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BIODIVERSITY RESEARCH

Projected impacts of climate change on three freshwater fishes and potential novel competitive interactions

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ABSTRACT

Aim As global air temperatures continue to rise in response to climate change, environmental conditions for many freshwater fish species will change. Warming air temperatures may lead to warming lake temperatures, and subsequently, the availability of suitable thermal habitat space. Our objectives are to identify the responses of three fish species from three thermal guilds to climate change in Ontario and consequently, the potential for novel competitive interactions between two top predators. We focus on lakes in Ontario because it is a dynamic region that encapsulates the northern and southern range extents of warm and cold-water fish species.

Location Ontario, Canada.

Methods Using lake morphology, water chemistry, climate and fish occurrence data for smallmouth bass (warmwater predator), walleye (coolwater predator) and cisco (cold-water forage fish), we modelled the occurrence rates of three fish in 2050 and 2070 under 126 scenarios of climate change. We also calculated the percentage change in co-occurrence of walleye and smallmouth bass in 2050 and 2070.

Results Smallmouth bass occurrence rates were predicted to increase by ~306% (ranging between 55 and 422%) by 2070 relative to their current distributions. Walleye were projected to decline by 22% (−42 to a +6% change) and cisco by 26% (−7 to −47%) by 2070. By 2070, walleye–smallmouth bass co-occurrence was predicted to increase by 11%, with walleye in central and northern Ontario at greatest vulnerability due to increased competition with smallmouth bass.

Main conclusions These results highlight three unique responses to climate change: range expansion, northward range shift, and range contraction for warmwater, coolwater and cold-water fish species, respectively. Alterations in distributions of these three ecologically important fish species may lead to shifts in fish community structure and novel species interactions in Ontario lakes, exacerbating the vulnerability of native coolwater predators to climate change.

Keywords

biotic interactions, cisco, climate change, competition, invasive species, range shifts, smallmouth bass, thermal guilds, walleye.

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INTRODUCTION

Climate change and biological invasions are two major threats to biodiversity (Sala *et al.*, 2000), and the interacting impacts of multiple environmental stressors may further increase vulnerability of ecosystems (Sala *et al.*, 2000; Rahel & Olden, 2008). As climate warms, species have been observed to shift their range northwards, including Australian *Banksia* flowers at rates of 5 km per decade (Fitzpatrick *et al.*, 2008), voles in Yosemite National Park at

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elevation rates of 50 m per decade (Moritz *et al.*, 2008), and marine commercial fishes, including cod, halibut, sole and herring (Mueter & Litzow, 2008). As climate warms, invasive species have also moved northwards including deer (Lankester, 2010; Frelich *et al.*, 2012) and warmwater sunfishes (Alofs *et al.*, 2014). In freshwater systems, as global air temperatures rise, lake water temperatures are expected to also increase (Livingstone & Lotter, 1998). Changing water temperatures can influence the distribution of fish across landscapes by altering their available thermal habitat space (Magnuson *et al.*, 1990; Adrian *et al.*, 2009) and may also eliminate barriers that have historically prevented warmwater invasive species from colonizing these lakes (e.g. Vinebrooke *et al.*, 2004; Rahel & Olden, 2008). The combination of climate change and invading warmwater sunfishes has been associated with large declines of cyprinids (Jackson & Mandrak, 2002), salmonids (Vander Zanden *et al.*, 1999) and percids (Fayram *et al.*, 2005) in northern lakes.

Our research focuses on how future changes in climate may modify distributions and potential future interactions of fish that prefer warm (~28 °C), cool (~24 °C), and cold-water (~15 °C) habitats (Magnuson *et al.*, 1990). Fish from each of these habitat guilds are expected to respond differently to climate change (e.g. Shuter *et al.*, 2002; Chu *et al.*, 2005). Within the past 30 years, sportfish in Ontario have shifted their range northwards by 12.5–17.5 km per decade while baitfish have shifted southwards in response to a changing climate and species interactions (Alofs *et al.*, 2014). Previous research has predicted that warm and coolwater fish will expand northward (Chu *et al.*, 2005; Sharma *et al.*, 2007) while cold-water fish will decline from their current ranges and potentially shift their distributions northward under future scenarios of climate change (Sharma *et al.*, 2011; Herb *et al.*, 2014). We aim to predict the impacts of climate change on species from each guild: smallmouth bass (*Micropterus dolomieu*; warmwater, non-native), walleye (*Sander vitreus*; coolwater, native), and cisco (*Coregonus artedii*; coldwater, native) and changes in co-occurrence and potential for biotic interactions between invasive and native species.

Alterations in warmwater, coolwater and cold-water fish species distributions resulting from climate change may facilitate changes in food web dynamics and ecosystem function with novel biotic interactions, leading to greater competition and predation pressures (Vander Zanden *et al.*, 1999; Sharma *et al.*, 2009). Non-native species expansions, such as smallmouth bass in Ontario, can have devastating effects on native biota, trophic structure and ecosystem processes (Vander Zanden *et al.*, 1999; Jackson & Mandrak, 2002; Sharma *et al.*, 2009). Increases in co-occurrence of walleye and smallmouth bass across Ontario in lakes where the two species have not historically co-occurred may result in novel competitive interactions for shared food resources (Johnson & Hale, 1977; Frey *et al.*, 2003; Wuellner *et al.*, 2011).

OBJECTIVES

The overall goal of this study was to identify the differential responses of ecologically important predatory and forage fishes from all thermal guilds to climate change and how distributional changes may alter the potential for biotic interactions. We focus our study in the province of Ontario, an especially dynamic region that encapsulates the northern range extent of warmwater species and the southern range extent of cold-water species. More specifically, our first objective was to identify the important abiotic and climatic predictors of non-native smallmouth bass and native walleye, and cisco occurrence in Ontario lakes.

Our second objective was to develop a predictive model to forecast future occurrences of smallmouth bass, walleye and cisco in the years 2050 and 2070. We projected the occurrence of smallmouth bass, walleye and cisco under all 126 IPCC climate change scenarios in order to identify the likelihood of expansion or extirpation of each species by incorporating uncertainties in air temperature and precipitation from each climate model.

Our third objective was to determine how co-occurrence rates of walleye and smallmouth bass, and walleye and cisco will change in response to changing temperature and precipitation regimes. We anticipate that these changes in co-occurrence will vary spatially across Ontario. For example, as both walleye and smallmouth bass consume similar prey, it is expected that increased co-occurrence rates will lead to interactions in novel locations. As smallmouth bass are slightly stronger competitors than walleye (Wuellner *et al.*, 2011), increases in smallmouth bass habitat suitability across Ontario could lead to increased walleye vulnerability. These interactions may be further exacerbated with the onset of climate change, threatening to alter aquatic species community composition in the future.

METHODS

Background information on three fish species

Smallmouth bass are a warmwater (preferred water temperatures: 20–29 °C) predatory fish found mainly in the central United States and southern Ontario (Shuter *et al.*, 1980; Scott & Crossman, 1998). Their current range is expanding throughout North America via natural and human-mediated dispersal (Sharma & Jackson, 2008). The distribution of smallmouth bass has been historically limited to the south and south-central regions of Ontario where July air temperatures exceed 18 °C (Shuter *et al.*, 1980). In regions where July air temperatures are below 16.6 °C, young-of-the-year smallmouth bass cannot grow to sufficient sizes to successfully overwinter (Shuter *et al.*, 1980; Wismer *et al.*, 1985). Under scenarios of climate change, smallmouth bass have been predicted to expand their range northward (e.g. Chu *et al.*, 2005; Sharma *et al.*, 2007).

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Walleye are a coolwater (preferred water temperatures: 18–25 °C) predatory species, whose native range extends from the Gulf coast of Alabama in the United States, up into the Yukon territories of Canada (Koenst & Smith, 1975; Scott & Crossman, 1998). Previous studies have suggested that increases in air temperature and changes in precipitation will translate to a greater number of habitable northern lakes for walleye, allowing them to expand their distributions northerly (Chu *et al.*, 2005; Fayram *et al.*, 2014). Warmer spring air temperatures can lead to earlier spring ice break-up, and warmer spawning waters which can increase young-of-year growth, and increase the risk of walleye predation in northern lakes (Fayram *et al.*, 2014;).

Cisco are a cold-water forage species (preferred water temperature: 8–17 °C) that are vital to the growth and success of many top predators (e.g. lake trout) in Canada and the northern United States (Matuszek *et al.*, 1990; Scott & Crossman, 1998; Jacobson *et al.*, 2010). As air temperatures increase under climate change, cisco distributions are predicted to shift northerly and decline from many of their southern extents (Jacobson *et al.*, 2010; Sharma *et al.*, 2011; Fang *et al.*, 2012). Cisco prefer cold temperatures of the hypolimnion and become stressed as oxygen levels in this layer are depleted; this forces them to move into warm waters that are unsuitable for growth, survival or reproduction (Aku *et al.*, 1997; Ficke *et al.*, 2007).

Data acquisition: Survey and climate data

Historical data were obtained from the Ontario Ministry of Natural Resources (OMNR) Aquatic Habitat Inventory (AHI) for 9885 lakes between 1957 and 1986 (Dodge *et al.*, 1985). The survey collected data on lake geography (latitude and longitude), morphology (e.g. mean depth, surface area) and chemistry (e.g. secchi depth, pH). Additional lake data were also obtained from the OMNR Broad Scale Monitoring Program (BSM) for 722 lakes between 2008 and 2012 (Sandstrom *et al.*, 2010). Similar variables for lake geography, morphology and chemistry data were included in this contemporary data set. Of the 722 lakes, 606 overlapped with the AHI data set, which were subsequently updated to reflect more recent data. With 116 new lakes added from the BSM, we compiled a data set of 10,001 Ontario lakes (Table S1). A data set comprised of 9736 lakes was resolved from the 10,001 as 265 lakes contained incomplete data. Fish occurrence data on 134 fish species from the AHI and 100 species from the BSM were also provided. Surveys in the contemporary period were able to effectively sample for both large and small-bodied fish with the use of a wider range of gillnet and trapnet mesh sizes, while historical data likely undersampled smaller fish. Northern regions of Ontario and the Hudson Bay lowlands continue to be undersampled (Minns, 1986; Sandstrom *et al.*, 2010).

Historical climate data and future climate change scenarios were obtained from the Intergovernmental Panel on Climate Change (IPCC, 2013). Historical climate data were represented as climate averages between 1950 and 2000. Variables were total monthly precipitation, and monthly mean, minimum, and maximum air temperatures (Hijmans *et al.*, 2005). Future climate scenarios for 2050 (average for 2041–2060) and 2070 (average for 2061–2080) were also obtained from the latest IPCC 5 report (IPCC, 2013). Projected air temperature and precipitation values from 19 general circulation models (GCMs) under four greenhouse gas scenarios (representative concentration pathway (RCP) 2.6, 4.5, 6.0 and 8.5) were extracted for 2050 and 2070. Eleven of the 19 GCMs projected future climate under all four RCPs for 2050 and 2070, while the remaining GCMs predicted for only select scenarios. Each GCM is unique and calculates climate values based on various assumptions of atmosphere, ocean, sea-ice and land components (Hijmans *et al.*, 2005; IPCC, 2013; Stocker, 2013). The scenarios of future greenhouse gas concentrations (including RCP 2.6, 4.5, 6.0 and 8.5) represent a gradient where RCP2.6 is the most conservative estimate of future greenhouse gas (GHG) emissions, projecting a decrease in overall emissions by 2100, while RCP 8.5 is the 'business-as-usual' scenario, which estimates continuous increases of GHG emissions through 2100 (Moss *et al.*, 2010; van Vuuren & Riahi, 2011; Rojeli *et al.*, 2012). A total of 126 climate change scenarios were used to project smallmouth bass, walleye and cisco occurrence.

How climate data were utilized in the models

To better understand the uncertainty in species range expansions and contractions, we projected species distributions using all 19 GCMs and their RCPs, over 2 time periods (mid-century and late-century), totalling 126 different climate change scenarios from the most recent IPCC assessment (IPCC, 2013). Previous studies have commented on the large variability between GCMs and resulting implications for species distribution forecasts (e.g. Thuiller, 2004; Buisson *et al.*, 2008; Sharma *et al.*, 2011). This variability can be attributed to several differences among GCMs, including their spatial and vertical resolutions, their representation and calculations of various physical processes (such as clouds, water vapour, ocean mixing processes, etc.), and their representation of climate feedback mechanisms (e.g. their ability to simulate feedbacks relating to clouds, water vapour and snow) (Beaumont *et al.*, 2008; IPCC, 2013). As such, using a wide range of climate change scenarios has been recommended by the IPCC to reduce the uncertainty inherent within each GCM and better reflect the likelihood of species expansion or extirpation within a particular site (Beaumont *et al.*, 2008; Sharma *et al.*, 2011).

Data analysis: Fish occurrence models

We developed logistic regression models for smallmouth bass, walleye and cisco occurrence in Ontario lakes. We divided our combined AHI-BSM data set (n = 9736) into two random and independent subsets: 80% of the data set was retained for model training, 20% for model validation. Variables were assessed for normality using a Shapiro–Wilk test; surface area, maximum depth, mean depth and secchi depth data were log-transformed to meet the assumptions of normality. Multicollinearity was found to be low ($r < 0.7$) among environmental predictor variables used in each species distribution model. The null model contained only the intercept and the global model from which explanatory variables were selected contained lake geography (latitude, longitude), lake morphology (lake elevation, lake surface area, perimeter, maximum depth and mean depth), water chemistry (secchi depth, pH, total dissolved solids, conductivity and dissolved oxygen) and climate (mean July, August, and annual air temperature, July and summer precipitation) variables. In addition, the global model contained interactions between all pairs of climatic variables and quadratic terms of climatic variables. See Table S1 for summary information on these variables in our data set. To develop each species distribution model, a forward selection procedure with a dual-criterion ($\alpha = 0.05$ and R^2_{adj}) was used to identify significant environmental predictor variables for smallmouth bass, walleye and cisco occurrence including climate interaction and polynomial terms (Blanchet *et al.*, 2008).

We used receiver operating characteristics (ROC) curves to identify thresholds (0–1) that maximize the sensitivity (percentage of correctly predicted presences) and specificity (percentage of correctly predicted absences) of each species distribution model. This procedure is recommended when species presences and absences are not equal within the data (Fielding & Bell, 1997; Sharma & Jackson, 2008). All analyses were performed in the R-language environment (R Development Core Team, 2015).

Fish projections under climate change

We predicted smallmouth bass, walleye and cisco occurrences under 126 future climate scenarios for the years 2050 and 2070. We used all possible climate scenarios to incorporate the variability between GCMs and RCPs on fish projections. The probability of fish occurrence was calculated for each lake by averaging the predicted species occurrence rates under each climate scenario for both 2050 and 2070. Ordinary kriging was performed using ArcGIS 10.1 to illustrate the probability of each fish occurrence across the landscape of Ontario in 2050 and 2070 (ESRI, 2011) under 126 scenarios of climate change. Ordinary kriging is a smoothing process that interpolates the probability of fish occurrence across landscapes. The probability of occurrence for each pixel across Ontario's landscape was calculated by averaging the probability of occurrence of the nearest 50 lakes.

Percentage change in walleye–smallmouth bass or cisco co-occurrence

Percentage change in walleye and smallmouth bass or cisco co-occurrence was calculated in Ontario lakes under historical and future climate change scenarios using the AHI lakes ($n = 9641$, 244 of the 9885 AHI lakes were omitted due to incomplete data). Lakes were categorized as follows: walleye only, smallmouth bass or cisco only, and co-occurrence of walleye and smallmouth bass or cisco. The median percentage change in occurrence between historical and future periods was calculated for each category and for three different latitudinal regions of Ontario. The latitudes between 50.5°N and 48.1°N were classified as central Ontario ($n_{central} = 3546$), while northern latitudes were above 50.5°N ($n_{northern} = 674$), and southern latitudes were below 48.1°N ($n_{southern} = 5421$). Percentage change in co-occurrence of walleye and smallmouth bass or cisco in these regions was calculated to better incorporate spatial variability in biotic interactions across the province.

RESULTS

Fish occurrence models

Models predicted that smallmouth bass were more likely to occur in larger, clearer lakes, in regions with higher temperatures and lower precipitation (Table 1). Model validation yielded a classification success of 84% (Table 2). Walleye models indicate a preference for larger, turbid lakes, in cooler regions with higher precipitation (Table 1). This model had a classification success of 80% (Table 2) when

Table 1 Coefficients of significant ($P < 0.01$) predictors for logistic regression models for smallmouth bass, walleye and cisco populations. Mean conditions in lakes with fish present and fish absent.

Selected variables	Model coefficients	Environmental characteristics with fish present	Environmental characteristics with fish absent
Smallmouth Bass			
Surface area (ha)	1.33	615.5	293.9
Secchi depth (m)	1.54	4.1	3.5
Mean July air temperature (°C)	1.03	18.8	17.5
July precipitation (mm)	−0.07	76.7	83.5
Walleye			
Surface area (ha)	2.09	944.6	118.5
Secchi depth (m)	−2.52	3.0	3.9
Mean August air temperature (°C)	−0.11	16.1	16.5
Mean summer precipitation (mm)	0.02	86.5	84.4
Cisco			
Surface area (ha)	1.62	1037.0	148.5
Mean depth (m)	1.75	7.8	4.9
Mean annual air temperature (°C)	−0.09	1.9	2.7

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Table 2 The classification success, specificity, sensitivity and kappa statistic values of the predictive smallmouth bass, walleye and cisco occurrence models.

	Classification success (%)	Specificity (%)	Sensitivity (%)	Kappa statistic
Smallmouth bass	84	89	59	0.48
Walleye	80	86	66	0.52
Cisco	80	87	56	0.43

tested on an independent validation data set. Cisco were predicted to occur more frequently in larger, deeper lakes, in cooler regions of Ontario (Table 1). A classification success rate of 80% was observed from this model (Table 2).

Fish projections

Smallmouth bass were present in 19% ($n_{\text{smallmouth bass}}$ = 1834, n_{total} = 9736) of south-central Ontario lakes (Fig. 1a). By 2050 and 2070, smallmouth bass are predicted to expand their range northerly, occupying many lakes in north-western Ontario (Fig. 1b,c). Under the most conservative scenario, in 2050 (RCP 2.6), there was a 0–40% likelihood of smallmouth bass expansion into central and northern Ontario lakes (see Fig. S1). In the most extreme scenario, in 2070 (RCP 8.5), there was an 80–100% likelihood of smallmouth bass expansion in all northern regions of Ontario (Fig. S1). Smallmouth bass are also predicted to invade 7873 new lakes by 2070 under the most extreme scenario. Changes in temperature and precipitation under future scenarios of climate warming may result in a −8 to +418% ($\bar{x}$ = 260% increase) change in smallmouth bass occurrence by 2050 and a 55–422% increase ($\bar{x}$ = 306% increase) by 2070 (Fig. 2a,b). All Ontario lakes became suitable for smallmouth bass under climate scenarios if mean July air temperatures increases by more than 4 °C.

Walleye were present in 28% (n_{walleye} = 2781, n_{total} = 9736) of lakes sampled in Ontario (Fig. 1d). By 2050 and 2070, walleye are predicted to become extirpated from lakes in southern and south-central Ontario, leaving populations in central Ontario the most vulnerable to

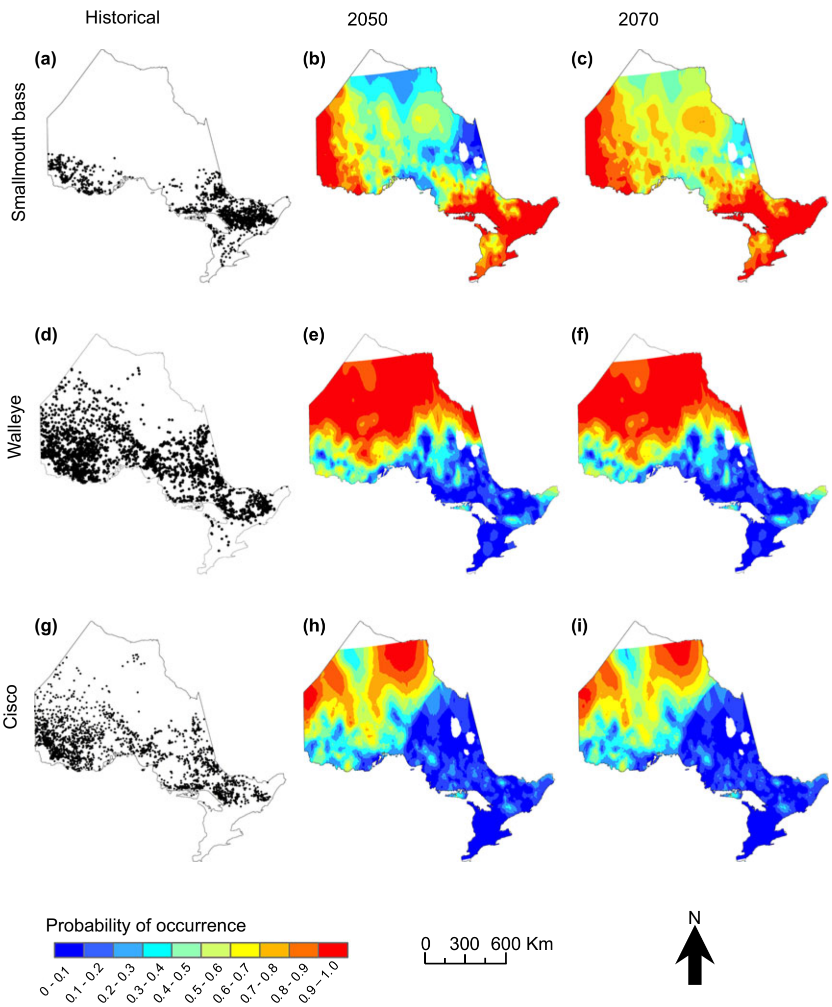

Figure 1 Distributions of smallmouth bass (a) historically, (b) in 2050 and (c) in 2070 under 126 scenarios of climate change. Distributions of walleye (d) historically, (e) in 2050 and (f) in 2070. Distributions of cisco (g) historically, (h) in 2050 and (i) in 2070.

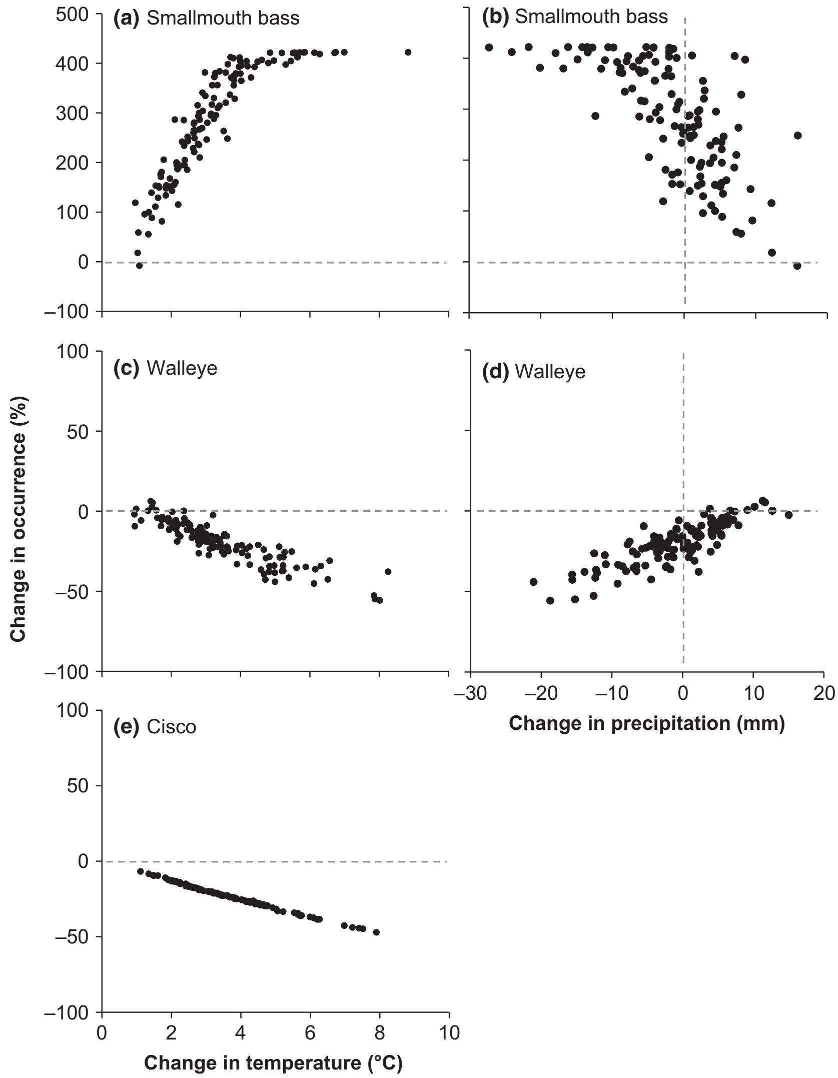

Figure 2 Percentage change in (a) smallmouth bass, (c) walleye and (e) cisco occurrence as temperature changes under 126 climate change scenarios in 2050 and 2070. Percentage change in (b) smallmouth bass and (d) walleye as precipitation increases under climate change.

extirpation under scenarios of climate change (Fig. 1e,f). The most conservative greenhouse gas scenario predicts a loss of 14% of walleye populations by 2050 (Fig. S2). If greenhouse gas emissions continue to follow this conservative trajectory, we can expect a 12% decline in walleye occurrence rates by 2070; this indicates a 2% increase in walleye occurrences from the 2050 projection (Fig. S2). Changes in temperature and precipitation may result in a −42 to a +6% change ($\bar{x}$ = 17% decline) in walleye occurrence by 2050 and a −56 to a +1% change ($\bar{x}$ = 22% decline) by 2070 (Fig. 2c,d).

Cisco were present in 23% ($n_{\text{cisco}} = 2257$, $n_{\text{total}} = 9736$) of lakes. By 2050 and 2070, cisco populations are projected to become extirpated from their southern and east-central range (Fig. 1h,i). Increasing greenhouse gas emissions will further squeeze cisco populations into small regions of northern Ontario (Fig. S3). Warming air temperatures correspond to a decline of cisco occurrence ranging from −8 to −37% ($\bar{x}$ = −20%) by 2050, and a loss of up to −7 to −47% ($\bar{x}$ = −26%) by 2070 (Fig. 2e).

Walleye–smallmouth bass and walleye–cisco co-occurrence

The number of lakes with walleye–smallmouth bass co-occurrence is expected to increase across Ontario by 10% by 2050 and 11% by 2070 ($n_{\text{historical co-occurrence}} = 633$ lakes) under projected scenarios of climate change (Fig. 3a; Fig. S4). Specifically, walleye-only lakes are predicted to decline by 15% in 2050 and 19% in 2070 while smallmouth bass only lakes are predicted to increase by 41% in 2050 and 51% in 2070 (Fig. 3a; Fig. S4). Co-occurrence is likely to increase across the province because smallmouth bass are predicted to invade regions historically occupied by walleye. Grouping lakes by region (south, central and north) suggests that in 2070, walleye–smallmouth bass co-occurrence will decline by 0.3% in southern Ontario (Fig. 3b), and increase by 20% and 68% in the central and northern regions, respectively (Fig. 3c,d). Walleye-only lakes are expected to decline by 32% in the central region and 67% in the northern region of Ontario by 2070, whereas smallmouth bass only lakes are

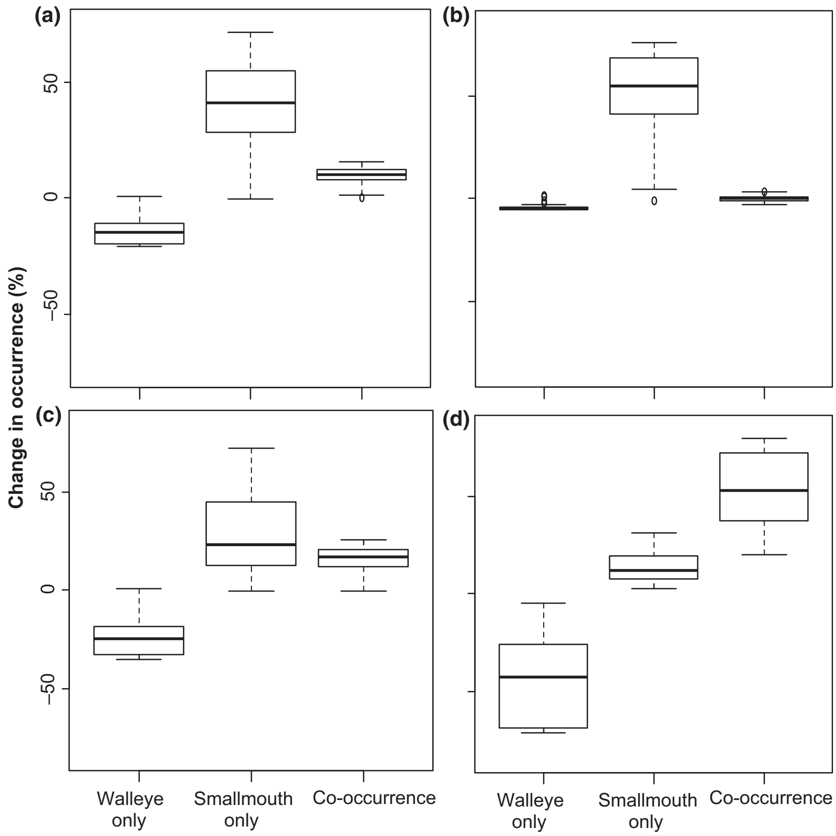

Figure 3 Projected change in walleye and smallmouth bass occurrence in 2070 in (a) all of Ontario, (b) southern Ontario, (c) central Ontario and (d) northern Ontario.

expected to increase by 39% and 18% for central and northern regions, respectively (Fig. 3c,d).

Changes in walleye–cisco co-occurrence rates are far less pronounced, increasing by 0.3% across all Ontario by 2070 while walleye-only and cisco-only lakes declined by 5.6% and 4.9%, respectively, under scenarios of climate change (Fig. 4a; Fig. S5). Changes in walleye–cisco co-occurrence in southern and central Ontario are predicted to increase by 2.9% and 0.9% respectively (Fig. 4b,c). Co-occurrence rates of walleye and cisco are expected to increase by 14.4% in the northern regions of Ontario Fig. 4d).

DISCUSSION

This study highlights three unique responses of fish species from each thermal guild to climate change in an especially sensitive region where warmwater fishes are at their current northern extent and cold-water fishes are near their southern extent. We forecasted how the warmwater predatory fish, smallmouth bass, would expand their range northwards and invade the majority of Ontario lakes. Walleye, a coolwater predator, were projected to shift their range northwards and undergo extirpations from southern regions within Ontario where they are currently found in high abundances. We found that cisco, a cold-water forage fish, may undergo range contractions and experience a thermal squeeze into the most northern regions of the province. Lastly, we determined that co-occurrence of smallmouth bass and walleye would increase, specifically in central and northern regions of Ontario. We expect that fish distributions will change faster and at times, in unexpected directions (e.g. walleye) than previously projected by older climate models (e.g. projections made using earlier climate data). For example, extreme scenario fish projections based on earlier climate models (e.g. Chu *et al.*, 2005; Sharma *et al.*, 2007) are now considered conservative estimates of fish distribution changes as greenhouse gas emissions continue to increase. Even in the past 30 years, increases in mean annual air temperatures have been linked to northerly range shifts of warm- and coolwater sportfish species and southern range contractions of many bait fish at rates much faster than expected (Alofs *et al.*, 2014). Such drastic changes in projections for ecologically important predatory and forage fish from all thermal guilds will have implications for species interactions and community assembly for lakes in the future.

Smallmouth bass

We project that smallmouth bass may expand their range northwards under scenarios of climate change. If July air temperatures increase by more than 4 °C, smallmouth bass thermal habitat increases, making all lakes in Ontario suitable for smallmouth bass. Historically, populations of smallmouth bass in Ontario have been limited to the south and south-central regions of Ontario. This boundary has largely been attributed to cooler summer temperatures in central

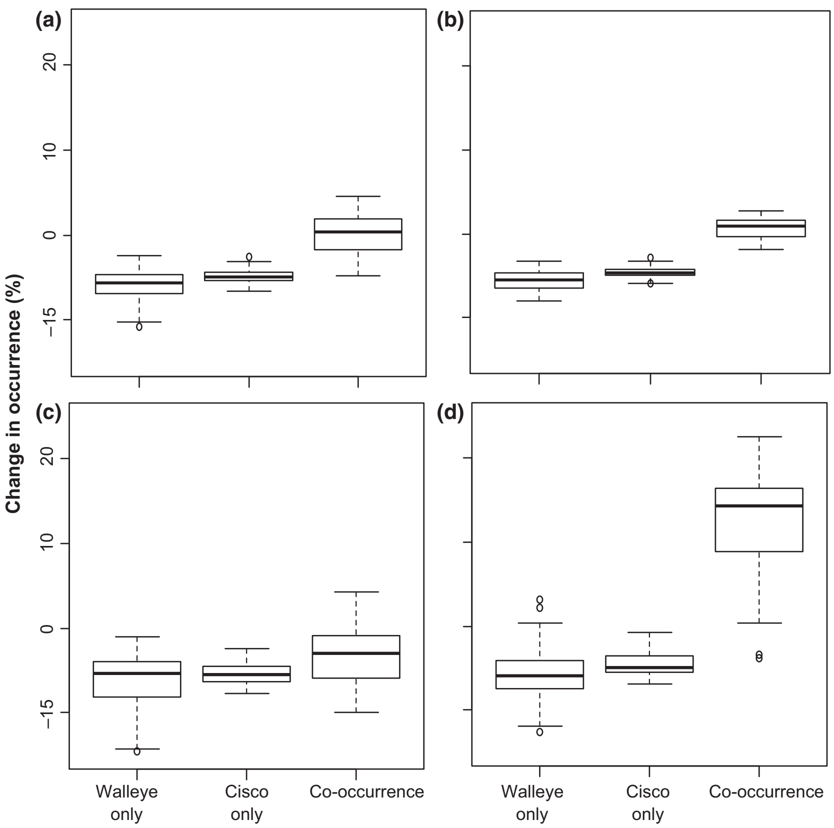

Figure 4 Projected change in walleye and cisco occurrence in 2070 in (a) all of Ontario, (b) southern Ontario, (c) central Ontario and (d) northern Ontario.

and northern Ontario lakes, which reduce the size of young-of-year smallmouth bass and prevent successful overwintering, thereby limiting northern shifts (Shuter *et al.*, 1980; Wismer *et al.*, 1985; Sharma *et al.*, 2007). In a recent publication, Alofs *et al.* (2014) documented that this boundary is already beginning to expand northward as warmwater sportfish (including smallmouth bass) are able to colonize lakes in many previously uninhabitable northern lakes at rates of 12.5–17.5 km per decade. Further increases in air temperatures through 2050 and 2070 will create more thermally suitable lakes for smallmouth bass in northern regions of Ontario (Sharma *et al.*, 2009). Recent circuit theory lake connectivity models have suggested that lakes are highly connected and highly accessible across southern and central Ontario (Melles *et al.*, 2015), thereby facilitating dispersal into more northern habitats. These high accessibility scores ultimately contributed to a higher invisibility scores across Ontario, which were then further exacerbated under warming climate regimes (Melles *et al.*, 2015). In regions north of the Canadian Shield, the dispersal of smallmouth bass would likely be further accelerated due to the northern drainage flow of river (Jackson & Mandrak, 2002; Sharma *et al.*, 2007).

This expansion may be further accelerated by decreasing precipitation rates under scenarios of climate change (IPCC, 2013). Carter *et al.* (2010) demonstrated that smallmouth bass feed less selectively in clearer lakes. As precipitation and sediment run-off into lakes decreases, lakes in Ontario are expected to become clearer (Miller & Russell, 1992), thereby facilitating potentially stronger smallmouth bass predation and competition pressures on other native fish (Sweka & Hartman, 2003).

Walleye

We predict that walleye will shift their range northwards, become extirpated in many southern and central Ontario lakes, and remain sensitive to extirpation in many north-central Ontario lakes. As temperatures are projected to increase at greater rates than previously anticipated (IPCC, 2013), lakes in southern and south-central Ontario will become thermally unsuitable for walleye. Previous studies have predicted expansions of walleye under older scenarios of climate change. For example, under a scenario of doubled atmospheric CO_2 concentrations walleye populations were predicted to undergo a slight northward shift (Shuter *et al.*, 2002), while a ‘business-as-usual’ scenario suggested a 54% expansion across Canada by 2050 (Chu *et al.*, 2005). Historical climate change between 1957 and 2011 suggested more favourable climates for coolwater fish (e.g. Alofs *et al.*, 2014), however as air temperatures continue to increase through 2050 and 2070, it is expected that these habitats will shift to thermally unsuitable states. Increasing air temperatures may affect walleye spawning behaviour as they tend to spawn in cold (6–12 °C), shallow waters (McMahon *et al.*, 1984). In 6–12 °C water walleye egg-survival rates range from 61.5 to

84%, while a drop to 15% survival is observed in 13 °C waters (Koenst & Smith, 1975). Larger increases in air temperatures may lead to longer periods of lake stratification (Adrian *et al.*, 2009), which can negatively affect walleye survival by increasing oxidative stress in the epilimnion (Leach *et al.*, 1977; McMahon *et al.*, 1984). The latest IPCC climate models also predict that summer precipitation levels in Ontario will decline by 0.4 mm in 2050 and 1.2 mm in 2070 (IPCC, 2013). We show that decreasing precipitation can be expected to negatively impact walleye as sediment run-off would be reduced into lakes, thereby decreasing lake turbidity (Miller & Russell, 1992). As adult walleye exhibit a negative phototactic response (Lester *et al.*, 2004), and require low-light conditions to feed (Ryder, 1977), decreasing precipitation could lead to increased starvation rates, as well as greater competition with fish that prefer clear waters.

Cisco

We predict that by 2070, cisco will undergo a southern range contraction and will become extirpated from 80 to 100% of lakes in southern and central Ontario. In recent studies, it has been suggested that cisco are already becoming extirpated from their southern range as a result of climate change and the invasion of cold-water rainbow smelt (Sharma *et al.*, 2011; Fang *et al.*,2012; Jiang *et al.*, 2012). On average, one-fourth of cisco populations could be extirpated by 2070 and remaining cisco populations could be squeezed into small regions of northern Ontario. Cisco populations can only persist if well-oxygenated, cold-water habitat is available as they prefer larger, deeper lakes in cooler geographic regions. Well-oxygenated, cold-water habitat provides suitable habitat refugia for cisco to grow and reproduce (Rudstam & Magnuson, 1985; Jacobson *et al.*, 2010; Fang *et al.*, 2012). In the late summer, however, these cold, well-oxygenated habitats become threatened, as insufficient dissolved oxygen concentrations in the hypolimnion decrease cisco survival. Cisco are then forced by this temperature–oxygen squeeze (Coutant, 1985; Ficke *et al.*, 2007), where the epilimnion becomes too warm and the hypolimnion becomes hypoxic, into unsuitable regions in the water column, resulting in reduced growth and higher summer kill rates (Becker, 1983; Aku *et al.*, 1997). With climate change predicted to increase water temperatures and decrease hypolimnetic dissolved oxygen concentrations, late summer mortalities of cisco may be exacerbated, leading to devastating losses of cisco populations at the southern extents of their range (e.g. Jacobson *et al.*, 2010; Sharma *et al.*, 2011).

Implications of climate change on biotic interactions

We estimate that the co-occurrence of walleye and smallmouth bass will increase by 20% in central Ontario and 68% in northern Ontario by 2070 under scenarios of climate change. In northern Ontario, we also predict that walleye–cisco co-occurrence will increase by 14%. The projected northward expansion of smallmouth bass and the range shift of walleye populations in Ontario could lead to competitive interactions in lakes where both species have not historically co-occurred, further increasing the vulnerability of native walleye populations in central and northern Ontario. These competitive interactions could be reduced in lakes where walleye and cisco co-occur because cisco are predated upon by walleye (Colby *et al.*, 1987; Scott & Crossman, 1998). In lakes where all three species co-occur walleye could utilize cisco as a pelagic prey buffer if they are unable to compete with smallmouth bass.

Smallmouth bass are voracious predators that have been found to out-compete cold-water predators, such as lake trout, for energetically rewarding littoral prey fish (Vander Zanden *et al.*, 1999). The effect of smallmouth bass expansion on coolwater fish is less clear because there are large geographic regions of habitat overlap, and evidence that suggests co-existence is possible when prey availability is high (Johnson & Hale, 1977; Frey *et al.*, 2003; Galster *et al.*, 2012). Individual lake studies have often yielded mixed results: Johnson & Hale (1977) found that smallmouth bass invasions reduced walleye populations in three of four Minnesota lakes, while Kempinger & Carline (1977) found that walleye introductions in smallmouth bass lakes caused bass to decline. A more recent study by Galster *et al.* (2012) analysed stable carbon and nitrogen isotope changes in walleye before and after smallmouth bass colonization in four lakes and found that walleye tissue became more nitrogen-rich and carbon-negative after colonization, indicating a shift in consumption of benthic to pelagic prey. It is possible that this shift occurs because smallmouth bass display competitive territorial behaviour in the presence of other predators, which could exclude walleye from near-shore prey resources (Wuellner *et al.*, 2011; Galster *et al.*, 2012). This agonistic behaviour could have negative effects on walleye populations in smaller lakes where prey is limited, as smallmouth bass have been found to be more effective predators under prey-limiting conditions (Wuellner *et al.*, 2011).

Competitive exclusion is more likely to occur under future climate change for four main reasons: (1) smallmouth bass invasions cause declines in prey resources (especially cyprinids) in northern regions (MacRae & Jackson, 2001); (2) increased metabolic rates create additional food demands at higher temperatures (Brett, 1971); (3) reductions in precipitation across Ontario (IPCC, 2013) are likely to increase water clarity, creating more ideal feeding environments for smallmouth bass, and relegating walleye feeding to night-hours; and (4) the range contractions of many forage species that have already begun in response to changing temperature regimes will become more pronounced (Alofs *et al.*, 2014). As smallmouth bass are such effective predators, it is likely that their colonization of northern Ontario lakes would either displace coolwater predators or decrease their total abundance, as many of these fish compete for the same littoral resources.

CONCLUSION

With climate change, as smallmouth bass invade new lakes, the persistence of native fish assemblages becomes threatened. These colonizations can result in homogenized lake communities, which may decrease the profitability of certain fisheries (Jackson, 2002; Rahel, 2002). Smallmouth bass represent a strong competitive pressure to native top predators, in both cool- (e.g. walleye) and cold-water (e.g. lake trout) fish guilds. We project that the likelihood of invasion of smallmouth bass and extirpation of walleye and cisco are substantially reduced under conservative climate change scenarios and reduced greenhouse gas emissions (e.g. RCP 2.6). Curbing greenhouse gas emissions is urgently needed to limit the invasion of warmwater predators into northern lakes and the extirpation of coolwater and cold-water predators from southern lakes.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Figure S1 Probability of smallmouth bass occurrence in 2050 and 2070.

Figure S2 Probability of walleye occurrence in 2050 and 2070.

Figure S3 Probability of cisco occurrence in 2050 and 2070.

Figure S4 Projected change in walleye and smallmouth bass co-occurrence in 2050.

Figure S5 Projected change in walleye and cisco co-occurrence in 2050.

Table S1 Summary of variables of the lakes in our dataset.

BIOSKETCH

Thomas M. Van Zuiden and **Miranda Chen** are the two primary authors of this manuscript. Both Thomas and Miranda are graduate students at York University under the supervision of Prof. Sapna Sharma. Their research interests primarily include how climate change may impact fish distributions in Ontario.

Author contributions: S.Sh. conceived the ideas; T.V.Z., M.C., S.St., L.L. and S.Sh collected the data; T.V.Z., M.C., S.St., L.L. analysed the data; and T.V.Z., M.C., S.St., L.L. and S.Sh led the writing.

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