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The contribution of cold winter temperatures to the 2003 alewife population collapse in Lake Huron

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ABSTRACT

The Lake Huron ecosystem has recently undergone dramatic changes. As part of those changes, the once highly abundant non-native alewife *Alosa pseudoharengus* population crashed in 2003 and has yet to recover. The purpose of this study was to evaluate whether temperature played a role in the population crash, because historically alewife have been subject to die-off events in response to cold temperatures in other lakes. Long-term climate data (1973–2009) showed that the winter of 2002–2003 exhibited the largest drop in degree days relative to the previous year, had the most extensive average March ice coverage, and was among the coldest years on record. However, since 2003, winter temperatures have not been overly cold, and air temperature has shown an increasing trend. Also, the relationship between temperature and alewife abundance between 1975 and 2006 was non-significant. Therefore, although we found evidence that cold winter temperatures contributed to the abrupt decline of alewife in 2003, they could not explain why the population failed to recover as it had after previous cold winters. Historically, Chinook salmon abundance contributed to long-term trends in alewife abundance, however, we found predation by Chinook to play a lesser role on the 2003 alewife collapse. In the absence of direct estimates of food availability, analyses of alewife length data suggest that a declining prey base altered the ecosystem conditions for alewife, possibly contributing to their collapse and lack of recovery.

Introduction

Planktivorous prey fish are notorious for their large fluctuations in abundance. Rapid increases in abundance, followed by periods of die-offs or decline, have been observed in Japanese sardine *Sardinops melanostictus* (Takasuka et al., 2007), Peruvian anchoveta *Engraulis ringens* (Chavez et al., 2003), and Great Lakes rainbow smelt *Osmerus mordax* (Lantry and Stewart, 2000; Nsembukya-Katuramu et al., 1981). Variable recruitment and survival of prey fish can be caused by several potentially confounding factors such as bottom-up effects that drive changes in food availability, top-down effects that alter predation rates, and large-scale environmental change. Understanding the nature of these fluctuations is important because prey fish play a key role in freshwater and marine ecosystems, providing the linkage between primary producers and top predators.

Alewife (*Alosa pseudoharengus*), a small planktivorous and mostly offshore prey fish, have undergone large fluctuations in abundance since its colonization of the Laurentian Great Lakes (e.g., Henderson and Brown, 1985; Madenjian et al., 2005; Ridgway et al., 1990). Alewife were present in Lake Ontario by at least 1873, although there is some debate as to their origin (Miller, 1957; Smith, 1970). The species was first reported in Lake Erie during the 1930s, after which it spread to the other Great Lakes (Miller, 1957). In Lakes Huron and Michigan, alewife abundance increased through the 1940s and peaked in the 1950s and 1960s in the virtual absence of piscivores which had been heavily fished and predated upon by sea lamprey (e.g., Berst and Spangler, 1973; Hatch et al., 1981; O'Gorman and Stewart, 1999). Large die-offs were observed during this period, with millions of dead alewife washing up along shorelines (Wells and McLain, 1973). After the introduction of Pacific salmon and the implementation of control measures for sea lamprey, alewife populations became somewhat reduced and massive die-offs were not as common (e.g., Henderson and Brown, 1985; Madenjian et al., 2002, 2005; O'Gorman and Stewart, 1999). Then, about a decade ago, an unprecedented collapse of the alewife population was observed in Lake Huron. Between 2002 and 2003, there was a large decline in adult alewife abundance in the lake (Riley et al., 2008). Since that time, the population has remained at low levels and failed to rebound (Riley et al., 2012). As the number of alewife declined in the lake, so too did the total biomass of demersal species (Riley et al., 2008, 2012), and the number of benthic fish schools (Dunlop et al., 2010).

Alewife play a key role in the fish community, preying on zooplankton (e.g., *Mysis*) and benthic invertebrates (e.g., *Diporeia*) (Janssen and Brandt, 1980; Pothoven and Madenjian, 2008), and provide a major source of food for large predators such as lake trout and Chinook salmon

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Oncorhynchus tshawytscha (Jacobs et al., 2013). Alewife have been implicated in the decline of many endemic fish species in the Great Lakes (Madenjian et al., 2008). Alewife are suspected to prey on the larvae of several species, including lake trout *Salvelinus namaycush*, emerald shiner *Notropis atherinoides*, and walleye *Sander vitreus* (Fielder et al., 2007; Krueger et al., 1995; Madenjian et al., 2008). Thiamine deficiency has been observed in lake trout (Fisher et al., 1996) that feed on alewife and the offspring of these thiamine-deficient lake trout suffer from Thiamine Deficiency Complex (Fitzsimons et al., 1995; Riley et al., 2011). There is some evidence that adversely affected species are recovering now that alewife have collapsed (Fielder et al., 2007; Riley et al., 2007). The extent to which any reversal of the negative impacts will continue depends on whether the alewife population will recover.

There are several potential causes of Lake Huron's alewife population collapse. Stocking of Chinook salmon began in the late 1960s to control nuisance levels of alewife and to provide recreational fishing opportunities (Johnson et al., 2010). Chinook stocking reached a peak during the 1990s (Dobiesz et al., 2005), and continues today despite high rates of natural reproduction (Johnson et al., 2010), potentially contributing to high rates of predation on alewife in the years leading up to the collapse. About the same time as the alewife collapse, a dramatic shift was observed in lower trophic levels. Most notably the benthic amphipod, *Diporeia* spp., once highly abundant in offshore waters, became almost non-existent in most areas of Lake Huron (Barbiero et al., 2011b; Nalepa et al., 2007, 2009), and there was a decline in Lake Huron's open-water zooplankton populations (Barbiero et al., 2009). In Lake Michigan, where alewife growth has declined due to *Diporeia* reductions, it was suggested that the increasing predatory demand by Chinook salmon on smaller alewife might have an impact on alewife recruitment (Jacobs et al., 2013). Climate might have also played a role in Lake Huron's alewife collapse, as cold winter temperatures have been associated with alewife mass mortality events in Lake Ontario (Ridgway et al., 1990). Conversely, alewife recruitment can be positively influenced by warm spring temperatures (Henderson and Brown, 1985). Although several studies have speculated as to the cause of the 2003 alewife collapse (Barbiero et al., 2009; Bunnell et al., 2011; Dunlop et al., 2010; Riley et al., 2008), no previous study has investigated the potential role of abiotic factors. The primary purpose of this study was to explore the possibility that cold winter temperatures contributed to the collapse of alewife in Lake Huron. Our approach was to analyze long-term trends in alewife abundance and available climate and temperature data. A secondary objective was to investigate the role of other potential factors in explaining long-term trends in alewife abundance. We lacked data to analyze the role of food availability and predation directly, but we did examine trends in alewife length and Chinook salmon abundance to provide some information on whether changes in the food web might have contributed to alewife population dynamics.

Methods

Climate data

Daily air temperature data were obtained for 1975–2006 from an Environment Canada weather station at the Sarnia airport (42°59′32.058″ N; 82°18′17.088″ W), in close vicinity (<4 km) to the southern shoreline of Lake Huron. Daily historical climate data for the Sarnia airport weather station were downloaded from the Environment Canada climate website (www.climateweatheroffice.gc.ca) and include daily minimum, maximum, and mean air temperatures. We chose 1975 as the first year of our time series because this was the first year for which quantitative estimates of alewife abundance were available (see below). The Sarnia whether station was chosen because of an extensive time series that corresponded with the alewife data. Although water temperature data would have been preferred, adequate time series data for the winter months at depths and regions occupied by alewife were not available (e.g., see Dobiesz and Lester, 2009). Water intake data from water treatment plants were available, but these time series contained many more gaps than the Sarnia air temperature data and they were collected from nearshore areas and depths (typically at the surface or 1 m below the surface) where alewife do not typically occur. Air and water temperatures in lakes are related (Dobiesz and Lester, 2009; Matuszek and Shuter, 1996), but to verify this for our Lake Huron data, we compared the monthly average air temperature at Sarnia to the monthly average water temperature at the Bay City, Michigan water treatment plant intake (data available through the Great Lakes Environmental Research Laboratory, www.glerl.noaa.gov). There was a strong positive correlation (Pearson correlation coefficient = 0.96; $P < 0.05$) between air temperature and water temperature for the subset of years (1970–1993) for which both types of data were available.

From the Sarnia daily air temperature records, we calculated growing degree days during the winter months as: $GDD_{\mathrm{w}} = \sum_{\mathrm{w}}[0.5(T_{\max,d} + T_{\min,d}) - T_{\mathrm{base}}]$, where $T_{\max,d}$ is the maximum air temperature of day d, $T_{\min,d}$ is the minimum air temperature of day d, and T_{base} is a base temperature, defined in this study as 10 °C. Winter months were defined as November to April. In the case of missing data (a total of nine days), data were substituted from the nearest station (Petrolia Town; approx 30 km away). We first performed a least squares linear regression between Sarnia and Petrolia air temperatures for each month and year, and then used the regression (which was highly significant in all cases; R^2 values all above 0.9), to predict Sarnia air temperature from the observed Petrolia air temperature. The effect of this substitution on the total winter growing degree days was assumed to be negligible. We also calculated the GDD_{w} deviation, representing the GDD_{w} of the winter year in question (*Year*) minus the GDD_{w} of the previous winter (*Year*-1).

Ice cover data for Lake Huron was obtained from the NOAA Great Lakes Environmental Research Laboratory Ice Cover Atlas (www.glerl.noaa.gov) in order to provide another measure of winter climate (e.g., Assel, 2003; Assel et al., 2003). The ice cover data include daily estimates of total ice cover for Lake Huron from which we calculated the average ice cover in March for Lake Huron for 1973–2009. March was chosen because ice coverage is close to its peak in March and the ice coverage in March reflects a measure of the overall severity of the winter (Assel, 2003).

Alewife abundance

Alewife abundance was estimated using data from the USGS Great Lakes Science Center (GLSC) annual fall (mid October to mid November) day-time bottom trawl survey (Riley et al., 2008, 2012). During the day, alewife can be found along the lake bottom (Dunlop et al., 2010; Janssen and Brandt, 1980), where they can be caught in very high numbers with benthic trawls (Riley et al., 2008, 2012). The GLSC has annually surveyed fish abundance from 1975 to 2006 using 12 m headrope (1975–1991) and 21 m headrope (1992–2009) bottom trawls at fixed transects at five ports in the Michigan waters of Lake Huron. Both trawls used a 4.76 mm square mesh cod end. To make density estimates from the two trawls comparable, we multiplied density estimates from the 12-m trawl (1976–1991) by species-specific fishing power corrections (Adams et al., 2009).

During the bottom-trawl surveys, the same fixed transects were sampled each year from the USGS R/V *Kaho* during 1973–1977 and from the USGS R/V *Grayling* during 1978–2009. Year-specific length cut-offs were determined from length-frequency data and used to apportion alewife into age-0 fish (young-of-the-year, or YOY) and those age-1 or older (yearling and older, or YAO). Alewife mature early in life, and therefore many YAO individuals are adults. Further details of sampling are described by Riley et al. (2008, 2012).