

Walleye out of the frying pan and into the fire: how will climate change influence Ontario walleye (*Sander vitreus*) and smallmouth bass (*Micropterus dolomieu*) populations? Do smallmouth bass invasions negatively influence walleye abundance?

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ABSTRACT

Climate change will impact freshwater fish communities in Ontario. Warmwater species are expanding their ranges northward while cool and coldwater species are expected to shift or decline under the current rates of warming. Our first objective was to examine how a warmwater predator, smallmouth bass (*Micropterus dolomieu*) and a coolwater predator, walleye (*Sander vitreus*), will respond to climate change. Our second objective was to determine if smallmouth bass expansions negatively influence Ontario walleye abundances. Data was provided by the Ontario Ministry of Natural Resources, Intergovernmental Panel on Climate Change, and Climatic Research Unit. We projected that smallmouth bass will undergo range expansions throughout Ontario while walleye will become extirpated in their southern ranges and shift into northern waters. We also observed that there were fewer walleye at the landscape scale when they share lakes with smallmouth bass. These findings underscore the importance of proactive fisheries management and curbing climate change.

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Appendix figure 1: Methodological workflow overview, outlining the steps required to repeat this chapter 1 of this project. Red boxes indicate our approach to answering research questions while blue boxes expand on these approaches with more specific detail.

GENERAL INTRODUCTION

The most recent climate report from the Intergovernmental Panel on Climate Change (IPCC 2013) predicts that global air temperatures will rise by 0 to 4.8°C by the year 2100. These changes are expected to affect global biodiversity across multiple biomes (Sala *et al.*, 2000; Newbold *et al.*, 2015), leading to numerous extinction events (e.g. Thomas *et al.*, 2004; Bellard *et al.*, 2012), as well as range contractions, shifts, and expansions of certain species depending on their temperature preferences (e.g. Walther *et al.*, 2002; Parmesan & Yohe, 2003; Chu *et al.*, 2005). Freshwater systems are especially vulnerable to climate change, whereby previous research has demonstrated how physical, chemical and biological properties of lakes respond rapidly to climate-related changes (ACIA 2004; Adrian *et al.*, 2009). In Ontario, temperatures are projected to increase while precipitation is predicted to decrease (IPCC, 2013). Higher air temperatures coupled with decreased precipitation rates will lead to higher water temperatures, earlier and longer periods of lake stratification, and decreased run off into lakes (De Stasio *et al.*, 1996; Livingston & Lotter, 1998; Adrian *et al.*, 2009).

Freshwater fishes are particularly sensitive to these changes as they require specific climatic conditions to effectively grow, feed, and spawn (Magnuson *et al.*, 1990; Shuter & Post, 1990). Climate projections from previous research have indicated that climate change will result in future range contractions for coldwater fish, expansions or shifts for coolwater fish, and range expansions for warmwater fish (Shuter *et al.*, 2002; Chu *et al.*, 2005; Sharma *et al.*, 2007). More recently Alofs *et al.* (2014) documented unprecedented northerly expansions of many warmwater predators between 1957 and 2011 in Ontario lakes, indicating that the predicted effects of climate change have already begun to occur in freshwater systems.

We chose to research the effects of climate change on Ontario walleye (*Sander vitreus*) populations because they are freshwater predators that play an important role in shaping aquatic

communities through top-down trophic interactions, and are also sensitive to changes in temperature and water clarity (McMahon *et al.*, 1984; Lester *et al.*, 2004; Pandit *et al.*, 2013). Walleye tend to prefer waters that are between 18 and 25°C (Koenst & Smith Jr., 1975; Hokanson 1977). Optimal growth occurs between 20 and 24°C and if possible, walleye seek refuge in waters above 24°C (McMahon *et al.*, 1984). They also tend to prefer turbid lakes because of a reflective tissue layer in their retina called the tapetum lucidum that makes them sensitive to light (Lester *et al.*, 2002). If lakes are too oligotrophic, walleye feeding hours become limited to after dusk (Lester *et al.*, 2002).

We were also interested in predicting the effects of climate change on smallmouth bass (*Micropterus dolomieu*) populations in Ontario. Smallmouth bass are aggressive warmwater predators that are currently undergoing northerly range expansions (Alofs *et al.*, 2014) and have been previously observed to outcompete other top predators for prey resources (Vander Zanden *et al.*, 1999; Johnson *et al.*, 2008). Typically smallmouth bass live in waters that are between 20 to 32°C, however their ideal temperatures for growth are between 26 and 29°C (Clancey 1980; Shuter *et al.*, 1980; Edwards *et al.*, 1983). Historically, temperature has been the most limiting factor preventing northerly smallmouth bass range expansions as their growth stops in waters below 14°C (Edwards *et al.*, 1983). If mean water temperatures do not reach 14°C during the summer, smallmouth bass are unable to grow to an adequate size that would allow them to successfully overwinter (Shuter *et al.*, 1980).

As temperatures are expected to increase as a result of climate change, warm and coolwater species may undergo range contractions, shifts, or expansions depending on their thermal preferences (Magnuson *et al.*, 1997; Rahel, 2002; Chu *et al.*, 2005). These distribution changes may lead to novel biotic interactions in lakes colonised by non-native species (Sharma *et*

al., 2009; Alofs & Jackson, 2015), increased competition and predation pressure on native species (MacRae & Jackson, 2001; Sharma *et al.*, 2007), and changes in ecosystem food web dynamics (Vander Zanden *et al.*, 1999; Galster *et al.*, 2012).

Our research objectives for this project were twofold: first we wanted to predict how climate change would alter the distributions of both walleye and smallmouth bass across Ontario's landscape; second, we were interested in examining how the projected smallmouth bass invasions may influence walleye abundance in Ontario lakes. Smallmouth bass invasions have previously been associated with cyprinid declines (MacRae & Jackson, 2001) as well as declines of some predator species (especially salmonids) (Vander Zanden *et al.*, 1999; Vander Zanden *et al.*, 2004) and may negatively influence walleye populations. This would be damaging to the economy of the Great Lakes region because their recreational and commercial walleye fisheries produce over 10-million dollars per year (Kinnunen 2003; Pandit *et al.* 2013). We hypothesized that under climate change scenarios smallmouth bass would continue to expand their range northward while walleye populations would either undergo northerly range expansions as well, or undergo northerly range shifts (Shuter *et al.*, 2002; Chu *et al.*, 2005; Sharma *et al.*, 2007). We further hypothesized that as smallmouth bass ranges expand, they will cause reductions in native walleye abundance.

CITATIONS FOR CHAPTERS SUBMITTED FOR PUBLICATION

This thesis was written as a series of two manuscripts, in collaboration with co-authors from Sapna Sharma's lab that have been submitted to journals for consideration for publication. The following is the citation list, including co-authorship from this thesis:

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Note 1: * signifies co-first authors of this manuscript.

Note 2: All cisco writing and analysis were completed by M. Chen, and therefore excluded from this thesis.

Note 3: Analysis of smallmouth bass projections performed by Samantha Stefanoff; boxplots created by Lianna Lopez.

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Chapter 1

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

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Keywords: climate change, smallmouth bass, walleye, thermal guilds, range shifts, biotic interactions, competition

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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 two fish species from different guilds to climate change in Ontario and consequently, the potential for novel competitive interactions between them. We focus on lakes in Ontario because it is a dynamic region that encapsulates the northern range extents of many warmwater fish species.

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

Results: Smallmouth bass occurrence rates were predicted to increase by ~306% by 2070 relative to their current distributions while walleye were projected to decline by 22%. By 2070, walleye-smallmouth bass co-occurrence was predicted to increase by 11%, increasing walleye vulnerability in central and northern Ontario as a result of increased competition with smallmouth bass.

Main conclusions: These results highlight two unique responses to climate change: range expansions, and northward range shifts, for warmwater, and coolwater fish species, respectively. Alterations in distributions of these two 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.

INTRODUCTION

Mean global air temperatures are predicted to rise by 0.3-4.8°C by the year 2100 (IPCC, 2013) – a major concern for the structure and functioning of aquatic ecosystems. Lakes are particularly vulnerable because surface water temperatures, water levels, ice phenology, lake chemistry, and the intensity of biotic interactions are all sensitive to changes in air temperature and precipitation caused by climate change (Adrian *et al.*, 2009). This vulnerability is exacerbated by their relative isolation from one another within landscapes and their overexploitation by humans (Woodward *et al.*, 2010). 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). Fish are expected to respond to these habitat modifications differently based on their individual thermal preferences. Our research focuses on how future changes in climate may modify distributions and potential future interactions of fish that prefer warm (~25-29°C), and cool (~20-24°C), (Magnuson *et al.*, 1990). Fish from these guilds are expected to respond differently to climate change (e.g. Shuter *et al.*, 2002; Chu *et al.*, 2005; Sharma *et al.*, 2007). Within the past 30 years, sportfish in Ontario have shifted their range northwards by 12.5-17.5 kilometres 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 coldwater 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 how climate change will impact warm and coolwater predator species and analyse how these changes may lead to increased rates of co-occurrence and potential biotic

interactions. Smallmouth bass (*Micropterus dolomieu*) was chosen to represent the warmwater guild, and walleye (*Sander vitreus*) was chosen as our coolwater species

Smallmouth bass are a warmwater (preferred water temperatures: 26-29°C) predatory fish found mainly in the central United States and southern Ontario (Shuter *et al.*, 1980; Edwards *et al.*, 1983; 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 are predicted to expand their range northward (e.g. Chu *et al.*, 2005; Sharma *et al.*, 2007).

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 Jr., 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).

Alterations in warmwater and coolwater fish species distributions resulting from climate change may facilitate changes in food web dynamics and ecosystem function, increasing the frequency of 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 may result in novel competitive interactions for shared food resources (Johnson & Hale, 1977; Frey *et al.*, 2003; Wuellner *et al.*, 2011).

Research objectives

The overall goal of this study is to identify the differential responses of ecologically important predatory fishes from warm and coolwater guilds to climate change and how distributional changes may alter the potential for biotic interactions between invasive and native top predators. We focus our study in the province of Ontario, a dynamic region that encapsulates the northern range extent of warmwater species and is in the middle range of coolwater species. More specifically, our first objective is to identify the important abiotic and climatic predictors of smallmouth bass and walleye occurrence in Ontario lakes.

Our second objective is to develop predictive models to forecast future occurrences of smallmouth bass and walleye in the years 2050 and 2070. We projected the occurrence of smallmouth bass and walleye 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. We hypothesize that smallmouth bass and walleye populations will expand across Ontario.

Our third objective is to determine how co-occurrence rates of two predatory fish, walleye and smallmouth bass, will change in response to changing temperature and precipitation regimes. We anticipate that these changes in co-occurrence will vary spatially across Ontario. Since both

predatory fish consume similar prey (Frey *et al.*, 2003), it is expected that increased co-occurrence rates will lead to novel competitive interactions. As smallmouth bass are stronger competitors than walleye (Wuellner *et al.*, 2011), increases in smallmouth bass habitat suitability across Ontario could increase 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

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 (i.e. mean depth, surface area), chemistry (i.e. secchi depth, pH) and climate variables (i.e. growing degree days). Additional data were also obtained from the OMNR Broad Scale Monitoring (BSM) Program 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 dataset. Of the 722 lakes, 605 overlapped with the AHI dataset which were subsequently updated to reflect more recent data. With 117 new lakes added from the BSM program, we compiled a dataset of 10,001 Ontario lakes (Table S1). A dataset 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 under-sampled 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 1950-2000. Variables included 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; Stocker *et al.*, 2013; IPCC, 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 (van Vuuren & Riahi, 2011; Moss *et al.*, 2010; Rojeli *et al.*, 2012). A total of 126 climate change scenarios were used to project smallmouth bass, walleye and cisco occurrence.

Data analysis: fish occurrence models

We developed logistic regression models for smallmouth bass and walleye occurrence in Ontario lakes. We divided our combined AHI-BSM dataset (n=9736) into two random and independent subsets: 80% of the dataset was retained for model training, 20% for model validation. Variables were assessed for normality: 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 among environmental predictor variables used in each species distribution model. 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 predictor variables for smallmouth bass, walleye and cisco occurrence (Blanchet *et al.*, 2008).

We used Receiver Operating Characteristics (ROC) curves to identify thresholds (0 – 1) that maximize the sensitivity (percent of correctly predicted presences) and specificity (percent 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). A Cohen's Kappa statistic for each logistic model was also calculated to assess the model's predictive power (Fielding & Bell, 1997). All analyses were performed in the R-language environment (R Development Core Team, 2012).

Fish projections under climate change

We predicted smallmouth bass and walleye 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.

Percent change in walleye-smallmouth bass co-occurrence

Percent change in walleye and smallmouth bass 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 only, and co-occurrence of walleye and smallmouth bass. The median percent 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 ($n_{\text{central}}=3546$), while northern latitudes were above 50.5°N ($n_{\text{northern}}=674$), and southern latitudes were below 48.1°N ($n_{\text{southern}}=5421$). Percent change in co-occurrence of walleye and smallmouth bass in these regions was calculated to better incorporate spatial variability in biotic interactions across the province.

RESULTS

Fish occurrence models

Smallmouth bass preferred larger, clearer lakes, in regions with higher temperatures and lower precipitation (Table 1). Model validation yielded a classification success of 84% (Table 2). Walleye preferred larger, turbid lakes, in cooler regions with higher precipitation (Table 1). This model had a classification success of 80% (Table 2) when tested on an independent validation dataset.

Fish projections

Smallmouth bass were present in 19% ($n_{\text{smallmouth bass}} = 1834$, $n_{\text{total}} = 9736$) 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). Ontario lakes became completely saturated by smallmouth bass under climate scenarios if mean July air temperatures increases by more than 4°C.

Walleye were present in 28% ($n_{\text{walleye}} = 2781$, $n_{\text{total}} = 9736$) 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 extirpation under

scenarios of climate change (Fig. 1e,f). 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). 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).

Walleye-smallmouth bass 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,b). 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. 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 walleye-smallmouth bass co-occurrence is expected to increase by 20% and 68% in the central and northern regions respectively, by 2070. 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 expected to increase by 39% and 18% for central and northern regions respectively. Conversely, the southern region may experience a slight decline in walleye-smallmouth bass co-occurrence by 0.3%, (Fig. S4).

DISCUSSION

This study highlights two unique responses of fish species from warm and coolwater guild to climate change in an especially sensitive region where warmwater fishes are at their current northern extent and coolwater fishes are in the middle of their 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. 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 the IPCC 2001 data). For example, fish projections using ‘extreme’ climate scenarios 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 baitfish 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.

How climate data was utilised in the models

To better understand the uncertainty in species range expansions and contractions, we projected species distributions using all 19 General Circulation Models (GCMs) and their respective greenhouse gas emissions scenarios (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).

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, allowing smallmouth bass to saturate all lakes in Ontario. 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 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 colonise lakes in many previously uninhabitable northern lakes at rates of 12.5 to 17.5 kilometres per decade. Under climate change, July air temperatures are projected to increase by 2050 and 2070,

allowing more lakes to become thermally suitable for smallmouth bass, enabling them to expand their range northerly provided that smallmouth bass continue to disperse at current rates via natural and human-mediated pathways (Sharma *et al.*, 2009; Alofs *et al.*, 2014). 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 runoff 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 CO₂ 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 61.5-84%, while a drop to 15% survival is observed in 13°C waters (Koenst & Smith Jr., 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 0.4mm in 2050 and 1.2mm in 2070 (IPCC, 2013). We show that decreasing precipitation can be expected to negatively impact walleye as sediment runoff would be reduced into lakes, thereby decreasing lake turbidity (Miller & Russel, 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.

Implications of climate change on biotic interactions

We estimate an increase in walleye-smallmouth bass occurrence by 20% in central Ontario and 68% in northern Ontario by 2070 under scenarios of climate change. The projected northward expansion of smallmouth bass and the range shift of walleye populations in Ontario could lead to novel competitive interactions, further increasing the vulnerability of native walleye populations in central and northern Ontario.

Smallmouth bass are voracious predators that have been found to out-compete coldwater 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 suggest co-existence is possible when prey availability is high (Johnson & Hale, 1977; Frey *et al.*, 2003; Galster *et al.*, 2012). Competitive exclusion is more likely to occur under future climate change for three main reasons: (1) smallmouth bass invasions cause declines in prey resources (e.g. cyprinids) in northern regions (MacRae & Jackson, 2001); (2) increased metabolic rates create additional food demands at higher temperatures

(Brett, 1971); and (3) 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). Furthermore, a study by Wuellner *et al.*, (2011) suggests that smallmouth bass are slightly more effective predators than walleye, which could give them a slight advantage during times of resource limitation. As smallmouth bass are such effective predators, it is likely that their colonisation 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

The impacts of climate change on ecologically important predatory fishes across two thermal guilds also have significant implications for commercial and recreational fisheries (Matsuzek *et al.*, 1990; Post *et al.*, 2002; Dove-Thompson *et al.*, 2011). Canadian recreational fisheries alone are valued at over 4.6 billion dollars annually (Shuter *et al.*, 1998). With climate change, as smallmouth bass invade new lakes, the persistence of native fish assemblages becomes threatened. These colonisations can result in homogenised lake communities, which may decrease the profitability of certain fisheries (Rahel, 2002; Jackson, 2002). Smallmouth bass represent a strong competitive pressure to native top predators, in both cool- (e.g. walleye) and coldwater (e.g. lake trout) fish guilds. We project that the likelihood of smallmouth bass invasions and extirpations of walleye are substantially reduced under conservative climate change scenarios of reduced greenhouse gas emissions (e.g., RCP 2.6). Consequently, co-occurrences of smallmouth bass and walleye are also reduced under the more conservative scenarios, thus lowering the probability of potentially competitive biotic interactions. Curbing greenhouse gas emissions is urgently needed to limit the invasion of warmwater predators into northern lakes and the extirpation of coolwater and coldwater predators from southern lakes.

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TABLES

Table 1: Coefficients of significant ($p < 0.01$) predictors for logistic regression models for smallmouth bass and walleye populations. Mean conditions of environmental characteristics in lakes with fish present and 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

Table 2: Classification success, specificity, sensitivity, and kappa statistic values of the predictive smallmouth bass and walleye occurrence models.

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

FIGURES

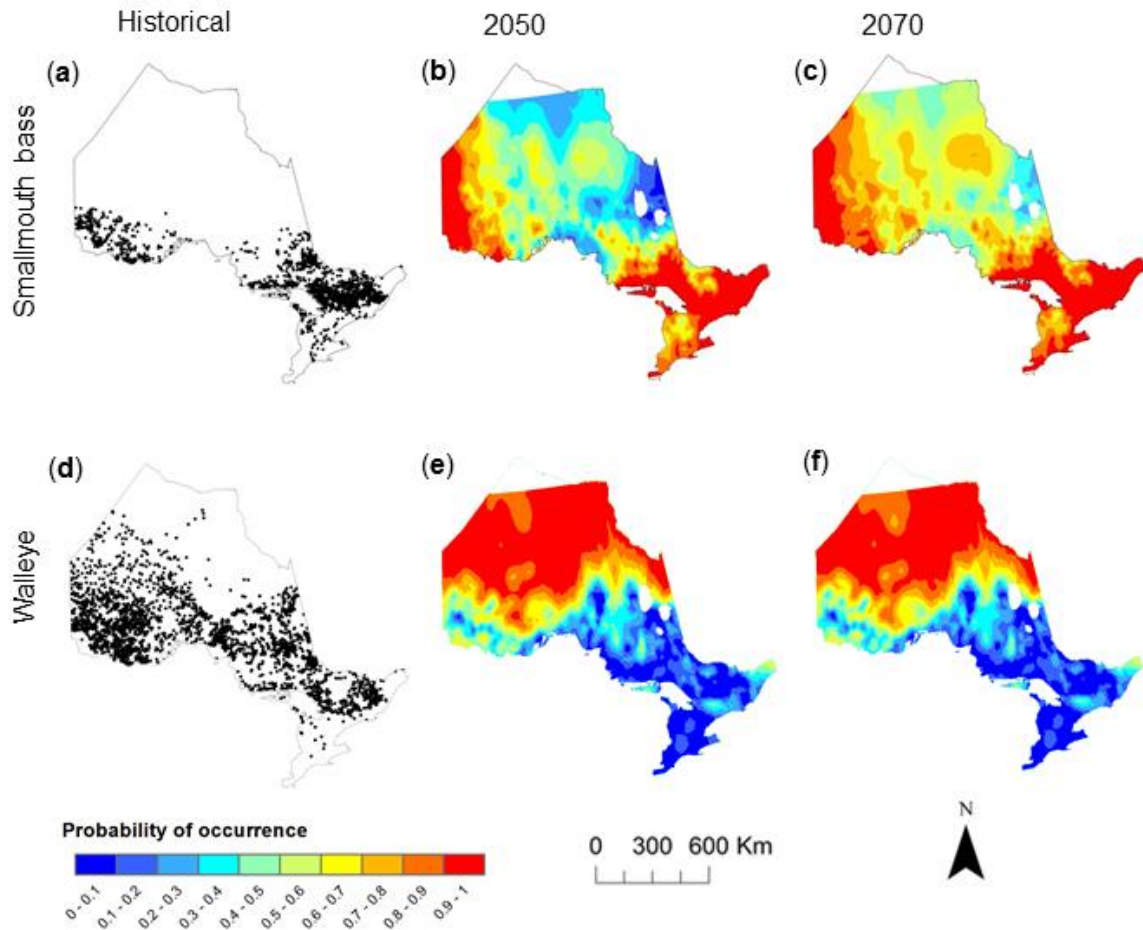


Figure 1: Distributions of smallmouth bass (a) historically, (b) in 2050, and (c) in 2070 under 126 scenarios of climate change. Distributions of walleye (d) historically, (e) in 2050, and (f) in 2070. Mean probabilities of occurrence were calculated in 2050 and 2070 using all climate change scenarios for each period.

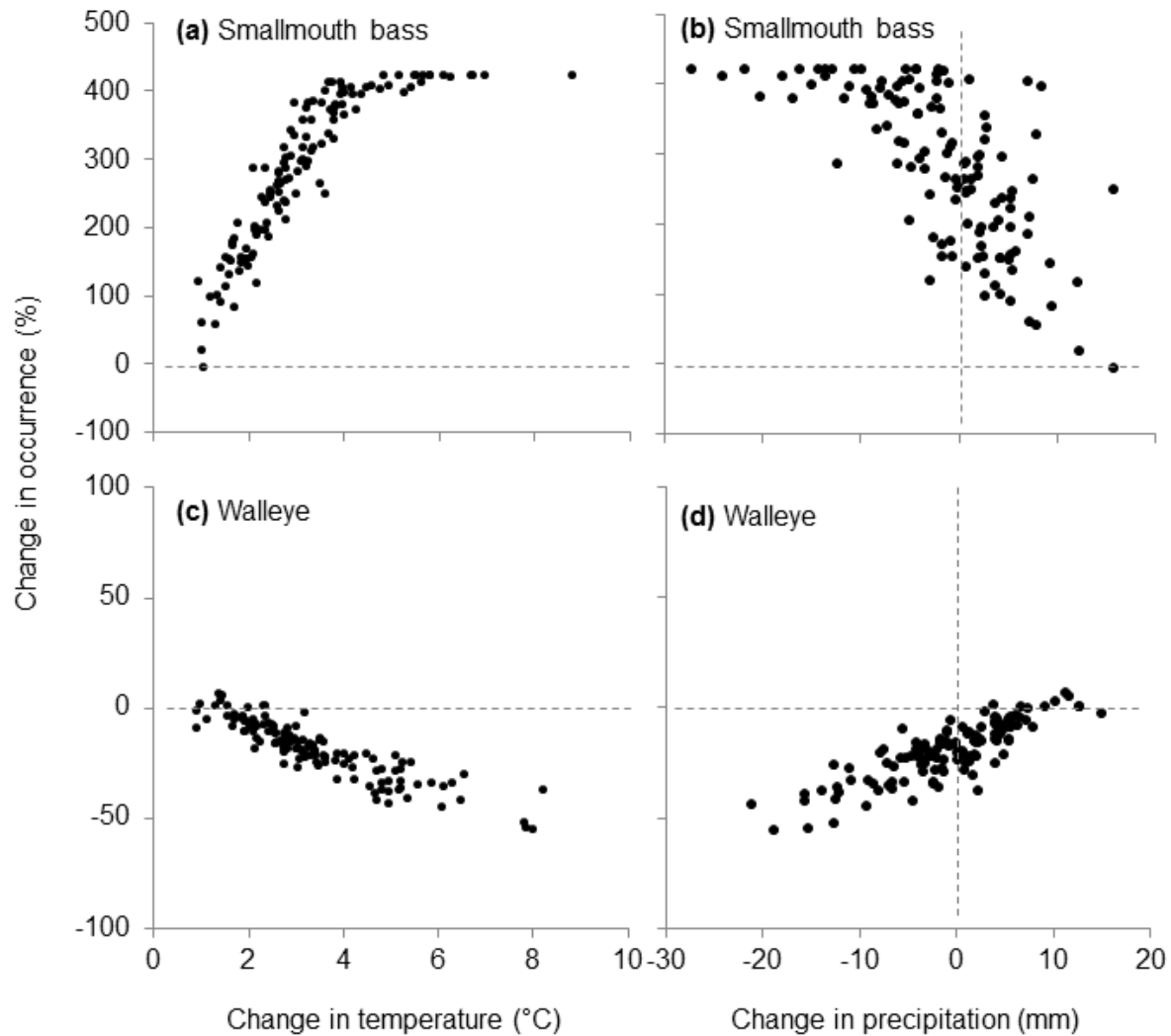


Figure 2: Percent change in occurrence of smallmouth bass under 126 scenarios of climate change in 2050 and 2070 as temperature changes (a), and as precipitation changes (b). Percent change in occurrence of walleye under climate change scenarios as temperature changes (c), and as precipitation changes (d).

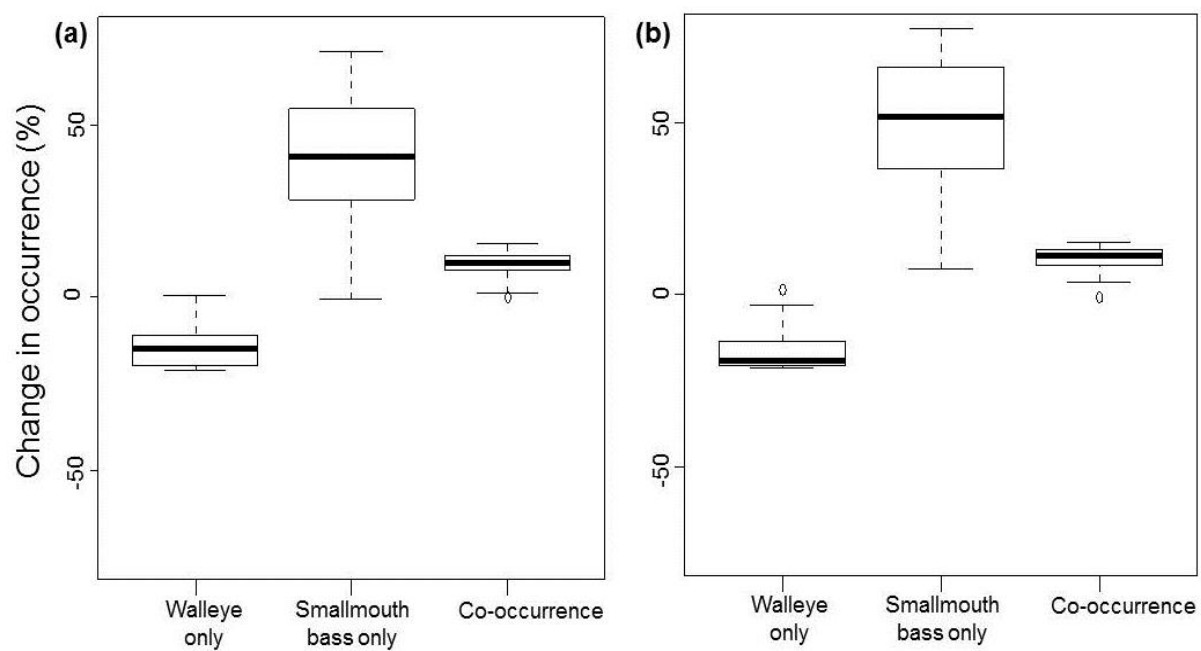


Figure 3: Projected change in walleye and smallmouth bass occurrence (a) in 2050 and (b) in 2070.

SUPPORTING INFORMATION

Table S1: Summary of geographic, environmental and climate variables of the lakes in our dataset.

Variable	Minimum	Maximum	Mean
Latitude	42.1	55.3	47.6
Longitude	-95.1	-74.5	-83.6
Surface area (ha)	0.1	79771.6	354.4
Perimeter (km)	0.1	938.3	14.0
Lake elevation (m)	42.0	875.0	338.9
Maximum depth (m)	0.2	213.5	17.0
Mean depth (m)	0.1	47.5	5.6
Secchi depth (m)	0.2	22	3.6
pH	4.0	10.0	7.4
Total dissolved solids (mg/L)	2.0	1294.0	59.1
Conductivity (uS/cm)	3.0	1243.1	86.8
Dissolved Oxygen (mg/L)	0.7	15.4	8.4
Mean July air temperature (°C)	14.1	22.4	17.8
Mean August air temperature (°C)	12.9	21.6	16.4
Mean annual air temperature (°C)	-4.2	9.5	2.5
July precipitation (mm)	55	106	82.2
Mean summer precipitation (mm)	66.7	97.3	85.0

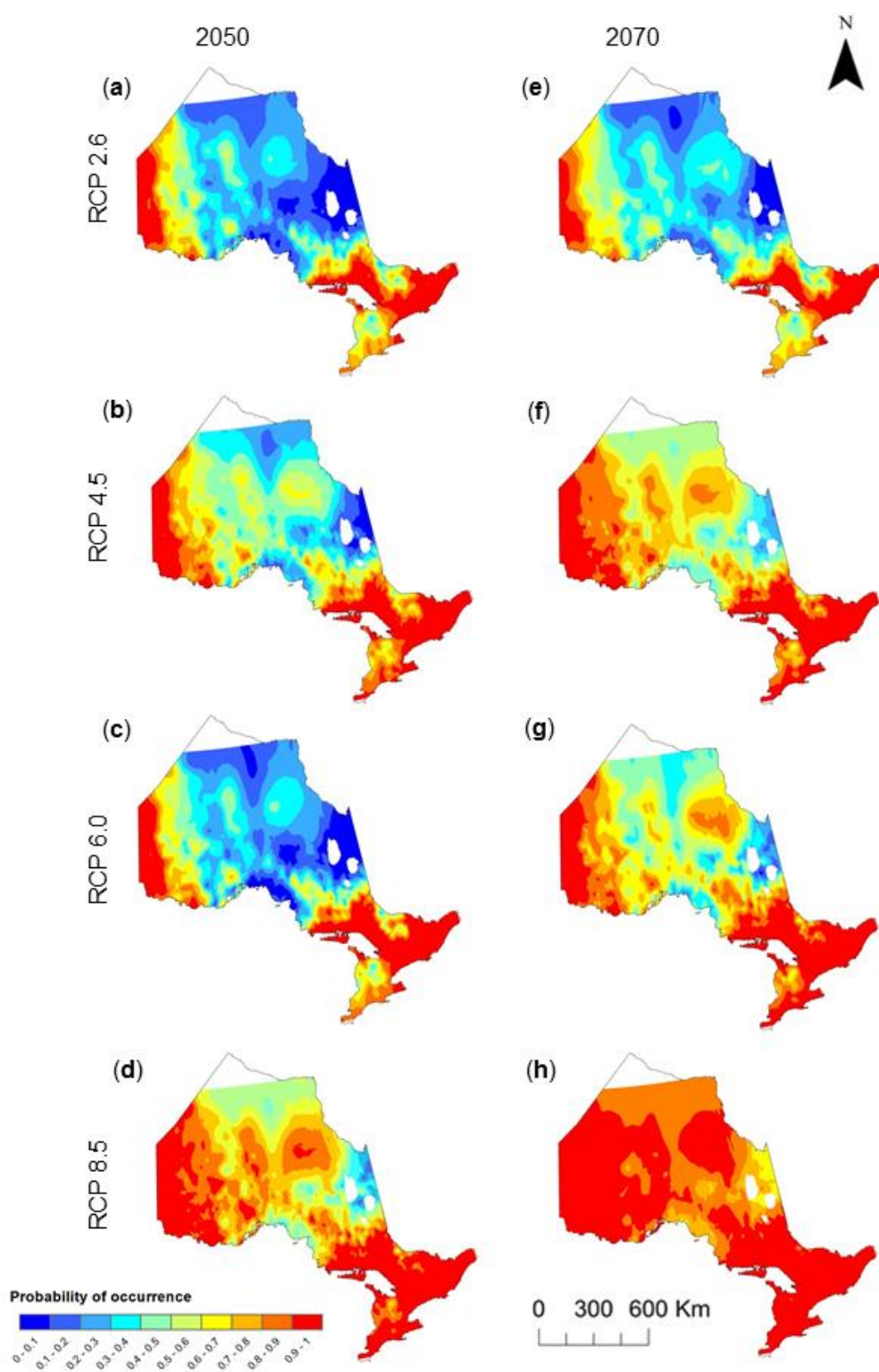


Figure S1: Probability of smallmouth bass occurrence for each greenhouse gas scenario in 2050 and 2070.

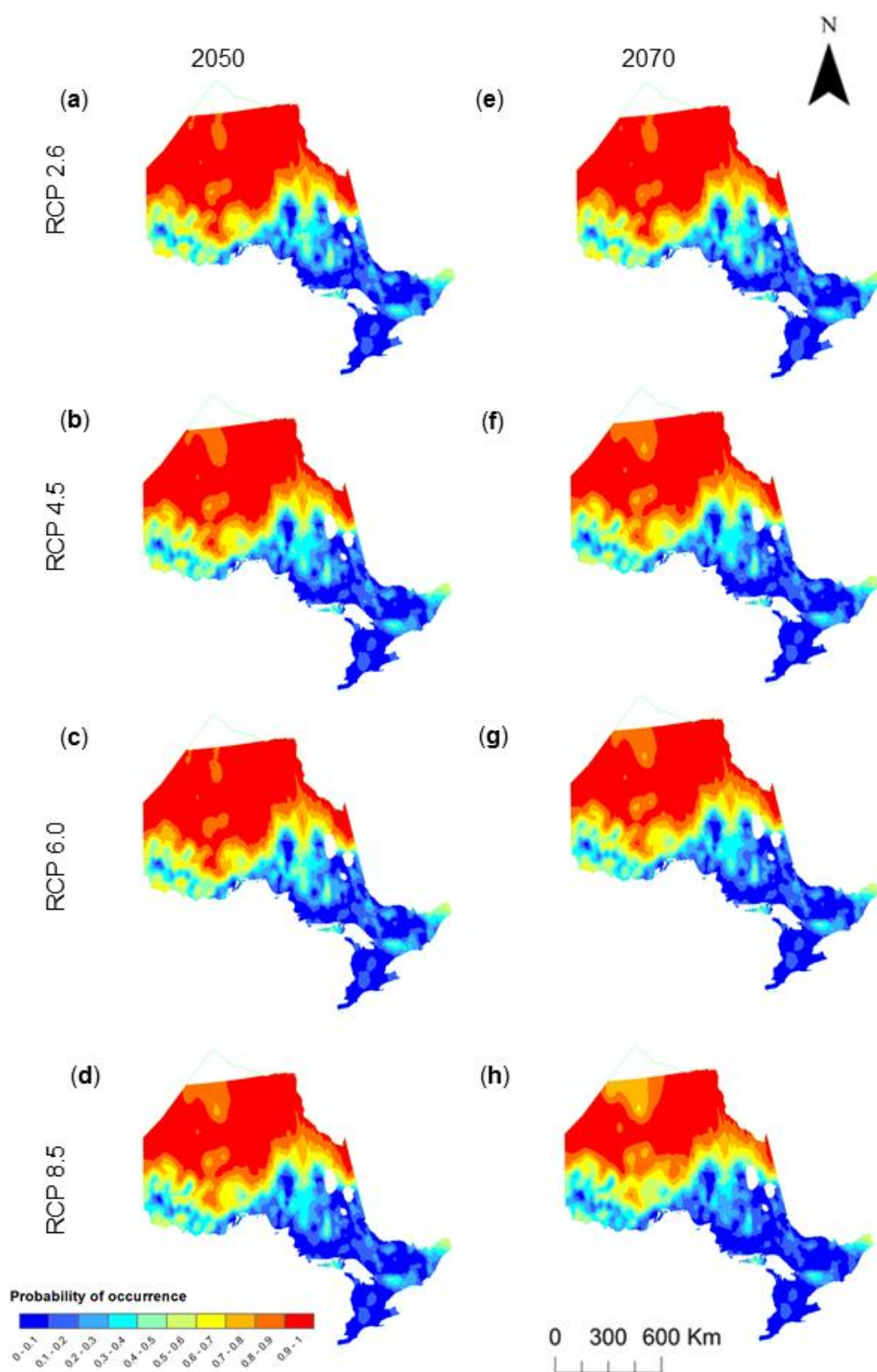


Figure S2: Probability of walleye occurrence for each greenhouse gas scenario in 2050 and 2070.

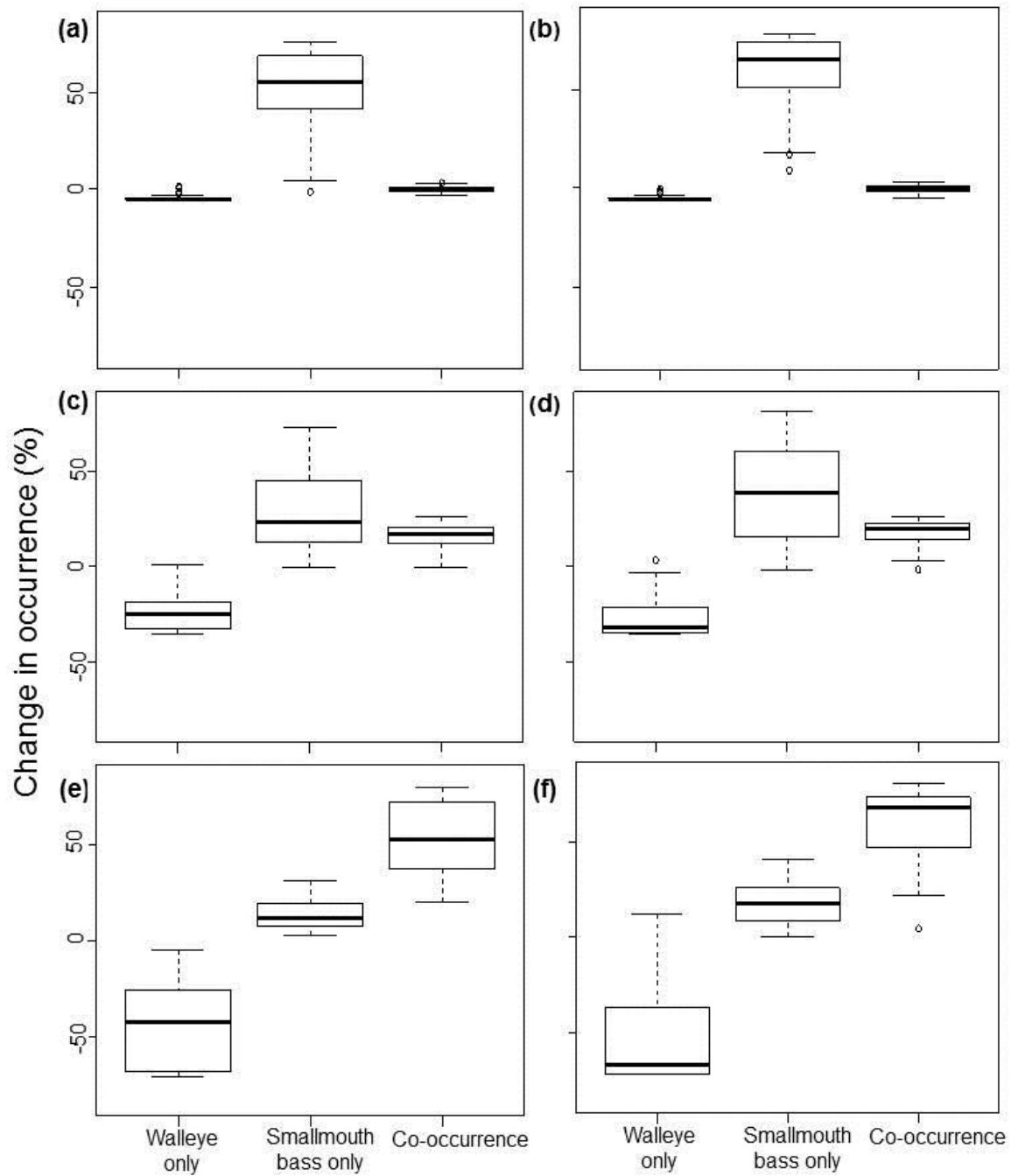


Figure S3: Projected change in walleye and smallmouth bass occurrence in southern (a,b), central (c,d) and northern (e,f) regions of Ontario in 2050 (a,c,e) and 2070 (b,d,f).

Chapter 2

Examining the influence of smallmouth bass invasion on walleye populations in Ontario lakes: Can walleye beat the heat?

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Keywords: walleye, smallmouth bass, co-occurrence, climate change, biotic interactions, competition

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ABSTRACT

Increases in global air temperatures associated with climate change are expected to facilitate northerly range expansions of smallmouth bass, and range shifts of walleye populations in Ontario. Continued northward smallmouth bass expansion may create novel competitive interactions in northern lakes where smallmouth bass have been historically absent. We aim to identify how the invasion of smallmouth bass influences walleye abundances across Ontario at the landscape scale. Smallmouth bass were found to prefer different lake environmental conditions than walleye, however, when walleye and smallmouth bass were found in the same lakes, walleye abundance was reduced. Multiple-regression and zero-inflated negative binomial models suggested that walleye abundance is negatively influenced by smallmouth bass occurrence. Subsequently, we predicted that under future scenarios of climate change the overlapping occurrence of walleye and smallmouth bass will increase by 86% to 332% by the year 2070. As walleye abundance is reduced in lakes with smallmouth bass, we predict that increased co-occurrence between smallmouth bass and walleye will result in Ontario-wide walleye reductions under scenarios of climate change.

INTRODUCTION

Walleye (*Sander vitreus*) are a coolwater predator species (Koenst & Smith Jr. 1975) that play an important role in lake-ecosystem dynamics by shaping aquatic communities through top-down trophic cascades (Bowlby et al. 2010; Pandit et al. 2013). Walleye are also popular angling targets for commercial and recreational fisheries, generating over ten million dollars in revenue annually for the economy of the Great Lakes region (Kinnunen 2003; Pandit et al. 2013).

Smallmouth bass (*Micropterus dolomieu*) are warmwater predators (Edwards et al. 1983) and an invasive species in central and northern Ontario (Vander Zanden et al. 2004). Unlike walleye, who only feed in dim-light conditions, smallmouth bass are opportunistic, generalist feeders that eat constantly over 24-hour periods (Johnson & Hale 1977; Warren 2009; Wuellner et al. 2011). Historically, lakes that have been invaded by smallmouth bass (either naturally or by human stocking) see declines in prey-fish density (especially cyprinids) (Macrae & Jackson 2001; Jackson 2002; Sharma et al. 2007). Many predator species, such as salmonids also experience population declines after smallmouth bass invasions (Vander Zanden et al. 1999). Laboratory studies have revealed smallmouth bass to be stronger competitors than walleye under food-limiting conditions (Wuellner et al. 2011). Whole lake studies however, yielded mixed results, some illustrating that smallmouth bass introductions have negative effects on walleye population levels (Johnson & Hale 1977; Inskip & Magnuson 1983) while others have found smallmouth bass have no effect on walleye fitness (Hall & Rudstam 1999; Fayram et al. 2005).

Research objectives

Our primary research objective is to identify how smallmouth bass influence walleye populations in Ontario lakes. Smallmouth bass are a voracious, competitive species that are expected to experience range expansions under increasing temperature regimes (e.g. Sharma et

al. 2007; Van Zuiden & Chen et al. in review). The consequence of these expansions on walleye populations at the landscape level has not been previously explored. Ontario was chosen as our study region because it contains a popular, valuable walleye fishery (Lester et al. 2003; Pandit et al. 2013), and comprises the northern range limit of smallmouth bass (Shuter et al. 1980; Scott & Crossman 1998; Sharma et al. 2007). Our research objective comprises four questions: i) Do walleye and smallmouth bass prefer the same lakes? ; ii) how does the presence of smallmouth bass influence walleye abundance?; iii) which environmental conditions favour smallmouth bass and walleye co-occurrence?; and iv) how will smallmouth bass-walleye co-occurrence alter in Ontario under scenarios of climate change? We hypothesize that smallmouth bass will negatively influence walleye populations as they may outcompete walleye (Galster et al. 2012). As smallmouth bass are projected to increase their range northwards (Sharma et al. 2007; Sharma & Jackson 2008; Van Zuiden & Chen et al. in review) and walleye populations are projected to be extirpated in southern Ontario and shift their range northwards (Van Zuiden & Chen et al. in review), we hypothesize that co-occurrence of walleye and smallmouth bass will increase under climate change, further exacerbating walleye populations in Ontario under scenarios of climate change.

METHODS

Lake survey and climate data acquisition

The Ontario Ministry of Natural Resources (OMNR) Broadscale Monitoring (BSM) Program collected data on 722 lakes between 2008 and 2012. The program was designed to sample fish habitats at several different depths (Sandstrom et al. 2010). Variables measured in this program include lake geography (latitude, longitude), morphology (surface area, depths), chemistry (pH, secchi depth, oxygen levels, etc.), climate (growing degree days), fish occurrence, and fish abundance of over 100 different species.

Climate data for historical (1950-2000) and contemporary (2000-2012) periods was obtained from both the fifth climate assessment report by the IPCC (2013), and the Climatic Research Unit, University of East Anglia (Harris et al. 2014). Climate data for these periods are represented as averages across all years. Climate variables include values for monthly mean, minimum, and maximum air temperatures, as well as total monthly precipitation. Future climate projections for 2050 (2041-2060 average) and 2070 (2061-2080 average) were also obtained from the fifth IPCC climate assessment report (IPCC 2013). Projected future air temperature and precipitation values were extracted from 19 general circulation models (GCMs), each containing between one to four representative concentration pathways (RCPs) that correspond to differing levels of greenhouse gas (GHG) emissions. Each of the 19 GCMs projects climate values using unique calculations and assumptions of atmosphere, ocean, sea-ice, and land components (Hijmans et al. 2005; Stocker et al. 2013; IPCC 2013). The RCP2.6 scenario has the lowest projected GHG emissions in 2050 and 2070 while the RCP8.5 is the “business as usual” scenario and projects the highest GHG emissions (IPCC 2013). The RCP4.5 and 6.0 are intermediate climate scenarios, corresponding to moderate increases in future GHG emissions (IPCC 2013).

Do walleye and smallmouth bass prefer the same lakes?

A redundancy analysis (RDA) was utilised to identify the environmental conditions that structure fish community composition in Ontario lakes. From the 722 lake dataset (Fig. 1), 645 lakes were used to construct the RDA. We excluded 77 lakes because they were missing data for many of the predictor variables that were included (most notably total phosphorus and dissolved organic carbon).

Response variables in the RDA include occurrence of walleye and smallmouth bass, and fishes from the percid, centrarchid, pike, cyprinid, gasterpsteid, sculpin, catostomid, and salmonid families. A species was excluded if it was rare (occurred in fewer than 5% of lakes). Lake morphology (surface area; maximum depth), water chemistry (secchi depth; dissolved organic carbon; total phosphorus), and climate (2000-2012 July mean temperature and total precipitation) were used as explanatory variables to explain variation in the fish community of Ontario lakes.

In the RDA, fish are represented as points in ordination space while the environmental predictors are represented by arrows. If a fish point is oriented close to an arrow, it suggests that the fish tends to occur in lakes where that specific environmental variable is high. If the fish point occurs 180° opposite of the arrow, it suggests that the fish species tends to occur in lakes where that environmental variable has low values.

How does the presence of smallmouth bass influence walleye abundance?

Boxplots were constructed to determine the abundance of walleye (expressed as catch per unit effort: CPUE) in lakes with and without smallmouth bass. We developed multiple linear regression models to identify the influence of smallmouth bass occurrence and environmental conditions on walleye abundance. Multiple linear regression models were utilised because

walleye CPUE is a continuous variable with integer values, and these models perform best when the response variable is continuous. Using CPUE as a response variable in place of total catch is preferable because it accounts for sampling effort of fish habitats at different depths (Tonn & Magnuson 1982; Jackson & Harvey 1997).

In addition to multiple linear regressions, zero-altered negative binomial (ZANB) models, and zero-inflated negative binomial models (ZINB) were also used to identify the influence of smallmouth bass occurrence and environmental conditions on walleye abundance. Zero inflated models were utilised because approximately 31% of lakes in the BSM dataset contain walleye abundances of zero. ZANB and ZINB models will only run when count data are used as the response variable, thus total walleye catch was used for these models. To accommodate for sampling effort in the ZANB and ZINB models, the total number of nets used in each lake was specified as an offset value to adjust the response variable such that sampling effort was considered (Zuur et al. 2009).

Poisson and zero-inflated Poisson models were excluded from this analysis because of the considerable overdispersion in both walleye CPUE and total catch data (see Wenger & Freeman 2008; Zuur et al. 2009). A negative binomial model was also excluded as it could not compensate for the large proportion of zeros present in the BSM dataset.

We divided the 697 lakes into two random, independent data subsets. Eighty percent of the data was kept for model training while the remaining 20% was used for model validation. All predictor variables were tested for normality: lake surface area, maximum depth, and secchi depth were log-transformed to meet assumptions of normality. Multicollinearity among predictor variables in each subsequent model was found to be low. A forward selection procedure containing a double-stop criterion ($\alpha = 0.05$, and R^2_{adj}) developed by Blanchet et al. (2008) was

then implemented to identify which factors were important predictors of walleye abundance. The effectiveness of each model was evaluated by observing how well it was able to predict walleye abundance values from the validation dataset (i.e. we used the model with the highest fit on validation data).

Which environmental conditions favour smallmouth bass and walleye co-occurrence?

We developed a logistic regression model for walleye-smallmouth bass co-occurrence in Ontario inland lakes. Data from the 605 lakes where the BSM program resampled lakes from the Aquatic Habitat Inventory (AHI) survey were used. The AHI survey was conducted between 1957 and 1986 and we chose to analyse the 605 overlapping lakes so that we could compare the rates of walleye-smallmouth bass co-occurrence between historical and contemporary time periods. Similar to the walleye abundance models, these 605 lakes were divided into 80% training and 20% validation datasets; predictor variables were tested for normality, and were subsequently transformed if assumptions were not met; and were subjected to a double-stop criterion forward selection procedure (Blanchet et al. 2008) for variable selection. To maximise the sensitivity (proportion of true positives) and specificity (proportion of true negatives) of the walleye-smallmouth bass co-occurrence model, Receiver Operating Characteristics (ROC) curves were used. ROC curves are recommended as the number of co-occurrences and non-co-occurrences were not equal within the data (Fielding & Bell 1997; Sharma & Jackson 2008). Lastly a Cohen's Kappa statistic was calculated to evaluate the model. A Kappa statistic between 0-0.4, 0.4-0.75, and 0.75-1 represent poor, good, and excellent predictive models respectively (Fielding & Bell 1997).

Projections of walleye-smallmouth bass co-occurrence under future climate change regimes

The strongest predictive model of walleye-smallmouth bass co-occurrence was used to project future co-occurrence under all 126 future climate scenarios for the years 2050 and 2070. The percent change in co-occurrence for each of the 126 scenarios was then calculated relative to contemporary (2008-2012) co-occurrence rates. The R-coding environment was used to perform all statistical analyses (R Development Core Team, 2015).

RESULTS

Do walleye and smallmouth bass prefer the same lakes?

Twenty percent of the variation in the fish community in Ontario lakes can be explained by lake morphology, water chemistry, and climate. The RDA suggests that walleye prefer larger, more turbid lakes (low secchi depth), in addition to other members of the percid family, many of which are prey for walleye, and pike species (Fig. 2). The RDA also revealed that smallmouth bass along with other centrarchids prefer lakes that are in warmer regions (Fig. 2). This RDA suggests that walleye and smallmouth bass do not prefer similar environmental conditions.

How does the presence of smallmouth bass influence walleye abundance?

Despite their preference for different environmental conditions, walleye and smallmouth bass still coexist in 37% of the lakes from the BSM dataset. Walleye abundance was approximately 2.5 times lower in lakes that also contain smallmouth bass (Fig. 3). The median CPUE of walleye in lakes with smallmouth bass was 1.26 whereas lakes without smallmouth bass had a median walleye CPUE of 3.16 (Fig. 3).

Multiple linear regression models were used to evaluate how smallmouth bass presence influences walleye abundance. The most parsimonious model included lake surface area, maximum lake depth, mean July temperature (2000-2012), mean July precipitation (2000-2012), and the occurrence of smallmouth bass as predictor variables of walleye abundance (expressed as CPUE) (Table 1). The model indicates that walleye abundance increases in larger, shallower lakes, with lower temperatures, high precipitation, and no smallmouth bass (Table 1). After adjusting for the number of predictor variables used, this model was found to explain 32% of the variation in walleye abundance ($R^2_{\text{adj}} = 0.32$).

The most effective ZINB model included lake surface area, maximum lake depth, mean July precipitation (2000-2012), and the occurrence of smallmouth bass as predictor variables of walleye abundance (expressed as a total catch with number of nets used as an offset value to accommodate for sampling effort) (Table 1). This model indicates that walleye abundance increases in larger, shallower lakes, with more precipitation, when smallmouth bass are not present (Table 1). The ZINB model performed slightly better than the ZANB model as it had a higher adjusted R^2 value, higher Pearson, and Spearman correlations, and a lower RMSE calculation (Table S1). The RMSE of this model on the validation dataset was 76.9, indicating that mean error in predicted abundance would be 76.9 walleye counts. Overall this model was found to explain 41% of the variation in walleye abundance in Ontario lakes ($R^2_{\text{adj}} = 0.41$).

Which environmental conditions favour smallmouth bass and walleye co-occurrence?

Smallmouth bass and walleye co-occurred in 240 lakes in the 2008-2012 sampling period, an increase of 100 co-occurrences, or 71.4% from the initial sampling of those lakes between 1957 and 1986. The logistic regression model suggested that walleye and smallmouth bass were found to co-occur in large lakes, in warm regions, with lower precipitation rates (Table 2). This model had a classification success rate of 75%, a sensitivity of 69%, specificity of 78% and a kappa statistic of 0.44, indicating that it was a “good” predictor of walleye-smallmouth bass co-occurrence (Fielding & Bell 1997).

How will co-occurrence change under future climate projections?

Changes in temperature and precipitation are projected to lead to a 246% increase (ranging between 48-332%) in walleye-smallmouth bass co-occurrence by 2050 and a 269% increase (between 86-332%) in co-occurrence by 2070 (Fig. 4) relative to the number of co-occurrences in the historical period (between 1957 and 1986). Lower temperatures (projected by

the RCP2.6 scenario) more frequently produce fewer co-occurrences while the scenarios with higher temperature projections (e.g. the RCP8.5) have higher incidences of co-occurrence (Fig. 4). If changes in July temperatures exceed 4°C, or if precipitation declines by more than 25mm, a saturation effect is predicted whereby all lakes in the dataset are projected to contain both walleye and smallmouth bass (Fig. 4).

DISCUSSION

Although our study demonstrates that walleye and smallmouth bass prefer different environmental conditions, we found that when they both occur in the same lakes, walleye abundance is reduced at the landscape level. Other studies have documented that smallmouth bass are better competitors than walleye in food-limited laboratory conditions (Wuellner et al. 2011), and that they displace walleye from feeding in littoral zones by outcompeting them for prey and by displaying aggressive territorial behavioural at the individual lake level (Galster et al. 2012). Our study is the first to describe a negative relationship between walleye abundance and smallmouth bass occurrence across a landscape of 697 lakes. Specifically, we found that walleye prefer lakes that are larger, and have low secchi depths (low water clarity) while smallmouth bass prefer lakes that are in warmer regions. This illustrates how temperature is the primary limiting abiotic factor for smallmouth bass (and all centrarchids). In lakes where temperature is not limiting and where smallmouth bass and walleye co-exist, we found that walleye abundance was reduced in the presence of smallmouth bass and that smallmouth bass presence was a significant, negative predictor of walleye abundance. Future climate projections suggest that temperatures will rise in response to increased greenhouse gas emissions in Ontario (IPCC 2013). Under these future climate regimes, it was projected that walleye-smallmouth bass co-occurrence increases on average by 257% as a result of increased temperatures that facilitate smallmouth bass expansions, potentially further exacerbating vulnerability of walleye populations.

Climate change impacts on Ontario Lakes

Climate change has already begun to affect fish communities in Ontario lakes. The range boundaries of some coolwater, and many warmwater predators have undergone northerly

expansions in response to increasing temperatures between 1957 and 2011 (Alofs et al. 2014). This is especially true of species from the centrarchid family, all of which are expected to expand northward in response to climate change (Sharma et al. 2007; Alofs & Jackson 2015; Van Zuiden and Chen et al., in review). Climate change projections for smallmouth bass indicate that by mid-to-late century they could expand their range across all of Ontario (Van Zuiden & Chen et al. in review), and potentially across the entirety of Canada (Sharma et al. 2007). Alternatively, cold and some coolwater species are expected to be negatively affected by increasing temperatures, and are projected to decline in the future due to climate change (Hari et al. 2006; Sharma et al. 2011; Van Zuiden & Chen et al. in review). Walleye in Ontario are projected to experience northerly range shifts under climate change projections, whereby they become extirpated from their southern ranges, vulnerable in their central ranges, and increase in their northern ranges (Van Zuiden & Chen et al. in review).

There are numerous mechanisms through which this shift in walleye distributions could be facilitated. The availability of spawning waters could decline under warming temperature regimes as walleye prefer spring water temperatures 6-12°C (McMahon et al. 1984). Shallow lakes preferred by walleye (McMahon et al. 1984; STC 2007) are expected to warm faster than deeper lakes (Williamson et al. 2008; Adrian et al. 2009), which could cause the availability of suitable habitat to decline. Lower future precipitation rates (IPCC 2013) will reduce lake turbidity, forcing walleye to feed less frequently during the day. Walleye could also experience increased incidences of competitive interactions as more warmwater predators invade lakes that were historically too cold for them (Alofs et al. 2014; Alofs & Jackson 2015). Walleye growth and survival could be negatively affected by these additional stresses, hence facilitating their northern shift into more suitable habitats.

How smallmouth bass negatively influence walleye abundance?

We found that walleye abundance is reduced across a landscape in the presence of smallmouth bass. A number of different mechanisms could explain why walleye abundance is reduced when lakes are shared with smallmouth bass. The first is predation, whereby smallmouth bass have been observed to eat young walleye, causing an inverse relationship of abundances between the two species when they both live in the same lakes (Johnson & Hale 1977; Zimmerman 1999; Hoxmeier et al. 2006). This predation is more prevalent when habitat conditions are favourable for smallmouth bass i.e. when lakes are smaller, warmer, and less turbid (Krishka et al. 1996). As walleye are already heavily predated upon by other pike and centrarchid species (Bozek et al. 1999; Fayram et al. 2005), the added pressure of smallmouth bass predation could explain why walleye abundance is reduced in lakes shared by both species.

Competition for space and prey resources is another possible reason for walleye reductions in the presence of smallmouth bass. Early research on which species is the stronger competitor yielded mixed results. Kempinger & Carline (1977) noted that smallmouth bass populations in northern Wisconsin lakes declined when walleye were introduced while Johnson & Hale (1977) found that walleye populations declined after smallmouth bass introductions in Minnesota lakes. Together these studies illustrate that introductions of either walleye or smallmouth bass into lakes where the other dominates results in a reduction of the native predator. As most lakes in Ontario are native to walleye and not smallmouth bass, it is more likely that the results from the Johnson & Hale (1977) study will be mirrored across Ontario's landscape.

The competitive mechanism for this reduction in walleye is not well understood. Although walleye and smallmouth bass utilise many of the same prey resources (Fedoruk 1966;

Zimmerman 1999) the proportions of each prey item consumed differ. Diet overlap studies have found that the gut contents of adult walleye contain mostly fish while those of adult smallmouth bass contain invertebrates and fish (Johnson & Hale 1977; Frey et al. 2003). The difference in prey preferences may not directly explain why walleye reductions occur when smallmouth bass are present, however it is possible that prey items preferred by walleye share similar diets to smallmouth bass. For example, yellow perch (*Perca flavescens*) are a preferred prey species of walleye (Nielsen 1980; Kerr et al. 1997; Scott & Crossman 1998) and feed on littoral invertebrates similar to smallmouth bass (Brown et al. 2009). If smallmouth bass outcompete yellow perch for the same prey resources, walleye reductions could occur as a by-product of yellow perch declines. Walleye may also be competitively excluded from sharing the same resources as smallmouth bass when both are present in the same system, potentially explaining why overlap of prey preferences was found to be low in some studies (Frey et al. 2003; Wuellner et al. 2011).

Walleye reductions can also occur if smallmouth bass displace them from littoral feeding zones. Galster et al. (2012) found that walleye typically derive their energy from benthic prey resources in the absence of smallmouth bass whereas they rely more heavily on pelagic prey resources when smallmouth bass are present. This dietary shift likely occurs because smallmouth bass exhibit agonistic feeding behaviour in the presence of competitors, aggressively eating at all times when other predators (including other smallmouth bass) are present (Wuellner et al. 2011). This voracious feeding behaviour has been linked with massive littoral prey declines (especially cyprinids) in lakes where smallmouth bass have been introduced (MacRae & Jackson 2001; Jackson 2002; Sharma et al. 2007). In smaller lakes where pelagic prey resources are limited, walleye abundance would likely decline in the presence of smallmouth bass as they tend to

diminish the availability of prey before other predators get a chance to feed (Wuellner et al. 2011). In oligotrophic systems this would be especially problematic for walleye as they would only be able to feed during the night due to their negative phototactic response (Lester et al. 2002; Lester et al. 2004) while smallmouth bass are able to feed consistently throughout the day (Johnson & Hale 1977; Warren 2009).

Implications of increasing co-occurrence

To project future co-occurrence rates of walleye and smallmouth bass, all climate change climate change scenarios were utilised, as advised by the IPCC due to the large amount of variability between each GCM. This variability is attributable to how each GCM represents and calculates physical processes (e.g. clouds, water vapour, ocean mixing processes), and climate feedback mechanisms (Beaumont et al. 2008; IPCC, 2013). As each GCM is highly variable, using more of them creates a broader uncertainty envelope that is better able to reflect the likelihood of future co-occurrence rates (Sharma et al. 2011).

Many scenarios of future climate change predict that temperatures across Ontario will increase, while precipitation will decrease (IPCC 2013). Earlier studies suggest that these climatic changes will have positive effects on smallmouth bass distributions, and potential negative effects on walleye populations (Chu et al. 2005; Sharma et al. 2007; Van Zuiden & Chen et al. in review). The occurrence rates of smallmouth bass are projected to increase faster than walleye are projected to decline (Van Zuiden & Chen et al. in review). This likely occurs because lakes become suitable for smallmouth bass more quickly than they become unsuitable for walleye under future climate projections. Ultimately, this leads to increased rates of co-occurrence, particularly in central and northern Ontario (Van Zuiden & Chen et al. in review). Smallmouth bass-walleye co-occurrence rates have already increased by approximately 71%

since 1957-1986 and are projected to increase by an average of 269% by 2070. As co-occurrence rates are predicted to continue to increase, we predict walleye abundance will decline due to the increased presence of a superior competitor. These declines are likely to be further exacerbated under future climate scenarios as lake temperatures increase because the availability of preferable thermal habitat for smallmouth bass is likely to increase, while thermal habitat space for walleye is expected to decrease (Hokanson 1977; Shuter et al. 1980; Edwards et al. 1983; McMahon et al. 1984).

Although our model predicts that walleye and smallmouth bass could co-occur in all lakes under future climate regimes, it is unlikely that small lakes would be able to sustain populations of both species (Krishka et al. 1996). Walleye prefer lakes that are larger than 400 ha, but are able to establish themselves in lakes closer to 100 ha if they form larger, highly connected systems (Colby et al. 1979; Kerr et al. 1997). Approximately 15% of lakes used in this model are smaller than 100 ha, and will therefore be unlikely to support walleye, let alone a combination of both walleye and smallmouth bass.

Conclusions

The implications of our study will be important when making future fisheries management decisions as northerly invasions of smallmouth bass will continue to decimate native prey populations as air temperatures increase (MacRae & Jackson 2001; Sharma et al. 2007; Van Zuiden & Chen et al. in review). Forage fish contractions have already begun to occur as a result of climate change and it is highly probable these contractions are exacerbated further by the expansions of warmwater predators (Alofs et al. 2014). The over-predation of forage fish and their subsequent range contractions not only negatively affect walleye, but also other native northern predators such as lake trout (e.g. Vander Zanden et al. 1999; Sharma et al. 2009).

Despite the overwhelming evidence that fish community composition is heavily influenced by predator-prey relationships (Harvey, 1981; Jackson et al. 1992; Jackson 2002), ecologists have largely ignored how species interactions affect biodiversity when examining the effects of climate change (Gilman et al. 2010).

It is important to take these relationships into consideration in future studies as there is considerable value in Canada's freshwater fisheries (approximately 4.7 billion dollars) (Shuter et al. 1998). As climate change continues to facilitate smallmouth bass invasions into new lakes, Canada's native fisheries are at greater risk of collapse. These consequences underline the importance of reducing greenhouse gas emissions and invasion of non-native species in the future, as the continued existence of native fisheries is at stake.

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TABLES

Table 1: The most parsimonious models used to predict walleye abundance and walleye-smallmouth bass co-occurrence in lakes across Ontario.

Model	Response variable	Predictor variables	Model coefficients	Significance level (p-value)
Multiple linear regression	Walleye abundance (CPUE)	Surface area (ha)	1.67	< 0.01
		Max depth (m)	-3.83	< 0.01
		Mean summer temperature (°C) (2000-2012)	-0.40	< 0.01
		Mean July precipitation (mm) (2000-2012)	0.02	< 0.01
		Occurrence of smallmouth bass	-0.48	0.01
Zero-inflated negative binomial	Walleye total catch	Surface area (ha)	0.54	< 0.01
		Max depth (m)	-1.63	< 0.01
		July precipitation (mm) (2000-2012)	0.02	< 0.01
		Occurrence of smallmouth bass	-0.53	< 0.01
Logistic regression	Walleye-smallmouth bass co-occurrence	Surface area (ha)	1.01	< 0.01
		Mean August temperature (°C) (2000-2012)	0.81	< 0.01
		Mean August precipitation (mm) (2000-2012)	-0.04	0.03

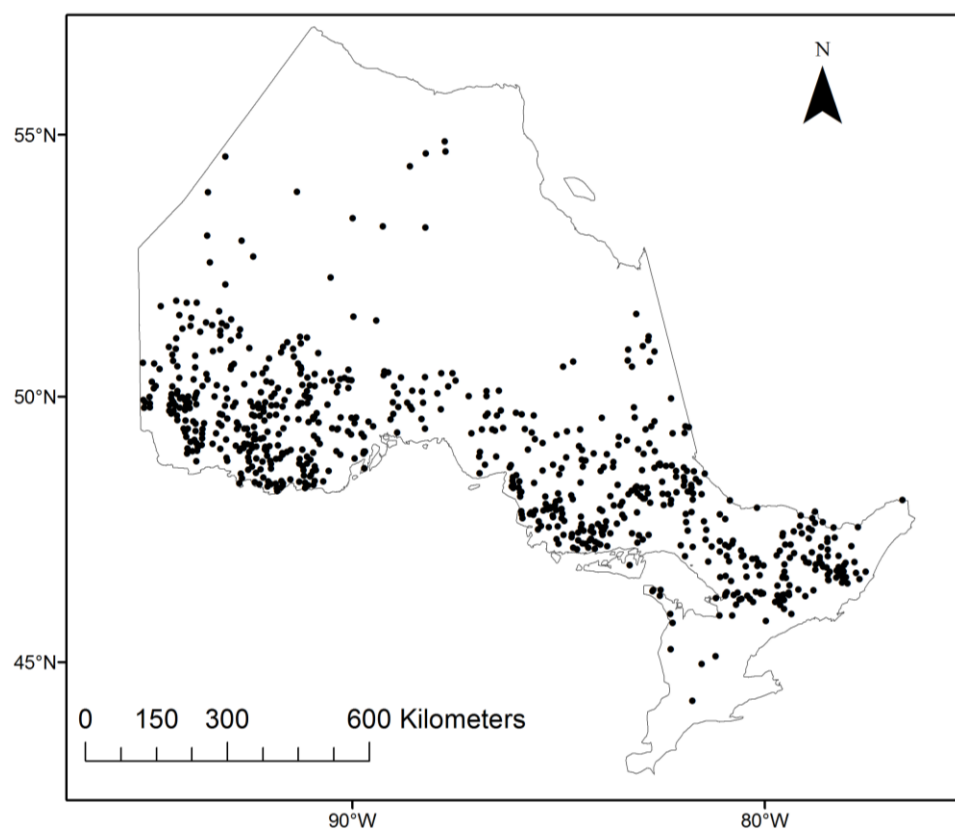
FIGURES

Figure 1: Distribution of the 722 lakes surveyed in the BSM program during 2008 and 2012.

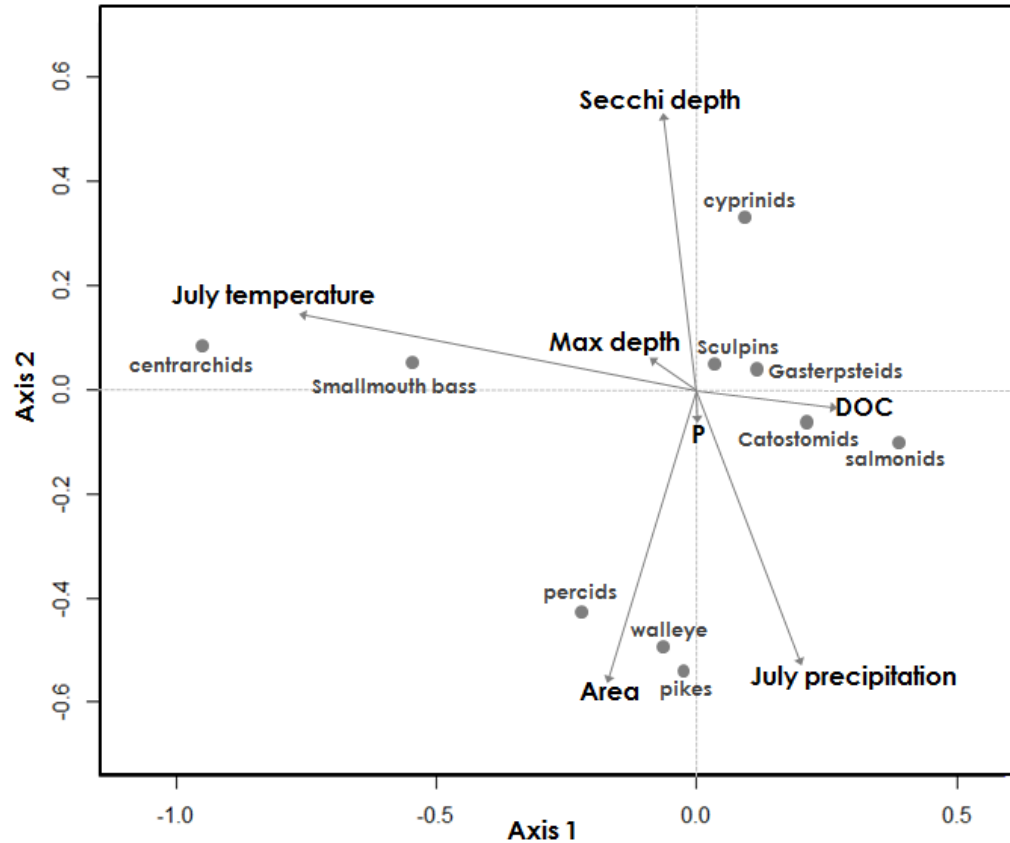


Figure 2: Redundancy analysis describing the association between fish and their environments across Ontario lakes. Fish species and families are represented by points. Lake characteristics and climate variables are represented by arrows. Environmental variables used are as follows: secchi depth, dissolved organic carbon (DOC), mean July precipitation between 2000 and 2012, total phosphorus (P), lake surface area, mean July temperature between 2000 and 2012, and maximum lake depth. Environmental variables describe 20% of the variation in fish communities in Ontario lakes ($R^2_{\text{adj.}} = 0.20$). The relationship between fish and their environments is significant ($p < 0.05$).

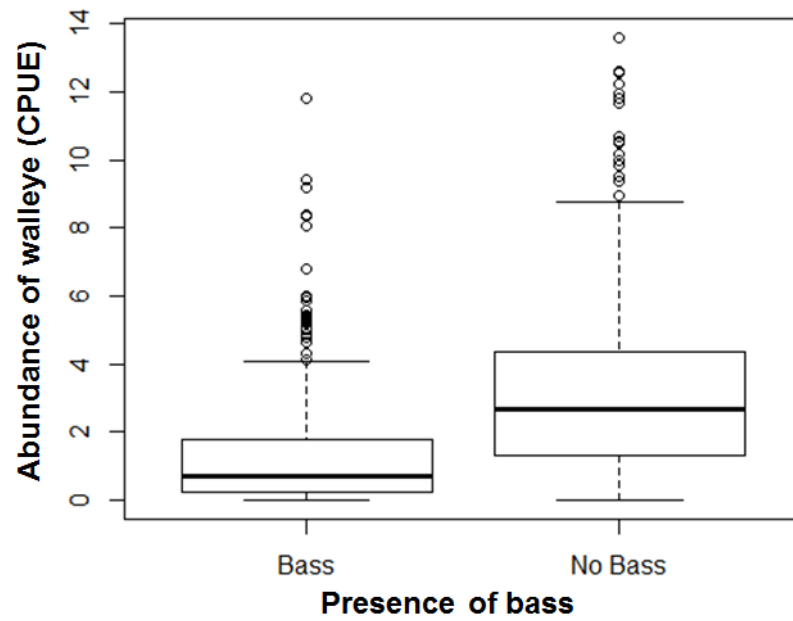


Figure 3: Walleye abundances in lakes when smallmouth bass are present (left box plot) and they are absent (right box plot). The median abundance of walleye when bass are present is 1.26 and is 3.16 when they are absent.

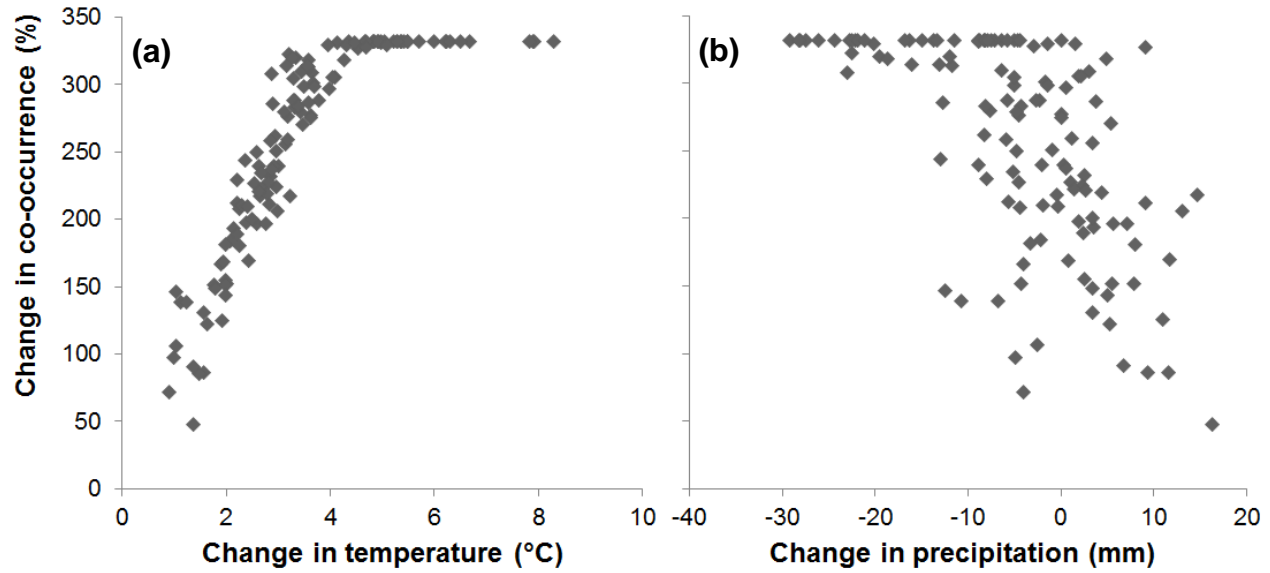


Figure 4: Percent change in walleye-smallmouth bass co-occurrence under 126 climate change scenarios in 2050 and 2070 as temperature increases (a), and precipitation changes (b). Calculations for percent change in co-occurrence are relative to the historical period (1957-1986) when there were 140 lakes in which walleye and smallmouth bass co-occurred.

SUPPORTING INFORMATION

Table S1: Model comparison of zero-altered and zero-inflated negative binomial (ZANB and ZINB, respectively) models. Total walleye catch was used as a response variable for both models below and number of nets was used as an offset value to allow the models to take the sampling effort of each lake into consideration.

Model	Predictor variables	Adj. R^2	r	p	RMSE	SMB effect size
ZANB	SA - MxD + July pre - SMB	0.407	0.641	0.702	77.2	-0.53
ZINB	SA - MxD + July pre - SMB	0.409	0.643	0.707	76.9	-0.53

Note: Values calculated for each model include Adjusted- R^2 (Adj. R^2), Pearson correlation coefficient (r), Spearman rank correlation (p), and root mean square error (RMSE). Abbreviated terms for predictor variables are as follows: lake surface area (SA); lake maximum depth (MxD); July precipitation for the years 2000-2012 (July pre.); occurrence of smallmouth bass (SMB).

SUMMARY AND CONCLUSIONS

Using climate data from the most recent IPCC climate assessment report (2013) we were interested in predicting how walleye, a coolwater fish, and smallmouth bass, a warmwater fish, would respond to future changes in temperature and precipitation as a result of climate change. Walleye were projected to undergo northerly range shifts in response to climate change; a novel response, as previous research using older IPCC climate data projected future walleye expansions (e.g. Shuter *et al.*, 2002; Chu *et al.*, 2005). Smallmouth bass were predicted to expand across Ontario in response to climate change. Although this finding is agreement with previous literature (e.g. Sharma *et al.*, 2007) we were shocked to observe that projections from “the business as usual” scenarios often yielded complete saturation of Ontario lakes with smallmouth bass by the year 2070. As smallmouth bass were projected to expand into numerous walleye lakes, we were also interested in elucidating how walleye abundance is affected by the presence of smallmouth bass. We found that walleye abundance was reduced in lakes where smallmouth bass were present at the landscape level and that under future climate projections walleye-smallmouth bass co-occurrence increased.

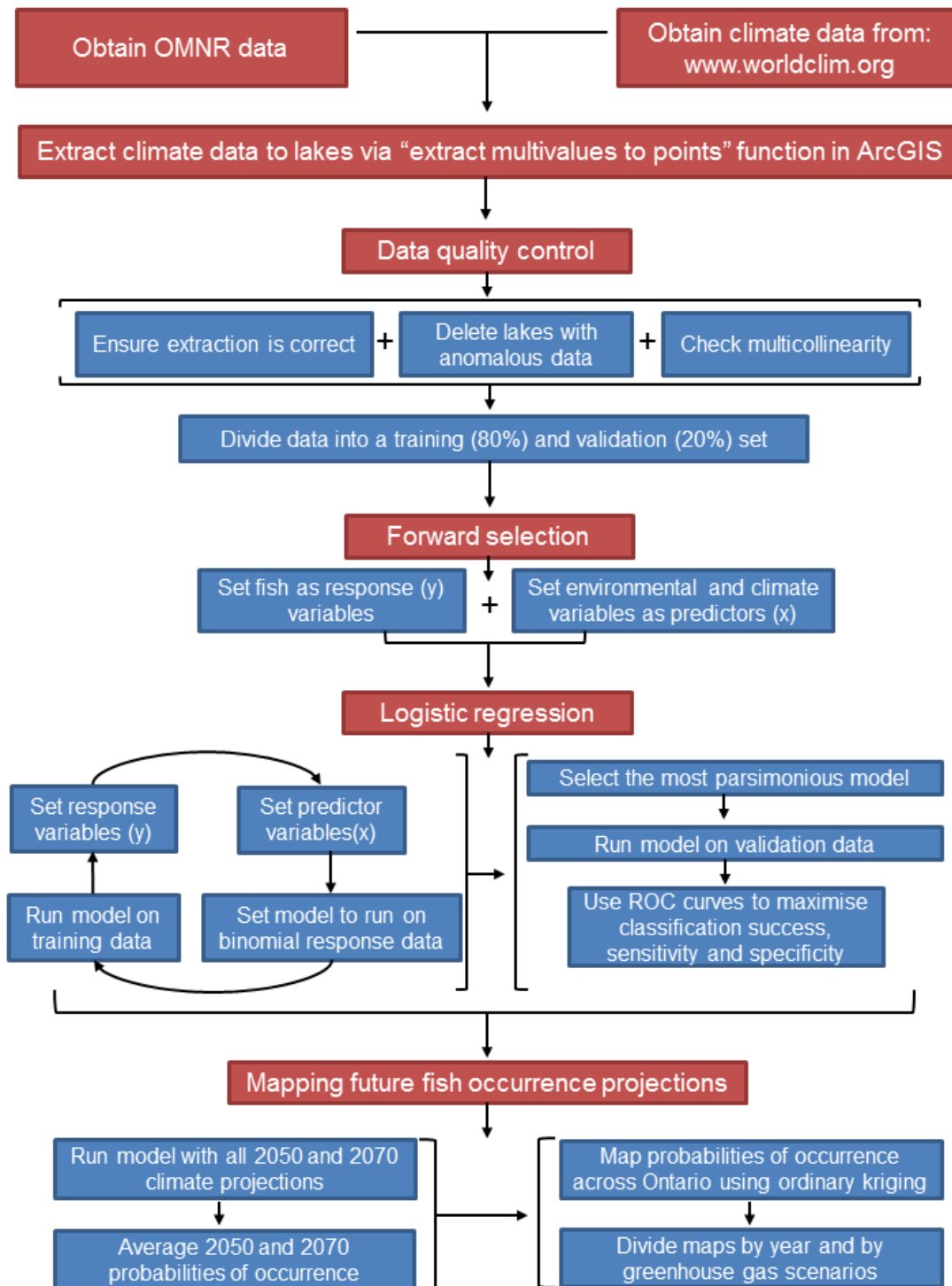
As water temperatures become more ideal for smallmouth bass and less favourable for walleye it is likely that naturally occurring walleye populations will experience declines or extirpations as smallmouth bass populations continue to expand northward. This presents fisheries managers with a difficult task, as northern fisheries might be in danger of becoming homogenised or collapsing upon smallmouth bass invasion (MacRae & Jackson, 2001; Rahel, 2002; Jackson, 2002). To date, fisheries managers have facilitated smallmouth bass expansions in Ontario through the introduction of stocking programs (Jackson, 2002). These stocking efforts continue despite the growing evidence that smallmouth bass are a “winner-species” that easily

outcompete other top predators under scenarios of climate change (Vander Zanden *et al.*, 2004; Sharma *et al.*, 2007; Pease & Paukert, 2014). In order to maintain a viable walleye fishery across Ontario, management of smallmouth bass expansions will need to become more stringent in the future. Although preventative management decisions could slow the impending expansion of smallmouth bass, continued attention must also be paid to curbing greenhouse emissions. If temperatures are allowed to increase along their current trajectory the outcome for Ontario fisheries could be disastrous.

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APPENDIX



Appendix figure 1: Methodological workflow overview, outlining the steps required to repeat this chapter 1 of this project. Red boxes indicate our approach to answering research questions while blue boxes expand on these approaches with more specific detail.

Chapter 1 workflow

Data quality control

1. Ensure extraction is correct
 - a) Check all lakes to ensure that extracted climate values have a numerical value that is not 0 or 9999
2. Delete lakes with anomalous data
 - a) Lakes with recorded depths or surface areas of 0 were deleted
 - b) Lakes where mean depth or secchi depth of the lake exceeded max depths were deleted
 - c) Lakes with latitudes or longitudes with inappropriate signs were deleted
3. Check multicollinearity
 - a) To test which environmental variables are correlated with one another, create a correlation matrix in the computer program R using the “cor.test” function
 - b) The resulting correlation matrix will display the correlation coefficients (r-values) between all environmental variables
 - c) If a resulting correlation coefficient between two variables is higher than 0.70, they cannot both be simultaneously in any of the following variable selection or model creation steps
4. Randomly divide data into 80% training, and 20% validation subsets

Forward selection

- a) Install the “packfor” package in R to use the “forward.sel” function
- b) From the training dataset, group environmental variables (including climate) and fish occurrence variables separately
- c) Set either walleye or smallmouth bass occurrence as the response variable and the group of non-correlated environmental variables as explanatory variables in the “forward.sel” equation
- d) Explanatory variables that were found to be significant ($p < 0.05$) predictors of either walleye or smallmouth bass occurrence were used in the following steps
- e) Lakes with missing data for important predictor variables were deleted

Logistic regression

1. Model training
 - a) Using the “glm” equation in R, set walleye or smallmouth bass occurrence as the response variable
 - b) Set a combination environmental variables that were significant predictors of walleye or smallmouth bass occurrence from forward selection as explanatory variables in the logistic regression model
 - c) Ensure that the “glm” equation is set to model binomial response data by adding “family=binomial” to the equation

- d) Ensure model is running on the training data
- e) Run numerous models with various combinations of explanatory variables to assess which is the best predictor of either walleye or smallmouth bass occurrence

2. Model validation

- a) Run the model again using the validation subset of data
- b) Use Receiver Operating Characteristic (ROC) curves to determine a threshold that optimizes the sensitivity and specificity of the model using the “roc” function in R

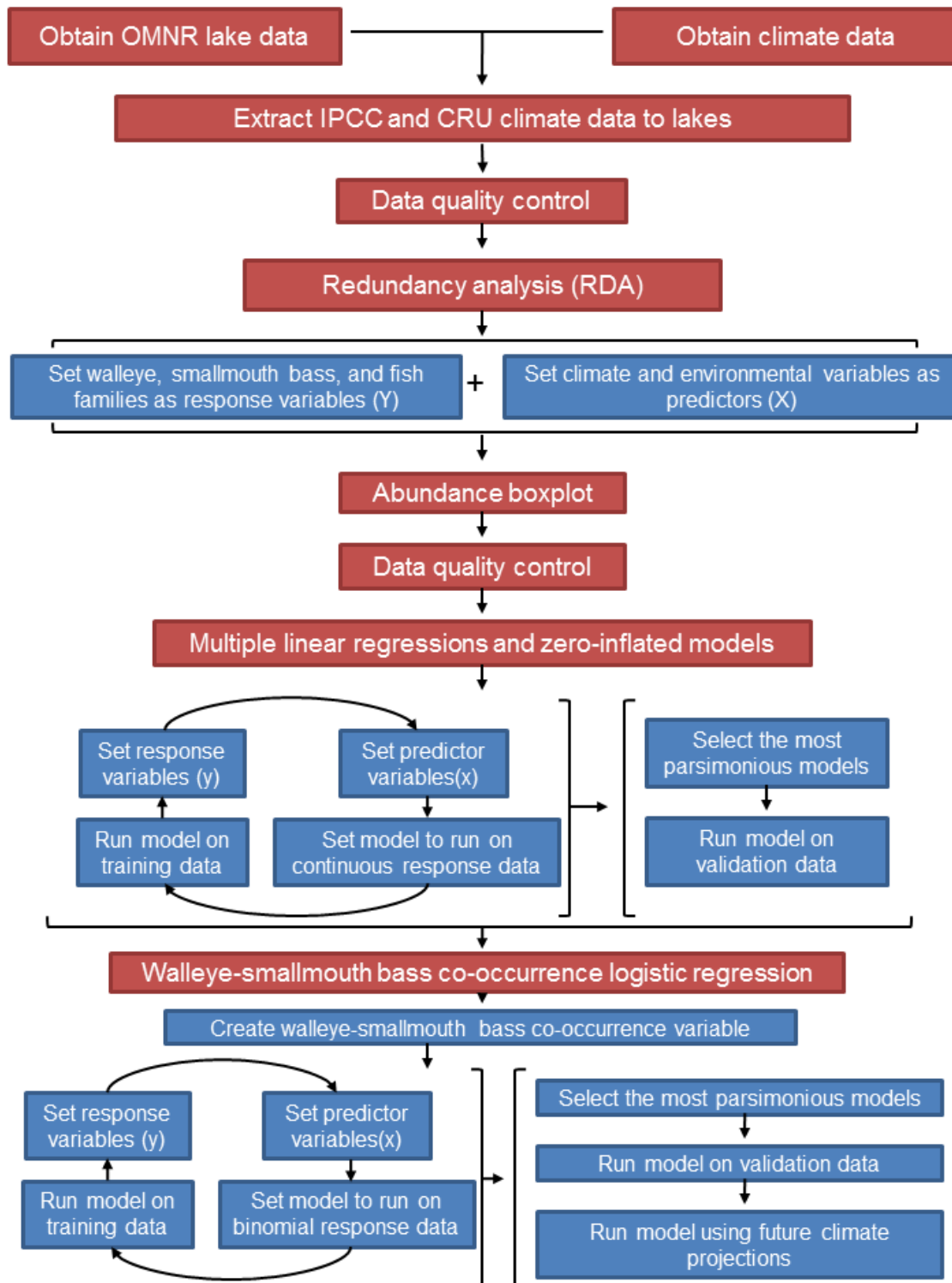
Mapping future projections of fish occurrence

1. Projecting occurrence rates for 2050 and 2070

- a) Use the optimized logistic regression model with optimized ROC curve threshold to project the occurrence of walleye and smallmouth bass using data from 2050 and 2070 scenarios of projected climate change
- b) Calculate probabilities of occurrence using all 126 scenarios of climate change
- c) Calculate the average projected occurrence rates for walleye and smallmouth bass in 2050 and 2070 by averaging the occurrence rates from all scenarios of climate change for each year

2. Creating maps for 2050 and 2070

- a) Using ArcGIS, plot the average projected occurrence rates of walleye and smallmouth bass in 2050 and 2070 as points
- b) Use the “ordinary kriging” function in ArcGIS to interpolate the probability of walleye and smallmouth bass occurrence across the landscape of Ontario
- c) Ensure that the probability of each interpolated pixel is calculated by using the mean probability of the nearest 50 lakes



Appendix figure 2: Methodological workflow overview, outlining the steps required to repeat this chapter 2 of this project. Red boxes indicate our approach to answering research questions while blue boxes expand on these approaches with more specific detail.

Chapter 2 workflow

Data quality control

1. Ensure extraction is correct
 - a) Check all lakes to ensure that extracted climate values have a numerical value that is not 0, or 9999
2. Delete lakes with anomalous data
 - a) Lakes with recorded depths or surface areas of 0 were deleted
 - b) Lakes where mean depth or secchi depth of the lake exceeded max depths were deleted
 - c) Lakes with latitudes or longitudes with inappropriate signs were deleted

Redundancy analysis (RDA)

- a) Group fish species into their respective families (excluding walleye and smallmouth bass)
- b) Omit lakes from the RDA where environmental variables are missing data
- c) Set walleye and smallmouth bass occurrence as response variables using “rda” code in the R statistical programming software
- d) Set fish family richness as response variables
- e) Set environmental and climate variables as predictors of the fish response variables

Abundance boxplots

- a) Create a comparative boxplot in R by plotting walleye abundance in lakes where smallmouth bass are present against walleye abundance in lakes where smallmouth bass are absent

Data quality control

1. Check multicollinearity
 - a) To test which environmental variables are correlated with one another, create a correlation matrix in the computer program R using the “cor.test” function
 - b) The resulting correlation matrix will display the correlation coefficients (r-values) between all environmental variables
 - c) If a resulting correlation coefficient between two variables is higher than 0.70, they cannot both be simultaneously in any of the following variable selection or model creation steps
2. Randomly divide data into 80% training, and 20% validation subsets
3. Forward selection
 - a) Install the “packfor” package in R to use the “forward.sel” function
 - b) From the training dataset, group environmental variables (including climate) and fish occurrence variables separately

- c) Set either walleye or smallmouth bass occurrence as the response variable and the group of non-correlated environmental variables as explanatory variables in the “forward.sel” equation
- d) Explanatory variables that were found to be significant ($p < 0.05$) predictors of either walleye or smallmouth bass occurrence were used in the following steps
- e) Lakes with missing data for important predictor variables were deleted

Multiple linear regression and zero-inflated models

1. Multiple linear regression model training
 - a) Using the “glm” equation in R, set walleye abundance (CPUE) as the response variable
 - b) Set a combination environmental variables that were significant predictors of walleye abundance from forward selection (including smallmouth bass occurrence) as explanatory variables in the logistic regression model
 - c) Ensure that the “glm” equation is set to model continuous response data by adding “family=family” to the equation
 - d) Ensure model is running on the training data
 - e) Run numerous models with various combinations of explanatory variables to assess which is the best predictor of walleye abundance
2. Multiple linear regression model validation
 - a) Run the model again using the validation subset of data
 - b) Analyse how well the model fits the validation data ($R^2_{\text{adj. value}}$)
3. Zero-inflated negative binomial model training
 - a) Using the “zeroinfl” equation in R, set walleye abundance (as count values) as the response variable
 - b) Set a combination environmental variables that were significant predictors of walleye abundance from forward selection (including smallmouth bass occurrence) as explanatory variables in the logistic regression model
 - c) Add an offset value to the model by including “offset(sampling effort variable name)” syntax so that sampling effort is taken into account when modeling pure count values
 - d) Ensure that the “zeroinfl” equation is set to model continuous response data by adding “family=family” to the equation
 - e) Ensure model is running on the training data
 - f) Run numerous models with various combinations of explanatory variables to assess which is the best predictor of walleye abundance
4. Zero-inflated negative binomial model validation
 - a) Run the model again using the validation subset of data
 - b) Analyse how well the model fits the validation data ($R^2_{\text{adj. value}}$)

Walleye-smallmouth bass co-occurrence logistic regression model

1. Create a co-occurrence variable by summing walleye and smallmouth bass occurrences together

2. Use the forward selection procedure to identify important predictors of co-occurrence of walleye and smallmouth bass
3. Model training
 - a) Using the “glm” equation in R, set walleye-smallmouth bass co-occurrence as the response variable
 - b) Set a combination environmental variables as predictors of co-occurrence
 - c) Ensure that the “glm” equation is set to model binomial response data by adding “family=binomial” to the equation
 - d) Ensure model is running on the training data
 - e) Run numerous models with various combinations of explanatory variables to assess which is the best predictor of either walleye or smallmouth bass occurrence
4. Model validation
 - a) Run the model again using the validation subset of data
 - b) Use Receiver Operating Characteristic (ROC) curves to determine a threshold that optimizes the sensitivity and specificity of the model using the “roc” function in R