

Ecological change alters the evolutionary response to harvest in a freshwater fish

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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.

Key words: density-dependent growth; eco-evolutionary dynamics; fisheries-induced evolution; individual-based model; Lake Huron; probabilistic maturation reaction norm; regime change; sea lamprey; stock–recruitment relationship.

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 behaviors 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.

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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 differs 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 (Wang et al. 2008, Morbey and Mema 2018; Appendix S2: 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 (Appendix S1: Table S1) 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 S1.

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

$$h_t = h_{\max}/(1 + a \times B_t) \quad (1)$$

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

$$R_t/S_t = r_{\max} \times \exp(-\beta \times S_t) \quad (2)$$

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: (1) a constant level of natural background

mortality and (2) 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 S2: Figs. S2 and S3).

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 favorable ecosystem conditions ($h_{\max} = 14.4$ and $r_{\max} = 9$, Appendix S1: Table S1). 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 $r_{\max} = 3$, Appendix S1: Table S1). These scenarios were based on 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 (Appendix S1: Table S1).

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, C), was described by a double-logistic function

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

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, D), followed a logistic function

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

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).

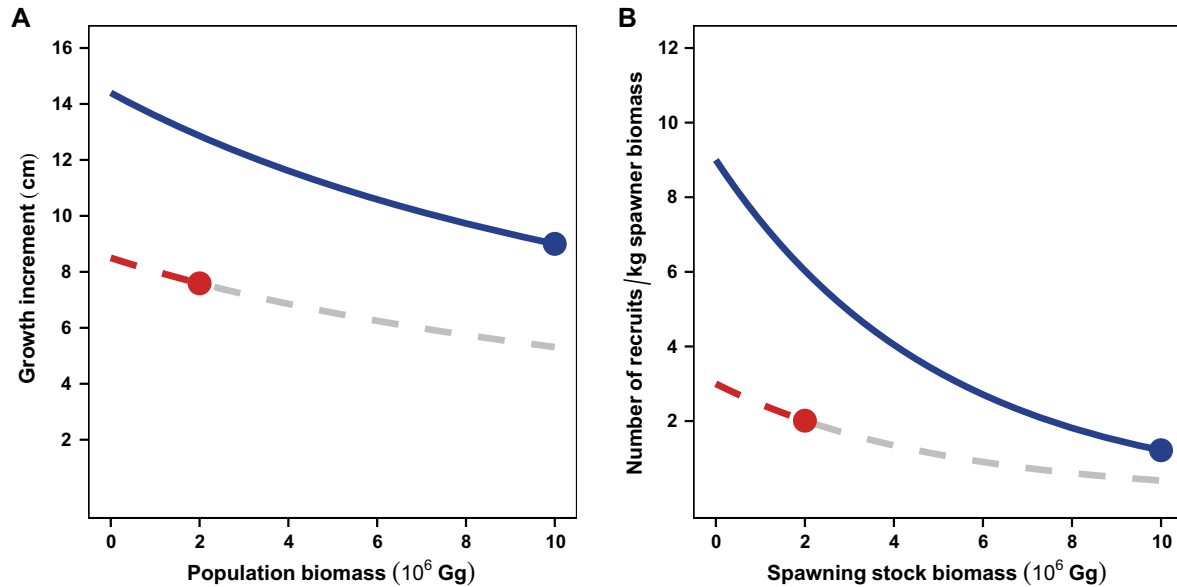


FIG. 1. Model scenarios used to examine the effects of ecosystem conditions before and after the dreissenid invasion on lake whitefish. (A) Growth potential and (B) recruitment potential are reduced between the pre-invasion scenario (solid blue lines; maximum growth rate, $h_{\max} = 14.4$ and maximum recruitment per unit of spawner biomass, $r_{\max} = 9$) 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 solid circles), measured as the population biomass equilibrium value in the absence of harvest (Gobin et al. 2016). Gray curves extending beyond the carrying capacity (i.e., population sizes not achieved during simulations) are shown to facilitate visual comparisons of relationships.

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 yr. 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, 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 (Figs. 3 and 4). The gill net fishery induced somewhat more evolution than the trap net fishery except with small mesh sizes at low harvest rates (Figs. 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 favorable, vs. downward-shifting PMRNs when ecosystem conditions were poor (Fig. 4). Most of the evolutionary response came about through evolution of the PMRN

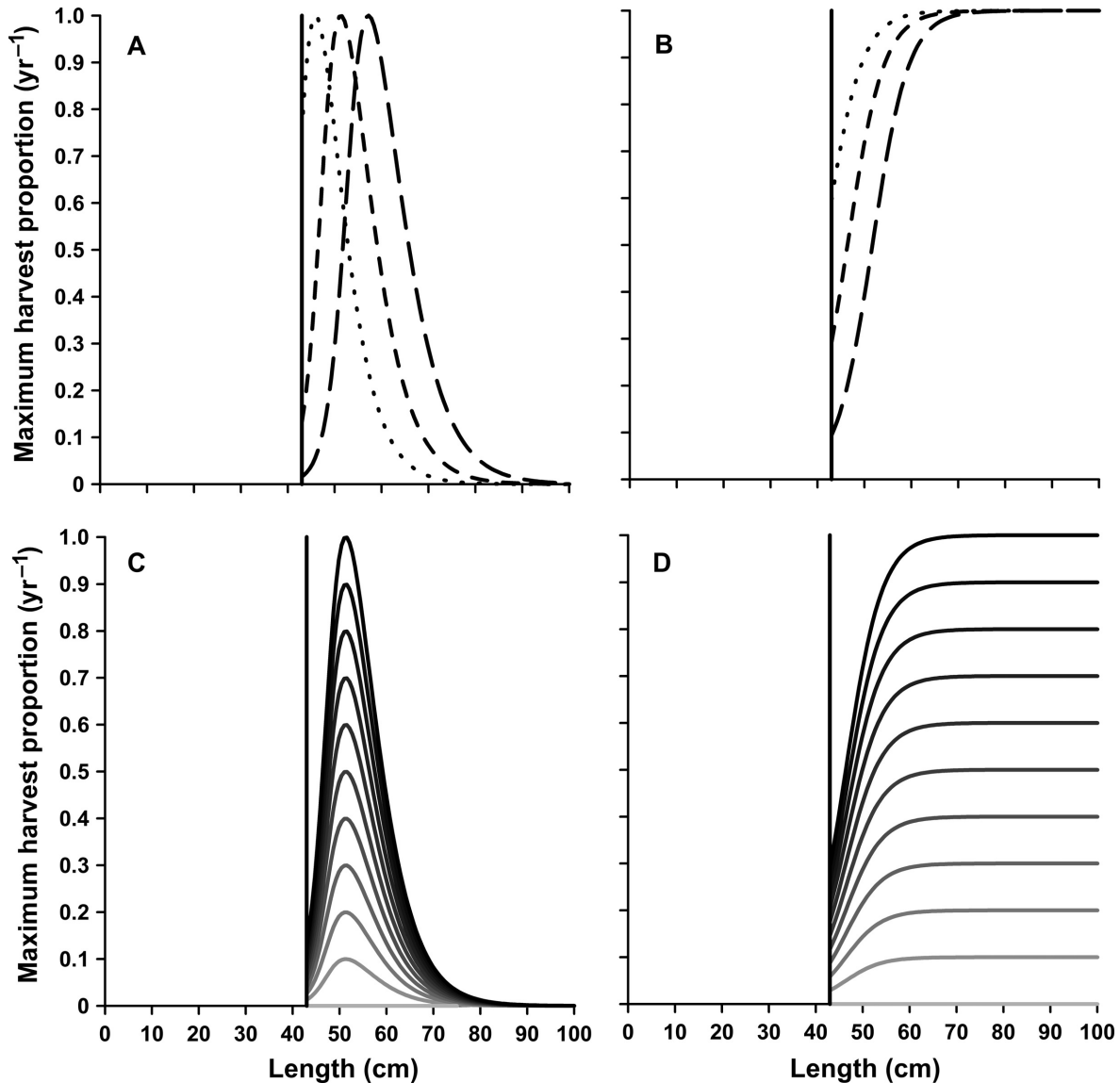


FIG. 2. Size-selective fishing regimes implemented in the eco-genetic model for lake whitefish. Vertical black lines mark the minimum size limit of the fishery, below which fish could not be harvested. Gill net selectivity curves (shown in panels A and C) are defined by a double-logistic function, whereas 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).

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 would also 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 S2: Figs. S4 and S5). 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 S2: Figs. S4 and S5). Declines in mean

age and size at maturation were greater when fishing with gill nets than when fishing with trap nets (Fig. 5A; Appendix S2: Figs. S4 and S5).

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 S2: Figs. S4–S7). 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 S2: Fig. S8). The exploitable biomass (i.e., the biomass of fish above the minimum size limit) and yield exhibited trends

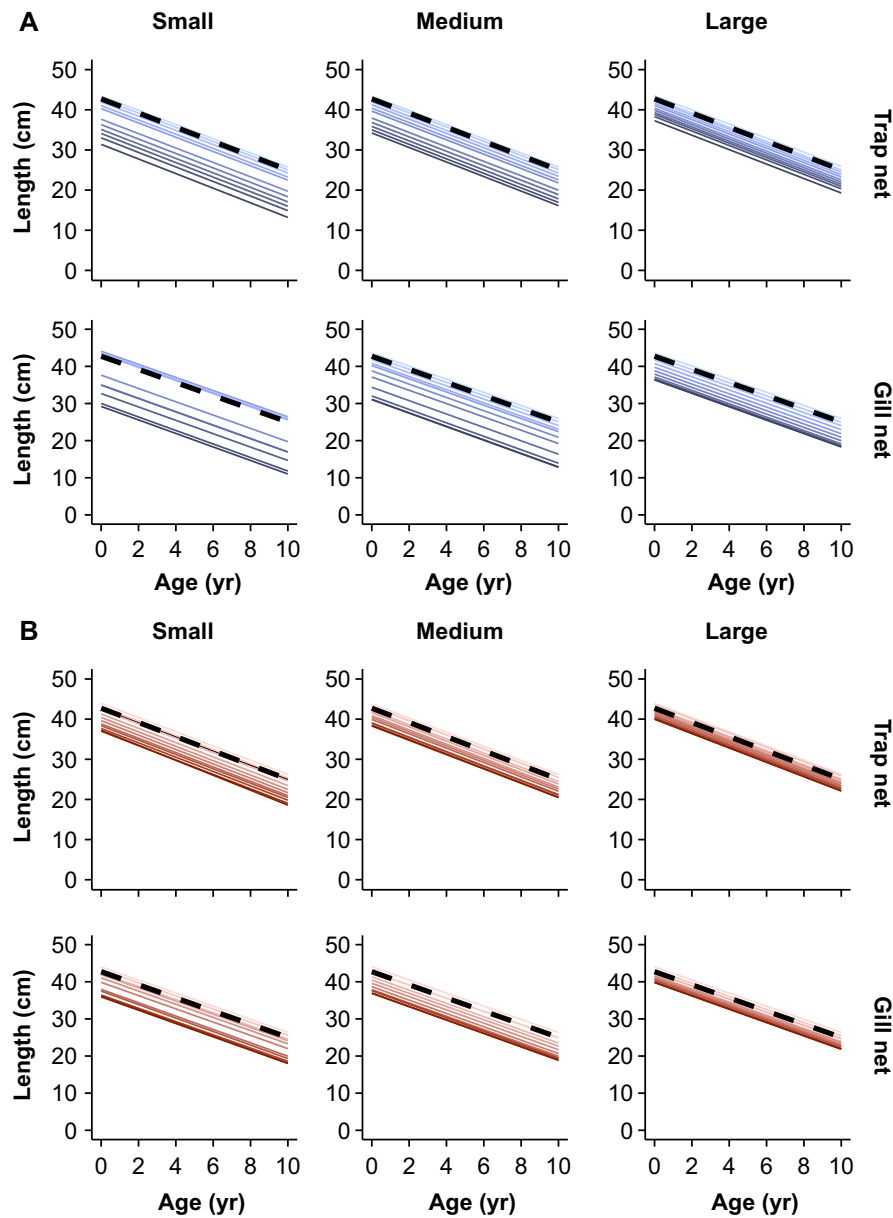


FIG. 3. Fisheries-induced evolution of mean probabilistic maturation reaction norms (PMRNs) for different ecological conditions. Top panels (A) shown in blue have a higher growth and recruitment potential (pre-invasion) and lower panels (B) shown in red have a lower growth and recruitment potential (post-invasion). 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 yr of harvest. Darker lines represent higher harvest rates. Results shown are population means averaged across replicate simulation runs.

similar to population biomass (Appendix S2: Fig. S8). 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 favorable 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, B), resulting in an overall reduced evolutionary response (Figs. 3 and 4). This contrasted with the

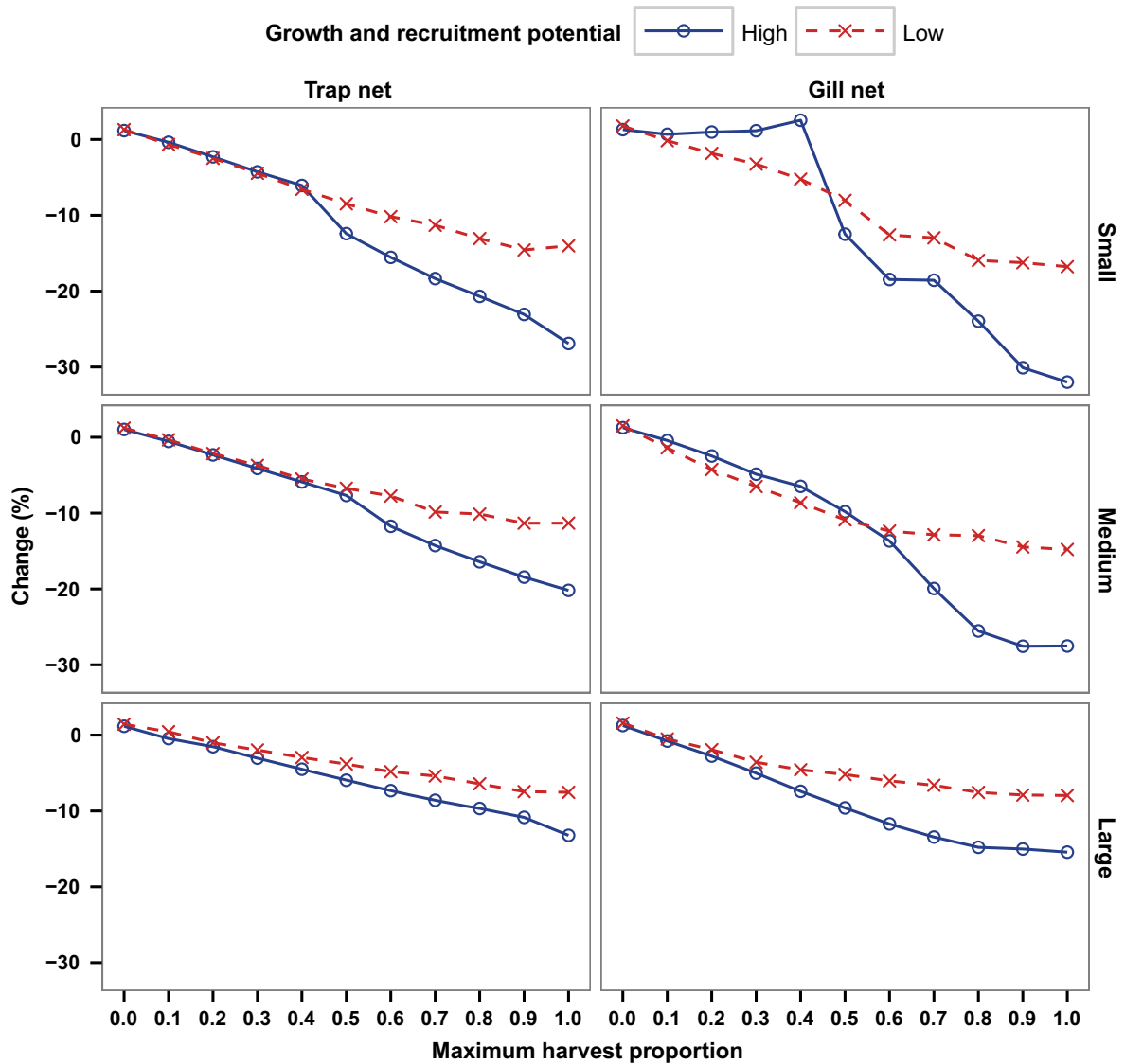


FIG. 4. Mean percent change in PMRN intercepts over a period of 100 yr of harvest. Negative values represent declines in the PMRN intercept whereas positive values represent increases in the PMRN intercept. Results shown are changes in population means averaged across replicate simulation runs.

pre-invasion scenario when the stock had a much steeper increase in vulnerability to harvest with age due to faster growth rates (Fig. 5A, B), which enhanced the selective pressure for earlier maturation (Figs. 3 and 4). 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 favorable for growth and recruitment. Reducing the vulnerability of younger age classes, in turn, reduced selection pressure favoring 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 (Figs. 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 favoring 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

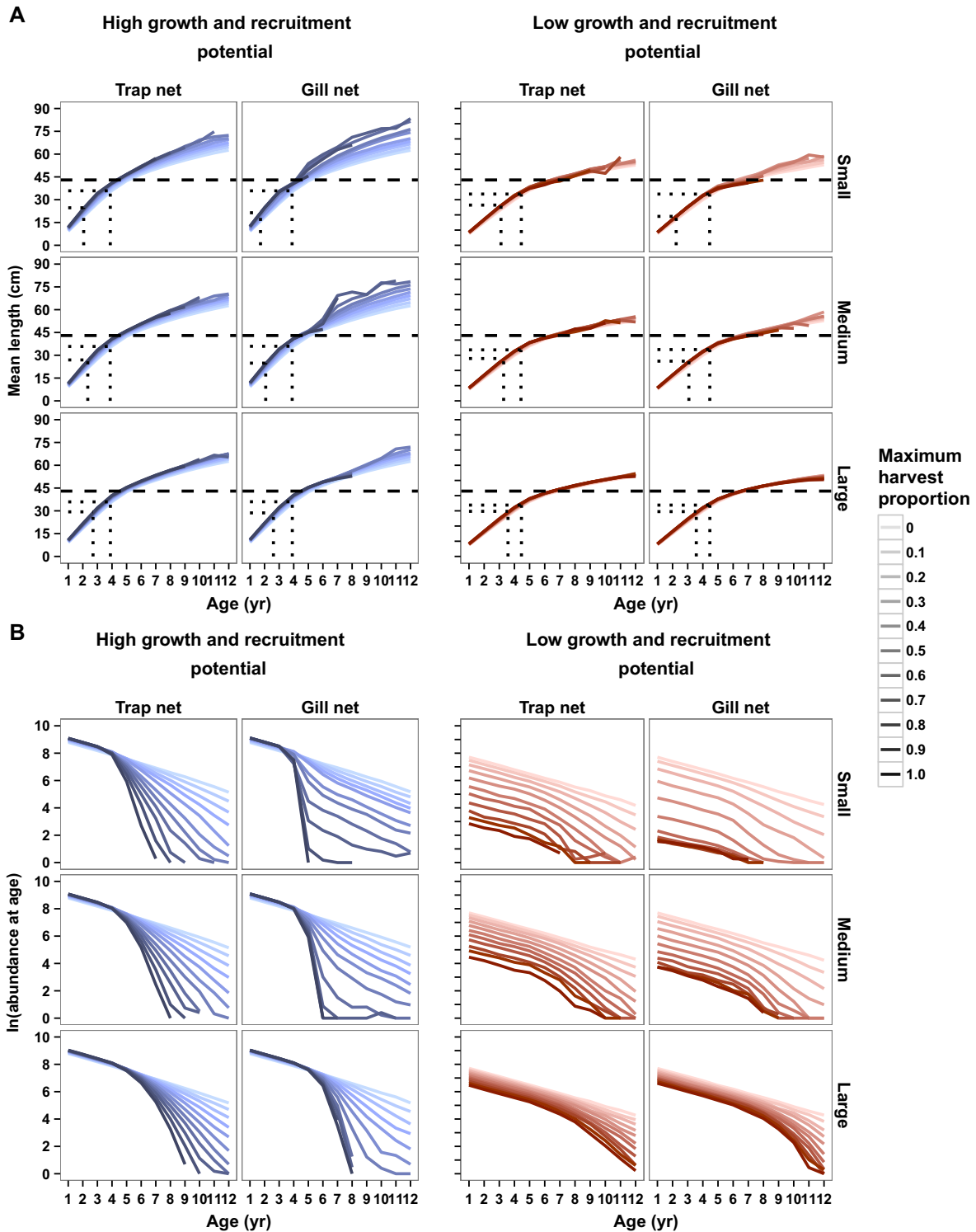


FIG. 5. (A) Predicted mean length-at-age and (B) natural-log-transformed mean abundance at age in the final year of harvest for different ecological conditions (blue, high growth and recruitment; red, low growth and recruitment) and mesh sizes (small, medium, large). In panel A, the dotted lines in each 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 panel 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.

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 S2: Fig. S1), 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 (Dunlop et al. 2015, Eikeset et al. 2016) 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 S2: Fig. S8). 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 2013, 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 (with a dome-shaped selectivity curve) generally induced slightly more evolution in maturation reaction norms than trap nets (with an S-shaped curve), except with small mesh sizes and low harvest rates when ecosystem conditions were favorable. 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 (Figs. 2 and 5B). 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 favorable. 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 S2: 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. 2012). 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 favor 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 S2: Figs. S2 and S3). 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.

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DATA AVAILABILITY

Data available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.3g227m5>