Failure to detect ecological and evolutionary effects of harvest on exploited fish populations in a managed fisheries ecosystem

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Abstract: Overexploitation and collapse of major fisheries raises important concerns about effects of harvest on fish populations. We tested for ecological and evolutionary mechanisms by which harvest could affect exploited fish populations in Lake Erie over the last four decades, over most of which intensive fisheries management was implemented. We did not detect evidence of long-term negative effects of harvest on yellow perch (Perca flavescens), walleye (Sander vitreus), white perch (Morone americana), or white bass (Morone chrysops) populations, either through recruitment success or through alteration of maturation schedules. Current fisheries management in Lake Erie has been relatively successful with respect to minimizing negative harvest effects, such that the dynamics of exploited fish populations in Lake Erie were more strongly affected by environment than harvest. Our study adds to the evidence that effective fisheries management is capable of rebuilding depleted fisheries and (or) maintaining healthy fisheries. Nevertheless, fisheries management needs to move beyond the ecological dimension to incorporate economic, social, and institutional aspects for society to be better assured of the sustainability of fisheries in rapidly changing ecosystems.

Introduction

The rapid increase of global harvest, and associated overexploitation and collapse of important fisheries, raises important concerns about effects of harvest on fish populations (Branch et al. 2011). However, it has proven difficult to disentangle effects of harvest from effects of environmental variation (e.g., ecosystem regime shift and climate change) on the dynamics of fish populations (Lluch-Belda et al. 1992). Simple evaluation of fisheries status using reference points derived from classical stock assessment models may not accurately reflect the effects of harvest on fish populations, especially when the variation in background ecological conditions coincides with systematic changes in the distribution, productivity, and (or) life history of fish populations (Punt et al. 2014; Szuwalski and Hollowed 2016). In such cases, a mechanistic approach that explicitly tests for the ecological and evolutionary mechanisms through which harvest could affect fish populations may be needed to better understand the risk that harvest poses, relative to other considerations, on the sustainability of fisheries.

Yellow perch (Perca flavescens), walleye (Sander vitreus), white perch (Morone americana), and white bass (Morone chrysops) are four main harvested species in Lake Erie (Fig. 1A). Since 1984, yellow perch and walleye have been co-managed by several jurisdictions around Lake Erie (i.e., Ontario, Ohio, Michigan, Pennsylvania, and
New York) under a management system comprising annual total allowable catches, quota allocation among jurisdictions, and individual transferable quotas (ITQs) (Belore et al. 2013; Wills et al. 2014). White perch and white bass are not managed via total allowable catch, quota allocations, or ITQs (i.e., fisheries for these species are largely open access), although minimum size limits are applied in Ohio waters (ODNR 2016). In recent decades, large ecosystem changes occurred in Lake Erie, the result of introductions of non-native species and eutrophication, among other anthropogenic activities (Ludsin et al. 2001; Bunnell et al. 2014), which coincided with changes in the dynamics of fish populations and associated fisheries (Jones et al. 2016). Debates as to the causes of fish population dynamics among stakeholders raised a basic, but important, question: to what extents are commercially and recreationally exploited fish populations in Lake Erie affected by harvest and (or) environment? To address this question, we launched a project under the Canadian Fisheries Research Network. In this paper, we (i) elaborate on general ecological and evolutionary mechanisms by which harvest may affect fish populations, (ii) summarize evidence about these general effects of harvest on exploited fish populations in Lake Erie, and (iii) discuss the implications of this evidence for fisheries management on Lake Erie and globally.

General mechanisms by which harvest affects fish population dynamics

Ecological and evolutionary processes can interactively affect fish population dynamics via recruitment success and maturation schedule (Hidalgo et al. 2014). In fisheries science, recruitment is typically defined as the youngest fish fully vulnerable to fishing gear, which is usually considered as a proxy of population birth rate (Caley et al. 1996). Fish recruitment usually exhibits strong temporal variation, which can strongly affect population dynamics (Fogarty et al. 1991; Koslow 1992). With respect to maturation schedule, the size and age at maturation can also affect fish population dynamics by influencing lifetime reproductive success (Stearns 1989; Bernardo 1993). Declines in age and size at maturation are usually correlated with reductions in fecundity, potentially decreasing the productivity of fish populations (Heino et al. 2013; Kuparinen et al. 2014; Dunlop et al. 2015) and possibly signaling population collapse (Olsen et al. 2004).

Harvest can affect recruitment success by reducing spawning stock biomass (SSB) and (or) altering spawning stock age structure. SSB was traditionally considered as an important factor affecting recruitment success (Myers and Barrowman 1996), and the stock–recruitment relationship is one of the most widely accepted concepts in fisheries science (Hilborn and Walters 1992). When the SSB is fished down to a very low level (ascending part of the stock–recruitment curve), recruitment will be substantially reduced due to reduced egg production, leading to recruitment overfishing (Sissenwine and Shepherd 1987). Additionally, harvest can affect the age structure of the spawning stock through disproportionate removal of older, larger, and potentially more reproductively valuable individuals (Bernely et al. 2004a), thereby affecting recruitment. For many fish species, offspring number and survival are positively correlated with the age and size of spawning fish (Berkeley et al. 2004a), so a population age structure skewed towards younger and smaller fish will lead to reduced population productivity (Marteinsdottir and Thorarinsson 1998; Berkeley et al. 2004b).

Harvest can also induce adaptive changes in age or size at maturation through developmental and (or) evolutionary mechanisms (Rochet 1998). Harvest that lowers fish density reduces inaspecific competition may release resources for surviving fish via density-dependent mechanisms, causing fish to grow faster and mature at younger age and often at smaller size (Trippel 1995). Many studies have indicated that the intensity of harvest is related to the direction and speed of changes in age and size at maturation (Law 2007; Heino and Dieckmann 2008). Additionally, persistent size-selective harvest can favor the evolution of younger age and smaller size at maturation (Heino et al. 2002; Grift et al. 2003; Barot et al. 2004), causing fisheries-induced evolution (Heino and Dieckmann 2008). Analyses of probabilistic maturation reaction norms (PMRNs) are widely used to measure evolutionary changes in fish size and age at maturation; downward shifts in PMRNs have been observed in many harvested fish populations, indicating evolutionary change towards lower age at maturity (Sharpe and Hendry 2009; Devine et al. 2012).

If harvest significantly affected fish population dynamics via these ecological and evolutionary mechanism, we predicted that (i) harvest that was sufficient to reduce SSB in the range of the ascending part of the stock–recruitment curve would lead to positive correlations between SSB and recruitment (Fig. 2A); (ii) harvest that induced change in age structure and affected fish recruitment would lead to recruitment positively correlated with mean age of spawning stock (Fig. 2B); (iii) fish maturation schedules sufficiently changed by harvest intensity would lead to negative correlations between harvest intensity and length at 50% maturity ($L_{50}$) (Fig. 2C); and (iv) persistent harvest that was sufficient to cause earlier maturation would lead to declines in $L_{50}$ over the period of harvest (Fig. 2D).

Ecological and evolutionary effects of harvest on exploited fish populations in Lake Erie

To test for the effects of SSB and mean age of spawning stock on recruitment of yellow perch and walleye in Lake Erie, we used age-specific biomass and abundance of yellow perch and walleye estimated from two statistical catch-at-age (SCAA) models used by the Yellow Perch Task Group and Walleye Task Group, respectively (Belore et al. 2016; Wills et al. 2016). Owing to time differences in the initialization of yellow perch and walleye stock.
assessments, yellow perch and walleye data were available from 1975 and 1978 forward, respectively. Additionally, biomass and abundance estimates from SCAA models are most uncertain for the most recent years, so we did not use the data after 2013. Detailed methods are shown in Zhang et al. (2015) and Gíslason et al. (2018).

To test for effects of harvest on $L_{50}$ of yellow perch, walleye, white perch, and white bass stocks in Lake Erie, we used the age-specific abundance data for age-1 and older fish collected from Partnership Gillnet Index Surveys (PGIS), as well as biological data (e.g., length, mass, age and maturity status) estimated from PGIS. The PGIS started in 1989, and we restricted our $L_{50}$ analyses between 1991 and 2013. Harvest data for yellow perch, walleye, white perch, and white bass included both commercial and recreational fisheries in both Canada and the United States.

No significant effects of harvest on recruitment success were detected for Lake Erie yellow perch and walleye fisheries over the last four decades, either through reduction of SSB or alteration of spawning stock age structure. In contrast with our predictions (Figs. 2A and 2B), for Lake Erie yellow perch and walleye, there were no significant correlations between SSB and recruitment (Figs. 3A and 3B), and the mean age of the spawning stock did not positively affect recruitment (Figs. 3C and 3D). At annual scale, Zhang et al. (2017a) compared the relative effect of SSB with multiple abiotic and biotic factors (e.g., water temperature, dissolved oxygen, wind speed, warming rate, zooplankton, and predatory fish) on recruitment of Lake Erie yellow perch and found that yellow perch recruitment was mainly driven by biophysical processes (i.e., spring warming rate, wind speed, and yearling walleye density) at pelagic larval and early juvenile life-history stages (Zhang et al. 2017a). At decadal scale, the stock–recruitment relationship of yellow perch varied in response to the ecosystem changes associated with eutrophication and invasive species, suggesting strong effects of ecological factors on yellow perch recruitment (Zhang et al. 2017b). In both cases, any effect of SSB on yellow perch recruitment was largely obscured (Zhang et al. 2017a, 2017b). Consistently, no significant effect of yellow perch spawning stock age structure on recruitment was detected (Zhang et al. 2015). For walleye fisheries, neither the probability of overexploitation nor undesirable economic outcomes for the commercial fishery were sensitive to the timing of harvest (before or after the spawning season), implying that walleye recruitment may not be strongly affected by harvest-induced changes in SSB (Reid 2016).

Harvest-induced changes in maturation schedules were not detected in Lake Erie yellow perch, walleye, white perch, and white bass fisheries over the last 30 years. Neither correlations between harvest intensity and $L_{50}$ (Fig. 4) nor declining temporal trends in female $L_{50}$ (Fig. 5) were detected among any of the four species. Both results were contrary to predictions of whether harvest affected changes in length at maturation (Figs. 2C and 2D). Rapid variation in age and size at maturity were detected for Lake Erie yellow perch, which could not be explained by variation in harvest (Gíslason et al. 2018). Similar results were observed for Lake Erie walleye, white perch, and white bass (Gíslason 2017). Instead, age and size at maturity of yellow perch, walleye, white perch, and white bass fluctuated synchronously over time, independent of harvest, implying that some large-scale ecological process(es), more so than harvest, drove temporal variation in age and size at maturity (Gíslason 2017). Additionally, PMRNs of female yellow perch actually shifted upwards over time (Gíslason 2017), contrary to expectation under the hypothesis that these fisheries might have induced evolution of important life-history traits that could affect productivity (Heino and Dieckmann 2008).

We infer from the results of this comparative approach that, under the fisheries management regime in place on Lake Erie since the mid-1980s, recruitment success and maturation schedules of yellow perch and walleye, as well as the maturation schedules of white perch and white bass, have been predominantly affected by ecological processes related to large-scale environmental changes, rather than harvest.

**Implications for fisheries management**

**Ecological success of Lake Erie fisheries management**

In contrast with the large amount of literature documenting collapse of exploited fish populations (Paula et al. 1998; Myers and Worm 2003; Sharpe and Hendry 2009), the yellow perch, walleye, white perch, and white bass fisheries in Lake Erie have been persistent during the past four decades. We propose three, not mutually exclusive, hypotheses that may account for the results: (i) Lake Erie commercial and recreational fisheries have become smaller in scale, losing the capacity to affect fish population dynamics, even in the cases of white perch and white bass, for which there is no direct control over fishing mortality; (ii) Lake Erie fisheries management has been effective in avoiding the negative effects of harvest on fish populations; and (iii) Lake Erie white perch, white bass, yellow perch, and walleye populations are inherently resilient to the effects of harvest.

Commercial fisheries in Lake Erie can be traced back to 1815, and the fishing gear has evolved from low-efficiency twine nets and seines to high-efficiency gillnets (Applegate and van Meter 1970). Increasing harvest pressure together with habitat destruction contributed to the collapse of cisco (*Coregonus artedi*) in the 1920s (Beeton 1961). Harvest capacity peaked in the 1950s and coincided with declines and collapse of several historically important fish species (e.g., lake whitefish (*Coregonus clupeaformis*) and blue pike (*Sander vitreus glaucus*); Applegate and van Meter 1970; Hatch et al. 1987). Since the mid-1980s, fishing effort in both the commercial and recreational fisheries was greatly reduced. Commercial fishing with gill nets was banned in the Ohio waters of Lake Erie in 1984. Following the implementation of the ITQ system in Ontario, the number of commercial gill-netting tugs working in the Canadian waters of Lake Erie declined from about 145 in 1984 (Cowan and Paine 1997) to fewer than 60 in 2016 (K. Soper, Ontario Ministry of Natural Resources and Forestry (OMNRF), personal communication). The Ohio recreational fishery also
Fig. 3. Effects of spawning stock biomass (SSB) and mean age of spawning stock (MA) on recruitment (R) for Lake Erie yellow perch and walleye; (A) relationship between SSB and R for yellow perch between 1975 and 2015; (B) relationship between SSB and R for walleye between 1978 and 2015; (C) relationship between MA and recruitment residual after accounting for effects of SSB (Res-R) for yellow perch between 1975 and 2015; (D) relationship between MA and Res-R for walleye between 1978 and 2015.

Fig. 4. Effect of harvest on female length at 50% maturity ($L_{50}$) for four harvested species in Lake Erie; (A) relationship between harvest and female $L_{50}$ 2 years later for yellow perch ($r = 0.12, p = 0.69$); (B) relationship between harvest and female $L_{50}$ 2 years later for walleye ($r = 0.04, p = 0.57$); (C) relationship between harvest and female $L_{50}$ 2 years later for white perch ($r = 0.14, p = 0.72$); (D) relationship between harvest and female $L_{50}$ 2 years later for white bass ($r = 0.04, p = 0.58$). CPUE, catch per unit effort.
experienced a significant reduction in fishing capacity over this period. Walleye fishing effort dropped from 8042 thousand rod hours (mean 1984–1989) to 2334 thousand rod hours in 2015, and yellow perch fishing effort dropped from 1724 to 1089 thousand hours over the same period (ODNR 2016). It is plausible that, where at one time they did, the capacity of Lake Erie fisheries simply no longer strongly affects fish population dynamics.

In 1984, a system of quota management for the commercial yellow perch and walleye fisheries was implemented in Lake Erie (Hatch et al. 1987). The Lake Erie Committee establishes annual total allowable catches for yellow perch and walleye fisheries based on stock assessment. Under the Lake Erie Committee, the Yellow Perch Task Group and Walleye Task Group use SCAA models to estimate and project population sizes of yellow perch and walleye, based on extensive data from fisheries-dependent and -independent surveys. The implementation of annual quotas is enforced within the administrative institutions of the province and states (Ontario, Michigan, Ohio, Pennsylvania, and New York) around Lake Erie. Meanwhile, active engagement by industry stakeholders with management agencies facilitated data acquisition, which helped to reconcile some of the conflicts between stakeholders and managers. For example, the Lake Erie Partnership Index Fishing Survey is the result of a 26-year partnership between the Ontario commercial fishing industry and the OMNRF. The data collected from this survey are used for stock assessment and management by the OMNRF and other Lake Erie agencies. Additionally, stakeholders began to actively participate in agency-driven processes such as structured decision making (Gregory et al. 2012) and management strategy evaluation (Butterworth 2007) for the development of harvest control rules and management plans for Lake Erie percids (Jones et al. 2016). Formed in 2010, the Lake Erie Percid Management Advisory Group (Jones et al. 2016) included stakeholders from all jurisdictions and user groups, all of whom were able to engage with the Lake Erie Percid Management Advisory Group science and facilitation team and each other during a long and technically sophisticated structured decision making – management strategy evaluation process (Jones et al. 2016). This active engagement of stakeholders in the management of Lake Erie percids led to a consensus on a stock assessment model, harvest strategy, and harvest control rule that improved sustainability and contributed to the recent eco-certification of Lake Erie yellow perch (gill net and trap net) and walleye (gill net) fisheries as sustainable by the Marine Steward Council (Adlerstein et al. 2015).

Overall, the current system for Lake Erie walleye and yellow perch fisheries management is characterized by reliable stock assessment, strict harvest control rules, comprehensive enforcement, and active stakeholder engagement, all of which are identified as important attributes of effective fisheries management (Melnichuk et al. 2016). Thus, it is plausible that important assessment and management decisions, e.g., updating stock assessment models, implementation of ITQs contributed to reduce the

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Fig. 5. Female length at 50% maturity ($L_{50}$) from 1991 to 2012 for four harvest species in Lake Erie; (A) female $L_{50}$ for yellow perch ($y = -432.63 + 0.299 \cdot \text{year}; R^2 = 0.04, p = 0.38$); (B) female $L_{50}$ for walleye ($y = -4368.24 + 2.4030 \cdot \text{year}; R^2 = 0.33, p < 0.005$); (C) female $L_{50}$ for white perch ($y = -2279 + 1.23 \cdot \text{year}; R^2 = 0.29, p < 0.01$); (D) female $L_{50}$ for white bass ($y = -5350 + 2.79 \cdot \text{year}; R^2 = 0.52, p < 0.0003$).
potential negative effects of harvest on fish populations, consistent with the idea that effective fisheries management is capable of rebuilding depleted fisheries and (or) maintaining sustainable fisheries (Worm et al. 2009; Hilborn and Ovando 2014). For example, the major quota reductions for yellow perch (1991–1993; Kenyon et al. 1991) and walleye (2001–2003; MacLennan et al. 2001) may have led to their recovery in recent decades (Adlerstein et al. 2015). Harvesters compensated for the reductions in commercial quotas for yellow perch and walleye by increasing commercial harvest of non-quota white perch and white bass, coinciding with increased probability of overexploitation in relatively unmanaged white perch and white bass fisheries during the 1990s (Adlerstein et al. 2015). The fisheries status indicators for white perch and white bass have improved since quotas were increased, initially for yellow perch in the late 1990s and later for walleye (Adlerstein et al. 2015). Despite periodic variation in fishery status, the fisheries management system in Lake Erie seems to contribute to the long-term persistence of yellow perch, walleye, white perch, and white bass fisheries.

Lake Erie yellow perch, walleye, white perch, and white bass all exhibit a periodic life-history strategy (Winemiller and Rose 1992; McCann and Shuter 1997). Periodic life-history strategies tend to be medium to larger-sized fishes with delayed maturation, higher fecundity, and longer life span. The periodic strategy represents a risk-spreading tactic via interannual variation (Winemiller and Rose 1992), over which periodic strategists exhibit large variation in recruitment of annual cohorts that may dominate the adult population for many years (Winemiller 2005). Thus, periodic strategists have a high capacity to offset variation in mortality (Rose et al. 2001) and are relatively resilient to harvest pressure (Rose 2005). In the case of the Lake Erie multispecies fishery, our failure to observe the negative effects of harvest on either recruitment or maturation schedule of any of these species may also be attributable to their shared periodic life-history strategy.

Over the past few decades, reduced commercial and recreational fishing capacity, effective fisheries management, and the periodic life-history strategy of exploited species may have collectively contributed to the insignificant effects of harvest on exploited fish populations in Lake Erie that we observed. In that respect, therefore, we offer that Lake Erie fisheries management has been relatively successful with respect to meeting the ecological prerequisite of sustainable fisheries, namely, avoiding or minimizing the negative effects of harvest on fish populations, consistent with results from successful fisheries management in marine fisheries (Hilborn and Ovando 2014).

Moving beyond the ecological dimension

At the global scale, fisheries management varies greatly among countries and regions, leading to dichotomous prospects for fisheries. For example, fisheries are effectively managed in some developed countries and regions in North America and Europe, but poorly regulated or not managed at all in many developing countries and regions in Asia and Africa (Costello et al. 2016; Melnychuk et al. 2016). Unfortunately, the majority of global catch comes from areas without effective fisheries management, and a large proportion of global fisheries are overexploited or collapsed (Costello et al. 2012). In this context, conservative and precautionary fisheries management is encouraged at global scales (Hilborn et al. 2001) to rebuild depleted fisheries and avoid “fisheries collapse” in areas without effective fisheries management (Worm et al. 2009; Worm 2016). However, at the same time, overemphasizing the precautionary principle may cause otherwise sustainable commercial fisheries to suffer opportunity costs imposed by reductions of harvest that are too restrictive, such that economic and social interests of fishing communities are compromised (Hilborn et al. 2001; Hilborn and Ovando 2014).

Fisheries management and governance should be pragmatically structured based on ecological, economic, social, and institutional objectives (Kloppenberg 1996; Stephenson et al. 2017). In previous decades, global fisheries research and management largely focused on the ecological objective of protecting exploited fish populations; the economic and social objectives of protecting fishing industries and communities were not adequately considered (Hilborn et al. 2001; Stephenson et al. 2017). The results of our project suggested that ecological processes may be the driving force affecting fish population dynamics and fisheries production, emphasizing the importance of taking into account complex ecological processes in fisheries management (Pikitch et al. 2004). To take this evolution a step further, so as to better integrate ecological and human dimensions into decisions about fisheries management, emerging perspectives about fisheries as complex, adaptive social–ecological systems should bring new insights for improving fisheries policy and management (Regier et al. 2002; Levin et al. 2013). For example, by considering humans as part of the social–ecological food web, classical food web theories may offer innovative ways to address sustainability of social–ecological fisheries systems (Worm and Paine 2016; Bieg et al. 2017).

In summary, no significant effects of harvest on four exploited fish populations, neither through changes in recruitment success nor through alteration of maturation schedules, were detected in Lake Erie over the past four decades. For yellow perch and walleye, this may be attributable to a Lake Erie fisheries management and governance system that features reliable stock assessment, strict harvest control, comprehensive enforcement, and, more recently, active stakeholder engagement. In the case of the unmanaged, essentially open access white perch and white bass fisheries, our failure to detect harvest-induced change is likely attributable to a combination of relatively low landed value (less preferred by fishermen) compared with walleye and yellow perch, life history–related resilience to harvest, and reduced fishing capacity. Our results are consistent with the idea that pragmatic fisheries management can avoid or reduce negative effects of harvest on fish populations and help to rebuild depleted fisheries and (or) maintain sustainable fisheries (Worm et al. 2009; Hilborn and Ovando 2014). Meanwhile, we recognize the potential risks of being over-conservative in fisheries management, when the ecological objective of protecting fish populations is emphasized at the expense of economic and social objectives for the sustainability of fishing industries and communities (Hilborn et al. 2001). To integrate the ecological, economic, and social objectives of fisheries management, future research should benefit from considering fisheries in an interdisciplinary context as complex, adaptive social–ecological systems, rather than from the perspective of humans as external to fisheries’ ecosystems.

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