



Changes in depth occupied by Great Lakes lake whitefish populations and the influence of survey design



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ABSTRACT

Understanding fish habitat use is important in determining conditions that ultimately affect fish energetics, growth and reproduction. Great Lakes lake whitefish (*Coregonus clupeaformis*) have demonstrated dramatic changes in growth and life history traits since the appearance of dreissenid mussels in the Great Lakes, but the role of habitat occupancy in driving these changes is poorly understood. To better understand temporal changes in lake whitefish depth of capture (D_w), we compiled a database of fishery-independent surveys representing multiple populations across all five Laurentian Great Lakes. By demonstrating the importance of survey design in estimating D_w , we describe a novel method for detecting survey-based bias in D_w and removing potentially biased data. Using unbiased D_w estimates, we show clear differences in the pattern and timing of changes in lake whitefish D_w between our reference sites (Lake Superior) and those that have experienced significant benthic food web changes (lakes Michigan, Huron, Erie and Ontario). Lake whitefish D_w in Lake Superior tended to gradually shift to shallower waters, but changed rapidly in other locations coincident with dreissenid establishment and declines in *Diporeia* densities. Almost all lake whitefish populations that were exposed to dreissenids demonstrated deeper D_w , following benthic food web change, though a subset of these populations subsequently shifted to more shallow depths. In some cases in lakes Huron and Ontario, shifts towards more shallow D_w are occurring well after documented *Diporeia* collapse, suggesting the role of other drivers such as habitat availability or reliance on alternative prey sources.

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Introduction

Behavior is an important determinant of the life history outcomes of aquatic species (Giacomini et al., 2013; Rennie et al., 2012b; Rogers et al., 2002). Major ecological changes, such as species invasions, have been demonstrated to alter the foraging behavior of fish populations (Vander Zanden et al., 1999). Additionally, changes in depth distribution have the potential to alter predator–prey interactions (O’Gorman et al., 2000) as well as the thermal habitat experienced by fishes, both of which can significantly alter vital bioenergetic rates such as growth (Rennie et al., 2012b). The stability and predictability of fish populations can be altered by changes in their habitat selection and/or changes in the energetic linkages between adjacent habitats (e.g., benthic and pelagic habitats, Rooney et al., 2006). Depth distributions have also been used to demonstrate the degree of spatial overlap (and therefore identify potential resource competition) between fish

species (Madenjian & Bunnell, 2008). These examples illustrate that understanding changes in habitat usage may provide important insights into the ecological function and stability of fish stocks of significant economic or intrinsic importance.

Substantial changes in the ecology of lake whitefish (*Coregonus clupeaformis*) from the Great Lakes have been observed since the late 1990s. Declines in growth rate and condition have been observed in populations from all the Great Lakes, including lake Ontario (Hoyle et al., 2008), Erie (Lumb & Johnson, 2012), Huron (Gobin et al., 2015; Rennie et al., 2009a), Michigan (DeBruyne et al., 2008; Pothoven et al., 2001) and Superior (Rennie, 2013). With only a few notable exceptions (Rennie, 2013; Fera et al., 2015), the most dramatic declines appear to have occurred among populations where dreissenids have established or where deepwater *Diporeia* have declined, suggestive of a bottom-up negative influence on lake whitefish foraging efficiency that in turn has had a negative effect on individual growth efficiency (Rennie et al., 2012b) and growth rate.

A major information gap in our understanding of these changes in lake whitefish biology deals with potential changes in their spatial distribution, given the predicted shift in the concentration of production

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from offshore to nearshore environments due to dreissenid invasion (Hecky et al., 2004). Consequently, one might expect the distribution of fishes to reflect this spatial change in production, a pattern that was observed for lake whitefish in the inner basin of South Bay, Lake Huron (Rennie et al., 2009b). However, elsewhere in Lake Huron, contrasting anecdotal accounts indicated a movement of whitefish-targeted commercial fishing effort offshore into deeper waters, during the 1990s (Mohr et al., 2005). These accounts were subsequently supported by an analysis of depth-of-capture from the main basin of Lake Huron (Riley & Adams, 2010). Given the limited existing data on lake whitefish depth distribution in Lake Huron waters, and opposing trends reported in the scientific literature, a need for a more comprehensive evaluation of changes in the depth distribution among additional populations in the Great Lakes was identified.

The goal of the current study was to determine the extent to which lake whitefish have altered their depth distribution following the establishment of dreissenid mussels throughout the Great Lakes Basin. To accomplish this goal, we examined long-term records of fishery independent index netting surveys to determine whether the mean depth-of-capture (D_w) of lake whitefish has changed systematically over time, and whether observed changes were temporally consistent with dreissenid establishment and/or declines in *Diporeia* abundance. To ensure our results were not simply reflections of variation in survey methodology, we additionally sought to evaluate and account for the effect of survey design on D_w , and in doing so describe a novel method for detecting survey-based bias in D_w estimates.

Methods

Index survey data were gathered from a number of federal, state and provincial government agencies (Table 1). Two populations from western Lake Superior were included as a reference for D_w trends not under

the influence of dreissenids or major *Diporeia* declines (Table 1). Index survey data from all populations except Lake Ontario were based on gillnetting. For each sampling event in each survey, we estimated lake whitefish catch-per-unit-effort (CPUE). For gillnet surveys, CPUE was estimated as biomass (kg) of fish per kilometer of gillnet per day (standardized to a 24 hour period). Mesh sizes of gillnets employed varied among populations, but were consistent within populations over time. Changes in gillnet material over time were adjusted to reflect catch in monofilament nets using correction factors (Rennie et al., 2009a), where appropriate (Table 1). CPUE is used as a weighting function in this study, and we found that increasing multifilament to monofilament conversion factor values from the published value of 1.8 to as high as 2.8 had no effect on our weighted depth of capture estimates (Electronic Supplementary Material (ESM) Appendix S1). CPUE from Lake Ontario bottom trawl surveys were estimated as biomass (kg) of fish per minute of trawl tow time.

For each sampling event, an estimate of mean depth (e.g., [minimum depth – maximum depth] / 2, or, where reported, the mid-net depth of the set, expressed as D , in m) and lake whitefish CPUE (see above) was available.

Annual means of lake whitefish D_w (m) were estimated as the within-year mean D weighted by CPUE estimates using the following equation (e.g., Madenjian & Bunnell, 2008; O’Gorman et al., 2000; Riley & Adams, 2010):

$$D_w = \frac{\sum_i C_i D_i}{\sum_i C_i} \quad (1)$$

where D_w is the weighted mean depth of capture for lake whitefish in each year, C_i is the CPUE estimate corresponding to sampling event i

Table 1
Data sources for lake whitefish depth of capture (D_w) and catch-per-unit-effort (CPUE) estimates.

Population	Abbreviation ^b	Years sampled	Depth range included (m)	Dreissenid establishment ^c	<i>Diporeia</i> collapse ^c	Agency ^d	Survey period	Survey method
<i>Lake Superior</i>								
Apostle Islands	WI-1 _{sp}	1987–2013	16–49	n/a	n/a	WiDNR	April–May	Gillnet
	WI-1 _{sum} ^a	1970–2013	5–103	n/a	n/a	WiDNR	July–August	Gillnet
	WI-2 _{sp}	1981–2013	23–49	n/a	n/a	WiDNR	April–May	Gillnet
	WI-2 _{sum} ^a	1970–1995, 1997–2012	8–129	n/a	n/a	WiDNR	July–August	Gillnet
<i>Lake Michigan</i>								
WFM-05	WFM-05	1980–1990; 1997, 1999–2001; 2003–2005	1–88	1993 ⁽ⁱ⁾	1998–2000 ⁽ⁱⁱ⁾	MDNR	May–June	Gillnet
WFM-06	WFM-06	1980–1990; 1997–2005	3–85	1993 ⁽ⁱ⁾	1998–2000 ⁽ⁱⁱ⁾	MDNR	April–June	Gillnet
WFM-07	WFM-07	1980–1990; 1997–2005	4–53	1993 ⁽ⁱ⁾	1998–2000 ⁽ⁱⁱ⁾	MDNR	April–June	Gillnet
WFM-08	WFM-08	1980–82; 1986–88; 1997–2005	11–51	1993 ⁽ⁱ⁾	1998–2000 ⁽ⁱⁱ⁾	MDNR	April–May	Gillnet
<i>Lake Huron</i>								
South Bay (Inner Basin) ^a	SB	1951, 1953, 1954–55, 1959–67, 1969–84, 1986–92, 1997, 2001–08	4–59	1997 ⁽ⁱⁱⁱ⁾	1997 ⁽ⁱⁱⁱ⁾	OMNRF	Late August	Gillnet
Cape Rich, Georgian Bay ^a	CR	1979–2010	11–90	1996 ^(iv)	2000–2003 ^(v)	OMNRF	Early August	Gillnet
Southampton ^a	SH _{sum}	1981–2000, 2002–08, 2010	9–121	1991 ^(vi)	2003 ^(v)	OMNRF	June–July	Gillnet
	SH _{fall}	1982–2010	6–121				August–Sept	Gillnet
Grand Bend ^a	GB _{sp}	1985–1995, 1997–2000, 2002–10	5–88	1991 ^(vi)	2003 ^(v)	OMNRF	May–June	Gillnet
	GB _{fall}	1984, 1985–1995, 1997–2010	9–76				Sept–Oct	Gillnet
<i>Lake Erie</i>								
Eastern Basin	ER	1985–2009	12–44	1989 ^(vii)	1993 ^(viii)	NYDEC	June–July	Gillnet
<i>Lake Ontario</i>								
US waters	ON _{sp}	1978–2011	7–175	1993 ^(ix)	1993–1995 ^(viii)	USGS	April–May	Trawl ^e
	ON _{sum}		5–219				June–July	
	ON _{fall}		5–175				August, Oct–Nov	

^a Catches corrected for changes in gillnet material (e.g., multifilament to monofilament), based on correction factors reported in Rennie et al. (2009a). See also “Supplementary Material”.

^b Subscripts denote season of survey in cases where multiple surveys exist for a single population: sp = spring, sum = summer.

^c Dreissenid establishment and *Diporeia* collapse based on the following references: ⁽ⁱ⁾Nalepa et al. (1998); ⁽ⁱⁱ⁾Nalepa et al. (2006); ⁽ⁱⁱⁱ⁾McNickle et al. (2006); ^(iv)Rennie et al. (2012b); ^(v)Nalepa et al. (2007); ^(vi)Nalepa et al. (1995); ^(vii)Nicholls and Hopkins (1993); ^(viii)Dermott and Kerec (1997); ^(ix)Mills et al. (1993).

^d Agency acronyms: WiDNR = Wisconsin Department of Natural Resources; MDNR = Michigan Department of Natural Resources; OMNRF = Ontario Ministry of Natural Resources and Forestry; NYDEC = New York Department of Environmental Conservation; USGS = United States Geological Survey.

^e Trawl method is parallel to shore at a target depth.

in a given year, and D_i is the mean depth of sampling event i in a given year.

Standard errors around weighted means (SEM_w) for each year were estimated according to equations presented in Gatz and Smith (1995):

$$SEM_w = \sqrt{\frac{n}{(n-1)(\sum C_i^2)} \left[\sum (C_i D_i - \bar{C} D_w)^2 - 2 D_w \sum (C_i - \bar{C})(C_i D_i - \bar{C} D_w) + D_w^2 \sum (C_i - \bar{C})^2 \right]} \quad (2)$$

where n is the sample size of sampling events in a given year, and \bar{C} is the mean CPUE of sampling events in a given year.

This estimation of standard errors for weighted means is reported to be similar to those estimated via bootstrapping (Gatz & Smith, 1995). Bootstrapping assumes an independence of observations, which may not be true of the error distribution around our weighted mean estimates; due to the nature of government fisheries survey designs, sampling sites are not necessarily randomly chosen, target a specific species (e.g., lake whitefish), or are only randomly assigned within specific depth strata. As such, we recognize the possibility that our error estimates may be more conservative than might be expected based on a random bootstrap of truly independent data.

Estimates of SEM_w were used in this study for (a) graphical display, and (b) as a way of determining cut-offs for excluding data from years that were heavily influenced by sampling design (e.g., bias in sampling depth allocation so as to cause a deviation from a known distribution typical of this species; see *Standardizing survey data*, below). We therefore recognize that our standardization procedure, based on SEM_w estimates derived in this fashion and applied to these specific survey data, may be more conservative (i.e., we may have excluded years with data that would have otherwise been included using a more liberal selection criteria), compared with error estimates from government surveys that employ fully random survey designs.

Lake whitefish are a coldwater species, and may alter their distribution with the season according to thermal stratification in lakes (but see Selgeby & Hoff, 1996). To attempt to control for seasonal variation in depth distribution, we divided our datasets into spring/early summer (April to June, where whitefish are less subject to stratification) and late summer/fall (summer being July to September, when stratification is developed and whitefish are thermally limited, and fall defined as September–October when thermal gradients break down and fish prepare to spawn).

Simulations: effects of variable fishing survey depths

An initial examination of data indicated that the mean fishing depth (D) and both the minimum and maximum fishing depth within a number of the surveys included in our study varied dramatically over time, and suggested a very strong correspondence between mean annual sampling depth and estimated annual D_w . The depth at which fish are captured in any survey is necessarily a function of what depths are actually sampled. For coldwater fish species, like lake whitefish, their distribution could extend beyond typical survey depths; Government fish community surveys are not typically conducted across the maximum range of depths encountered in the Great Lakes. Thus, year-to-year variability in the distribution of fishing effort across depths (which can be influenced by weather, vessel type, changes in maximum target depth of the survey, personnel changes, etc.) could generate variability in the mean D_w in any particular survey year. Because it was our goal to evaluate actual changes in the distribution of lake whitefish, we needed a means of disentangling the effects of annual variation in survey design from our estimates of fish depth distributions. To do this, we first demonstrated the effect of survey design on the estimated D_w by using computer simulations. These simulations examined a fishery that varies systematically in design, as applied to a hypothetical distribution of fish around a known (fixed) depth.

In our first simulation, data for an idealized lake whitefish population were generated from a normal distribution around a mean depth of 60 m (with 1 standard deviation = 15 m; Fig. 1; values arbitrarily chosen) from a water body of 244 m depth (e.g., Lake Ontario). The initial survey sampled depths between 5 m and 40 m at 5 m intervals. Every third iteration, we added another sampling site to the previous simulation that was 5 m greater than the maximum depth in the previous iteration (e.g., minimum depth fixed at 5 m, but maximum depth of survey increased from 40 m to 45 m, then to 50 m, then to 55 m, etc.). In our second simulation scenario, we increased both the maximum and minimum survey depth (60 m and 1 m initially, respectively), each by the number of the iteration in the simulation, and sampled the population at 5 m intervals between these two depths.

Standardizing survey data

Having demonstrated a strong and predictable effect of variation in survey design and effort across depth in the previous simulation exercise, we extended this approach to assist with data standardization on our own fishery independent survey data from among our survey sites. For all surveys conducted, we applied the actual annual sampling depths of fishing gear applied in government index survey data used here to simulated whitefish depth distributions that approximate actual reported distributions in the literature (see justification below for selection of depth distributions used in this data standardization exercise). Survey years where the 95% confidence intervals ($D_w \pm SEM_w * 1.96$) around the estimated mean D_w from this exercise did not include the “known” simulated depth distribution were identified as spurious (i.e., resulting from a change in survey design in that particular year) and were excluded from further analysis. Additionally, we excluded data from years where the sampled depths were grossly different from other survey years in a given population, even if the effect on mean depth of capture from the simulation exercise failed to indicate its removal (see Results). For sites with very sparse data (Lake Michigan), 2 to 3 adjacent years of distributional data were combined to provide sufficient sample sizes from across a reasonable range of samples (Table 2).

When evaluating data for standardization using the above exercise, we simulated lake whitefish distributions around a mean depth of 35 m (normally distributed with a coefficient of variation, or CV = 20%) based on previously published data (Riley & Adams, 2010; Selgeby & Hoff, 1996). More shallow mean depths were used in a minority of instances when a depth of 35 m would have rendered the number of years included in the simulations too few to analyze (Table 1 – 20% CV was applied in all cases). Results from these populations (Cape Rich, Southampton, Lake Erie) should therefore be interpreted with some caution, as the sampling design in these regions may not have been sufficient to capture whitefish at the deep end of their distribution in all years surveyed (as per Fig. 1a,b).

Statistical analysis

All analyses, including data simulations and figure generation, were carried out using the statistical program R (Development Core Team, 2013). After filtering data to include only those cases where sampling design (e.g., depths sampled) would not cause artifactual patterns in the data, we evaluated changes in mean depth of capture among dreissenid-invaded populations using mixed effects models (R package *lme4*). Within each population, we modeled individual depths of gear sets, weighted by CPUE, as a function of food web change (FWC, fixed effect) and year (nested random effect within FWC). Food web change was represented by either a two-level (e.g., before dreissenids, after dreissenid establishment) or a three-level (before dreissenids, after dreissenid establishment/pre-*Diporeia* collapse, post-dreissenid/post-*Diporeia* collapse) factor. Dates of dreissenid establishment and *Diporeia* declines are as reported from the literature (Table 1). We

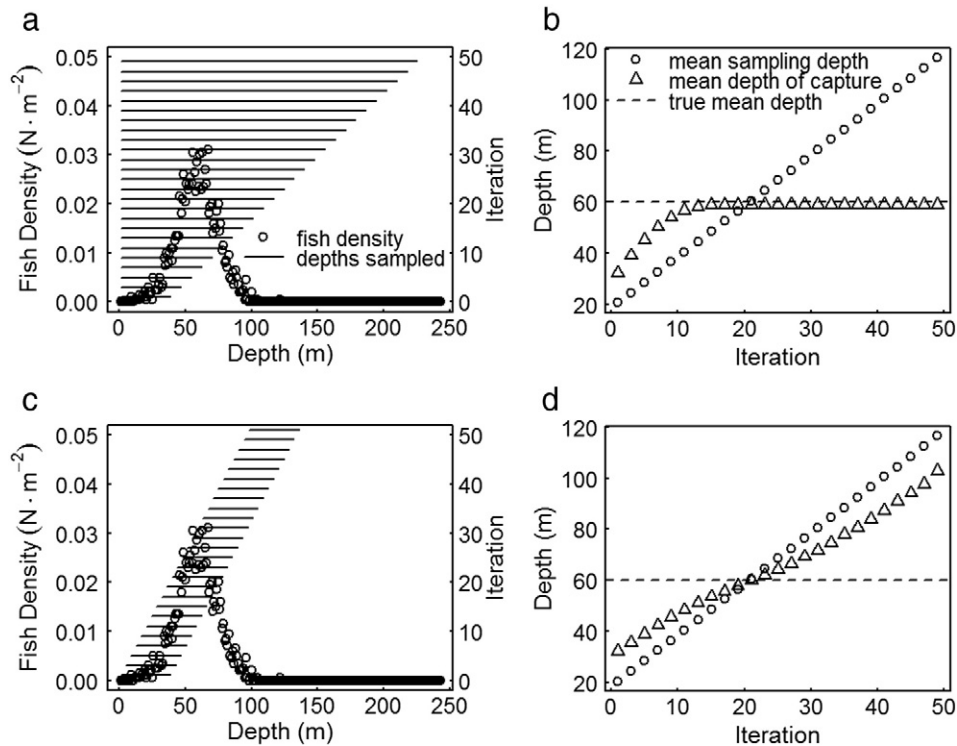


Fig. 1. Influence of sampling depth range on depth of capture (D_w) for a simulated fish distribution with an arbitrary mean depth of 60 m (standard deviation = 15 m). We explored two likely scenarios observed in fishing surveys, adding additional deeper samples (top two panels) and maintaining static effort but shifting the range of depths sampled (bottom two panels). Left panels (a,c) illustrate the simulated fish density (open circles) and the range of fishing depths employed (solid horizontal lines) while the right panels (b, d) illustrate the resulting estimated mean D_w (triangles), the mean sampling depth (circles) and the true mean depth of the simulated population (dashed line).

evaluated the significance of FWC by comparing nested models with and without the fixed FWC effect using log-likelihood tests, and report associated P -values and test statistics.

Where mixed-effects models were found to be non-significant, we evaluated linear trends in our dreissenid-established whitefish populations, using linear regression. Within each population, the depth of the gear set, weighted by CPUE, was modeled as a function of Year (considered here as a continuous variable). Where regressions were found to be significant, we included the variable describing FWC in our models. We then compared linear models as a function of Year, with and without the FWC variable using ANOVA tests, to determine if the FWC effect explained significant additional variance in D_w beyond simple linear trends.

In our reference sites (Lake Superior), we similarly examined the data for trends over time, using linear regression as described above. To determine whether the punctuated changes we observed in dreissenid-invaded populations could also be seen in our reference populations (suggesting the existence of a more global driver of the changes observed here not related to FWC), we included a “Before–After” categorical variable that corresponded with the mean dreissenid-establishment date from sites included here in lakes Michigan and Huron (1993). We then compared the linear models as a function of year, with and without the “Before–After” factor using an ANOVA test to determine whether it explained any more variation in our models beyond a simple linear trend in the data.

Mean annual D_w (Eq. (1)) were also examined for trends in time using a breakpoint regression approach (package *segmented*, Muggeo, 2003) in order to determine changes in depth distribution that did not necessarily coincide with years assigned to represent dreissenid establishment and/or *Diporeia* declines. In each case, the breakpoint model is tested for significance against a linear regression model using an ANOVA test. Breakpoint regression was applied to the estimated annual means (as opposed to analyzing individual data using the approach

described above) because the function we employed does not permit the use of a weighting function in the estimator.

To investigate general patterns among major Great Lakes regions (Lake Superior, Lake Michigan, Northeast Lake Huron, Main Basin Lake Huron, Lake Erie and Lake Ontario), we averaged the estimated mean annual D_w , treating data across all sites and seasons within a region and within a given year as a replicate value. These lake-wide annual D_w averages were investigated for patterns of dreissenid establishment using t -tests (with a Welch correction to degrees of freedom to account for heterogeneous variance) and linear regression. Lake Huron data were grouped into Main Basin (GB, SH) and Northeast (SB, CR) in order to reflect differential timing of dreissenid establishment between the two regions (Table 1).

Results

Simulation results: idealized population, sampling depths

Simulation results from our idealized population and sampling design revealed two important findings. First, that D_w can be sensitive to varying the extent of the sampling depth in the survey, but only if the minimum or maximum depth of the survey does not extend to the tail of the depth distribution of the organism under study (Fig. 1, a,b). This is illustrated in Fig. 1 (a, b) by holding the shallow extent of the survey constant, and varying the deeper extent of the survey. Once the sampling design encompasses the majority of the distribution of the organism, the estimated D_w converges with the known D_w of the simulated population. If the shallow extent of the survey becomes deeper over time such that it fails to capture the upper bound of the depth distribution, then D_w will be overestimated (Fig. 1, c,d); similarly, if the depth extent of the survey becomes too shallow, then D_w will be underestimated (Fig. 1, a,b). However, extending the survey beyond the distribution of the study organism does not affect D_w , providing

Table 2

Statistical results (linear or breakpoint regression, linear mixed effects models) evaluating temporal changes in lake whitefish depth of capture (D_w) with food web change (FWC). Negative slope coefficients indicate trends towards shallower D_w .

Population	Simulated mean depth	Years included ^a	Linear weighted (Lw) or breakpoint (Bp) regression slopes ^b	Model comparisons	Notes
<i>Lake Superior</i>	35 m				
WI-1 _{sp}		1987–2013	Lw: -0.6 m/yr, $F_{1,230} = 32.0, P < 0.0001$	ANOVA comparing linear model with and without “before–after 1993” factor, $F = 1.6, P = 0.2$	
WI-1 _{sum}		1981–2013 (odd years only)	Lw: $F_{1,177} = 1.1, P = 0.3$	ANOVA comparing linear model with and without “before–after 1993” factor, $F = 0.02, P = 0.9$	
WI-2 _{sp}		1981–2013	Lw: -0.13 m/yr, $F_{1,610} = 10.3, P = 0.001$; Bp = 1985 ± 0.5 yrs 81–85: -2.8 m/yr 85–2013: -0.13 m/yr $F = 26.5, P < 0.0001$	ANOVA comparing linear model with and without “before–after 1993” factor, $F = 0.7, P = 0.4$	
WI-2 _{sum}		1980–1994, 1998–2012 (even years only)	Lw: -0.3 m/yr, $F_{1,658} = 36.5, P < 0.0001$	ANOVA comparing linear model with and without “before–after 1993” factor, $F = 0.9, P = 0.3$.	
<i>Lake Michigan</i>	35 m				
WFM-05		(1980–81 ^c), (1982–83 ^c), 1984, (1985–86), (1987–88), (1989–90), (1999–2000), 2003, 2004, 2005	Lw: 0.6 m/yr, $F_{1,126} = 17.0, P < 0.0001$	$X^2 = 3.69, P = 0.055$; ANOVA comparing linear model with and without FWC factor, $F = 7.0, P = 0.009$	Greatest decline during 2004–05
WFM-06		(1980–82), (1987–89), (1997–99), (2000–01), 2002–2005		$X^2 = 11.27, P = 0.0008$; $^dX^2 = 11.31, P = 0.004$	16 m deeper after dreissenid establishment, <i>Diporeia</i> collapse
WFM-07		(1980–82), (1984–86), (1988–90), (1997–99), (2000–02), (2003–05)		$^dX^2 = 21.64, P < 0.0001$	Decline following <i>Diporeia</i> collapse
WFM-08		(1986–87), 1988, (2000–01), 2002–05	Lw: $F_{1,37} = 2.1, P = 0.15$	$^dX^2 = 3.07, P = 0.22$	Appears deeper 2003–05, after <i>Diporeia</i> collapse
<i>Lake Huron</i>					
SB	35 m	1951, 1954–55, 1963, 1965, 1969–74, 1976–1980, 1986–88, 1997, 2001–03, 2006–07	Bp = 1988 ± 9.3 yrs, 1951–88: 0.16 m/yr 1988–2007: -0.68 m/yr $F = 7.1, P = 0.004$	$X^2 = 14, P = 0.0002$	More shallow by 7 m after dreissenid establishment/ <i>Diporeia</i> collapse
CR	25 m	1979–81, 1983, 1985–90, 1993, 1997, 2000–01, 2004–05, 2007–10		$^dX^2 = 16.8, P = 0.0002$	More shallow (from 25 to 22 m) after dreissenids, but deeper (to 31 m) after <i>Diporeia</i> collapse
SH _{sum}	25 m	1981, 1984–88, 1990–93, 1995–2004, 2006–2010	Bp = 2007 ± 1.28 yrs, 1981–2007, 1 m/yr; 2007–10, -3.5 m/yr $F = 3.64, P = 0.046$	$X^2 = 15.0, P = 0.0001$; $^dX^2 = 22.4, P < 0.0001$	Deeper (from 17 to 26 m) after dreissenids, and deeper (to 34 m) after <i>Diporeia</i> collapse (but see breakpoint results)
SH _{fall}	30 m	1984–1988, 1994, 1997–2001, 2003, 2005–2009	Lw: 0.8 m/yr, $F_{1,209} = 52.5, P < 0.0001$	$^dX^2 = 4.34, P = 0.11$; ANOVA comparing linear model with and without FWC factor, $F = 17.4, P < 0.0001$	Deeper by 11 m after dreissenids, but 5 m shallower after <i>Diporeia</i> collapse
GB _{sp}	35 m	1987, 1997, 2000, 2002, 2005, 2008–10	Lw: 0.4 m/yr, $F_{1,135} = 4.9, P = 0.03$	$X^2 = 3.34, P = 0.19$; ANOVA comparing linear model with and without FWC factor, $F = 6.7, P = 0.01$	Deepest 2008–2010
GB _{fall}	35 m	1984, 1995, 1999–2001, 2003, 2006–10	Bp = 1999 ± 1.5 yrs, 1984–99, 0.9 m/yr 99–2010, -1.5 m/yr $F = 7.26, P = 0.03$	$X^2 = 5.69, P = 0.017$; $^dX^2 = 11.1, P = 0.004$	Deeper (from 25 to 36 m) after dreissenids, and more shallow (to 32 m) after <i>Diporeia</i> collapse
<i>Lake Erie</i>	30 m				
ER		1985, 1987, 1991–1998, 2002–04, 2006, 2008–09	Lw: -0.19 m/yr, $F_{1,298} = 37.4, P < 0.0001$	$^dX^2 = 3.03, P = 0.22$; ANOVA comparing linear model with and without FWC factor, $F = 6.5, P = 0.002$	Deepest D_w in 1992 after dreissenids; more shallow after <i>Diporeia</i> collapse
<i>Lake Ontario</i>					
ON _{sp}	35 m	1978–94, 1996–2011	Bp = 1996 ± 1.26 yrs, 1999 ± 1.02 yrs, 1978–96, 0.7 m/yr; 1996–99, 23.8 m/yr 99–2011, -29.6 m/yr $F = 6.5, P = 0.002$	$X^2 = 9.3, P = 0.002$	Depth increased, 40 to 67 m on average (but see breakpoint results)
ON _{sum}		1978, 1981–94, 1996–2000, 2002–11	Bp = 1998 ± 1.9 yrs, 2002 ± 2 yrs, 1978–98, 1.8 m/yr; 1999–02, -7.2 m/yr; 2002–11, 7.2 m/yr $F = 2.8, P = 0.05$	$X^2 = 5.2, P = 0.02$	Depth increased, 33 to 44 m on average (but see breakpoint results)

Table 2 (continued)

Population	Simulated mean depth	Years included ^a	Linear weighted (Lw) or breakpoint (Bp) regression slopes ^b	Model comparisons	Notes
ON _{fall}		1980–88, 1990–91, 1993–97, 1999–2000, 2002, 2010	Bp = 1992 ± 1.2 yrs, 1997 ± 0.9 yrs 1980–92, 0.3 m/yr; 1992–97, 10.3 m/yr; 1997–2002, –13.7 m 7.2/yr F = 4.9, P = 0.042	$\chi^2 = 16.5$, $P < 0.0001$	Depth increased, 32 to 70 m on average (but see breakpoint results)

^a Brackets indicate years combined for analyses.

^b Bp indicates a breakpoint estimate from segmented regression models. F statistics and P values provided for breakpoint regressions are of an ANOVA comparison between the model with breakpoints vs. a linear regression with no breakpoints. Regression statistics as otherwise indicated.

^c Samples from shallow strata (0–15 m) were reduced by 75% by subsampling randomly to down-weight representation of shallow sites and permit inclusion in the analysis.

^d Indicates where FWC is a 3-level factor to indicate the following time periods: (i) no dreissenids; (ii) dreissenids present, *Diporeia* abundant; (iii) dreissenids present, *Diporeia* rare. Otherwise, FWC is a two level factor described by (i) no dreissenids, and (ii) dreissenids present.

that the extent of the survey encompasses the majority of the distribution of the organism under study.

Therefore, if the survey design can be structured such that the spatial coverage is relatively standardized and is likely to encompass the depth range of the distribution of the organism under study, then an accurate description of D_w should be achievable. Where this is not the case, understanding the relationship between

survey design and D_w can still provide some context for cautious interpretation.

General patterns among Great Lakes regions

In our study, Lake Superior represents the reference state for our estimates of D_w (e.g., patterns expected in the absence of influence

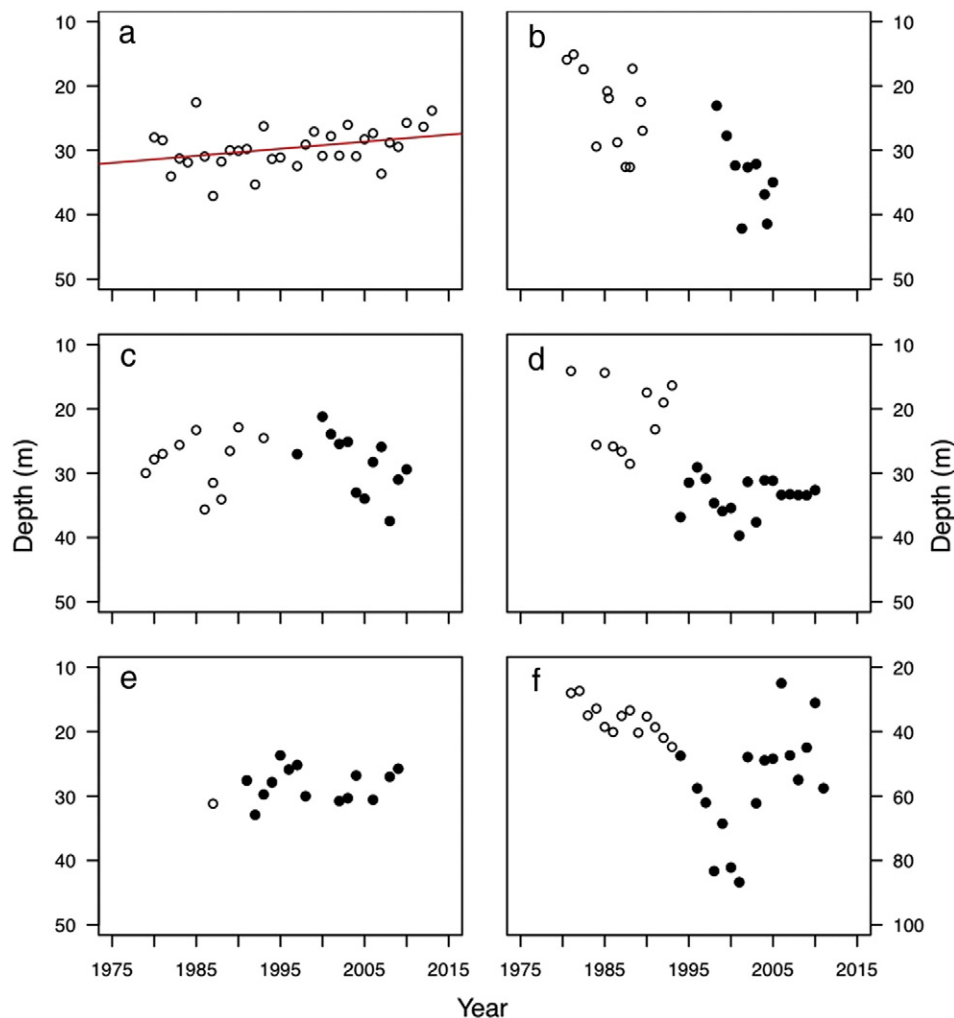


Fig. 2. Trends in lake whitefish depth of capture (D_w), averaged across all sites and time periods within a particular Great Lakes region. Panel (a), Lake Superior (reference sites); (b), Lake Michigan; (c), northeastern Lake Huron; (d), main basin Lake Huron; (e), Lake Erie, and (f), Lake Ontario. Open symbols indicate years pre-dreissenid establishment, closed symbols are post-dreissenid establishment.

from either widespread dreissenid establishment or *Diporeia* collapse). Combining data from all survey regions over all time periods, lake whitefish D_w tended to be found at more shallow depths over time (Fig. 2a), though the effect was marginal ($F_{1,30} = 4.03$, $P = 0.0537$).

Patterns from other Great Lakes regions were different than those observed in Lake Superior (Fig. 2, b–f). In both Lake Michigan and the main basin of Lake Huron, mean lake whitefish D_w became deeper by approximately 10 m on average following dreissenid establishment (Lake Michigan, t -test, $t_{28.3} = 4.38$, $P = 0.0001$; main basin Lake Huron, t -test, $t_{22.3} = 5.33$, $P < 0.0001$). Among northeastern Lake Huron sites, no significant change was observed (Fig. 2c). In contrast to lakes Michigan and Huron, Lake Erie mean D_w was significantly more shallow after dreissenid establishment by approximately 4 m on average (one-sample t -test, $t_{22.3} = 4.3$, $P = 0.0008$). There was no significant linear change in Lake Erie D_w over time ($P > 0.05$). In Lake Ontario, mean lake whitefish D_w became deeper by twice the change observed in either lakes Michigan or Huron (21 m; t -test, $t_{44.6} = 5.27$, $P < 0.0001$). Breakpoint regression revealed a slightly more complicated pattern in Lake Ontario, with D_w becoming increasingly deep around 1994 (± 1.7 years), then becoming more shallow from 1998 (± 1.2 years) to present (ANOVA, $F = 9.7$, $P < 0.0001$).

Reference populations: Lake Superior, spring and summer surveys

Lake whitefish D_w became increasingly shallow in three of four surveys we examined from the Apostle Islands region of Lake Superior. Further, we found no evidence of a significant change in distributions before or after 1993; in no cases did linear models with a “Before–After 1993” variable explain any significant component of variance over a linear model with only year included as an independent variable (Table 2). Visual inspection of the data further confirmed the absence of any punctuated changes in depth distributions corresponding with this time period (Fig. 3a,b, Fig. 4a,b).

Both spring surveys in Lake Superior indicated that lake whitefish have occupied increasingly shallow depths since the mid-1980s (Fig. 3a,b). In WI-2_{sp}, the depth distribution became more shallow during the early 1980s, but the slope of the relationship was less steep following that period (Table 2). Lake whitefish D_w was more shallow by 17.2 m (WI-2_{sp}) and 10.5 m (WI-1_{sp}) on average by 2013 compared with the beginning of the temporal record analyzed. No years were rejected for analysis based on simulations from either spring survey (Tables 1 and 2).

During summer surveys, only one location in Lake Superior demonstrated a significant change in D_w with time (WI-2_{sum}; Fig. 4b). Similar to the two spring surveys, lake whitefish D_w at this location was more shallow by 9.6 m on average between the earliest and latest reported survey dates. Surveys conducted between 1970–1979 underestimated mean depth of capture from the simulated population and were excluded; additionally, odd sample years between 1980–2000 in WI-2_{sum} were excluded due to a lack of sufficient sampling effort across depths (range 27–37 m in odd sample years vs. 5–120 m in even sample years), and were removed from the analysis (Tables 1, 2).

Dreissenid-invaded populations: spring and early summer surveys

In contrast to reference sites, lake whitefish D_w during spring among locations with dreissenids tended to move deeper over time, and changed in a punctuated fashion that was typically consistent with FWC representing either local dreissenid establishment or *Diporeia* collapse (Fig. 3, Table 2). In Lake Michigan, surveys of lake whitefish from more northern sites (WFM-05, WFM-06 and WFM-07) demonstrated significantly deeper D_w whereas the southernmost location (WFM-08) did not (Table 2). Plots of the data suggest a similar trend among Lake Michigan populations; the deepest D_w observed over the time series for WFM-08 was greatest following *Diporeia* collapse (Fig. 3). The lack of statistical significance for trends in WFM-08 are

likely due to what appears to be a 3 to 5 year delay in the shift of D_w to deeper depths following dreissenid establishment/*Diporeia* collapse (Fig. 3). Where a significant linear trend towards greater depths was detected (WFM-05), the effects of FWC explained a significant additional amount of variance in D_w (Table 2). Data from Lake Michigan populations were not available after 2005.

Distribution of lake whitefish in Lake Huron during spring/early summer surveys also tended to be found deeper after dreissenid establishment/*Diporeia* collapse. In Grand Bend (GB_{sp}), the deepest observed D_w of lake whitefish during the spring was observed five or more years following *Diporeia* collapse (Fig. 3g). Though FWC was not a significant variable in our mixed effects model for the Grand Bend population during spring, a significant effect of FWC was revealed after taking into account the linear trend towards greater depths between 1997 and 2010 (Table 2).

Patterns in Lake Ontario (ON_{sp}) were partially consistent with those observed in lakes Michigan and Huron. In Lake Ontario, lake whitefish D_w became deeper in the years following *Diporeia* collapse, but then became shallower about a decade later (Fig. 3h). Breakpoint analysis indicated significant breaks in the trend around 1996 and 1999, with depths becoming more shallow by 0.7 m per year between 1978–1996, going deeper by 24 m per year between 1996–1999 (following *Diporeia* collapse), and then becoming more shallow by 30 m per year between 1999 and 2011 (Table 2). Lake whitefish D_w for Lake Ontario was also notably more variable after 2005.

Dreissenid-invaded populations: late summer and fall surveys

Lake whitefish D_w during late summer and fall were also different than those observed in reference populations. Like spring surveys, changes appeared to be punctuated around dreissenid invasion and *Diporeia* collapse, though directionality was somewhat less consistent.

In South Bay (SB), lake whitefish D_w reversed in trend from approaching deeper depths prior to dreissenid establishment to more shallow distributions following dreissenid establishment, as revealed by breakpoint analysis (Fig. 4c, Table 2). Lake whitefish D_w was more shallow by 7 m on average in South Bay following dreissenid establishment and *Diporeia* collapse.

Cape Rich (CR) lake whitefish D_w was significantly more shallow following dreissenid establishment (by 3 m), but slightly deeper (by 6 m) after *Diporeia* collapsed. It is worth noting that the shallower D_w of Cape Rich lake whitefish was observed despite the survey including greater depths during this period (Fig. 4d), opposite of what would be expected if patterns were driven by changes in survey design (as per Fig. 1).

During summer surveys, mean D_w of lake whitefish in Southampton (SH_{sum}) was deeper by 9 m following dreissenid establishment, and a further 8 m on average following *Diporeia* collapse (Table 2, Fig. 4e). Similar to the Cape Rich survey, the decline in summer Southampton lake whitefish D_w preceded changes in survey design to include deeper depths by 7 years; this suggests that the observed shift in depth distribution during this period was independent of changes in survey design. Breakpoint regression analysis for this survey detected a slightly different trend, with a significant shift in Southampton lake whitefish D_w near 2007; D_w became deeper at a rate of 1 m per year between 1981–2007, and became more shallow by 3.5 m per year from 2007–2010. Models proposing 2 or 3 breakpoints did not explain any additional variance compared with the single breakpoint (at 2007) model. A significant linear trend towards greater depth was observed during the fall survey of Southampton (SH_{fall}, Table 2), and the inclusion of FWC as a variable explained significantly more variance in lake whitefish D_w compared with the linear trend alone.

At Grand Bend during the fall survey (GB_{fall}), lake whitefish D_w became significantly deeper following dreissenid establishment from 20 m to 36 m, but then became more shallow following *Diporeia* collapse, to 32 m on average (Fig. 4g). Breakpoint analysis confirmed

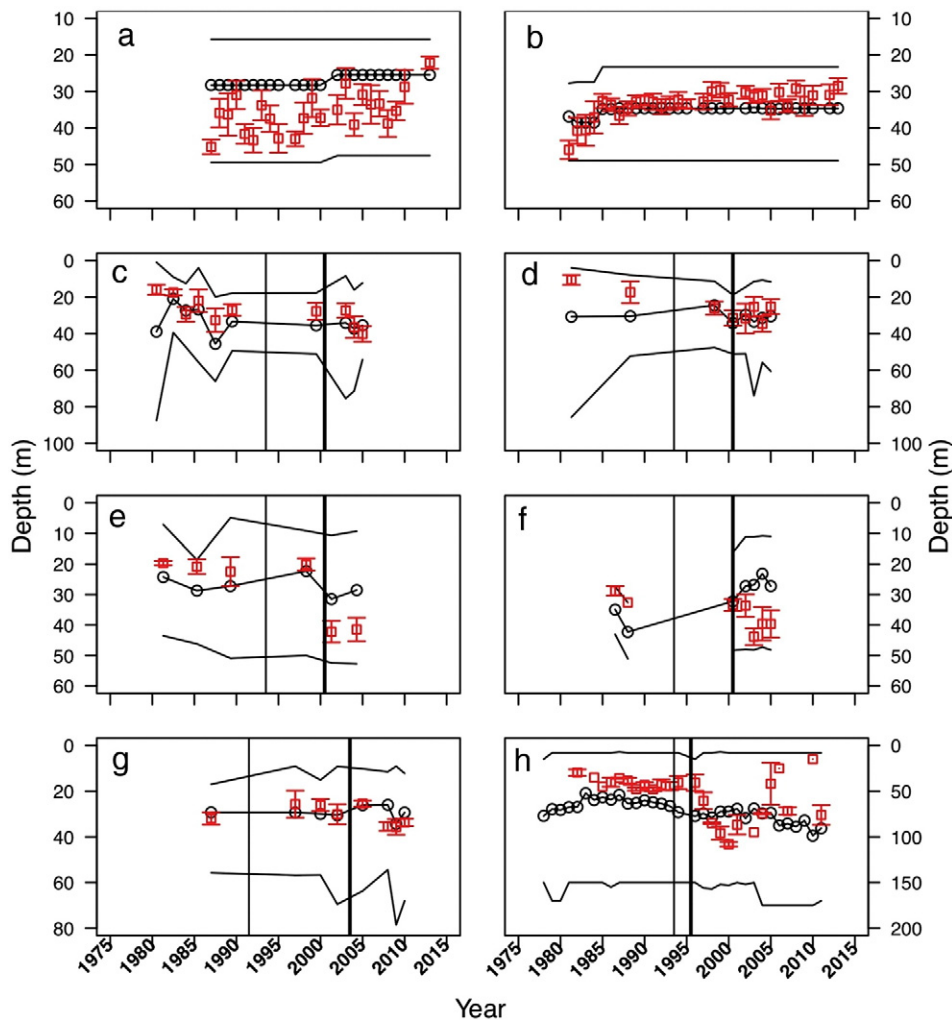


Fig. 3. Lake whitefish mean depth of capture (D_w , squares) and mean sampling depth (circles) among populations surveyed during the period between April and July. Only years of data that were not biased by sample design in a particular year are presented (see text). Upper and lower horizontal solid lines indicate the minimum and maximum sampling depth in a given survey year. Light vertical line indicates timing of dreissenid establishment; heavy vertical line indicates timing of *Diporeia* decline (see Table 1 for dates and abbreviations of populations where applicable, below). Lake Superior locations (reference sites) are WI-1_{sp} (a) and WI-2_{sp} (b) in the Apostle Islands; Lake Michigan sites are WFM-05 (c), WFM-06 (d), WFM-07 (e) and WFM-08 (f); Lake Huron sites are Grand Bend, GB_{sp} (g) and Lake Ontario is ON_{sp} (h).

this trend, and indicated that Grand Bend lake whitefish D_w shifted from increasingly deep to more shallow habitats after 1999 (Table 2).

In the eastern basin of Lake Erie (ER), dreissenid establishment was not a significant variable in our mixed effects statistical models, but, unlike the regression based on only mean annual D_w , the linear weighted regression revealed a significant linear trend towards shallow depths. The inclusion of a FWC variable explained significantly more variance in lake whitefish D_w than the linear trend alone (Table 2). Similar to South Bay, Lake Huron, the deepest observed D_w for Lake Erie lake whitefish were observed prior to *Diporeia* collapse, and the most shallow distributions observed following *Diporeia* collapse (Fig. 4h).

Late-season trends in Lake Ontario D_w were examined in both summer (ON_{sum}; June and July) and late summer/fall surveys (ON_{fall}, during the months of August, October and November combined). Data in this latter category were too sparse within any single month to permit estimation of D_w over enough years to evaluate trends, as were data with October and November surveys combined. Like the spring survey in Lake Ontario, depth distributions were significantly deeper following dreissenid establishment during summer and fall surveys (Table 2), but breakpoint analysis revealed a more detailed structure in temporal changes. During summer surveys, Lake Ontario whitefish D_w became deeper up to 1999, then more shallow to 2002, and then became deep again. During late summer/fall surveys in Lake Ontario, whitefish D_w

became gradually deeper to 1992, sharply deeper between 1992 and 1997, and then shallower thereafter to 2002 (the last year with useable data available from this survey).

Discussion

The survey information and simulation exercise presented here represent both a novel approach to evaluating survey-based bias in D_w estimates, as well as a comprehensive analysis of patterns of lake whitefish depth distribution across the Laurentian Great Lakes. Importantly, our study illustrates that in nearly all cases, the patterns of lake whitefish depth of capture (D_w) changed in a punctuated fashion about the same time as changes in the benthic invertebrate community (i.e., after dreissenids established and/or *Diporeia* declined). Further, temporal patterns in locations with dreissenids were very different from the gradual, increasingly more shallow distributions observed among Lake Superior locations where dreissenids are not widely established and *Diporeia* populations have not undergone the dramatic declines observed elsewhere (Scharold et al., 2004). Where linear trends were detected in populations experiencing dreissenid establishment, the inclusion of a FWC variable explained significant additional variance compared to the linear trend alone in every case. This sum of evidence strongly suggests a dramatic impact of changes in the benthic

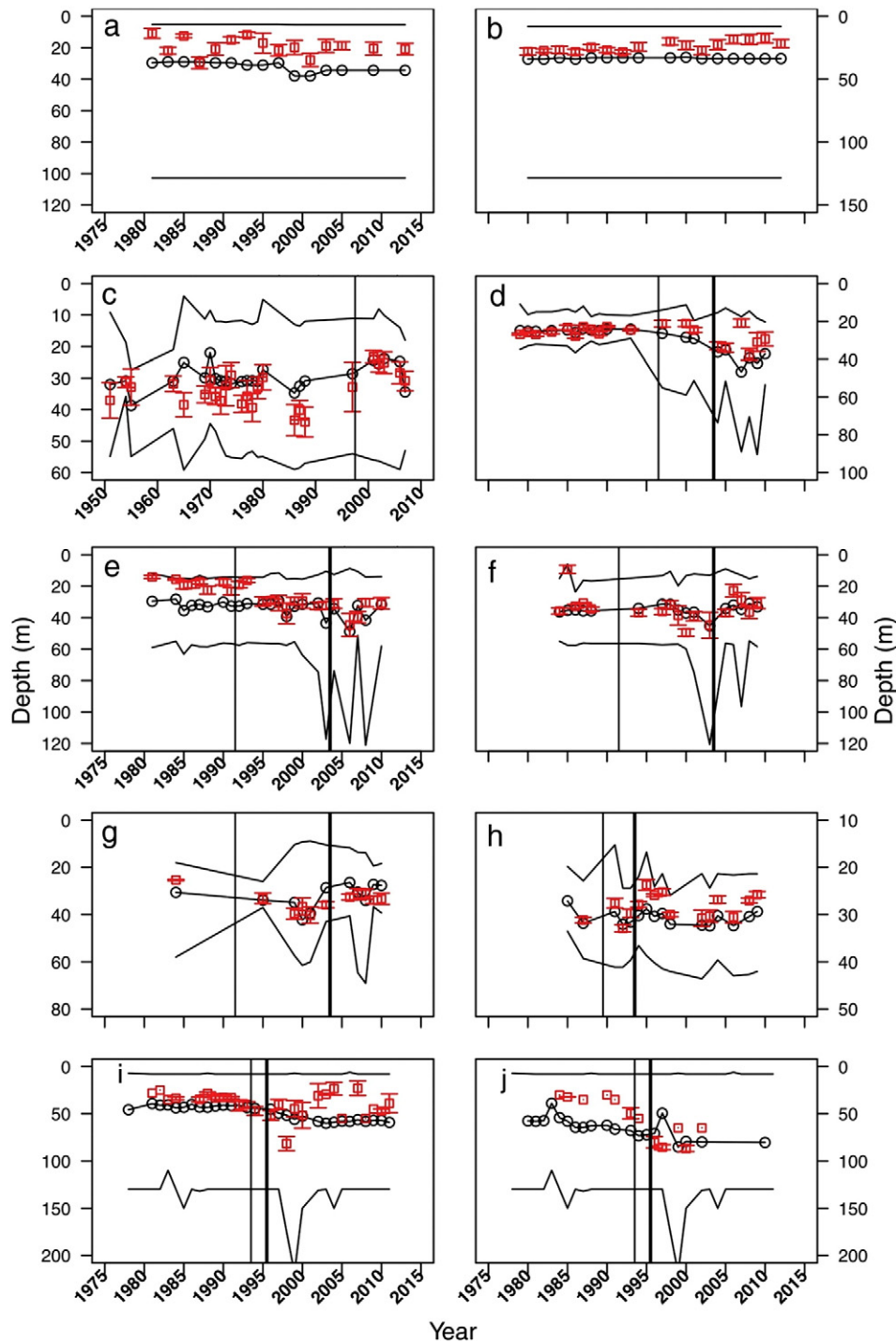


Fig. 4. Mean depth of capture (D_w , squares) and mean sampling depth (circles) among populations surveyed during the period between July and November. Only years of data which were not biased by sample design in a particular year are presented (see text). Symbols as in fig. 2; abbreviations and dates from Table 1. Lake Superior locations (reference sites) are WI-1_{sum} (a) and WI-2_{sum} (b); Lake Huron sites are South Bay, SB (c), Cape Rich, CR (d), Southamptn, SH_{sum} (e), and SH_{fall} (f), Grand Bend, GB_{fall} (g), Lake Erie is ER (h), and Lake Ontario is ON_{sum} (i), and ON_{fall} (j). Note change of scale in x-axis for panel c.

invertebrate community on Great Lakes lake whitefish depth distribution, and may help to explain significant changes observed in lake whitefish growth and condition reported elsewhere (Pothoven et al., 2001; Rennie, 2013; Fera et al., 2015).

The most common response observed in lake whitefish D_w was to seek deeper habitats following *Diporeia* collapse with no evident shift towards shallower distributions thereafter (WFM-05, 06, 07, 08, GB_{sp}, ON_{fall}). One population (CR) became slightly more shallow following dreissenid establishment, then went deeper following *Diporeia* collapse.

Only two groups of lake whitefish (SB and ER) showed evidence of shallower distributions soon after dreissenid establishment/*Diporeia* collapse. In other sites, we observed more shallow D_w only after a period of deeper distribution that was initiated immediately after dreissenid establishment/*Diporeia* collapse (GB_{fall}, SH_{sum}, SH_{fall}, ON_{sp}, ON_{sum}).

The reasons behind these different regional responses in lake whitefish D_w are not clear, but may relate to the availability of alternative prey. A number of studies have demonstrated that offshore benthic invertebrate abundance and biomass has declined significantly along

with the collapse of *Diporeia*, whereas abundance and biomass of benthic invertebrates in the nearshore have increased (McNickle et al., 2006; Ozersky et al., 2011; Rennie & Evans, 2012). Diets of lake whitefish also vary seasonally (Rennie et al., 2009b; Pothoven & Madenjian, 2013), and may influence D_w . Lake whitefish also appear to be capable of consuming dreissenids in great number (Madenjian et al., 2010; Pothoven & Nalepa, 2006; Rennie et al., 2012a,b), suggesting that the increase in nearshore benthic production due to dreissenids themselves can provide forage for lake whitefish. Additionally, larger individuals (>400 mm) of some Great Lakes populations of lake whitefish appear to have recently transitioned to a more piscivorous feeding mode (since 2006), with an emphasis on round goby (*Neogobius melanostomus*) as prey (He et al., 2015; Pothoven & Madenjian, 2013). In Southampton, round goby predation may have played a part in shifts to shallower regions since 2007, where 87% of the catch was greater than 400 mm (fork length). By comparison, in Grand Bend, only 14% of the catch was greater than 400 mm, suggesting round goby predation may be less important for shallower depth distributions in this part of the lake. In support of this observation, lake whitefish in Southern Lake Huron (which encompasses Grand Bend) fed on round gobies only during winter and spring months, but they were consumed spring through fall in the central part of the lake that encompasses Southampton sites (Pothoven & Madenjian, 2013). In Lake Ontario, round gobies appear to occupy primarily nearshore environments starting in May/June, but shift to greater (>70 m) depths in October (Weidel et al., 2013). Our surveys were conducted primarily within the window during the period where round gobies in this lake are more nearshore (Table 1). Round gobies were first detected in Lake Ontario trawl surveys in 2002 (Weidel et al., 2013), and lake whitefish depth distribution in our Lake Ontario surveys shifted to more shallow regions after 2000.

The pattern we observed of increasingly deep D_w for lake whitefish around the time of dreissenid establishment, followed by an increase in D_w occurring at or sometime after *Diporeia* collapse is consistent with patterns reported in another study of Lake Huron. Riley and Adams (2010) reported this same pattern (deeper following dreissenid establishment, more shallow around 2003) for a number of benthic species combined (deep benthic, shallow benthic) based on trawl surveys in Lake Huron. When considering lake whitefish alone, Riley and Adams (2010) reported a shift towards deeper depths of capture following dreissenid establishment, with no evidence of subsequent movement to shallower depths. Similarly, a number of our populations appear to occupy only deeper depths following dreissenid establishment/*Diporeia* collapse. However, in a number of cases (WFM-05, 06, 07, 08; ON_{fall}), the datasets that were available ended earlier than others considered in this analysis (2005 for Lake Michigan populations; in the case of ON_{fall}, too few whitefish were captured past 2002 to assess D_w).

Dense aggregations of quagga mussels further offshore in the Great Lakes (Mills et al., 1993; Nalepa et al., 2007, 2009) may further disrupt inshore-offshore coupling and prey availability, and may further alter lake whitefish resource availability and feeding strategies as reflected by habitat use in these systems. Deepwater or “profunda” morph quagga mussels have a more narrow shell morphology relative to their counterparts found in more shallow habitats (Nalepa et al., 2013); this narrow shell may make profunda morphs better suited to burrowing, but also potentially easier to crush and therefore more susceptible to whitefish predation. If so, it may explain the general pattern of deeper distributions of lake whitefish in the main basins of lakes Michigan, Huron and Ontario.

In the absence of dreissenids, our study suggests that lake whitefish D_w should remain stable or show evidence of a gradual (rather than punctuated) increase as a result of other regional drivers not explicitly considered here. While the magnitude of the shift to shallower depths over time is similar in South Bay, Lake Huron (7 m) to that of our reference populations (WI-1, WI-2), the pattern and timing of the shift (following dreissenid establishment) is unlike the pattern observed in

our reference populations. Additionally, stable isotope and diet data from the South Bay population provide independent evidence to support the hypothesis that lake whitefish in this location are indeed feeding at shallower depths (Rennie et al., 2009a). If D_w in the other dreissenid-invaded populations reported here reflect the actual distribution of lake whitefish in the water column, and this in turn reflects the depths at which they are feeding, then we would expect trends in stable isotope ratios of C and N to reflect those of D_w (e.g., more negative $\delta^{13}\text{C}$ and heavier $\delta^{15}\text{N}$, indicating shifts towards greater depths, and a reversal of this trend where more shallow D_w is observed). Stable isotope data are currently being analyzed from these populations in order to make this assessment. Indeed, comparing differences in feeding behavior and vital rates among lake whitefish populations with different responses to dreissenid establishment (deeper vs. more shallow) may prove instructive for understanding response strategies of this fish to major ecosystem-level change.

Climate change represents a significant potential driver of lake whitefish depth distributions across the entire Great Lakes region (Lynch et al., 2015; Kao et al., 2015; Rennie, 2013; Rennie et al., 2010). Potential changes in thermal stratification in the Great Lakes associated with climate warming in the region may be responsible for the patterns observed in our Lake Superior (reference) sites, where dreissenids are too limited in their distribution to have significant whole-lake effects. Thermocline depths in the Great Lakes (King et al., 1997; McCormick, 1990; Rennie et al., 2009b) and elsewhere (Keller, 2007; Keller et al., 2006; King et al., 1999; Snucins & Gunn, 2000) are typically reported to have become shallower with increasing air temperature. As thermoclines become more shallow, this permits occupancy of more shallow depths to stenothermic species like lake whitefish.

Though density-dependence may also potentially play a role in changing depth distributions of lake whitefish, it is not clearly manifest in the patterns in our data, nor clear what one might predict based on available evidence. In South Bay, Lake Huron, CPUE was at its highest during the 1960s and most recently during the 2000s (Rennie et al., 2009b). By contrast, D_w reported here was deeper during the 1960s, and more shallow only during the most recent period. In the Apostle Islands region of Lake Superior (our WI-2 sites), passive index netting methods went from a period of relative stability to a dramatic increase beginning around the early to mid-1990s (Seider & Schram, 2011). In contrast, our data from this site do not show a dramatic change in depth distribution during this time, but rather a gradual increase over the length of the entire data record with any major changes in D_w preceding this increase in reported density. Further, CPUE from an independent netting program based on active (trawl) sampling in the same region reported no similar change in CPUE (Fera et al., 2015). This difference in CPUE results between passive (Seider & Schram, 2011) vs. active (Fera et al., 2015) sampling methods may suggest potential changes in whitefish behavior influencing catch in passive gear, rather than changes in density *per se* (e.g., Rudstam et al., 1984). Further, there is no consistent pattern in depth of capture with density dependence among populations considered here. Where lake whitefish densities were reported to have increased in Lake Superior (Seider & Schram, 2011), we observed more shallow depths. Similarly, in Lake Huron (Gobin et al., 2015; Fera et al., 2015) and Lake Ontario (Hoyle et al., 2008), where reported densities declined, depth of capture also increased towards greater depths (with perhaps only recent shifts towards more shallow depths). By contrast, in Lake Michigan, where whitefish are reported to have increased in density (DeBruyne et al., 2008), we also observe whitefish at greater depths.

Basin morphology may also affect the response of lake whitefish to dreissenid establishment and *Diporeia* collapse. More shallow D_w appears to be associated with locations with relatively shallow mean depths (South Bay, 16 m, King et al., 1997; Lake Erie, 18 m, Rawson, 1952). This contrasts with the typically deeper lake whitefish D_w observed in the main basin of Lake Michigan, Huron and Ontario which have much greater mean depths (84, 59 and 86 respectively; Assel

et al., 2003; Rawson, 1952). Shallow lakes are more likely to have a greater proportion of benthic area available to respond to increased light penetration; as a result, they may experience a greater overall increase in nearshore benthic production relative to deeper lakes more typically dominated by offshore processes (Rennie, 2013). Other relatively shallow lakes that support both dreissenids and lake whitefish, like Lake Simcoe (mean depth = 14 m; Eimers et al., 2005) and Lake Champlain (mean depth = 19.5 m; Herbst et al., 2011) might therefore be predicted to demonstrate more shallow D_w after dreissenid establishment.

Our study adds to a number of investigations that document significant shifts in fish depth distributions with dreissenid establishment. Both shallow and deep benthic fishes in Lake Huron shifted towards greater depths in Lake Huron after zebra mussel establishment, but appeared to occupy shallower depths after the invasion of Quagga mussel (Riley & Adams, 2010). Declines in the depth distribution of pelagic species in Lake Huron were more closely associated with the establishment of *Bythotrephes longimanus* (Riley & Adams, 2010). In contrast, pelagic fish species in Lake Ontario (alewife, rainbow smelt, young lake trout) were shown to shift towards deeper water between 1991 and 1994 after dreissenid establishment (O'Gorman et al., 2000); these dates are consistent with those observed for lake whitefish in this study, which shifted to deeper habitats around 1995, but varied from between 1992 and 1998 depending on the season of sampling data used (Table 2). Deepwater sculpin (*Myoxocephalus thompsonii*) in Lake Michigan may have also shifted towards greater depths following the establishment of deepwater morph quagga mussels and *Diporeia* collapse during the late 1990s and early 2000s (Madenjian & Bunnell, 2008), though the opposite pattern was observed among Lake Huron deepwater sculpin (Riley & Adams, 2010). Consistencies in pattern and/or timing of shifts among many lakes and species warrant additional investigation to better appreciate how behavioral responses of fishes to ecosystem change have influenced the pathways of energy and nutrients through Great Lakes food webs.

Finally, we argue that it is highly unlikely that our data selection procedure has shaped our conclusions. Recall that years with data that were estimated to have fallen outside the 95% confidence interval of an idealized lake whitefish depth distribution were excluded. If our methods of error estimation were too conservative, we would expect to see no patterns with time due to the exclusion of years of data with extreme values. Despite this conservative approach and the exclusion of suspect years of data, we observed strong and consistent patterns (e.g., clear increases with time in 3 of 4 Lake Superior sites, clear change-points and shifts over time in the data of dreissenid-affected populations). Indeed, the inclusion of so many years of data across data sourced from a number of government agencies indicates that the survey designs in most years should be capable of detecting whitefish within their expected distributional ranges, based on historical values (Riley & Adams, 2010; Selgeby & Hoff, 1996).

Conclusion

In populations where dreissenids are absent, we observed either no shift in lake whitefish D_w with time or a very gradual change towards more shallow distributions. By contrast, in populations where dreissenids have invaded, we observed sudden changes in lake whitefish D_w coincident with benthic food web changes in these regions. Typically, lake whitefish D_w became deeper following dreissenid establishment; in a subset of locations, this was followed by a shift to more shallow distributions some time following the collapse of *Diporeia*. Variation in the response of lake whitefish D_w to changes in the benthic food web may be mediated by differences in access to deep-water refuge or alternative deep-water forage for lake whitefish within a particular region, or differences in basin bathymetry which may amplify the nearshore benthification of lakes with relatively shallow mean depths. Importantly, our analysis stresses the importance

of taking into account potential changes in sampling design over time, due either to directional shifts in depths sampled or year-to-year variation in sampling programs, when investigating distributional changes in fish habitat occupancy.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <http://dx.doi.org/10.1016/j.jglr.2015.09.014>.

References

- Assel, R.A., Cronk, K., Norton, D., 2003. Recent trends in Laurentian Great Lakes ice cover. *Clim. Chang.* 57, 185–204.
- 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.
- Eimers, M.C., Winter, J.G., Scheider, W.A., Watmough, S.A., Nicholls, K.H., 2005. Recent changes and patterns in the water chemistry of Lake Simcoe. *J. Great Lakes Res.* 31, 322–332.
- Fera, S.A., Rennie, M.D., Dunlop, E.S., 2015. Cross-basin analysis of long-term trends in the growth of lake whitefish in the Laurentian Great Lakes. *J. Great Lakes Res.* 41, 1138–1149.
- Gatz, D.F., Smith, L., 1995. The standard error of a weighted mean concentration. 1. Bootstrapping vs other methods. *Atmos. Environ.* 29, 1185–1193.
- Giacomini, H.C., Shuter, B.J., Lester, N.P., 2013. Predator bioenergetics and the prey size spectrum: do foraging costs determine fish production? *J. Theor. Biol.* 332, 249–260.
- Gobin, J., Lester, N., Fox, M., Cottrill, R.A., 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.
- He, J.X., et al., 2015. Coupling age-structured stock assessment and fish bioenergetics models: a system of time-varying models for quantifying piscivory patterns during the rapid trophic shift in the main basin of Lake Huron. *Can. J. Fish. Aquat. Sci.* 72, 7–23.
- Hecky, R., Smith, R., Barton, D., Guildford, S., Taylor, W., Charlton, M., 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.
- Herbst, S.J., Marsden, J.E., Smith, S.J., 2011. Lake whitefish in Lake Champlain after commercial fishery closure and ecosystem changes. *N. Am. J. Fish. Manag.* 31, 1106–1115.
- 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.
- Kao, Y., Madenjian, C.P., Bunnell, D.B., Lofgren, B.M., Perroud, M., 2015. Potential effects of climate change on the growth of fishes from different thermal guilds in Lakes Michigan and Huron. *J. Great Lakes Res.* 41, 423–435.
- Keller, W., 2007. Implications of climate warming for Boreal Shield lakes: a review and synthesis. *Environ. Rev.* 15, 99–112.
- Keller, W., Heneberry, J., Leduc, J., Gunn, J., Yan, N., 2006. Variations in epilimnion thickness in small Boreal Shield Lakes: relationships with transparency, weather and acidification. *Environ. Monit. Assess.* 115, 419–431.
- King, J.R., Shuter, B.J., Zimmerman, A.P., 1997. The response of the thermal stratification of South Bay (Lake Huron) to climatic variability. *Can. J. Fish. Aquat. Sci.* 54, 1873–1882.
- King, J.R., Shuter, B.J., Zimmerman, A.P., 1999. Signals of climate trends and extreme events in the thermal stratification pattern of multibasin Lake Opeongo. *Ontario. Can. J. Fish. Aquat. Sci.* 56, 847–852.
- Lumb, C.E., Johnson, T.B., 2012. Retrospective growth analysis of lake whitefish (*Coregonus clupeaformis*) in Lakes Erie and Ontario, 1954–2003. *Adv. Limnol.* 63, 429–454.

- Lynch, A.J., Taylor, W.W., Beard Jr., D.T., Lofgren, B.M., 2015. Climate change projections for lake whitefish (*Coregonus clupeaformis*) recruitment in the 1836 Treaty Waters of the Upper Great Lakes. *J. Great Lakes Res.* 41, 415–422.
- Madenjian, C.P., Bunnell, D.B., 2008. Depth distribution dynamics of the sculpin community in Lake Michigan. *Trans. Am. Fish. Soc.* 137, 1346–1357.
- Madenjian, C.P., et al., 2010. Dreissenid mussels are not a “dead end” in Great Lakes food webs. *J. Great Lakes Res.* 36, 73–77.
- McCormick, M.J., 1990. Potential changes in thermal structure and cycle of Lake Michigan due to global warming. *Trans. Am. Fish. Soc.* 119, 183–194.
- 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.
- Mills, E.L., Leach, J.H., Carlton, J.T., Secor, C.L., 1993. Exotic species in the Great Lakes – a history of biotic crises and anthropogenic introductions. *J. Great Lakes Res.* 19, 1–54.
- Mohr, L.C., Ebener, M.P., Nalepa, T.F., 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 Technical Report 66, pp. 105–126.
- Muggeo, V.M.R., 2003. Estimating regression models with unknown break-points. *Stat. Med.* 22, 3055–3071.
- Nalepa, T.F., et al., 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., Lang, G.A., 2009. 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., 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., 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., Pavlova, V., Wong, W.H., Jannsen, J., Houghton, J.S., Mabrey, K., 2013. Variation in the Quagga mussel (*Dreissena rostriformis bugensis*) with emphasis on the de-water morphotype in Lake Michigan. In: Nalepa, T.F., Schloesser, D.W. (Eds.), *Quagga and Zebra Mussels: Biology, Impacts and Control*, 2nd Edition CRC Press, Boca Raton, Florida, pp. 315–329.
- Nalepa, T.F., Wojcik, J.A., Fanslow, D.L., Lang, G.A., 1995. Initial colonization of the zebra mussel (*Dreissena polymorpha*) in Saginaw Bay, Lake Huron: population recruitment, density, and size structure. *J. Great Lakes Res.* 21, 417–434.
- Nicholls, K.H., Hopkins, G.J., 1993. Recent changes in Lake Erie (north shore) phytoplankton: cumulative impacts of phosphorus loading reductions and the zebra mussel introduction. *J. Great Lakes Res.* 19, 637–647.
- O’Gorman, R., et al., 2000. Shifts in depth distributions of alewives, rainbow smelt, and age-2 lake trout in southern Lake Ontario following establishment of dreissenids. *Trans. Am. Fish. Soc.* 129, 1096–1106.
- Ozersky, T., Barton, D.R., Evans, D.O., 2011. Fourteen years of dreissenid presence in the rocky littoral zone of a large lake: effects on macroinvertebrate abundance and diversity. *J. N. Am. Benthol. Soc.* 30, 913–922.
- 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.
- Development Core Team, R., 2013. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.
- Rawson, D.S., 1952. Mean depth and the fish production of large lakes. *Ecology* 33, 513–521.
- Rennie, M.D., 2013. Context-dependent changes in lake whitefish populations associated with dreissenid invasion. In: Nalepa, T.F., Schloesser, D.W. (Eds.), *Quagga and Zebra Mussels: Biology, Impacts and Control*, 2nd Edition CRC Press, Boca Raton, Florida, pp. 661–680.
- Rennie, M.D., Ebener, M.P., Wagner, T., 2012a. Can migration mitigate the effects of ecosystem change? Patterns of dispersal, energy acquisition and allocation in Great Lakes lake whitefish (*Coregonus clupeaformis*). *Adv. Limnol.* 63, 455–476.
- Rennie, M.D., Evans, D.O., 2012. Decadal changes in benthic invertebrate biomass and community structure in Lake Simcoe. *Freshw. Sci.* 31, 733–749.
- Rennie, M.D., Johnson, T.B., Sprules, W.G., 2012b. Energy acquisition and allocation patterns of lake whitefish (*Coregonus clupeaformis*) are modified when dreissenids are present. *Can. J. Fish. Aquat. Sci.* 69, 41–59.
- Rennie, M.D., Sprules, W.G., Johnson, T.B., 2009a. Factors affecting the growth and condition of lake whitefish (*Coregonus clupeaformis*). *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., Sprules, W.G., Vaillancourt, A., 2010. Changes in fish condition and mercury vary by region, not *Bythotrephes* invasion: a result of climate change? *Ecography* 33, 471–482.
- 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.
- Rogers, S.M., Gagnon, V., Bernatchez, L., 2002. Genetically based phenotype-environment association for swimming behavior in lake whitefish ecotypes (*Coregonus clupeaformis* Mitchill). *Evolution* 56, 2322–2329.
- Rooney, N., McCann, K., Gellner, G., Moore, J.C., 2006. Structural asymmetry and the stability of diverse food webs. *Nature* 442, 265–269.
- 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, 1251–1255.
- 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.
- Seider, M.J., Schram, S.T., 2011. Population Dynamics of Lake Whitefish in the Apostle Islands Region of Lake Superior. Wisconsin Department of Natural Resources Fisheries Management Report No. 154 20 pp.
- Selgeby, J.H., Hoff, M.H., 1996. Seasonal Bathymetric Distributions of 16 Fishes in Lake Superior, 1958–75. 7. U.S. Fish and Wildlife Service (14 pp.).
- Snucins, E., Gunn, J., 2000. Interannual variation in the thermal structure of clear and colored lakes. *Limnol. Oceanogr.* 45, 1639–1646.
- Vander Zanden, M.J., Casselman, J.M., Rasmussen, J.B., 1999. Stable isotope evidence for the food web consequences of species invasions in lakes. *Nature* 401, 464–467.
- Weidel, B.C., Walsh, M.G., Connerton, M.J., 2013. Benthic prey fish assessment. Lake Ontario (16–24 pp.).