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Review

Potential for fisheries-induced evolution in the Laurentian Great Lakes

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ABSTRACT

Fisheries are selective, capturing fish based on their body size, behaviour, life stage, or location. Over time, if harvest pressure is strong enough and variation in traits heritable, evolution can occur that affects key aspects of the ecology of fish stocks. Most compelling examples of rapid evolution in response to harvest have come from marine systems. Here, we review the state of knowledge on fisheries-induced evolution (FIE) in the Laurentian Great Lakes where subsistence, commercial, and recreational fisheries have operated for centuries. We conclude that stocks experienced harvest rates high enough and for long enough to undergo evolution. While historical fisheries exploited more juveniles, some contemporary Great Lakes fisheries target primarily adult size-classes thus reducing current selection for earlier maturation; however, other traits and behaviours could evolve (e.g., growth, timing of spawning, boldness). While commercial harvest previously dominated, recreational fishing is now expected to be a strong contributor to harvest selection in the Great Lakes. Environmental variation, density-dependence, invasive species, and the genetic legacy of population bottlenecks and stocking interact with, and make it more challenging to detect, FIE in the Great Lakes than in marine systems. Case studies are presented for Great Lakes stocks of yellow perch *Perca flavescens* and lake whitefish *Coregonus clupeaformis* for which FIE has been investigated. The evidence for FIE in the Great Lakes is currently sparse, potentially because of the low research focus on this topic or because of the interacting influence of environmental variation and anthropogenic stressors.

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Introduction

Fishing can exert strong selective pressures on a stock, causing rapid evolution of key traits and behaviours (see reviews by Heino et al., 2015; Hutchings and Fraser, 2008; Law, 2007). Size-selective fishing is

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typically expected to select for earlier maturation, slower or faster growth, and increased investment to reproduction (e.g., Dunlop et al., 2009b). Even fishing that is not size-selective could induce evolution of life history traits because overall increased mortality selects for earlier maturation and increased reproductive effort (Gårdmark and Dieckmann, 2006; Heino et al., 2015). Fisheries-induced evolution (FIE) has been studied in several freshwater and anadromous populations, dating back decades (e.g., Edeline et al., 2007; Handford et al., 1977; Nusslé et al., 2009; Philipp et al., 2009; Ricker, 1981). However, the majority of research on FIE has focused on marine fisheries, and most of the likely cases of FIE in the wild have come from marine systems (Jørgensen et al., 2007). Given the long history of subsistence, commercial, and recreational fisheries, it is possible that many fish stocks in the Laurentian Great Lakes have also undergone FIE and experienced resultant changes in population productivity and stability (Dunlop et al., 2015; Kuparinen et al., 2016; Uusi-Heikkilä et al., 2015).

Detecting FIE can be challenging (Heino and Dieckmann, 2008; Heino et al., 2015). In addition to causing evolution, harvest can have several other consequences on the life history traits of fish populations, including causing demographic changes and responses through phenotypic plasticity (Law, 2000). By reducing the fitness of fish that delay maturation (because those fish have a higher chance of being harvested prior to reproducing and passing on their genes), intense size-selective harvesting of both juveniles and adults is expected to select for earlier maturation (Fig. 1). As growth slows down after maturation (Lester et al., 2004), sizes of fish may decrease as a result of harvest. In some cases, harvest could also select for slower growing genotypes (Conover and Munch, 2002). However, intense size-selective fishing might not only lead to FIE, but could also lead to a demographic shift toward smaller individuals in the fished population simply via removal of large, old individuals (size truncation) meaning the simple observation of a decline in mean size coinciding with increased fishing does not represent evidence of FIE. In addition, fishing could reduce population biomass and improve the conditions for growth via compensatory density-dependence, which could also lead to earlier maturation (Law, 2000; Rijnsdorp, 1993). Thus, even if harvest brings about FIE and genetically slower growth rates, observed (phenotypic) growth of individual fish could nonetheless increase and ages at maturity decrease because of density-dependent release (Dunlop et al., 2009b).

Despite these challenges, evaluating the extent to which FIE has occurred in fish populations is important from a management perspective for several reasons. First, the life history traits expected to evolve define vital processes that determine population productivity and potential fisheries yield. Second, some of the more common evolutionary responses (e.g., earlier maturation and slower growth) can be viewed as undesirable because they have negative consequences for the ecosystem services provided by fish stocks (Jørgensen et al., 2007), such as net present value and the likelihood of capturing trophy-sized fish (e.g., Eikeset et al., 2013). Third, evolution can occur on timescales short enough to interact with ecological processes and to be of relevance to management (e.g., within a few decades; Fraser, 2013). This can result in changes to population dynamics (Dunlop et al., 2015; Nusslé et al., 2016), including potentially decreased stability (Hsieh et al., 2006; Kuparinen et al., 2016), as well as trophic level responses and effects on other species in the food web (Bodin et al., 2012; Kindsvater and Palkovacs, 2017). Additionally, evolution can alter the reference points commonly relied upon when evaluating the status of stocks and defining harvest control rules (Heino et al., 2013). Fourth, reversing FIE is predicted to take longer than the evolution that occurs during intense harvesting (Conover et al., 2009; Dunlop et al., 2009b; Enberg et al., 2009), although the pace of reversal will depend on the costs associated with the initial evolutionary response or other ecological factors (e.g., Feiner et al., 2015).

Strong selection from human harvesting capable of causing evolution has now been reported as occurring in a variety of taxa, including marine and freshwater fish and wildlife populations (Allendorf and Hard, 2009; Chiyo et al., 2015; Douhard et al., 2017; Heino et al., 2015;

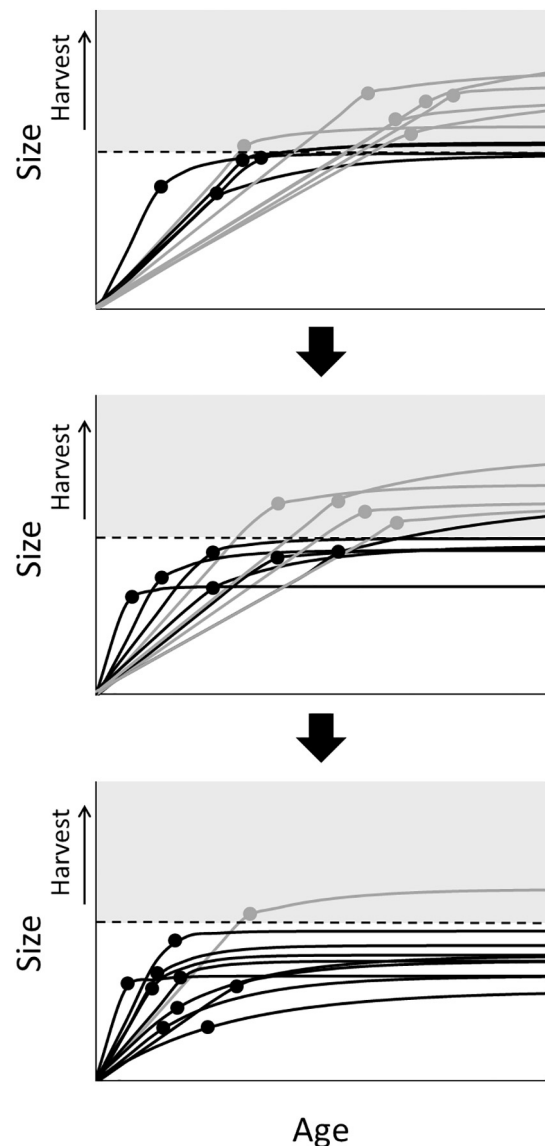


Fig. 1. Theoretical expectations for the evolution of maturation over time (moving from top to bottom) in fish stocks experiencing size-selective harvest. The horizontal dashed line and shaded area denote the size at which fish become susceptible to the fishery. Each solid line represents a potential growth trajectory for an individual fish, with the point along the line indicating the size and age at which that individual becomes mature. Growth is linear before maturation and slows after maturation due to allocation of energy toward reproduction. Individuals with black growth curves mature before they become susceptible to harvest, and therefore are more likely to reproduce successfully before they are harvested. In contrast, individuals with gray growth curves do not mature until after they are large enough to be harvested, and therefore may be harvested before they are able to reproduce. This selection against late maturation leads to an evolutionary reduction in the size and age at maturation of individuals over time.

Kvalnes et al., 2016). Here, we provide an assessment of whether FIE is expected to occur within the Laurentian Great Lakes (herein referred to as Great Lakes) and whether it should be of concern from a management perspective. We begin with describing the potential for FIE within the Great Lakes based on the harvest pressure, selectivity patterns, and environment experienced by fish stocks. We then review specific Great Lakes examples where FIE has been studied, explain why FIE should be relevant to Great Lakes managers, and discuss research priorities.

Is harvest pressure high enough to cause FIE in Great Lakes stocks?

There is a long enough history of substantial harvest pressure of Great Lakes stocks to support the possibility that FIE has already taken

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