak exploitation rate. Size-selectivity was described using a double logistic function (Fig. 1G):

$$V_t = (1/(1 + \exp(-\delta_1 * (Q_t - \varepsilon_1)))) * (1 - 1/(1 + \exp(-\delta_2 * (Q_t - \varepsilon_2)))), \tag{11}$$

where Q_t is the ratio of the length of the fish (L_t) to the gillnet mesh size (G): L_t/G, and δ_1, ε_1, δ_2, and ε_2 are parameters that were empirically derived for Lake Huron lake whitefish (Y. Zhao, OMNRF*, unpublished data*). This selectivity curve was scaled to the peak exploitation rate (P_{max}), defined as the proportion of fish harvested of the most selected size, to calculate the probability of an individual being harvested (P_t):

$$P_t = (V_t/P_{max}). \tag{12}$$

Individuals were vulnerable to harvest above a minimum size limit based on the existing commercial fishing regulations for Lake Huron lake whitefish (Ebener, 2008).

Model scenarios

We evaluated three density-dependent scenarios: a baseline scenario and two alternative scenarios (Fig. 2). For our baseline scenario, density-dependent growth and recruitment relationships reflect pre-dreissenid conditions with relatively high maximum growth and recruitment rates (Gobin et al., 2015). Because lake whitefish growth in the southern main basin has clearly declined, only the maximum growth rate was reduced in the first alternative scenario (i.e. low growth rate). Both maximum growth and recruitment rates were reduced in the second alternative scenario (i.e. low growth and recruitment rates), because a decline in recruitment potential may have also occurred (Gobin et al., 2015). The two alternative scenarios reflected declines in growth and recruitment rates observed in southern Lake Huron after dreissenid invasion (Gobin et al., 2015) by manipulating maximum rates (h_{max}, *and* R_{max} in Equations 4 and 7).

Simulated populations were initialized with parameters representing one of the three scenarios (i.e. baseline, low growth rate, low growth and recruitment rates). Harvest was initiated 100 years later, well after populations became stable. Simulations were run for an additional 400 years (500 years in total) to assess whether populations stabilized and persisted after harvest began.

To assess effects on fishery yield and sustainable harvest rates, we conducted simulations in which we varied the peak exploitation rate (P_{max}) from 0.1 to 1.0 (Fig. 1F). We defined sustainable harvest rates as those from which populations persisted for the duration of the simulation (i.e. abundance was not reduced to zero individuals).

When reporting our results, we compare population density metrics, commercial harvest, and individual life history traits in the last year of the simulations (i.e. year 500). All results were depicted as means of ten independent simulation runs (as in Dunlop et al., 2015).

RESULTS

Growth

In the baseline scenario, mean length increment varied between 9-12.5 cm/year, depending upon the harvest rate. When the maximum growth rate was reduced (scenario 2), mean length increment varied between 6-7 cm/year, a 30-45% decline compared to the baseline scenario (Fig 3A). Reducing both the maximum growth and recruitment rates (scenario 3) led to 18-19% declines in mean length increment to 7.5-8.5 cm/year (Fig. 3A). Higher harvest rates yielded higher growth rates and larger mean sizes at age due to density-dependence; this was most apparent in the baseline scenario (Fig. 3A and B). As the peak exploitation rate was increased, mean sizes at age were also affected by age truncation in the baseline scenario (Fig. 4A).

Recruitment

In the baseline scenario, the rate of recruitment varied between 1-5 recruits/kg spawner biomass, depending on the harvest rate. Reducing the maximum growth rate (scenario 2) led to recruitment rates varying between 3-4.5 recruits/kg spawner biomass; relative to the baseline scenario, this represented a 23-145% increase in relative recruitment when the peak exploitation rate was less than 0.7 or a 8-11% decline in relative recruitment when peak exploitation rates were 0.7 or greater (Fig.5A). Increases in relative recruitment were inversely related to the harvest rate (i.e. the lowest peak exploitation rate produced the greatest increase in relative recruitment). When both maximum growth and recruitment rates were reduced, relative recruitment varied between 2-3 recruits/kg spawner biomass, a 27-60% decline compared to the baseline scenario, with lower harvest rates yielding greater declines (Fig. 5A). The number of recruits produced by the population increased by up to 26% or decreased by up to 3%, depending on the harvest rate, when maximum growth rate was reduced (scenario 2) (Fig. 5B). When both maximum growth and recruitment rates were reduced (scenario 3), the number of recruits declined by 77-100% compared to the baseline scenario (Fig. 5B).

Mortality

In the baseline scenario, older fish experienced higher overall mortality rates with individuals between the ages of 4 and 7 years old experiencing the highest mortality as reflected by steeper slopes of catch curves (Fig. 4A). This resulted from the combined effects of sea lamprey mortality increasing with age, the size-selectivity of gill nets, and the effects of growth rate on vulnerability to lamprey or fishing (Fig. 4B). Age truncation (i.e. older aged individuals became rare) also became apparent in the baseline scenario when the peak exploitation rate exceeded 0.8. Reducing the growth rate (scenario 2) delayed the ages experiencing the highest mortality rates to 7 years and older (Fig. 4A). In scenario 2, age-specific differences in mortality resulted purely from fishing as background mortality and lamprey predation were fairly constant across the ages of 1 to 12 years (Fig. 4B). When both growth and recruitment rates were reduced (scenario 3), increased mortality rates associated with fishing began at around 6 years of age, and age truncation became apparent at the highest harvest rate that was sustainable (Fig. 4A and B). Differences in catch curves for various harvest rates over ages at which fish are not susceptible to harvest in scenario 3 (Fig. 4A) reflect effects of harvest on levels of recruitment through the stock-recruitment relationship.

Response in population abundance metrics, yield, and sustainable harvesting

In the baseline scenario, populations were stable over a wide range of harvest rates (Fig. 6A and B). Reducing the growth rate alone (scenario 2) resulted in slightly higher population abundance compared to the baseline scenario (Fig. 6A). However, all other population abundance metrics (e.g. population biomass, and exploitable abundance and biomass) declined across all harvest rates for scenario 2 and these declines varied between 26% and 78% (Fig. 6A and B). When both growth and recruitment rates were reduced (scenario 3), all population abundance metrics including population abundance were reduced substantially, by at least 76% for population abundance, 84% for population biomass, 87% for exploitable abundance, and 89% for exploitable biomass (Fig. 6A and B).

In the baseline scenario, yield varied 4 to 6-fold depending on the harvest rate (Fig. 6A and B). When only growth rate was reduced (scenario 2), yield declined by 71-85%, but harvest remained sustainable at all levels of exploitation. When both growth and recruitment rates were reduced (scenario 3), harvest declined by at least 85%, but was sustainable as long as peak exploitation equaled 0.4 or less. Harvest became unsustainable (i.e. abundance reduced to zero) when both growth and recruitment rates were reduced, and the peak exploitation rate exceeded 0.4. Sustainable harvest was maximized when the peak exploitation rate equaled 0.7 in the baseline scenario, 1.0 in the low growth scenario, and 0.2 in the low growth and recruitment scenario (Fig. 6A and B).

DISCUSSION

Our model predicts that the changes in growth and recruitment occurring in Great Lakes' lake whitefish stocks are affecting stock productivity, which translates into effects on fisheries yield. Juvenile growth of lake whitefish in the southern main basin of Lake Huron is now approximately half of what it was 25 years ago (Gobin et al., 2015). Similar declines in growth have been observed in Lakes Ontario and Michigan (Ebener, 2013; Fera et al., 2015; Lumb et al., 2007). Reductions in recruitment have also been reported for lake whitefish in Lakes Ontario and Huron (Gobin et al., 2015; Hoyle et al., 2008). Given the importance of lake whitefish to the commercial fisheries in the Great Lakes, with Lake Huron supplying the majority of the commercial harvest for the species (Brenden et al. 2013), these declines have led to concerns regarding sustainable harvest rates (Gobin et al., 2015; Brenden et al., 2010). In a previous study, trends in growth and recruitment of Lake Huron lake whitefish were partly attributed to changes in density-dependent relationships associated with ecosystem changes following the establishment of dreissenid mussels (Gobin et al., 2015). In the present study, our model predicts that these changes in density-dependent growth and recruitment will result in reduced fisheries yield and unsustainable harvest at several harvest rates that the population could previously support.

Declines in size-at-age caused substantial reductions in yield (by at least 71%) when density-dependent growth was altered (scenario 2). Although population abundance increased in the low growth rate scenario (scenario 2), population biomass and yield consistently declined compared to the baseline scenario due to reductions in somatic growth. Slower growth also affected the age structure of the population by delaying the age at which fish recruited to the fishery. Declines in growth and population biomass, combined with fish taking longer to recruit to the fishery were primarily responsible for the predicted yield declines. Conversely, reductions in yield observed when the rate of recruitment was also lowered (scenario 3) were due to declines in size at age as well as abundance. Although declines in population biomass led to growth and sizes at age that were intermediate between the baseline scenario and the low growth rate scenario (scenario 2), density-dependent increases in growth rate were not sufficient to compensate for declines in abundance. These results demonstrate how density-dependent growth and recruitment processes interact, with effects that scale from the level of individuals to the population; and by altering individual life history traits, regulate population productivity and bound sustainable harvest rates (Lester et al., 2014).

In our model, reducing maximum growth rate alone (scenario 2) resulted in either increases or minor decreases in recruitment. It was only when changes in density-dependent recruitment were also included (scenario 3), that we predicted substantial reductions in the number of recruits. Given the declines in both growth and recruitment observed in Lake Huron (Gobin et al. 2015; OMRNF unpublished data), this would suggest that both density-dependent relationships have changed in response to the altered ecosystem conditions. The changes in the density-dependent relationships (i.e. reductions in the maximum growth and recruitment rates) we simulate in our model could come about if the stock's carry capacity has been reduced, a possible result of the recent ecosystem changes.

Altering density-dependent relationships also affected sustainable harvest rates and the harvest rates at which yields were maximized. According to Zhou et al. (2012), sustainable yield is maximized when the level of natural mortality (M) on average equals 0.87 times the level of fishing mortality (F) in teleost fishes; this varies with density-dependent growth, density-dependent recruitment, and life history traits of the population. In our study, M equaled 0.3, and maximum instantaneous fishing mortality rate (F) for fully vulnerable fish varied from 0.1 to infinity (instantaneous fishing mortality approaches infinity when the annual proportion harvested equals 1). Our model also included mortality from sea lamprey with probabilities varying between 0 and 0.6, depending on the length of the fish; these probabilities were generally small compared to other sources of mortality, for example ranging from one-tenth of natural mortality in the alternative scenarios to rarely exceeding the natural mortality in the baseline scenario. Reducing the growth rate alone shifted the harvest rate that maximized sustainable yields upwards (i.e. to a higher harvest level), whereas adding the reduced recruitment rate shifted it downwards (i.e. to a lower harvest level). In both cases, however, yields declined notably compared to when growth and recruitment were higher in the baseline scenario. Harvest also became unsustainable when both growth and recruitment rates were reduced, and the peak exploitation rate exceeded 0.4 (the equivalent of a maximum instantaneous fishing mortality rate of approximately 0.5).

Based on our model, it seems likely that the lake whitefish commercial yields that were achieved during the 1990s in Lake Huron will no longer be attainable given the recent ecosystem changes. The current fish community objective for coregonids in Lake Huron is for populations to remain capable of sustaining harvests of 3.8 million kg annually (DesJardines et al., 1995). However, this objective was not met for the most recent reporting period in which coregonid harvest averaged 3.3 million kg, of which lake whitefish comprised 97% (Ebener, 2013). Our model predictions bring into question whether this fish community objective is achievable in the present context of reduced stock productivity and the state of the ecosystem. The statistical catch-at-age model for QMA 4-5 used by OMNRF also predicts that some age classes have experienced considerably higher fishing mortality in recent years (Fig. A1), which could be of concern if these harvest rates continue.

Declines in estimates of harvest and abundance of Lake Huron lake whitefish have been observed in recent years. Commercial harvest has declined by approximately 35% since its peak in the late 1990s, with 13% of declines occurring between 2005 and 2010 (Ebener, 2013). The stock assessment model for Lake Huron lake whitefish in QMA 4-5 predicts declines in lake whitefish abundance in the order of 15%, as well as 20% declines in biomass across the main basin, since dreissenid mussels became established (Ebener, 2013). Declines in the catch-per-unit effort (CPUE) of age 4 lake whitefish (Gobin et al., 2015), as well as in the biomass CPUE of lake whitefish (Fera et al. 2015) in the fishery-independent gill netting survey also occurred between the 1990s and 2010. These declines could have also resulted from several factors, including reduced fishing effort and catchability brought about by increased water clarity and clogging of nets with filamentous algae (Ebener, 2013). Changes in the depth distribution of lake whitefish that might have occurred following dreissenid mussel invasion and the collapse of *Diporeia* (Rennie et al., 2009b; Rennie et al., 2015) could also affect harvest or estimated abundance if effort hasn't been re-adjusted (or if there was a lag) to reflect the new spatial distributions. Although these other factors could have contributed to the observed trends, our model predictions provide evidence that the fundamental changes in growth and recruitment on their own are substantial enough to have caused the declines observed in abundance and harvest.

Delayed recruitment to the fishery due to slower growth reflected by increased mean age of the commercial catch (Fig. A2) could also be affecting yields in the southern main basin of Lake Huron. In Lake Ontario where lake whitefish growth and recruitment decreased after dreissenid establishment, harvest declined by over 90% (Hoyle et al., 2008). In Lake Michigan, however, commercial yields increased by 13% for the most recent reporting period (2005-2010) despite similar declines in growth and condition to those observed in Lakes Huron and Ontario (Clapp et al., 2012). Age 3 recruitment in Lake Michigan has also remained relatively strong, and although lower somatic growth has delayed recruitment to the fishery, increasing trends in the commercial harvest reflect overall increases in population biomass (Clapp et al., 2012). Variability in the dynamics and harvest of lake whitefish observed across the Great Lakes could be due to a number of factors such as lake size, rates of exploitation, or the extent of recent ecosystem changes.

Our model has several limitations that could be improved by including additional details or processes that might affect lake whitefish dynamics in Lake Huron. First, other than the positive relationship between body size and fecundity, our model does not account for parental effects on recruitment, such as those that would occur if the older or higher condition spawners experience higher reproductive success. In recent years, the condition of lake whitefish has declined in many regions of the Great Lakes, including the southern main basin of Lake Huron (Ebener, 2013; Lumb et al., 2007; Rennie et al., 2009a), and the effects on recruitment remain unknown. However, Muir et al. (2010) found that neither parental condition nor egg quality affected the physiological condition of juvenile lake whitefish. Similarly, Johnston et al. (2012) found that lake whitefish allocate increasingly smaller proportions of body lipid to gonadal development as they age. Condition could also affect maturation or population dynamics in other complex ways that are not included in our model. For example, the reduced condition of lake whitefish observed following the ecosystem changes in Lakes Huron and Michigan might also result in higher natural mortality because of increased susceptibility to disease (Wagner et al., 2010). Our model also does not account for any migration of lake whitefish from different areas; however, this is likely to have minimal effects on our conclusions given that the growth rate and recruitment declines observed in the southern main basin are occurring in several other locations in the Great Lakes (Fera et al. 2015; OMNRF unpublished data from the statistical-catch at age model). Furthermore, our model does not permit any evolution of life history traits in response to selection from fishing. A previous model of lake whitefish predicted that evolution in response to fishing could increase population productivity and reduce the risk of collapse from over-fishing (Dunlop et al. 2015).

The harvest regime implemented in our model was intentionally simplistic. We assumed a constant peak exploitation rate, whereas in reality, fishing mortality would be expected to fluctuate annually with the complex dynamics that occur between catch, effort, management, and other variables such as climate and water clarity. It should be noted, however, that although our peak exploitation rate was constant, the realized fishing mortality of individuals varied with age and size in the model, as observed for this stock (Fig. A1), and the mean fishing mortality rate could also vary through time as growth conditions change. We purposefully chose our approach to permit generalizations to other systems and ecosystem conditions, and to facilitate the interpretation of simulation results.

In Lake Huron, the spatial extent of recent ecosystem changes and effects observed among multiple trophic levels suggest that a regime shift has occurred (Ridgway, 2010; Ridgway and Middel, 2015). Regime shifts have been observed in a variety of systems, whereby large-scale ecosystem changes occur abruptly and stabilize at a new alternative state (Scheffer et al., 2001). Such drastic changes in aquatic ecosystems are predicted to increase in frequency with future climate change and increased human disturbance (Meyer et al., 1999). Density-dependent relationships and life history traits that affect the productivity of fish populations, and in turn fishery yields, harvest sustainability, and population resilience are also affected by these ecosystem changes. With this in mind, effective management of exploited populations can be limited by our ability to understand and account for how several complex processes, and the interactions among these processes, respond to ecosystem change. Our study provides insight into the potential effects of changes in two key density-dependent relationships on the productivity and sustainability of a Great Lakes commercial fishery. Given that growth and recruitment of Lake Huron lake whitefish are a fraction of what they once were, these populations are not expected to be able to support the same level of harvest when growth or recruitment was higher. Changes in growth or recruitment caused solely by changing population density (i.e. movement along the same density-dependent curve) would be more readily reversible with future changes in population biomass; conversely, reductions in productivity associated with changes in the actual density-dependent relationships themselves (i.e. a shift to a different relationship altogether) are inherently different and may have longer-lasting effects. Lake whitefish have shown a history of decline and increase in the past and have previously recovered following periods of higher fishing mortality. However, the impact of ecosystem changes on density-dependent relationships puts a limit on productivity that could alter the rate and extent of recovery potential in this valuable resource.

ACKNOWLEDGMENTS

We are grateful to the staff of the Upper Great Lakes Management Unit of the OMNRF for providing the data necessary to conduct this work. In particular, we thank Adam Cottrill for providing assistance with the data and for providing estimates from the SCAA model. Funding was provided by the Great Lakes Fishery Commission. We also thank Mark Ebener and an anonymous reviewer whose valuable suggestions improved our paper.

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Table 2.1. Parameter values and sources used in the individual-based model for lake whitefish in the southern main basin of Lake Huron.

Description	Symbol	Source	Value
Gonado-somatic index GSI	GSI	1	0.2
Gonado-somatic index conversion factor	b	2	1.73
Constant in length-weight relationship (kg/cm)	c	3a	3.318e-6
Exponent in length-weight relationship	d	3a	3.29
Mean probabilistic maturation reaction norm slope (cm/yr)		3b	-1.77
Mean probabilistic maturation reaction norm intercept (cm)		3b	42.7
Mean probabilistic maturation reaction norm width (cm)		3b	10.6
Exponent of length-fecundity relationship	J	4	3.83
Slope of length-fecundity relationship (eggs/mm^{k})$^{-10\textasciicircum 3}$	a	4	1.1e-6
Background natural mortality (year^{-1})	M_B	5	0.30
von Bertalanffy asymptotic growth (cm)	L_∞	5	60.0
Brody's growth coefficient	k	5	0.25
Water temperature T (°C)	T	5	6°C
Wounding probability logistic model coefficient	p	6	8.60
Wounding probability logistic model coefficient (mm^{-1})	n	6	0.01
Lamprey mortality probability		7	0.75
Double logistic gillnet selectivity function	δ_1	8	5.84
Double logistic gillnet selectivity function	ε_1	8	4.19
Double logistic gillnet selectivity function	δ_2	8	2.19
Double logistic gillnet selectivity function	ε_2	8	4.74
Gillnet selectivity mesh size (mm)	G	8,9	114
Fishery minimum size limit (mm)		9	430

1. Based on estimates from Johnston et al., 2012; Lumb et al., 2007; Cook et al., 2005.
2. Lester et al., 2004.
3a. OMNRF survey data for years 1984-1992.
3b. OMNRF survey data for years 1984-2009.
4. Kratzer et al. (2007) Alpena study site for years 1986-1987.
5. OMRNF Statistical catch-at-age stock assessment model for QMA 4-5 based on Ebener et al. (2005).
6. McLeod et al. (2011) southern main basin for the year 2000.
7. Spangler et al. 1980.
8. YM Zhao, OMNRF, unpublished data.
9. Ebener et al. (2008).

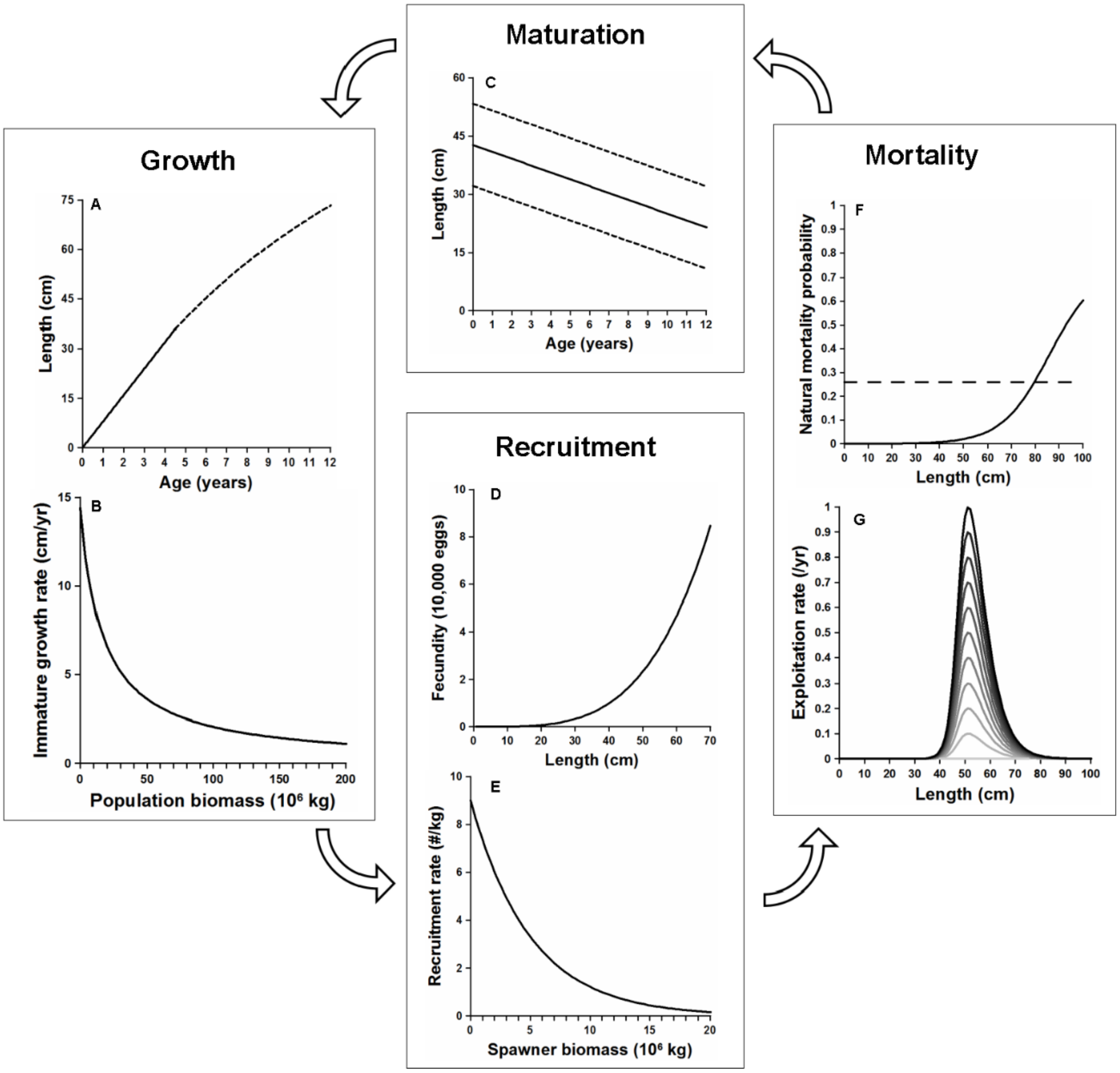


Figure 2.1. An overview of the individual-based life history model used to simulate harvest dynamics of lake whitefish. Individuals undergo four processes in an annual time-step: maturation, growth, reproduction, and mortality; the arrows indicate the order in which these processes occur in the model. A) Mean length at age based on the bi-phasic growth model; the solid line shows pre-maturation growth and the dotted line shows post-maturation growth. B) The density-dependent growth relationship. C) The population mean probabilistic maturation reaction norm; the solid line shows the midpoint at which individuals have a 50% probability of maturing, and the dotted lines depict the lower and upper bounds representing 25% and 75% probabilities of maturing, respectively. D) The length-dependent fecundity relationship. E) Density-dependent recruitment bases on the Ricker stock–recruitment relationship. F) Sources of natural mortality; the dotted line depicts constant background mortality, and the solid line represents length-dependent predation by sea lamprey. G) The length- dependent commercial gillnet fishery scaled to peak exploitation rates ranging between 0 and 1, shown by the darkness of the line.

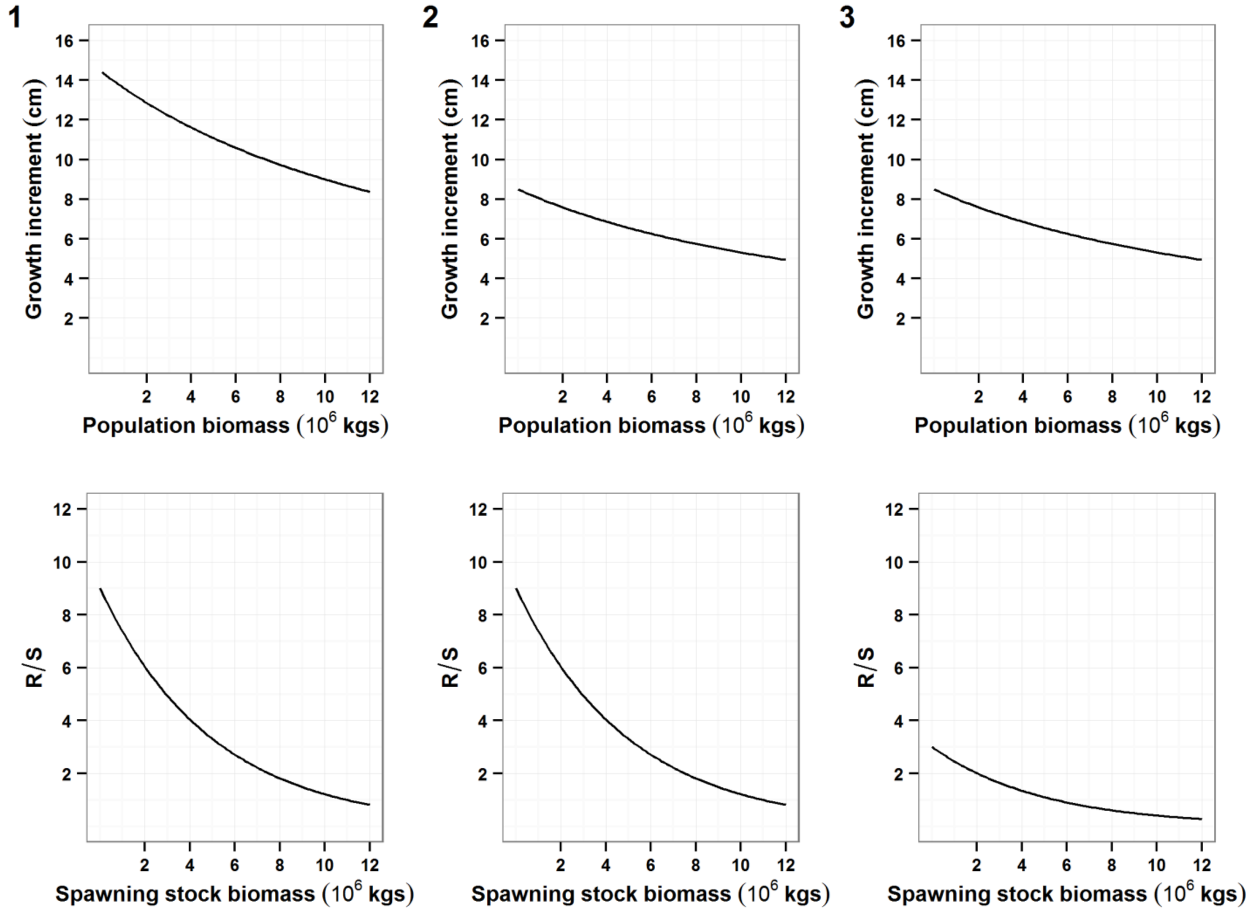


Figure 2.2. Model scenarios used to predict the effects of changes in density-dependent growth (upper panels) and recruitment (lower panels) on harvest dynamics of lake whitefish. Scenario 1 – the baseline scenario representative of pre-dreissenid years characterized by relatively high growth and recruitment rates (h_{max} = 14.4 and r_{max} = 9). Scenario 2 – low growth rate scenario characterized by reduced growth rate (h_{max} = 8.5 and r_{max} = 9). Scenario 3 - low growth and recruitment rate scenario characterized by reduced growth and recruitment rates (h_{max} = 8.5 and r_{max} = 3).

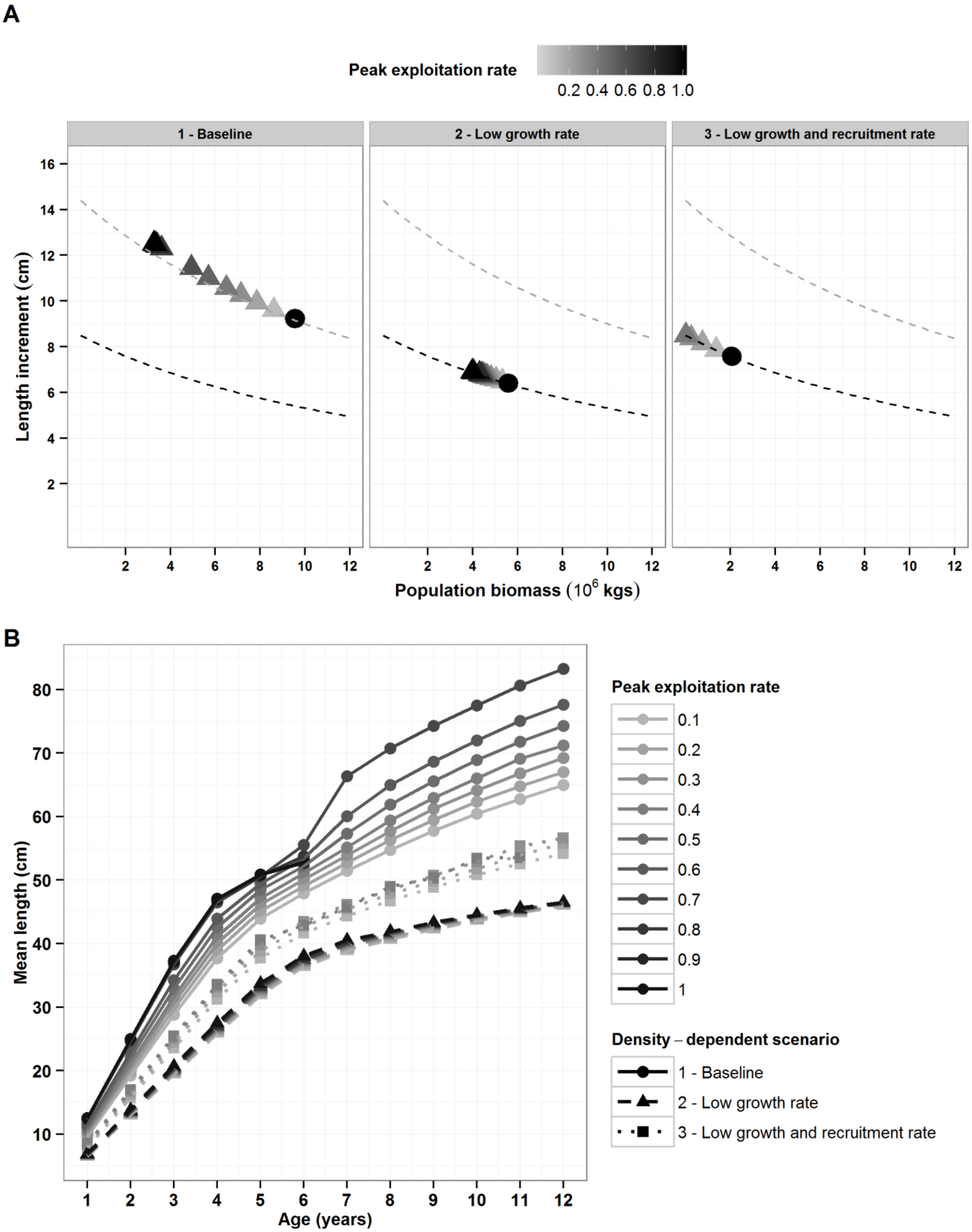


Figure 2.3. Model predictions and emergent dynamics for growth and biomass. A) Mean juvenile growth (i.e. length increment) as determined by the population biomass; the black circle represents the equilibrium value prior to harvest in the model (year 100), triangles represent values achieved in the final year of model simulations (year 500) for various levels of harvest.

Dotted lines represent the density-dependent growth relationships implemented for each scenario (darker line is the reduced growth rate scenario; lighter line is the baseline growth rate scenario) and the symbols depict the emergent model predictions. B) Mean length-at-age in the final year of model simulations (year 500).

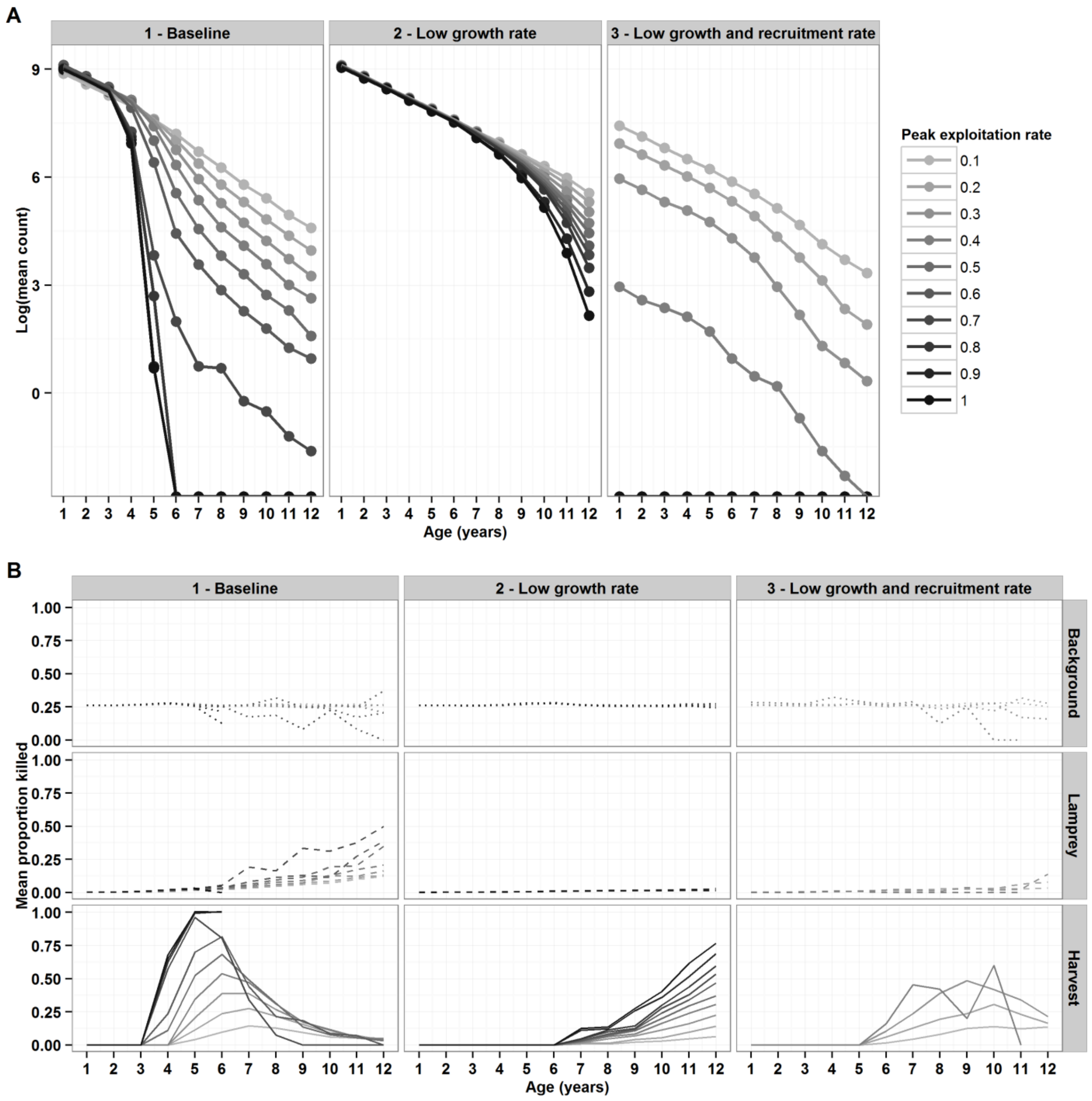


Figure 2.4. Model predictions related to harvest. A) Catch curves based on all individuals in the model between the ages of 1 to 12 years old, and B) age specific mortality due to natural sources (constant background and sea lamprey predation) and harvest, in the final year of model simulations (year 500).

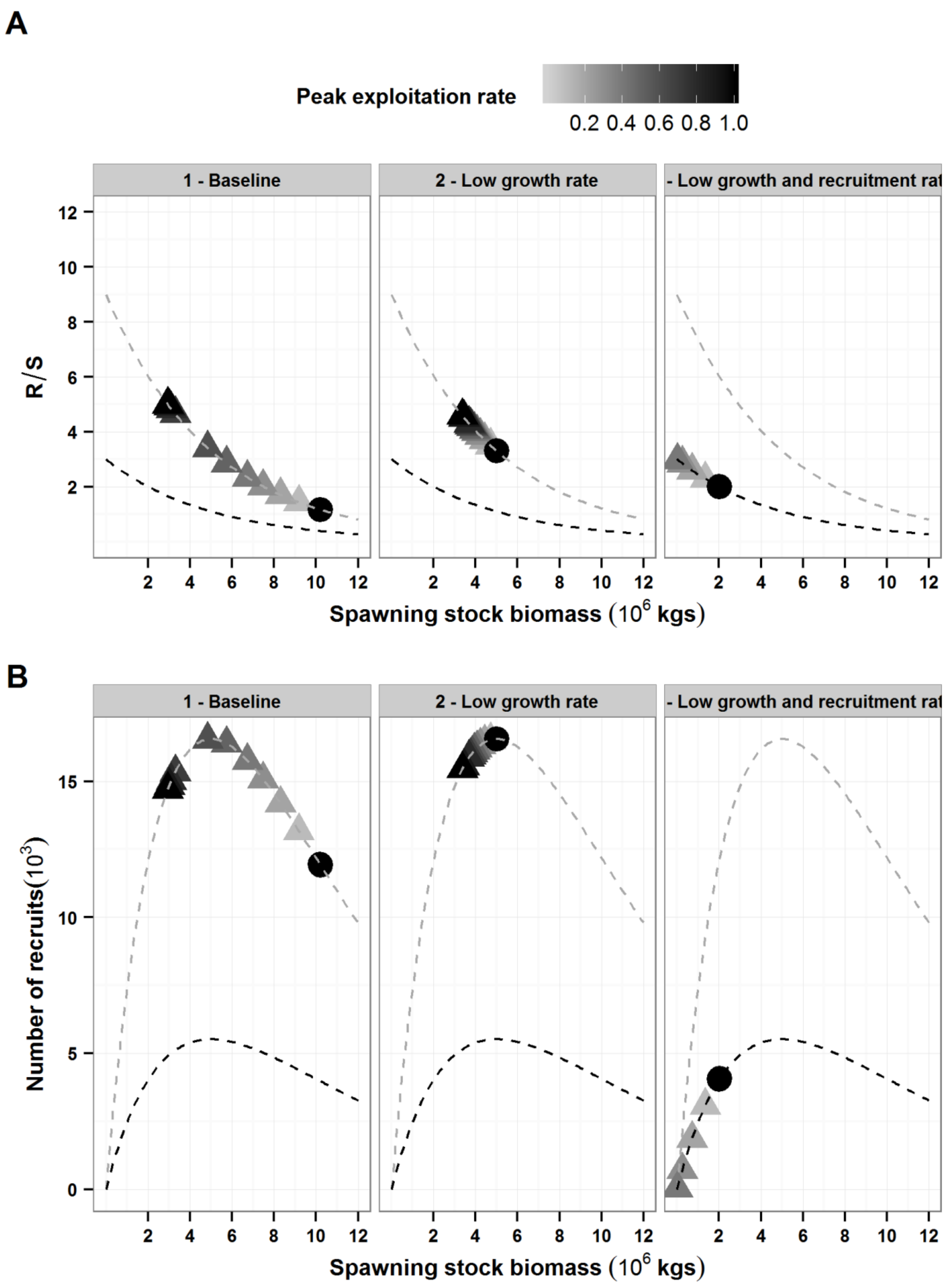


Figure 2.5. Model predictions and emergent dynamics for recruitment. A) Recruitment rate (R/S; the number of recruits per kg spawner biomass), and B) absolute recruitment as determined by the biomass of the spawning stock; the black circle represents the equilibrium value prior to harvest in the model (year 100), triangles represent values achieved in the final year of model

simulations (year 500) for various levels of harvest. Dotted lines represent the density-dependent recruitment relationships implemented for each scenario (darker line is the reduced recruitment rate scenario; lighter line is the baseline recruitment rate scenario) and the symbols depict the emergent model predictions.

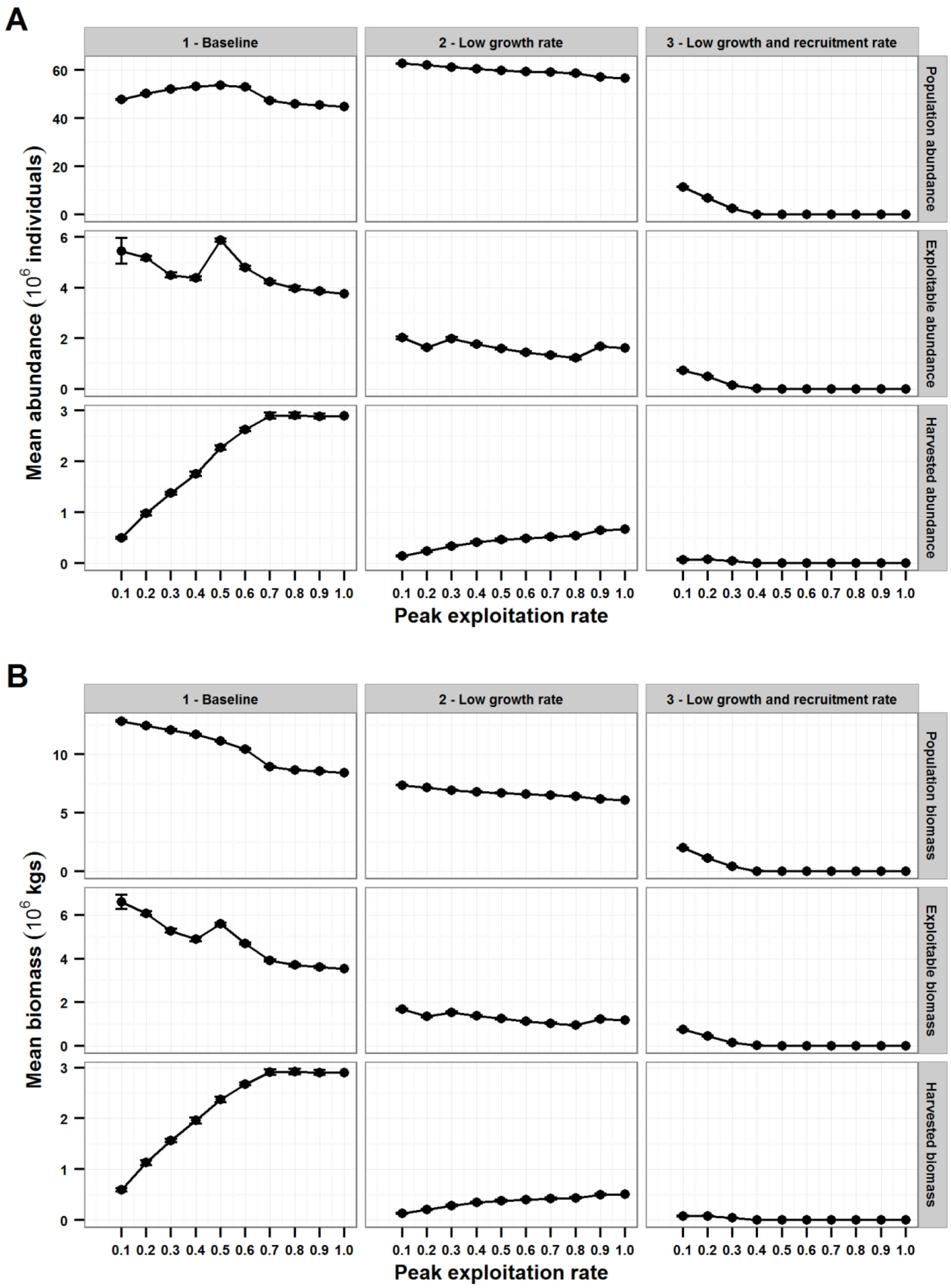
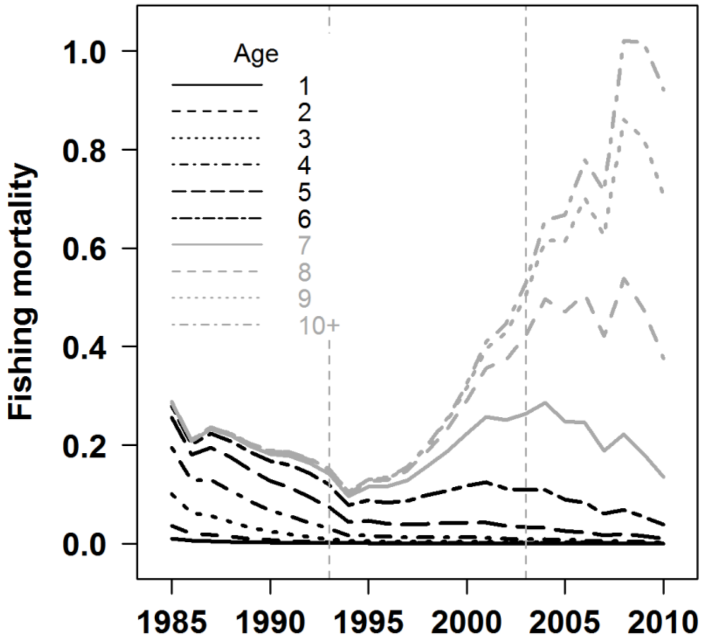


Figure 2.6. Model predictions for population abundance metrics and harvest. Depicts the mean population density and harvest metrics (± SD) in the final year of model simulations (year 500) measured in terms of A) abundance, and B) biomass.

Figure A1. Age-specific instantaneous commercial gillnet fishing mortality estimates from the OMNRF statistical-catch-at-age stock assessment model (based on Ebener et al. 2005) for lake whitefish in the southern main basin of Lake Huron, from 1985 to 2010.



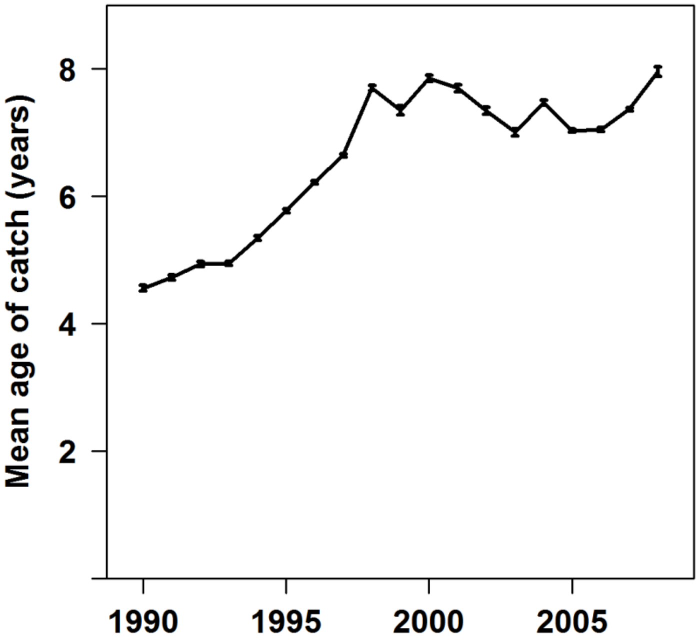


Figure A2. Mean age of lake whitefish in the commercial catch from the southern main basin of Lake Huron between 1990 and 2008 (OMNRF unpublished data).

CHAPTER 3: ECOLOGICAL CHANGE ALTERS THE EVOLUTIONARY RESPONSE TO HARVEST IN A FRESHWATER FISH

This chapter has been accepted for publication in the journal Ecological Applications. Manuscript ID: EAP17-0781.

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ABSTRACT

Harvesting can induce rapid evolution in animal populations, yet the role of ecological change in buffering or enhancing that response is poorly understood. Here, we developed an eco-genetic model to examine how ecological changes brought about by two notorious invasive species – zebra and quagga mussels– influence harvest-induced evolution and resilience in a freshwater fish. Our study focused on lake whitefish (*Coregonus clupeaformis*) in the Laurentian Great Lakes, where the species supports valuable commercial and subsistence fisheries, and where the invasion of dreissenid (zebra and quagga) mussels caused drastic shifts in ecosystem productivity. Using our model system, we predicted faster rates of evolution of maturation reaction norms in lake whitefish under pre-invasion ecosystem conditions when growth and recruitment of young to the population were high. Slower growth rates that occurred under post-invasion conditions delayed when fish became vulnerable to the fishery, thus decreasing selection pressure and lessening the evolutionary response to harvest. Fishing with gill nets and traps nets generally selected for early maturation at small sizes, except when fishing at low levels with small mesh gill nets under pre-invasion conditions; in this latter case, evolution of delayed maturation was predicted. Overall, the invasion of dreissenid mussels lessened the evolutionary response to harvest, while also reducing the productivity and commercial yield potential of the stock. These results demonstrate how ecological conditions shape evolutionary outcomes and how invasive species can have a direct effect on evolutionary responses to harvest and sustainability.

KEYWORDS

Eco-evolutionary dynamics, density-dependent growth, probabilistic maturation reaction norm, fisheries-induced evolution, individual-based model, Lake Huron, stock-recruitment relationship, regime change, sea lamprey.

INTRODUCTION

Human activities can induce rapid evolutionary change in animal populations, with resulting ecological consequences and impacts to society (Hendry et al. 2017). One of the most profound ways in which humans alter populations is through harvest (Darimont et al. 2009), having both short-term consequences and longer-lasting effects. Harvesting often reduces population biomass, leading to rapid changes in growth and population productivity related to density dependence (Trippel 1995). Harvesting is also selective, targeting animals with certain characteristics such as large body size, which can lead to short-term changes in age and size structure, as well as the evolution of life-history traits and behaviours over time (Heino et al. 2015). Both the ecological and evolutionary impacts of harvest can lead to further responses in the food web, which has implications for ecosystem services (Jørgensen et al. 2007, Rudman et al. 2017).

Research has highlighted the potential ways in which reciprocal feedback between ecological and evolutionary dynamics, referred to as eco-evolutionary dynamics, influence the response of populations to anthropogenic stressors, including harvest (Palkovacs 2011, Hendry et al. 2017). As an example of the ecology to evolution pathway, the presence of density-dependent growth can buffer harvest-induced selective pressure favoring earlier maturation, and thus lessen the evolutionary response (Lester et al. 2014, Dunlop et al. 2015, Eikeset et al. 2016). In the evolution to ecology pathway, models have shown that life-history evolution in response to harvest can alter population growth rate and the recovery potential of a population (Dunlop et al. 2015). Recent research has also shown the significance of considering eco-evolutionary feedbacks beyond single species. For example, Kindsvater and Palkovacs (2017) predicted that the extent to which fishing alters the trophic level of a stock depends on whether joint demographic and evolutionary changes are included in models. Audzijonyte and Kuparinen

(2016) examined whether predictions of the effects of evolution on population growth rate in single population models were conserved in a multi-species model. These studies are raising awareness of the significance of eco-evolutionary dynamics in the management of harvested populations and more broadly to the future health and resilience of ecosystems.

Animals are harvested from environments that undergo significant ecological change. Yet, despite recent advances in considering the broader impacts of harvest beyond single species, there remains a paucity of research on how ecological changes affect a stock's adaptation to harvest. Understanding these eco-evolutionary responses in a single species context can provide a basis on which to broaden management approaches to account for eco-evolutionary effects. The need for this type of research is growing because the occurrence of rapid and severe ecosystem change is expected to increase with human population growth and climate change. Owing to their size, ease of access, and proximity to human development, freshwater systems are affected by a variety of stressors beyond harvest, such as invasive species, habitat loss, and eutrophication. The ways in which these stressors affect a stock's evolutionary response to harvest remains poorly understood.

Ecological changes have the potential to mask, outweigh, or interact with the effects of harvest within a population. For example, Lake Erie yellow perch (*Perca flavescens*) support large commercial and recreational fisheries, yet rapid changes in life-history traits appeared independent of harvest pressure and were attributed to changing environmental conditions (Gíslason et al. 2017). The relative role of the environment or density dependence in phenotypic change in freshwater fishes likely differ from what occurs in some large marine fish stocks where rates of life-history change are strongly linked with fishing intensity (Sharpe and Hendry 2009) and where many of the prominent examples of harvest-induced evolution have focused

(Devine et al. 2012). Such differences in the responses of marine and freshwater fishes could call for different approaches and priorities for management (Dunlop et al. 2018).

Invasive species are a major driver of broad-scale ecosystem change and have had particularly strong impacts in freshwater systems. Invasive species can affect multiple trophic levels in the ecosystems they invade (Townsend 2003), leading to effects on ecosystem services (Pejchar and Mooney 2009). Species invasions can also drive evolutionary changes in native species (Colautti and Lau 2015), which can in turn affect ecological processes such as population growth rate and resource competition (Gillis and Walsh 2017, Rudman et al. 2017).

In this study, we focus on how invasive species can modify the adaptive response of a fish stock to harvest by altering the vital ecological processes of density-dependent growth and recruitment. We investigate the influence of ecological change on harvest-induced evolution of maturation traits in lake whitefish (*Coregonus clupeaformis*), a broadly distributed freshwater fish. In the Laurentian Great Lakes, lake whitefish are an important linkage between the nearshore benthic and offshore pelagic food webs (Rennie et al. 2009) and are harvested by commercial and subsistence fisheries (Brenden et al. 2013). The ecological changes we studied were brought about by the invasion of dreissenid mussels (*Dreissena polymorpha* and *Dreissena bugensis*) (Gobin et al. 2015, 2016), two of the world's most impactful and notorious aquatic invasive species (Higgins and Vander Zanden 2010, Karatayev et al. 2015).

Lake whitefish stocks in the Great Lakes experienced broad-scale shifts in diet, habitat usage, growth, and recruitment stemming from the invasion of dreissenid mussels (Fera et al. 2015, 2017, Gobin et al. 2015, Rennie et al. 2015). These changes included a reduction in growth potential and recruitment rate, consistent with a reduced carrying capacity (Gobin et al. 2015, 2016). Maturation ages and sizes of these stocks also shifted over time (Morbey and Mema 2018, Wang et al. 2008, Fig. S1). We are aware of no previous studies examining the effects of dreissenid mussels on the eco-evolutionary effects of fishing, even though dreissenid mussels have invaded aquatic systems across multiple countries. A previous study (Gobin et al. 2016) modeled the influence of the growth and recruitment changes on lake whitefish harvest sustainability, but did not consider potential evolutionary responses. Morbey and Mema (2018) considered how two different growth trajectories in a lake whitefish population influenced harvest-induced evolution of maturation size, but did not allow for continuous, reciprocal feedbacks between ecological and evolutionary processes and did not consider changes in recruitment. Here we build on these previous studies by developing an eco-genetic model (Dunlop et al. 2009) that enables a broader examination of how the ecological changes caused by an invasive species alter a stock's adaptation and resilience to harvest. We further investigate the effects of multiple selectivity curves that are representative of two commonly used types of fishing gear (trap nets and gill nets) and explore the effects of various mesh sizes and harvest rates, making our findings more generally applicable to other fisheries.

METHODS

We used an eco-genetic modeling framework, a tool that enables joint and seamless interacting effects between ecological and evolutionary processes (Dunlop et al. 2009). This type of model has been employed in many other studies of eco-evolutionary dynamics in fish (e.g. Vincenzi et al. 2014, Ivan and Höök 2015). The model used for this study is individual-based, and modified from a previous evolutionary model of lake whitefish that included more general (i.e. non stock-specific) density-dependent growth and stock-recruitment models (Dunlop et al. 2015), and a previous non-evolutionary version of the present model with the same parameterization (Gobin et al. 2016).

The parameterization of the model (Table A1) is based on empirical data for lake whitefish, but the life-history processes and inheritance structure are described by general relationships that are broadly applicable to other fish species. For example, growth is described using a bi-phasic model derived from bioenergetic principles (Lester et al. 2004). This growth model has been demonstrated with empirical data to fit the growth trajectories of many fish species (Quince et al. 2008), and has been used in numerous studies modeling growth in fish and other taxa (e.g. Cadeddu et al. 2012, Johnston et al. 2013). The previously published non-evolutionary model developed for lake whitefish differed from the present model only in that the genetic variance was set to 0 in the former, thus preventing evolution and making all individuals in the model genetically identical (Gobin et al. 2016). Thus, we only provide an overview of the model here and focus on the evolutionary process that sets the two models apart. Additional details for the full eco-genetic model are provided in Appendix A1.

Individuals in the model undergo birth, somatic growth, maturation, reproduction, inheritance, phenotypic expression, and mortality in annual time steps. Individual traits are tracked, and mean population genotypes and phenotypes are emergent properties of the model. Population-level processes such as density-dependent effects on growth and recruitment are also incorporated into the model, and population metrics such as abundance, spawning stock biomass, and yield are also emergent.

An individuals' annual growth rate h_t was density dependent, being scaled according to the population biomass B following Walters and Post (1993):

$$h_t = h_{max}/(1 + a^*B_t), \tag{1}$$

where a represents the loss of food resources due to intraspecific competition and h_{max} describes the maximum growth rate when $B = 0$. Prior to maturation, an individual's length L at age t was a linear function of h_t, whereas after maturation, this growth rate was reduced owing to reproductive investment (Lester et al. 2004).

Phenotypic plasticity in the size and age at reproduction was included by modeling probabilistic maturation reaction norms (PMRNs), which enables important eco-evolutionary feedback between growth and maturation. The PMRN describes the probability of maturation as a function of an individual's age and size in a given year, thereby accounting for variation in the timing of maturation due to variability in growth rates (Heino et al. 2002). Two evolving traits are present in the model, the slope and intercept of a linear PMRN. No other traits (e.g. growth, reproductive investment) were permitted to evolve. The PMRN slope, a measure of the degree of phenotypic plasticity, and the PMRN intercept, a description of the size-based likelihood of maturing, can evolve over time and represent an individual's genetic trait values. Following a basic quantitative genetics approach, an individual's genetic traits are randomly assigned at birth by drawing from a normal distribution centered on the mid-parental trait value and with variance equal to the genetic variance. Genetic variation is set in the initial population by assuming a given value for the coefficient of genetic variation, CV_G (representing a percentage of the mean initial trait value). The CV_G influences evolvability, having a direct effect on the rate of evolution (Dunlop et al. 2015). We assumed constant genetic variation with a $CV_G = 8\%$, which has been shown to produce modest rates of evolution (Dunlop et al. 2015). An individual's genetic trait values are then expressed phenotypically by the inclusion of environmental variation that is held constant at a level determined by a heritability value assumed in the initial population. In summary, the probability that an individual will mature in a given year is a function of the individual's PMRN phenotype and its age and body length in that year.

Recruitment is density dependent and modeled using a Ricker stock-recruitment relationship:

$$R_t/S_t = r_{max} * \exp(-\beta * S_t), \qquad (2)$$

where R/S is the rate of recruitment of age 0 fish, S is biomass of spawning fish in the population, β is the parameter describing the strength of density-dependence in recruitment, and r_{max} describes the maximum recruitment per unit of spawner biomass.

In addition to the recruitment mortality imposed from the egg to the young-of-year stage through the stock-recruitment relationship, two other sources of natural mortality were included: (i) a constant level of natural background mortality and (ii) predation mortality by sea lamprey (*Petromyzon marinus*), an introduced parasitic fish that preferentially targets larger individuals. Note that although lamprey-induced mortality increases with body size of its prey, its inclusion had very little effect on model results (Appendix A2: Fig. A2 and A3).

Model scenarios

We contrasted model predictions under two separate ecological scenarios that affect the density-dependent processes for growth and recruitment (Fig. 1). The first is a baseline (pre-invasion) scenario represented by high recruitment and growth potential, consistent with a higher carrying capacity and overall more favourable ecosystem conditions (h_{max} = 14.4 and r_{max} = 9, Table A1). The second (post-invasion) scenario is characterized by low recruitment and growth potential, consistent with a reduced carrying capacity and poorer ecosystem conditions (h_{max} = 8.5 and r_{max} = 3, Table A1). These scenarios were based upon density-dependent growth and recruitment relationships observed in Lake Huron lake whitefish before and after the dreissenid mussel invasion (Gobin et al. 2015, 2016). We thus refer to our scenarios as pre- and post-invasion ecological scenarios. All other parameters were set to the same initial values in both scenarios (Table A1).

Commercial harvest

Commercial fishing occurred using either trap nets or gill nets, the two types of gear used in the Great Lakes to target lake whitefish (Brenden et al. 2013). Trap nets operate by retaining fish in a compartment from which they cannot readily escape (like hoop and fyke nets), whereas gill nets retain fish that become wedged or entangled in the mesh. Size-selectivity curves reflect an individual's vulnerability to being caught by the gear given their body length, and were based on empirically-derived relationships for Lake Huron lake whitefish (Zhao and Morbey 2017). Gill net selectivity (V_t), which showed a dome-shaped response (Fig. 2A and C), was described by a double logistic function:

$$V_t = (1/(1 + \exp(-\delta_1 * (L_t/G - \varepsilon_1)))) * (1 - 1/(1 + \exp(-\delta_2 * (L_t/G - \varepsilon_2)))), \quad (3)$$

where L_t is fish length, G is the mesh size, and δ_1, ε_1, δ_2 and ε_2 are parameters. Trap net selectivity (X_t), which showed an S-shaped response (Fig. 2B and D), followed a logistic function:

$$X_t = 1/(L_t + \exp(-\gamma * (L_t - \lambda))), \quad (4)$$

where λ and γ are parameters describing the length of fish with 50% selectivity, and initial slope of the curve, respectively. The harvest rate in the model was varied by scaling these selectivity curves to the maximum harvest proportion P_{max} (the proportion of fish harvested of the most vulnerable length). This was achieved by standardizing the selectivity curve to a maximum value of 1 and multiplying by P_{max} to determine an individual's probability of being harvested (Gobin et al. 2016).

Parameter values for the selectivity curves were developed for the commercial fishing gear used for lake whitefish (Zhao and Morbey 2017). The fishery primarily employs 114 mm stretch mesh gill nets; we ran our scenarios for this mesh size (referred to as the "medium" mesh size), as well as smaller (102 mm) and larger (127 mm) mesh gill nets that are used to capture lake whitefish in fishery-independent surveys. Selectivity curves for small, medium, and large mesh trap nets were developed by shifting the midpoint of the logistic function, λ, to match that of the increasing side of gill net selectivity curves for the 102 mm, 114 mm, and 127 mm size mesh (Fig. 2A), and corresponded to 415 mm, 464 mm, and 517 mm, respectively (Fig. 2B). Our "medium" mesh trap net most closely matches the selectivity of standard trap nets employed by the fishery that have a midpoint (i.e. the length of fish with 50% selectivity) of 471 mm (Zhao and Morbey 2017).

A minimum size limit of 430 mm was implemented in all simulations, such that fish below this length could not be captured. The minimum size limit was based on that used in the southern Lake Huron lake whitefish fishery. Minimum size limits are used in many fisheries and result in a more exacerbated leading edge of the selectivity curve. In commercial fisheries with a minimum size limit restriction, as in Lake Huron, the targeting or capturing of undersized fish is not permitted and fishers avoid unwanted fines by modifying their behavior (e.g., fishing location or time of year) or the gear used (e.g., mesh size). The minimum size limit in our simulations is well below the peak selectivity for all mesh sizes and gear types considered (Fig. 2). Note also that the effect of changing the minimum size limit has been explored extensively in other studies (e.g., Dunlop et al. 2009). For simplicity, we did not investigate the effects of illegal bycatch of undersized fish.

Commercial fishing was initiated in year 100 (to allow stabilization of the population dynamics and traits prior to harvest) and then continued for 100 years. For each scenario, we varied the type of fishing gear employed (gill nets or trap nets), mesh size, and the maximum harvest proportion (Fig. 2). Maximum harvest proportions for each type of fishery and mesh size were varied between 0 and 1, in increments of 0.1 (Fig. 2C and D). The results shown represent the means of a given number of replicate runs. Ten runs were generally sufficient to produce clear trends in mean model results, except for low growth and recruitment rate scenarios for gill net fisheries with harvest proportions greater than 0.4. Due to low population abundance that increased variability in these scenarios, we ran 50 additional replicate simulations (60 replicates in total).

RESULTS

Probabilistic maturation reaction norms (PMRNs) evolved in response to fishing, but the magnitude depended on the underlying ecosystem conditions. Specifically, the evolution of younger ages and smaller sizes at maturation (characterized by a downward shift of the PMRN) was lessened under the post-invasion conditions of low growth and recruitment potential (Fig. 3 and 4). The gill net fishery induced somewhat more evolution than the trap net fishery except for small mesh sizes at low harvest rates (Fig. 3 and 4). The direction of evolution also switched for gill nets at these small mesh sizes and low harvest rates, whereby PMRN midpoints increased when ecosystem conditions were favourable, versus downward-shifting PMRNs when ecosystems conditions were poor (Fig. 4). Most of the evolutionary response came about through evolution of the PMRN intercept, as opposed to the PMRN slope (Fig. 3) as has been predicted and discussed in previous studies (Dunlop et al. 2009; Eikeset et al. 2016). Higher harvest proportions and smaller mesh sizes increased the evolutionary response, as also would be expected from previous eco-genetic models (Dunlop et al. 2009, 2015).

The post-invasion conditions for lake whitefish resulted in lesser declines in mean ages and sizes at maturation compared to pre-invasion conditions (Fig. 5A, Appendix A2: Fig. A4 and A5). Overall, growth rates were faster when fishing under pre-invasion conditions, except at low harvest rates where growth was more similar between scenarios (Fig. 5A, Appendix A2: Fig. A4 and A5). Declines in mean age and size at maturation were greater when fishing with gill nets than when fishing with trap nets (Fig. 5A, Appendix A2: Fig. A4 and A5).

In terms of population metrics, the population biomass, spawning stock biomass, and abundance declined by a greater proportion in response to fishing when growth and recruitment potential were lowered in the post-invasion scenario (Appendix A2: Fig. A4 – A7). Note however that proportional declines in population metrics between the two scenarios are not equivalent in absolute terms due to the different carrying capacity in each scenario (Appendix A2: Fig. A8). The exploitable biomass (i.e. the biomass of fish above the minimum size limit) and yield exhibited trends similar to population biomass (Appendix A2: Fig. A8). A reduction in mesh size resulted in more substantial declines in biomass as the harvest proportion increased. Trends were similar between the two gear types, with a slight tendency for effects to be greater for gill nets when ecosystem conditions were more favourable during the pre-invasion scenario. Age-specific abundances (and mortality) varied substantially between the pre- and post-invasion scenarios, and show the cumulative effect of the mesh size, minimum size limit, harvest rate, gear type, and invasion scenario on the population demographics (Fig. 5B).

DISCUSSION

Ecological changes imposed on lake whitefish by the invasion of dreissenid mussels were predicted to alter the evolutionary response of maturation to harvest and decrease the stock's productivity. When ecosystem conditions were relatively poor in the post-invasion scenario, such that recruitment and growth potential were reduced, slow growth trajectories delayed the ages at which fish became vulnerable to harvest (Fig. 5A and B), resulting in an overall reduced evolutionary response (Fig. 3). This contrasted with the pre-invasion scenario when the stock had a much steeper increase in vulnerability to harvest with age due to faster growth rates (Fig. 5A and B), which enhanced the selective pressure for earlier maturation (Fig. 3). Under the post-invasion scenario where growth and recruitment rates were compromised, the same harvest proportions lead to lower catch rates, particularly for younger age classes compared to when ecological conditions were more favourable for growth and recruitment. Reducing the vulnerability of younger age classes, in turn, reduced selection pressure favouring earlier maturation, much as would occur when minimum size limits are raised (Dunlop et al. 2009). The exception was when growth and recruitment potential were high, and populations were harvested with small mesh gill nets at low harvest rates (Fig. 3 and 4). In that case, the dome-shaped selectivity of the gill net and size of mesh, combined with sufficiently low harvest and faster growth, caused evolution in the opposite direction (an increase in the age and size at maturation) by offering a size refuge for larger fish.

Previous studies have shown how ecological processes like density-dependent growth can mediate evolutionary responses to exploitation (e.g. Lester et al. 2014, Dunlop et al. 2015, Eikeset et al. 2016). However, we took our model scenarios a step further and considered how a shift in growth and recruitment potential brought about by species invasions, alters predictions for harvest-induced evolution. When there is a strong relationship between individual growth and population biomass, fishing can lead to higher growth rates due to increased per capita availability of resources, which in turn leads to earlier maturation through the process of phenotypic plasticity (Trippel 1995). This plastic shift toward earlier maturation means that selection favouring the evolution of earlier maturation is not as strong (Dunlop et al. 2015, Eikeset et al. 2016). In our study, there was density-dependent growth, but the lower growth potential associated with a reduced carrying capacity lessened selection through a different mechanism – decreased vulnerability to size-selective harvest for younger age classes. This occurs despite there being some compensation in growth rate when population biomass is reduced by fishing and there are declines in recruitment.

The low growth and recruitment scenario we considered is consistent with a reduction in carrying capacity; in other words, ecological conditions do not allow the population to reach the same growth or recruitment levels that it once could. Carrying capacity has been defined as the maximum population biomass that can be sustained on a finite level of resources (Hayes et al. 1996). Changes in carrying capacity within aquatic ecosystems can occur in response to many factors, including nutrient loading, species invasions, habitat loss, and climate change (Vert-pre et al. 2013, Britten et al. 2016). In the Laurentian Great Lakes, profound changes have occurred coinciding with the establishment of dreissenid mussels, including catastrophic declines in key invertebrate and prey fish populations (reviewed in Higgins and Vander Zanden 2010). Lake whitefish have exhibited an increase in age at 50% maturity and decrease in length at 50% maturity (Appendix A2: Fig. A1), a different trend than would be expected if evolution of earlier maturation was a strong contributing factor. Although the potential for harvest-induced evolution still exists, our model predicts that the changes in carrying capacity for lake whitefish caused more substantial plastic responses in life history and population dynamics, rather than evolutionary responses in maturation. If poor ecological conditions persist, this would lessen the selection for earlier maturation, which sets lake whitefish apart from many of the harvested marine fish stocks where trends toward earlier maturation are observed (e.g. Devine et al. 2012). It appears that the strong density-dependence and substantial environmental forcing experienced by freshwater populations, including those in the Great Lakes, could result in different evolutionary responses compared to those found for the large marine fish stocks, where fisheries-induced evolution has been most prominently studied (Dunlop et al. 2018).

Evolution of maturation reaction norms contributed to the stock's resilience to collapse as in previous studies (Eikeset et al. 2013, Dunlop et al. 2015) in that populations in the current study withstood harvest levels that led to collapse under the same ecological conditions in the non-evolutionary version of this model (see Gobin et al. 2015, 2016). This can be seen as an example of fisheries-induced evolution having a positive effect on ecosystem services (Rudman et al. 2017), a somewhat different perspective than those studies focusing on the undesirable nature of trait changes that can also be of concern (Jørgensen et al. 2007). However, ecological changes stemming from the dreissenid-mediated effects had far greater effects on population productivity and yield than fisheries-induced evolution, often resulting in substantial declines in key metrics (Appendix A2: Fig. A8). Although these simulated populations persisted in the face of dreissenids, other indicators and reference points suggest that their long-term sustainability would be at risk. For example, the number of young fish recruited to the population declined with increasing harvest rate under post-invasion conditions even though these fish are not of a harvestable size (Fig. 5B). Such declines in recruitment are indicative of recruitment overfishing, resulting from reductions in the spawning stock biomass. At the same time, when growth and recruitment potential were higher, we observed little difference in population metrics between an evolving population and a non-evolving population (Gobin et al. 2016).

Taken together, the results of this study and those of Gobin et al. (2016) predict that the invasion of dreissenid mussels has altered the selective pressure of harvest, while also increasing the chances of collapse and reducing the commercial yield potential of the stock. Lake whitefish support highly valuable commercial and subsistence fisheries in the Laurentian Great Lakes, and are a binational management priority for multiple agencies and jurisdictions (Brenden et al. 2013). Fishery yield in several regions of the Great Lakes declined following the dreissenid invasion and have since remained below pre-invasion levels (Ebener 2012, Lantry et al. 2017). Considering the eco-evolutionary dynamics predicted, it is unlikely that fishery yield will return to pre-invasion levels or that harvesting at these levels would be sustainable without further environmental change or management intervention. Although our study focuses on a single widely distributed and economically important species, it has broader implications for other systems experiencing species invasions. The influence of species invasions on fisheries-induced evolution and more generally on fishery sustainability for native species has been rarely studied to date. One of the only examples we could find, is the study by Sharpe et al. (2012) where the introduction of Nile perch (*Lates niloticus*) into Lake Victoria combined with commercial fishing led to phenotypic life-history changes in a native cyprinid fish. Clearly, more research is needed on this topic given the global occurrence of species invasions and the impacts they have on food webs and harvested species within those systems (Pejchar and Mooney 2009).

Changing the gear type had subtler effects on the evolutionary response to harvest compared to altering harvest rates or mesh sizes. Gill nets (dome-shaped curve) generally induced slightly more evolution in maturation reaction norms than trap nets (S-shaped curve), except with small mesh sizes and low harvest rates when ecosystem conditions were favourable. Some studies have predicted that dome-shaped selectivity curves may slow rates of evolution compared to knife-edge or S-shaped selectivity curves by allowing older, larger individuals that experience disproportionately greater reproductive success to be retained in the population (Hutchings 2009, Jørgensen et al. 2009). Zimmermann and Jørgensen (2017) examined the effects of gear selectivity using a model for Northeast Arctic cod (*Gadus morhua*) and found that dome-shaped selectivity increased yield and reversed harvest-induced evolution compared to S-shaped selectivity. Alternatively, a model by Gårdmark and Dieckmann (2006) predicted evolution of smaller maturation sizes (and ages) even when size-selective mortality provided refuges for larger individuals. Our results build on these previous studies by showing that predictions depend on ecological conditions and other factors such as mesh size and harvest rate. One reason why our model predicts slightly faster evolution with a dome-shaped curve across all but lower harvest rates and smaller mesh sizes, is that there is a steeper increase in vulnerability to harvest as sizes increase toward the leading edge of the selectivity curve (Fig. 2, 6). Similar trends are predicted when harvesting fish just prior to the average onset of maturation (Dunlop et al. 2009, 2018). The potential effects of providing a size refuge to larger fish under dome-shaped selectivity, as predicted by Zimmermann and Jørgensen (2017), are experienced in our whitefish populations when harvest is low, mesh sizes are small enough, and ecosystem conditions are favourable. This was a similar result to that found by Morbey and Mema (2018), whereby small mesh gill nets buffered the evolution of size thresholds for maturation in lake whitefish fished at low rates under fast growing conditions. This is because more individuals are able to grow through and reach the protected size window. Thus, the benefits of providing refuges for older, larger fish in terms of evolutionary responses of maturation traits to size-selective harvest depend on interactions with ecological processes and harvest rates.

To broaden the results of our study beyond the Great Lakes, we investigated the response to changing mesh size, which could represent a potential management option for mitigating the undesirable effects of fisheries-induced evolution such as slow recovery, early reproduction, and economic losses. For both trap and gill nets, harvesting with larger mesh sizes generally resulted in less evolution of the PMRN, except for the case described previously when fishing at low rates with a small mesh gill net. The overall trend of reduced selection for earlier maturation when mesh size (or minimum size harvested) is increased has been observed in several previous studies (e.g. Dunlop et al. 2009, Mollet et al. 2016). In the context of Lake Huron, we note that the medium mesh size is what is currently used in the commercial fishery, resulting in most harvest being directed at fish that have already matured. This lessens selection for early maturation relative to some of the large marine fish stocks where higher proportions of juvenile fish are harvested (Dunlop et al. 2018). This particular aspect of size-selectivity in the Great Lakes whitefish fishery could be one reason why maturation age has not undergone consistent declines over the past several decades (Appendix 2: Fig. S1; Morbey and Mema 2018) despite continued commercial harvest pressure, as has been observed in almost all fish stocks where fisheries-induced evolution has been documented (Devine et al. 2012).

One limitation of our model is that while PMRN slopes and intercepts were permitted to evolve, other traits were not. Harvest can induce evolution of a variety of life history traits and behaviors (Heino et al. 2015). Growth declined in lake whitefish harvested through a gill net fishery in Lesser Slave Lake (Handford et al. 1977), despite the tendency of lake whitefish to exhibit compensatory growth in response to reductions in population size (Healey 1975). Common whitefish (*Coregonus lavaretus*) in Lake Constance experiencing an intense size-selective fishery and changes in lake phosphorus underwent shifts in reproductive investment, which the authors suggested could be the result of evolution, although other factors could have contributed as well (Thomas et al. 2009). We focused on PMRNs specifically because previous empirical studies have reported consistent and dramatic downward shifts in the PMRN midpoints of many fish stocks (Devine et al. 2012), consistent with rapid fisheries-induced evolution as predicted in numerous modeling studies (e.g., Dunlop et al. 2015, Mollet et al. 2016). Furthermore, previous modeling studies of multi-trait evolution have shown that PMRN intercepts undergo fisheries-induced evolution to a greater extent than other traits, including growth and reproductive investment, although the response does depend on the size-selectivity of harvest (Dunlop et al. 2009). We also felt that it was important to first investigate the role of ecological change on PMRNs, before including the further complexity of additional evolving traits. In this way, focusing on a well-studied trait allowed us to determine how the added complexity of ecological change altered previous predictions.

Growth rate is a particularly relevant trait that could evolve to be higher or lower in response to harvest, depending on the size-selectivity of the fishery, strength of density-dependence, and presence of phenotypic plasticity (Dunlop et al. 2009, Enberg et al. 2015). For example, a study of alpine whitefish (*Coregonus palaea*) measured selection differentials on growth in response to commercial harvest of 1-year old fish and found evidence of evolution toward slower growth (Nusslé et al. 2009). When mesh sizes or gear target mature fish, as is the case for many Great Lakes fisheries, this would favour evolution for slower growth while decreasing selection for earlier maturation (Dunlop et al. 2009). Condition factor (or girth) might be another trait under selection from gill nets, as was believed to be the case for lake whitefish in Lesser Slave Lake (Handford et al. 1977). Behavioral traits such as timidity or aggressiveness could also evolve in response to fishing with passive gear types including both gill and trap nets (Arlinghaus et al. 2017). Given the many interactions that occur between various life-history and other traits, our predictions could differ if multiple traits were permitted to evolve. Furthermore, these additional traits could evolve in response to other selective pressures besides harvest, including the changing ecosystem conditions themselves.

Another limitation was that our model did not consider multi-species responses and interactions. Dreissenid mussels have broadly impacted the food webs of the systems they have invaded (Higgins and Vander Zanden 2010). The growth and recruitment declines in lake whitefish represent an example of how the food web changes from dreissenids have manifested to impact a commercially harvested fish (Fera et al. 2015, 2017, Gobin et al. 2015, 2016). We then take these empirical findings one step further to predict how the changes might affect eco-evolutionary responses to harvest. We also included predation by sea lamprey as another form of size-dependent mortality, but this had little impact on the overall results due the relatively low mortality from sea lamprey compared to fishing, and because sea lamprey predation tends to target larger-sized fish that have already reproduced (Appendix A2: Fig. A2 and A3). A subsequent step could be to include additional species or trophic level responses. New and exciting research is emerging that shows how multi-species responses can alter the evolutionary effects of harvest and, more generally, are important in shaping eco-evolutionary dynamics (Audzijonyte and Kuparinen 2016, Kindsvater and Palkovacs 2017). However, we believe that there is still much to learn about how the eco-evolutionary dynamics of individual stocks are influenced by basic ecological processes that commonly undergo changes in response to stressors such as species invasions.

Our model illustrates the critical role of eco-evolutionary feedbacks when making predictions about the response of a population to harvest. The need to account for fisheries-induced evolution as part of an ecosystem-based management approach has been recognized (Francis et al. 2007), prompting recommendations for conducting evolutionary impact assessments for stocks of management importance (Laugen et al. 2014). Our findings indicate that adequately accounting for eco-evolutionary feedbacks is crucially important in any such evolutionary impact assessment. The use of an eco-genetic model in the evolutionary impact assessment for North Sea plaice (*Pleuronectes platessa*) demonstrates how interactions between density-dependence, phenotypic plasticity, and trait evolution can be integrated seamlessly (Mollet et al. 2016). Future evolutionary impact assessments could further benefit by considering changing environmental conditions as brought about by factors such as climate change and eutrophication, as they could interact with evolutionary dynamics in fundamental ways. The development and application of empirical approaches that consider not only how traits evolve in response to human-induced selection, but also how they interact with a constantly changing ecosystem, including multi-trophic level responses, will be important for demonstrating the significance of the eco-evolutionary feedback loop to issues of broad societal concern.

ACKNOWLEDGEMENTS

We thank the Upper Great Lakes Management Unit of the Ontario Ministry of Natural Resources and Forestry for providing data used in this study, and the Great Lakes Fishery Commission for funding. We also thank several anonymous reviewers whose feedback improved our manuscript.

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DATA AVAILABILITY

Data available from the Dryad Digital Repository: doi:10.5061/dryad.3g227m5

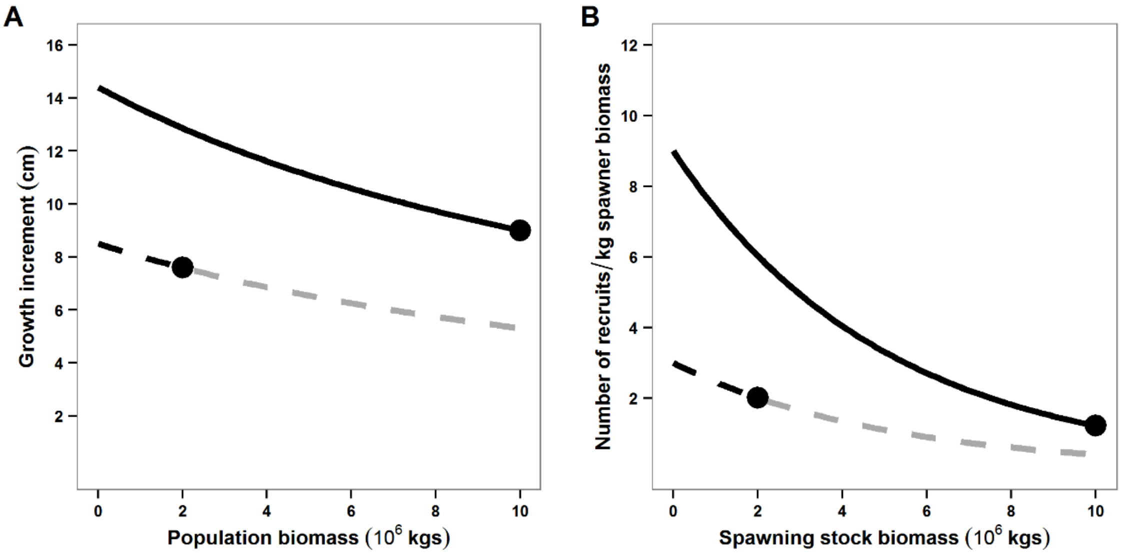

Figure 3.1. Model scenarios used to examine the effects of ecosystem conditions before and after the dreissenid invasion on lake whitefish. A) Growth potential and B) recruitment potential are reduced between the pre-invasion scenario (solid blue lines; h_{max} = 14.4 and r_{max} = 9) and the post-invasion scenario (dashed red lines; h_{max} = 8.5 and r_{max} = 3). Blue and red lines depict relationships up to the carrying capacity in each scenario (marked by filled circles ●), measured as the population biomass equilibrium value in the absence of harvest (Gobin et al. 2016). Grey curves extending beyond the carrying capacity (i.e. population sizes not achieved during simulations) are shown to facilitate visual comparisons of relationships.

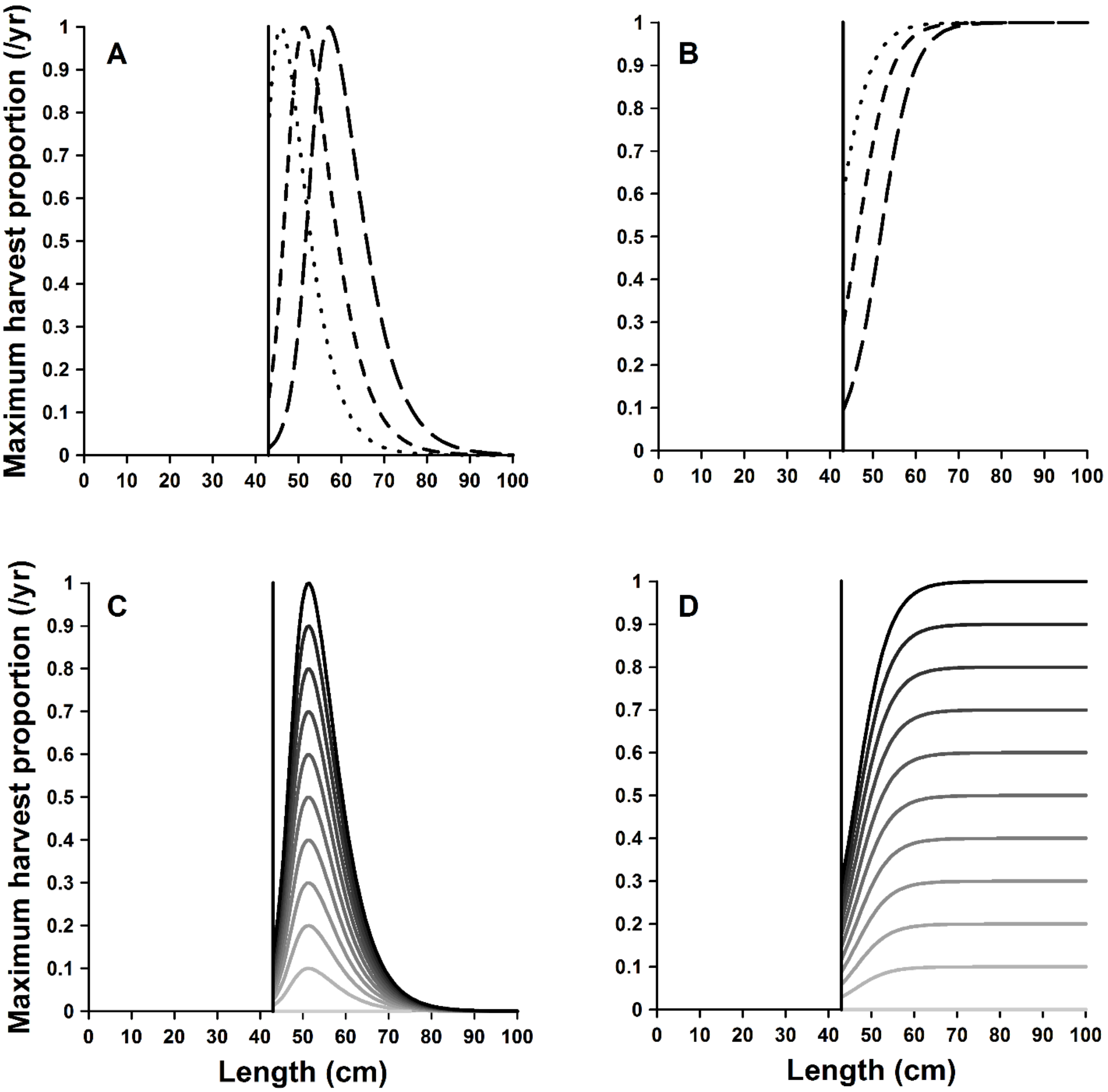

Figure 3.2. Size-selective fishing regimes implemented in the eco-genetic model for lake whitefish. Vertical black lines mark the minimum size limit of the fishery, below which fish could not be harvested. Gill net selectivity curves (shown in panels A and C) are defined by a double-logistic function, whereas trap net selectivity curves (shown in panels B and D) are defined by a logistic function. We varied mesh sizes from small to large (panels A and B; small mesh=short dash, medium mesh= medium dash, large mesh= long dash). Selectivity curves for small, medium, and large mesh gill nets represent 102 mm, 114 mm, and 127 mm mesh, respectively (panel A). Selectivity curves for small, medium, and large mesh trap nets corresponded to 415 mm, 464 mm, and 517 mm, respectively (panel B). Maximum harvest proportions were varied between 0 and 1 in increments of 0.1 (panels C and D; lines become darker with increasing harvest proportions and are shown for medium mesh sizes only).

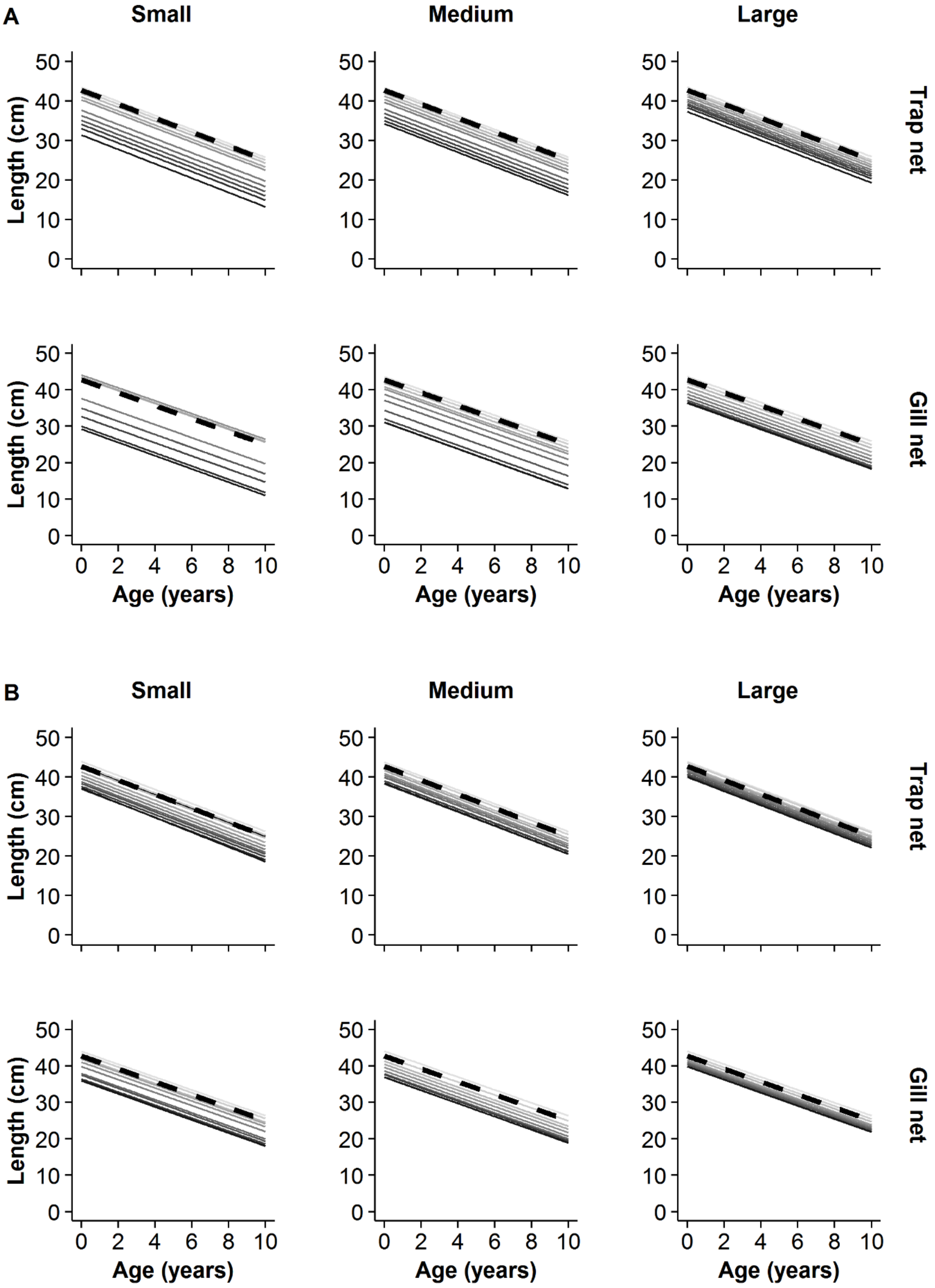
A
Small
Medium
Large
Trap net
Gill net
Length (cm)
0
10
20
30
40
50
Age (years)
0
2
4
6
8
10
B
Small
Medium
Large
Trap net
Gill net
Length (cm)
Age (years)

Figure 3.3. Fisheries-induced evolution of mean probabilistic maturation reaction norms (PMRNs) for different ecological conditions. Top panels (A) have a higher growth and recruitment potential (pre-invasion) and lower panels (B) have a lower growth and recruitment potential (post-invasion). Panels from left to right show results for different mesh sizes. In each panel, dashed black lines depict the initial population's mean PMRN (assumed to be the same in all scenarios) while solid lines show mean PMRNs in the final simulation year after 100 years of harvest. Darker lines represent higher harvest rates. Results shown are population means averaged across replicate simulation runs.

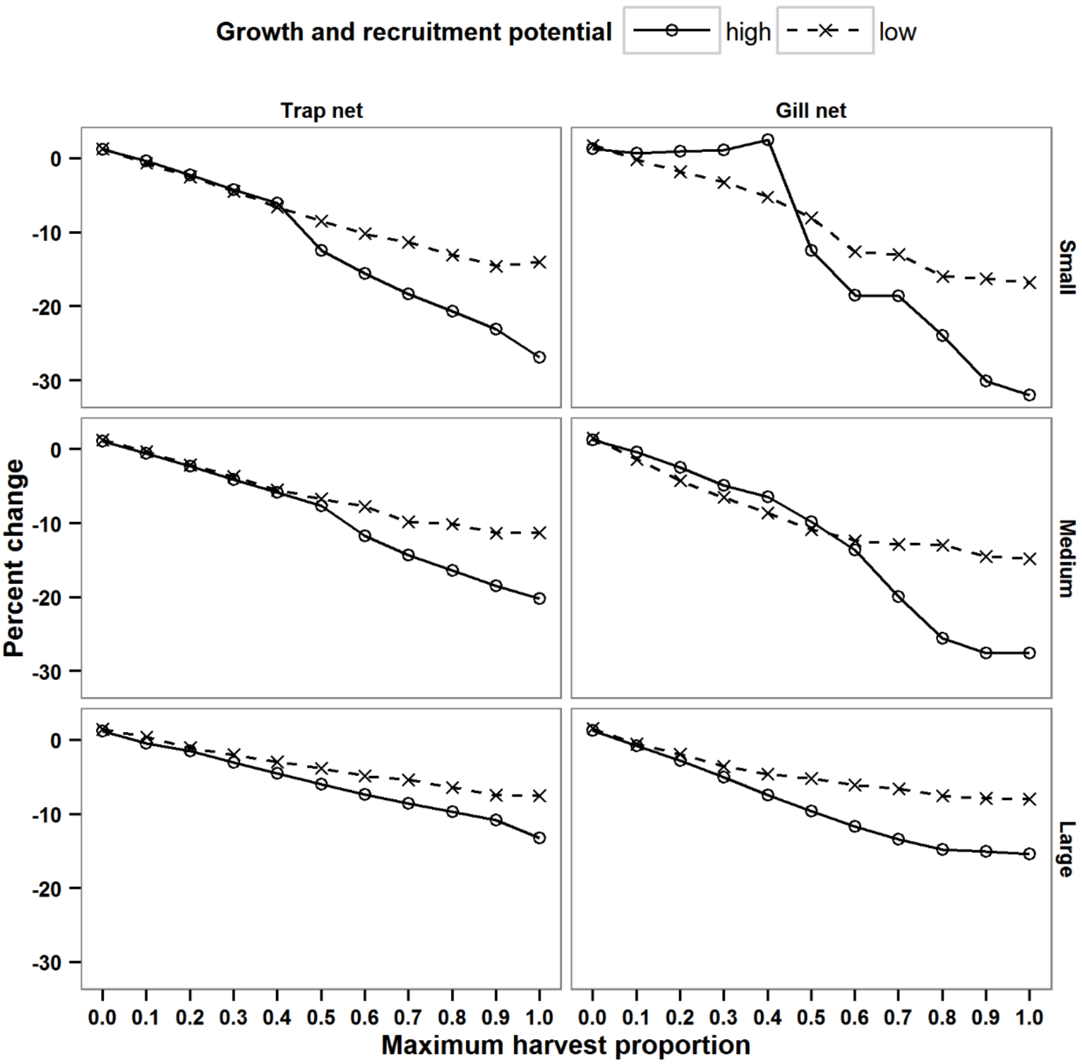

Figure 3.4. Mean percent change in PMRN intercepts over a period of 100 years of harvest. Negative values represent declines in the PMRN intercept whereas positive values represent increases in the PMRN intercept. Results shown are changes in population means averaged across replicate simulation runs.

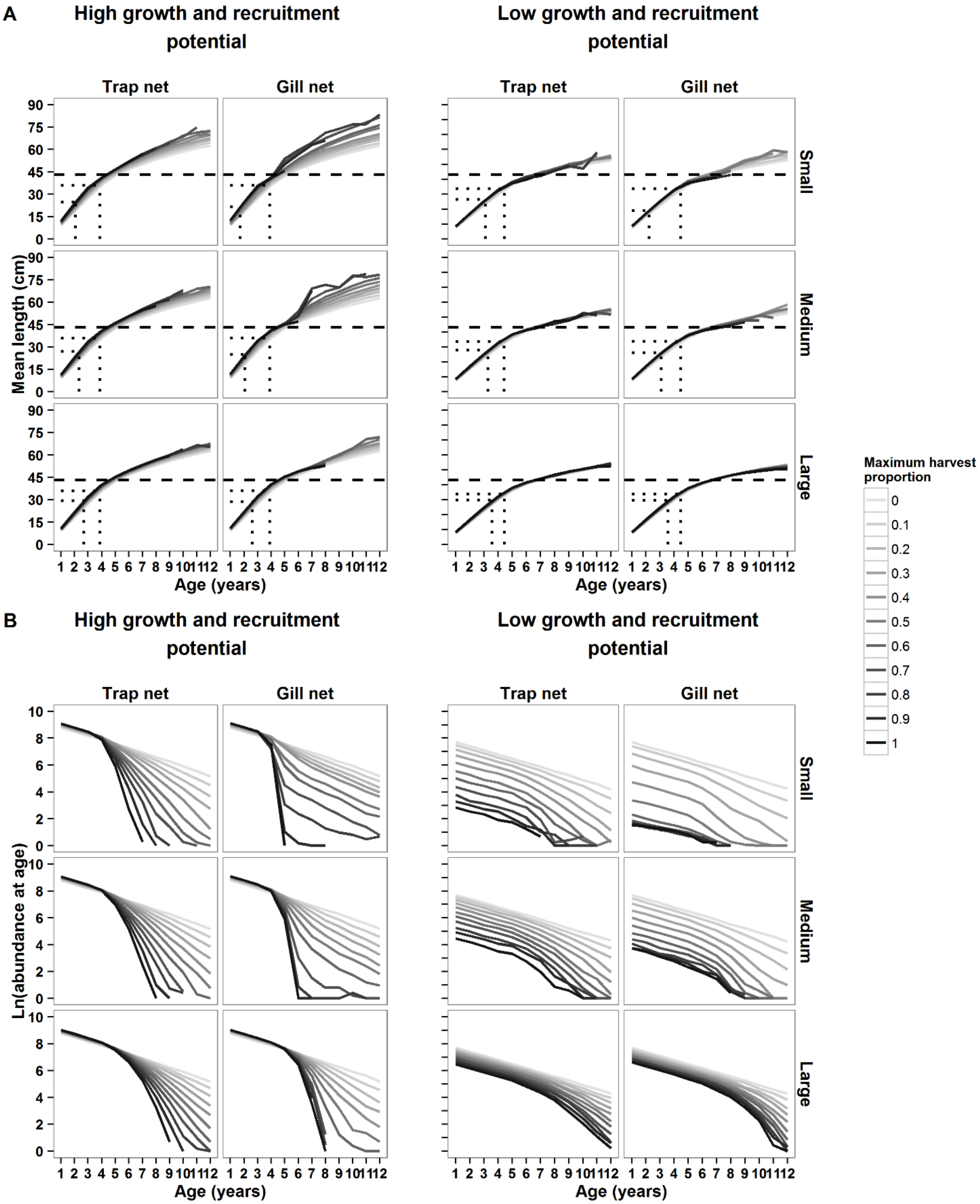

Figure 3.5. Predicted mean length-at-age (A) and natural log-transformed mean abundance at age (B) in the final year of harvest for different ecological conditions (high growth and recruitment, low growth and recruitment) and mesh sizes (small, medium, large). In (A), the dotted lines in each panel mark the range of mean ages and sizes at which fish matured and the horizontal

dashed line marks the minimum size limit for the fishery. In (B), the slopes of the lines reflect age-specific total mortality rates (where steeper slopes represent higher mortality). In both (A) and (B), the results shown are means of replicate simulation runs.

APPENDIX 3.1. MODEL DESCRIPTION

We used an individual-based eco-genetic model developed for lake whitefish stocks in Lake Huron (Gobin et al. 2016). This model was previously used to evaluate the effects of changes in density-dependent relationships on lake whitefish population dynamics and harvest in the absence of evolution (Gobin et al. 2016), and was based on an earlier model used to examine evolution of traits in several fish species, including lake whitefish (Dunlop et al. 2015). Individuals in the model are tracked from birth to death. The model runs on an annual time step, with individuals undergoing birth and inheritance, phenotypic expression, growth, maturation, reproduction, and mortality.

The annual growth rate h_t of individuals in the model is density dependent, following Walters and Post (1993):

$$h_t = h_{max}/(1 + a*B_t), \qquad \text{(A1)}$$

where B_t is population biomass in year t, a is the loss of food resources due to intraspecific competition, and h_{max} is the maximum growth rate when $B = 0$. An individual's lifetime growth is described by the mechanistically-based biphasic growth model described by Lester et al. (2004). Prior to maturation, the growth rate of individuals is linear where length L in year t is h_t*t. After maturation, a proportion of available energy is diverted away from growth and is invested in reproduction,

$$L_{t+1} = ((3/(3 + \mathrm{GSI})) * L_t) + (3*h_t/(3+\mathrm{GSI})), \qquad \text{(A2)}$$

where g is the reproductive investment (calculated by multiplying an energy conversion factor by the empirically measured ratio of gonad mass to body mass). For the purposes of calculating biomass measures in the model, an individual's length (L_t) was converted to body mass W_t assuming a simple relationship,

$$W_t = c * L_t^d, \tag{A3}$$

where c and d are parameters (Wootton 1998).

Phenotypic plasticity is included in the model using probabilistic maturation reaction norms (PMRNs), which allows for variation in the age and size at maturation as a function of the environment. Phenotypic plasticity is an important characteristic of fish stocks (Lorenzen 2016), and is a key component of the eco-evolutionary feedback loop (Dunlop et al. 2009). Including phenotypic plasticity allows us to capture a key trend observed in empirical studies where harvesting leads to changes in a stock's ages and sizes at maturation because growth rates increase from density-dependent compensation (Rose et al. 2001). PMRNs describe the probability that individuals will mature as a function of age ¥ and length L, thereby accounting for variation in the timing of maturation due to variability in growth rates (Heino et al. 2002). Lower and upper bounds encompassing the range of sizes over which individuals of a given age could mature (curves often representing the 25% and 75% probabilities of maturing at a given age and size) define the width ω of a PMRN. PMRNs were linear, being characterized by a slope s and intercept I, which define an individual's length when their probability of maturing is 50% (often termed the PMRN midpoint) at a given age,

$$L_{p50} = I + s * ¥. \tag{A4}$$

The individual's PMRN midpoint represents their maturation genotype. The slope and intercept are evolving traits in the model that are inherited independently at birth. Inheritance occurs by randomly drawing an individual's trait value from a normal distribution centered on the mid-parental value (the mean of the two parent trait values) and with a variance given by the genetic variation, σ_G^2. The genetic variation is held constant through time by assuming a coefficient of genetic variation CV_G, which is the standard deviation of the trait divided by the mean of that trait. The genetic variation is calculated by multiplying the assumed CV_G (e.g. 10%) by the mean trait value (to give the standard deviation), and then squaring the total. The mean trait value is estimated from empirical data in the initial population. In other words, CV_G defines the genetic variability of the trait, and has a direct effect on the rate and magnitude of evolution (Houle 1992, Dunlop et al. 2015). In our model, we assumed a CV_G of 8%, which produces modest rates of evolution (Dunlop et al. 2015). In a study by Dunlop et al. (2015), varying the CV_G from 0%-12% resulted in an approximately 3-fold difference in PMRN midpoints for lake whitefish at high harvest rates.

Following basic quantitative genetics, trait values of offspring are not expressed with perfect heritability (i.e., heritability < 1); in other words, offspring don't look exactly like their parents. We include phenotypic expression of genetic traits in our model by adding environmental variation. To do this, phenotypic trait values are drawn randomly from a normal distribution centered on the genetic trait value and with variation around the mean given by the environmental variation, σ_E^2. That environmental variation is given by,

$$\sigma_E^2 = \sigma_G^2(1/H - 1), \tag{A5}$$

where H is the population's initial heritability. Heritability is defined as the ratio between genetic and phenotypic variation, the latter being the sum of genetic (σ_G^2) and environmental (σ_E^2) variation. The above equation for σ_E^2 is simply a rearrangement of $H=(\sigma_G^2/\sigma_G^2{*}\sigma_E^2)$. For simplicity, σ_E^2 is held constant through time.

The probability that an individual will mature in a given year is given by,

$$p_m = \frac{1}{1+e^{-(L_t - L_{p50})/u}}, \tag{A6}$$

where $u = \omega$ /logit(upper limit of PMRN width) - logit(lower limit of PMRN width) = ω/(ln(0.75/0.25)-ln(0.25/0.75)).

Once an individual becomes mature, it can reproduce. Spawning pairs consisting of mature males and females are determined randomly. Offspring are allocated to parents by a random number draw scaled to the fecundity of the largest individual for each sex; an offspring is allocated to that mature individual if this random number is less than the value of that individual's fecundity. Therefore, fecundity is length-dependent, with larger females producing larger numbers of offspring in accordance with Kratzer et al. (2007).

Early survival rates were applied through a Ricker stock-recruitment relationship, incorporating density-dependence in recruitment:

$$R/S = r_{max} * \exp(-\beta * S_t), \tag{A7}$$

where R/S is the rate of recruitment of age 0 fish, S is biomass of spawning fish in the population, β is the parameter describing the strength of density-dependence in recruitment, and r_{max} describes the maximum recruitment per unit of spawner biomass (Hilborn and Walters 1992). Equation (7) determines the total number of recruits produced (i.e. the new fish born into the population) in a given year. Sex is assigned randomly at birth.

In addition to the recruitment mortality from the egg to newborn stage, two other sources of natural mortality were implemented. First, a constant level of natural background mortality was applied to all individuals equally in the model. This was estimated using Pauly (1980), which theoretically accounts for all sources of mortality except fishing. Second, we included size-dependent predation by sea lamprey (*Petromyzon marinus*) as it is a unique component of the study system that contributes mortality disproportionately to larger fish. The sea lamprey is an invasive species introduced to the Great Lakes in the 1950s that preys on native fishes, including lake whitefish. The probability of a sea lamprey attack ($L_{attack,t}$) in our model increases with fish body length, following the wounding rate relationship described by McLeod et al. (2011), with a 75% mortality rate applied to an attack if it occurs (Spangler et al. 1980):

$$L_{attack,t} = 1/(1 + \exp(p - n * L_t)), \tag{A8}$$

where L is the individual's length in year t, and p and n are parameters. Given the potential for this additional size-dependent mortality cost to impact selection, we evaluated its effects in the absence of harvest by separately running simulations with and without sea lamprey predation.

Parameterization

The model parameterization is the same as that described in Gobin et al. (2016), and a list of parameter values with their sources are provided in Table A1. We developed the model for lake whitefish stocks in the southern main basin of Lake Huron, which supports a valuable commercial fishery and for which sufficient data is available to parameterize the model. The model was parameterized using (1) data collected by the Ontario Ministry of Natural Resources and Forestry (OMNRF) from their standardized offshore gill netting survey (Speers 2013); (2) the statistical catch-at-age stock assessment model for lake whitefish in the QMA 4-5 management area (based on Ebener et al. 2005); and (3) the published literature for parameters that could not be estimated from the first two sources. Mean population PMRN slope and intercept values used to initialize populations in the model were estimated from empirical data from the OMNRF surveys for the QMA 4-5 region using the method described by Barot et al. (2004). Because this method is not robust with small sample sizes, logistic regressions of size with maturity status (mature/immature) were only fit for consecutive age classes and cohorts with data available for >100 individuals, which was then used to estimate size-specific probabilities of maturing for each age. A linear regression was then fit to the maturation probability midpoints (p=0.5) for each age to calculate mean population PMRN slope and intercept values used to initialize the model. The PMRN slope and intercept values are then free to evolve over time.

Table A1. Parameter values and sources used in the individual-based eco-genetic model for lake whitefish in the southern main basin of Lake Huron.

Description	Symbol	Source	Value
Mean PMRN[*] intercept[†] (cm)	I	1	42.7
Mean PMRN slope[†] (cm/yr)	s	1	-1.77
Heritability[†]	H	2	0.2
Coefficient of genetic variation	CV_G	2	0.08
PMRN width (defining 0.25 and 0.75 probabilities) (cm)	ω	1	10.6
Mean maximum growth potential (cm)	h_{max}	3	14.4 (high), 8.5 (low)
Intraspecific competition food loss rate (kg^{-1})	a	3	6e-5
Reproductive investment[‡]	GSI	4,5	0.346
Mean maximum recruitment potential (# of recruits)	r_{max}	3	9 (high), 3 (low)
Ricker stock-recruitment parameter (kg^{-1})	β	3	2e-4
Constant in length-weight relationship (kg/cm^{d})	c	6	3.318e-6
Exponent in length-weight relationship	d	6	3.29
Exponent of length-fecundity relationship	j	7	3.83
Slope of length-fecundity relationship (eggs/mm^{j})$^{-10\text{^}3}$	i	7	1.1e-6
Background natural mortality[§] (year^{-1})	M_B	8	0.30
von Bertalanffy asymptotic length (cm)	L_∞	8	60.0
Brody's growth coefficient (in von Bertalanffy growth model) (year^{-1})	k	8	0.25
Water temperature T (°C)	T	8	6
Wounding probability logistic model coefficient	p	9	8.60
Wounding probability logistic model coefficient (mm^{-1})	n	9	0.01
Lamprey mortality probability		10	0.75
Double logistic gill net selectivity parameter (mm^{-1})	δ_1	11	5.84
Double logistic gill net selectivity parameter (mm)	ε_1	11	4.19

Double logistic gill net selectivity parameter (mm^{-1})	δ_2	11	2.19
Double logistic gill net selectivity parameter (mm)	ε_2	11	4.74
Gill net selectivity mesh size (mm)	G	11	102, 114, 127
Logistic trap net selectivity parameter (mm)	λ	11	415, 464, 517
Logistic trap net selectivity parameter	γ	11	0.026
Fishery minimum size limit (mm)		12	430

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[*] Probabilistic maturation reaction norm

[†] Values are defined for the initial population and are then free to change through time

[‡] Calculated by multiplying the gonadosomatic index (gonad mass divided by body mass) by a conversion factor of 1.73 to account for differences in the energetic content of gonad and somatic tissues (Lester et al. 2004).

[§] Background natural mortality was estimated from the relationship between von Bertlanffy growth model parameters and mean annual temperature (Pauly 1980, Ebener et al. 2005).

Data sources are:

1. OMNRF survey data for years 1984-2009.
2. Dunlop et al. (2009).
3. Gobin et al. (2016).
4. Based on estimates from Johnston et al. (2012); Lumb et al. (2007); Cook et al. (2005).
5. Lester et al. (2004).
6. OMNRF survey data for years 1984-1992.
7. Kratzer et al. (2007) Alpena study site for years 1986-1987.
8. OMRNF Statistical catch-at-age stock assessment model for QMA 4-5 based on Ebener et al. (2005).
9. McLeod et al. (2011) southern main basin for the year 2000.
10. Spangler et al. (1980).
11. Zhao and Morbey (2017).
12. Ebener et al. (2008).

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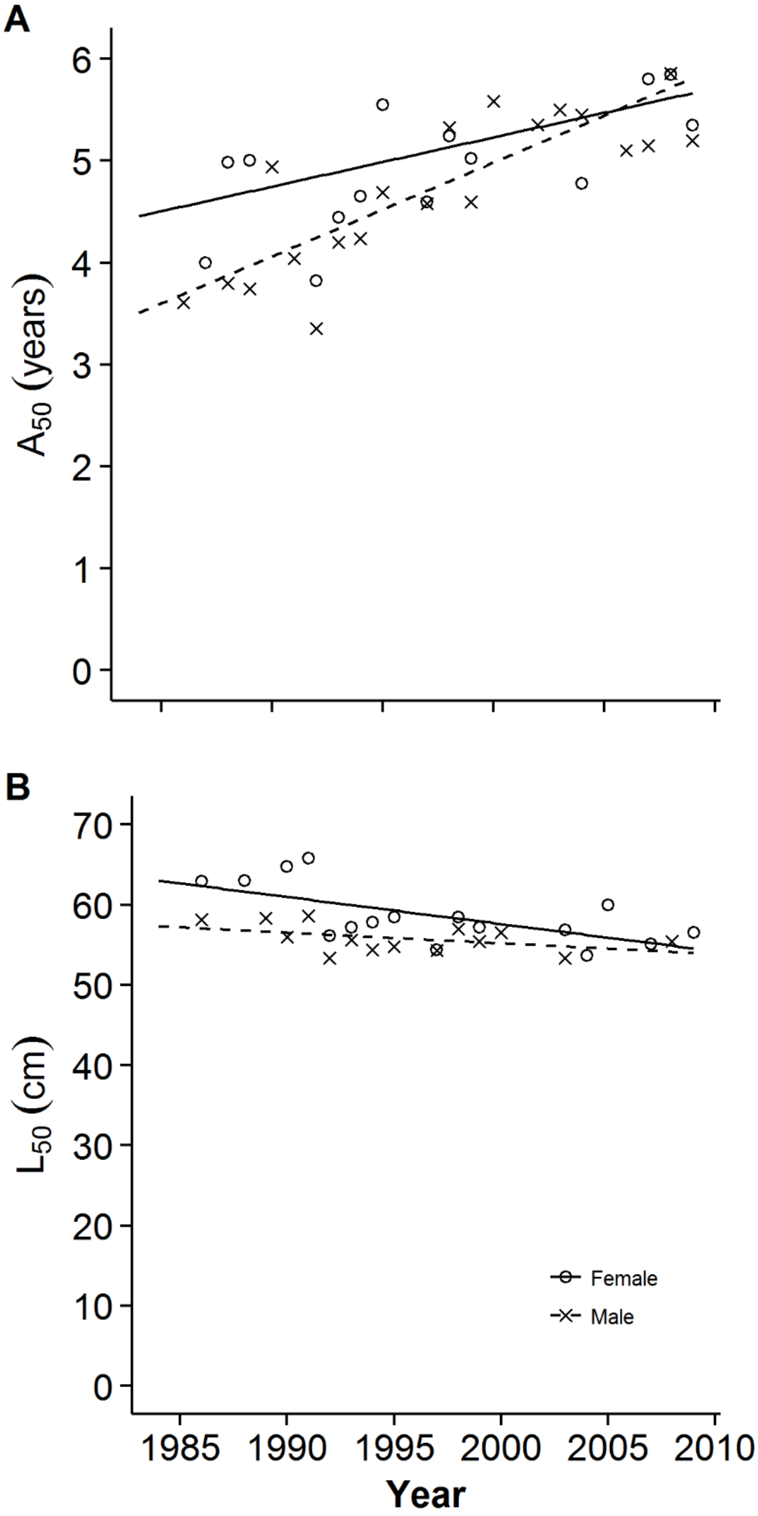
APPENDIX 3.2. SUPPLEMENTARY FIGURES

Figure A1. Observed mean (A) age and (B) size at 50% maturity of lake whitefish in the southern main basin of Lake Huron from 1985 to 2009 estimated from data collected through the Ontario Ministry of Natural Resources and Forestry offshore index netting survey using the method developed by Chen and Paloheimo (1994). Trend lines for age at 50% maturity over time show a significant increase in mean age for males from 3.7 to 5.8 years between 1986 and 2009 (F1,19 = 40.59, adj. R2 = 0.66, P <0.001), and a nearly significant increase from 4.6 to 5.6 years between 1987 and 2009 for females (F1,14 = 4.50, adj. R2 = 0.19, P =0.05). Female length at 50% maturity also declined significantly from approximately 62 to 55 cm (F1,14 = 10.05, adj. R2 = 0.37, P =0.007), whereas declines in mean length at 50% maturity were not statistically significant for males (F1,12 = 3.10, adj. R2 = 0.14, P =0.10).



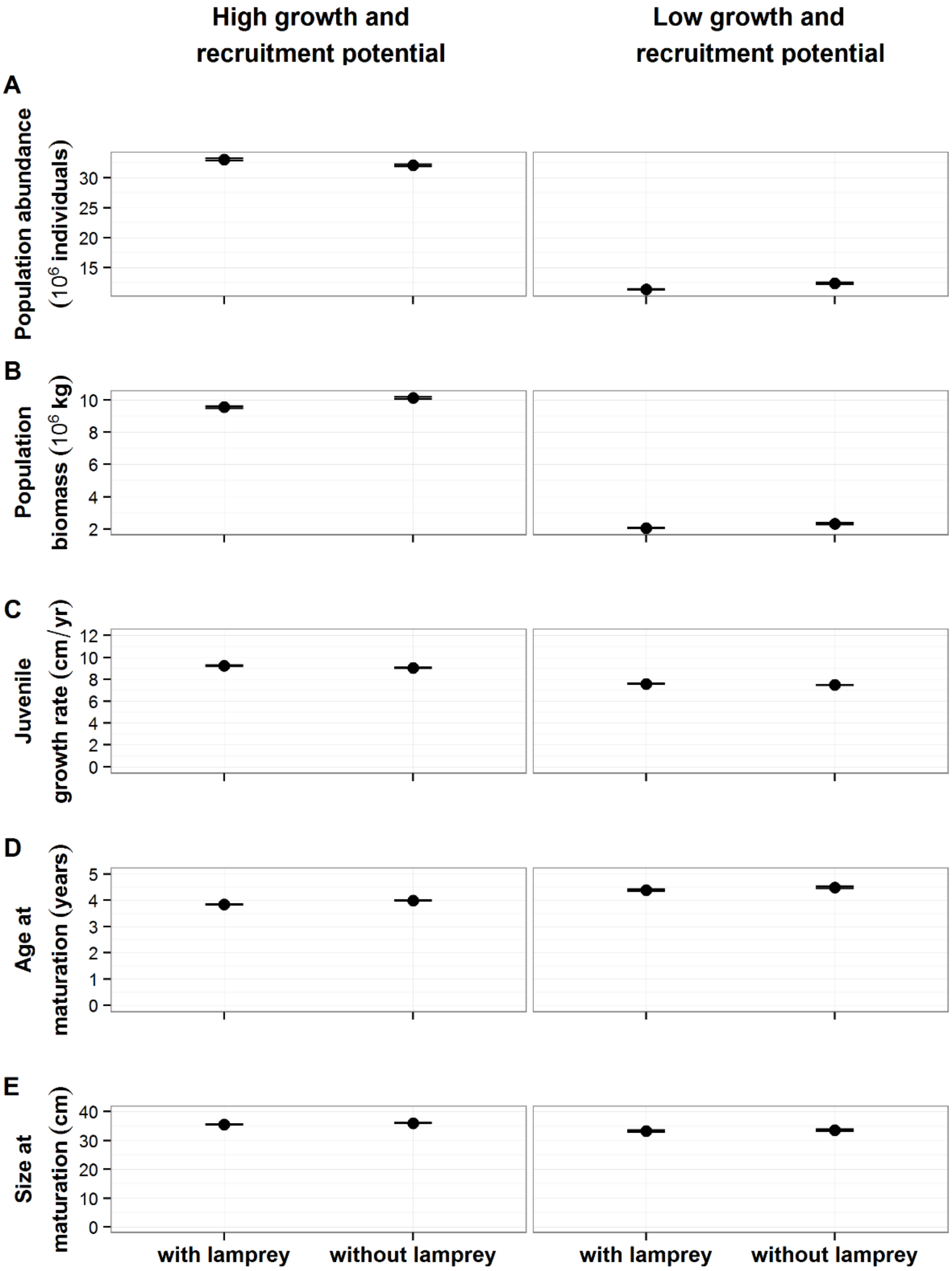


Figure A2. Effects of 100 years of size-selective lamprey mortality (in the absence of harvest) on model predictions for population abundance metrics expressed as a proportion of the population's carrying capacity (A-B) and life-history trait phenotypes (C-E) for pre-invasion and post-invasion scenarios. Results displayed are means ± SD for 10 replicate simulation runs.

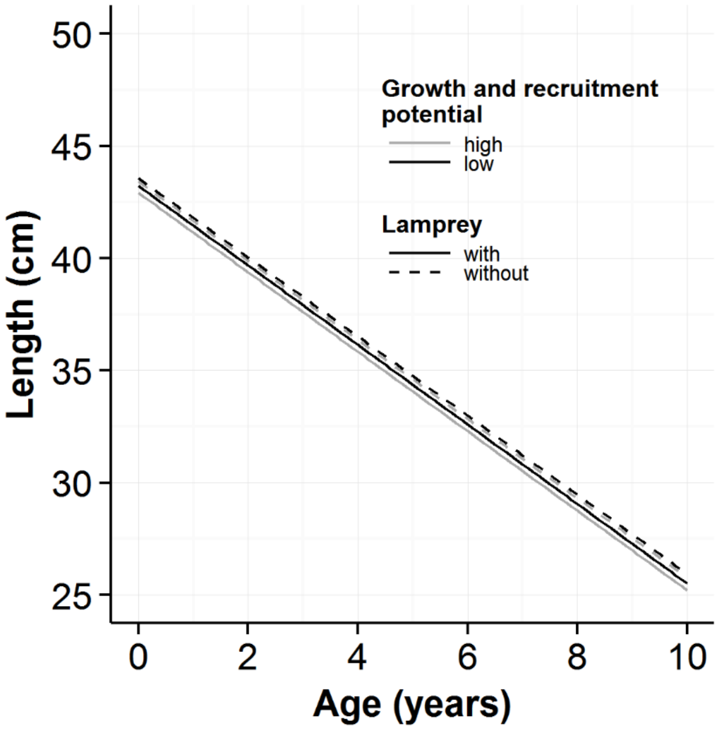


Figure A3. Effects of 100 years of size-selective lamprey mortality (in the absence of harvest) on probabilistic maturation reaction norms for pre-invasion and post-invasion scenarios. Results displayed are population means averaged across 10 replicate simulation runs.

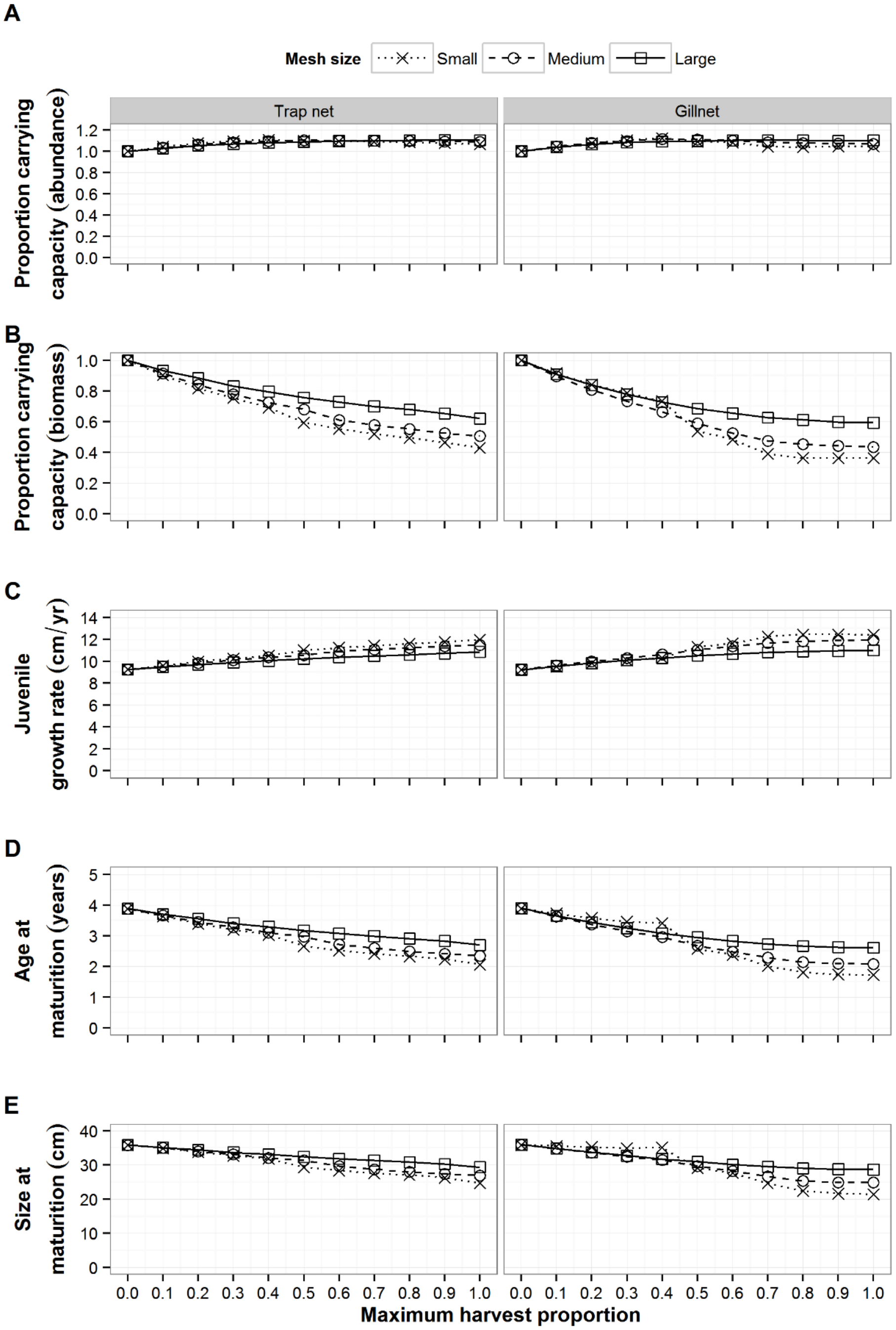


Figure A4. Model predictions for population abundance metrics expressed as a proportion of the population carrying capacity (A-B) and life-history trait phenotypes (C-E) for the pre-invasion scenario. Maximum harvest proportion is the proportion of fish harvested of the most vulnerable length. Results shown are the means of replicate simulation runs.

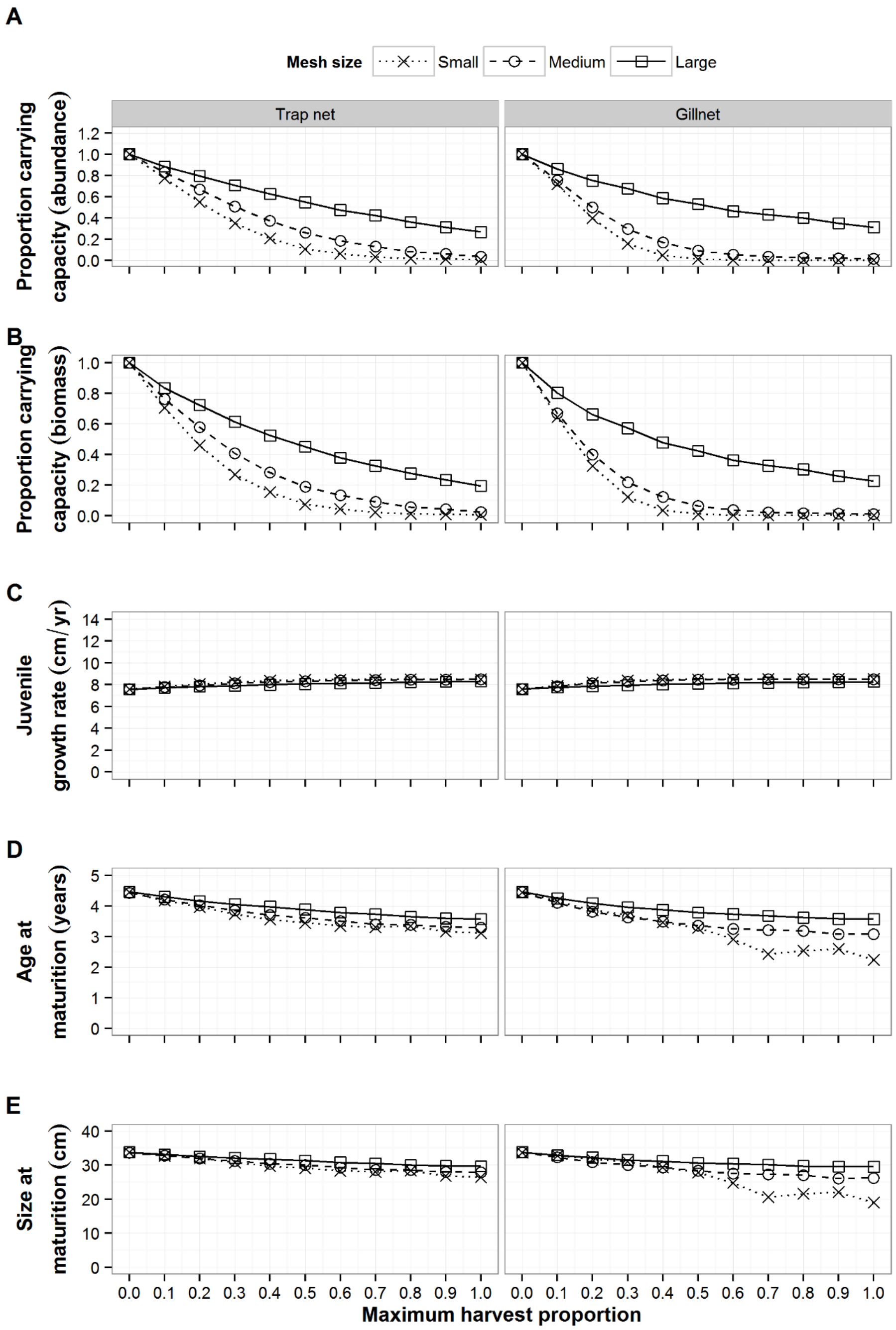


Figure A5. Model predictions for population abundance metrics expressed as a proportion of the population carrying capacity (A-B) and life-history trait phenotypes (C-E) for the post-invasion scenario. Maximum harvest proportion is the proportion of fish harvested of the most vulnerable length. Results shown are the means of replicate simulation runs.

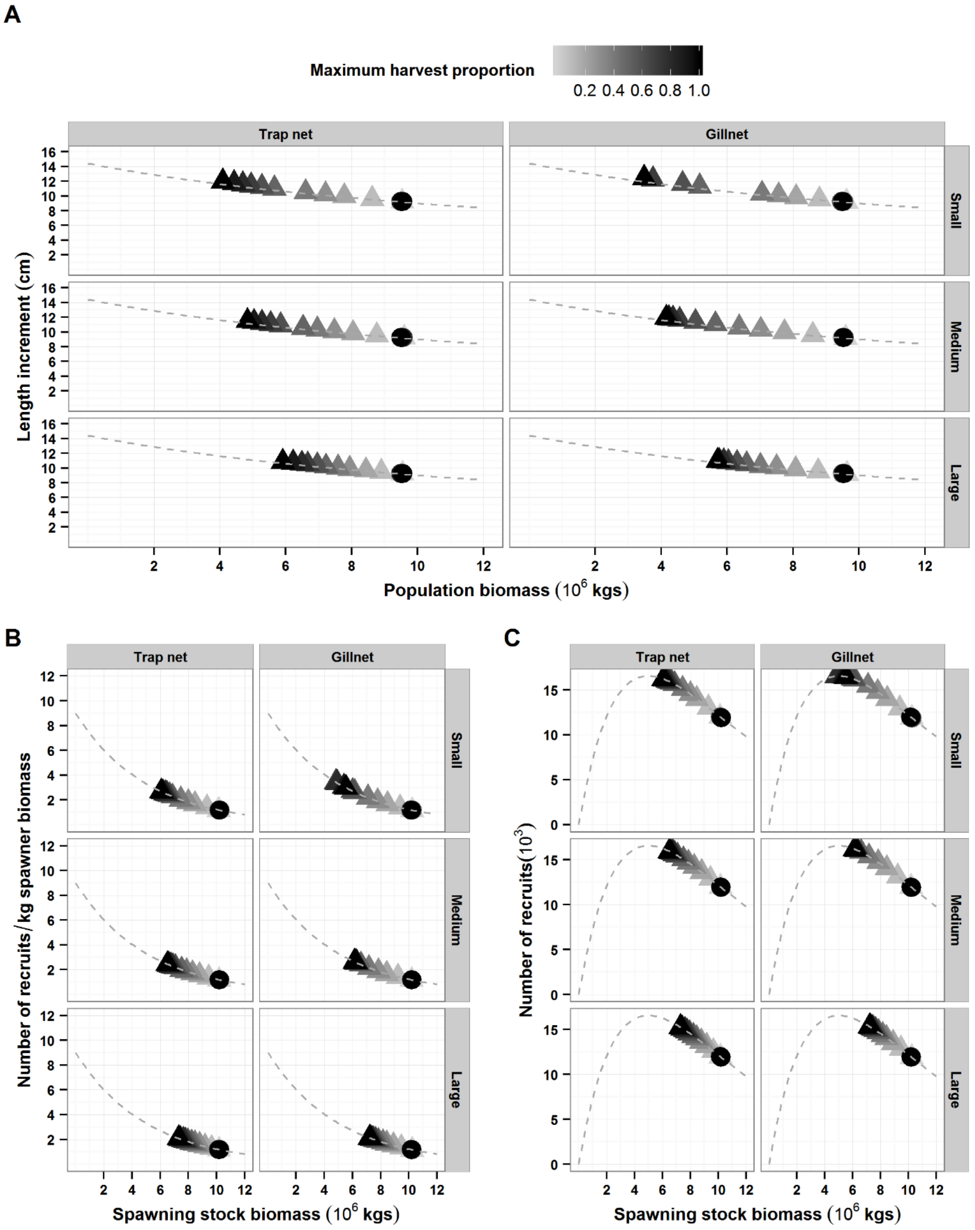


Figure A6. Emergent growth and recruitment relative to population and spawning stock biomass for the high growth and recruitment potential (i.e. pre-invasion) scenario. A) Mean juvenile growth rate. B) Recruitment rate (the number of recruits per kg spawner biomass). C) Number of age 0 fish (“recruits) produced by the spawning stock. Panels from top to bottom show results for different mesh sizes (small, medium, and large). In each panel, the population’s pre-harvest initial (black circle) and final values (triangles) are shown.

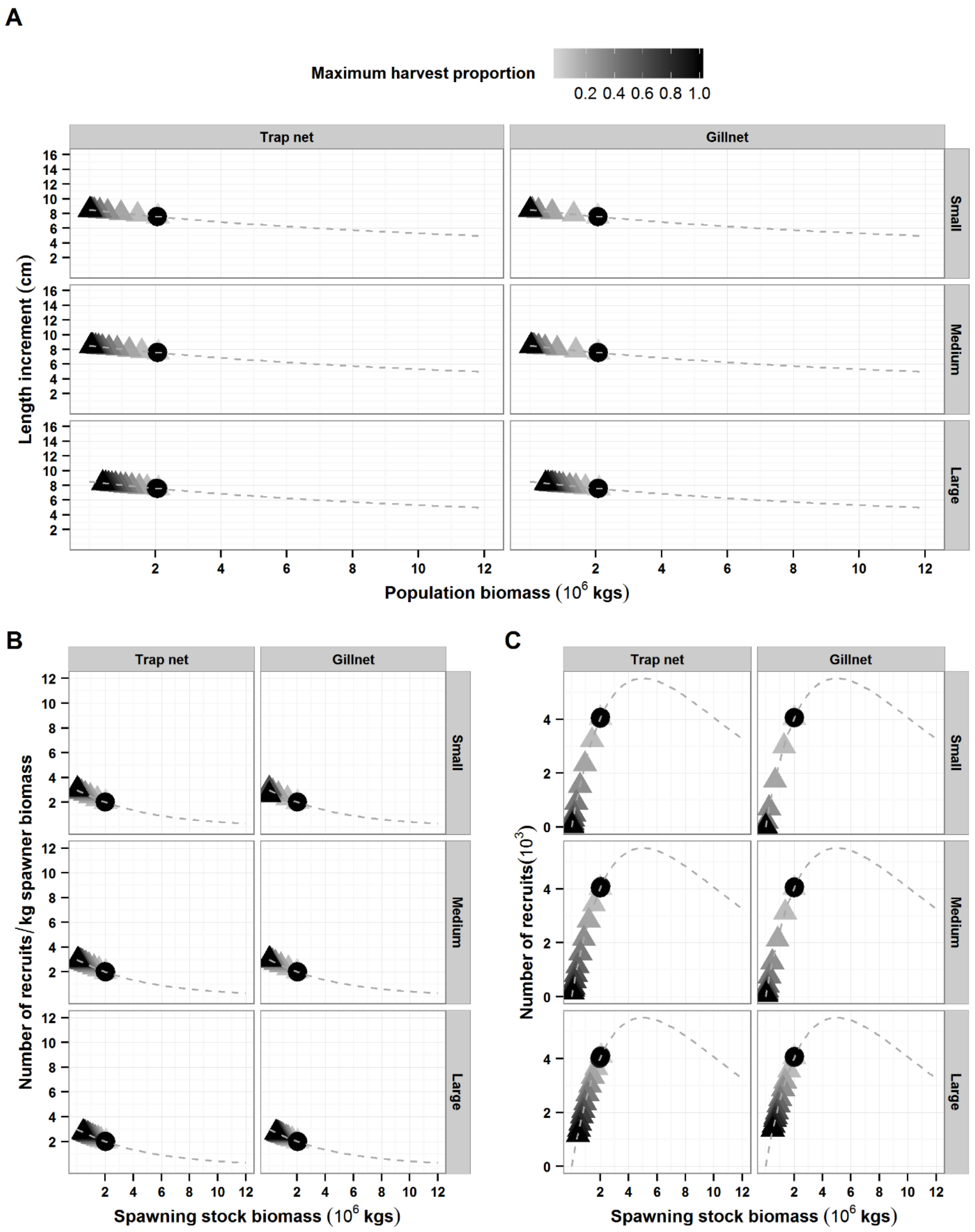


Figure A7. Emergent growth and recruitment relative to population and spawning stock biomass for the low growth and recruitment potential (i.e. post-invasion) scenario. A) Mean juvenile growth rate. B) Recruitment rate (the number of recruits per kg spawner biomass). C) Number of age 0 fish (“recruits) produced by the spawning stock. Panels from top to bottom show results for different mesh sizes (small, medium, and large). In each panel, the population’s pre-harvest initial (black circle) and final values (triangles) are shown.

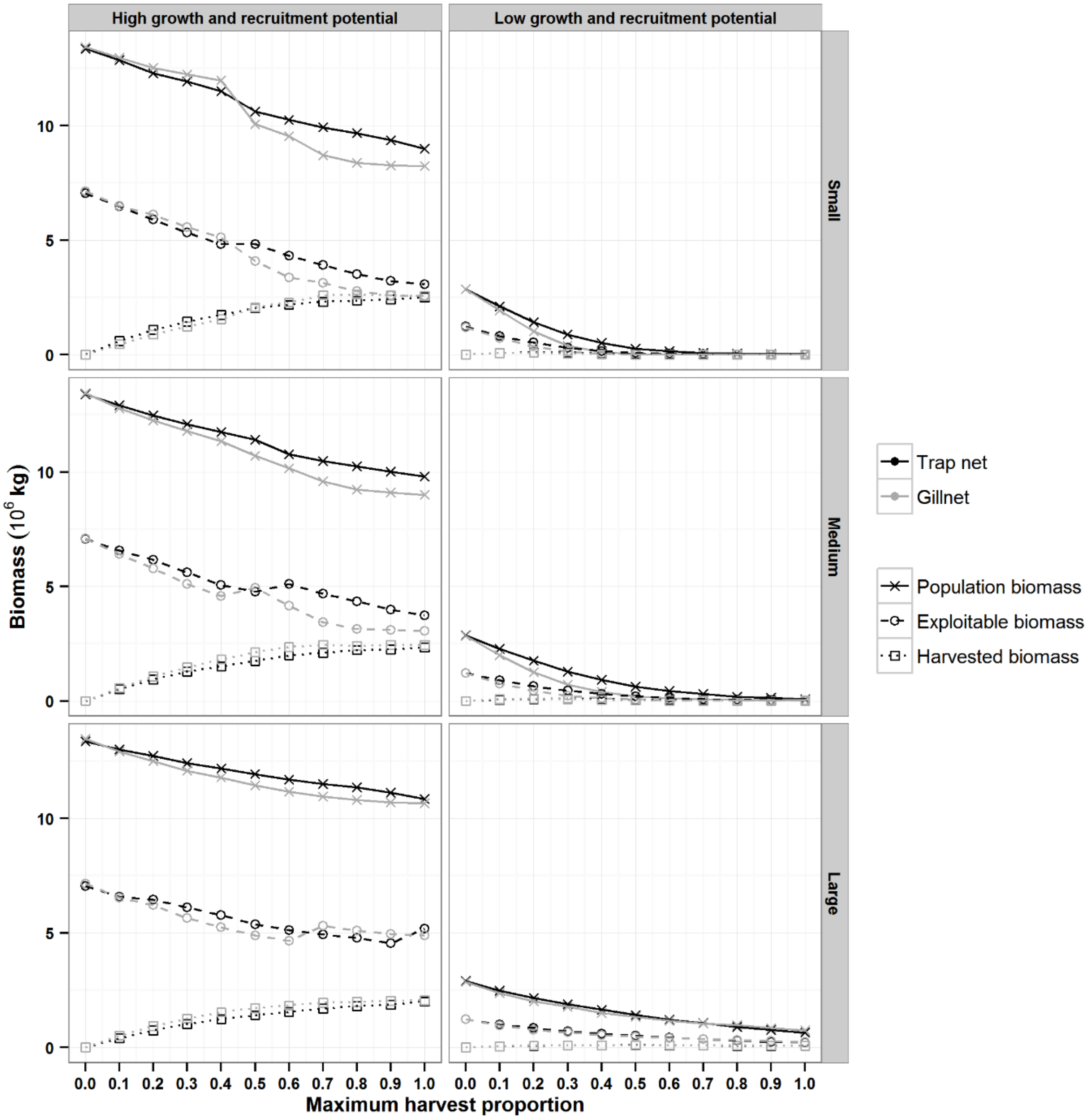


Figure A8. Model predictions for population abundance and harvest metrics in the final year of model simulations (year 200) for various harvest and ecological scenarios. Panels from top to bottom show results for various mesh sizes.

CHAPTER 4: HOW ECOLOGICAL AND EVOLUTIONARY CHANGE AFFECT MATURATION REACTION NORM ESTIMATES

ABSTRACT

Disentangling plastic from evolutionary trait change in wild populations is a major challenge that limits our ability to better understand evolutionary processes. Probabilistic maturation reaction norms (PMRNs) are commonly used to infer evolution of maturation age and size in wild fish stocks, but how well PMRNs estimated from phenotypic data reflect underlying genotypes has been the subject of much debate. We used an individual-based eco-genetic model to simulate populations undergoing various levels of fisheries-induced evolution and ecological feedbacks, to evaluate their effects on the estimation of PMRNs. We sampled these simulated populations and estimated PMRNs from phenotypic data (the age, length, and maturation status of individuals) as would be done for a wild population and compared these with the known maturation genotypes of individuals in the model. Individuals in the model matured earliest when PMRNs evolved in response to harvest and growth was density-dependent. PMRN estimates were for the most part robust to changes in density-dependent growth and high levels of fisheries-induced evolution. However, detection of slower rates of evolution was more limited, especially when individuals mature within a narrow range of ages. This study suggests that the widely applied method of estimating PMRNs is robust to some key factors that can vary in wild populations, while highlighting considerations for using phenotypic data to infer evolutionary change.

INTRODUCTION

The timing of maturation plays an important role in determining the productivity and resilience of fish stocks. Changes in maturation traits, generally towards earlier maturation at smaller sizes, have been observed in numerous exploited fish populations (Trippel 1995, Law 2000, Sharpe and Hendry 2009) and have often preceded substantial declines in stock productivity (Trippel 1995, Olsen et al. 2004). Fishing can lead to these maturation-related changes by three, non-mutually exclusive mechanisms. First, these changes can be demographic in nature, where fishing removes older, larger individuals, resulting in a truncation of the age and size distribution of the population (Heino and Dieckmann 2008). Second, these changes can be the result of phenotypic plasticity, whereby faster growth caused by the reduction in population density leads to earlier maturation (Trippel 1995). Third, they can be the result of genetic change brought about by the selection imposed by fishing, (i.e. harvest- or fisheries-induced evolution) (Hutchings and Fraser 2008, Heino et al. 2015). Changes that have a genetic basis, as opposed to those that are solely the result of phenotypic plasticity, could affect a stock's dynamics in fundamental ways (Dunlop et al. 2015), including altering the speed of recovery after harvesting has ceased (Enberg et al. 2009a, Dunlop et al. 2009, Uusi-Heikkilä et al. 2015). Fisheries-induced evolution also impacts economic returns from a fishery and could require specific evolutionarily enlightened management strategies (Eikeset et al. 2013). As a result, disentangling evolutionary from plastic responses to harvest has been the focus of intense research efforts and debate (Browman et al. 2008, Heino et al. 2008, Enberg and Jørgensen 2017).

Demonstrating evolutionary change in response to selection pressures in wild populations is challenging, requiring genetic evidence that is linked to the phenotypic traits undergoing selection. Recent technological advances are creating opportunities in this area of research that will improve our understanding of evolutionary processes in wild populations (Hemmer-Hansen et al. 2014). However, few studies to date have incorporated genetic evidence, such as changes in allele frequencies, when investigating evolutionary responses to harvest (some exceptions being Jakobsdóttir et al. 2011 and Therkildsen et al. 2013). Studies that have actually demonstrated genetic changes that are linked to the phenotypes under selective harvest (e.g. Van Wijk et al. 2013) are even more scarce. Thus, our current understanding of fisheries-induced evolution, remains to be highly reliant on inferring evolution from empirical phenotypic data (Merilä 2009, Heino et al. 2015).

Probabilistic maturation reaction norms (PMRNs) are commonly used to infer whether an underlying evolutionary change in maturation tendency has contributed to observed trends in age or size at maturation in wild fish stocks (Heino et al. 2015). The premise is that the estimation of PMRNs accounts for much of the plastic changes in growth that can occur during fishing (e.g. owing to density-dependence), and thus allows examination of the underlying evolutionary change in the stock's genetic propensity for maturation (Heino et al. 2002, Dieckmann and Heino 2007). PMRNs are also widely included in modeling studies of fisheries-induced evolution, in order to include the process of phenotypic plasticity (Enberg et al. 2009b, Dunlop et al. 2009, Mollet et al. 2016, Dercole and Della Rossa 2017). Maturation reaction norms describe the relationship between the age and length at which individuals of a given genotype (or group of genotypes) become mature (Stearns and Koella 1986, Heino et al. 2002, Barot et al. 2004). By defining the timing of maturation in terms of both age and length concurrently, PMRNs can account for variation in maturation associated with different growth trajectories (Stearns and Koella 1986, Heino et al. 2002, Dieckmann and Heino 2007). Therefore, changes in maturation that follow along the same reaction norm are interpreted as plastic responses to changes in growth rates (Fig. 1A), whereas shifts in the reaction norm itself, are interpreted as having a genetic basis (Fig. 1B) (Stearns and Koella 1986, Hutchings 2011). Heino et al. (2002) built upon the theory underlying maturation reaction norms by incorporating a probabilistic component that accounts for stochasticity in the maturation process. Probabilistic maturation reaction norms are typically depicted by a midpoint, representing the sizes and ages at which the probability of maturing is 50%. A PMRN width can also be defined, often shown as the distance between contour lines describing the 25% and 75% maturation probabilities (Fig. 1C). Barot et al. (2004) then developed a method for estimating PMRNs in fish stocks when the age and size at which individuals first become mature cannot be observed directly, as is often the case when using data available from fisheries monitoring programs.

Estimating probabilistic maturation reaction norms using the Barot et al. (2004) approach is now a widely-used method for characterizing maturation schedules in wild fish stocks and investigating ecological and evolutionary influences on maturation. Perhaps the most well-known application of PMRNs revealed that shifts in maturation to earlier ages and smaller sizes preceded the collapse of the northern cod (*Gadus morhua*) fishery (Olsen et al. 2004). Probabilistic maturation reaction norms have also been applied to other marine (e.g. North sea plaice *Pleuronectes platessa* - Grift et al. 2003, 2007; North sea sole *Solea solea* - Mollet et al. 2007, 2013; Japanese anchovy *Engraulis japonicus* - Yoneda et al. 2015) and freshwater (e.g. lake whitefish *Coregonus clupeaformis* - Wang et al. 2008; yellow perch *Perca flavescens* - Feiner et al. 2015, 2017; pikeperch *Sander lucioperca* - Kokkonen et al. 2015) fishes to assess trends in maturation and the factors driving them. The Barot et al. (2004) method has also been used to estimate probabilistic reaction norms for length and age at smoltification in anadromous salmonids (Jonsson et al. 2016).

Environmental factors such as temperature (Kuparinen et al. 2011) and social cues (Pauli and Heino 2013) have been found to influence maturation independently of their effects on growth, which could also affect PMRNs. In laboratory experiments, Uusi- Heikkilä (2011) induced variation in PMRNs of genetically similar zebrafish (*Danio rerio*) within a single generation, and found that accounting for condition factor in addition to length and age significantly increased the amount of this variation that could be explained. The question of whether an individual's growth history or size at age is more important in determining the timing of first maturation has also been raised (Morita and Fukuwaka 2006, Pauli and Heino 2013).

Plasticity in maturation in response to environmental factors can be accounted for in the PMRN estimation process when data are available (Dieckmann and Heino 2007). However, recent studies also found that accounting for plasticity in maturation (via growth or other mechanisms) failed to fully explain temporal trends in PMRNs (Hunter et al. 2015) and proportions of mature fish (Wright et al. 2014) in exploited stocks, leaving fisheries-induced evolution as the most parsimonious explanation for unexplained variation in maturation.

Although our understanding of PMRNs and the factors that influence them continues to develop, interpreting PMRN shifts in wild populations remains a challenge. This is because interpreting shifts in PMRNs requires not only knowledge of the factors affecting maturation, but how these factors could affect the statistical estimation of PMRNs as well. When calculating maturation probabilities using the Barot et al. (2004) method, we assume that age-specific rates of growth and mortality are the same for both mature and immature individuals of a given size (Barot et al. 2004) - conditions that are rarely met (Hutchings 1993). In fishes, mature individuals experience a trade-off with growth due to the allocation of energetic resources to reproduction (Charnov 1993, Charnov et al. 2001, Lester et al. 2004). Consequently, juveniles typically grow faster than adults. Growth is also affected by environmental conditions, often via density-dependence; individual growth rates decline as population biomass increases due to increased competition for resources (Lorenzen and Enberg 2002). Annual variation in population biomass associated with variable recruitment, mortality rates, and harvest are therefore also expected to impact growth rates.

While investigating the role of plasticity in shifting PMRNs has gained much attention (e.g. Morita et al. 2009, Uusi-Heikkilä et al. 2011, Pauli and Heino 2013), only a few studies have attempted to assess how the estimation process itself could be affected by natural conditions or violations of model assumptions. Barot et al. (2004) tested its robustness to violations of assumptions using artificial datasets for simulated populations with a known, non-evolving PMRN, whereas Pérez-Rodríguez et al. (2009) and Olsen et al. (2014) compared PMRN estimates with direct observations of first maturation events in wild populations. Based on these studies, it appears we can estimate PMRNs relatively well, even when assumptions are violated (Barot et al. 2004, Pérez-Rodríguez et al. 2009, Olsen et al. 2014). However, the robustness of PMRN estimated to changes in density-dependent changes in growth has never been formally tested. We also do not know to what extent PMRN estimates could be influenced by different rates of ecological and evolutionary change, or how this might affect our ability to detect evolution of maturation.

Here, we use an eco-genetic model to evaluate our ability to estimate PMRNs and detect harvest-induced evolution of maturation in the presence of ecological and evolutionary changes. We simulate changes in growth and maturation within populations for various ecological and evolutionary scenarios. We then estimate PMRNs from individual phenotypes and compare them with the populations' true maturation reaction norms based on the mean of individual genotypes. Given the relevance of growth to the maturation process, we explicitly consider the effects of density-dependent growth on the PMRN estimation process. This allows critical examination of one of the primary goals of estimating PMRNs – to remove the influence of changing growth through density-dependence on maturation age and size in order to reveal potential underlying evolutionary responses. In addition, we investigate the effects of different amounts of evolutionary change and environmental stochasticity by varying the coefficient of genetic variation and harvest rates in the model. We are aware of no previous studies that have explicitly tested whether different levels of density-dependent growth and evolutionary change affect the robustness of PMRN estimates.

METHODS

Model description

An individual-based eco-genetic model was developed for Lake Huron lake whitefish (*Coregonus clupeaformis*). It has previously been used to examine how ecological change affects (1) population dynamics and sustainable harvest in the absence of evolution (Gobin et al. 2016) and (2) the evolution of maturation in response to size-selective harvest (Gobin et al., in press). This model was based on earlier models used to study the evolution of traits in a variety of fish species (Dunlop et al. 2007, 2009, 2015). Individuals in the model experience growth, maturation, reproduction, inheritance, phenotypic expression, and mortality. Individuals also possess both genotypic and phenotypic traits related to maturation. Using this model, we investigated the effects of ecological conditions on the estimation of PMRNs by modifying the density-dependent growth relationship. We also varied the coefficient of genetic variation and harvest rates in the model to examine the effects of evolvability and environmental stochasticity.

Each individual in the model possesses its own linear probabilistic maturation reaction norm (PMRN), characterized by a slope (s) and intercept (I):

$$L_{mat} = I + s * ¥ , \tag{1}$$

where L_{mat} is the PMRN midpoint – i.e, the length at which that individual has a probability to mature given its age ¥. The PMRN slope and intercept are that individual's maturation genotype, defining its specific genetic propensity for maturation as a function of age. An individual's maturation phenotypes are the actual age and length at which the individual matures, defining the individual's maturation status in any given year (i.e., immature or mature). In the initial population, all individuals are assigned the same PMRN parameters; but these parameters are then free to evolve over time. Traits are inherited quantitatively, with parameter values of offspring being drawn randomly from a normal distribution centered on the mean value of the parents with a variance determined by an assigned coefficient of genetic variation (CV_G). The CV_G is the standard deviation (the square root of the genetic variation) divided by the mean trait value and is set between values of 0 and 0.12 (or 12% of the mean). In determining the genetic variance (σ_G^2) of PMRN parameters (i.e. slope and intercept values), the CV_G parameter influences how much these traits can evolve (Houle 1992, Dunlop et al. 2015).

Environmental stochasticity in traits (σ_E^2) is incorporated through its relationship with genetic variance (σ_G^2), and heritability (*H*):

$$\sigma_E^2 = \sigma_G^2(1/H - 1). \tag{2}$$

This is simply a rearrangement of the common equation describing heritability ($H= \sigma_G^2/ \sigma_P^2$ where $\sigma_P^2= \sigma_E^2+ \sigma_G^2$, the phenotypic variance). Heritability is set at 0.2 in the initial population (i.e. additive genetic variation accounts for 20% of the total phenotypic variation). The amount of environmental variation is then scaled (i.e. determined) by the level of genetic variation (via CV_G) in order to maintain the 20% heritability assumed initially. Environmental variation is calculated in this way for the initial population and is then held constant. This environmental variation is included in the expression of genetically inherited traits when determining a trait's phenotype.

In our simulations, we set the width of the PMRN (i.e. the distance between contours describing an individual's 25% and 75% probability of maturing) to zero. Doing so makes the PMRN midpoint equal to a maturation probability of 1, therefore making maturation deterministic (in effect, representing a MRN). We did this to avoid interactions with the coefficient of genetic variation that result in the realized PMRN width becoming wider over time than that originally specified in the model (Eikeset et al. 2016), and in order to keep the effects we are trying to test tangible.

The model incorporates ecological feedbacks in the form of density-dependent growth and recruitment (Dunlop et al. 2009). Growth (h) in the model declines with increasing population density (B) according to Walters and Post (1993):

$$h = h_{max}/(m + a * B), \tag{3}$$

where a and m represent the loss of food resources due to intraspecific competition and other natural causes, respectively, and h_{max} describes the maximum growth rate when $B = 0$ and $m = 1$.

Harvest is size-selective, where selectivity (V_t) follows a dome-shaped curve defined by a double-logistic function scaled to the maximum exploitation rate F_{max} (the proportion of fish harvested of the most selected length):

$$V_t = (1/(1 + \exp(-\delta 1 * (L_t/G - \varepsilon 1)))) * (1 - 1/(1 + \exp(-\delta 2 * (L_t/G - \varepsilon 2))))/V_{max} * E_{max}, \tag{4}$$

where L_t is the fish length, G is the mesh size, V_{max} is the maximum selectivity, and δ_1, ε_1, δ_2, and ε_2 are parameters (Zhao and Morbey 2017). A complete description of the model is provided in the Appendix of Chapter 3.

Parametrization

We parameterized the model for lake whitefish, with most data based on the stock in the southern main basin of Lake Huron. We used data collected by the Ontario Ministry of Natural Resources and Forestry (OMNRF) from their standardized offshore gillnetting survey (Speers 2013) and the statistical catch-at-age stock assessment model for lake whitefish in the QMA 4-5 management area (based on Ebener et al. 2005). Parameters that could not be estimated from available data were obtained from the published literature. A list of parameter values with their sources are provided in Table 1.

Model scenarios

We examined two growth scenarios: density-independent (i.e., constant) and density-dependent (i.e., growth declines with increasing population density) (Fig. 2A). For each of these scenarios, we varied the CV_G parameter such that the evolvability of traits was non-existent (CV_G= 0%), moderate (CV_G= 6%), or high (CV_G= 12%) (Figs. 2B and C). We also varied the exploitation parameter (F_{max}) such that populations experienced no (F_{max}= 0), moderate (F_{max}= 0.5), and high (F_{max}= 1) harvest (Fig. 2D). The minimum size limit of the fishery was set to 75% of the initial population PMRN intercept value (32 cm) to promote evolutionary change (Dunlop et al. 2015). Model simulations ran for a total of 200 years, with harvest being initiated in year 100. We ran five replicate simulations for each model scenario.

We simulated a very basic fishery-independent sampling program in our modeled population by randomly sampling 200 individuals of each age, for each year between model years 50-55 (referred to as the initial time period prior to harvest) and 170-175 (referred to as the final time period after harvest began). These time periods were chosen to represent populations before and after being subject to harvest, while allowing populations to stabilize following the initiation of model simulations and the initiation of harvest in the model, respectively. We then estimated PMRNs from this sample using the method by Barot et al. (2004), to mimic the estimation of PMRNs in a wild stock using typically collected data (age, length and maturation status). We then compared these estimated PMRNs to the population's true PMRN, represented by the mean of individual PMRN genotypic traits. In other words, we have perfect information on our simulated population's true (i.e. genetic) PMRN and compare that to estimates derived using the Barot et al. (2004) method. In this way, we can test the performance of Barot's estimation method when we vary conditions for growth and evolvability.

Empirical estimation of PMRNs from simulated data

A more direct estimation of PMRNs from phenotypic data requires individual-level observations on the timing of maturation, i.e. the age and size at maturation of a given fish. However, fishery data often provides only a description of maturation status - whether individuals are immature or mature in the year the sample was taken, i.e., the age and size at maturity. The sub-sample of fish defined as being mature would include fish that had matured in a previous (unknown) year, not allowing for the direct estimate of the probability of maturing. To make our analysis more applicable to how PMRNs are estimated most typically for wild stocks, we used the estimation approach of Barot et al. (2004), which indirectly estimates the probability of maturation when the age and size at maturation of individuals is not observed. This approach has been the mostly commonly applied method for estimating PMRNs in the wild (Heino et al. 2015), and has been used for numerous high profile stocks (Devine et al. 2012) such as northern cod (Olsen et al. 2004) and North Sea plaice (Grift et al. 2007).

Barot et al. (2004) estimates maturation probability m for a given age a and size s using available information on the proportion mature at age ($o(a,s)$) and age-specific growth rate $\Delta s(a)$,

$$m(a,s) = \frac{o(a,s) - o(a-1, s-\Delta s(a))}{1 - o(a-1, s-\Delta s(a))}.$$

(5)

The proportion of mature individuals is estimated by fitting the following model for each age and cohort separately:

$$logit(o) = \ln(\frac{o}{1-o}) = c_0 + s * c_1, \quad (6)$$

where logit (o) is the logit link function, and c_0 and c_1 are estimated as parameters. Annual age-specific growth rates are estimated for each cohort as the difference in mean sizes of consecutive ages. Equation (6) and age-specific growth rates are used to estimate probabilities of being mature at various ages and sizes that are inserted into equation (5); thereby calculating probabilities of maturing over the observed range of ages. Parameters summarizing maturation reaction norms are derived by fitting logistic regression models to maturation probabilities and sizes for each age and cohort:

$$logit(m) = d_0 + s * d_1, \quad (7)$$

where d_0 and d_1 are parameters. Probabilistic maturation reaction norm midpoints (i.e. the size at which an individual of a given age has a 0.5 probability of maturing) (s_{50}) are calculated by setting m=0.5 in equation (7):

$$s_{50} = \frac{-d_0}{d_1}. \quad (8)$$

We estimated PMRN midpoints for ages and cohorts of our simulated population where the proportion of mature fish fell in the range of 0.2 to 0.8, as having few fish that are either mature or immature can produce unrealistic reaction norm estimates (Barot et al. 2004). In the scenarios when CV_G is set to 0 in our simulated populations (removing the possibility of any evolution), there is no genetic variation or environmental stochasticity in a cohort's PMRN, and the cohort's observed size at maturation represented their estimated PMRN.

RESULTS

Density-dependent growth did not affect our ability to accurately estimate PMRNs and detect harvest-induced evolution; estimated PMRN midpoints were similar to the true (i.e. underlying genetic) PMRNs and reflected evolutionary shifts in true PMRNs (Fig. 3). However, we were generally limited in our ability to detect low to moderate amounts of evolution, regardless of the presence or absence of density-dependent growth, as shown by the overlap in midpoints estimated before and after harvest. In most cases, at least one midpoint (i.e. for one age) intersected with populations' true PMRNs. In two cases (when there was no harvest or high harvest in the density-dependent growth scenario), both midpoints estimated during the final time period (years 170-175) fell below those populations' true PMRNs. However, this did not affect our ability to detect evolution, as shifts in estimated PMRN midpoints remained apparent. The number of ages for which PMRN midpoints could be estimated was restricted to one or two based on the variability in growth and the timing of maturation. As expected, the ages for which we could estimate midpoints also tended to shift with changes in the mean age at maturation. When the CV_G= 0, PMRN midpoints estimated as the age and size at which all individuals within a cohort matured was consistently higher than the populations' true PMRNs because setting this parameter to zero in the model removes individual variation in growth and the timing of maturation; meaning that all individuals in a cohort grow at the same rate, thus surpassing the PMRN at the same time, and maturing at the same age and length.

Maturing earlier and at smaller sizes was partly due to harvest-induced evolution, but also driven by density-dependent growth. Probabilistic maturation reaction norms shifted downwards in response to harvest, but harvest also led to maturation at younger ages when growth was density-dependent and PMRNs were not permitted to evolve (CV_G=0). Individuals matured earliest when growth was density-dependent and evolution of PMRNs was permitted (Figs. 4 and 5). This was despite the tendency of populations' true PMRNs to exhibit slightly less evolution when growth was density-dependent, and evolvability and harvest were high (Fig 3). The rate at which PMRNs evolved in the presence and absence of density-dependent growth appear to be influenced by the tendency of PMRNs to naturally shift upwards with the former and downwards with the latter in the absence of harvest (Fig. 3). Differences in the trends observed in mean size at maturation between the two growth scenarios (Fig. 5) were therefore due to a combination of differences in the evolution of PMRNs, and density-dependence in growth.

Compared to the density-independent scenario, density-dependence reduced growth (Fig. 6), leading to delayed maturation at slightly older ages and smaller sizes (Figs. 4 and 5). When evolution was constrained in the model ($CV_G=0$), harvest altered ages and/or sizes at maturation through density-dependent growth, with moderate harvest resulting in maturation at similar ages and larger sizes, and high harvest leading to earlier maturation at smaller sizes (Figs. 4 and 5). When evolution was permitted in the model ($CV_G>0$), mean age and size at maturation both declined (to younger ages and smaller sizes) in response to harvest, in both the presence and absence of density-dependent growth (Figs. 4 and 5). Shifts to younger ages at maturation were greater when growth was density-dependent, whereas shifts to smaller sizes at maturation at maturation were greater when growth was density-independent and harvest was high. In all cases, shifts in maturation to earlier ages and smaller sizes with harvest was greater when evolvability was high (i.e. with higher coefficients of genetic variation leading to faster rates of evolution) (Figs. 4 and 5).

DISCUSSION

The estimation of probabilistic maturation reaction norms was robust to changes that (1) were purely ecological in nature or that (2) that had a strong evolutionary component. By simulating a population that could undergo various degrees of eco-evolutionary change, we were able to perform a model-based evaluation of a commonly used statistical method's ability to detect evolution. When a population's true PMRN underwent substantial evolution in response to high rates of harvest, estimated PMRN midpoints captured these shifts. Density-dependent growth similarly did not have a substantial impact on PMRN estimates or our ability to detect evolutionary change.

Numerous studies have used shifts in PMRNs as evidence of fisheries-induced evolution (Heino et al. 2015), which has instigated debate about the ability to detect evolution using indirect methods and specifically about the estimation of PMRNs (Marshall and Browman 2007, Marshall and McAdam 2007, Kuparinen et al. 2011). A concern with using estimates of PMRNs derived from phenotypic data to detect evolution is that a population might show phenotypic plasticity in maturation that occurs independently of changes in growth. In other words, there is concern that PMRN estimates could be affected by factors other than growing conditions that influence an individual's likelihood of maturing. Several studies have demonstrated that maturation can exhibit plastic responses to environmental factors independent of their effects on growth (Dhillon and Fox 2004, Kuparinen et al. 2011, Tobin and Wright 2011), and that not accounting for these can influence PMRN estimates (i.e. resulting in non-evolutionary shifts when not accounted for) (Kraak 2007, Uusi-Heikkilä et al. 2011, Pauli and Heino 2013). Fortunately, research addressing these concerns is growing, thus allowing for their effects to be incorporated into the PMRN estimation process (e.g. Hunter et al. 2015). Also of concern is how variation in maturation associated with an individual's growth history could impact PMRN estimates (Morita and Fukuwaka 2006, Pauli and Heino 2013). Non-random sampling has also been shown to affect PMRN estimation and could bias the interpretation of shifting PMRNs in wild populations (Sahashi and Morita 2015).

The interpretation of shifts in PMRNs is further complicated by the method having never been validated using simulated populations subject to eco-evolutionary processes that occur in nature. How robust PMRN estimates are to density-dependent changes in growth has never been formally examined, despite this being one of the key reasons for developing the PMRN approach. Previous studies evaluating the PMRN estimation method have involved either simulated datasets in which maturation was not evolving (Barot et al. 2004), or observations from wild populations where it is impossible to have certain knowledge of how the population's true PMRNs might be changing over time (e.g. Pérez-Rodríguez et al. 2009, Olsen et al. 2014). These studies also focused on evaluating PMRN estimates at a certain point in time rather than PMRNs evolving over a number of years, although Pérez-Rodríguez et al. (2009) does examine temporal trends in PMRN midpoint estimates. Here, we expand upon the previous understanding of the reliability of the PMRN estimation process by showing that the estimates derived from our simulated populations were robust to several key conditions found in nature, such as density-dependent growth and recruitment, various levels of mortality, and different amounts of evolutionary change. Our results provide support for the hypothesis that an important component of the PMRN shifts observed in several wild fish stocks could indeed represent evolution of those stock's overall genetic propensity to mature.

In some cases, the way in which density-dependence altered growth and evolutionary trajectories slightly reduced the accuracy of PMRN midpoint estimates. However, these effects were sufficiently small that they did not affect our ability to detect more substantial levels of harvest-induced evolution of maturation. Estimated PMRN midpoints that did not intersect with the population's true PMRNs generally fell below population PMRNs, suggesting a tendency to underestimate lengths at maturation. Density-dependent growth resulted in flatter growth curves (Fig. 6); at the same time, evolving population PMRNs shifted downwards in response to harvest (Fig. 3). Changes in growth curves and PMRNs would alter where they intersect, and in turn, could affect the proportion of mature and immature individuals. With Barot's method, errors in midpoint estimates can occur when there are few immature or mature individuals for a given age and cohort, as this affects the estimation of logistic regression parameters used to describe the proportion of mature individuals (also referred to as a maturity ogive) in equation (5) (Barot et al. 2004). We ensured a certain level of data quality when estimating midpoints by setting limits on the proportions of mature fish used to describe maturity ogives. Nonetheless, proportions that fall closer to these limits while remaining within them could produce midpoint estimates with larger errors than when the ratio of mature to immature individuals is approximately equal. Such errors became important when the evolution of maturation was low to moderate in magnitude. In these cases, slight inaccuracies in midpoint estimates relative to populations' true PMRNs could limit our ability to detect slow rates of maturation evolution.

As a first step in understanding how effectively PMRN estimates reflect populations' true underlying PMRNs and their evolution, we modeled maturation as a deterministic process. The probabilistic spread in estimated PMRNs generally captures variation in the wild resulting from micro- and macro-environmental factors that cannot be accounted for (Dieckmann and Heino 2007). We made maturation deterministic by setting the width of the PMRN in our model to zero. The width of a PMRN is generally defined as the distance between the contours that give the 25% and 75% maturation probabilities, providing a measure of the variation in sizes over which an individual of a given age could mature. Although the maturation process is clearly probabilistic in nature (Heino et al. 2002), the PMRN width and its potential role in eco-evolutionary dynamics remains poorly understood (Eikeset et al. 2016 Supporting Information, 2017). Removing the PMRN width from our model makes maturation deterministic (i.e. it simply becomes a MRN) such that individuals mature when they surpass a size at age threshold that is determined by their genotype (i.e. their individual slope and intercept values). We did this to avoid interactions with the coefficient of genetic variation that can occur in eco-genetic models that can result in the realized PMRN becoming wider than that originally specified for the initial population (Eikeset et al. 2016 Supporting Information).

Making maturation deterministic may have contributed to the limited number of PMRN midpoints that we could estimate by reducing inter-individual variation in the timing of maturation, which resulted in a narrow range of ages over which individuals in the model matured. However, many studies that employ PMRNs to detect evolution of maturation in natural populations are only able to estimate midpoints for a limited number of ages (e.g. Wang et al. 2008, Hidalgo et al. 2014, Feiner et al. 2015). This means that important information relating to the slope or shape of PMRNs when attempting to interpret shifts in PMRN midpoints over time or space is often lacking. Interpretation of trends with few PMRN midpoints is further complicated by the fact that the ages for which we are able to estimate midpoints also shifted with changes in the age and size at which individuals matured due to its effect on the ratio of mature to immature individuals.

In our model, the age and size at which individuals matured was determined solely by their length at age relative to their individual maturation reaction norm. This means that variation in the evolution of populations' true PMRNs and density dependent growth could only affect maturation through their influence on an individual's length at age. We did not include other environmental factors in our model that could affect maturation independently of growth. It would, however, be useful to incorporate variables besides growth that contribute to variation in the size and age at maturation (e.g. to condition - Uusi-Heikkilä et al. 2011; temperature - Dhillon and Fox 2004, Kuparinen et al. 2011; growth history – Morita and Fukuwaka 2006, Pauli and Heino 2013) into models like ours to evaluate the estimation method's sensitivity to growth-independent plasticity in maturation.

Our study demonstrates that PMRN estimates can be used to detect rapid evolution of maturation in response to harvest in the presence of key ecological feedbacks. Given the difficulty of detecting fisheries-induced evolution using direct genetic approaches (Jakobsdóttir et al. 2011, Casey et al. 2016), PMRNs remain the best approach for analyzing phenotypic changes in maturation in natural populations (Heino et al. 2015), and have become a fundamental way to model the evolution of maturation (e.g. Dunlop et al. 2007, 2009, 2015, Enberg et al. 2009, Mollet et al. 2016, Dercole and Della Rossa 2017). We also found that shifts towards earlier maturation were greatest when PMRNs evolved in response to high levels of harvest and growth was density-dependent. A thorough understanding of PMRNs is essential as we move forward with addressing gaps in our knowledge related to harvest-induced evolution in the wild, and particularly how it interacts with ecological processes like density-dependent growth. Further research investigating the PMRN width, and its role in the evolution of maturation, are especially needed (Eikeset et al. 2017, Enberg and Jørgensen 2017).

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Table 4.1. Parameter values and sources used in the individual-based eco-genetic model for lake whitefish in the southern main basin of Lake Huron.

Description	Symbol	Source	Value
Mean PMRN[*] intercept[†]	I	1	42.7
Mean PMRN slope[†]	S	1	-1.77
Heritability[†]	H	2	0.2
Coefficient of genetic variation	CV_G	2	0, 0.06, 0.12
PMRN width (defining 0.25 and 0.75 probabilities)	ω		0
Mean maximum growth potential	h_{max}	3	14.4
Intraspecific competition food loss rate	a	3	6e-5
Food loss rate from other causes	m	3	1.0
Reproductive investment[‡]	g	4,5	0.346
Mean maximum recruitment potential	r_{max}	3	9
Ricker stock-recruitment parameter	β	3	2e-4
Constant in length-weight relationship (kg/cm)	c	6	3.318e-6
Exponent in length-weight relationship	d	6	3.29
Exponent of length-fecundity relationship	j	7	3.83
Slope of length-fecundity relationship (eggs/mm^{k})$^{-10\text{\textasciicircum}3}$	i	7	1.1e-6
Background natural mortality[§] (year^{-1})	M_B	8	0.30
von Bertalanffy asymptotic length (cm)	L_∞	8	60.0
Brody's growth coefficient (in von Bertalanffy growth model)	K	8	0.25
Water temperature (°C)	T	8	6
Wounding probability logistic model coefficient	P	9	8.60
Wounding probability logistic model coefficient (mm^{-1})	N	9	0.01
Lamprey mortality probability		10	0.75
Double logistic gillnet selectivity parameter	δ_1	11	5.84
Double logistic gillnet selectivity parameter	ε_1	11	4.19
Double logistic gillnet selectivity parameter	δ_2	11	2.19
Double logistic gillnet selectivity parameter	ε_2	11	4.74
Gillnet selectivity mesh size (mm)	G	11	114
Fishery minimum size limit (mm)		12	320
Maximum exploitation rate	F_{max}		0, 0.5, 1

[*] Probabilistic maturation reaction norm

[†] Values are defined for the initial population and are then free to change through time

[‡] Calculated by multiplying the gonadosomatic index (gonad mass divided by body mass) by a conversion factor of 1.73 to account for differences in the energetic content of gonad and somatic tissues (Lester et al. 2004).

[§] Background natural mortality was estimated from the relationship between von Bertlanffy growth model parameters and mean annual temperature (Pauly 1980, Ebener et al. 2005)

1. OMNRF survey data for years 1984-2009.
2. Dunlop et al. (2009).
3. Gobin et al. (2016).
4. Based on estimates from Johnston et al. (2012); Lumb et al. (2007); Cook et al. (2005).
5. Lester et al. (2004).
6. OMNRF survey data for years 1984-1992.
7. Kratzer et al. (2007) Alpena study site for years 1986-1987.

8. OMRNF Statistical catch-at-age stock assessment model for QMA 4-5 based on Ebener et al. (2005).
9. McLeod et al. (2011) southern main basin for the year 2000.
10. Spangler et al. (1980).
11. Zhao and Morbey (2017).
12. Ebener et al. (2008).

Figure 4.1. A) Maturation reaction norms (solid black line) account for differences in the timing of maturation owing to variation in growth rates. An individual with a faster growth trajectory (dashed line) matures at an earlier age and larger body length (black circle) than an individual with a slower growth trajectory (dotted line) who matures at a later age and smaller body length (black square); both points depicting the ages and sizes at which these individuals mature intersect the same maturation reaction norm. B) Shifts in maturation reaction norms represent variation in the timing of maturation associated with factors that influence maturation independent of growth (e.g. genotypes, growth-independent plasticity in maturation). In this case, two individuals (black dashed and gray dotted lines) have similar juvenile growth rates but have different maturation reaction norms (black and gray solid lines), resulting in different ages and lengths at maturation (black and grey circles). This variation in the timing of maturation and tradeoffs between growth and reproduction are responsible for differences in lengths at age following maturation. C) Probabilistic maturation reaction norms incorporate a stochasticity in maturation. The midpoint (solid gray line) depicts the lengths and ages at which individuals have a 50% probability of maturing, lower and upper dashed lines represent the lengths and ages at which individuals have a 25% and 75% probability of maturing, respectively. Individuals can therefore mature over of a range of lengths for a given age with some set probability; the black dotted line and circle depict the growth trajectory and age and length at maturation of one individual as an example.

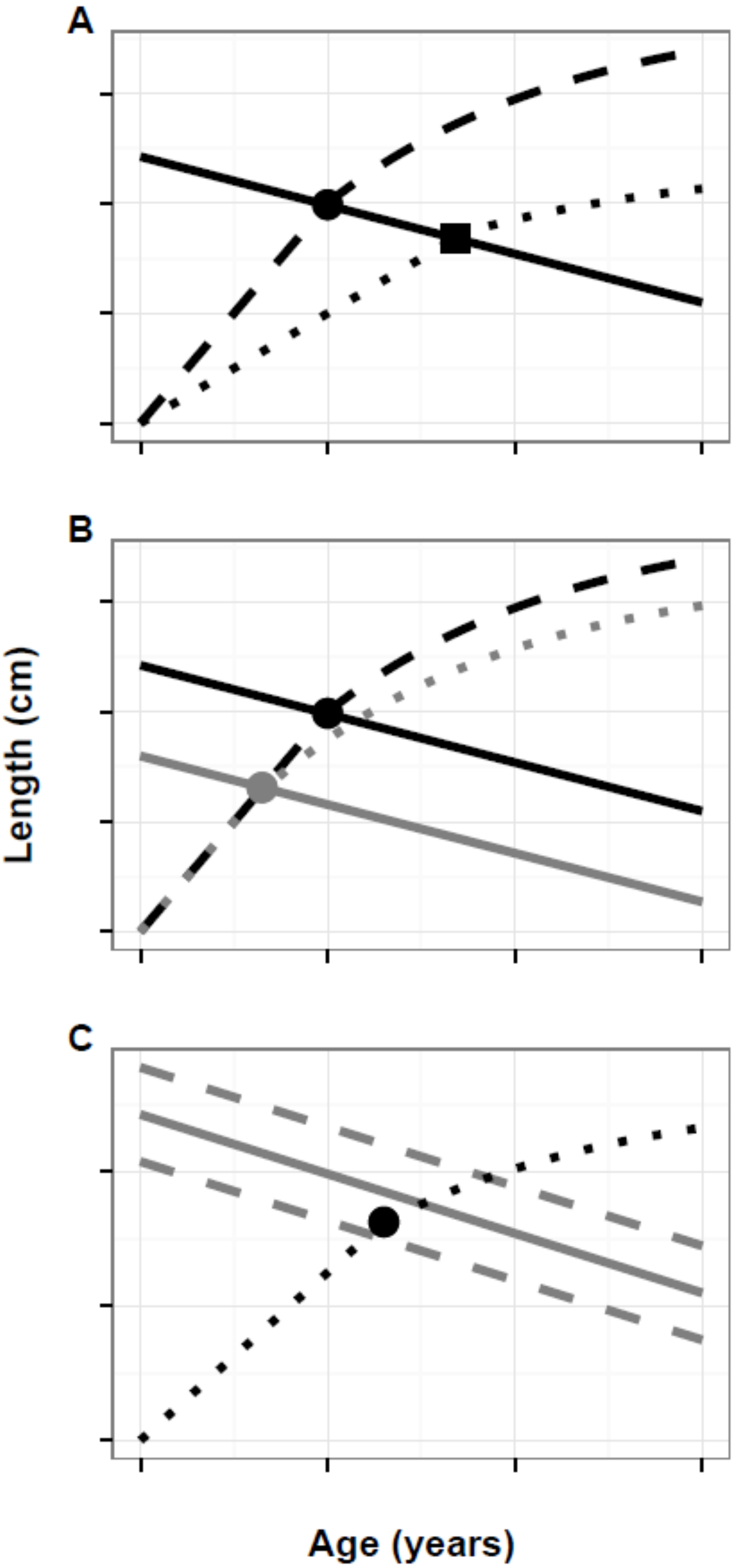


Figure 4.2. Model scenarios used to investigate the detection of harvest-induced evolution using probabilistic maturation reaction norms. A) Maximum growth potential in density-dependent and –independent growth scenarios. B) The probability distribution of genotypic traits (maturation reaction norm slope and intercept) when evolvability is high (CV_G=0.12), moderate (CV_G=0.06) and when evolution is constrained (CV_G=0). C) Size-selectivity curves for high (F_{max} = 1), moderate (F_{max} = 0.5), and no harvest (F_{max} = 0).

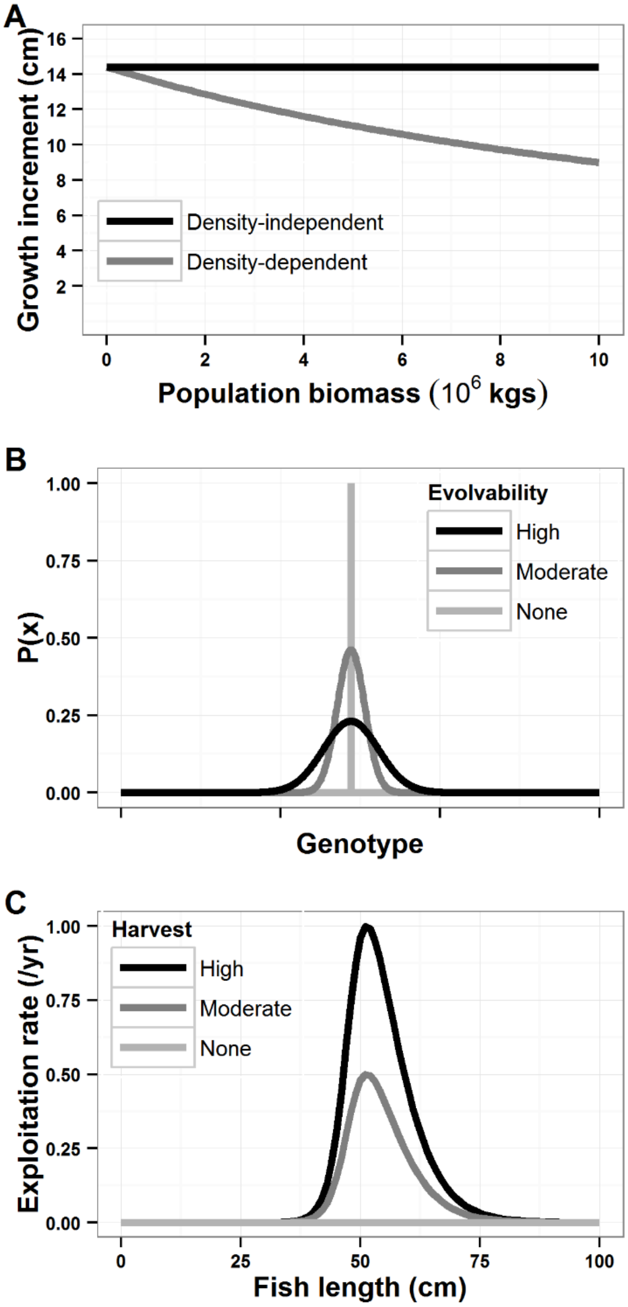


Figure 4.3. Comparison of true probabilistic maturation reaction norms (PMRNs) based on genotypes (lines) and estimated midpoints (points) based on phenotypic traits when growth is A) density-independent and B) density-dependent. Grey lines show the initial mean population PMRN (i.e. year 0 in simulation), black lines show the mean true PMRN in years 50-55 (i.e. initial PMRN before harvest, dashed line); and in years 170-175 (i.e. final PMRN after harvest, solid lines). In the absence of evolution, all lines overlap. PMRN midpoints were estimated using Barot et al.'s (2004) method, except when model parameters eliminated variation in the timing of maturation resulting in all individuals of a given cohort maturing at the same age and length (CV_G=0). In this case, instead of estimating PMRN midpoints, we compared populations' true PMRNs with the length at while individuals from the same cohort matured. No, moderate, and high evolvability represent coefficients of genetic variation of 0, 0.06, and 0.12, respectively. No, moderate, and high harvest represent maximum exploitation rates of 0, 0.5, and 1, respectively. Populations' true PMRNs and estimated PMRNs shown are means across cohorts for 5 replicate runs ± 1 SD.

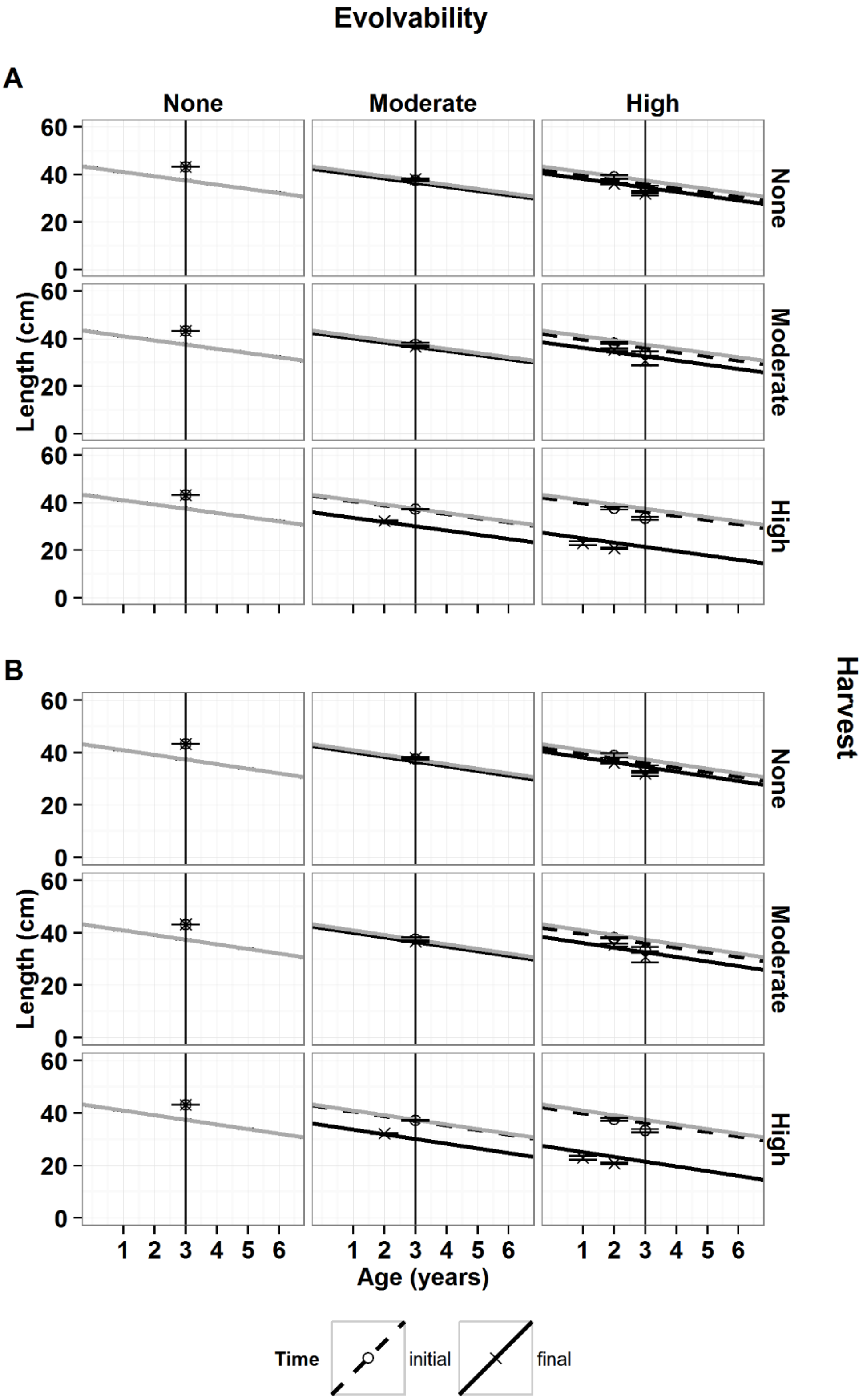


Figure 4.4. Mean age at maturation before (initial) and after (final) harvest, when growth is A) density-independent and B) density-dependent. No, moderate, and high evolvability represent coefficients of genetic variation of 0, 0.06, and 0.12, respectively. No, moderate, and high harvest represent maximum exploitation rates of 0, 0.5, and 1, respectively. Means depicted are for population samples taken during model years 50-55 (initial) and 170-175 (final); error bars show the average standard deviation across 5 replicate runs.

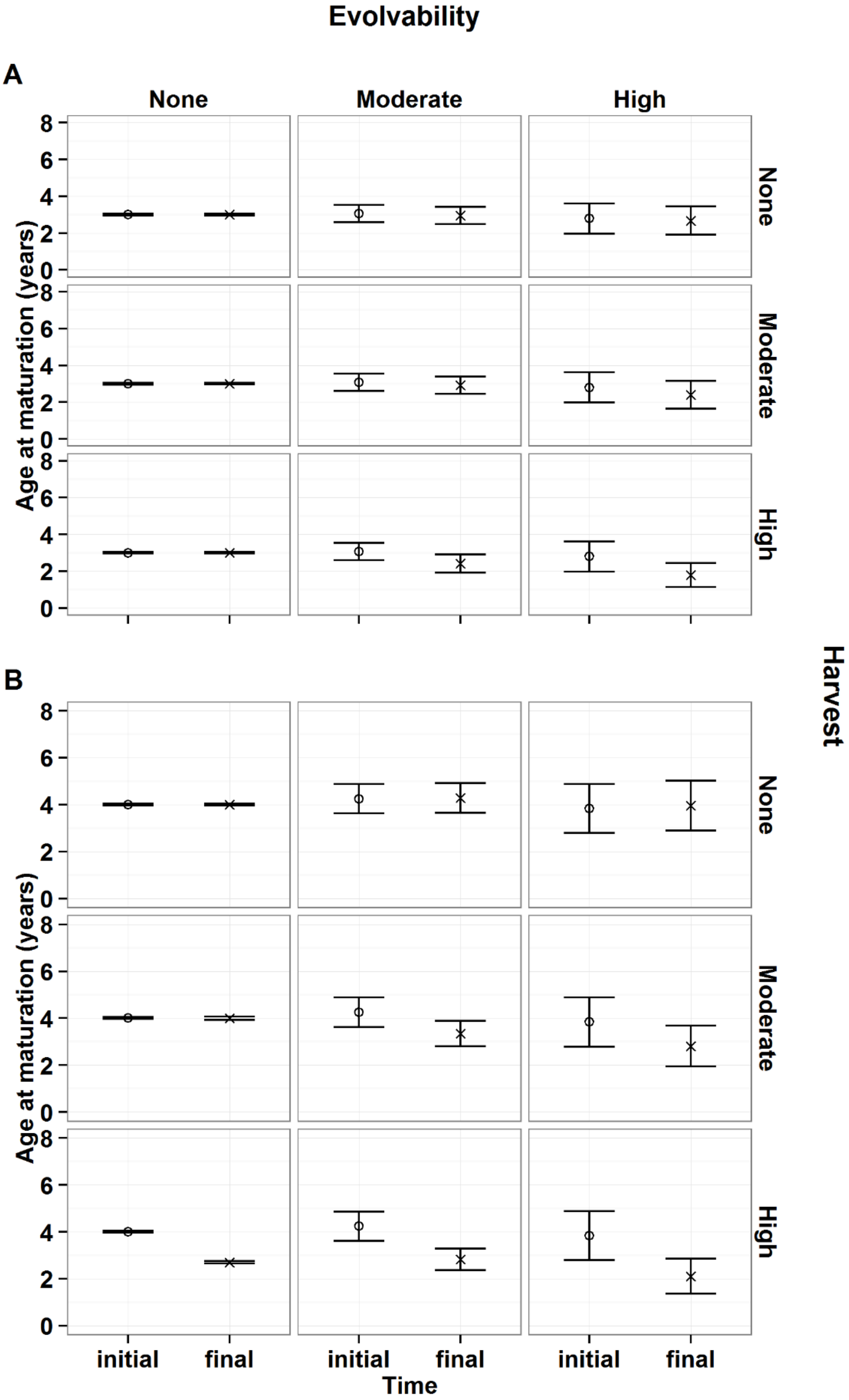
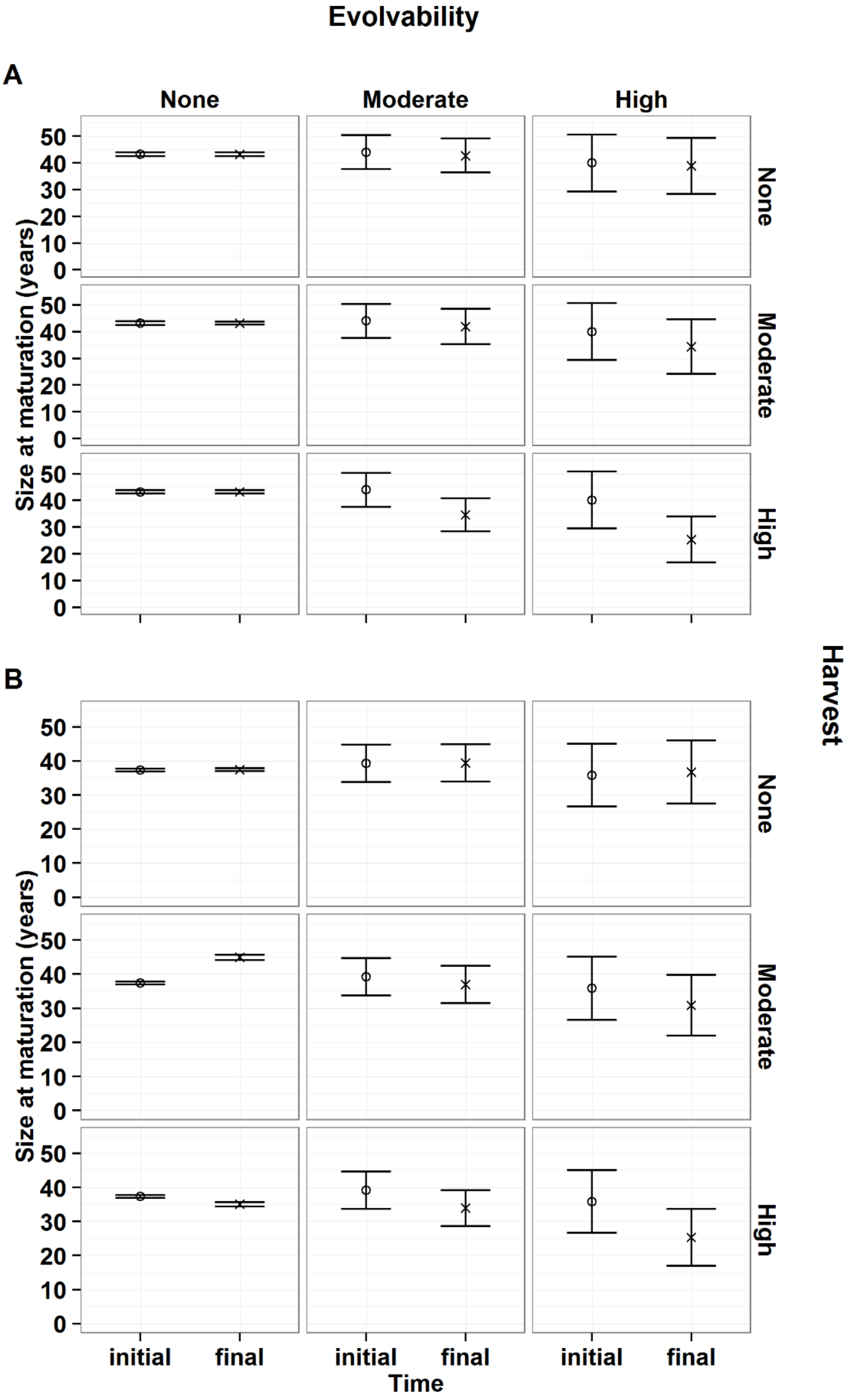


Figure 4.5. Mean size at maturation before (initial) and after (final) harvest, when growth is A) density-independent and B) density-dependent. No, moderate, and high evolvability represent coefficients of genetic variation of 0, 0.06, and 0.12, respectively. No, moderate, and high harvest represent maximum exploitation rates of 0, 0.5, and 1, respectively. Means depicted are for population samples taken during model years 50-55 (initial) and 170-175 (final); error bars show the average standard deviation across 5 replicate runs.



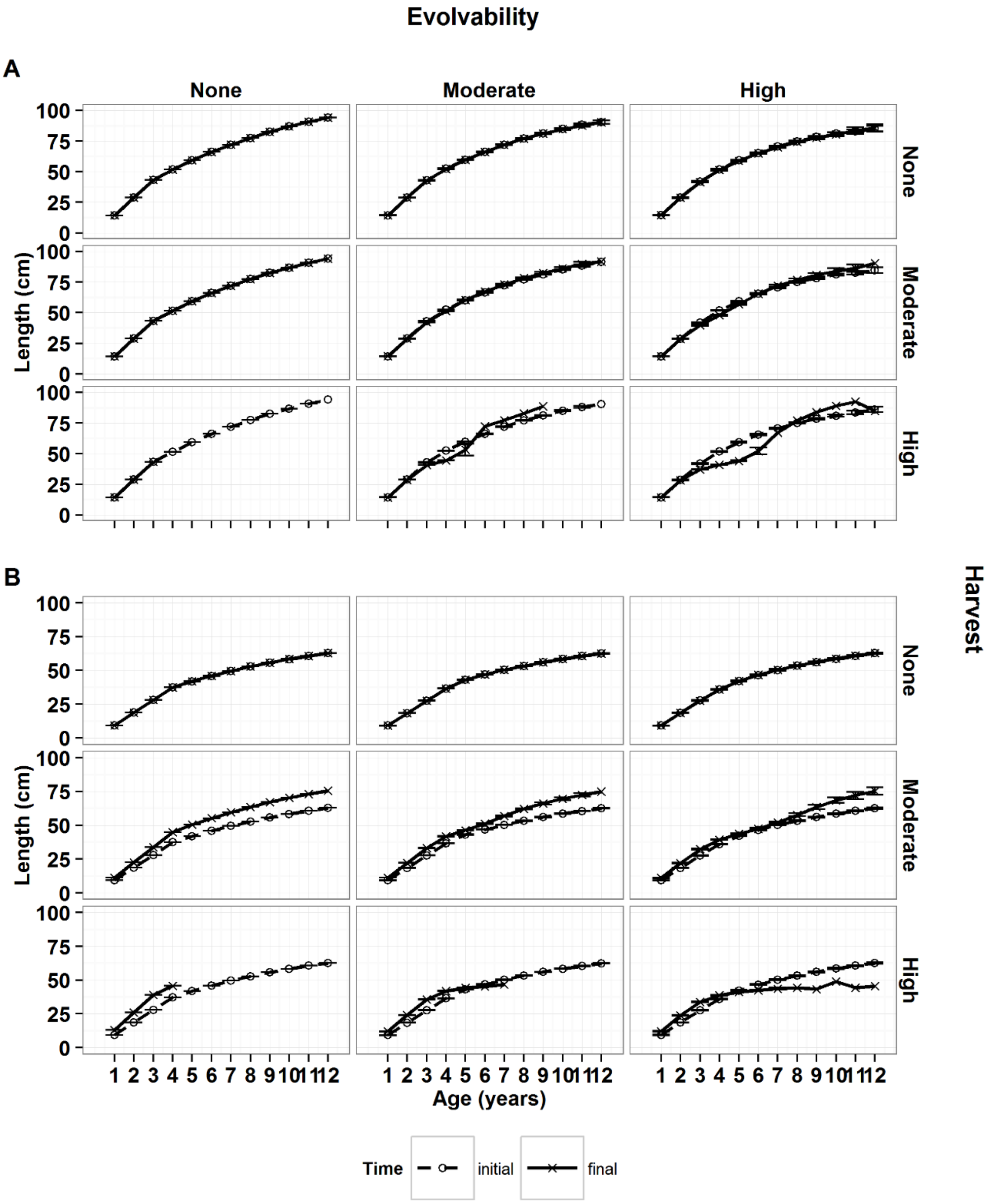


Figure 4.6. Mean lengths at age before (initial) and after (final) harvest, when growth is A) density-independent and B) density-dependent. No, moderate, and high evolvability represent coefficients of genetic variation of 0, 0.06, and 0.12, respectively. No, moderate, and high harvest represent maximum exploitation rates of 0, 0.5, and 1, respectively. Means depicted are for population samples taken during model years 50-55 (initial) and 170-175 (final); error bars show the average standard error across 5 replicate runs.

GENERAL DISCUSSION

With this dissertation, I aimed to investigate the role of eco-evolutionary dynamics in fisheries – a vital next step towards accounting for interactions between ecological and evolutionary processes in fisheries assessment and management. I accomplished this through the study of a commercially important lake whitefish stock in the Laurentian Great Lakes, a system that has undergone substantial ecological change over the last several decades. Using this system, I linked the timing of large-scale ecological change associated with a non-native species invasion with shifts in density-dependent growth and recruitment relationships for lake whitefish that likely reflect declines in the population carrying capacity (Gobin et al. 2015). Then using an individual-based model developed for this stock, I demonstrated how reductions in growth and recruitment potential associated with ecosystem change are predicted to negatively impact population productivity and sustainable harvest rates through demographic and plastic mechanisms (Gobin et al. 2016). By further incorporating an eco-genetic component to this model, I revealed how ecological processes could also affect evolutionary responses in maturation to harvest (Gobin et al., in press). Finally, using the same model, I show that the probabilistic maturation reaction norm (PMRN) approach that is commonly used to assess maturation and infer its evolution appears to be robust to ecological and evolutionary processes experienced by exploited stocks in the wild.

My first chapter contributes to our understanding of how large-scale ecosystem changes, such as those associated with species invasions, can impact ecological feedbacks in exploited fish stocks. In that chapter, I link large-scale ecological change stemming from a dreissenid mussel invasion with changes in density-dependent growth and recruitment relationships in Lake Huron lake whitefish. Accounting for the timing of two major events – the establishment of dreissenid mussels and a subsequent regime shift – greatly improved the fit of density-dependent growth and stock recruitment models to time series data spanning the years 1985 to 2012, providing evidence that changes in these relationships were associated with ecosystem changes, resulting in an altered carry capacity. Across the Great Lakes where dreissenid mussels have become established, lake whitefish have shifted towards a greater reliance on nearshore benthos (Rennie et al. 2009, Fera et al. 2015), including the zebra mussels that occupy these depths (Pothoven and Nalepa 2006, Lumb et al. 2007, Nalepa et al. 2009). A diet comprised of dreissenid mussels is energetically inferior in comparison to their historical diet that included *Diporeia* spp., and these diet shifts are thought to have contributed to declines in the growth, condition, and recruitment observed in lake whitefish across several of the Great Lakes (Pothoven and Madenjian 2008, Rennie et al. 2012, Fera et al. 2015). My work further shows that declines in growth and recruitment of Lake Huron lake whitefish coincide with shifts in key density-dependent relationships (Gobin et al. 2015). As the density-dependent feedbacks that regulate populations are scaled by the population carrying capacity (Hayes et al. 1996), these findings strongly suggest that ecosystem changes associated with the dreissenid mussel invasion have lowered the carrying capacity of Lake Huron lake whitefish. Consequently, these ecosystem changes have also altered how lake whitefish respond to changes in population density (e.g. via exploitation), with effects on harvest and the sustainability of the fishery.

In my second chapter, I show how the changes in ecological feedbacks via density-dependent growth and recruitment relationships interact to impact harvest in terms of yield and sustainability. Reducing the growth rate alone resulted in declines in yield that occurred through lower somatic growth that decreased population biomass and delayed when fish became vulnerable to the fishery. Also lowering the recruitment rate further decreased yield and sustainability through reductions in population abundance. Although this lower population density resulted in intermediate somatic growth rates owing to density-dependence, populations with reduced growth and recruitment rates exhibited the lowest yield and resilience to harvest. This study therefore demonstrates how both density-dependent growth and recruitment processes interact, and together with life history traits, regulate population productivity and determine sustainable harvest rates (Lester et al. 2014). Similar trends to those predicted here were observed in lake whitefish in several of the Laurentian Great Lakes following the establishment of dreissenid mussels. Lake whitefish in Lakes Ontario, Michigan, and Huron exhibited significant declines in growth (Lumb et al. 2007, Ebener 2013, Fera et al. 2015, Gobin et al. 2015) that were accompanied by reductions in recruitment in Lakes Ontario and Huron (Hoyle et al. 2008, Gobin et al. 2015). Commercial harvest of lake whitefish in Lakes Huron and Ontario also declined by 35% (Ebener 2013) and 90% (Hoyle et al. 2008), respectively. The declines in lake whitefish recruitment, relative abundance as measured in agency monitoring programs, and harvest are widespread in lakes Michigan and Huron, prompting significant concern among state, provincial, and binational management agencies and resulting in urgent requests for research related to lake whitefish dynamics. My thesis work, and the results of chapter 2 are thus timely, given that they describe the mechanisms underlying the changes observed, and point out that sustainable levels of harvest are predicted to be much lower than they used to be.

In my third chapter, I incorporated an eco-genetic component to the model presented in the previous chapter to investigate evolutionary responses to harvest and how these might be affected by ecological conditions. I examined how harvest-induced evolution is influenced by two ecological scenarios from the previous chapter: favourable, pre-invasion conditions characterized by high growth and recruitment rates, and poorer, post-invasion conditions with reduced rates of growth and recruitment. As in previous studies, harvest resulted in evolution of younger ages and smaller sizes at maturation (e.g. Dunlop et al. 2009, 2015). However, ecosystem conditions altered the evolutionary response to harvest such that less evolution of maturation occurred under post-invasion conditions when rates of growth and recruitment were reduced. Previous studies have demonstrated how evolutionary responses to harvest can be mediated by density-dependent growth (Lester et al. 2014, Dunlop et al. 2015, Eikeset et al. 2016). Increases in somatic growth when population density is reduced can shift maturation to younger ages through phenotypic plasticity (Trippel 1995); lessening selection for earlier maturation. In the current study, selective pressure was reduced through a different mechanism - slower growth that delayed recruitment to the fishery under less favourable ecological conditions. Although evolution in maturation allowed populations to persist when harvested at rates that led to collapse in the previous chapter, post-invasion conditions still resulted in less resilient populations overall, with diminished productivity compared to under pre-invasion conditions. This lower resilience is concerning given the economic, ecological, and cultural significance of this species in the Great Lakes. These findings also suggest that ecological changes resulting from the dreissenid invasion could have greater implications for the fishery and its sustainability compared to evolutionary responses to harvest. This differs from what has typically been found in marine stocks where fisheries-induced evolution has primarily been studied (e.g. Devine et al. 2012), and could be due to stronger density-dependence and environmental forcing experienced by freshwater populations.

In my fourth chapter, I investigated how a variety of factors relevant to exploited stocks in the wild, including the ecological setting, harvest rates, and evolution might affect our ability to accurately estimate probabilistic maturation reaction norms (PMRNs) and detect the evolution of maturation. The PMRN estimation method (Barot et al. 2004) is widely used to characterize age and size at maturation, and is the main approach used to infer evolution of maturation in fish stocks (Heino et al. 2015). However, the reliability of the approach when being applied to stocks in the wild has been questioned, due in part to the method having undergone little validation despite its widespread use. Barot et al. (2004) tested the method's robustness to violations of underlying model assumptions related to growth and mortality using simulated data for a single cohort, generated from a relatively simple model, with a non-evolving PMRN. Since then, only two additional studies (Pérez-Rodríguez et al. 2009, Olsen et al. 2014) have attempted to assess the estimation method, which they did by comparing estimated PMRNs with known timing of maturation observed in wild stocks. However, both of these studies focused on PMRN estimates for a single time period and were limited to comparing PMRN estimates with direct observations of maturation events, as a population's true PMRN in the wild can never actually be known. The individual-based eco-genetic model used in the current study allowed me to compare PMRNs estimated using the Barot et al. (2004) method with the population's true mean PMRN based on the maturation genotypes of the individuals in the population. That estimated PMRN midpoints aligned well with the population's true mean PMRN under various ecological conditions and with varying levels of harvest, and evolution, suggests that the estimation method is robust to these processes in the wild. Consequently, shifting PMRNs observed in wild stocks could reflect changes in the genetic propensity to mature at a given age and size, which is an important consideration for fisheries managers.

The research presented in this thesis highlights several exciting avenues for future research. When modeling ecological change, both density-dependent growth and recruitment relationships were often varied at the same time. While we might expect both relationships to be affected by large-scale ecosystem change, this approach provides little insight into the relative impacts of each type of ecological feedback individually. Therefore, studies that vary density-dependent relationships using a fully factorial design could provide valuable insight into the interactions between ecological feedbacks and evolutionary processes, with important implications for fisheries assessment and management. Similarly, rather than characterizing ecosystem change in terms of its effects on key density-dependent relationships in a single-species model, multispecies models (e.g. Audzijonyte and Kuparinen 2016) could provide another means of exploring eco-evolutionary dynamics among species and various trophic levels. Furthermore, investigation into how eco-evolutionary dynamics might differ in freshwater and marine fisheries is warranted. For my thesis work, I also focused on a single evolving trait, maturation, given that its influence on population productivity and its potential to evolve in response to harvest has already been widely demonstrated in the fisheries-induced evolution literature (Jørgensen et al. 2007, Dunlop et al. 2009, Devine et al. 2012). However, shifts in other life history traits (e.g. growth, reproductive investment) have been observed in exploited stocks and could readily evolve in response to harvest (Heino et al. 2015). Another logical step building on this work would therefore be to investigate the impacts of traits other than maturation, multiple evolving traits, or covariation among traits on eco-evolutionary dynamics in exploited stocks. Harvest could also select for behavioral (Uusi-Heikkilä et al. 2015, Andersen et al. 2018), morphological (Idris 2016), and physiological (Killen et al. 2015) traits. In the model used here, only an individual's genetic propensity to mature (i.e. PMRN slope and intercept) and their length at a given age influenced their probability of maturing. However, maturation can respond plastically to environmental and ecological factors independently of their effect on growth (e.g. temperature - Dhillon and Fox 2004, Kuparinen et al. 2011; social cues - Pauli and Heino 2013). Similarly, while growth rate influences length at age, these are not one in the same. Morita and Fukuwaka (2006) found maturation to be primarily influenced by recent growth history (i.e. growth rate) rather than length at age. Finally, the PMRN width reflects the probabilistic nature of maturation (Barot et al. 2004) and accounts for different types of variability in maturation at the level of the individual and the population. For individual-level PMRNs, the width would be influenced by plasticity in maturation that is independent of an individual's size-at-age, whereas for population-level PMRNs, it would be further influenced by genetic variation among individuals. However, the PMRN width in the current model does not allow these types of variation to be accounted for separately. Teasing apart the relative contribution of sources of variation in the PMRN width at the population level has been identified as a challenge (Eikeset et al. 2016, 2017, Enberg and Jørgensen 2017) that would be valuable to pursue.

A shift in fisheries assessment and management is currently underway. Historical approaches focused on single species over relatively small spatial and temporal scales. However, this approach limits our ability to account for the effects that various species have on one another, and how changes in these interactions over space and time could alter ecological and evolutionary responses to harvest. Large-scale ecological change is becoming ever more common with increasing rates of human disturbance and climate change (Meyer et al. 1999, Britten et al. 2016), and a need to integrate ecosystem monitoring and evolutionary biology more broadly when assessing wild populations has been identified (Brodersen and Seehausen 2014, Duckworth and Aguillon 2015). New research suggests that managing fisheries at the ecosystem level can increase efficiency (Jacobsen et al. 2017), and highlights how considering evolutionary responses to harvest can be used to promote productivity in exploited stocks (Mollet et al. 2016, Zimmermann and Jørgensen 2017). Assessment and management approaches that account for both ecological and evolutionary processes are still being developed, and those that incorporate reciprocal feedbacks between these processes remain to be seen. By demonstrating how interactions between ecological and evolutionary processes in exploited stocks together impact productivity and sustainability, this thesis serves as a next step in the integration of eco-evolutionary dynamics in the assessment and management of fisheries.

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