

## Changes in fish condition and mercury vary by region, not *Bythotrephes* invasion: a result of climate change?

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We compared changes in body condition (relative weight) and mercury concentrations ([Hg]) in two species of coregonid fish (lake herring *Coregonus artedii*, lake whitefish *C. clupeaformis*) among discrete populations in Ontario between 1967 and 2006. Temporal comparisons among populations were made to determine whether 1) the establishment of *Bythotrephes longimanus* had affected coregonid populations, or 2) if changes in body condition or [Hg] were related to regional differences in the degree of climate change during the time period investigated. Climate data from northwestern, northeastern and southern Ontario showed a general warming trend in all regions over the period of study. However, greater temporal changes in climate were observed in the northwest where growing degree days  $>5^{\circ}\text{C}$  (GDD) increased and precipitation declined over the study period compared with relatively little change in southern or northeastern Ontario. Correspondingly, northwestern Ontario coregonid populations demonstrated significantly greater declines in body condition relative to those from northeastern or southern Ontario. Declines in [Hg] of both species were also greater among northwestern populations compared with those from northeastern or southern Ontario but only significantly so for lake herring. These declines were independent of the invasion of non-native *Bythotrephes*, and declines in [Hg] were opposite predictions based on the hypothesis that *Bythotrephes* invasion lengthened aquatic food chains. Based on our findings and further evidence from the literature, we propose that warming regional climates are capable of contributing to declines in both condition and [Hg] of fishes. Because fish condition affects both reproductive success and overwinter survival, observed condition declines of the magnitude reported here could have profound implications for the structure of future aquatic ecosystems in a warming climate.

The world's fisheries have undergone profound change during the past century. Commercial (Pauly et al. 1998, Myers and Worm 2003) and recreational (Post et al. 2002, 2008) fishing beyond sustainable levels have directly altered many aquatic ecosystems. Indirectly, humans can affect fisheries – and the ecosystems they occupy – through the transmission of non-indigenous species (Smith and Tibbles 1980), and by contributing to global warming. Despite the potential role these indirect factors can play in affecting fisheries and their sustainable management, their effects on aquatic communities remain poorly understood.

North American freshwater fisheries support a multi-billion dollar industry through commercial (Kinnunen 2003) and recreational (Post et al. 2002) activities, of which coregonids are a major component. Lake whitefish *Coregonus clupeaformis* are profundal and fished widely for commercial (Scott and Crossman 1998) and subsistence purposes (Hopper and Power 1991). Lake herring *Coregonus artedii* are common forage for other commercially and recreationally important fish species (Kaufman et al. 2006, Morbey et al. 2007). Recent declines in growth rate

and condition of Great Lakes lake whitefish have been widely documented (Pothoven et al. 2001, Lumb et al. 2007, Rennie et al. 2009a), as has lake herring recruitment failure (Bronte et al. 2003). Coincident with these changes are the successful colonization of *Bythotrephes longimanus* (Bronte et al. 2003), and in the lower Great Lakes, dreissenids (Pothoven et al. 2001), leading to concern regarding the impact of these invasive species on the growth, condition and recruitment of coregonid fishes (Fernandez et al. 2009, Rennie et al. 2009a).

Concern also exists regarding the potential role of these non-indigenous species on elevating fish contaminant burdens. The filtering capacity of dreissenids may cause them to accumulate greater contaminant burdens compared with native invertebrates, which could then cause higher contaminant concentrations in consumer species (MacIsaac 1996). *Bythotrephes* is an invertebrate predator whose establishment may act to lengthen aquatic food chains. Food chain length is positively correlated with contaminant burdens in fish (Vander Zanden and Rasmussen 1996). Though *Bythotrephes* have reduced native zooplankton

diversity and size distributions (Yan and Pawson 1997, Barbiero and Tuchman 2004), few studies have described their potential effects on fish consumers. Both lake herring and lake whitefish feed actively on *Bythotrephes*, sometimes making up nearly 100% of the stomach volume in individual fish (Barnhisel and Harvey 1995, Coulas et al. 1998, Rennie et al. 2009b).

Regional climate warming may have also contributed to observed changes in Great Lakes coregonids. Weather patterns resulting from warmer air temperatures in Ontario are associated with more shallow thermoclines (King et al. 1997, 1999), which provides increased cold-water habitat volume for coregonids (Magnuson et al. 1990, Rennie et al. 2009b) but reduced volume for pelagic production in the epilimnion. Lake productivity affects both the abundance and individual growth rates of coregonids (Gerdeaux and Perga 2006). Changes in fish body condition have also been linked to climate change elsewhere (Möllmann et al. 2005), possibly mediated through climate-induced changes in the lower food web. Climate change may also affect bioaccumulation of atmospherically dispersed contaminants like mercury (Schindler 1997). Generally, northern latitudes are responding more rapidly to climate change than regions closer to the equator (IPCC 2007). Ontario climate models predict differences in subclimates among northwestern, northeastern and southern Ontario in the next 100 yr (Colombo et al. 2007), which might be reflected in varying degrees of temporal change in fish populations between these regions.

We therefore sought to evaluate the role of both food web disruption (lengthening of food chains via invasion of *Bythotrephes*) versus regional geographic effects (each region potentially reflecting different degrees of climate change) on changes in Hg concentrations ([Hg]) and body condition in Ontario coregonid populations during the past ca 30 yr. Populations with and without *Bythotrephes* present were selected from and compared among northeast, northwest and southern Ontario. In each geographic region, 30-yr trends in environmental factors likely to be affected by climate change were described. Our working hypothesis based on the available published literature was that fish [Hg] should increase and condition decline after *Bythotrephes* invasion compared with reference populations, and that northern populations (reflecting a stronger response to warming climates than those in the south) would increase in [Hg] and decline in condition compared with southern populations (Schindler 1997).

## Materials and methods

### Selection of populations

Candidate study populations were selected from across Ontario by cross-referencing a database listing *Bythotrephes* occurrence (Ontario Federation of Anglers and Hunters Invasive Species Watch Program, <[www.invadingspecies.com](http://www.invadingspecies.com)>), with one describing [Hg] ( $\mu\text{g g}^{-1}$ ), total length (cm) and round weight (g) for individual lake whitefish and lake herring (Ontario Ministry of Environment Sport Fish Contaminant Monitoring Program, <[www.ene.gov.on.ca/envision/guide/](http://www.ene.gov.on.ca/envision/guide/)>). We identified populations that had been

sampled at least once for lake whitefish or lake herring [Hg] before *Bythotrephes* invaded, as well as reference populations with historic observations of fish [Hg] where *Bythotrephes* had not been detected. We chose 1997 as our cut-off for considering data “historic” in our reference lakes, as this represented the average year of *Bythotrephes* detection in our invaded populations (Table 1). Only reference populations relatively unaffected by human disturbance were included; two heavily contaminated lakes on the English-Wabigoon river system (Clay Lake, Ball Lake) were excluded on this basis (Rudd et al. 1983, Kinghorn et al. 2007).

Populations were subdivided into three geographic regions: northwest populations (west of 84° longitude and north of 46° latitude); northeast populations (east of 84° longitude and north of 46° latitude), and southern populations (south of 46° latitude and east of 84° longitude; Fig. 1). These regions generally correspond with previous studies describing distinct regions of differences in fish Hg (Somers and Jackson 1993) or of predicted climate change in Ontario (Magnuson et al. 1990, Colombo et al. 2007). All but a single population (Lake Simcoe) was located on the Canadian Shield (Fig. 1).

Populations with only historic [Hg] data were sampled at least once during 2004–2007 (Table 1). Fish were captured in experimental multi-mesh gill nets (stretched mesh length between 19 and 156 mm). Fish sacrificed for contaminant analysis were measured, weighed and sex was determined. Skinless, boneless fillets were removed from each fish, sealed in plastic and frozen for later analysis.

### Description of climate trends

To examine differences in climate change among these regions during the time period under study, we compared trends in annual averages of mean daily air temperature ( $^{\circ}\text{C}$ ), annual growing degree days  $>5^{\circ}\text{C}$  (GDD,  $^{\circ}\text{C d}$ ), and total annual precipitation (mm) from 1967 to 2006. All data were obtained online from Environment Canada weather stations surrounding populations in each region. Northwestern Ontario weather stations were located near Sault Ste. Marie (Whitefish Bay, Lake Superior), Cameron Falls (Lake Nipigon) and Kenora (Lake of the Woods). Northeastern Ontario weather stations were those located near Monetteville (Lake Temagami), Kirkland Lake (Lake Abitibi) and Chapleau (Lake Wakami). Southern Ontario weather stations were located near Meaford (Cape Rich, Georgian Bay), Orillia (Lake Simcoe), and Algonquin Provincial Park (Lake Opeongo).

### Determination of fish mercury

Mercury concentrations [Hg] for most tissue samples were determined at the Ontario Ministry of Environment (OMOE) laboratories using cold-vapour flameless atomic absorption spectroscopy. Details regarding OMOE methods and quality assurance/quality control are outlined in detail elsewhere (French et al. 2006, Choy et al. 2008, Goulet et al. 2008). Remaining samples were analyzed on a Milestone DM-80 direct mercury analyzer following EPA method 7473 SW-846. Between 0.1 and 0.2 g of thawed

Table 1. Populations included in the study.

Invaded/reference	Region	Population/lake	Location	Species analyzed	Year <i>Bythotrephes</i> reported
Invaded	S	Boshkung Lake <sup>A</sup>	45°04', 78°44'	LW	2003
	S	Drag Lake <sup>A</sup>	45°05', 78°24'	LH	2003
	S	Georgian Bay (Cape Rich) <sup>A</sup>	44°43', 80°37'	LW <sup>C</sup>	1984 <sup>1</sup>
	S	Gull Lake <sup>A</sup>	44°51', 78°47'	LH	2003
	S	Lake Huron (Grand Bend)	43°10', 82°10'	LW <sup>C</sup>	1984 <sup>1</sup>
	S	Lake Joseph <sup>A</sup>	45°10', 79°44'	LW <sup>C</sup> , LH	1989
	S	Lake Ontario (Bay of Quinte)	44°06', 76°54'	LW <sup>C</sup>	1985 <sup>2</sup>
	S	Lake Rosseau <sup>A</sup>	45°10', 79°35'	LH	1989
	S	Lake Simcoe <sup>A</sup>	44°20', 79°19'	LW <sup>C</sup> , LH	1993
	S	Round Lake <sup>A</sup>	45°38', 77°30'	LW	2004
	S	Stony Lake <sup>A</sup>	44°33', 78°06'	LH	2001
	S	Twelve Mile Lake <sup>A</sup>	45°01', 78°43'	LW, LH	2003
	S	Young Lake <sup>A</sup>	45°13', 79°33'	LH	2005
	NW	Lake Nipigon <sup>A</sup>	49°50', 88°30'	LW, LH	2001
	NW	Lake Superior (Black Bay)	48°40', 88°25'	LH	1987 <sup>3</sup>
	NW	Lake Superior (Michipicoten Island)	47°37', 85°22'	LH	1987 <sup>3</sup>
	NW	Lake Superior (Whitefish Bay) <sup>A</sup>	46°38', 84°39'	LW	1987 <sup>3</sup>
	NE	Lake Temagami <sup>A</sup>	47°00', 80°05'	LW, LH	1992
	NE	Red Cedar Lake <sup>A</sup>	46°45', 79°54'	LH	2004
	Reference	S	Chandos Lake <sup>A</sup>	44°48', 78°03'	LH
S		Farrell Lake <sup>A</sup>	44°46', 76°30'	LH	n/d
S		Gillies Lake <sup>A</sup>	45°12', 81°20'	LH	n/d
S		Lake Clear	45°26', 77°12'	LW	n/d
S		Opeongo Lake <sup>A</sup>	45°42', 78°23'	LW	n/d
S		Papineau Lake <sup>B</sup>	45°21', 77°49'	LH	n/d <sup>B</sup>
S		Smoke Lake <sup>A</sup>	45°31', 78°41'	LW	n/d
S		Trout Lake <sup>A</sup>	45°35', 80°10'	LH	n/d
NW		Abamasagi Lake	50°28', 87°15'	LW	n/r
NW		Big Trout Lake	53°43', 90°06'	LW	n/r
NW		Dogtooth Lake	49°43', 94°10'	LW	n/r
NW		Eagle Lake	49°42', 93°13'	LW	n/r
NW		Favel Lake	50°00', 94°00'	LW	n/r
NW		Hawley Lake	54°30', 84°39'	LW	n/r
NW		Kenogamisis Lake	49°42', 86°53'	LW	n/r
NW		Lake of the Woods (Whitefish Bay) <sup>A</sup>	49°24', 93°53'	LW	n/d
NW		Long Lake	49°30', 86°50'	LW	n/r
NW		Sandybeach Lake	49°49', 92°21'	LW	n/r
NW		Separation Lake	50°14', 94°24'	LW, LH	n/r
NW		Wabigoon Lake	49°44', 92°44'	LW	n/r
NE		Lake Abitibi	48°42', 79°45'	LW	n/r
NE		Larder Lake	48°05', 79°38'	LW	n/r
NE		Net Lake <sup>A</sup>	47°06', 79°46'	LH	n/d
NE	Opeepeesway Lake	47°37', 82°15'	LW	n/r	
NE	Round Lake	48°01', 80°02'	LH	n/r	
NE	Wakami Lake	47°29', 82°51'	LW	n/r	

Notes: table indicates lakes invaded by *Bythotrephes* or those non-invaded (reference). Year of *Bythotrephes* detection based on records from Ontario Federation of Anglers and Hunters unless otherwise noted; n/d = not detected, n/r = not reported, but assumed uninvaded based on distance from known source populations. LW = lake whitefish, LH = lake herring.

<sup>1</sup>(Bur et al. 1986), <sup>2</sup>(Lange and Cap 1986), <sup>3</sup>(Cullis and Johnson 1988).

<sup>A</sup>Lakes sampled during 2004–2007 to provide contemporary estimates of fish [Hg].

<sup>B</sup>*Bythotrephes* detected in 2006; not detected in 2003 or 2004; contemporary samples for Hg collected in 2000.

<sup>C</sup>Lake whitefish populations that also support invasive dreissenids.

fish muscle tissue (boneless, skinless) was weighed into nickel boats and loaded onto the analyzer. Mean estimates of NRC reference material DORM-2 ranged between 4.51 and 4.75  $\mu\text{g g}^{-1}$  in each of 11 runs conducted during the study (based on 2–5 determinations per run), and 4.66  $\mu\text{g g}^{-1}$  averaged over all runs, well within the 95% confidence limits reported by NRC ( $4.64 \pm 0.26 \mu\text{g g}^{-1}$ ). Duplicate samples of tissues were not significantly different (paired t-test,  $t_{40} = -1.16$ ,  $p_{\text{two-tailed}} = 0.25$ ), indicating good repeatability of results using this method. Subsets of tissues analyzed using both the DM-80 and OMOE methods were not statistically different (paired t-test,

$t_{45} = 0.7$ ,  $p_{\text{two-tailed}} = 0.49$ ), indicating good agreement between both methods.

### Estimation of condition

We used relative weight ( $W_r$ ; expressed as a percentage of standard weight) as a measure of fish condition. Standard weight was estimated using published equations for lake herring (Fisher and Fielder 1998) and lake whitefish (Rennie and Verdon 2008). Published standard weight equations for both species were generated using the

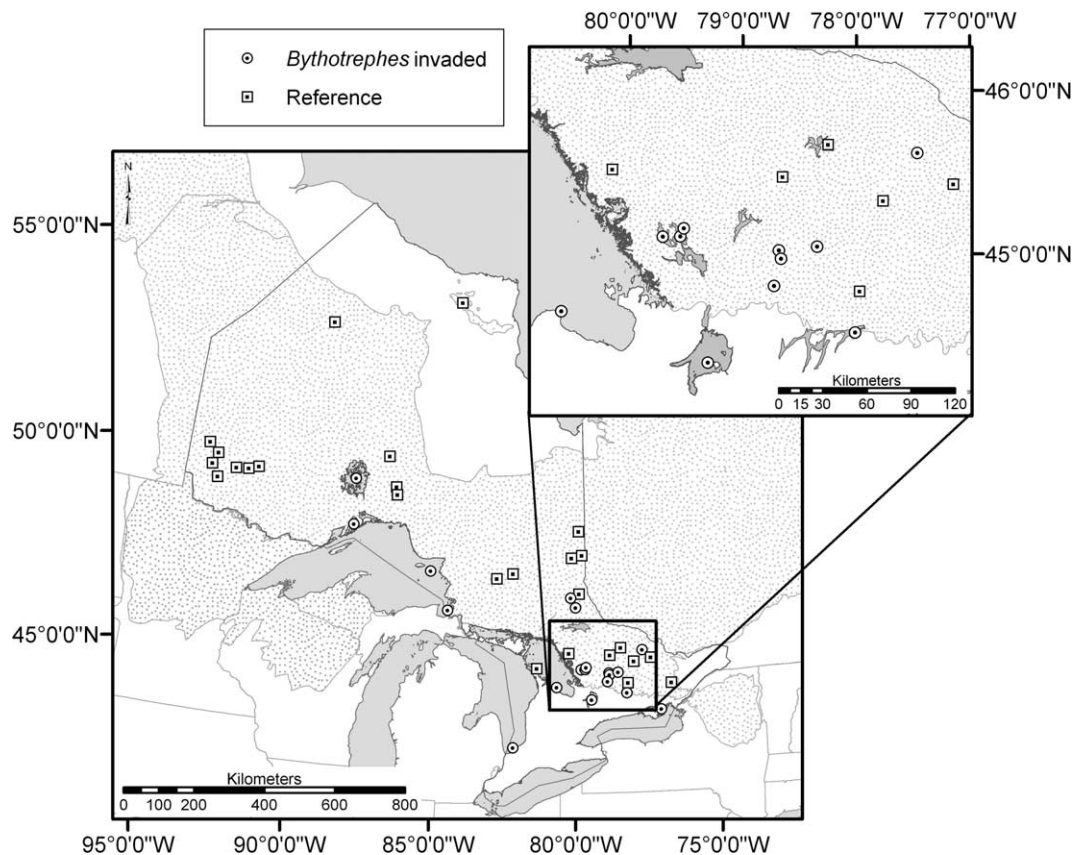


Figure 1. Spatial distribution of populations of lake herring *Coregonus artedii* and/or lake whitefish *Coregonus clupeaformis* included in the study. Shaded region indicates boundary of Canadian Shield.

regression length-percentile method (RLP, Wege and Anderson 1978). RLP- $W_r$  correlates significantly with other proximate measures of condition in lake whitefish (% lipid content, % dry mass, energy density) while removing potentially confounding length-related bias from estimates (Rennie and Verdon 2008).

### Statistical analysis

Response variables in our analyses were fish [Hg] ( $\mu\text{g g}^{-1}$  fresh weight,  $\log_{10}$  transformed), size (total length, cm) and condition ( $W_r$ , % of standard weight). Mean fish [Hg], size and condition of lake whitefish (LW) and lake herring (LH) were estimated for each population in both historic (pre-invasion) and contemporary (post-invasion) time periods (Supplementary material Appendix 1). Because fish [Hg] increases with body size (Somers and Jackson 1993), fish length was included as a response variable to compare with fish [Hg] patterns.

To evaluate the effect of *Bythotrephes* invasion on LW and LH, response variables were subjected to two-factor ANOVA, considering the effects of TIME (historic, contemporary), INVASION (invaded, reference) and the interaction between these factors. Due to unequal sample sizes among groups, we used “Type III” sums of squares (and appropriate contrast statements) in the car package for R (R Development Core Team 2006). To facilitate comparisons between historic and contemporary periods

within populations, differences between historic and contemporary mean response variables (contemporary minus historic) were estimated for each population; differences were then compared between invaded and reference populations using t-tests employing a Welch correction, allowing for heterogeneous variance among groups (Zar 1999).

Differences in the degree of climate change among regions (mean annual temperature, growing degree days and total annual precipitation) were compared using ANCOVA, with YEAR as a covariate, followed by contrasts of adjusted means where appropriate. Differences in slopes among regions indicated regional differences in response to climate change.

The effects of geographic location on LW and LH response variables were evaluated by replacing the factor INVASION in the previous two-factor ANOVA with LOCATION (northwest, northeast, south). The effects of region on contemporary – historic differences in response variable means were evaluated using single-factor ANOVA. Differences were  $\log_{10}(x+1)$  transformed where necessary to normalize residual distributions.

Fish size can influence the interpretation of patterns in fish [Hg]. Multivariate approaches have been suggested to better account for body size effects of fish [Hg] patterns (Somers and Jackson 1993). Applying these multivariate approaches to our data, correlations among mean fish [Hg] and body size were weak (Supplementary material Appendix 2). Furthermore, most of the variation in these analyses was

captured by statistics regarding fish [Hg] (Supplementary material Appendix 2), suggesting that fish size did not have an overwhelming influence on mean fish [Hg] in our data.

## Results

### *Bythotrephes* invasion

*Bythotrephes* invasion had no effect on LW and LH, as indicated by nonsignificant interactions among time and invasion for all response variables. Mean [Hg] was not different between historic and contemporary time periods for either LW or LH (Fig. 2a–b), and the general trend was a decrease in all populations, rather than the hypothesized increase in fish [Hg] in invaded populations relative to reference populations. Mean length in LW and LH populations was similar over time (Fig. 2c–d), though mean size was significantly and consistently greater in LW invaded populations compared to reference populations (ANOVA,  $F_{1,56} = 10.5$ ,  $p = 0.002$ ). Mean condition of both species declined over time in both reference and invaded populations (Fig. 2e–f), though only significantly so for LH (LH: ANOVA,  $F_{1,38} = 4.60$ ,  $p = 0.038$ ; LW: ANOVA,  $F_{1,56} = 3.45$ ,  $p = 0.069$ ). There were no

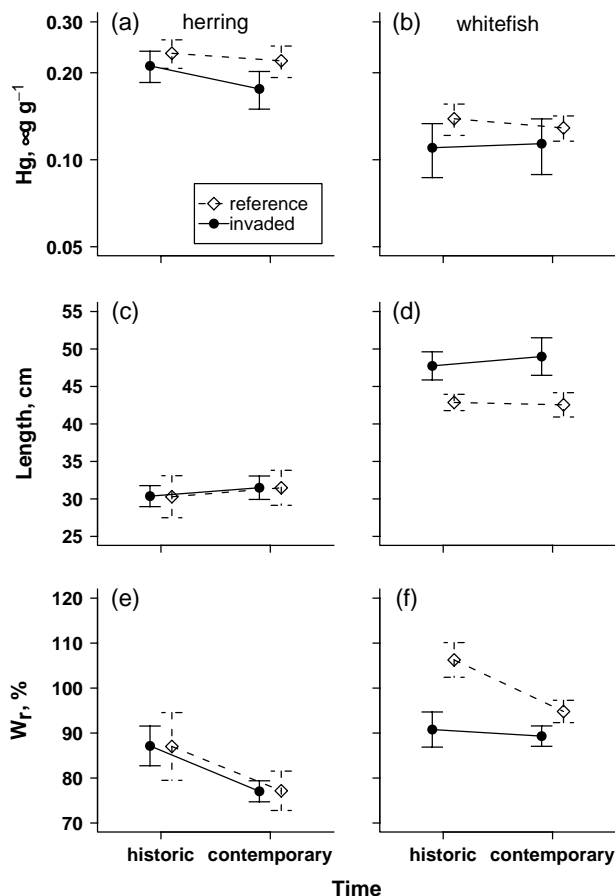


Figure 2. Mean mercury concentration ([Hg],  $\mu\text{g g}^{-1}$ ), total length (cm), and condition (relative weight,  $W_r$ , % of standard weight) over time among populations without (reference) and with (invaded) *Bythotrephes*. Left panels (a, c, e) are lake herring, right panels (b, d, f) are lake whitefish. Error bars are  $\pm 1$  standard error.

significant within-population differences over time for [Hg] ( $\Delta[\text{Hg}]$ ), size ( $\Delta\text{TL}$ ) or condition ( $\Delta W_r$ ) between reference and invaded populations for either species (t-tests, all  $p > 0.05$ ).

### Evaluating regional environmental change

Significant warming effects in all regions were detected (ANCOVA,  $F_{1,116} = 14.9$ ,  $p < 0.0001$ , Fig. 3a). The southern region was warmer than the northwest (planned contrasts,  $t = 19.2$ ,  $p < 0.0001$ ) as was the northwest compared with the northeast (planned contrasts,  $t = 13.8$ ,  $p < 0.0001$ ). The interaction between region and year for mean annual temperature was non-significant (test for heterogeneity of slopes,  $F_{2,114} = 0.082$ ,  $p = 0.9$ ). GDD did not significantly increase with time in southern Ontario (linear regression,  $F_{1,38} = 3.56$ ,  $p = 0.067$ ), but did increase in northwestern (linear regression,  $F_{1,38} = 15.63$ ,

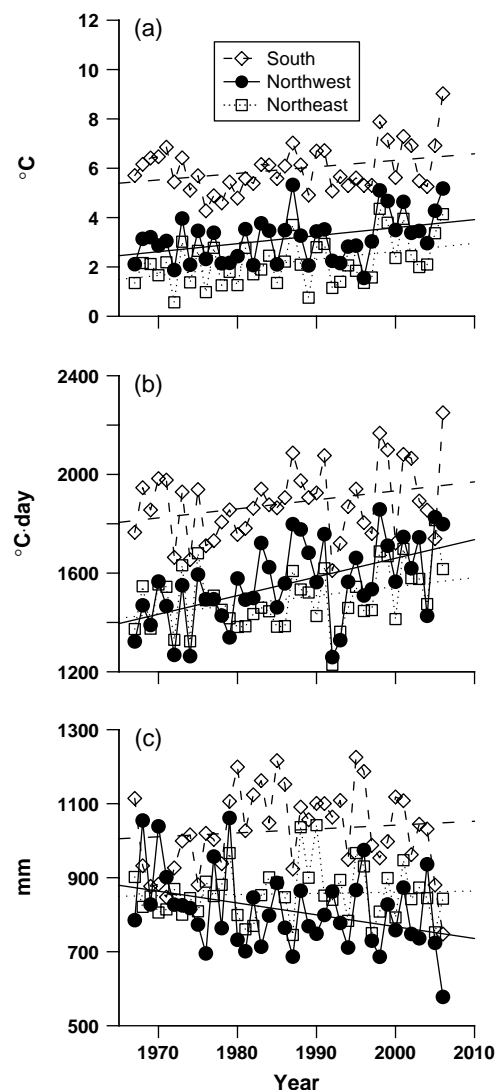


Figure 3. Patterns in mean annual temperature (a), growing degree days  $>5^\circ\text{C}$  (b) and precipitation (c) during the study period (1967–2006) in northwest, northeast and southern Ontario. Straight lines show trends over time; secondary lines join adjacent points.

$p = 0.0003$ ) and northeastern (linear regression,  $F_{1,38} = 5.22$ ,  $p = 0.028$ , Fig. 3b) Ontario during the study period. However, the interaction between region and year on GDD was non-significant (test for heterogeneity of slopes,  $F_{2,114} = 1.53$ ,  $p = 0.22$ ). There was a significant interaction between region and year in total annual precipitation (test for heterogeneity of slopes,  $F_{2,114} = 3.29$ ,  $p = 0.04$ , Fig. 3c). Annual precipitation declined significantly over the study period in northwestern Ontario (linear regression,  $F_{1,38} = 5.31$ ,  $p = 0.027$ ), but not in the south (linear regression,  $F_{1,38} = 0.47$ ,  $p = 0.5$ ) nor in the northeast (linear regression,  $F_{1,38} = 0.1$ ,  $p = 0.8$ ).

## Regional patterns

Though both species appeared to show [Hg] declines in northwest compared with northeastern or southern populations (Fig. 4a, b), the pattern was not statistically significant using 2-factor ANOVA. Body sizes of both species were not significantly different over time among regions (Fig. 4c–d), though southern LW populations tended to be larger-bodied than northeast populations (ANOVA,  $p = 0.09$ ). The interaction among region and time was very near significance for LH condition, (Fig. 4e; ANOVA,

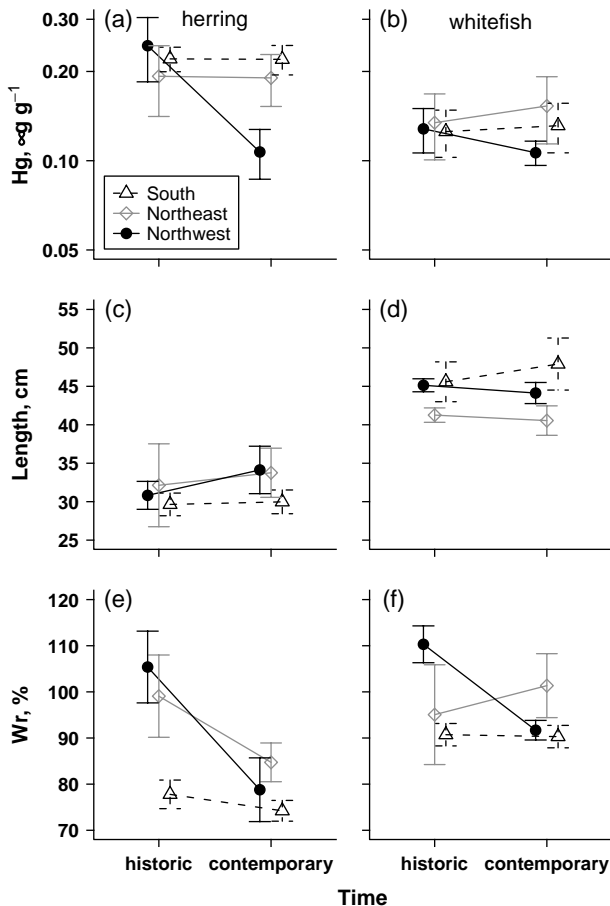


Figure 4. Temporal changes in mean [Hg], total length, and condition among regions in Ontario. Left panels (a, c, e) are lake herring, right panels (b, d, f) are lake whitefish. Error bars are  $\pm 1$  standard error.

$F_{2,36} = 3.25$ ,  $p = 0.050$ ), and significant for LW (Fig. 4f; ANOVA,  $F_{2,54} = 5.24$ ,  $p = 0.009$ ). Lake herring  $W_r$  from contemporary samples was lower in all regions (ANOVA,  $F_{1,36} = 13.01$ ,  $p = 0.0009$ ), and tended to be higher overall in northern populations (Fig. 4e; ANOVA,  $F_{2,36} = 9.59$ ,  $p = 0.0004$ ). Lake whitefish  $W_r$  declined in northwestern populations, and did not change significantly in north-eastern or southern regions (Fig. 4f).

Within-population changes among regions provided a somewhat clearer picture. Consistent with climate change hypotheses, lake herring  $\Delta$ [Hg] was significantly different among regions (ANOVA,  $F_{2,18} = 3.57$ ,  $p = 0.0496$ ); northwestern LH [Hg] declined by 47% on average, significantly more than southern lakes which were relatively unchanged (Fig. 5a; Tukey's HSD:  $p = 0.046$ ). The trend in lake whitefish  $\Delta$ [Hg] was similar but non-significant; mean LW [Hg] declined by 2% on average in northwestern populations, and increased very slightly in the other regions. (Fig. 5b;  $p > 0.05$ ). There were no significant regional differences for  $\Delta$ TL in either species (ANOVA,  $p > 0.05$ ). Also consistent with climate change hypotheses, significant regional differences of  $\Delta W_r$  were detected in both species (LH: ANOVA,  $F_{2,18} = 5.15$ ,  $p = 0.017$ ; LW: ANOVA,  $F_{2,27} = 9.20$ ,  $p = 0.0009$ ). There were regional declines in condition of LH and LW of 10 and 8% respectively across all populations. As with  $\Delta$ [Hg], condition for LH and LW declined significantly more in northwestern (25%, 19%) than in southern (5%, 0.5%) populations respectively (Fig. 5c–d; LH: Tukey's HSD,  $p = 0.016$ ; LW: Tukey's HSD,  $p = 0.0056$ ). Further, LW condition declines were greater in northwestern than in northeastern populations (Tukey's HSD,  $p = 0.0034$ ).

## Discussion

Regional differences in the degree of climate change better explained observed declines in coregonid condition and [Hg] than did food web disruption via *Bythotrephes* invasion. Mean condition of coregonids declined significantly during the study period, though the greatest declines were among northwest populations for both species. Declines in [Hg] were observed for both LW and LH populations in northwestern Ontario, but only significantly so for LH. Though climates appear to have warmed similarly among all three regions in Ontario based on trends in mean annual temperature, northwestern Ontario has shown a more rapid increase in GDD and a more dramatic reduction in precipitation compared with either northeast or southern regions. These changes are also consistent with predicted regional responses to climate warming during the next 100 yr (Colombo et al. 2007), which describes more dramatic change in northwestern Ontario, particularly with respect to precipitation, compared to northeast or southern regions of the province. As the patterns reported here between mercury and condition with change in climate are associative, it is difficult to assign causality. However, there is evidence from the literature (discussed below) that suggests climate might play a role in the declines of both fish condition and mercury.

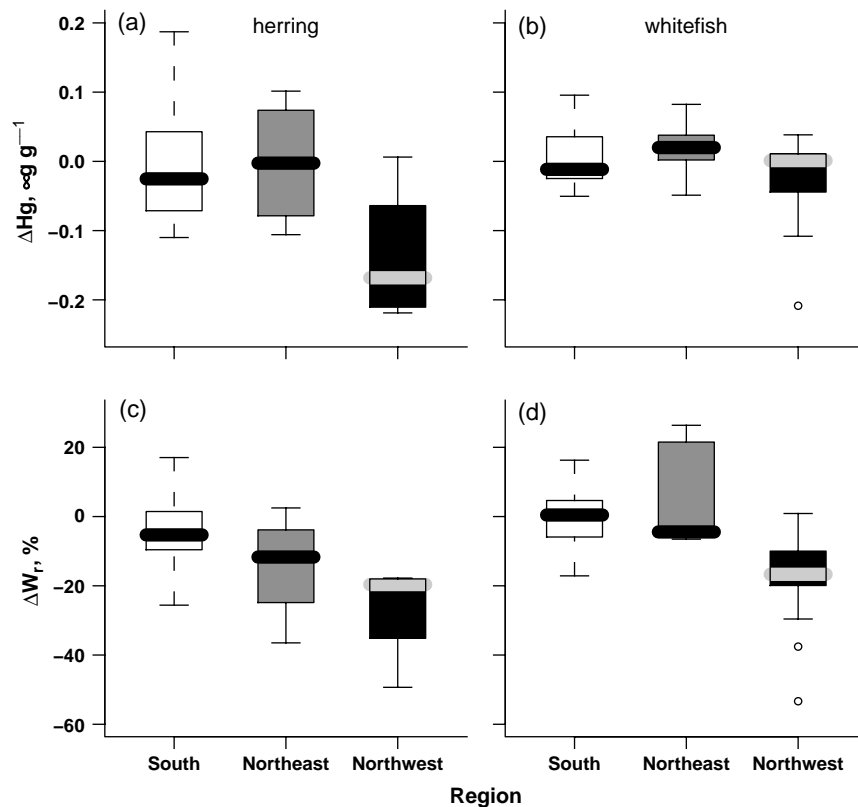


Figure 5. Boxplots of within-population differences in [Hg] and condition over time (contemporary minus historic). Comparisons are among regions. Left panels (a, c) are lake herring, right panels (b, d) are lake whitefish. Heavy bars are medians. Boxes are interquartile ranges, whiskers are 95% confidence intervals. Points falling outside the 95% confidence intervals are shown as circles.

### Potential role of climate in condition declines

Widespread and consistent declines in coregonid condition observed in this study are indicative of a broad-scale environmental impact such as climate change (Stenseth et al. 2002). We propose that condition declines in North American coregonids are likely a bottom-up process, stemming from higher regional temperatures which in turn have reduced whole-lake annual pelagic productivity. The thermocline depth (and epilimnetic volume) of oligotrophic Shield lakes is negatively correlated with mean temperature and GDD (King et al. 1999, Keller 2007, Rennie et al. 2009a, b). Stratification periods have also become significantly extended (Winder and Schindler 2004b, Jensen et al. 2007). Thus, a reduced volume during a longer stratified period may result in a reduction in primary productivity as regional climates warm. As a result, less energy would be delivered to either pelagic or profundal habitats during the stratified period under warmer conditions. While increased epilimnetic temperatures can increase photosynthetic rates, these increases would likely be negligible with respect to total productivity in the absence of increased nutrient inputs (Elliott et al. 2006, Staehr and Sand-Jensen 2006) relative to declines in epilimnetic volumes (Rennie et al. 2009a). Fish condition is known to decline with decreased lake productivity (Mills 1985, Milbrink et al. 2008) and prey availability (Liao et al. 1995, Rennie and Verdon 2008). Warming climates have also been demonstrated to disrupt synchrony of events around spring algal blooms, which can also negatively impact

upward rates of energy and nutrient transfer through food webs (Winder and Schindler 2004a).

While our study is the first to report broad-scale condition declines in North American freshwater fish populations, climate-related condition declines in anadromous and marine species have been observed in marine habitats. Declines in condition of Atlantic salmon *Salmo salar* have been related to climate-induced pelagic food web changes in the northeast Atlantic (Todd et al. 2008). Declines in condition of Baltic herring *Clupea harengus* have also been linked to climate-induced changes in the zooplankton community (Möllmann et al. 2003, Rasmussen et al. 2007). Warm El Niño years have also been associated with a 7.5% reduction in condition of *Sebastes mistinus* (Ventresca et al. 1995).

Condition is directly related to rates of energy acquisition and expenditure (Van Noordwijk and Dejong 1986, Reznick et al. 2000, Bajer and Hayward 2006). Broad-scale declines in fish condition could therefore portend additional changes in lentic cold water fish populations, including delayed spawning (Ali and Wootton 1999, Engelhard and Heino 2006), reduced fecundity (Henderson and Morgan 2002, Óskarsson et al. 2002), reduced survival (Sogard and Olla 2000, Pangle et al. 2004, Engelhard and Heino 2006) and increased susceptibility to predation (Mesa et al. 1994). Reductions in prey (i.e. lake herring) condition may also have further negative consequences on their predators (Davoren and Montevicchi 2003).

Condition may also decline with increasing population density, presumably through increased resource competition

(Aku and Tonn 1997, Casini et al. 2006). Evidence from a subset of our populations with catch data available suggests that this is an unlikely explanation for our results. Herring abundance throughout the Great Lakes and Lake Simcoe have declined, not increased during the past 20 yr (Supplementary material Appendix 3). Where lake whitefish CPUE data were available (Lumb et al. 2007, Rennie 2009), declines took place in six (Lake Ontario, Cape Rich, Lake of the Woods, Smoke Lake, Lake Nipigon, Lake Superior-Whitefish Bay) of the populations in this study and increased in only two (Lake Opeongo and Lake Simcoe). Further, while condition declines in lake whitefish on the Great Lakes appear to be associated with dreissenid-induced food web changes, specifically the loss of *Diporeia* (DeBruyne et al. 2008, Rennie and Verdon 2008), we do not believe that these changes have contributed significantly to the patterns observed in our study. Though the relative contributions of these factors to fish condition can be difficult to tease apart, recent work has suggested that population density, rather than the abundance of *Diporeia* plays a more important role in affecting condition, whereas *Diporeia* abundance more directly affects growth rates of lake whitefish (Rennie et al. 2009a). Of the lake whitefish populations included in this study that support dreissenids (Table 1), all occur in our southern region. However, lake whitefish condition declines were only significant in northwest populations in our study, where dreissenids are uncommon. The greater changes in precipitation and GDD associated with climate in the northwest relative to other regions in Ontario and the effects this will have on thermal structure and ecosystem productivity are a more likely explanation for declines in lake whitefish condition there.

### Potential role of climate in mercury declines

Reported declines in fish [Hg] from remote lakes has been attributed to reductions in sulfate deposition and associated changes in precipitation chemistry related to industrial emissions legislation passed in the United States and Canada in the 1970s (Drevnick et al. 2007). While reduced sulfate deposition provides an explanation for fish [Hg] declines on a broad geographic scale, it does not sufficiently explain the clear regional patterns we observed in our study. Sulfate deposition and lake sulfate concentrations in lakes in northwestern and southern Ontario have demonstrated similar patterns of decline since the 1980s (Jeffries et al. 2003). Thus, were sulfate deposition the driving force behind our patterns, we would have expected equivalent declines in fish [Hg] in both northern and southern regions. Instead, our study found fish [Hg] declines only in regions more affected by changes in climate. While all our inland study lakes save one are located on the Canadian Shield (Fig. 1), lakes in our northwest region sit on calcareous glacial till which has allowed many lakes in this region to maintain non-acidic pH in the face of acidic precipitation (Kettles et al. 1991). Correlations between fish [Hg] and lake acidity are well documented (Suns and Hitchin 1990, Hrabik and Watras 2002). The increased buffering capacity provided by calcareous soils surrounding the northwestern lakes should

have a stabilizing effect on fish [Hg] in the region. We observed temporal declines in northwestern Ontario fish [Hg] despite this stabilizing force.

Regional effects on temporal changes in fish [Hg] have also been reported in Wisconsin (Rasmussen et al. 2007), where [Hg] of walleye *Sander vitreus* declined at northern latitudes, but increased at southern latitudes. Our observations for lake herring, a common prey item for walleye (Kaufman et al. 2006) support this general trend; increases in lake herring and lake whitefish [Hg] were only ever observed at southern latitudes, whereas declines were the general pattern in northern latitudes (Supplementary material Appendix 1). A more recent study on Minnesota lakes reported declines in standardized fish [Hg] between 1982 and 1992 followed by a recent but relatively small increase (Monson 2009). However, the study reports trends in fish [Hg] over time from both “new and resampled sites”, and no indication is given to what extent the trend reported is consistent among lakes that have multiple temporal observations. As a result, it is difficult to determine to what extent their trend might be a function of fish [Hg] collected from novel populations in recent years vs actual trends observed from a group of the same populations sampled over time (as in our study).

Though climate warming has been proposed to increase fish Hg burdens (Schindler 1997), recent examples from populations not otherwise influenced by anthropogenic activity (e.g. flooding, industrial or mining point-source contamination) most frequently indicate no change or declines comparing contemporary samples to those collected in previous decades. Of the 16 studies we reviewed (collected from searches using ISI Web of Science), only one example of increased fish [Hg] was reported, as was one example of decline followed by a more recent but small increase in fish Hg (Table 2).

Climate warming may negatively affect fish [Hg] through the impacts associated with declining precipitation and associated reductions in the transport of both atmospheric and terrestrial products to lakes which impact directly Hg delivery and methylation rates. Precipitation is a major vector for the delivery of atmospheric [Hg] deposition, either directly or via runoff from soils and material from the landscape (Watras and Morrison 2008). While there is evidence of declining mercury and sulfate concentrations in precipitation delivered to lakes and their watersheds since the implementation of clean air legislation in North America (Jeffries et al. 2003, Watras and Morrison 2008), observed reductions in Hg (Hrabik and Watras 2002, Givélet et al. 2003, Watras and Morrison 2008), sulfate (Drevnick et al. 2007) and hydrogen ion loading via wet deposition can also result from declining precipitation rates, each of which would act to reduce fish [Hg] (Hrabik and Watras 2002, Hammerschmidt and Fitzgerald 2006, Driscoll et al. 2007). In smaller lakes where terrestrial inputs are important sources of both carbon (dissolved organic carbon or DOC in particular) and mercury (Mierle and Ingram 1991, Garcia et al. 2007, Keller et al. 2008), climate-induced reductions in DOC and Hg transport to lakes due to reduced precipitation will likely reduce MeHg production and loading to aquatic ecosystems (Watras and Morrison 2008). Increased light penetration resulting from reduced DOC loading will



Table 2. Published accounts of fish [Hg] over time from lakes not subject to direct point-source impacts of Hg (i.e. reservoir flooding, mining or industrial activity).

Species	Region	No. of populations	Years examined	Reported trend in fish [Hg]	Reference
Lake whitefish <i>Coregonus clupeaformis</i>	Northwestern, northeastern, southern Ontario	14, 5, 11	1970–2006	No change*, no change, no change	This study
Lake herring <i>Coregonus artedii</i>	Northwestern, northeastern, southern Ontario	4, 4, 13	1967–2006	Decline, no change, no change	This study
Walleye <i>Sander vitreus</i> , northern pike <i>Esox lucius</i>	Minnesota	845	1982–2006	Decline to 1992, small increase thereafter	(Monson 2009)
Arctic charr <i>Salvelinus alpinus</i>	Nunavut	1	1990–2006	No change	(Gantner et al. 2009)
Spottail shiner <i>Notropis hudsonius</i>	St. Lawrence River	2 (reference sites only)	1979–2005	Decline	(Choy et al. 2008)
Northern pike <i>Esox lucius</i> , white sucker <i>Catostomus commersonii</i> , walleye <i>Sander vitreus</i> , yellow perch <i>Perca flavescens</i>	St. Lawrence River	4	1975–2005	Decline	(Goulet et al. 2008)
Northern pike, walleye, <i>Coregonus</i> spp. (whitefish and herring combined)	Isle Royale, Lake Superior	4	1930–2006	Decline	(Drevnick et al. 2007)
Smallmouth bass <i>Micropterus dolomieu</i>	Lake Erie, western Basin	3	1993–2003	No change	(Hogan et al. 2007)
Walleye	Northern Wisconsin	420	1982–2005	Decline	(Madsen and Stern 2007)
Walleye	Southern Wisconsin	421	1982–2005	Decline, Increase	(Rasmussen et al. 2007)
Chinook salmon <i>Oncorhynchus tshawytscha</i> , coho salmon <i>Oncorhynchus kisutch</i>	Credit River, Lake Ontario	1	1976–2003	Decline	(French et al. 2006)
Glacier lanternfish <i>Benthosema glaciale</i>	Atlantic Ocean (39°N, 70°W)	1	1936–1993	Decline	(Martins et al. 2006)
Arctic char	Arctic	3	1997–2003	No change	(Muir et al. 2005)
Lake trout <i>Salvelinus namaycush</i> , walleye, northern pike	Manitoba, Ontario	31	1977–2000	Decline, no change	(Johnston et al. 2003)
Yellow perch	Northern Wisconsin	1	1994–2000	Decline	(Hrabik and Watras 2002)
Walleye	Lake Huron, Lake Ontario, Lake St. Clair	3	1976–1994	No change, no change, decline	(Scheider et al. 1998)

\*General pattern was decline, but non-significant at  $\alpha = 0.05$ .

increase the loss rate of otherwise bio-available aqueous MeHg to photoreduction (Schindler 1997). Reductions in DOC would also reduce rates of MeHg uptake in algae, the primary point of MeHg uptake in aquatic foodwebs (Pickhardt and Fisher 2007). Low DOC is also associated with lower MeHg concentrations in zooplankton (Westcott and Kalff 1996, Garcia and Carignan 1999), benthic invertebrates (Rennie et al. 2005) and fish (Cope et al. 1990, Suns and Hitchin 1990, Qian et al. 2001). Though terrestrial inputs may be less important in deep, large oligotrophic lakes, shallower thermoclines associated with climate warming (Magnuson et al. 1990, King et al. 1997, 1999) will reduce the total sediment area within the epilimnion, likely counteracting any increase in net methy-

lation due to warmer epilimnetic temperatures alone (Schindler 1997).

### No effect of *Bythotrephes* invasion on fish [Hg], condition

The introduction of *Bythotrephes* had no influence on [Hg] or condition of coregonid fish. Other studies have also found no increase in contaminants of consumer species after the invasion of mid-trophic invasive species (Johnston et al. 2003, Hogan et al. 2007). This is despite other work documenting a general increase in consumer contaminant concentrations with increasing food chain length (Cabana

et al. 1994). One explanation for these patterns is that mid-trophic invaders like *Bythotrephes* share existing niches with other functionally similar species when they invade, and as such have no significant effect on trophic positions of consumer species. While growth dilution has been implied in cases where invaders are speculated to have had positive effects on consumer growth rates (Hogan et al. 2007), conclusions regarding true “growth dilution” vs an array of alternative factors are difficult to assess without knowledge regarding contaminant loads from fish diets, consumption rates and activity rates (Trudel and Rasmussen 2006). Alternatively, any increase in consumer contaminant loads as a result of mid-trophic species invasions might be overwhelmed by decreases driven by global trends in precipitation chemistry (e.g. declines in Hg, sulfate and H<sup>+</sup> deposition described above). Recent studies have suggested that processes affecting Hg methylation at the base of foodchains have a stronger influence on consumer [Hg] than does their trophic position (Chasar et al. 2009).

In conclusion, the pattern of change we observed in body condition and fish [Hg] in Ontario coregonid populations over the past three decades are consistent with regional differences in climate change. The widespread and consistent declines observed in coregonid body condition are of particular concern, as this may affect both reproductive output and overwinter survival of these fish. Further, our review of existing literature suggests that fish [Hg] might be expected to decline with warming climates in lakes where nutrients, carbon and Hg are largely supplied by terrestrial inputs and in large oligotrophic water bodies where thermal stratification occurs. Our study suggests that impending changes in climate pose a much greater threat to the health and continued exploitation of northern coregonid populations than does the threat of invasion by *Bythotrephes*.

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## References

Aku, P. M. K. and Tonn, W. M. 1997. Changes in population structure, growth, and biomass of cisco (*Coregonus artedii*)

- during hypolimnetic oxygenation of a deep, eutrophic lake, Amisk Lake, Alberta. – *Can. J. Fish. Aquat. Sci.* 54: 2196–2206.
- Ali, M. and Wootton, R. J. 1999. Effect of variable food levels on reproductive performance of breeding female three-spined sticklebacks. – *J. Fish Biol.* 55: 1040–1053.
- Bajer, P. G. and Hayward, R. S. 2006. A combined multiple-regression and bioenergetics model for simulating fish growth in length and condition. – *Trans. Am. Fish. Soc.* 135: 695–710.
- Barbiero, R. P. and Tuchman, M. L. 2004. Changes in the crustacean communities of Lakes Michigan, Huron, and Erie following the invasion of the predatory cladoceran *Bythotrephes longimanus*. – *Can. J. Fish. Aquat. Sci.* 61: 2111–2125.
- Barnhisel, D. R. and Harvey, H. A. 1995. Size-specific fish avoidance of the spined crustacean *Bythotrephes* – field support for laboratory predictions. – *Can. J. Fish. Aquat. Sci.* 52: 768–775.
- Bronte, C. R. et al. 2003. Fish community change in Lake Superior, 1970–2000. – *Can. J. Fish. Aquat. Sci.* 60: 1552–1574.
- Bur, M. T. et al. 1986. 1st records of a european cladoeran, *Bythotrephes cederstroemi*, in lakes Erie and Huron. – *J. Gt. Lakes Res.* 12: 144–146.
- Cabana, G. et al. 1994. Pelagic food-chain structure in Ontario lakes – a determinant of mercury levels in lake trout (*Salvelinus namaycush*). – *Can. J. Fish. Aquat. Sci.* 51: 381–389.
- Casini, M. et al. 2006. Inter-annual variation in herring, *Clupea harengus*, and sprat, *Sprattus sprattus*, condition in the central Baltic Sea: what gives the tune? – *Oikos* 112: 638–650.
- Chasar, L. C. et al. 2009. Mercury cycling in stream ecosystems. 3. Trophic dynamics and methylmercury bioaccumulation. – *Environ. Sci. Technol.* 43: 2733–2739.
- Choy, E. S. et al. 2008. Spatial and temporal trends of mercury concentrations in young-of-the-year spottail shiners (*Notropis hudsonius*) in the St. Lawrence River at Cornwall, ON. – *Arch. Environ. Contam. Toxicol.* 54: 473–481.
- Colombo, S. J. et al. 2007. Climate change projections for Ontario: practical information for policymakers and planners. – Queen’s printer for Ontario, ON.
- Cope, W. G. et al. 1990. Mercury accumulation in yellow perch in Wisconsin seepage lakes – relation to lake characteristics. – *Environ. Toxicol. Chem.* 9: 931–940.
- Coulas, R. A. et al. 1998. Selective predation on an introduced zooplankter (*Bythotrephes cederstroemi*) by lake herring (*Coregonus artedii*) in Harp Lake, Ontario. – *Freshwater Biol.* 40: 343–355.
- Cullis, K. I. and Johnson, G. E. 1988. 1st evidence of the cladoceran *Bythotrephes cederstroemi* Schoedler in Lake Superior. – *J. Gt. Lakes Res.* 14: 524–525.
- Davoren, G. K. and Montevecchi, W. A. 2003. Signals from seabirds indicate changing biology of capelin stocks. – *Mar. Ecol. Prog. Ser.* 258: 253–261.
- DeBruyne, R. L. et al. 2008. Lake whitefish relative abundance, length-at-age, and condition in Lake Michigan indicated by fishery-independent surveys. – *J. Gt. Lakes Res.* 34: 235–244.
- Drevnick, P. E. et al. 2007. Deposition and cycling of sulfur controls mercury accumulation in Isle Royale fish. – *Environ. Sci. Technol.* 41: 7266–7272.
- Driscoll, C. T. et al. 2007. Mercury contamination in forest and freshwater ecosystems in the northeastern United States. – *Bioscience* 57: 17–28.
- Elliott, J. A. et al. 2006. Testing the sensitivity of phytoplankton communities to changes in water temperature and nutrient load, in a temperate lake. – *Hydrobiologia* 559: 401–411.
- Engelhard, G. H. and Heino, M. 2006. Climate change and condition of herring (*Clupea harengus*) explain long-term

- trends in extent of skipped reproduction. – *Oecologia* 149: 593–603.
- Fernandez, R. J. et al. 2009. Changes in nearshore zooplankton communities associated with species invasions and potential effects on larval lake whitefish (*Coregonus clupeaformis*). – *Int. Rev. Hydrobiol.* 94: 226–243.
- Fisher, S. J. and Fielder, D. G. 1998. A standard weight equation to assess the condition of North American lake herring (*Coregonus artedii*). – *J. Freshwater Ecol.* 13: 269–277.
- French, T. D. et al. 2006. Long-term changes in legacy trace organic contaminants and mercury in Lake Ontario salmon in relation to source controls, trophodynamics, and climatic variability. – *Limnol. Oceanogr.* 51: 2794–2807.
- Gantner, N. et al. 2009. Temporal trends of mercury, cesium, potassium, selenium, and thallium in arctic char (*Salvelinus alpinus*) from Lake Hazen, Nunavut, Canada: effects of trophic position, size, and age. – *Environ. Toxicol. Chem.* 28: 254–263.
- Garcia, E. and Carignan, R. 1999. Impact of wildfire and clear-cutting in the boreal forest on methyl mercury in zooplankton. – *Can. J. Fish. Aquat. Sci.* 56: 339–345.
- Garcia, E. et al. 2007. Seasonal and inter-annual variations in methyl mercury concentrations in zooplankton from boreal lakes impacted by deforestation or natural forest fires. – *Environ. Monit. Assess.* 131: 1–11.
- Gerdeaux, D. and Perga, M. E. 2006. Changes in whitefish scales  $\delta^{13}\text{C}$  during eutrophication and reoligotrophication of subalpine lakes. – *Limnol. Oceanogr.* 51: 772–780.
- Givélet, N. et al. 2003. Predominant anthropogenic sources and rates of atmospheric mercury accumulation in southern Ontario recorded by peat cores from three bogs: comparison with natural “background” values (past 8000 years). – *J. Environ. Monit.* 5: 935–949.
- Goulet, R. R. et al. 2008. Temporal trends and spatial variability of mercury in four fish species in the Ontario segment of the St. Lawrence River, Canada. – *Arch. Environ. Contam. Toxicol.* 54: 716–729.
- Hammerschmidt, C. R. and Fitzgerald, W. F. 2006. Methylmercury in freshwater fish linked to atmospheric mercury deposition. – *Environ. Sci. Technol.* 40: 7764–7770.
- Henderson, B. A. and Morgan, G. E. 2002. Maturation of walleye by age, size and surplus energy. – *J. Fish Biol.* 61: 999–1011.
- Hogan, L. S. et al. 2007. How non-native species in Lake Erie influence trophic transfer of mercury and lead to top predators. – *J. Gt. Lakes Res.* 33: 46–61.
- Hopper, M. and Power, G. 1991. The fisheries of an Ojibway community in northern Ontario. – *Arctic* 44: 267–274.
- Hrabik, T. R. and Watras, C. J. 2002. Recent declines in mercury concentration in a freshwater fishery: isolating the effects of de-acidification and decreased atmospheric mercury deposition in Little Rock Lake. – *Sci. Total Environ.* 297: 229–237.
- IPCC 2007. Climate change 2007: the physical science basis. – Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge Univ. Press.
- Jeffries, D. S. et al. 2003. Monitoring the results of Canada/USA acid rain control programs: some lake responses. – *Environ. Monit. Assess.* 88: 3–19.
- Jensen, O. P. et al. 2007. Spatial analysis of ice phenology trends across the Laurentian Great Lakes region during a recent warming period. – *Limnol. Oceanogr.* 52: 2013–2026.
- Johnston, T. A. et al. 2003. Temporal changes in mercury bioaccumulation by predatory fishes of boreal lakes following the invasion of an exotic forage fish. – *Environ. Toxicol. Chem.* 22: 2057–2062.
- Kaufman, S. D. et al. 2006. Muscle enzymes reveal walleye (*Sander vitreus*) are less active when larger prey (cisco, *Coregonus artedii*) are present. – *Can. J. Fish. Aquat. Sci.* 63: 970–979.
- Keller, W. 2007. Implications of climate warming for Boreal Shield lakes: a review and synthesis. – *Environ. Rev.* 15: 99–112.
- Keller, W. et al. 2008. Relationships between dissolved organic carbon concentrations, weather, and acidification in small Boreal Shield lakes. – *Can. J. Fish. Aquat. Sci.* 65: 786–795.
- Kettles, I. M. et al. 1991. Surficial geochemistry, south-central Canadian Shield – implications for environmental assessment. – *J. Geochem. Explor.* 41: 29–57.
- King, J. R. et al. 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. et al. 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.
- Kinghorn, A. et al. 2007. Temporal and spatial trends of mercury in fish collected in the English-Wabigoon river system in Ontario, Canada. – *Sci. Total Environ.* 372: 615–623.
- Kinnunen, R. E. 2003. Great Lakes commercial fisheries, – <www.miseagrant.umich.edu/downloads/fisheries/GLCommercialFinal.pdf>, accessed 5-11-2009.
- Lange, C. and Cap, R. 1986. *Bythotrephes cederstroemi* (Schodler). (Cercopagidae, Cladocera) – a new record for Lake Ontario. – *J. Gt. Lakes Res.* 12: 142–143.
- Liao, H. S. et al. 1995. Relative weight ( $W_r$ ) As a field assessment-tool – relationships with growth, prey biomass, and environmental-conditions. – *Trans. Am. Fish. Soc.* 124: 387–400.
- Lumb, C. E. et al. 2007. Comparison of lake whitefish (*Coregonus clupeaformis*) growth, condition, and energy density between lakes Erie and Ontario. – *J. Gt. Lakes Res.* 33: 314–325.
- MacIsaac, H. J. 1996. Potential abiotic and biotic impacts of zebra mussels on the inland waters of North America. – *Am. Zool.* 36: 287–299.
- Madsen, E. R. and Stern, H. S. 2007. Time trends of methylmercury in walleye in northern Wisconsin: a hierarchical Bayesian analysis. – *Environ. Sci. Technol.* 41: 4568–4573.
- Magnuson, J. J. et al. 1990. Potential changes in the thermal habitat of Great Lakes fish after global climate warming. – *Trans. Am. Fish. Soc.* 119: 254–264.
- Martins, I. et al. 2006. Temporal and spatial changes in mercury concentrations in the North Atlantic as indicated by museum specimens of glacier lanternfish *Benthoosema glaciale* (Pisces: Myctophidae). – *Environ. Toxicol.* 21: 528–532.
- Mesa, M. G. et al. 1994. Are all prey created equal – a review and synthesis of differential predation on prey in substandard condition. – *J. Fish Biol.* 45: 81–96.
- Mierle, G. and Ingram, R. 1991. The role of humic substances in the mobilization of mercury from watersheds. – *Water Air Soil Pollut.* 56: 349–357.
- Milbrink, G. et al. 2008. Long-term effects of nutrient enrichment on the condition and size-structure of an alpine brown trout population. – *Environ. Biol. Fishes* 81: 157–170.
- Mills, K. H. 1985. Responses of lake whitefish (*Coregonus clupeaformis*) to fertilization of Lake-226, the Experimental Lakes Area. – *Can. J. Fish. Aquat. Sci.* 42: 129–138.
- Möllmann, C. et al. 2003. The marine copepod, *Pseudocalanus elongatus*, as a mediator between climate variability and fisheries in the central Baltic Sea. – *Fish Oceanogr.* 12: 360–368.
- Möllmann, C. et al. 2005. Climate, zooplankton, and pelagic fish growth in the central Baltic Sea. – *ICES J. Mar. Sci.* 62: 1270–1280.
- Monson, B. A. 2009. Trend reversal of mercury concentrations in piscivorous fish from Minnesota lakes: 1982–2006. – *Environ. Sci. Technol.* 43: 1750–1755.
- Morbey, Y. E. et al. 2007. Dynamics of piscivory by lake trout following a smallmouth bass invasion: a historical reconstruction. – *Trans. Am. Fish. Soc.* 136: 477–483.

- Muir, D. et al. 2005. Spatial and temporal trends of mercury and other metals in landlocked char from lakes in the Canadian Arctic archipelago. – *Sci. Total Environ.* 351: 464–478.
- Myers, R. A. and Worm, B. 2003. Rapid worldwide depletion of predatory fish communities. – *Nature* 423: 280–283.
- Óskarsson, G. J. et al. 2002. Predictions of realised fecundity and spawning time in Norwegian spring-spawning herring (*Clupea harengus*). – *J. Sea Res.* 48: 59–79.
- Pangle, K. L. et al. 2004. Overwinter survival of juvenile lake herring in relation to body size, physiological condition, energy stores, and food ration. – *Trans. Am. Fish. Soc.* 133: 1235–1246.
- Pauly, D. et al. 1998. Fishing down marine food webs. – *Science* 279: 860–863.
- Pickhardt, P. C. and Fisher, N. S. 2007. Accumulation of inorganic and methylmercury by freshwater phytoplankton in two contrasting water bodies. – *Environ. Sci. Technol.* 41: 125–131.
- Post, J. R. et al. 2002. Canada's recreational fisheries: the invisible collapse? – *Fisheries* 27: 6–17.
- Post, J. R. et al. 2008. Angler numerical response across landscapes and the collapse of freshwater fisheries. – *Ecol. Appl.* 18: 1038–1049.
- Pothoven, S. A. et al. 2001. Changes in diet and body condition of lake whitefish in southern Lake Michigan associated with changes in benthos. – *North Am. J. Fish. Manage.* 21: 876–883.
- Qian, S. S. et al. 2001. A predictive model of mercury fish tissue concentrations for the southeastern United States. – *Environ. Sci. Technol.* 35: 941–947.
- R Development Core Team 2006. R: a language and environment for statistical computing. – <[www.R-project.org](http://www.R-project.org)>, accessed 1-1-2008.
- Rasmussen, P. W. et al. 2007. Temporal trends of mercury concentrations in Wisconsin walleye (*Sander vitreus*), 1982–2005. – *Ecotoxicology* 16: 541–550.
- Rennie, M. D. 2009. Influence of invasive species, climate change and population density on life histories and mercury dynamics of *Coregonus* spp. – Ph.D. thesis, Univ. of Toronto.
- Rennie, M. D. and Verdon, R. 2008. Development and evaluation of condition indices for the lake whitefish. – *North Am. J. Fish. Manage.* 28: 1270–1293.
- Rennie, M. D. et al. 2005. Predictive models of benthic invertebrate methylmercury in Ontario and Quebec lakes. – *Can. J. Fish. Aquat. Sci.* 62: 2770–2783.
- Rennie, M. D. et al. 2009a. Factors affecting the growth and condition of lake whitefish (*Coregonus clupeaformis*). – *Can. J. Fish. Aquat. Sci.*, in press.
- Rennie, M. D. et al. 2009b. Resource switching in fish following a major food web disruption. – *Oecologia* 159: 789–802.
- Reznick, D. et al. 2000. Big houses, big cars, superfleas and the costs of reproduction. – *Trends Ecol. Evol.* 15: 421–425.
- Rudd, J. W. M. et al. 1983. The English Wabigoon River system. 1. A synthesis of recent research with a view towards mercury amelioration. – *Can. J. Fish. Aquat. Sci.* 40: 2206–2217.
- Scheider, W. A. et al. 1998. Current status and temporal trends in concentrations of persistent toxic substances in sport fish and juvenile forage fish in the Canadian waters of the Great Lakes. – *Environ. Monit. Assess.* 53: 57–76.
- Schindler, D. W. 1997. Widespread effects of climatic warming on freshwater ecosystems in North America. – *Hydrol. Process.* 11: 1043–1067.
- Scott, W. B. and Crossman, E. J. 1998. *Freshwater fishes of Canada*. – Galt House Publ., Oakville.
- Smith, B. R. and Tibbles, J. J. 1980. Sea lamprey (*Petromyzon marinus*) in lakes Huron, Michigan, and Superior – history of invasion and control, 1936–78. – *Can. J. Fish. Aquat. Sci.* 37: 1780–1801.
- Sogard, S. M. and Olla, B. L. 2000. Endurance of simulated winter conditions by age-0 walleye pollock: effects of body size, water temperature and energy stores. – *J. Fish Biol.* 56: 1–21.
- Somers, K. M. and Jackson, D. A. 1993. Adjusting mercury concentration for fish-size covariation – a multivariate alternative to bivariate regression. – *Can. J. Fish. Aquat. Sci.* 50: 2388–2396.
- Staehr, P. A. and Sand-Jensen, K. 2006. Seasonal changes in temperature and nutrient control of photosynthesis, respiration and growth of natural phytoplankton communities. – *Freshwater Biol.* 51: 249–262.
- Stenseth, N. C. et al. 2002. Ecological effects of climate fluctuations. – *Science* 297: 1292–1296.
- Suns, K. and Hitchin, G. 1990. Interrelationships between mercury levels in yearling yellow perch; fish condition and water-quality. – *Water Air Soil Pollut.* 50: 255–265.
- Todd, C. D. et al. 2008. Detrimental effects of recent ocean surface warming on growth condition of Atlantic salmon. – *Global Change Biol.* 14: 958–970.
- Trudel, M. and Rasmussen, J. B. 2006. Bioenergetics and mercury dynamics in fish: a modelling perspective. – *Can. J. Fish. Aquat. Sci.* 63: 1890–1902.
- Van Noordwijk, A. J. and Dejong, G. 1986. Acquisition and allocation of resources – their influence on variation in life history tactics. – *Am. Nat.* 128: 137–142.
- Vander Zanden, M. J. and Rasmussen, J. B. 1996. A trophic position model of pelagic food webs: impact on contaminant bioaccumulation in lake trout. – *Ecol. Monogr.* 66: 451–477.
- Ventresca, D. A. et al. 1995. EL Nino effects on the somatic and reproductive condition of blue rockfish, *Sebastes mystinus*. – *Calif. Coop. Ocean. Fish. Invest. Rep.* 36: 167–174.
- Watras, C. J. and Morrison, K. A. 2008. The response of two remote, temperate lakes to changes in atmospheric mercury deposition, sulfate, and the water cycle. – *Can. J. Fish. Aquat. Sci.* 65: 100–116.
- Wege, G. J. and Anderson, R. O. 1978. Relative weight ( $W_r$ ): a new index of condition for largemouth bass. – In: Novinger, G. D. and Dillard, J. G. (eds), *New approaches to the management of small impoundments*. American Fisheries Society, Bethesda, pp. 79–91.
- Westcott, K. and Kalff, J. 1996. Environmental factors affecting methyl mercury accumulation in zooplankton. – *Can. J. Fish. Aquat. Sci.* 53: 2221–2228.
- Winder, M. and Schindler, D. E. 2004a. Climate change uncouples trophic interactions in an aquatic ecosystem. – *Ecology* 85: 2100–2106.
- Winder, M. and Schindler, D. E. 2004b. Climatic effects on the phenology of lake processes. – *Global Change Biol.* 10: 1844–1856.
- Yan, N. D. and Pawson, T. W. 1997. Changes in the crustacean zooplankton community of Harp Lake, Canada, following invasion by *Bythotrephes cederstroemi*. – *Freshwater Biol.* 37: 409–425.
- Zar, J. H. 1999. *Biostatistical analysis*. – Prentice Hall.

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