Examining the effects of climate change and species invasions on Ontario walleye populations: can walleye beat the heat?

Thomas M. Van Zuiden and Sapna Sharma*

Department of Biology, York University, Toronto, ON M3J 1P3, Canada

*Correspondence: Sapna Sharma, Department of Biology, York University, 4700 Keele Street, Toronto, ON M3J 1P3, Canada.
E-mail: sharma11@yorku.ca

ABSTRACT

Aim The combined effects of multiple environmental stressors continue to threaten global biodiversity, yet predicting how biotic interactions between native and invasive species may change across a landscape in a multiple stressor environment is relatively understudied. We aim to identify how the invasion of smallmouth bass (*Micropterus dolomieui*) may influence native walleye (*Sander vitreus*) populations across Ontario lakes at the landscape scale in a changing climate.

Location Ontario, Canada.

Methods Using a database that included the abundance and occurrence of over 130 fish species, lake chemistry and lake morphology for 722 lakes, a redundancy analysis was conducted to identify environmental conditions preferred by walleye and smallmouth bass. Multiple linear regression models were then developed to identify the relationship between walleye and multiple stressors (including climate change and biotic interactions with invasive species). Using future scenarios of climate change, we were then able to project future walleye–smallmouth bass co-occurrences.

Results Smallmouth bass were found to prefer different environmental conditions than walleye; however, when walleye and smallmouth bass were found in the same lakes, walleye abundance was reduced almost threefold. Multiple regression models further suggested that there are fewer walleye in lakes with smallmouth bass. Subsequently, we predicted that under future scenarios of climate change the overlapping co-occurrence of walleye and smallmouth bass may increase by 86–332% by the year 2070.

Main conclusions We illustrate the importance of including multiple environmental stressors in statistical models when attempting to understand how native species will be impacted by invasive species and climate change. While independently climate change is anticipated to lower walleye abundances across Ontario, this change is expected to be exacerbated by invasions of warmwater predators.

Keywords biotic interactions, climate change, competition, co-occurrence, invasive species, smallmouth bass, walleye.

INTRODUCTION

Threats to global biodiversity continue to increase as systems are affected by multiple environmental stressors (Sala et al., 2000), yet how these stressors impact species interactions between native and invasive species at a landscape scale is relatively understudied (Olden et al., 2010). While research that investigates the independent effects of climate change or invasive species on biodiversity continues to grow (e.g. Sala et al., 2000), integrating the effects of climate change and species invasions on native species that are simultaneously affected by both stressors becomes increasingly important (Olden et al., 2010). Here, we directly include the influence of climate change and an invasive species on a native
coolwater fish across hundreds of lakes, expanding on earlier studies investigating the effects of multiple stressors on endangered marsupials (Bateman et al., 2012), butterflies (Araújo & Luoto, 2007), cold-water fishes (Sharma et al., 2009) and others (e.g. Blois et al., 2013).

Evidence suggests that climate change profoundly impacts biodiversity on a global scale, across all biological systems (Sala et al., 2000; Walther et al., 2002). In freshwater ecosystems, warming air temperatures are directly responsible for increased surface water, and epilimnetic temperatures as well as increased thermal stratification, and decreased lake-mixing (Livingston & Lotter, 1998; Adrian et al., 2009). These changes can all affect the availability of suitable thermal habitat for many freshwater fish species, hence altering their distributions across landscapes (Magnuson et al., 1990; Ficke et al., 2007). In turn, many species that prefer cold or cool waters that decline in response to climate change may additionally face increased pressure (via competition or predation) from invasive species that prefer warmer temperatures.

As climate change increases epilimnetic water temperatures, it facilitates the potential invasion of warmwater species into northern lakes that have historically been too cold for them to occupy (Sharma et al., 2007). The consequences of these invasions can range from lowering the abundances of certain fish, invertebrate or plant populations to decimating entire populations (MacRae & Jackson, 2001; Kolar et al., 2007; Sharma et al., 2007, 2009). The Centrarchidae are one such family of warmwater species that have, until recently, been limited to southern Canada due to cold-water temperatures (Shuter et al., 1983). Recent research, however, has demonstrated that the historical northern limit of their range may now contain suitable thermal habitat and that centrarchids are being found in northern lakes where they have never occurred historically (Alofs et al., 2014). Centrarchids, particularly bass (e.g. smallmouth bass, Micropterus dolomieui), are of particular concern due to their effectiveness as predators (Krishka et al., 1996; Wuellner et al., 2011) and their tendency to substantially lower the population of prey species in invaded lakes (MacRae & Jackson, 2001) and directly influence salmonid predators (Vander Zanden et al., 1999; Sharma et al., 2009).

Walleye (Sander vitreus) are a native coolwater predator species (Koenst & Smith, 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 Canadian dollars in revenue annually for the economy of the Great Lakes region (Kinnunen, 2003; Pandit et al., 2013). Walleye are currently under threat in Ontario lakes by climate change and the invasion of smallmouth bass. Studies examining the effect of smallmouth bass competition with walleye have only been conducted at the individual lake level (Johnson & Hale, 1977; Frey et al., 2003; Galster et al., 2012) or in laboratory studies (Wuellner et al., 2011) and have largely reported mixed findings.

Research objectives

Our primary research objective is to identify how smallmouth bass influence walleye populations across the landscape of Ontario. Smallmouth bass are a competitive predatory species that are expected to experience range expansions under increasing temperature regimes (Sharma et al., 2007; Van Zuiden et al., 2016). 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: (1) Do walleye and smallmouth bass prefer the same lakes? (2) how does the presence of smallmouth bass influence walleye abundance? (3) which environmental conditions favour smallmouth bass and walleye co-occurrence?, and (4) how will smallmouth bass-walleye co-occurrence change as Ontario’s climate warms? 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 expand their range northwards (Sharma et al., 2007; Sharma & Jackson, 2008; Van Zuiden et al., 2016) and walleye populations are projected to be extirpated in southern Ontario and shift their range northwards (Van Zuiden et al., 2016), we hypothesize that co-occurrence of walleye and smallmouth bass will increase under climate change, further exacerbating walleye vulnerability in Ontario under scenarios of climate change.

METHODS

Lake survey and climate data acquisition

The Ontario Ministry of Natural Resources (OMNR) Broad-scale Monitoring (BSM) Programme collected data on 722 lakes between 2008 and 2012. The programme was designed to sample fish habitats at several different depths (Sandstrom et al., 2010). Variables measured in this programme include lake location (latitude, longitude), morphology (surface area, depths), chemistry (pH, secchi depth, oxygen levels, etc.), fish occurrence and fish abundance of over 100 different species. To sample fish abundances, the BSM survey used large and small mesh gill nets to target fish larger or smaller than 20 cm, respectively (Sandstrom et al., 2010). Large mesh nets were set up to sample for 16–22 h while small mesh nets sampled for 12–22 h (Sandstrom et al., 2010). The sampling effort on each lake was largely dependent on lake size and depth, whereby a greater effort was utilized in larger, deeper lakes (Sandstrom et al., 2010). Climate data for historical (1950–2000) and contemporary (2000–2012) periods were 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; IPCC 2013; Stocker, 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 RCP6.0 are intermediate climate scenarios, corresponding to moderate increases in future GHG emissions (IPCC 2013).

Do walleye and smallmouth bass prefer the same lakes?

First, a map was created to illustrate the contemporary distributions of walleye and smallmouth bass in Ontario inland lakes using the 722 lakes from the BSM survey (Fig. 1). From the 722 lake dataset, 645 lakes were used to perform a redundancy analysis (RDA) ordination. An RDA was used to identify the environmental conditions that structure fish community composition in Ontario lakes. We used data from 645 lakes because 77 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 the occurrence of walleye and smallmouth bass, and the sum of occurrences of other fishes from the percid, centrarchid, esocid, cyprinid, gasterosteid, cottid, 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. Fish families or individual species that are closer to one another in the ordination tend to prefer similar environmental conditions.

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 from 645 lakes because 77 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 the occurrence of walleye and smallmouth bass, and the sum of occurrences of other fishes from the percid, centrarchid, esocid, cyprinid, gasterosteid, cottid, 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. Fish families or individual species that are closer to one another in the ordination tend to prefer similar environmental conditions.

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 from 645 lakes because 77 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 the occurrence of walleye and smallmouth bass, and the sum of occurrences of other fishes from the percid, centrarchid, esocid, cyprinid, gasterosteid, cottid, 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. Fish families or individual species that are closer to one another in the ordination tend to prefer similar environmental conditions.

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

Figure 1 Distribution of the 722 lakes surveyed in the BSM programme during 2008 and 2012. Open circles represent lakes in which neither smallmouth bass nor walleye occur (156 lakes); closed grey circles represent lakes where only walleye occur (229 lakes); black squares represent lakes in which only smallmouth bass occur (61 lakes); ‘Plus’ signs represent lakes in which walleye and smallmouth bass co-occur (276 lakes). Map created using ArcGIS 10.1 software.
with or without smallmouth bass. Additional boxplots were created to identify if the observed effect of smallmouth bass on walleye CPUE was actually a reflection of habitat quality (abiotic variables) alone. If walleye CPUE is lower in lakes with bass in both ideal and subideal habitats, we can attribute some of this difference to smallmouth bass presence and only not habitat quality. Typically walleye prefer larger, shallower lakes that are in cooler geographical regions.

We developed multiple linear regression models to identify the influence of smallmouth bass occurrence and environmental conditions on walleye CPUE. Multiple linear regression models were utilized 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).

We divided the 697 lakes into two random, independent data subsets. Eighty percentages 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 605 Ontario inland lakes. Our co-occurrence variable was binary and was classified as a lake in which walleye and smallmouth bass both occur. The 605 lakes were chosen specifically because they were sampled in both the 2008–2012 BSM survey, and in the Aquatic Habitat Inventory (AHI) survey that was conducted between 1957 and 1986. We chose to analyse the 605 overlapping lakes so that we could compare the 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 maximize the sensitivity (proportion of true positives) and specificity (proportion of true negatives) of the walleye–smallmouth bass co-occurrence model, receiver operating characteristic (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 percentage change in co-occurrence for each of the 126 scenarios was then calculated relative to contemporary (2008–2012) co-occurrence. 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 esocid 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). We were also able to confirm that this difference in abundance was likely attributed to smallmouth bass, as walleye CPUE was consistently lower in lakes when smallmouth bass were present, regardless of whether or not environmental conditions were favourable for walleye (Fig. S1 in Supporting Information).

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 summer temperature (2000–2012), 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 ($R_{adj}^2 = 0.20$). The relationship between fish and their environments is significant ($P < 0.05$).

**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 ($R_{adj}^2 = 0.20$). The relationship between fish and their environments is significant ($P < 0.05$).

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

From the 605 lake subset, we found that smallmouth bass and walleye co-occurred in 240 lakes during the 2008–2012 sampling period, an increase of 71.4% from the initial sampling of those lakes between 1957 and 1986 during the AHI study period. 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. 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% and 332%) in walleye–smallmouth bass co-occurrence by 2050 and a 269% increase (between 86 and 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 25 mm, a saturation effect is predicted whereby all lakes in the dataset are projected to contain both walleye and...
smallmouth bass (Fig. 4). Although we expect walleye populations to decline and shift northward under future climate scenarios, it is likely we see walleye–smallmouth bass co-occurrence increasing because smallmouth bass are invading lakes more quickly than walleye are becoming extirpated.

DISCUSSION

We illustrate the importance of using a multiple stressor framework across a landscape scale to identify the potential vulnerability of an ecologically and economically important coolwater predator. By examining two top predator sportfish with different thermal preferences, we were able to elucidate the influence of climate change and biotic interactions on walleye populations in Ontario. Using an approach that allows for the incorporation multiple stressors into native species models helps identify more realistic predictions when determining the potential effects of climate change on species distributions (Preston et al., 2008; Olden et al., 2010; Bate man et al., 2012).

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 behaviour 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 hundreds of lakes. Specifically, we found that walleye prefer larger, shallower lakes that have lower 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 prefer larger, shallower lakes that have lower water clarity while smallmouth bass prefer lakes that are in warmer regions. 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 invasions, potentially further exacerbating vulnerability of walleye populations.

Climate change impacts on Ontario Lakes

Lake summer surface water temperature trends have increased by 0.45 °C per decade in Ontario lakes (Appendix S1, Ontario lakes data adapted from O’Reilly et al., 2015) and are already influencing fish communities in

<table>
<thead>
<tr>
<th>Model</th>
<th>Response variable</th>
<th>Predictor variables</th>
<th>Model coefficients</th>
<th>Significance level (P-value)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Multiple linear</td>
<td>Walleye abundance (CPUE)</td>
<td>Surface area (ha)</td>
<td>1.67</td>
<td>&lt; 0.01</td>
</tr>
<tr>
<td>regression</td>
<td></td>
<td>Max depth (m)</td>
<td>−3.83</td>
<td>&lt; 0.01</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Mean summer temperature (°C) (2000–2012)</td>
<td>−0.40</td>
<td>&lt; 0.01</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Mean July precipitation (mm) (2000–2012)</td>
<td>0.02</td>
<td>&lt; 0.01</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Occurrence of smallmouth bass</td>
<td>−0.48</td>
<td>0.01</td>
</tr>
<tr>
<td>Logistic regression</td>
<td>Walleye–smallmouth bass co-occurrence</td>
<td>Surface area (ha)</td>
<td>1.01</td>
<td>&lt; 0.01</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Mean August temperature (°C) (2000–2012)</td>
<td>0.81</td>
<td>&lt; 0.01</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Mean August precipitation (mm) (2000–2012)</td>
<td>−0.04</td>
<td>0.03</td>
</tr>
</tbody>
</table>
Ontario lakes (Alofs et al., 2014; Van Zuiden et al., 2016). The range boundaries of many warmwater predators have already 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 et al., 2016). Climate change projections for smallmouth bass indicate that by mid-to-late century they could expand their range across all of Ontario (Van Zuiden et al., 2016), 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 et al., 2016). 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 et al., 2016).

There are numerous mechanisms through which this shift in walleye distributions could be facilitated. First, the availability of spawning waters could decline under warming temperature regimes as walleye prefer spring water temperatures between 6 and 12 °C (McMahon et al., 1984). Second, 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. Third, lower future precipitation rates (IPCC 2013) will reduce lake turbidity, forcing walleye to feed less frequently during the day. Lastly, walleye could 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). The interconnected network of Ontario lakes would allow for these changes in fish distributions. Melles et al. (2015) developed lake connectivity models using circuit theory to demonstrate how Ontario lakes form a network of highly connected systems that allow for the dispersal of invasive warmwater species into northern lakes. Under climate warming scenarios, it is possible that these highly accessible systems would then be invaded due to the creation of new ideal habitats in more northerly regions (Melles et al., 2015).

**How do smallmouth bass negatively influence walleye abundance?**

We found that walleye abundance is reduced across a landscape in the presence of smallmouth bass. We found that there is higher walleye CPUE in lakes without bass regardless of lake size, lake depth and temperature (Fig. S1). We were able to rule out that the reduced abundance of walleye occurred solely because of habitat quality alone. 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). Predation is more prevalent when habitat conditions are favourable for smallmouth bass, that is when lakes are smaller, warmer and less turbid (Krishka et al., 1996). As walleye are already heavily preyed 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 result 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 utilize 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 byproduct 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 while 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, 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 scenarios were used, 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 et al., 2016). Although we have shown a decrease in walleye abundance in the presence of smallmouth bass, there is a higher likelihood of detecting an invasion of smallmouth bass into thermally suitable lakes under climate change scenarios than walleye extirpation from thermally unsuitable lakes. Further, some individual walleye may be able adapt or find thermal refugia within a lake (Van Zuiden et al., 2016). Thus, the likelihood of co-occurrence increases, particularly in central and northern Ontario, within the next 50 years. Specifically, 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 smallmouth bass–walleye co-occurrence is predicted to continue increasing, we predict walleye abundance will decline due to the increased presence of a superior competitor. In the interim, it is possible that expanding walleye stocking efforts could mitigate some of the smallmouth bass pressure, as currently there are only 52 inland lakes with walleye stocking programmes in Ontario (Kerr, 2008). Future walleye declines, however, are likely inevitable under scenarios of climate change as lake temperatures increase the availability of preferable thermal habitat for smallmouth bass while decreasing its availability for walleye (Edwards et al., 1985; McMahon et al., 1984; Van Zuiden et al., 2016).

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 in 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 et al., 2016). 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 (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 underlie the importance of reducing greenhouse gas emissions and invasions of non-native species in the future, as the continued existence of native fisheries is at stake.

**ACKNOWLEDGEMENTS**

We would like to thank Nigel Lester for providing updated fish community data as well as Lianna Lopez for helping us run co-occurrence models under climate change scenarios. We would also like to thank Miranda Chen for editing the final version of this manuscript. Funding for this research was provided by an NSERC Discovery Grant and York University to S.S.
REFERENCES


**SUPPORTING INFORMATION**

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

**Figure S1** Walleye CPUE when bass are absent in lakes larger than 1000 ha (A), between 100 and 1000 ha (B), smaller than 100 ha (C), shallower than 30 m (D), deeper than 30 m (E), in regions with cooler air temperatures than 17 °C (F), and in regions with warmer air temperatures than 17 °C (G).

**Appendix S1** Data from the Sharma et al. (2015) publication were adapted to illustrate how trends in summer surface water temperatures (SSWT) are increasing in a subset of 24 Ontario inland lakes.

**BIOSKETCHES**

Thomas Van Zuiden is a York University MSc graduate under the supervision of Prof. Sapna Sharma. His research involves analysing how climate change may impact fish distributions in Ontario.

Sapna Sharma is an Assistant Professor in the Department of Biology at York University. Her research investigates how environmental stressors, including climate change and invasive species, impact lake water temperatures, ice phenology, water quality, species distributions and ecosystem function.

Author contributions: TVZ and SS conceived the study. TVZ conducted data analyses. TVZ and SS wrote the manuscript.

Editor: Hugh MacIsaac