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Effects of changes in density-dependent growth and recruitment on sustainable harvest of lake whitefish

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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 for lake whitefish in the southern main basin of Lake Huron that 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. Also, fishing 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.

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), and 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 and habitat) determines a population's 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

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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 the 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 (*Micropterus 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 by a conversion factor b to account for the difference in energetic content between gonads and somatic tissue (Lester et al., 2004):

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

This investment is limited by the individual's body length and growth rate such that $g \le (3 * h) / L_t$ (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