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# Cross-basin analysis of long-term trends in the growth of lake whitefish in the Laurentian Great Lakes



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#### ABSTRACT

We conducted a basin-wide analysis of trends in the growth rate of lake whitefish (Coregonus clupeaformis), a commercially harvested species in the Laurentian Great Lakes. Juvenile growth (measured as the growth between ages 1 and 2 years) was back-calculated from agency archived scale collections going back as far as the 1950s. We examined trends for 11 locations within the Great Lakes, and investigated the role of multiple explanatory factors (dreissenid mussel establishment; lake whitefish relative abundance; growing degree days) in contributing to the variation observed. Juvenile growth rates declined in all but one location where dreissenid mussels have had widespread establishment. Growth of juvenile lake whitefish from Lake Ontario showed the largest decline following dreissenid establishment, decreasing by 32%. In several locations, lake whitefish growth rates declined or had breakpoints prior to dreissenid establishment and have stabilized or increased in recent years, thus indicating the contribution of other factors. One location in Lake Superior (Apostle Islands) also showed a marked decline and subsequent increase in growth, whereas the other two Lake Superior locations showed no obvious trends. Changes in relative abundance of lake whitefish and growing degree days contributed to growth patterns among locations, but the effect was inconsistent and in most cases weaker than that from the timing of dreissenid establishment. Although our study cannot identify a specific mechanism involved, the suite of changes at the base of the food web that coincided with the timeline of dreissenid establishment appear to have had a broad-scale impact on lake whitefish. © 2015 International Association for Great Lakes Research. Published by Elsevier B.V. All rights reserved.

#### Introduction

Lake whitefish (*Coregonus clupeaformis*) are of considerable economic importance, contributing more to commercial fisheries yield over the past decade than any other species in the Laurentian Great Lakes (Brenden et al., 2013). Given this, growth and abundance trends of this native, cold water fish species are of particular interest to resource management agencies. Inhabiting each of the Great Lakes, lake whitefish contribute to nutrient cycling in the pelagic zone and facilitate upper and lower food web energy transfer by feeding in the benthic region of the lake (Scott and Crossman, 1973; Mohr and Ebener, 2005). Over the past two decades, declines in the growth and condition of lake whitefish have been observed for many regions of the Laurentian Great Lakes. In some locations, these growth rate declines are occurring together with declines in recruitment (Gobin et al., 2015), raising concerns over the status of the commercial fisheries these stocks support.

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Several factors could have led to these trends. Diporeia spp. (herein "Diporeia"), a freshwater amphipod that is a source of food for lake whitefish, declined in abundance and experienced a contraction of their spatial distribution as dreissenid mussel populations (zebra mussels Dreissena polymorpha, and guagga mussels Dreissena bugensis) invaded and expanded in the Great Lakes (Dermott and Kerec, 1997: Nalepa et al., 2009a). This time period corresponds with the lake whitefish growth rate declines observed in Lakes Huron, Michigan and Ontario (Pothoven et al., 2001; Hoyle, 2005; Lumb et al., 2007; Nalepa et al., 2007; Rennie et al., 2009b), suggesting a possible linkage (Pothoven et al., 2001; Nalepa et al., 2007). Although lake whitefish historically consumed a variety of prey items, the lipid content of *Diporeia* (Kainz et al., 2010) coupled with its being the most abundant benthic invertebrate in many offshore regions within the Great Lakes prior to dreissenids could have made it an important source of energy for lake whitefish (McNickle et al., 2006; Nalepa et al., 2007). For example, when Diporeia populations declined in South Bay (Lake Huron), lake whitefish, at least initially, switched their diet to one reliant on lower calorie prey items, including dreissenid mussels (McNickle et al., 2006; Rennie et al., 2009b). However, lake whitefish make use of other potentially energy dense prey items including Mysis, prey fish, and fish eggs (McNickle et al., 2006; Pothoven and Madenjian, 2013; Sierszen et al., 2014; Stockwell et al., 2014),







which could limit the impact of declining *Diporeia* on lake whitefish growth in some locations.

As ecosystem engineers, dreissenid mussels could be responsible for altering energetic pathways throughout the Great Lakes where they have become established (Hecky et al., 2004). Dreissenid mussels have contributed to large reductions in phytoplankton and increases in water clarity (Barbiero and Tuchman, 2004; Higgins and vander Zanden, 2010), and consequently, a reduction in zooplanktonic species has also been observed in several regions (Noonburg et al., 2003; Bowen and Johannsson, 2011). At a more fundamental level, dreissenid mussels are implicated in the re-direction of nutrients from offshore to nearshore areas (Hecky et al., 2004). A shift in the concentration of energy away from pelagic or profundal pathways towards more nearshore or benthic pathways could have profound effects on profundal lake whitefish. Such drastic changes in the availability of resources at the base of the food web will likely impact growth of fishes occupying higher trophic levels.

Changes in lake whitefish growth could also arise through densitydependent regulation, whereby population abundances have increased and caused reductions in per capita food availability, and therefore suppression of growth rates (Brenden et al., 2010). For example, in Lake Huron (Mohr and Ebener, 2005), Lake Ontario (Hoyle, 2005; Hoyle et al., 2008), and northern Lake Michigan (DeBruyne et al., 2008), commercial catches of lake whitefish showed signs of recovery in the 1990s following many years characterized by lower catches. Such increases in catch could be indicative of increasing population density which could also contribute to declines in growth and condition through increased competition for resources.

The objective of this study was to provide a comprehensive, cross-basin comparison of juvenile lake whitefish growth rates over the past several decades. We conducted back-calculations of length-at-age to reduce biases associated with gear selectivity and changes in other life history traits, which both are affected by growth rate changes themselves and in turn can affect size-at-age measurements of fish (Enberg et al., 2012). Archived scale samples that spanned decades were obtained from government agencies around the Great Lakes basin. We furthermore examined the potential role of several explanatory factors in contributing to growth rate variation. We focused on three explanatory variables for which data were available for the majority of our populations: the presence of established populations of dreissenid mussels, lake whitefish relative abundance, and growing degree days. We also included populations from Lake Superior, where dreissenid mussels are present in low numbers in some limited coastal areas, but have not had widespread establishment as they have in the other four Great Lakes.

#### Methods

Lake whitefish scales were obtained from agency index netting programs and commercial fishing monitoring programs for 11 locations within the Great Lakes, including eight locations where dreissenids have become established and three locations in Lake Superior where dreissenids have not had widespread establishment (Fig. 1; Table 1). The index netting programs use standardized collection procedures and are designed to monitor fishery independent trends in relative fish abundance over time. Commercial fishing activities are monitored by Great Lakes agencies, who collect samples (e.g., aging structures) and information (e.g., fish length, effort, sampling locations), and they provided us with scales for this project. Sampling location names are in most cases those used by the collection agency and refer to the nearest town or port from which sites are accessed; however, we recognize that the fish are collected from a larger geographic area of the lake (e.g., Ebener et al., 2010) which varies depending on the specific monitoring program. Scales collected from commercial fisheries are typically taken from a broader sampling area (they correspond to the commercial fishing locations for a particular year). Statistical analyses for all scale measurements were performed within each location rather than by pooling among all locations, to account for the different sources of data and lengths of the time series available for each sampling location.

For each location where we obtained scale samples we identified the year of substantial dreissenid presence ("establishment") from published sources, where possible (Table 1). We chose to use this year of dreissenid establishment, as opposed to a first sighting date, to reflect the period of time when effects of dreissenids on the ecosystems they occupied are likely to have been observed. Given the difficulty in determining the exact year of establishment for a species, there could be some variability among locations in when effects were observed relative to the particular establishment year. The establishment year was used to determine whether trends in growth coincided with the establishment of dreissenid mussels for each location, and it was also used as an explanatory variable in statistical analyses (described below).

#### Lake whitefish growth

We estimated back-calculated length-at-ages and re-created the growth history of fish from birth to age at capture (Francis, 1990). This allowed us to measure juvenile growth of fish from a body size where the entire cohort is susceptible to the sampling gear (Gobin et al., 2015). We specifically examined growth of fish from ages 1 to 2 years when the fish are still in the juvenile phase, but are expected to be benthivorous (Reckahn, 1970; Claramunt et al., 2010). Focusing on juvenile growth avoids any bias associated with changes in maturation schedule or reproductive investment that can affect post-maturation growth (Enberg et al., 2012). Mature 3-year olds were observed in the dataset, indicating that some fish are investing in reproduction between ages 2 and 3 years; growth up to age 2 was therefore selected to represent juvenile growth across all populations examined (see also Gobin et al., 2015). Growth is approximated by a linear growth curve in the juvenile phase for many fish (Lester et al., 2004), which also seems to be the case for lake whitefish (Gobin et al., 2015). We therefore consider growth between ages 1 and 2 to be representative of the juvenile growth rate.

Five year old fish were targeted from the scale archives for backcalculations to balance gear recruitment with the reliability of aging, as the determination of growth of lake whitefish using scales becomes increasingly unreliable at ages beyond 5 years (Muir et al., 2008; Rennie et al., 2009a). From each sampling location, up to 20 randomly-selected fish were collected from each year to use for growth analyses. In cases where twenty age-five fish were not available, age four or six year-old fish were substituted instead, or more rarely ages three, seven and eight so that we had 20 samples per year wherever possible. When the scales were damaged or determining the age was particularly difficult and unreliable, the fish was removed from the analysis and another individual was randomly chosen (this occurred for less than 1% of samples). Those fish that could not be confidently aged were excluded from the sample (this occurred for less than 7 fish per sampling location).

The distance from the scale focus to each annulus and the scale edge was measured on the anterior-lateral axis. These distances were then converted into scale radii following the validated backcalculation procedure by Dunlop and Shuter (2006), which assumes that body length is an allometric function of the scale radius as follows,

 $Body length = alpha (Scale radius)^{beta}.$ 

We estimated beta (the slope of the relationship between log body length and log scale radius) using a representative population



Fig. 1. Map of the Great Lakes indicating the source of lake whitefish scale samples used in this study.

(Dunlop and Shuter, 2006).

Length<sub>(at annulus a)</sub>

possible to estimate an unbiased slope for each location. For each

fish, the length at an individual annulus was estimated as follows

All back-calculations were performed by a single, trained individual

(S. Fera). Although the agencies provided the original aging information

used to target fish of particular ages, the final age and growth rates

assigned to the fish were from S. Fera. Note that age assignment errors

 $= Length_{at\,capture} \big( scale_{radius\,at\,annulus\,a} / scale_{radius\,at\,capture} \big)^{0.79}$ 

of lake whitefish (Grand Bend, Lake Huron) for which there were 658 fish and a large range of ages and sizes sampled, including young and small fish (Gobin et al., 2015). Previous studies have shown that slopes of this relationship are similar within a species even when growth varies widely (Dunlop et al., 2005; Dunlop and Shuter, 2006), so we assumed a common slope (beta = 0.79) among all lake whitefish populations (Electronic Supplementary Material (ESM) Fig. S1). The length- and age-at-capture for each population were also visually inspected to ensure that the common slope was reasonable (ESM Fig. S2). The approach of choosing a common slope is needed because our samples for each location did not include younger or smaller fish not fully recruited to the gear, making it not

# Table 1

Dreissenid timelines and sources of lake whitefish scale samples used in this study. First sighting of dreissenids per lake based on Carlton (2008) for Erie, Griffiths et al. (1991) for Ontario, and Benson (2013) for Michigan, Huron and Superior. Timelines based on Rennie et al. (2009a) using the USGS and OFAH Invasive species watch programs. Locations in Lake Superior are defined as "Not established", because dreissenids are not established at the basin level and are only present in very low numbers in a few locations. Agency: OMNRF = Ontario Ministry of Natural Resources and Forestry, CORA = Chippewa Ottawa Resource Authority, USGS = United States Geological Survey.

Lake	Location	Dreissenid first sighting per lake	Dreissenid establishment per location	Sample years	Source of scale samples	Agency
Superior	Thunder Bay	1989	Not established	1962-2009	Commercial netting	OMNRF
	Whitefish Bay		Not established	1966-2005	Commercial netting	CORA
	Apostle Islands		Not established	1978-2005	Research trawl netting	USGS
Ontario	Glenora	1989	1993	1958-2009	Assessment gill netting	OMNRF
Erie	Dunkirk	1986	1989	1953–2003 <sup>a</sup>	Commercial and assessment gill netting	OMNRF
Huron	Grand Bend	1990	1994	1985-2007	Assessment gill netting	OMNRF
	Southampton		1993	1981-2006	Assessment gill netting	OMNRF
	Cape Rich		1996	1985-2007	Assessment gill netting	OMNRF
	Cheboygan		2000	1980–2006 <sup>a</sup>	Commercial netting	CORA
	Detour Village		2000	1980–2006 <sup>a</sup>	Commercial netting	CORA
Michigan	Naubinway	1989	1994	1991-2007 <sup>a</sup>	Commercial netting	CORA

<sup>a</sup> Locations with gaps in available scale samples.

would not have a significant effect on our results because we focused on back-calculated growth occurring between ages 1 and 2 years.

#### Climate data

Growing degree days (GDD) was used as a measure of the cumulative thermal energy stimulating ecosystem production over the course of a given growing season. A daily  $GDD_d$  was calculated as,

$$GDD_d = \frac{T_{\max,d} + T_{\min,d}}{2} - T_{\text{base}}$$

where,  $T_{\max,d}$  is the maximum air temperature for a given day,  $T_{\min,d}$  is the minimum air temperature of a given day, and  $T_{\text{base}}$  is a constant base temperature, which we set to 10 °C. Given the findings in Chezik et al. (2013), that there are a broad range of threshold air temperatures that are equally effective in describing growth of freshwater fish using the degree days method, we chose a standardized threshold temperature within their recommendations. The daily values were then summed over the growing season (here defined as May to September) to give a  $GDD_{\nu}$  for a particular year. We recognize that lake whitefish could grow outside of our defined growing season (Madenjian et al., 2006), but the number of gaps in the daily temperature records increased beyond September, making the inclusion of data beyond this time period not feasible. Air temperatures were used because water temperature time series were not available for the years, geographic locations, and water depths representative of all regions included in the study. To confirm that air temperatures and water temperatures were related, we compared surface water temperature data from the Belleville, ON water treatment plant (for 1973-1986) with air temperature data from the Picton, ON weather station over the same period of time. Mean daily temperatures were significantly correlated between the two sources ( $F_{1,12} = 40.22$ , *p*-value < 0.001,  $R^2 = 0.75$ ).

For lake whitefish sampling locations within Canada, we used Environment Canada's National Climate Data and Information Archive (http://climate.weatheroffice.gc.ca). NOAA's National Data Buoy Center (http://www.ncdc.noaa.gov) was used as a source of daily air temperatures for locations within the United States. All temperature values were compiled from a primary weather station located near the scale collection offices, with interpolation from another nearby station when there were gaps in the data. While sampling locations for the fish scales likely represent a larger area for commercial fisheries samples, it is expected that the GDD would capture any large, broad shifts in climate that might influence lake whitefish growth within the full sampling region (Matuszek and Shuter, 1996). Where needed, we confirmed that the nearby weather stations showed a similar weather pattern (e.g., linear regression of the two locations of substitution to the Picton weather stations indicate 94% and 69% correlation: Glenora  $F_{1,151} = 2367, p < 0.001,$  $R^2 = 0.94$ ; and Belleville;  $F_{1,151} = 334$ , p < 0.001,  $R^2 = 0.69$ ). For Cape Rich (Lake Huron), there were years where we directly substituted temperatures from a station 23 km away, because there was a 4-year period where it was the only station with reliable data. Though this substitution is not as accurate as the substitutions with interpolation, we believe that any notable trends in temperature will still be captured over this time period given the short distances between stations (Matuszek and Shuter, 1996). Reliable climate data for the Apostle Islands was not available prior to 1984, and we could not find a suitable substitute; therefore GDD was calculated from 1984 to present even though growth data is available from 1978.

#### Catch per unit effort

Lake whitefish catch-per-unit-effort (CPUE) data were compiled from the relevant agencies for all but one location (Dunkirk, Lake Erie, due to a lack of data) as an estimate of annual relative lake whitefish abundance. CPUE is a measure of the number or weight of fish caught per standardized amount of fishing effort. Where appropriate, mesh sizes were standardized through time. For four locations (Cape Rich, Southampton, Grand Bend, Thunder Bay), we applied a conversion factor following Collins (1979) to account for the switch from multi- to mono-filament nets that occurred (switch occurred in 1971 for Thunder Bay and 1994 for the other three). This conversion factor (multi-filament net catch  $\times$  1.8) was calculated prior to the arrival of dreissenid mussels and it is possible that environmental changes (e.g., increases in water clarity) have influenced net catchability. However, we are aware of no other published conversion factors. For Lake Erie, robust annual CPUE estimates were not available for the years we had samples for and we instead used commercial fishing harvest, recognizing that it doesn't fully capture trends in relative population abundance and it is not corrected for effort. The time series for CPUE at our sample locations, and the GDD at those stations are given in ESM Fig. S3 and Fig. S4.

#### Statistical analyses

We chose three approaches to evaluate the role of explanatory variables in affecting growth rate variation. First, we created a series of generalized linear models (GLMs) which included four explanatory variables (year, dreissenid status, catch per unit effort, growing degree days) and all possible subsets. Dreissenid establishment status ("*Dreissenid*") was included as a fixed factor, with *Year* nested as a random effect. *Year* was also included as a fixed effect to account for unexplained variation that varied systematically through time. Intercepts were included in all models and the GLMs assumed a normal distribution. The full model was,

## Growth = Year + (Dreissenid|Year) + GDD + CPUE.

In Lake Superior locations, there was no *Dreissenid* factor and in Lake Erie, *Harvest* was used in place of *CPUE*. Note that all possible model combinations were run, allowing comparison between models that did or did not contain particular variable combinations. The relative goodness of fit of each model was ranked using an Akaike Information Criterion (AIC) to identify the highest-ranked models (Sakamoto et al., 1986). AIC was calculated as,

# AIC = -2 \* log likelihood - k \* npar

where k = 2, and *npar* is the number of parameters in the model. We used the AICcmodavg package in R (Version 1.35; Mazerolle, 2013) to select the top models, identified as those with a delta AIC  $\leq$  3 compared to the top model. We furthermore experimented with including the timeline of the recent food web shift (signaled by the 2003 collapse of alewife) for Lake Huron locations (Riley et al., 2008). However, given that the shift was never present in the top ranked model, did not contribute much explanatory power, and was never present in models with delta AIC  $\leq$  3 except when all other variables were included, we did not include it in our final results.

Second, to examine the individual explanatory power of each factor, we performed a variance partitioning exercise. We used the Hier.part package in R (version 1.0-4; Walsh and MacNally, 2013) to identify the relative independent contribution of each parameter. In doing so, we address the issue of multi-collinearity among the variables by identifying both the independent and joint contributions of each parameter in the model, thus improving our ability to identify driving mechanisms of lake whitefish growth. We found that the full models were ranked closely with the top model according to the AIC model selection exercise, so we choose to use a model containing *Dreissenid*, *CPUE* and *GDD* in our variance partitioning to observe the contribution of each variable. We could not include nested variables in the variance partitioning exercise and so we ran our analysis without *Year* in the model. In this case, the time period is captured in part by the dreissenid establishment factor.

Our third approach was to perform segmented regression (breakpoint analysis) to identify whether breakpoints existed in the time series for each location. The purpose is to aid in the interpretation of trends through time and whether changes are associated with key events (i.e., the particular dreissenid establishment year for a given location). We used JoinPoint software, version 4.0.4 from the National Cancer Institute (http://surveillance.cancer.gov/joinpoint/), which uses permutation tests to select the statistically best model fit. The permutation test evaluates how often a test statistic is in favor of the alternative hypothesis (no breakpoint, or an additional breakpoint). The program also identifies if there was a statistically significant Annual Percent Change (APC), an indicator of both the scale and the direction of slope change between breakpoints.

The contribution of explanatory variables to growth rate variation was considered on a cohort basis in all analyses. In other words, the growth of the cohort between ages 1 and 2 (our response variable) was compared to the growing degree days or CPUE of the population for the corresponding year in which that cohort was growing. The dreissenid establishment year was similarly adjusted in the statistical models to correspond to the year in which the cohort was age 2.

# Results

Growth rates prior to dreissenid establishment were variable among locations, where some locations showed decreases, some locations showed increases, and others showed no obvious patterns over time (Fig. 2). In all but one location where dreissenids have become established, the overall trend was a decrease in growth following the designated dreissenid establishment year (Fig. 2; Table 2). Following

#### Table 2

Mean growth between ages 1 and 2 years for lake whitefish in years pre- and postdreissenid mussel establishment. Locations are listed in order of the largest percentage drop in growth between the pre and post time periods (negative % change indicates growth declined whereas positive % change indicates that growth increased post dreissenids).

Location	Pre growth mean (mm)	Pre growth standard deviation (mm)	Post growth mean (mm)	Post growth standard deviation (mm)	% change	
Glenora	107.4	25.2	72.9	20.6	-32.1	
Grand Bend	96.9	25.1	70.3	24.2	-27.5	
Cheboygan	76.4	23.3	56.9	23.3	-25.5	
Southampton	90.0	15.8	67.7	18.0	-24.8	
Naubinway	85.8	19.9	66.4	35.9	-22.6	
Detour Village	70.7	24.1	56.6	25.2	-20.1	
Cape Rich	85.6	19.6	69.8	15.7	-14.9	
Dunkirk	98.2	25.7	102.4	25.3	+4.1	
Thunder Bay*	82.0	23.0	Growth range: 8.7–174.5 mm		mm	
Apostle Islands*	39.9	14.3	Growth range: 20.1–95.1 mm			
Whitefish Bay*	83.3	24.4	Growth range: 30.5–163.3 mm			

\* Dreissenid mussel populations have not had widespread establishment in Lake Superior.

dreissenid establishment, decreases in growth ranged from 32.1% (Glenora, Lake Ontario) to 14.9% (Naubinway, Lake Michigan) across Lake Huron, Michigan and Ontario. In contrast, average growth in Dunkirk (Lake Erie) increased by 4.1%. While the variability in individual growth rates of fish remained consistent between the pre- and postestablishment periods in Grand Bend, Detour Village, Cheboygan and Dunkirk, growth was more variable in Southampton and Naubinway



Fig. 2. Growth between ages 1 and 2 for lake whitefish in Glenora (Lake Ontario), Dunkirk (Lake Erie), Grand Bend (Lake Huron), Southampton (Lake Huron), Cape Rich (Lake Huron), Cheboygan (Lake Huron), Detour Village (Lake Huron), and Naubinway (Lake Michigan). Lengths at ages were back-calculated from scale samples of (primarily) age 5 fish. Vertical line indicates the year of dreissenid mussel establishment in each location for the cohort when it was age 2.



Fig. 3. Growth between ages 1 and 2 for lake whitefish in Lake Superior. Lengths at ages were back-calculated from scale samples of (primarily) age 5 fish.

#### Table 3

Generalized linear models examining variation in growth of lake whitefish between ages 1 and 2 years. Highest-ranked models by AIC in each location are given ( $\Delta$ AIC  $\leq$  3). Model weights,  $R^2$  value for the top model, number of parameters (*npar*), and negative log likelihood (-LL) are shown. Whitefish Bay (Lake Superior) models not shown because of extremely poor predictive power ( $R^2 < 0.001$ ).

Lake	Location	Model	$R^2$	npar	ΔAIC	Weight	-LL
Superior	Thunder Bay <sup>a</sup>	GDD	0.02	3	0	0.48	3120.8
*	-	GDD + CPUE		4	1.3	0.25	3120.4
		Year + GDD		4	2.0	0.18	3120.8
Superior	Apostle Islands <sup>a</sup>	Year + GDD + CPUE	0.26	5	0	0.66	337.2
		Year + GDD		4	1.9	0.26	339.2
Erie	Dunkirk	Year + Dreissenid + Harvest	0.14	6	0	0.34	569.3
		Year + GDD		4	1.6	0.15	572.3
		Year + Dreissenid + GDD		6	1.9	0.14	570.2
		Year + Dreissenid + GDD + Harvest		7	2.0	0.13	569.1
		Year + Harvest		4	2.1	0.12	572.5
Ontario	Glenora	Year + Dreissenid + CPUE	0.32	7	0	0.56	3664.5
		Year + Dreissenid + GDD + CPUE		6	0.48	0.44	3665.3
Huron	Grand Bend	Dreissenid + GDD	0.31	5	0	0.28	1904.5
		Dreissenid + CPUE		5	0.3	0.25	1904.6
		Year + Dreissenid + GDD		6	1.2	0.16	1904.1
		Dreissenid + GDD + CPUE		6	1.4	0.14	1904.1
		Year + Dreissenid + CPUE		6	2.2	0.09	1904.6
Huron	Southampton	Year + Dreissenid + GDD	0.33	6	0	0.50	1844.1
		Year + Dreissenid		5	1.6	0.23	1845.9
Huron	Cape Rich	Year + Dreissenid + CPUE	0.31	6	0	0.55	1928.3
		Year + Dreissenid		5	2.3	0.17	1930.5
Huron	Cheboygan	Year + CPUE	0.12	4	0	0.41	1263.7
		Year + GDD + CPUE		5	1.4	0.21	1263.4
		Dreissenid + GDD		5	3.0	0.09	1264.2
Huron	Detour Village	GDD + CPUE	0.07	4	0	0.57	1568.8
		Year + GDD + CPUE		5	1.4	0.28	1568.5
Michigan	Naubinway	Year + Dreissenid + CPUE	0.40	6	0	0.42	946.5
		Dreissenid + CPUE		5	1.1	0.24	948.1
		Year + Dreissenid + GDD + CPUE		7	2.1	0.14	946.5
		Dreissenid + GDD + CPUE		6	2.1	0.14	947.6

<sup>a</sup> Dreissenids not included in the models for Lake Superior locations because dreissenid populations have not had widespread establishment there as in the other Great Lakes.

(Table 2; Fig. 2). Growth rates in Lake Superior showed variable patterns. In Apostle Islands, growth rates declined in about the early 1990s, but then increased again (Fig. 3). Growth rates in Thunder Bay and Whitefish Bay showed no clear temporal trend (Fig. 3).

# AIC model selection and hierarchical partitioning

#### Locations with dreissenids

AIC model selection identified *Dreissenid* in the highest-ranked models in 6 of 8 locations investigated (Table 3). The highest-ranked models had  $R^2$  values ranging from 0.07 to 0.40. *Dreissenid* was not in the highest ranked models for either Detour Village or Cheboygan in Lake Huron, but the predictability of the top models for both these locations was the lowest among dreissenid-established locations ( $R^2 = 0.07$  and 0.12, respectively). From the hierarchical partitioning, the independent contribution of dreissenid mussels was between 0.1% (Dunkirk, Lake Erie) and 91.8% (Naubinway, Lake Michigan) of the variation explained, with other variables contributing varying amounts depending on the location (Table 4).

# Lake Superior locations

The  $R^2$  was extremely low for the top GLM for Thunder Bay, which included only *GDD* (Table 3). Hierarchical partitioning for Thunder Bay found *GDD* to explain the majority of the variation (99%), again, with a very low  $R^2$  overall (Table 4). The Apostle Islands top GLM explained 26% of the variation and included *Year*, *GDD* and *CPUE* (Table 3). Hierarchical partitioning for Apostle Islands found that *CPUE* explained the highest percentage of the variation (81%), compared to *GDD* which explained 19% (Table 4). Results are not shown for the model selection exercise for Whitefish Bay because the sample size was low relative to the number of parameters and the resulting  $R^2$  was less than 1%. The hierarchical partitioning exercise identified that *Year* and *CPUE* contributed equally in Whitefish Bay, although the model explained almost none of the variation (Table 4).

#### Segmented regression

A single breakpoint was detected in Naubinway, Glenora, Cheboygan, and the Apostle Islands (Fig. 4). Two breakpoints were detected in Southampton, and no breakpoints were detected in Cape Rich or Detour Village (Fig. 4). In Southampton, two slope changes occurred: one in 1986 (95% confidence interval, CI: 1983 to 2000), and once in 2000 (CI: 1995 to 2004). Between 1986 and 2000, there was a statistically significant Annual Percent Change (APC) of -3.18. Cheboygan showed a breakpoint at 1997 (CI: 1991 to 2001), and a significant APC of -7.9 from 1997 to 2003. In Naubinway, a breakpoint was identified at 1992 (CI: 1990 to 1997), with a significant APC of -5.18 between 1992 and 2003. Note that there was a gap in scale samples for Naubinway in 1993 and 1994, and we do not know if a peak in growth occurred in one of those years. Growth in Glenora (Lake Ontario) steadily increased, at which point we saw a slope change in 1980 (CI: 1973 to 1988) and a corresponding decline in growth. Statistically significant APCs were seen in Glenora: 1.2 from 1952 to 1980 and -2.4after 1980

There were no breakpoints detected for Cape Rich or Detour Village, but there were statistically significant slope decreases over the full sampling period (APC was -2.02 for Cape Rich and -2.16 for Detour Village). A breakpoint was detected for the Apostle Islands at 1995 (95% CI: 1992 to 1998) with a statistically significant slope before and after the breakpoint (ACP was -5.47 for 1977–1995 and 6.04 for 1995–2003). Grand Bend, Dunkirk, Thunder Bay, and Whitefish Bay did not have statistically significant temporal trends in growth (Fig. 4).

Patterns before and after the breakpoints were variable among locations. In 7 locations, trends in growth were apparent prior to dreissenid

Table 4

Results of hierarchical partitioning analysis explaining variation in growth of lake whitefish between ages 1 and 2 years. Model examined included catch per unit effort (*CPUE*) + growing degree days (*GDD*) + *Dreissenids*.

Lake	Location	Model R <sup>2</sup>	Variable	Independent <sup>a</sup>	Joint <sup>a</sup>	Direction	Independent %
Superior	Thunder Bay <sup>b</sup>	0.02	GDD	84.1	0.1	_	99.4
	5		CPUE	0.5	0.1	_	0.6
Superior	Whitefish Bay <sup>b</sup>	< 0.001	CPUE	118.1	118.1	_	50.0
	5		GDD	118.1	118.1	_	50.0
Superior	Apostle Islands <sup>b</sup>	0.02	GDD	0.1	-0.1	+	18.9
*	*		CPUE	0.5	-0.1	-	81.1
Ontario	Glenora	0.26	Dreissenids	89.2	28.6	-	72.3
			CPUE	22.1	21.2	+	17.9
			GDD	12.1	6.8	-	9.8
Erie	Dunkirk	0.05	Harvest	342.1	341.1	+	49.9
			Dreissenids	1.9	-1.8	-	0.1
			GDD	341.9	341.1	+	49.8
Huron	Grand Bend	0.24	CPUE	59.2	47.2	+	46.3
			GDD	37.4	37.3	_	29.2
			Dreissenids	31.3	9.9	_	24.5
Huron	Southampton	0.31	Dreissenids	46.0	33.3	+	44.6
			GDD	3.1	-0.7	+	3.0
			CPUE	0.6	-0.2	-	0.5
Huron	Cape Rich	0.19	Dreissenids	37.2	5.1	-	77.4
			GDD	3.2	1.1	_	6.6
			CPUE	7.7	1.8	_	16.0
Huron	Cheboygan	0.11	CPUE	87.4	89.6	+	48.7
			GDD	82.9	83.7	+	45.7
			Dreissenids	10.0	7.1	_	5.5
Huron	Detour Village	0.07	CPUE	4.8	2.6	+	37.1
			GDD	4.8	0.1	_	37.1
			Dreissenids	3.2	3.8	+	25.8
Michigan	Naubinway	0.39	Dreissenid	49.7	-0.8	_	91.8
	-		CPUE	3.8	-0.5	+	7.0
			GDD	0.7	-0.6	-	1.2

<sup>a</sup> These quantities represent the relative contribution of each parameter to the full model. The sum of the independent and joint contributions in each model is equal to the goodness of fit measure for the full model, minus the goodness of fit measure for the null model.

<sup>b</sup> Dreissenids not included in the models for Lake Superior because they have not had widespread establishment there as in the other Great Lakes.



Fig. 4. Segmented regression of mean lake whitefish growth per cohort between ages 1 and 2. Two break points were observed in Southampton; one breakpoint was observed in Naubinway, Glenora, Cheboygan and Apostle Islands; no breakpoints were observed in Cape Rich and Detour Village. No significant trends (therefore regression lines not shown) were observed in Grand Bend, Dunkirk, Thunder Bay, or Whitefish Bay. Vertical line indicates the year of dreissenid mussel establishment in each location for the cohort when it was age 2. Dreissenids have not had widespread establishment in Lake Superior.

establishment and where significant breaks were detected, the breakpoints occurred prior to the establishment year (Fig. 4).

### Discussion

We found that lake whitefish populations have undergone notable reductions in juvenile growth rate in nearly all regions examined except two locations in Lake Superior and one location in Lake Erie. These trends in lake whitefish growth have occurred against a back-drop of ecosystem changes that have taken place over the past several decades in the Great Lakes. To varying degrees among the lakes, there have been increases in water clarity, and declines in phytoplankton, native invertebrates, and prey fish populations (Nalepa et al., 1998; Riley et al., 2008; Bunnell et al., 2013). In Lake Huron, food web changes have been particularly profound since about 2003 when alewife, once the most abundant prey fish in offshore areas, crashed (Riley et al., 2008; Dunlop and Riley, 2013). The establishment of dreissenid mussels has been implicated in the water quality and lower trophic level changes (Bunnell et al., 2013), and to some extent in some of the changes observed in fish populations (Rennie et al., 2009b; Riley and Adams, 2010; Gobin et al., 2015). However, as noted by Bunnell et al. (2013), the effects of dreissenid mussels on higher trophic levels remain uncertain.

The relatively large-scale pattern of growth declines we report suggests a broad driver of change that is consistently present in many regions throughout the basin. Our analyses provide evidence that the establishment of dreissenid mussels was the most consistently present factor where growth rate declines occurred. In 7 of 8 locations where dreissenids have become established, lake whitefish growth rates declined in years following the location-specific dreissenid establishment year (Table 2). The largest decline was observed for Glenora (Lake Ontario) where growth decreased by 32.1% following dreissenid establishment. Dreissenid establishment did occur in the top model for the majority of locations and overall explained more variation in the top models than any other variable. In two of the three locations in Lake Superior, where dreissenids have not had widespread establishment, no notable trends in growth were apparent. One location with established dreissenid populations where we did not observe a growth rate decline was Lake Erie, which is different than the pattern reported by Lumb and Johnson (2008); however, our Lake Erie time series contained significant gaps and it is difficult to draw conclusions from the limited data we had.

Clearly, variables other than dreissenid mussels contributed to trends in lake whitefish growth. In several locations, declines in growth began prior to the first sighting of dreissenids in the system (Table 1 lists year of first sighting). For example, in Cape Rich, declines in growth occurred from the beginning of the time series in the 1980s, before dreissenid presence and establishment. An overall growth decline also occurred in Detour Village, although our models have very low predictive power (7%). Some of the prior trends in growth might be the result of uncertainty in our estimated year of dreissenid establishment. We chose to include the establishment year in our models instead of the year of first sighting because we wanted to more fully represent the timeline when dreissenids would begin to have detectable effects on the surrounding ecosystem. Prior to the year we classified as the establishment year of first sighting (Table 1), in several locations (most notably Cape Rich), declines in growth were occurring prior to the dreissenid invasion. What we do not know is whether these trends would have otherwise decelerated or ceased if dreissenids didn't become established.

One hypothesis for observed growth rate declines of lake whitefish has been that increasing whitefish abundance has led to reduced growth through density-dependent processes. Indeed, whitefish commercial catches in Lakes Michigan and Huron were at recorded highs during the late 1990s, substantially higher than historically observed (Brenden et al., 2013). Our models included measures of relative abundance (CPUE or harvest) so that we could test this hypothesis more explicitly. We did not, however, find evidence that density was consistently changing in a pattern that could broadly explain the growth rate declines. This is not to imply that density did not contribute to the variation observed or that it does not impact lake whitefish growth, but rather that it's effect was not clearly apparent nor consistent with the expected direction and magnitude in our dataset. CPUE (or harvest) was present in the top model in 7 of 9 locations. One location with a substantial contribution from CPUE was for Grand Bend, where it accounted for 33% of the variation explained by the full model. However, in Grand Bend, the association between CPUE and growth in the full model was positive (opposite the expectation if high abundances were suppressing growth rates). Relative abundance did explain more of the overall variance in the full models than GDD across locations, but with both variables explaining less variation overall than the establishment of dreissenids. The lack of a consistent direction of contribution from density could be because of the declines in relative abundance that seem to be occurring in the most recent years in several locations (ESM Fig. S3). Inconsistent patterns between growth and CPUE could also arise if the strength or shape of the density-dependent relationship has changed. In Lake Huron, there is evidence that the relationship between growth and population biomass of lake whitefish switched from being negative (i.e., as expected if population biomass suppresses growth) to one that is more positive (i.e., both growth and population biomass decline concurrently) following dreissenid mussel establishment (Gobin et al., 2015).

Growing degree days (GDD) also contributed to growth rate variation, but to a lesser extent than the other explanatory variables. GDD was present in the top model in 4 of 9 locations; however, the largest contributions from GDD were found in locations where our models had low predictive power (Dunkirk  $R^2 = 0.05$ ; Cheboygan  $R^2 = 0.11$ ). Altogether, 7 of 11 locations showed a negative relationship with GDD, while the other 4 locations showed a positive relationship with GDD. This minor and inconsistent effect of temperature on growth is similar to a few previous studies. For example, a review of temperature effects on European fishes showed that the consequences of changing temperatures vary greatly among populations of Coregonus spp., being particularly dependent on lake depth and altitude (Jeppesen et al., 2012). Gobin et al. (2015) found that GDD was not a good predictor of lake whitefish growth rates in the southern main basin of Lake Huron. However, another previous study did find a negative relationship between GDD and lake whitefish growth that appears to be mediated through a reduction of primary productivity (Rennie et al., 2009a).

Although there was a broad trend of slower growth, local-scale effects are also apparent across our study locations. This once again points to the presence of factors other than dreissenids in contributing to some of the growth rate variation. Local effects are made obvious by the different directions of growth rate trends in some locations prior to dreissenids, the variation in explanatory power of our models, and the direction of effects of different variables. In some locations, increases in growth occurred before dreissenid establishment (e.g., Naubinway, Glenora) or growth was more stable prior to dreissenid establishment (Cheboygan, Grand Bend, Dunkirk, Thunder Bay, and Whitefish Bay). *Year*, which is expected to capture some of the variation caused by unexplained factors that are systematically changing through time, was also present in the top model in 7 of 9 locations.

Local effects appear to be occurring within Lake Superior. Apostle Islands was the one location in Lake Superior where there was an obvious trend in growth. Growth steadily declined between the late 1970s and 1995 when a breakpoint occurred, followed by a subsequent increase in growth (Fig. 4). In this population, Year was the most important factor (in a hierarchical partitioning model including Year + GDD + CPUE, Year explained 76% of the total variation), highlighting the role of an unaccounted for variable. Dreissenid mussels are present in low numbers in some areas of Lake Superior. To aid interpretation of our results, we ran a posthoc analysis where we included the year at which dreissenids were observed in Lake Superior as a factor in our full GLMs (the same as we did for our established locations). Results for this posthoc analysis are provided in ESM Tables S1, S2 and S3. In Thunder Bay, growth was found to increase slightly (ESM Table S1), with the overall variation explained being extremely low ( $R^2 = 0.03$ ) for the top model (ESM Table S2), which did not include dreissenids as a factor. In Whitefish Bay, dreissenids were a factor in the top model, but the variation explained was so minimal (<0.0001), that the effect on the interpretation of the model is meaningless. In Apostle Islands, however, dreissenids were a contributing factor, with a drop in growth pre and post of about 32% (as can be seen in Fig. 4; ESM Table S2). Low abundances of dreissenids have been detected in Duluth Harbor, about 100 km away from the Apostle Islands; however, tagging studies have suggested that Apostle Islands lake whitefish remain relatively local (Seider and Schram, 2010), and it seems unlikely that low numbers of dreissenids would have a substantial effect on fish growth from such a distance

Instead, there are two other potential drivers of the changes observed in Apostle Islands. First, there were decreases in Diporeia in the Apostle Islands region of Lake Superior during the 1990s (Scharold et al., 2004). Lake whitefish in the Apostle Islands do consume Diporeia, although other prey items have a high frequency of occurrence (most notably sphaeriid clams, fish eggs, and chironomids) depending on the season, depth, and size of the fish (Seider and Schram, 2010). The second possibility is related to changes in relative abundance. Catch per unit effort from USGS bottom trawl surveys (the source of the data analyzed here) was not closely associated with trends in lake whitefish growth (Table 3); trawl CPUE estimates do not show an obvious directional trend in the years where growth was changing (ESM Fig. S3). However, a separate gill netting survey conducted by the Wisconsin Department of Natural Resources shows a fairly substantial increase in CPUE between the mid-1970s and early 2000s (Seider and Schram, 2010). When we plot CPUE from the summer gill netting survey with our growth rate estimates from the USGS trawl surveys, there is some evidence for a negative relationship; in other words, growth declines as CPUE increases as would be expected if densitydependent growth were occurring in this population (ESM Fig. S5). Furthermore, although there was significant interannual variability, commercial harvest and sport harvest of lake whitefish in the Apostle Islands showed evidence of increases between the 1970s and early 2000s, perhaps signaling an increase in abundance (Seider and Schram, 2010). A spring large mesh gill netting survey also observed an increasing CPUE up until the early 2000s, although the relationship with growth was less evident (ESM Fig. S5). It is not clear why the trawl survey shows a different pattern. Trawl nets are an active gear, exploiting a different behavioral response than passive gear such as a gill net (He, 2010). There could be other differences in the habitats or

sizes of fish sampled by the different gears. Differences between the surveys could also be related to potential behavioral changes in lake whitefish activity; increased movement or activity rates could cause differences in encounter rates (and therefore estimated CPUE) between passive and active survey methods (Rudstam et al., 1984, sensu Rennie et al., 2009b).

Our statistical models explained between 0 and 40% of the variation in growth, indicating a large degree of unaccounted for variation. Some of the unexplained variability could be driven by uncertainty in the study design. We used CPUE (or in one case, harvest) as an estimate of relative abundance. However, changes in water quality or other variables that impact catchability could affect the relationship between CPUE and true abundance. Most notably, the increases in water clarity brought about by dreissenids might have decreased the catchability of gill nets. Similarly, the presence of dreissenid mussels on the lake-bed might alter catchability of gear, as appears to be the case for bottom trawls (Kocovsky and Stapanian, 2011). Furthermore, the conversion between multi-filament nets and mono-filament nets (see the Methods section) could potentially interact with water clarity. The increases in Cladophora observed in many regions (Brooks et al., 2015) could also reduce catchability of gill nets because of net fouling. Changing survey catchability is a pervasive issue in the monitoring programs of agencies throughout the Great Lakes and is in need of further investigation. The other explanatory variable in our analysis, growing degree days (GDD), is based on air temperature data, and although closely related to water temperature (see the Methods section), would not capture all of the variation within the habitats and depths in which lake whitefish reside. Lake whitefish in Lake Huron were captured at depths between 6 m and 111 m in OMNRF assessment gill nets (range of depths fished was 4-121 m; OMNRF unpublished data). Deriving an annual estimate that represents the water temperatures experienced by lake whitefish would not be straightforward. Despite these uncertainties, however, our models were able to explain a good degree of variation (as high as 40%). This is noteworthy given the inherent complexity of these systems and the number of potential variables that could have local effects (e.g., water quality, fishing pressure, habitat). Our analysis provides a quantitative assessment over a broad geographical region that contributes to identifying large, systematic changes in a few key variables that are driving trends in lake whitefish growth. The fairly consistent declines in lake whitefish growth that have been occurring in most of the Great Lakes, suggest the role of a factor with a broad basis. Dreissenid mussels and the suite of ecosystem changes associated with their establishment (Higgins and vander Zanden, 2010) appear to be the most obvious contributor to the overall growth rate declines.

Observed declines in Diporeia are a possible mechanism by which dreissenid mussels have influenced lake whitefish growth (Hoyle, 2005; Rennie et al., 2009b). Unprecedented declines in Diporeia coincided with the introduction and population expansion of dreissenids throughout the Great Lakes (Nalepa et al., 2009a). Large areas within each of the Great Lakes except Lake Superior are now devoid of Diporeia, where they were once abundant (Nalepa et al., 2006, 2009b). Declines in Diporeia were first noted at a few sites in the early 1990s (Dermott and Kerec, 1997; Nalepa et al., 1998), with prominent declines being apparent by the late 1990s in Lakes Michigan, Huron, and Ontario (Barbiero et al., 2011). In Lake Superior, dramatic reductions in Diporeia have not occurred, although there is still notable variability among years and sites (Scharold et al., 2004; Barbiero et al., 2011). The close temporal correspondence between dreissenid establishment and Diporeia declines suggests a linkage (Nalepa et al., 2007, 2009a), but the exact mechanism remains unknown (Foley et al., 2014).

Lake whitefish eat a variety of benthic prey items, varying by season and location. Several diet studies have indicated that while lake whitefish regularly consume *Diporeia* when present, they make use of other prey items such as sphaeriid clams, oligochaetes, chironomids, *Mysis*, fish eggs, and small fish (Pothoven et al., 2001; Rennie et al., 2009b; Seider and Schram, 2010; Stockwell et al., 2014). However, the lipid content of *Diporeia* might have made them an important source of calories that was once abundant but is no longer available in many regions. Wright and Ebener (2007), for example, found that *Diporeia* consumption has a positive relationship with lipid content of lake whitefish in northern Lake Michigan, which in turn contribute to higher growth rates observed there. It could also be that the prey items available to lake whitefish following the establishment of dreissenids and disappearance of *Diporeia* do not provide the same energy density (McNickle et al., 2006).

Lake whitefish growth rate declines after the establishment of dreissenids in South Bay, Lake Huron were associated with a 13–29% lower caloric intake by lake whitefish (Rennie et al., 2009b). Stomach samples from South Bay in 1947 and 1981 (prior to dreissenids) indicated that lake whitefish were dependent on profundal prey sources (e.g. *Diporeia*, chironomids, oligochaetes), whereas samples from 2005 (post dreissenids) indicated a heavy dependence on littoral prey, dominated by gastropods and dreissenids (Rennie et al., 2009b). Lake whitefish from South Bay had higher activity costs associated with increased foraging activity in an environment with less energy available from prey, which could explain observed growth declines (Rennie et al., 2012). Similarly, a bioenergetics model for Lakes Huron and Michigan predicted that substantial increases in lake whitefish consumption would have been needed to maintain growth rates given the changes in diet that occurred (Pothoven and Madenjian, 2008).

To explore the causal links more fully in our study, it would have been preferred to include Diporeia abundance as a parameter in our models; however, long-term and annual trends in Diporeia were not available in our sampling regions. Similarly, annual estimates of dreissenid density would have been preferred. Lacking this level of detailed information, we had to rely on the timeline of dreissenid establishment as a presence or absence factor to reflect changes in available diet items, and to capture the coinciding ecosystem changes. It would not be surprising if the changes in the benthic invertebrate communities of the Great Lakes following dreissenid establishment have affected the foraging behavior and diet of benthic fish, in turn having an impact on their bioenergetics. Local differences in food availability and population density have also likely contributed to growth variation, but the dramatic declines in Diporeia (Nalepa et al., 2007, 2009a; Barbiero et al., 2011) and the evidence of caloric reductions and bioenergetics costs in lake whitefish diets (McNickle et al., 2006; Pothoven and Madenjian, 2008; Rennie et al., 2009b; Rennie et al., 2012) are compelling.

There have been signs of stabilization and even increases in lake whitefish growth in very recent years for some locations. Growth rates in Glenora, Cape Rich, and Naubinway appear to have reached the lower limit of declines. We observed possible signs of increased growth in recent years in Southampton, Grand Bend and Detour Village. Declining lake whitefish CPUE in Southampton was observed between 2005 and 2009 (ESM Fig. S3), which could be indicative of lowered population abundance supporting faster growth rates. Similarly, lake whitefish CPUE has been low in Detour Village since 2000 (ESM Fig. S3). A downward trend in CPUE in Cape Rich and Grand Bend is also observed (ESM Fig. S3), but is not coupled with higher growth rates in the late 2000s; Cape Rich growth continues to decline until 2006, and Grand Bend growth rates continue to decline until 2009. Variability in prey items might explain some of the divergent growth patterns observed among locations in recent years. In Lake Huron, for example, there was high variability in lake whitefish diets across the lake between 2002-2004 (e.g., Pothoven and Nalepa, 2006).

In some locations, lake whitefish could also be feeding on round gobies (*Neogobius melanostomus*) as a new source of prey (Pothoven and Madenjian, 2013). Pothoven and Madenjian (2013) found that those lake whitefish obtaining the longest lengths (over 400 mm), consumed more fish. They also noted that gobies are a more energetically rich prey than dreissenids, and bioenergetics modeling indicated that diets containing round gobies could allow lake whitefish to attain predreissenid growth levels. By extending the time series to more recent

years, and including mature growth in our analysis, we might have observed further increases in growth as a result of recent changes in diet composition.

The declines in lake whitefish growth have implications for the commercial fisheries in the Great Lakes. Decreases in growth rates have preceded fishery crashes in the past (Brenden et al., 2010). Sustained slow growth rates could result in delayed maturation, thereby influencing spawning stock biomass and recruitment. In the southern main basin of Lake Huron, declines in lake whitefish recruitment and an altered relationship between population biomass and growth have taken place, signaling potential changes in the population's carrying capacity (Gobin et al., 2015). Declines in lake whitefish recruitment have also been observed in other locations within Lake Huron (OMNRF unpublished data). This highlights the need for increased vigilance in the monitoring and management of these valuable fishery resources in light of the profound ecosystem changes that have taken place in the Great Lakes. The results of our study furthermore highlight the insights that can be gained by comparing trends among basins of the Laurentian Great Lakes, which can help elucidate the role of regional versus local drivers of change.

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#### Appendicesx 1–4. Supplementary material

Supplementary material to this article can be found online at http://dx.doi.org/10.1016/j.jglr.2015.08.010.

#### References

- Barbiero, R.P., Tuchman, M.L., 2004. Long-term dreissenid impacts on water clarity in Lake Erie. J. Great Lakes Res. 30, 557–565.
- Barbiero, R.P., Schmude, K., Lesht, B.M., Riseng, C.M., Warren, G.J., Tuchman, M.L., 2011. Trends in *Diporeia* populations across the Laurentian Great Lakes, 1997–2009. J. Great Lakes Res. 37, 9–17.
- Benson, A., 2013. Chronological history of zebra and quagga mussels (Dreissenidae) in North America, 1988–2010. In: Nalepa, T.F., Schloesser, D.W. (Eds.), Quagga and Zebra Mussels: Biology, Impacts and Control, 2nd Edn CRC Press, Boca Raton, pp. 9–31.
- Bowen, K.L., Johannsson, O.E., 2011. Changes in zooplankton biomass in the Bay of Quinte with the arrival of the mussels, *Dreissena polymorpha* and *D. rostiformis bugensis*, and the predatory cladoceran, *Cercopagis pengoi*: 1975 to 2008. Aquat. Ecosyst. Health Manag. 14, 44–55.
- Brenden, T.O., Ebener, M.P., Sutton, T.M., Jones, M.L., Arts, M.T., Johnson, T.B., Koops, M.A., Wright, G.M., Faisal, M., 2010. Assessing the health of lake whitefish populations in the Laurentian Great Lakes: lessons learned and research recommendations. J. Great Lakes Res. 36, 135–139.
- Brenden, T.O., Brown, R.W., Ebener, M.P., Reid, K., Newcomb, T., 2013. Great Lakes commercial fisheries: historical overview and prognoses for the future. In: Taylor, W.W., Lynch, A.J., Leaonard, N.J. (Eds.), Great Lakes Fisheries Policy and Management. Michigan State University Press, East Lansing, pp. 339–397.
- Brooks, C., Grimm, A., Shuchman, R., Sayers, M., Jessee, N., 2015. A satellite-based multitemporal assessment of the extent of nuisance *Cladophora* and related submerged aquatic vegetation for the Laurentian Great Lakes. Remote Sens. Environ. 157, 58–71.

- Bunnell, D.B., Barbiero, R.P., Ludsin, S.A., Madenjian, C.P., Warren, G.J., Dolan, D.M., Brenden, T.O., Briland, R., Gorman, O.T., He, J.X., Johengen, T.H., Lantry, B.F., Lesht, B.M., Nalepa, T.F., Riley, S.C., Riseng, C.M., Treska, T.J., Tsehaye, I., Walsh, M.G., Warner, D.M., Weidel, B.C., 2013. Changing ecosystem dynamics in the Laurentian Great Lakes: bottom-up and top-down regulation. Bioscience 64, 26–39.
- Carlton, J.T., 2008. The zebra mussel *Dreissena polymorpha* found in North America in 1986 and 1987. J. Great Lakes Res. 34, 770–773.
- Chezik, K.A., Lester, N.P., Venturelli, P.A., 2013. Fish growth and degree-days I: selecting a base temperature for a within-population study. Can. J. Fish. Aquat. Sci. 71, 47–55. Claramunt, R.M., Muir, A.M., Johnson, J., Sutton, T.M., 2010. Spatio-temporal trends in the
- food habits of age-0 lake whitefish. J. Great Lakes Res. 36, 66–72. Collins, I.I. 1979. Relative efficiency of multifilament and mono-filament nylon gill net to-
- Comms, J.J., 1979. Relative enciency of muturinament and mono-manient myon gin net towards lake whitefish (*Coregonus cluperaformis*) in Lake Huron. J. Fish. Res. Board Can. 36, 1180–1185.
- DeBruyne, R.L., Galarowicz, T.L., Claramunt, R.M., Clapp, D.F., 2008. Lake whitefish relative abundance, length-at-age, and condition in Lake Michigan indicated by fishery-independent surveys. J. Great Lakes Res. 34, 235–244.
- Dermott, R., Kerec, D., 1997. Changes to the deepwater benthos of eastern Lake Erie since the invasion of *Dreissena*: 1979–1993. Can. J. Fish. Aquat. Sci. 54, 922–930.
- Dunlop, E.S., Riley, S.C., 2013. The contribution of cold winter temperatures to the 2003 alewife population collapse in Lake Huron. J. Great Lakes Res. 39, 682–689.
- Dunlop, E.S., Shuter, B.J., 2006. Native and introduced populations of smallmouth bass differ in the concordance between climate and somatic growth. Trans. Am. Fish. Soc. 135, 1175–1190.
- Dunlop, E.S., Orendorff, J.A., Shuter, B.J., Rodd, F.H., Ridgway, M.S., 2005. Diet and divergence of introduced smallmouth bass, *Micropterus dolomieu*, populations. Can. J. Fish. Aquat. Sci. 62, 1720–1732.
- Ebener, M.P., Brenden, T.O., Wright, G.M., Jones, M.L., Faisal, M., 2010. Spatial and temporal distributions of lake whitefish spawning stocks in Northern lakes Michigan and Huron, 2003–2008. J. Great Lakes Res. 36, 38–51.
- Enberg, K., Jorgensen, C., Dunlop, E.S., Varpe, O., Boukal, D.S., Baulier, L., Eliassen, S., Heino, M., 2012. Fishing-induced evolution of growth: concepts, mechanisms and the empirical evidence. Mar. Ecol. Evol. Perspect. 33, 1–25.
- Foley, C.J., Bowen, G.J., Nalepa, T.F., Sepulveda, M.S., Hook, T.O., 2014. Stable isotope patterns of benthic organisms from the Great Lakes region indicate variable dietary overlap of *Diporeia* spp. and dreissenid mussels. Can. J. Fish. Aquat. Sci. 71, 1784–1795.
- Francis, R.I.C.C., 1990. Back-calculation of fish length: a critical review. J. Fish Biol. 36, 883–902.
- Gobin, J., Lester, N.P., Cottril, A., Fox, M.G., Dunlop, E.S., 2015. Trends in growth and recruitment of Lake Huron lake whitefish during a period of ecosystem change, 1985 to 2012. J. Great Lakes Res. 41, 405–414.
- Griffiths, R.W., Schloesser, D.W., Leach, J.H., Kovalak, W.P., 1991. Distribution and dispersal of the zebra mussel (*Dreissena polymorpha*) in the Great Lakes region. Can. J. Fish. Aquat. Sci. 48, 1381–1388.
- He, P., 2010. Behavior of Marine Fishes: Capture Processes and Conservation Challenges. Wiley-Blackwell, Ames, Iowa.
- Hecky, R.E., Smith, R.E.H., Barton, D.R., Guildford, S.J., Taylor, W.D., Charlton, M.N., Howell, T., 2004. The nearshore phosphorus shunt: a consequence of ecosystem engineering by dreissenids in the Laurentian Great Lakes. Can. J. Fish. Aquat. Sci. 61, 1285–1293.
- Higgins, S.N., vander Zanden, M.J., 2010. What a difference a species makes: a metaanalysis of dreissenid mussel impacts on freshwater ecosystems. Ecol. Monogr. 80, 179–196.
- Hoyle, J.A., 2005. Status of lake whitefish (*Coregonus clupeaformis*) in Lake Ontario and the response to the disappearance of *Diporeia* spp. In: Mohr, L.C., Nalepa, T.F. (Eds.), Proceedings of a Workshop on the Dynamics of Lake Whitefish (*Coregonus clupeaformis*) and the Amphipod *Diporeia* spp. in the Great Lakes. Great Lakes Fishery Commission, Ann Arbor, MI, pp. 47–86.
- Hoyle, J.A., Bowlby, J.N., Morrison, B.J., 2008. Lake whitefish and walleye population responses to dreissenid mussel invasion in eastern Lake Ontario. Aquat. Ecosyst. Health Manag. 11, 403–411.
- Jeppesen, E., Mehner, T., Winfield, I.J., Kangur, K., Sarvala, J., Gerdeaux, D., Rask, M., Malmquist, H.J., Holmgren, K., Volta, P., Romo, S., Eckmann, R., Sandstrom, A., Blanco, S., Kangur, A., Stabo, H.R., Tarvainen, M., Ventela, A.M., Sondergaard, M., Lauridsen, T.L., Meerhoff, M., 2012. Impacts of climate warming on the long-term dynamics of key fish species in 24 European lakes. Hydrobiologia 694, 1–39.
- Kainz, M.J., Johannsson, O.E., Arts, M.T., 2010. Diet effects on lipid composition, somatic growth potential, and survival of the benthic amphipod *Diporeia* spp. J. Great Lakes Res. 36, 351–356.
- Kocovsky, P.M., Stapanian, M.A., 2011. Influence of dreissenid mussels on catchability of benthic fishes in bottom trawls. Trans. Am. Fish. Soc. 140, 1565–1573.
- Lester, N.P., Shuter, B.J., Abrams, P.A., 2004. Interpreting the von Bertalanffy model of somatic growth in fish: the cost of reproduction. Proc. R. Soc. Lond. B 271, 1625–1631.
- Lumb, C.E., Johnson, T.B., 2008. Retrospective growth analysis of lake whitefish (*Coregonus clupeaformis*) in Lakes Erie and Ontario, 1954–2003. In: Tallman, R.F., Howland, K.L., Rennie, R.D., Mills, K. (Eds.), Biology and Management of Coregonid Fishes 2008. Proceedings of the Tenth International Symposium on the Biology and Management of Coregonid Fishes 2008, Advances in Limnology 63, pp. 429–454.
- Lumb, C.E., Johnson, T.B., Cook, H.A., Hoye, J.A., 2007. Comparison of lake whitefish (*Coregonus clupeaformis*) growth, condition, and energy density between lakes Erie and Ontario. J. Great Lakes Res. 33, 314–325.
- Madenjian, C.P., O'Connor, D.V., Pothoven, S.A., Schneeberger, P.J., Rediske, R.R., O'Keefe, J.P., Bergstedt, R.A., Argyle, R.L., Brandt, S.B., 2006. Evaluation of a lake whitefish bioenergetics model. Trans. Am. Fish. Soc. 135, 61–75.
- Matuszek, J.E., Shuter, B.J., 1996. An empirical method for the prediction of daily water temperatures in the littoral zone of temperate lakes. Trans. Am. Fish. Soc. 125, 622–627.

- Mazerolle, M.J., 2013. Model selection and multimodel inference based on (Q)AIC(c). Version 1.35. Available at:, http://cran.r-project.org/web/packages/AICcmodavg/ AICcmodavg.pdf (Accessed November 2013).
- McNickle, G.G., Rennie, M.D., Sprules, W.G., 2006. Changes in benthic invertebrate communities of South Bay, Lake Huron following invasion by zebra mussels (*Dreissena polymorpha*), and potential effects on lake whitefish (*Coregonus clupeaformis*) diet and growth. J. Great Lakes Res. 32, 180–193.
- Wohr, L.C., Ebener, M.P., 2005. Status of lake whitefish (*Coregonus clupeaformis*) in Lake Huron. In: Mohr, L.C., Nalepa, T.F. (Eds.), Proceedings of a Workshop on the Dynamics of Lake Whitefish (*Coregonus clupeaformis*) and the Amphipod *Diporeia* spp. in the Great Lakes. Great Lakes Fishery Commission, Ann Arbor, MI, pp. 105–126.
- Muir, A.M., Ebener, M.P., He, J.X., Johnson, J.E., 2008. A comparison of the scale and otolith methods of age estimation for lake whitefish in Lake Huron. N. Am. J. Fish Manag. 28, 625–635.
- Nalepa, T.F., Hartson, D.J., Fanslow, D.L., Lang, G.A., Lozano, S.J., 1998. Declines in benthic macroinvertebrate populations in southern Lake Michigan, 1980–1993. Can. J. Fish. Aquat. Sci. 55, 2402–2413.
- Nalepa, T.F., Fanslow, D.L., Folley III, A.J., Lang, G.A., Eadie, B.J., Quigley, M.A., 2006. Continued disappearance of the benthic amphipod *Diporeia* spp. in Lake Michigan: is there evidence for food limitation? Can. J. Fish. Aquat. Sci. 63, 872–890.
- Nalepa, T.F., Fanslow, D.L., Pothoven, S.A., Foley, A.J., Lang, G.A., 2007. Long-term trends in benthic macroinvertebrate populations in Lake Huron over the past four decades. J. Great Lakes Res. 33, 421–436.
- Nalepa, T.F., Fanslow, D.L., Lang, G.A., 2009a. Transformation of the offshore benthic community in Lake Michigan: recent shift from the native amphipod *Diporeia* spp. to the invasive mussel *Dreissena rostriformis bugensis*. Freshw. Biol. 54, 466–479.
- Nalepa, T.F., Pothoven, S.A., Fanslow, D.L., 2009b. Recent changes in benthic macroinvertebrate populations in Lake Huron and impact on the diet of lake whitefish (*Coregonus clupeaformis*). Aquat. Ecosyst. Health Manag. 12, 2–10.
- Noonburg, E.G., Shuter, B.J., Abrams, P.A., 2003. Indirect effects of zebra mussels (*Dreissena polymorpha*) on the planktonic food web. Can. J. Fish. Aquat. Sci. 60, 1353–1368.
- Pothoven, S.A., Madenjian, C.P., 2008. Changes in the consumption by alewives and lake whitefish after dreissenid mussel invasions in lakes Michigan and Huron. N. Am. J. Fish Manag. 28 (1), 308–320.
- Pothoven, S.A., Madenjian, C.P., 2013. Increased piscivory by lake whitefish in Lake Huron. N. Am. J. Fish Manag. 33, 1194–1202.
- Pothoven, S.A., Nalepa, T.F., 2006. Feeding ecology of lake whitefish in Lake Huron. J. Great Lakes Res. 32, 489–501.
- Pothoven, S.A., Nalepa, T.F., Schneeberger, P.J., Brandt, S.B., 2001. Changes in diet and body condition of lake whitefish in southern Lake Michigan associated with changes in benthos. N. Am. J. Fish Manag. 21, 876–883.

- Reckahn, J.A., 1970. Ecology of young lake whitefish (*Coregonus clupeaformis*) in South Bay, Manitoulin Island, Lake Huron. In: Lindsay, C.C., Woods, C.S. (Eds.), The Biology of Coregonid Fishes. University of Manitoba Press, Winnipeg, pp. 437–460.
- Rennie, M.D., Sprules, W.G., Johnson, T.B., 2009a. Factors affecting the growth and condition of Jake whitefish (Coregonus cluneaformis). Can. J. Fish. Aquat. Sci. 66, 2096–2108.
- Rennie, M.D., Sprules, W.G., Johnson, T.B., 2009b. Resource switching in fish following a major food web disruption. Oecologia 159, 789–802.
- Rennie, M.D., Johnson, T.B., Sprules, W.G., 2012. Energy acquisition and allocation patterns of lake whitefish (*Coregonus clupeaformis*) are modified when dreissenids are present. Can. J. Fish. Aquat. Sci. 69, 41–59.
- Riley, S.C., Adams, J.V., 2010. Long-term trends in habitat use of offshore demersal fishes in western Lake Huron suggest large-scale ecosystem change. Trans. Am. Fish. Soc. 139, 1322–1334.
- Riley, S.C., Roseman, E.F., Nichols, S.J., O'Brien, T.P., Kiley, C.S., Schaeffer, J.S., 2008. Deepwater demersal fish community collapse in Lake Huron. Trans. Am. Fish. Soc. 137, 1879–1890.
- Rudstam, L.G., Magnuson, J.J., Tonn, W.M., 1984. Size selectivity of passive fishing gear A correction for encounter probability applied to gill nets. Can. J. Fish. Aquat. Sci. 41 (8), 1252–1255.
- Sakamoto, Y., Ishiguro, M., Kitagawa, G., 1986. Akaike Information Criterion Statistics. D. Reidel Publishing Company, Dordrecht, The Netherlands.
- Scharold, J.V., Lozano, S.J., Corry, T.D., 2004. Status of the amphipod Diporeia spp. in Lake Superior, 1994–2000. J. Great Lakes Res 30, 360–368.
- Scott, W.B., Crossman, E.J., 1973. Freshwater fishes of Canada. J. Fish. Res. Board Can. 184. Seider, M.J., Schram, S.T., 2010. Population Dynamics of Lake Whitefish in the Apostle Islands Region of Lake Superior. Wisconsin Department of Natural Resources Fisheries Management, Bayfield, WI (Report No. 154).
- Sierszen, M.E., Hrabik, T.R., Stockwell, J.D., Cotter, A.M., Hoffman, J.C., Yule, D.L., 2014. Depth gradients in food-web processes linking habitats in large lakes: Lake Superior as an exemplar ecosystem. Freshw. Biol. 59, 2122–2136.
- Stockwell, J.D., Yule, D.L., Hrabik, T.R., Sierszen, M.E., Isaac, E.J., 2014. Habitat coupling in a large lake system: delivery of an energy subsidy by an offshore planktivore to the nearshore zone of Lake Superior. Freshw. Biol. 59, 1197–1212.
- Walsh, C., MacNally, R., 2013. Package "hier.part", version 1.04. Available at:, http://cran.rproject.org/web/packages/hier.part/hier.part.pdf (Accessed April 2014).
- Wright, G.M., Ebener, M.P., 2007. Potential effects of dietary lipid reduction on growth and reproduction of lake whitefish in Northern Lake Michigan. In: Jankun, M., Brzuzan, P., Hliwa, P., Luczynksi, M. (Eds.), Proceedings of the Ninth International Symposium on the Biology and Management of Coregonid Fishes – 2005. Advances in Limnology 60, pp. 311–330.