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Non-stationary recruitment dynamics of rainbow smelt: The influence of environmental variables and variation in size structure and length-at-maturation

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ABSTRACT

Fish stock-recruitment dynamics may be difficult to elucidate because of nonstationary relationships resulting from shifting environmental conditions and fluctuations in important vital rates such as individual growth or maturation. The Great Lakes have experienced environmental stressors that may have changed population demographics and stock-recruitment relationships while causing the declines of several prey fish species, including rainbow smelt (*Osmerus mordax*). We investigated changes in the size and maturation of rainbow smelt in Lake Michigan and Lake Huron and recruitment dynamics of the Lake Michigan stock over the past four decades. Mean lengths and length-at-maturation of rainbow smelt generally declined over time in both lakes. To evaluate recruitment, we used both a Ricker model and a Kalman filter-random walk (KF-RW) model which incorporated nonstationarity in stock productivity by allowing the productivity term to vary over time. The KF-RW model explained nearly four times more variation in recruitment than the Ricker model, indicating the productivity of the Lake Michigan stock has increased. By accounting for this nonstationarity, we were able identify significant variations in stock productivity, evaluate its importance to rainbow smelt recruitment, and speculate on potential environmental causes for the shift. Our results suggest that investigating mechanisms driving nonstationary shifts in stock-recruit relationships can provide valuable insights into temporal variation in fish population dynamics.

Introduction

Predicting recruitment variability in fishes requires the identification of biotic and abiotic factors that control the production and survival of larval and juvenile fish. Historically, the basis of many evaluations of fish recruitment were founded on correlations between levels of recruitment and potentially important density-dependent (e.g., intraspecific and interspecific) and density-independent (e.g., environmental) variables derived from analysis of long-term time series (Ricker, 1975). However, many stock-recruitment models have been beset by high levels of uncertainty (Touzeau and Gouzé, 1998) and inconsistent replication of results (Myers, 1998), often leaving the exact sources of recruitment variation poorly understood.

Nonstationary relationships between recruitment variability, stock characteristics, and environmental variables may contribute to the high levels of uncertainty observed in many stock-recruitment analyses. Strong shifts in ecological and climatic conditions may significantly alter relationships between stock size, environmental factors, and annual recruitment variation (Vert-pre et al. 2013). These types of nonstationary ecological relationships have long been recognized as potentially important (Walters, 1987) and are often cited as probable causes for the inconsistent replication of environmental influences in many stock-recruitment models (e.g., Myers, 1998). Including nonstationarity in stock-recruitment analyses can potentially integrate and detect the influences of environmental variation that can be difficult to measure (Payne et al., 2009; Polovina, 2005; Wayte, 2013) but which have the potential to strongly influence the importance of environmental variables (Brander, 2005; Ottersen et al., 2006).

In addition to environmental influences, properly defining and measuring spawning stock size and productivity is crucial for developing useful stock-recruitment models, as errors in measurement or estimation of the reproductive potential of the spawning stock, due to factors such as altered growth rates or maturation schedules in adult fish, can have pronounced effects on the perceived relationship between stock size and recruitment (Walters and Ludwig, 1981). Evaluating and accounting for nonstationarity in stock productivity (Vert-pre et al., 2013) may therefore allow for a clearer understanding of recruitment

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dynamics in populations that have experienced shifts in demography (Bunnell et al., 2006; Peterman et al., 2000). However, most of the research into nonstationary shifts in stock productivity have considered mainly marine (e.g., Atlantic cod [*Gadus morhua*]; Minto et al., 2013) or anadromous (e.g., Pacific salmon [*Oncorhynchus* spp.]; Dorner et al., 2008) species, resulting in a poor understanding of these dynamics in freshwater systems (but see Collingsworth et al., 2014).

The Laurentian Great Lakes are a highly dynamic, freshwater system that has experienced a multitude of strong shifts in environmental conditions over the past century. Great Lakes food webs have been irreversibly changed by numerous species introductions, including sea lamprey (*Petromyzon marinus*), alewife (*Alosa pseudoharengus*), dreissenid mussels (*Dreissena* spp.), round goby (*Neogobius melanostomus*), and Pacific salmon, among others (Griffiths et al., 1991; Mills et al., 1994; Ricciardi, 2001; Ricciardi and MacIsaac, 2000). Ecosystem productivity has varied widely over time due to changes in phosphorous loadings and oligotrophication enhanced by filter-feeding dreissenid mussels (Chapra and Dolan, 2012; Dolan and Chapra, 2012; Evans et al., 2011; Hecky et al., 2004). More recently, lake levels have declined to record-low levels, which may be influencing habitat availability along shorelines, within tributaries, and affecting lake hydrological dynamics (Gronewold and Stow, 2013). The myriad physical, chemical, and biotic changes to Great Lakes ecosystems have resulted in benthification of energy pathways and altered zooplankton and macroinvertebrate species composition and abundance (Bunnell et al., 2014; Fahnenstiel et al., 2010; Nalepa et al., 2009; Pothoven et al., 2013; Vanderploeg et al., 2012).

These rapid, strong shifts in habitat and trophic structure may have had particularly strong impacts on the population dynamics of many forage fish species in the Great Lakes, such as alewife, bloater (*Coregonus hoyi*), and rainbow smelt (*Osmerus mordax*) (Bunnell et al., 2013; Gorman, 2013). These species represent an important trophic link, sustaining valuable sport and commercial fisheries while preying upon zooplankton, benthic macroinvertebrates, and early life stages of many different fish species (e.g., Jones et al., 1994; Kirn and Labar, 1996; Madenjian et al., 1998; Myers et al., 2009). Over the past two decades, many Great Lakes forage fish assemblages have experienced steep declines in lake-wide abundance and recruitment, especially in lakes Michigan (Bunnell et al., 2013) and Huron (Roseman et al., 2013), which have led to numerous cascading effects on lake food webs. The collapse of alewife in Lake Huron, for example, potentially enabled the recovery of walleye (*Sander vitreus*) (Fielder et al., 2007) and bloater (Collingsworth et al., 2014) while contributing to the marked decline of the Chinook salmon (*Oncorhynchus tshawytscha*) fishery (He et al., 2008). However, the highly dynamic nature of Great Lakes ecosystems is a primary reason for prey fish declines to remain elusive.

Rainbow smelt is an abundant constituent of the prey fish community in each of the five Laurentian Great Lakes and provides an important food source for walleye, lake trout (*Salvelinus namaycush*), and stocked salmon species (Diana, 1990; Fitzsimons and Brown, 1998; Gorman, 2007; Jones et al., 1994; Madenjian et al., 1998; Stewart et al., 1981). In addition, rainbow smelt predation can influence other species by both consumption of young fish and resource competition with other planktivores. For example, predation by adult rainbow smelt on larval fishes was implicated in the decline of cisco (*Coregonus artedi*) in Lake Michigan and Lake Superior (Gorman, 2012; Myers et al., 2009), and zooplanktivory by rainbow smelt may be sufficiently high to induce competitive interactions with bloater and alewife, although the strength of these interactions may depend on the spatial overlap of these species (Frie and Spangler, 1985; Pothoven et al., 2009; Stewart et al., 1981; Urban and Brandt, 1993). Through this suite of trophic interactions with other species, fluctuations in the abundance of rainbow smelt can potentially influence multiple levels of Great Lakes' food webs. In recent years, the biomass of rainbow smelt in four of the five lakes (all but Lake Erie) is less than 15% of the peak biomass that was observed in the 1970s (Lake Superior) or 1980s (lakes Michigan, Huron, and Ontario; Gorman 2013), and recruitment has been consistently poor. Despite its widespread occurrence throughout the basin, no single mechanism has been identified to consistently explain these declines in recruitment and population abundance of rainbow smelt across the Great Lakes.

Several factors have been suggested to contribute to rainbow smelt recruitment patterns in the Great Lakes, including variation in temperature and precipitation patterns (Hoff, 2004; O'Brien et al., 2014, 2012), predation by piscivores (Hoff, 2004; O'Brien et al., 2014; Stewart et al., 1981), and cannibalism (Henderson and Nepszy, 1989; Parker Stetter et al., 2007). In addition to these factors, other characteristics of rainbow smelt populations may have changed dramatically over time, including reduced growth rates (Henderson and Nepszy, 1989; Lantry and Stewart, 2000; Parker Stetter et al., 2005) and truncated age-structure (i.e., few fish older than age-3; Gorman, 2007; Lantry and Stewart, 2000, 1993; Owens, 1982; Walsh et al., 2008). Therefore, the productivity and variability of rainbow smelt stock-recruitment patterns may have shifted over time in response to shifts in environmental conditions and population demography (Hsieh et al., 2010; Lantry and Stewart, 2000), potentially leading to the development of novel recruitment dynamics in recent years. However, the magnitude and direction of potential demographic shifts remain poorly understood in most Great Lakes rainbow smelt populations.

In this paper, we sought to use data spanning four decades to 1) describe temporal changes in the size structure and maturation schedules of rainbow smelt in Lake Michigan and Lake Huron, which may be influencing stock productivity and population dynamics in both lakes, and 2) determine the importance of environmental variables and adult rainbow smelt abundance in explaining long-term variation in the recruitment of young-of-the-year (YOY) rainbow smelt in Lake Michigan. We focused our recruitment models solely on Lake Michigan because previous studies have examined recruitment patterns in Lake Huron (O'Brien et al., 2014) and we wished to examine potential similarities in recruitment dynamics between stocks. Moreover, recruitment models in Lake Huron have yielded sufficient explanatory power to suggest important drivers of recruitment in that lake (O'Brien et al., 2014, 2012), while recruitment dynamics in Lake Michigan are poorly understood and appear far more variable and uncertain (this study). Thus, our results could provide important insights into reasons underlying the decline of rainbow smelt in the Great Lakes, identify important similarities or differences in dynamics among stocks, and may be used to develop hypotheses for the declines of prey fishes in this and other systems.

Methods

Data collection

We used data from annual fall (September-November) bottom trawl surveys conducted by the U.S. Geological Survey throughout Lake Michigan from 1973-2012 and Lake Huron from 1973-2013. Each year, 10-minute tows were conducted using a 12-m headrope bottom trawl towed along contours at 9 m depth increments between 9 and 110 m at each of seven transects around Lake Michigan: Manistique, Frankfort, Ludington, and Saugatuck, Michigan; Waukegan, Illinois; and Port Washington and Sturgeon Bay, Wisconsin, USA (see Fig. 1 in Collingsworth et al., 2014) and seven transects in Lake Huron: De Tour, Hammond Bay, Alpena, Au Sable Point, and Harbor Beach, Michigan, USA; and Goderich, Ontario, Canada (see Fig. 1 in O'Brien et al., 2014). Methodological survey details are described elsewhere (Bunnell et al., 2013; O'Brien et al., 2014). Briefly, for each tow the abundance and biomass of rainbow smelt were estimated (through complete counts and weights or through sub-sampling), and up to fifty individuals were measured (nearest 1 mm total length [TL]). Annual estimates of mean lakewide abundance of rainbow smelt were