Changing Fish Biodiversity: Predicting the Loss of Cyprinid Biodiversity Due to Global Climate Change

DONALD A. JACKSON

Department of Zoology, University of Toronto, Toronto, Ontario M5S 3G5, Canada Phone: 416-978-0976, Fax: 416-978-8532, E-mail: Jackson@zoo.utoronto.ca

NICHOLAS E. MANDRAK

Department of Fisheries and Oceans, Burlington, Ontario L7R 4A6, Canada Phone: 905-336-4842, Fax: 905-336-6437, E-mail: MandrakN@dfo-mpo.gc.ca

Abstract.—Substantial changes in the patterns of global temperature and precipitation are predicted to occur over the next century. Changes in the thermal habitat will alter the thermal boundaries that currently limit the distribution of many species. Species such as smallmouth bass Micropterus dolomieu are currently limited in their northern distribution by temperature-related effects as the length of the growing season determines population viability through overwinter survival of the young-of-the-year. Using a climate change scenario, we estimate the additional area and number of lakes within Ontario that will provide suitable thermal habitat sufficient for their viability. Smallmouth bass are known to have strong negative impacts on many other aquatic species. We estimate their impact, in extirpating four cyprinid species, northern redbelly dace Phoxinus eos, finescale dace Phoxinus neogaeus, fathead minnow Pimephales promelas, and pearl dace Margariscus margarita, in Ontario. We estimate that in excess of 25,000 populations of these species may be lost and discuss the relative sources of errors within our modeling approach.

Introduction

Changes in atmospheric composition are predicted to lead to altered climate for the planet. The predictions are for increased temperatures globally with greater effects towards the poles. Effects may vary during different times of the year and the implications for the hydrologic cycle are more uncertain than for the temperature regimes. Considerable concern has been expressed about the implications of these changes to climate for terrestrial environments such as agricultural areas, forested lands, and other terrestrial ecosystems. One of the principal concerns is the ability of these systems to adjust and shift to appropriate locales in response to the changing climate. Given the great rate of temperature change, the rates of movement and distance that must be moved are considerable and pose substantial challenges to the biota.

To date, less attention has been paid to the potential effects on aquatic systems, despite the fact that these systems are currently among our most ecologically threatened and susceptible to loss of biodiversity (Naiman et al. 1995; Ricciardi and Rasmussen 1999). Aquatic ecosystems in deserts are obviously at considerable risk with climate change due to their current threatened status, limited number of sites, and vulner-

ability to increased temperature and evaporation combined with possibly decreased precipitation. However, many other freshwater systems will be impacted and exhibit associated changes in biodiversity, productivity, and recreational and commercial fishing opportunities. In more northerly environments, there is the potential for new species to become established (e.g., Mandrak 1989) from more southerly locales, but existing resident species will likely decline due to direct or indirect effects related to climate change.

Our study considers the potential impacts of a predatory fish species, smallmouth bass Micropterus dolomieu, on native cyprinid species in northern Ontario under a climate-warming scenario. The northern range of the smallmouth bass is currently limited by temperature; however, changes in climate may lead to a change in this northern boundary. Shuter et al. (1980) showed the strong linkage between the viability of smallmouth bass populations and air temperature (Figure 1). They showed that the overwinter viability of the young-ofthe-year (YOY) smallmouth bass was strongly dependent on temperature (indexed as the July average air temperature) as this influenced the growth rate and size of the YOY entering their first winter and their ability to avoid starvation during the winter. The range between 18°C and 16°C was critical, with most populations hav2 Author

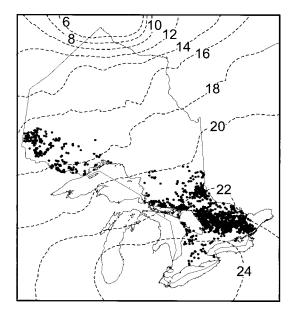


Figure 1. Current distribution of smallmouth bass and mean July air temperature.

ing high viability towards the higher end of this range whereas viability was essentially zero as the mean July temperature approached 16°C. The northern boundary of the smallmouth bass distribution was strongly related to the July mean temperature across a wide geographic range (Shuter et al. 1980). Therefore, if the temperature regime is shifted northwards due to global climate change, we can expect the thermal range limits of smallmouth bass distribution to also change, with the potential for smallmouth bass to exist further north than at present.

The presence of littoral predators, such as smallmouth bass, largemouth bass M. salmoides, and northern pike Esox lucius, has been shown to be strongly associated with the absence of many species of cyprinids (Harvey 1981; Tonn and Magnuson 1982; Jackson and Harvey 1989; Robinson and Tonn 1989; Jackson et al. 1992; Findlay et al. 2000). Jackson (2002) showed the strong negative association between Micropterus species and various cyprinids (Figure 2), notably northern redbelly dace *Phoxinus eos*, finescale dace *P. neogeaus*, fathead minnow Pimephales promelas and pearl dace Margariscus margarita. In general, where either species of *Micropterus* was present, these cyprinid species were absent. Although the bass species have restricted distributions within Ontario, these cyprinids are common throughout much of the province. Global warming would lead to additional northern areas of the province (and the associated lakes) having suitable thermal habitat for bass. However, when bass become established within a lake, there would likely be a corresponding loss in the cyprinid biodiversity with some cyprinids being more affected than others. Our study models the potential impact of smallmouth bass on four species of cyprinids in areas of northern Ontario that may become suitable for smallmouth bass under global warming.

Methods

Data

The Ontario Lake Inventory Database provides data on fish species composition and lake environmental conditions for approximately 10,000 lakes. This sample of the approximately 250,000 lakes in Ontario (Cox 1978) has been shown to be biased in the size of the lakes chosen, has an over-representation of sport fishes and particular combinations of sport fishes (Minns 1986), and is poorly sampled for both northern regions of the province and for nonsport fishes. Much of the sampling was done using gillnets to target sport fishes, so most of the lakes have not been sampled adequately to determine the occurrence of small fishes, particularly cyprinids. However, these data provide approximations of whether certain species are found in particular regions of Ontario. These regions can be defined on the basis of drainage basins. In Canada, drainages are defined as primary, secondary and tertiary watersheds and we used tertiary watersheds are our operational geographic unit (see Figure 3 for a map of these tertiary watersheds in Ontario). We used 96 of the 144 tertiary watersheds in Ontario, excluding the southernmost watersheds that contain few, if any lakes or where smallmouth bass are present now. We excluded those watersheds where smallmouth bass are present now as we are primarily interested in the potential expansion of their range rather than possible changes to fish communities within their current range. Cox (1978) provided summaries of the number of lakes in different size classes per watershed. He classified lakes into groups based on surface areas of less than 1 ha, 1–10 ha, 10–100 ha, 100–1,000 ha, greater than 1,000 ha. Based on the combination of the Lake Inventory Database and the data provided by Cox (1978), we estimated the number of lakes in each size-class per watershed and summarized the occurrence of each species of interest, i.e. smallmouth bass, northern pike, northern redbelly dace, finescale dace, fathead minnow, and pearl dace, in each watershed across the province (Figure 4). In general, sampling in many areas of northern Ontario has been limited; therefore, the absence of records for various species in these watersheds may be due to the lack of sampling, not necessarily the actual absence of these cyprinids.

Given the sampling biases in the inventory database, we could not estimate the frequency of occurrence Chapter Title 3

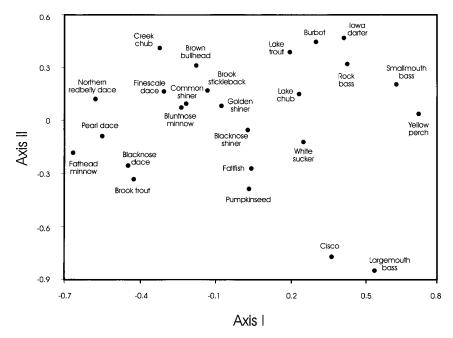


Figure 2. Plot of the first two axes from a Principal Coordinates Analyses of the species presence-absence from 52 lakes in the Black and Hollow River drainages of south-central Ontario. The measure of association between species was calculated using the Phi similarity coefficient. Relative position of species provides a measure of their association with other species within this watershed. Species positioned adjacent to one another are frequently found to co-exist whereas species at opposite ends of Axis 1 are generally not found together. This figure is reproduced from Jackson (2002).



Figure 3. Tertiary watersheds in Ontario. Lines represent watershed boundaries.

of these species within size classes of lakes nor within watersheds. To provide estimates of incidence rates (i.e., frequency of occurrence), we required data from sampling programs that systematically targeted all fish species within given sets of lakes. Datasets from the Black and Hollow River watersheds and Algonquin Provincial Park in central Ontario (Jackson 1988, 2002; Mandrak, unpublished data) provided estimates of the incidence of these cyprinids in these lake size classes for lakes where smallmouth bass were present and for lakes where they were absent. The Black and Hollow River watersheds were sampled intensively using multimeshed gill nets, trap nets, Plexiglas traps, and baited minnow traps. The Algonquin lakes were sampled using multi-meshed gill nets, baited minnow traps and seine nets. Pike were absent from all lakes in these studies with the exception of a few lakes in Algonquin Provincial Park (Mandrak, unpublished data). Estimates for the incidence of pike, and cyprinids in the presence or absence of pike, were obtained from datasets for northwestern Ontario (Crossman 1976; Beamish et al. 1976) and northeast of Lake Superior (Somers and Harvey 1984). Due to the northern location of lakes in these datasets, bass were rare or absent in each of them. Therefore, none of these datasets permit estimates of the relative impact on cyprinids of smallmouth bass and pike 4 Author

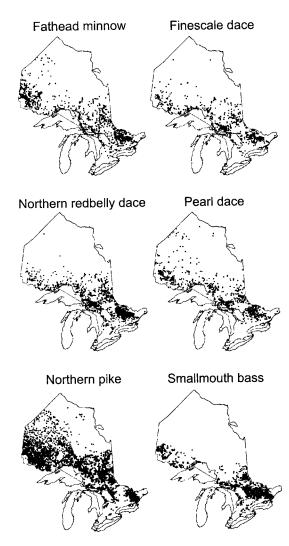


Figure 4. Distributions of the six fish species used in the analysis. The poor representation of these species, particularly cyprinids, in northern areas of the province greatly underestimates their actual occurrence.

occurring together. Collectively, these datasets used to estimate incidence rates are referred to as the intensively sampled lakes in contrast to the lake inventory database.

Data for average July mean temperatures were obtained from Environment Canada for 364 climate stations across Ontario for the period of 1960–1989. These data provided the baseline temperature conditions used in our modeling. Predicted July mean temperatures were obtained from the Canadian Global Coupled model Version 2 (CGCM2) Scenario A2 for July 2050 and July 2100 (Environment Canada). These data provide the basis for determining which watersheds will have suitable temperature regimes for the survival of smallmouth

bass. These data were used to create isotherms using Inverse Distance Weighting Interpolation (12 nearest neighbors) in ArcView 3.2.

Estimation of Species Incidence

Using the intensively sampled lakes from central Ontario, we estimated the incidence rates for the four cyprinid species in the absence of smallmouth bass and in the presence of smallmouth bass. Within each of the five size classes of lakes, the proportion of lakes containing each cyprinid species was determined where smallmouth bass (and largemouth bass) was absent. This proportion represents the incidence rate for a given sizeclass in the absence of bass. Similar calculations were made for lakes where smallmouth bass (but not largemouth bass) was present. In addition, the incidence rate of smallmouth bass was calculated. We estimated the incidence for pike in an identical fashion but using a different set of intensively sampled lakes.

Impact Factor on Cyprinid Inc idence due to Predation

For each size-class of lakes, we determined the relative impact of smallmouth bass occurrence by the reduction in incidence rates between lakes with bass absent to lakes with bass present. This difference was then divided by the incidence rate for bass-absent lakes to determine a relative impact factor. This impact factor provided a standardized estimate of the reduction in cyprinid incidence in lakes with smallmouth bass relative to lakes without smallmouth bass. We estimated the impact factor for pike in an identical fashion, but using a different set of intensively sampled lakes. For the smallest size-class of lakes (approximately 60,000 lakes), we were not able to estimate the impact factor because too few lakes have been sampled in this class to calculate incidence rates for these species.

The estimation of the number of populations for each of the four cyprinids within a watershed proceeded as follows: determine from the lake inventory database whether pike, smallmouth bass, and the four cyprinids are known from the watershed. As an example, assume pike is present, bass is currently absent, and fathead minnow is present; determine the number of lakes in each size-class within the watershed from Cox (1978); based on the pike incidence rate from the intensively sampled data, estimate the number of lakes within each size-class where pike is present and the number where pike is absent; for lakes without pike, use the incidence data for fathead minnow from the intensively sampled lakes to estimate the number of lakes within each sizeclass that contain fathead minnow; for lakes with pike, use the incidence data for fathead minnow from the inChapter Title 5

tensively sampled lakes without pike to estimate the number of lakes within each size-class that contain fathead minnow and reduce this number by the impact factor. This is equivalent to using the incidence rate for fathead minnow from lakes with pike; as smallmouth bass are absent from the watershed, we do not need to consider their impact. Therefore, the estimated number of fathead minnow populations is the total of those from the nonpike lakes and the pike lakes (i.e., steps 4 and 5 combined); if bass are present in the watershed currently, we estimate their impact similarly for both the pike and nonpike lakes, e.g. the pike lakes are then further divided in pike with smallmouth bass and pike without smallmouth bass. There is no change in the lakes estimated not to have bass present, but a further reduction in the fathead minnow in the bass present lakes according to the associated impact factor. The estimate of the number of fathead populations is then based on the sum of the four conditions representing the presence or absence of pike and smallmouth bass. Following these calculations for each size-class of lakes within each watershed, the overall total number of populations is estimated for all the watersheds. This provides the present-day baseline estimate for each of the cyprinid species considered.

Using projected changes in climate, we determined whether each watershed currently contained bass or may become thermally suitable for smallmouth bass, i.e. those with predicted average July maximum temperatures greater than 18°C for 2050 or 2100. We considered only those watersheds where smallmouth bass is currently absent, recently introduced, or rare (i.e., typically only one or two records since 1980 from dozens to hundreds of lakes within a watershed). This adjustment takes into account that a few populations have become established within watersheds, but are either very recent occurrences (without time to impact the cyprinids in the remainder of the lakes) or are restricted in their expansion due to unfavorable environments, likely temperature related. Most of these special cases are located along the north and western shore of Lake Superior. Those watersheds with recent or restricted cases are considered to be the same as the watersheds where bass is completely unknown within the watershed because the bass populations are minimal or nonexistent in both cases. After determining which watersheds currently lack smallmouth bass, but would be thermally suitable in either 2050 or 2100, we reran the model for those watersheds. The results provide an estimate of the reductions in the number of populations for each of the cyprinid species due to possible range expansion of smallmouth bass as a result of temperature change. We focus our detailed results on the 2100 scenario, but the reader can assess where differences arise between the 2050 and 2100 scenarios by considering the differences in the predicted temperature regimes.

Results

There is a substantial change in the temperature patterns from the present-day average July maximum to that predicted for both 2050 and 2100 (Figure 5). Current distributions show that only regions from the southeastern one-third of Ontario have temperatures reaching 20°C. In contrast, this area expands to cover approximately two-thirds of Ontario by 2050 and all but the most extreme northern part in 2100. Currently, areas as far north as the region east of the lower parts of Lake Superior show temperatures suitable for viable populations of smallmouth bass. Regions north of this area and immediately west and northwest of Lake Superior are areas where the population viability is reduced, representing the current northern thermal boundary for the species. North and east of Lake Superior, as well as most of the northern half of Ontario, are currently too cold for bass viability. The results for 2050 show most of the province will provide suitable thermal habitat and the area of reduced viability is restricted to the far northwestern area. By 2100, virtually all of Ontario exceeds 18°C, the lower limit for population viability with the exception of a small region in the extreme north.

An example set of calculations for watershed 4EC bordering on James Bay shows the predicted changes over time. The watershed has 2880 lakes and the watershed currently contains pike, but not smallmouth bass. Based on the incidence rate for fathead minnow, we would expect 1122 lakes to have fathead minnow present (or 1122 populations) if there was no impact due to pike predation (Table 1). Including the predation impact of pike, we estimate that 934 populations of fathead minnow occur at present. As bass are not present in the watershed, there is no current impact by them. However, inferring bass expansion into the area following climate change, we expect that they will reduce the number of fathead minnow populations to 800 for a net loss of 134 populations. Extending this model to the entire province, we have an expected reduction in the number of fathead minnow populations from 85,443-77,442 for a net loss of 7,991 populations. Results for northern redbelly dace, finescale dace, and pearl dace provide net losses of 6,064, 5,510, and 5, 260 respectively (Table 1).

The spatial distribution of population losses shows that the watersheds to the north and northwest of Lake Superior will likely experience the greatest loss of the four cyprinid species (Figure 6). There are many watersheds in the northern part of the Ontario that show no change in the number of populations, likely due to the

6 Author

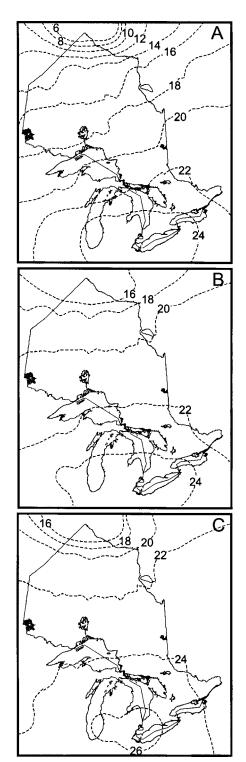


Figure 5. Mean July air temperature for Ontario based on data for years 1960–1989 (A), and on predicted values derived from the CGCM2 using scenario A2 for the year 2050 (B) and the year 2100 (C).

uncertainty of whether these cyprinids are present in these watersheds today. The species show many comparable changes across the watersheds, but there are some watersheds that show changes for some species, but not all.

Discussion

Assuming the temperature models to be reasonably accurate in their prediction of future climate for this area, almost all of Ontario will have July average air temperatures exceeding 18°C. Only the far northern areas of the province will not have temperatures above this range by 2050 and almost none of it by 2100. Such temperatures changes will lead to most lakes in Ontario having temperatures that would allow YOY smallmouth bass to grow to sufficient size to result in populations surviving shortened winters. Only in the extreme northern part of the province will lakes fall into the zone where some lake populations may be viable and others may not be. As a result of these temperature model predictions, most populations will not be limited due to the effect of overwinter starvation as YOY would be of sufficient size to contain the energy reserves sufficient to survive. It is apparent that the thermal limits to the range of smallmouth bass will shift northwards and that based on this scenario, virtually all of Ontario will provide the minimum temperature required for population viability.

The expansion of smallmouth bass further north will have substantial effects on the aquatic systems into which they become established. We have estimated the impact that bass may have on four cyprinid species over the next century. These species are notable in their sensitivity to smallmouth bass occurrence. They have a strong negative association in their occurrence with bass as shown in various studies (e.g., Tonn and Magnuson 1982; Jackson et al. 1992; MacRae and Jackson 2001), and the cyprinids are reduced or eliminated from lakes when littoral predators such as bass or pike are introduced. These effects are also strongly influenced by the size of the lake in which the species are found (Jackson et al. 2001). Given that small lakes are much more common than large lakes within Ontario, and that the effects are most notable in smaller lakes, we expect large numbers of lakes to have the potential to lose one or more cyprinid. Although we focus on only four minnow species, we estimate that the potential loss exceeds 20,000 populations. Many other cyprinid species are known to have negative associations with littoral predators such as smallmouth bass, so there is the potential for the loss of many times this number of cyprinid popu-

The impacts of bass extends beyond the loss of other fish species, but include changes in the size struc-

Chapter Title 7

Table 1. Results from the predation-impact model for tertiary watershed 4EC, and the totals from all watersheds. This watershed currently has pike present. Smallmouth bass are not present currently but thermal habitat would be suitable in 2050 and 2100 AD based on CGCM2 results. N = number of populations.

	Northern redbelly dace	Finescale dace	Fathead dace	Pearl minnow
N assuming no pike impact	0	728	1122	996
N assuming pike impact	0	635	934	811
N assuming future bass and current pike impact	0	540	800	714
Reduction in N due to futurebass impact	0	95	134	97
Total reduction across all watersheds	6,064	5,510	7991	5260
% Reduction across all watersheds	7.48	8.78	9.35	7.61

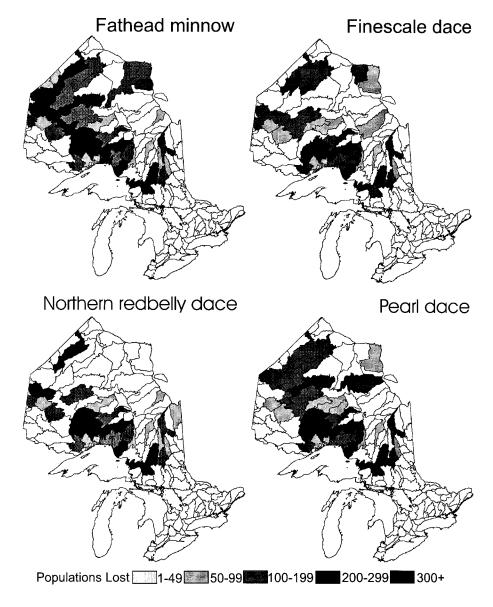


Figure 6. Number of populations per watershed predicted to be lost as a result of bass predation. Note that some northern watersheds show no change, but this may also be due to lack of records for the species within that watershed.

ture of zooplankton favoring large-bodied zooplankton and associated changes in the phytoplankton community (see Jackson 2002 for a review of effects). The presence of bass can lead to changes in the behavior of benthic invertebrates and fishes to minimize the risk of predation, thereby resulting in effects such as increased accumulations of filamentous algae due to reduced grazing. Introduction of smallmouth bass to lakes can alter the energy flow within lakes. Lake trout average approximately 60% of their energy intake from cyprinids where bass and pelagic forage fish are absent, but this intake is reduced to approximately 20% when smallmouth bass or rock bass Amboloplites rupestris were introduced (Vander Zanden et al. 1999). Therefore, lakes which bass colonize can be expected to undergo changes ranging from the loss of cyprinid biodiversity to complex ecosystem changes.

If the thermal habitat becomes available, how likely are bass to expand their range, follow this potential northern boundary and lead to these biological effects? Various portions of the current northern range of smallmouth bass did not contain the species historically. They have been expanding rapidly in the areas immediately west of Lake Superior during the past few decades (K. Armstrong, Ontario Ministry of Natural Resources, personal communication). The areas where we sampled fish communities to estimate both bass and cyprinid incidence (i.e., Algonquin Provincial Park and the Black-Hollow River watersheds) did not contain bass historically. Smallmouth bass were introduced into these areas in the late 1800s, often into lakes adjacent to the railway lines. The authors have found bass populations establishing in additional lakes during the past 15 years (unpublished data), with the expected effects on the cyprinid populations. These new bass populations are ones that have either become established following illegal introductions or have colonized from other lakes. Jackson et al. (2001) reported considerable rates of movement of smallmouth bass between lakes. Many lakes around the Sudbury region of Ontario were populated by lake trout Salvelinus namaycush, but did not contain smallmouth bass. These lakes became acidified due to smelting activity, but have since recovered following a reduction in emissions. As water quality conditions improved, smallmouth bass populations have been established in these systems (E. Snucins and J. Gunn, Ontario Ministry of Natural Resources, personal communication), either a result of unauthorized introductions or colonization from adjacent populations.

Once bass are introduced into a new watershed, they have the potential to colonize through the connecting waterways (Jackson et al. 2001). In particular, once bass become established within a watershed in northern Ontario, it is much simpler for them to colonize further

north due to the direction of river drainage. In contrast to most systems along the north shore of the Great Lakes, most of the lakes in northern Ontario drain via rivers flowing to the north, to James Bay and Hudson Bay. This direction of flow, often along low gradient systems, provides river systems ideal for the subsequent further northward expansion of bass.

Although the focus of this study has been to model the change in the thermal limits to smallmouth bass under a climate change scenario, another major consideration in their expansion will relate to changes in the hydrologic cycle. The various climate change models tend to be more consistent in their predictions of temperature regimes than in predictions of future precipitation and associated evapotranspiration. If water levels in lakes or in the connecting waterways, were to decrease in future, we can expect that the ability of smallmouth bass to disperse throughout watersheds and colonize additional lakes will be reduced. The more fragmented these drainage systems become due to reduced flows in streams and rivers, the lower the proportion in which bass will become established. However, the loss of these connecting waterways may also eliminate some of the refuges (i.e., streams or small lakes) used by cyprinids to avoid bass (e.g., He and Kitchell 1990; He and Wright 1992; Jackson et al. 2001)

Although we predict the potential for substantial expansion in the range of smallmouth bass and an associated loss of many cyprinid populations, we must consider some of the potential errors associated with our predictions. The incidence of bass, pike and the four cyprinid species were estimated from several detailed data sets that encompass several hundred lakes. These subsets of Ontario lakes were chosen because they were sampled with much greater effort than during the provincial inventories and have much more accurate records for the cyprinid occurrences. Based on repeated surveys of lakes, smallmouth bass are known to be expanding into additional lakes in the subsets where their incidence has been estimated (Jackson and Mandrak, unpublished data). Therefore, we have likely underestimated the incidence of bass in each of the size classes of lakes, and as a result, underestimated the number of predicted extirpations.

Due to the biogeography of pike and smallmouth bass, they have mutually exclusive distributions throughout most of these intensively sampled lakes. Therefore, we cannot estimate the interaction effect between pike and smallmouth bass in these lakes and the resulting combination of their effects on the cyprinids. Our model assumes an additive effect such that if bass colonize a lake containing pike, their additional effect is the same as if bass colonize a lake without pike and they eliminate a certain proportion of the existing cyprinid popu-

lations. However the combined effect of both pike and bass leads to a lower incidence of each cyprinid than if either pike or bass alone are present. Error from this lack of interaction between bass and pike may increase or decrease the number of populations that we expect to be extirpated, but it is more likely to overestimate the number. Our estimation of the incidence of each cyprinid species appears appropriate when compared between the data sets, but may vary in other watersheds within the province. The effect of this form of error depends on whether the incidence rates are higher or lower in other watersheds relative to the areas from which they were estimated.

Our study focuses on the effect of temperature on population viability due to overwinter survival of smallmouth bass in their first year. This is a function of their growth during the summer versus the starvation period during the winter. However there is another temperature-related feature that must be considered. The length of the ice-covered period is expected to decrease substantially due to a later freeze-up and an earlier breakup of the ice on lakes (Magnuson, this volume). In small Ontario and Wisconsin lakes, winterkill is a phenomenon known to occur and affects the large predatory species to a greater extent than the cyprinids (Casselman and Harvey 1975; Tonn and Magnuson 1982; Jackson et al. 1992). The longer that a lake is covered with ice, the greater is the probability that dissolved oxygen will be depleted and lead to fish mortalities. An outcome of global warming will be a reduction in the period of ice cover, and therefore a reduction in the probability of pike and bass winterkill. Therefore, the incidence rates of bass and pike are expected to increase, in particular in the smaller lakes where this winterkill effect is greatest. It is in these smaller lakes where the predation effect of bass and pike is greatest. Therefore, this effect will lead to an increase in the number of extirpated cyprinid populations within existing (i.e., those watersheds not considered in the predictive model of this study) and expanded ranges. This effect has the potential to greatly increase the number of populations expected to be lost. Not only is there the potential loss of these populations, these small winterkill lakes contain species assemblages that are unique to those environments and maintained due to the winterkill effect (J. Magnuson, personal communication). Therefore, we have the potential to not only reduce the number of populations of various cyprinids, but also lose entire assemblages and further contribute to a homogenization of our fish fauna (Radomski and Goeman 1995; Rahel 2000; Jackson et al. 2001)

There are other factors, not considered here, that will affect the changes in these minnow populations. Such factors include the rates at which smallmouth bass

are able to colonize these habitats. Our model assumes that they will have access to all of these watersheds and the lakes within the watersheds (or at least the proportion that they have been able to access in the intensively sampled lakes). Reduced rates of introduction or colonization will reduce the number of extirpated populations. However, another important factor is the potential for other species (e.g., largemouth bass and rock bass) to also colonize more northerly lakes. The addition of these predators will undoubtedly increase the number of extirpated populations. Under global warming, thermal habitat suitable for largemouth bass will also be available throughout much of Ontario also.

We have inadequate data for the distribution of cyprinids within northern Ontario. Various watersheds may contain these species, but because few lakes have been sampled and the sampling has targeted large-bodied species, we do not know whether many species of cyprinids exist within some of these watersheds. If they do exist in these watersheds, we would expect bass colonization to lead to extirpations and therefore, we are likely to greatly underestimate the number of population losses as a result of this factor.

Conclusions

It appears likely that climate change will occur, but considerable uncertainty remains about the specific changes in temperature and precipitation. Based on a common scenario for climate change and the relationship between July air temperatures and the population viability of smallmouth bass, we estimated the number of lakes where we expect bass to become established. The impact of bass will be the extirpation of many species of cyprinids and we conservatively estimate that in excess of 25,000 local populations of four cyprinids species may be lost. There is the potential for this number to greatly underestimate the outcome due to changes in effects such as winterkill and the range expansion of other predatory species. The loss of these cyprinids will reduce the overall number of populations and assemblages unique to small winterkill lakes within Ontario. The expansion of bass and related predators will lead to substantial changes within the ecosystems of vast numbers of Ontario lakes, with effects ranging from losses in cyprinid biodiversity, to gains in centrarchid biodiversity, to reductions in growth and yield of recreational species such as lake trout.

Acknowledgments

We would like to acknowledge funding support from the Ontario Ministry of Natural Resources, the Ontario Renewable Resources Research Grant Program, the Department of Fisheries and Oceans, and the Natural Sciences and Engineering Research Council of Canada. Carolyn Bakelaar provided GIS assistance. We thank Henry Regier, Nature McGinn, and an anonymous reviewer for their comments and challenges. Our study has benefited as a result.

Refernces

- Beamish, R. J., L. M. Blow, and G. A. McFarlane. 1976. A fish and chemical study of 109 lakes in the Experimental Lakes Area (ELA), northwestern Ontario, with appended reports on lake whitefish ageing errors and the northwestern Ontario baitfish industry. Fisheries Research Board of Canada Technical Report Number 607, Environment Canada.
- Casselman, J. M., and H. H. Harvey. 1975. Selective fish mortality due to low winter oxygen. Internationale Vereinigung für theoretische und angewandte Limnologie Verhandlungen 19:2418–2429.
- Cox, E. T. 1978. Counts and Measurements of Ontario Lakes. Ontario Ministry of Natural Resources. Toronto, Ontario, Canada.
- Crossman, E. J. 1976. Quetico Fishes. Miscellaneous Publication, Royal Ontario Museum, Toronto, Ontario, Canada.
- Findlay, C. S., D. G. Bert, and L. G. Zheng. 2000. Effect of introduced piscivores on native minnow communities in Adirondack lakes. Canadian Journal of Fisheries and Aquatic Sciences 57:570–580.
- Harvey, H. H. 1981. Fish communities of the lakes of the Bruce Peninsula. Internationale Vereinigung f[mac]ür Theoretische und Angewandte Limnologie 21:1222– 1230.
- He, X., and J. F. Kitchell. 1990. Direct and indirect effects of predation on a fish community: a whole-lake experiment. Transactions of the American Fisheries Society 119:825–835.
- He, X., and R. A. Wright. 1992. An experimental study of piscivore-planktivore interactions: population and community responses to predation. Canadian Journal of Fisheries and Aquatic Sciences 49:1176–1183.
- Jackson, D. A. 1988. Fish communities in lakes of the Black and Hollow River watersheds, Ontario. Master's thesis, University of Toronto, Toronto, Ontario, Canada.
- Jackson, D. A., and H. H. Harvey. 1989. Biogeographic associations in fish assemblages: local *versus* regional processes. Ecology 70:1472–1484.
- Jackson, D. A., K. M. Somers, and H. H. Harvey. 1992.Null models and fish communities: evidence of non-

- random patterns. American Naturalist 139:930-951.
- Jackson, D. A. 2002. Ecological Effects of Micropterus Introductions: the Dark Side of Black Bass. In D. Phillip and M. Ridgway, editors. Ecology, Conservation and Biology of Black Bass. American Fisheries Society, Bethesda, Maryland.
- Jackson, D. A., Peres-Neto, P. R., and J. D. Olden. 2001. What controls who is where in freshwater fish communities – the roles of biotic, abiotic and spatial factors? Canadian Journal of Fisheries and Aquatic Sciences 58:157–170.
- MacRae, P. S. D., and D. A. Jackson. 2001. The influence of smallmouth bass (*Micropterus dolomieu*) predation and habitat complexity on the structure of littoral-zone fish assemblages. Canadian Journal of Fisheries and Aquatic Sciences 58:342–351.
- Mandrak, N. E. 1989. Potential invasion of the Great Lakes by fish species associated with climatic warming. Journal of Great Lakes Research 15:306–316.
- Minns, C. K. 1986. Analyses of the Ontario lake inventory data base. Ontario Fisheries Technical Report Series.
- Naiman, R. J., J. J. Magnuson, D. M. McKnight, and J. A. Stanford. 1995. The Freshwater Imperative: A Research Agenda. Island Press, Washington.
- Radomski, P. J., and T. J. Goeman. 1995. The homogenizing of Minnesota lake fish assemblages. Fisheries 20:20–23.
- Rahel, F. J. 2000. Homogenization of fish faunas across the United States. Science 288:854–856.
- Ricciardi, A., and J. B. Rasmussen. 1999. Extinction rates of North American freshwater fauna. Conservation Biology 13:1220–1222.
- Robinson, C. L. K., and W. M. Tonn. 1989. Influence of environmental factors and piscivory in structuring fish assemblages in small Alberta lakes. Canadian Journal of Fisheries and Aquatic Sciences 46:81–89.
- Shuter, B. J., MacLean, J. A., Fry, F. E. J., and H. A. Regier. 1980. Stochastic simulation of temperature effects on first-year survival of smallmouth bass. Transactions of the American Fisheries Society 109:1–34.
- Somers, K. M., and H. H. Harvey. 1984. Alterations of lake fish communities in response to acid precipitation and heavy metal-loading near Wawa, Ontario. Canadian Journal of Fisheries and Aquatic Sciences 41:20–29.
- Tonn, W. M., and J. J. Magnuson. 1982. Patterns in the species composition and richness of fish assemblages in northern Wisconsin lakes. Ecology 63:1149–1166.
- Vander Zanden, M. J., J. M. Casselman, and J. B. Rasmussen. 1999. Stable isotope evidence for the food web consequences of species invasions in lakes. Nature (London) 401:464–467.