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Research

Quantifying the potential effects of climate change and the invasion of smallmouth bass on native lake trout populations across Canadian lakes

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Climate change and invasive species are two stressors that should have large impacts on native species in aquatic and terrestrial ecosystems. We quantify and integrate the effects of climate change and the establishment of an invasive species (smallmouth bass *Micropterus dolomieu*) on native lake trout *Salvelinus namaycush* populations. We assembled a dataset of almost 22 000 Canadian lakes that contained information on fish communities, lake morphologies, and geography. We examined the pelagic-benthic and littoral forage fish community available to lake trout populations across three lake size classes in these aquatic ecosystems. Due to the decreased presence of alternate prey resources, lake trout populations residing in smaller lakes are more vulnerable to the effects of smallmouth bass establishment. A detailed spatially and temporally explicit approach to assess smallmouth bass invasion risk in Ontario lakes suggests that the number of Ontario lakes with vulnerable lake trout populations could increase from 118 (~1%) to 1612 (~20%) by 2050 following projected climate warming. In addition, we identified nearly 9700 lake trout populations in Canada threatened by 2100, by the potential range expansion of smallmouth bass. Our study provides an integration of two major stressors of ecosystems, namely climate change and invasive species, by considering climate-change scenarios, dispersal rates of invasive species, and inter-specific biotic interactions.

Climate change and invasive species are two stressors threatening native ecosystems throughout the world. Non-native species can have large ecological (Lodge 1993, Ricciardi and MacIsaac 2000, Simon and Townsend 2003, McKinney and LaSorte 2007) and economical impacts (associated annual costs approximating $120 billion in the United States) (Pimentel et al. 2005). Climate change is expected to exacerbate non-native species invasions as conditions at any given site become less suitable for existing species and may become more suitable for invasive species (Dukes and Mooney 1999) owing to climate-related impacts on local habitats. As such, there is a need to improve estimates of invasion risk using models that account for habitat suitability under climate-change scenarios, the dispersal rate of an invasive species, and its interactions with native species within the community (Dukes and Mooney 1999). The ability to spatially and temporally quantify the impacts of invasive species is imperative to identify the number of potentially threatened native populations.

We present a spatially and temporally explicit framework quantifying the effects of climate change and the invasion of a non-indigenous species on native populations. The general framework involves first developing species distribution and habitat models that yield high predictive power on current environmental scenarios, followed by forecasting future predictions of habitat availability and species distribution under scenarios of climate change. The forecasted ecological models will provide an indication of potential range expansion. Subsequently, dispersal rates are calculated to determine if in fact the species can disperse to the predicted potential future habitat as suggested by the previous models. If a species is able to disperse to the forecasted regions in the time-frame set by the climate-change scenario (i.e. 50 or 100 yr), a quantification of the impact of successful species establishment on native species is appropriate. As such, assuming that a non-indigenous species establishes itself in the new region, if there is a negative impact on native species, native populations will be considered vulnerable. However, if there is no impact of a species introduction on native species, native populations will be buffered to the effects of the biological invasion. This framework can serve as a general approach provided the availability of information that incorporates aspects of habitat suitability under climate change, dispersal rates, and biotic interactions.

In this study, we quantify the effects of climate change and the invasion of smallmouth bass on native lake trout populations across Canadian lakes. The abundance of lake trout, a native cold-water fish species, has declined from overexploitation, habitat degradation, acidification, eutrophication, and fish stocking (Vander Zanden et al. 2004a). In central Ontario, the number of native lake trout populations has declined by ca 5% (Olver et al. 1991). Lake trout will continue to experience additional stressors, for example, alteration of habitat, increased road access, climate change, and invasion of aquatic species (Gunn and Pitblado 2004).

Increases in water temperature due to climate change, will introduce additional stress on lake trout populations. Global air temperatures are predicted to increase by between 1.4 and 5.8°C owing to the increased emissions of greenhouse gases into the atmosphere (IPCC 2001). Climate change will alter thermal habitat and the distribution and growth of aquatic organisms (Casselman 2002). As climate warms, suitable habitat for lake trout may decrease while suitable habitat for cool and warmwater fish species may increase (Shuter and Post 1990, Schindler et al. 1996, Gunn and Pitblado 2004, Shuter and Lester 2004) causing lake trout to be more vulnerable to introductions of warmwater and coolwater competitors (Gunn and Pitblado 2004). Some fishes are expected to expand their range northward (Rahel 2002) by ca 500 or 600 km (Magnuson et al. 1997). One such species is the smallmouth bass for whom the northern range could be extended by hundreds to thousands of kilometers owing to the expansion of optimal thermal habitat for this species under climate-change scenarios (Sharma et al. 2007). This northward range expansion of smallmouth bass could have dramatic impacts on native lake trout and cyprinids populations, as well as impacting all trophic levels of the ecosystem (Jackson and Mandrak 2002).

Smallmouth bass, a warmwater fish species, and lake trout, a coldwater fish species, inhabit different habitats. However, the northward range expansion of smallmouth bass may affect lake trout populations as they share similar food resources especially in fall, winter, and spring (Vander Zanden et al. 1999). In the absence of bass and pelagic-benthic forage fish, lake trout diet consists of ca 60% littoral cyprinids (Vander Zanden et al. 1999). When littoral predators like smallmouth bass are present, the littoral prey assemblage is eliminated or reduced in abundance (Jackson et al. 1992, MacRae and Jackson 2001, Jackson and Mandrak 2002). Thus, lake trout forage predominantly on pelagic prey, rather than littoral prey in lakes with smallmouth bass (Vander Zanden et al. 1999, 2000). Where pelagic forage fish are absent in lakes with smallmouth bass, lake trout consume zooplankton as their primary food source (Vander Zanden et al. 1999, 2000) and only ca 20% of the lake trout diet is composed of littoral cyprinids (Vander Zanden et al. 1999). This shift in diet to less energetically rewarding prey has negative implications for growth and reproduction of lake trout (Vander Zanden et al. 2004a).

The primary objective of our study is to provide a framework to quantify the impacts of invasive species under climate-change scenarios on native populations using a spatially and temporally explicit approach. Our purpose is to quantify the impact of smallmouth bass, currently experiencing range expansion, on native lake trout populations by inferring the vulnerabilities of lake trout populations to smallmouth bass under climate-change scenarios for different sized Canadian lakes. We examine the pelagic-benthic and littoral forage fish communities available to lake trout and potentially to smallmouth bass for: small (10–100 ha), medium (100–1000 ha) and large (>1000 ha) lakes. Lake trout populations may be vulnerable to the co-occurrence of smallmouth bass in lakes if only littoral forage fish are available. Conversely, lake trout populations may be buffered from the influence of smallmouth bass in a lake where both pelagic-benthic and littoral forage are available. We hypothesize that smaller lakes will be more vulnerable to the effects of smallmouth bass because they are less likely to contain both pelagic-benthic and littoral forage fishes.

Methods

We gathered data on lake morphology and corresponding fish communities from a variety of academic and government institutions across Canada. We obtained fish community data from 21 975 Canadian lakes for which 15 551 lakes also included surface area (Table 1). The methodological framework for this study is summarized in Fig. 1.

Lake data

We used several approaches to estimate lake counts because many Canadian maps, in particular maps providing coverage of northern areas, underestimate the number of small lakes owing to limited mapping resolution (Lehner and Doll 2004) when covering large spatial scales. To reduce uncertainty in lake counts, we only used lakes >10 ha. In a global analysis of aggregated lake size data, Lehner and Doll (2004) and Downing et al. (2006) showed that observed distributions of lakes approximate the Pareto distribution. We estimated Pareto distribution parameters for each of the secondary watersheds in Canada. The Pareto distribution follows the function, $N_{a=A} = \alpha A^{\beta}$ where N is the number of lakes with area (a) greater than or equal to a threshold area (A). The Pareto distribution parameters were subsequently used to estimate the number of lakes per size class in each secondary watershed for lakes <10 000 ha in surface area. For lakes >10 000 ha we used remote sensing data and the Global Lakes and Wetland Database to approximate lake area (Lehner and Doll 2004, A. Davidson pers. comm.).

The database for the Manitoba province presented some unique issues. Although fish community data within Manitoba were available, we could not obtain corresponding information on lake surface area, although some lakes did contain data on maximum lake depth. For lakes that contained unique identifiers such as lake name and a corresponding geographic location, we searched the Global Lakes and Wetland Database for information on surface area. For lakes not addressed this way, we developed a regression relationship between maximum depth and surface area. This was completed using a bootstrapped

Table 1. Summary of the number of lakes with fish community data assembled for this study.

Province	Fish data	Fish data with area	Data sources
British Columbia	3860	3423	Dept of Fisheries and Oceans, Univ. of Calgary, Univ. of Toronto
Alberta	141	140	Atlas of Alberta Lakes, Univ. of Calgary, Robinson and Tonn 1989
Saskatchewan	587	587	Dept of Fisheries and Oceans
Manitoba	1001	243	Dept of Fisheries and Oceans
Ontario	9886	9883	Ontario Ministry of Natural Resources
Quebec	5299	117	Québec Ministère de Ressources Naturelles et de la Faune, Dept of Fisheries and Oceans, Univ. du Québec à Montréal, Univ. du Québec à Trois Rivières
Nova Scotia	911	869	Dept of Fisheries and Oceans
New Brunswick	19	19	Hansen 2004
Newfoundland	149	149	Dept of Fisheries and Oceans
Northwest Territories	13	12	Dept of Fisheries and Oceans, Univ. of Toronto
Nunavut	0	0	–
Yukon	109	109	Univ. of Calgary
Total	21975	15551	

Model II regression to obtain a more accurate slope given common levels of error associated with both area and depth (Chen et al. 1994). Lakes in north-western Ontario and northern Saskatchewan were chosen for the Model II regression analyses based on their having similar surficial and bedrock geology to geographically adjacent lakes in southern and northern regions of Manitoba respectively. We bootstrapped the Model II regression 1000 times to determine the relationship between maximum depth and surface area and applied this relationship to lakes in Manitoba.

Fish community data

The provinces of Ontario, British Columbia, Nova Scotia and Saskatchewan provided detailed records of fish community, lake morphology and water chemistry (Table 1). We have greater confidence in estimates of buffered and vulnerable lake trout populations for these provinces. There were records of fish community data for the island of Newfoundland where there are no lake trout, whereas no community data were available for lakes in Labrador where lake trout are known to exist. Although we obtained large fish community presence/absence datasets for Manitoba and Quebec lakes, there were few lakes that could be matched with corresponding surface area data owing to the nature of the databases. The majority of lakes for which we had fish community data in those two provinces could not be included in the analysis because they lacked information on lake size. Most lakes in the Yukon for which we had fish community data contained lake trout. These lakes have good records of pelagic-benthic forage fishes, but not littoral fishes.

For each of the provincial and territorial datasets, fish communities were categorized into lakes that had surface areas between 10–100, 100–1000, and >1000 ha. Within each size class, we determined the fraction of lakes with lake trout. In addition, we identified the fraction of lakes in which lake trout populations are buffered from the invasion of smallmouth bass, that is lakes that contained lake trout, and both pelagic-benthic and littoral fishes. If smallmouth bass establish in these lakes, lake trout would have an alternate forage fish base and should not experience a major reduction in growth and fecundity (Vander Zanden et al. 2004a). We identified the fraction of lakes in which lake trout populations will be vulnerable to the effects of smallmouth bass establishment. These lakes contain lake trout and littoral prey species, but no pelagic-benthic forage fishes (Fig. 1).

Species categorization was based on forage preferences of lake trout populations throughout their Canadian range. Fishes categorized as pelagic-benthic forage fish were: alewife *Alosa pseudoharengus*, lake herring *Coregonus artedi*, Atlantic herring *Clupea harengus*, Nipigon cisco *Coregonus nipigon*, lake whitefish *C. clupeaformis*, round whitefish *Prosopium cylindraceum*, mountain whitefish *P. williamsoni*, arctic grayling *Thymallus arcticus*, rainbow smelt *Osmerus mordax*, emerald shiner *Notropis atherinoides*, spottail shiner *N. hudsonius*, trout-perch *Percopis omiscomaycus*, ninespine stickleback *Pungitius pungitius*, logperch *Percina caprodes*, prickly sculpin *Cottus asper*, slimy sculpin *C. cognatus*, spoonhead sculpin *C. ricei*, and deepwater sculpin *Myoxocephalus thompsoni* (McDonald et al. 1998, Scott and Crossman 1998, Vander Zanden et al. 2000). Fishes categorized as littoral prey were: central mudminnow *Umbra limi*, northern redbelly dace *Phoxinus eos*, finescale dace *P. neogaeus*, lake chub *Couesius plumbeus*, golden shiner *Notemigonus crysoleucas*, common shiner *Luxilus cornutus*, fathead minnow *Pimephales promelas*, redside shiner *Richardsonius balteatus*, pearl dace *Margariscus margarita*, and brook stickleback *Culaea inconstans* (Scott and Crossman 1998, Jackson and Mandrak 2002).

Ontario fish community analyses

We used the Ontario Habitat Inventory database that consists of nearly 10 000 lakes, to identify invasion risk of smallmouth bass and its effects on lake trout populations in Ontario lakes under climate change scenarios. Analyses were conducted at a tertiary watershed level (i.e. the third level in a hierarchical watershed classification system; see Jackson

I. Lake data

Estimate total number of lakes by size (10–100, 100–1000, and > 1000 ha) using:

Pareto distribution (for lakes < 10 000 ha)

(for Manitoba lakes, lake size needed to be estimated first using a Model II regression for lakes < 10 000 ha)

Global Lakes and Wetland Database (for lakes > 10 000 ha)

Remote sensing methods (for lakes > 10 000 ha)

Model II regression (for Manitoba lakes < 10 000 ha)

II. Fish community data

Categorized by size classes (10–100, 100–1000, and >1000 ha):

Fraction of lakes with lake trout

Fraction of lakes with lake trout and at least one pelago-benthic forage fish species (Buffered)

Fraction of lakes with lake trout and at least one littoral forage fish species, and no pelago-benthic forage fish species (Vulnerable)

III. Population estimates

For each lake size category (10–100, 100–1000, and > 1000 ha):

Estimate of total number of lake trout populations =

Total number of lakes (from Part I) × Fraction of lakes with lake trout (from Part IIa)

Estimate of total number of buffered lake trout populations =

Total number of lakes (from Part I) × Fraction of buffered lakes (from Part IIb)

Estimate of total number of vulnerable lake trout populations =

Total number of lakes (from Part I) × Fraction of vulnerable lakes (from Part IIc)

Figure 1. Methodological framework used to estimate the numbers of lake trout populations, buffered lake trout populations, and vulnerable lake trout populations.

and Mandrak (2002) for a map of the tertiary watersheds) to attain a more accurate estimate of the number of buffered and vulnerable lake trout populations using the Ontario Habitat Inventory database and the Counts and Measurements of Ontario Lakes database (Cox 1978).

We calculated dispersal rates to determine the potential for smallmouth bass to disperse to the northern regions of the province assuming that smallmouth bass will invade every lake that has a suitable temperature based on our previous model (Sharma et al. 2007) and that dispersal barriers and unsuitable local conditions will not stop colonization – a situation that has been shown to be the case repeatedly due to large-distance dispersal events aided by humans. To determine smallmouth bass dispersal rates, we calculated Euclidean distances between locations at the northern extent of the front during successive time periods (whether smallmouth bass had dispersed or not) using the spatial analyst tools available in ArcGIS. We used smallmouth bass distribution based on 1970–1975 and 1975–1980 time intervals and calculated the average distance smallmouth bass had moved during that time period. We only used the lakes sampled between 1970 and 1980 to calculate dispersal rate because there were a greater number of lakes sampled throughout Ontario in those years relative to other decades. Based on the average dispersal rate, we estimated whether smallmouth bass would be able to disperse to northern Ontario by 2050 and 2100 assuming that suitable thermal conditions exist. It should be noted that the data did not permit us to differentiate between natural dispersal and human-mediated translocations, but rather provided an integrated measure summarizing the minimum average distance that the northern range boundary expanded during this time period.

Canadian fish community analyses

In a similar approach to the analyses conducted on the Ontario fish community dataset, we identified the fraction of lakes in which lake trout populations were buffered or vulnerable to the effects of smallmouth bass establishment for each province. This provided an estimate of the gross number of potentially impacted small, medium, and large lakes across Canada. The province of Quebec contains many lakes and we were unable to obtain fish community and corresponding lake morphology data for most lakes. We expect that Quebec and adjacent areas of Ontario, its neighbouring province, likely share similar relationships in their lake trout populations. Therefore, we also used Ontario lake trout and fish community relationships to attain a more realistic estimate of vulnerable lake trout populations in Quebec.

Uncertainty analyses

Because fish community data are often biased, we conducted an uncertainty analysis by using both half and twice the current frequency of predicted lake trout, pelago-benthic and littoral forage fishes. Based on the uncertainty analyses, we calculated the median, first quartile, and third quartile using each of the combinations (e.g. 0.5 × lake trout and 0.5 × forage fish, 0.5 × lake trout and 1 × forage fish, through to the combination of 2 × lake trout and 2 × forage fish) to estimate a potential range of buffered and vulnerable lake trout populations for each province/territory.

Results

Lakes

Using the Global Lakes Wetland Database (Lehner and Doll 2004), the Pareto distribution as described by Downing et al. (2006), and remote sensing analyses conducted by Environment Canada, it is estimated that Canada contains >3 706 900 lakes >10 ha (Table 2; Supplementary material Appendix 1).

Risk assessment of invasion of smallmouth bass in Ontario lakes

In Ontario, there are currently an estimated 8178 lakes that contain lake trout populations. There are 933 lakes in which lake trout and smallmouth bass co-occur, of which 286 lake trout populations are buffered from the effects of smallmouth bass. At present, there are 118 lake trout populations that are vulnerable to the effects of smallmouth bass presence (Table 3).

We calculated smallmouth bass dispersal rates for the five-year period between 1970 and 1975 to be ca 14.7 km yr^{-1}. The average distance dispersed northwards by smallmouth bass in the five-year period between 1975 and 1980 was 9.5 km yr^{-1}. Therefore, on average, smallmouth bass dispersed north by 12.1 km yr^{-1} during that decade. From the current smallmouth bass distribution, smallmouth bass would need to disperse ca 700 km to reach the northern limits of Ontario. Using the average dispersal rate of 12.1 km yr^{-1}, this can be achieved by 2050.

Table 2. Predicted counts of lakes for different lake size categories (ha) across Canadian provinces and territories. The counts were determined by using the Pareto distribution as outlined in Downing et al. (2006) and through remote sensing (A. Davidson pers. comm.). Provincial abbreviations are as follows: BC (British Columbia), AB (Alberta), SK (Saskatchewan), MB (Manitoba), ON (Ontario), QC (Quebec), NB (New Brunswick), NS (Nova Scotia), PEI (Prince Edward Island), LB (Labrador), ND (Newfoundland), YK (Yukon Territory), NWT (Northwest Territories), and NT (Nunavut Territory).

	10–100 ha	100–1000 ha	>1000 ha
BC	19288	1245	165
AB	16497	1294	136
SK	58126	4832	476
MB	73374	6405	3658
ON	82333	6483	2431
QC	185763	18194	6602
NB	1656	2338	1236
NS	2317	1368	496
PEI	194	13	2
LB	24757	2478	232
ND	8342	5214	3242
YK	12509	1344	91
NWT	151875	10596	6384
NT	171061	22260	14745

Assuming that habitat would be thermally suitable for smallmouth bass in 2050 and 2100 and that smallmouth bass would be able to disperse to northern Ontario by 2050, we predicted the potential risk to lake trout under climate-change scenarios. The number of Ontario lakes with vulnerable lake trout populations could increase from 118 (∼1%) to 1612 (∼20%) following projected climate warming (Table 3).

Risk assessment of invasion of smallmouth bass in Canadian lakes

The risk assessment of invasion of smallmouth bass for Canadian lakes assumed that smallmouth bass would disperse across Canada by 2100 following Sharma et al. (2007) and Sharma and Jackson (2008). We calculated the median number, and first and third quartiles of lakes that contained buffered and vulnerable lake trout populations by province for small, medium, and large lakes across the country (Table 4). There are an estimated 87 125 lake trout populations in Canadian lakes of which 29 000 (∼33%) lake trout populations are buffered to potential effects of smallmouth bass establishment – that is these lakes contain both pelagic-benthic and littoral forage fish species. There are 9668 (∼11%) lake trout populations that would be vulnerable to smallmouth bass invasion because these lakes do not have an alternate pelagic-benthic forage fish base for lake trout. Based on frequency of vulnerabilities, lake trout populations found in smaller lakes tend to be more vulnerable to the effects of smallmouth bass establishment, whereas larger lakes tend to be more buffered to the impacts of smallmouth bass. The re-analyses of Quebec fish community data estimated 84 290 lake trout populations across Canadian lakes of which 21 620 (∼26%) lake trout populations are buffered from the effects of the potential invasion of smallmouth bass. There are 19 940 (23%) lake trout populations that would be vulnerable to the invasion

Table 3. Predicted estimates of current number of lake trout populations, buffered lake trout populations (lakes that contain pelago-benthic and littoral forage fishes), vulnerable lake trout populations (lakes that only contain littoral forage fishes), buffered and vulnerable lake trout populations under climate change scenarios based on smallmouth bass introductions in Ontario lakes.

	10–100 ha	100–1000 ha	>1000 ha	Total
Lake trout populations	6274	1624	280	8178
Smallmouth bass populations	2758	929	193	3880
Lake trout and smallmouth bass co-occurrence	482	344	107	933
Buffered lake trout populations	119	107	60	286
Vulnerable lake trout populations	94	23	1	118
Buffered lake trout populations – climate change	3279	583	137	3999
Vulnerable lake trout populations – climate change	1440	166	6	1612

Table 4. Estimates of number of lake trout populations, buffered lake trout populations (lakes that contain pelago-benthic and littoral forage fishes), and vulnerable lake trout populations (lakes that only contain littoral forage fishes) assuming that smallmouth bass has dispersed throughout Canada by 2100. The median number of lakes is presented with the 25th quartile and 75th quartile presented from the uncertainty analyses in brackets. Re-estimates of Quebec are based on using the proportions found within the large database of lakes for the adjacent region of Ontario.

	10–100 ha	100–1000 ha	> 1000 ha
British Columbia			
Lake trout populations	251 (188, 376)	153 (115, 230)	50 (38, 76)
Buffered lake trout populations	71 (35, 141)	67 (33, 133)	23 (12, 46)
Vulnerable lake trout populations	24 (12, 47)	0	2 (1, 4)
Alberta			
Lake trout populations	434 (326, 651)	55 (41, 83)	23 (17, 35)
Buffered lake trout populations	0	28 (14, 55)	12 (6, 23)
Vulnerable lake trout populations	0	0	0
Saskatchewan			
Lake trout populations	4912 (3684, 7368)	915 (6686, 1373)	192 (144, 287)
Buffered lake trout populations	0	293 (146, 586)	142 (71, 284)
Vulnerable lake trout populations	819 (409, 1637)	0	0
Manitoba			
Lake trout populations	843 (633, 1265)	1580 (1185, 2369)	1486 (1115, 2229)
Buffered lake trout populations	0	176 (88, 351)	171 (86, 343)
Vulnerable lake trout populations	0	176 (88, 351)	0
Ontario			
Lake trout populations	11504 (8628, 17256)	1996 (1497, 2993)	875 (656, 1313)
Buffered lake trout populations	2439 (1220, 4878)	(681 (341, 1363)	439 (220, 879)
Vulnerable lake trout populations	4993 (2497, 9987)	282 (141, 564)	11 (5, 22)
Quebec			
Lake trout populations	18576 (13932, 27864)	13646 (10234, 15920)	4548 (3411, 5575)
Buffered lake trout populations	11146 (5573, 22292)	4549 (2274, 9097)	293 (147, 587)
Vulnerable lake trout populations	0	1819 (910, 3639)	0
Quebec re-estimated			
Lake trout populations	25956 (19467, 38934)	5600 (4200, 8401)	2376 (1782, 3564)
Buffered lake trout populations	5503 (2752, 11006)	1912 (956, 3824)	1193 (597, 2386)
Vulnerable lake trout populations	11266 (5633, 22532)	791 (395, 1582)	30 (15, 60)
New Brunswick			
Lake trout populations	0	585 (438, 877)	0
Buffered lake trout populations	0	585 (292, 1169)	0
Vulnerable lake trout populations	0	0	0
Nova Scotia			
Lake trout populations	0	0	1 (0, 1)
Buffered lake trout populations	0	0	0
Vulnerable lake trout populations	0	0	0
Newfoundland			
Lake trout populations	0	0	0
Buffered lake trout populations	0	0	0
Vulnerable lake trout populations	0	0	0
Yukon			
Lake trout populations	9382 (7036, 10945)	1090 (818, 1217)	80 (60, 85)
Buffered lake trout populations	0	0	0
Vulnerable lake trout populations	0	0	0
Northwest Territories			
Lake trout populations	–	8477 (6358, 9536)	5472 (4104, 5928)
Buffered lake trout populations	–	4238 (2119, 8447)	3648 (1824, 6384)
Vulnerable lake trout populations	–	0	1824 (912, 3648)

of smallmouth bass as these lakes do not have an alternate pelagic-benthic forage base for lake trout.

Discussion

We quantified the effects of climate change and the northward range expansion of smallmouth bass on native lake trout populations in Canada. We estimated that there are ca 87 125 lake trout populations in Canadian lakes at present. Climate change will have dramatic impacts on native coldwater fishes, such as lake trout, even in the absence of invasion of competitors. Increases in water temperatures and longer stratification period may decrease hypolimnetic oxygen concentrations leading to increased frequency of anoxic waters, thereby reducing the amount of suitable habitat available and the abundance of lake trout populations in many Canadian lakes (Fang and Stefan 1999, King et al. 1999, Shuter and Lester 2004). For example, MacKenzie-Grieve and Post (2006) showed that temperature increases as low as 2°C would decrease thermal habitat and potential harvest of lake trout in southern Yukon lakes. Furthermore, changes in fish community composition resulting from changes in abiotic and biotic factors (such as range expansion of smallmouth bass and range contraction of cool- and cold-water pelago-benthic forage fish species) will increase stress on lake trout populations as lake trout potentially lose some of their habitat and forage base.

The decline in lake trout populations will be compounded by the invasion of smallmouth bass. Using the potential future suitable thermal habitat and distribution of smallmouth bass under climate change scenarios (Sharma et al. 2007, Sharma and Jackson 2008) and assuming that future lake trout distribution will not change, we derived conservative estimates of lake trout vulnerability. Although lake trout, a coldwater species, and smallmouth bass, a warmwater species, inhabit different habitats, they can have overlapping food resources (Jackson 2002, Vander Zanden et al. 2004a). In lakes containing bass, lake trout are forced to forage on pelagic fish prey or zooplankton rather than their preferred littoral prey assemblage, which are consumed by smallmouth bass (Jackson 2002, Shuter et al. 2002, Vander Zanden et al. 2004a). Assuming that smallmouth bass will be able to establish in most Canadian lakes by 2100, we estimate that 29 000 (33%) of the lake trout populations will be buffered to the invasion of smallmouth bass. We estimate that at least 9668 (11%) lake trout populations will be vulnerable to the effects of smallmouth bass invasion across Canadian lakes. Lake trout populations in smaller lakes tend to be more vulnerable to the effects of smallmouth bass, whereas those in larger lakes tend to be more buffered to the effects of smallmouth bass invasion. This difference results because larger lakes tend to contain both pelagic-benthic and littoral forage fishes, whereas smaller lakes typically only contain littoral forage fishes. Furthermore, larger lakes tend to contain cooler, more oxygenated areas available as refuge to lake trout. This finding stresses the importance of protecting lake trout populations residing in smaller lakes from the effects of smallmouth bass, because smaller lakes tend to only contain littoral forage fishes and are also more likely to contain more stressful abiotic conditions for lake trout, such as increased water temperatures and lower oxygen levels under climate-change scenarios.

The number of Ontario lakes with vulnerable lake trout populations could increase from 118 (~1%) to 1612 (~20%) following projected climate warming, provided that smallmouth bass are able to disperse northwards under climate change (which based on recent range extensions appears to be highly probable as climate change scenarios suggest that thermal habitat and distribution of smallmouth bass could expand northwards by hundreds to thousands of kilometres (Sharma et al. 2007, Sharma and Jackson 2008)). Despite less suitable thermal habitat being available to smallmouth bass in the past, we estimate that smallmouth bass have had their range expanded northwards by approximately twelve kilometers per year on average. It should be noted that our predictions are based on the assumption that dispersal rates remain the same in the future, although future rates of dispersal may change.

Currently the northward range expansion of smallmouth bass has been facilitated by both natural dispersal and human-mediated translocations. Unfortunately due to data limitations, we were unable to dissociate between the two modes of dispersal, although both modes of dispersal are expected to continue into the future. Human-mediated translocations have been facilitated by governmental agencies through stocking, and authorized, unauthorized and accidental introductions by anglers (Jackson 2002, Vander Zanden et al. 2004b). The human-induced component is particularly important as it is often over longer distances and barriers, e.g. into different watersheds. However, there is uncertainty associated with the estimates of human-mediated dispersal rates across barriers because we do not know how awareness among the public and authorities will change in the future. Of particular importance is whether or not humans will move fish across the continental divide. Continuing education will be required to reduce and stop the accidental and premeditated introductions of smallmouth bass into additional watersheds.

Natural dispersal is the second mode of dispersal and is facilitated by the ability of smallmouth bass to colonize adjacent waters (Jackson and Mandrak 2002). The northward expansion of smallmouth bass may be further assisted by the direction of the low gradient river systems in the north (Jackson and Mandrak 2002). As environmental conditions become suitable north of the continental divide, acceleration of smallmouth bass range expansion is expected due to the northward direction of flow of river systems as the direction of water flow changes from south to north above the continental divide (Jackson and Mandrak 2002, Sharma et al. 2007). However, if water levels decline as climate warms, the northward expansion of smallmouth bass may be hindered as drainage systems become fragmented (Jackson and Mandrak 2002).

The northward range expansion of smallmouth bass will have substantial impacts on lake trout populations by decreasing their growth and reproduction (Vander Zanden et al. 1999), but also on fish community composition (Jackson 2002). Many studies have reported that the presence of littoral predators like smallmouth bass, have been strongly associated with the lack of cyprinids (Harvey 1981, Tonn and Magnuson 1982, Jackson and Harvey 1989, Jackson et al. 1992, Vander Zanden et al. 2004a). Invasion of smallmouth bass into an aquatic system may relate to the loss of entire assemblages, leading to the homogenization of fish fauna (Jackson 2002). These effects on cyprinids appear to be more pronounced in smaller lakes (Jackson and Mandrak 2002). MacRae and Jackson (2001) found that, while controlling for lake size, lakes, with smallmouth bass contained an average of 2.3 fewer smaller-bodied species and attributed this difference to predation by bass but did not find similar impacts due to trout predation. Jackson and Mandrak (2002) estimated that $>$25 000 local populations of four cyprinid species, specifically northern redbelly dace, finescale dace, fathead minnow and pearl dace, may disappear within Ontario alone as climate warms and smallmouth bass invade. Although the habitat suitability for littoral forage fishes may increase under climate-change sceanarios, the association of smallmouth bass with a reduction in cyprinid species diversity, further reinforces the risk of smallmouth bass invasion on lake trout populations and the native fish community, particularly in smaller lakes.

Data limitations

The total number of freshwater lakes and their size distributions are subject to a large amount of uncertainty on a global scale (Lehner and Doll 2004, Downing et al. 2006). We estimated that there are over 3.7 million lakes in Canada $>$10 ha. The estimate of the number of Canadian lakes at small size classes, i.e. $<$10 ha, was significantly larger than previous accounts (Cox 1978; Supplementary material Appendix 1). Lakes $>$5000 ha tended to be well identified; however there was a large degree of uncertainty with lakes $<$100 ha (Lehner and Doll 2004). Under-representation of lakes $<$100 ha may be due to the difficulty in identifying an individual lake in GIS analyses because of low resolution in remote sensing and mapping, and owing to highly irregular shorelines resulting in lakes being combined and counted as one lake using remote sensing methods (Lehner and Doll 2004).

Fish community data were generally lacking in many regions of the country, particularly in association with lake surface area data. We attempted to document the obvious discrepancies in data collection. Fish community sampling tended to be biased towards sampling larger, more accessible lakes that contained targeted sport fishes while under-sampling smaller fishes, such as cyprinids (Minns 1986, Jackson and Mandrak 2002). Less-biased sampling would provide a more realistic risk assessment. This paucity of data stresses the need for unbiased and basic data collection in terms of lake morphology, water chemistry and community compositional data for a large number of lakes in each province that is publicly available to attain a more accurate estimate of the ecological status of aquatic systems in Canada.

Conclusions

There is a need for a more integrated approach to delineate areas of invasion concern and quantify the risk associated with a successful invasion on native populations owing to a combination of ecological stressors, such as climate change and invasion of non-indigenous species. We provide a framework to quantify the impact of the invasion of non-indigenous species under climate-change scenarios on native populations using a spatially and temporally explicit approach. The key elements of the general framework include: models linking current environments and species distribution; predictions of potential future habitat availability under climate-change scenarios; estimates of species rates of dispersal or range expansion (i.e. will the species be able to disperse to predicted future habitat in the time-period predicted by the climate-change scenarios, such as in 50 or 100 yr?); and, the quantification of the impact of successful species establishment on native species based on field studies or experiments. This combination of features permits the risk assessment for aquatic and terrestrial species, provided there is a sufficient understanding of the biology of the system, and if adequate spatially and temporally explicit data are available. Further understanding of the responses and linkages between invasive species, climate change and native species, will permit improved management and conservation of our native ecosystems. The potential decline in lake trout abundance will necessitate further attention to the development of regional fisheries management approaches (Vander Zanden et al. 2004a), particularly because this could have a great negative impact on the Canadian recreational fishery as anglers have already begun to lose interest in this economically important species (Vander Zanden et al. 2004b).

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