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Effects of walleye predation on variation in the stock-recruitment relationship of Lake Erie yellow perch

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ABSTRACT

Stock-recruitment relationships (SRRs) may vary over time due to temporal variation in ecological conditions, reducing confidence in projections from stock-recruitment models. We examined whether the time-varying SRRs detected for yellow perch (*Perca flavescens*) in the western basin of Lake Erie between 1977 and 2013 could be attributed to variation in yearling walleye (*Sander vitreus*) predation, indexed by variation in density. Annual variation in yearling walleye density was strongly associated with yellow perch recruitment dynamics, and positively correlated with temporal variation in density-dependence of yellow perch SSRs. However, non-stationary SRRs persisted after accounting for effects of yearling walleye density, and the extent of temporal variation in SRRs actually increased. In simulations, we showed that time-varying SRRs may result more from variation in low-frequency ecological factors on the order of decades, than from variation in high-frequency ecological factors on the order of years (*e.g.*, yearling walleye density) and thus may not be distinguishable from noise. Hence, of these two types of factors, the systematic identification, characterization and incorporation of those of low-frequency factors into stock-recruitment models (*e.g.*, exotic mussel invasions and eutrophication, in the case of Lake Erie) may offer greater promise to improve the reliability of long-term forecasts for sustainable harvests in this and other fisheries in dynamic ecosystems.

Introduction

Fish stock-recruitment relationships (SRRs) may vary with time-varying ecological conditions, leading to non-stationary SRRs (Walters, 1987). Non-stationary SRRs are typically characterized by variation in parameters of stock-recruitment models. For example, time-varying productivity in Ricker models was detected when fitted to data series from salmon (*Oncorhynchus* spp.) stocks in the Northeast Pacific (Dorner et al., 2008; Peterman and Dorner, 2012), cod (*Gadus morhua*) stocks in the North Atlantic (Minto et al., 2014) and rainbow smelt (*Osmerus mordax*) stocks in Lake Michigan (Feiner et al., 2015). Additionally, time-varying density-dependence in Ricker models was observed in European hake (*Merluccius merluccius*) stocks in the Northeast Atlantic (Hidalgo et al., 2014). It has been speculated that such non-stationary SRRs are associated with low-frequency ecological processes, *e.g.*, Pacific Decadal Oscillation (Dorner et al., 2008), the effects of which may vary slowly over decades and large areas, or with fisheries-induced systematic demographic changes (Hidalgo et al., 2014) or other high-frequency ecological factors that operate over shorter time scales.

Non-stationary SRRs pose a challenge for traditional approaches to fisheries management, which often assume time-invariant SRRs, reducing the reliability of such models to forecast future trends (Szuwalski and Hollowed, 2016). A mechanistic understanding and incorporation of the ecological factors that cause non-stationary SRRs may offer a means to improve predictions of stock-recruitment models. Previous studies on non-stationary SRRs in fish populations have been largely restricted to descriptions of temporal variation in SRRs and speculation of potential causes (Feiner et al., 2015; Minto et al., 2014; Peterman and Dorner, 2012); fewer have explicitly tested among potential mechanisms causing non-stationary SRRs.

The Laurentian Great Lakes experienced large changes in ecosystem dynamics over many decades, as a result of the combined effects of climate change, invasive species and anthropogenic activities (Bunnell et al., 2014). The most productive of the Great Lakes, Lake Erie, was strongly affected by eutrophication and invasive species, leading to large changes in water chemistry, the benthic community and fish production (Hecky et al., 2004; Ludsin et al., 2001; Vanderploeg et al., 2002). Coinciding with systemic ecosystem changes associated with low-frequency ecological processes in Lake Erie, *e.g.*, dreissenid invasion and eutrophication, yellow perch (*Perca flavescens*) exhibited strong

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temporal variation in SRRs (Zhang et al., 2017a). Previous studies in other ecosystems also associated non-stationary SRRs of fish populations with low-frequency ecological factors, *e.g.*, Pacific Decadal Oscillation (PDO), climate change and overfishing (Dorner et al., 2008; Hidalgo et al., 2014; Minto et al., 2014). In contrast to these low-frequency ecological factors acting on decadal time scales, Lake Erie yellow perch recruitment was also strongly affected by high-frequency biotic and abiotic factors that varied annually, *e.g.*, warming rate, wind speed, predation and food abundance (Farmer et al., 2015; Ludsin et al., 2014; Zhang et al., 2017b). However, it is unclear how these high-frequency ecological factors may contribute to the non-stationary SRRs.

Lake Erie's yellow perch populations, which have supported economically important commercial and recreational fisheries, have undergone systematic stock assessment since the 1970s (Belore et al., 2014; Wills et al., 2014). To reduce uncertainty in the management of Lake Erie yellow perch fisheries, it is important to understand the explicit mechanisms causing the non-stationary SRRs. In this study, instead of doing comprehensive analyses on the effects of multiple factors on the non-stationarity of SRRs (largely restricted by limited data availability), we focused on the effects of variation in walleye abundance, which had relatively long time-series of data (Wills et al., 2016). Previous diet analyses documented evidence of predation on yellow perch juveniles by yearling and older walleye in the western Lake Erie, which was considered responsible for low yellow perch recruitment in the late 1980s (Hartman and Margraf, 1993). Likewise, weak predation, presumably due to reduced visibility in the Maumee River plume (MRP), resulted in increased recruitment of yellow perch in the MRP (Reichert et al., 2010; Carreon-Martinez et al., 2014, 2015), and Zhang et al. (2017b) demonstrated that yearling walleye density was negatively correlated with yellow perch recruitment in the western basin of Lake Erie. Nevertheless, it remained unclear whether non-stationary SRRs of yellow perch could be attributed to walleye predation.

To test the hypothesis that non-stationary SRRs of yellow perch were caused by variation in yearling walleye density, we 1) re-established the non-stationarity of the SRRs of yellow perch in Lake Erie (Zhang et al., 2017a), and asked whether 2) yellow perch recruitment was strongly correlated with variation in yearling walleye density, 3) variation in yearling walleye density was correlated with temporal variation in SRRs, and 4) temporal variation in SRRs of yellow perch was primarily caused by variation in yearling walleye density. Further, we implemented a simulation to examine whether the frequency at which ecological factors operate might be critical with respect to whether they are important causal agents of non-stationary SRRs.

Methods

Study area and data collection

There are western, central and eastern basins in Lake Erie, across which yellow perch and walleye fisheries are managed in four and five management units (MUs), respectively. The western basin comprises one MU for both yellow perch and walleye (Fig. 1). Age-specific biomass of yellow perch (ages 2, 3, 4, 5, and 6+) in each MU has been annually estimated with a statistical catch-at-age model (Belore et al., 2014). Unlike yellow perch, walleye in the western and central basins are considered one stock, and their overall biomass-at-age has been estimated from a statistical-catch-at-age model since 1978 (Wills et al., 2014). Stock assessments of yellow perch and walleye have been based on both fisheries-dependent catch and effort data and fisheries-independent trawl and gillnet survey data (Belore et al., 2014; Wills et al., 2014). To align the temporal and spatial scales of yellow perch and walleye data, we restricted our study to the western basin between 1977 and 2013. We confirmed that yearling walleye density in the western basin could be indexed by age-2 walleye biomass across the western and central basins, lagged by one year (Electronic Supplementary Material (ESM) Appendix S2).

In Lake Erie, yellow perch recruit to the fishery at age 2; thus age-2 yellow perch biomass estimated from a statistical catch-at-age model was used to index recruitment (Belore et al., 2014). The summed biomass of females aged 2 and older (S_t) is calculated as,

$$S_t = \sum_{a=2}^{n} p_a * B_{a,t} * s$$

where, p_a is the mean percentage of maturation of age a class, $B_{a,t}$ is the biomass of age a class in year t, and s is the sex ratio of the spawning stock. The mean percentages of maturation for age 2 and 3 females were calculated based on the Ontario fisheries-independent annual gillnet index survey co-conducted by Ontario Ministry of Natural Resources and Forestry and Ontario Commercial Fisheries' Association (Belore et al., 2016). Females aged 4 and older were assumed to be mature with probability of 1, and the sex ratio was assumed constant at 1:1 for each age class in each year (Belore et al., 2016).

Direct measures of yearling walleye density from trawling surveys were only available after 1988 in the western basin (Thomas et al., 2014); however, the estimates of age 2 walleye biomass extended back to 1978 in the western and central basins (Wills et al., 2014). Estimated overall biomass of age-2 walleye across the western and central basins and yearling walleye density the previous year in the western basin were highly correlated (Supplementary Materials). Thus, we used the age-2 walleye biomass in the western and central basins in year t to index yearling walleye density in the western basin in year $t-1$.

Effect of yearling walleye density on yellow perch recruitment

A Ricker model (Ricker) and an augmented Ricker model accounting for effects of yearling walleye density (Ricker-Walleye) were fit to time

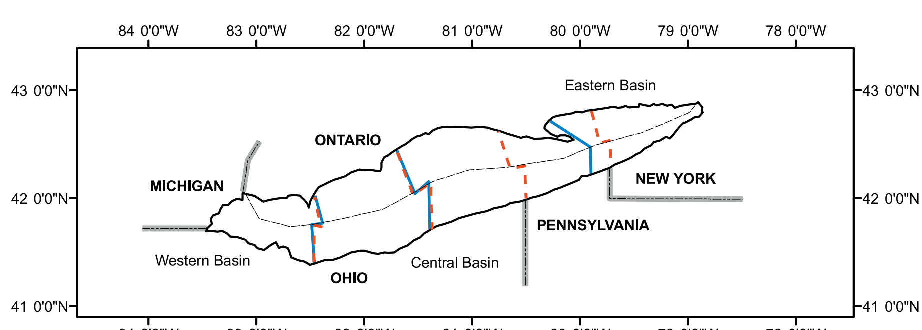

Fig. 1. Management units (MUs) for yellow perch and walleye in Lake Erie. Solid blue lines are boundaries of yellow perch MUs, and dashed red lines are boundaries of walleye MUs. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

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