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Impact of Piscivorous Fish Introduction on Fish Communities of Small Temperate Lakes in Gatineau Park, Québec, Canada

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Abstract

Small temperate lakes are under increasing pressure from a number of anthropogenic sources, including but not limited to: habitat alteration, invasive species, climate change, and pollution. In Gatineau Park, Québec, Canada small temperate lakes have been demonstrated to be under threat from introduced piscivores, among other potential stressors. Here, I assessed the historical impact of four introduced piscivores on minnow, small fish and total fish species richness for a set of small Gatineau Park lakes. Fish community data were obtained from two previously published studies and a lake survey conducted in the summers of 2006 and 2007. I used a modified Control/Impact study design and repeated measures analysis of variance to test the hypothesis that introduced piscivores negatively affect species richness over time. My results strongly demonstrate that piscivores have had a negative effect on minnow and small fish species richness over time, whereas total fish species richness was unaffected. Assuming that these introduced piscivores pose a risk to the parks small temeprate lakes, I then assessed what lake characteristics best predict piscivore invasion risk. To do this, I estimated invasion risk employing two different analytical approaches for a total of 42 small lakes located in Gatineau Park using current and historical data collected in 1971, 1981, 1991 and 2006. Bootstrapped logistic regression was used to predict historical occurrence, and whether or not a lake was invaded/not invaded over time using predictor variables that included lake anthropogenic, spatial-isolation, and morphometric factors. For both logistic regression analyses, lake area and small fish species richness were found to be excellent predictors of piscivore invasion risk and historical occurrence, while lake spatial-isolation factors were also found to be excellent predictors of piscivore historical occurrence. The

bootstrapped models with the most support based on Akaike's Information Criterion corrected for small sample size (AICc) were then used to identify lakes at greatest risk for future invasion. My results support the contention that introducing top predators into novel aquatic environments has detrimental impacts on native fish communities, and that these impacts are not always immediately obvious, but are indeed discernable over time. In conclusion, I make specific recommendations to guide the conservation and management of small temperate lake ecosystems.

Résumé

Les petits lacs tempérés sont sous soumis à une pression grandissante d'un certain nombre de facteurs anthropogéniques, incluant, mais non limités, aux altérations d'habitat, aux espèces envahissantes, aux changements climatiques, et à la pollution. Dans le parc de la Gatineau (Québec, Canada) les petits lacs tempérés sont sous la menace, entre autres facteurs, de l'introduction de poissons piscivores. J'ai évalué l'impact historique de l'introduction de quatre espèces de piscivores sur les cyprins (Cyprinidae), sur les espèces de poissons de petite taille ainsi que sur la richesse totale en poissons pour un ensemble de petits lacs du parc de la Gatineau. Des données sur la communauté de poissons ont été obtenues à partir de deux études passées et d'une enquête sur des lacs menée durant les étés 2006 et de 2007. J'ai utilisé une analyse commande/impact modifiée et j'ai effectué une analyse de variance à mesures répétées pour vérifier l'hypothèse que l'introduction des piscivores affecte négativement la richesse des espèces dans le temps. Mes résultats ont démontré que les piscivores ont eu un impact négatif sur la richesse des cyprins et de petites espèces poissons dans le temps, alors que la richesse totale d'espèces de poissons demeurait inchangée. En supposant que la présence des piscivores pose un risque dans les petits lacs du parc, j'ai alors tenté d'évaluer quelles étaient les principales caractéristiques d'un lac qui permettaient de prédire le risque d'invasion de piscivores. Pour ce faire, j'ai estimé le risque d'invasion par deux approches analytiques différentes pour 42 petits lacs situés dans le parc de la Gatineau en utilisant des données récentes (2006) et historiques (1971, 1981 et 1991) de communautés de poissons. Des régressions logistiques par *bootstrap* ont été utilisées pour prédire l'occurrence historique d'une invasion de piscivores dans un lac, et prédire cette invasion en utilisant des variables prédictives telles que les facteurs anthropogéniques, l'isolement spatial et les caractéristiques morphométriques des lacs. Pour les deux analyses de régression logistiques, la superficie du lac et la richesse en petites espèces se sont avérées d'excellents facteurs prédictifs du risque d'invasion de piscivores et d'occupation historique; alors que les facteurs d'isolement spatial s'avèrent également d'excellents éléments permettant de prédire l'occupation historique de piscivores. Les meilleurs modèles de *bootstrap* selon le Critère d'Information d'Akaike ajusté pour la petite taille de l'échantillon (AICc), ont alors été utilisés pour identifier les lacs ayant le plus grand risque d'être envahis par des piscivores. Mes résultats corroborent l'affirmation que l'introduction de prédateurs piscivores dans les petits environnements aquatiques a des impacts nuisibles sur les communautés indigènes de poissons et que ces impacts ne sont discernables qu'après un certain temps. Finalement, j'émets des recommandations spécifiques pour guider la conservation et la gestion des petits écosystèmes tempérés de lacs.

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General Introduction

Freshwater Fish Conservation and Management in Protected Areas

Threats to freshwater fish biodiversity include: habitat change and fragmentation, pollution, non-native species introduction, and overfishing (Richter et al. 1997; Allan et al. 2005; Dudgeon et al. 2006). These threats are particularly evident in North American small temperate lakes, where water chemistry alteration (i.e., acidification, eutrophication, mercury contamination), habitat modification, non-native fish introduction (Whittier et al. 2002), and a predicted reduction in precipitation caused by climate change (Carpenter et al. 1992; Lodge 1993) all threaten native freshwater fish species.

One potential solution to these problems is the establishment of protected areas. Protected areas, however, are often deemed inadequately designed to protect aquatic biota due in part to being originally designed to accommodate terrestrial rather than aquatic species (Saunders et al. 2002; Filipe et al 2004). This lack of appropriate design is further exasperated by increasing levels of environmental degradation, and inappropriate management actions aimed at mitigating anthropogenic threats (Ervin 2003). An excellent example of how protected areas have been unable to protect aquatic ecosystems is the proliferation of invasive piscivorous fish (for simplicity, henceforth referred to as piscivores) and the negative impacts these invasive species have had on the native fish (Chapleau et al. 1997), plankton (Parker et al. 2001), and amphibians (Knapp & Matthews 2000; Pilliod& Peterson 2001) of protected area lakes.

An important step to reducing threats to a native fish species is focusing conservation and management efforts on "ecosystems and natural environments" (National

Capital Commission 2005) rather than the historically utilitarian objectives of enhancing recreational fishing opportunities and human enjoyment (Pister 2001). In North America, the predominance of this utilitarian resource management ethic has resulted in a large number of lakes within many parks (including Gatineau Park) being stocked at the beginning of the 20th century with non-native piscivores such as bass (smallmouth (*Micropterus dolomieu*) and largemouth (*Micropterus salmoides*)), northern pike (*Esox lucius*), walleye (*Sander vitreus*) and yellow perch (*Perca flavenses*) for recreational fishing opportunities. Over time, however, it has been hypothesized that these predators have reduced native small fish species to near local extinction, and as a result, management authorities have tried to abandon stocking lakes for sheer human enjoyment and instead promote the conservation of ecosystems and natural environments.

To meet this objective, prescribed actions such as those outlined by Gatineau Park management are an excellent start, including: (1) developing a conservation plan; (2) preserving ecological links; (3) creating a research strategy directed at ecosystem conservation; (4) restoring significant ecosystems; (5) limiting human access to and presence in significant ecosystems; and (6) gradually relocate recreational activities not compatible with conservation objectives (National Capital Commission 2005). Even if new park management objectives are implemented, the state of lake ecosystems in Gatineau Park and other protected areas is relatively unknown. It is expected that introduced top predator populations have continued to persist in already colonized lakes and will or already have emigrated and colonized new lakes, potentially impacting previously unaffected fish communities. To mitigate future impact, the conservation and management of small temperate lake ecosystems requires gathering data on a management endpoint such as fish biodiversity, species richness or relative species abundance. Such knowledge will allow managers to assess change in ecosystem state over time and space, forecast state into the future, and attempt to solve potential problems (Yoccoz et al. 2001). For lentic ecosystems, this would entail identifying potential anthropogenic risks to fish biodiversity, and implementing management strategies designed to mitigate these risks.

Fish have been cited as one of the most threatened groups of vertebrates on the planet (Bruton 1995), and can be good indicators of small temperate lake ecosystem state. In particular, minnows (family Cyprinidae), a group of small, often ubiquitous, fish have been suggested to be among the most sensitive to chemical, biological and habitat perturbations, and are highly susceptible to extirpation. (Angermeir 1995; Whittier et al. 1997). For example, in Québec, two minnow species native to Gatineau Park, the brassy minnow (*Hybognathus hankinsoni*) and the bridle shiner (*Notropis bifrenatus*) are likely to be legally designated as threatened or vulnerable (Tardif et al. 2005). The brassy minnow has also been categorized by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC) as a species within the highest priority group for assessment, which includes species that are suspected to be at high risk of extirpation in Canada (COSEWIC 2008). Threats to minnow species vary, but a number of studies have demonstrated minnows to be greatly reduced in number or completely absent from acidified lakes (Somers & Harvey 1984; Rago & Wiener 1986; Rahel 1986; Matuszek & Beggs 1988; Minns 1989; Matuszek et al. 1990). More recent studies suggest minnow species richness is lower in lakes where introduced littoral zone piscivorous fish persist (Chapleau et al. 1997; Whittier et al. 1997; Findlay et al. 2001; MacRae & Jackson 2001; Jackson 2002). The common finding that cyprinids are often absent from anthropogenically impacted lakes have led some to suggest the use of these organisms as a potential indicator of ecosystem state in temperate regions (*i.e.*, Mills & Schindler 1986; Matuszek et al. 1990; Harig & Bain 1998).

In addition to cyprinids, local small-bodied fish species, including those belonging to two groups (Etheostomatinae [darters] of the family Percidae and sticklebacks of the family Gasterosteidae), and three species: margined madtom (*Noturus insignus*), banded killifish (*Fundulus diaphanus*), and central mudminnow (*Umbra limi*)) must also be considered. These small species (along with minnows) are susceptible to predation by introduced-gape limited-top predators due to their small body size (Chapleau et al 1997). One group of these small fish species - darters (from the family Percidae) have been recommended as a metric in the widely used Index of Biotic Integrity (IBI) because sedimentation and habitat alteration can reduce the number of these benthic invertebrate feeders (Karr 1991). A rare species, the margined madtom was designated threatened by COSEWIC in 1989, but has been reclassified as data deficient in 2002 due to a controversy surrounding its status as a native species in Canada (COSEWIC 2002). Finally, though stickleback species are widely distributed across Canada, the threespine stickleback exhibits morphologically distinct populations in Gatineau Park and are of special interest in terms of conservation (Patankar 2006).

In addition to introduced piscivorous fish species, access to lakes via roads or recreational trails is an important concern to park management authorities. Road density/access has been shown to negatively affect stream fish species abundance and occurrence (Thompson & Lee 2000; Steel et al. 2004; Wall et al. 2004; Ripley et al. 2005) and could potentially reduce fish species richness by impeding migration between local populations (Rieman & McIntyre 1995); facilitating the invasion of exotic species (Cowie & Werner 1993; Lonsdale & Lane 1994; Kaufman et al. 2009); and/or indirectly increasing angler harvest pressure (Gunn & Sein, 2000; Kaufman et al. 2009). In the Gatineau Park, it is highly probable that lakes stocked with non-native top predators were once easily accessible via trails or roads. If a lake stocking is now deemed unacceptable and lake access has been reduced, then alternative actions must be put in place to limit the proliferation of these non-native species.

Objectives

The overall objective of this thesis was to assess the current state of small temperate lake fish communities in Gatineau Park, Québec. The first objective was to assess current and past fish species richness and relative abundance for several Gatineau Park lakes. This was accomplished by collecting fish community and environmental data through (1) sampling 25 lakes during the summers of 2006 and 2007and (2) a literature review of past fish community studies done in the Park (Figure 0.1). Second, I assessed the impact of piscivore introductions on minnow, small and total fish species richness and two classical ecological relationships (specie-area and species-elevation) (Chapter 1). Third, I estimated piscivore invasion risk using lake anthropogenic, spatial and morphometric predictor variables (Chapter 2). Finally, I evaluated various management strategies intended to mitigate the effects of anthropogenic factors (focusing on introduced piscivores) on the small temperate lake ecosystems of Gatineau Park.

Figures and Tables

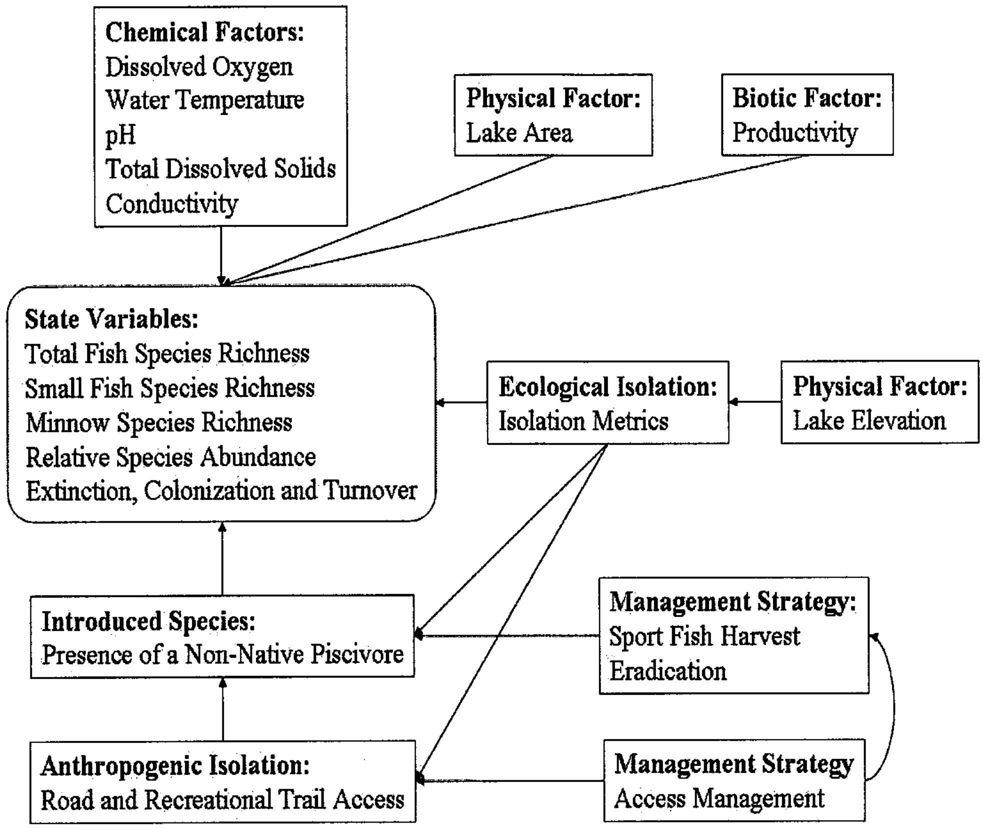

Figure 0.1. Conceptual model illustrating state variables, field collected covariates (chemical and biotic factors), GIS derived covariates (physical factors, ecological and anthropogenic isolation) and potential management strategies intended to mitigate risks to fish biodiversity.

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Chapter 1 Effect of piscivorous fish introduction on fish communities of small temperate lakes

Introduction

Aquatic biodiversity is diminishing at rates equivalent to that found in some of the most critically endangered ecosystems on earth (Ricciardi& Rasmussen 1999). At least some of this impoverishment is attributable to exotic introductions that represent a significant and increasing threat to biodiversity (Coblentz 1990; Soulé 1990; Sala et al. 2000; Allan et al. 2005; Dudgeon et al. 2006; Lodge 2001; Dextrase & Mandrak 2006), imperiled species (Richter et al. 1997; Wilcove 1998), biological conservation efforts (Allan and Flecker 1993; Richter et al. 1997; Walker & Steffen 1997), and human economies and health (Pimentel 2000). In aquatic ecosystems, non-native fish introductions are especially ominous as they often cause important ecological and economic damage (Kolar and Lodge 2001), and threaten native biota via competition, hybridization, predation, and the introduction of diseases (Allendorf 1991).

Of particular concern is the introduction of exotic piscivores. Given that native piscivores are important in structuring prey fish prey populations (Lyons & Magnuson 1987; Tonn & Paszkowski1986; Tonn et al. 1992; Bonar et al. 2005) and communities (Zaret & Paine 1973; Tonn & Magnuson 1982; Robinson & Tonn 1989; Jackson et al. 2001; Bystrom et al. 2007) it is unsurprising that the introduction of exotic predators often has negative effects on native prey that do not recognize novel predators or do not show appropriate avoidance behaviours (Shave et al. 1994, Kiesecker & Blaustein 1997; Nyström et al. 2001; Lockwood et al. 2007). A wide range of studies corroborate with the hypothesis that introduced exotic piscivores: (a) reduce populations of small-bodied fish species (Harvey 1981; Lyons & Magnuson 1987; He & Kitchell 1990; He & Wright 1992; Tonn et al. 1992; MacRae & Jackson 2001); (b) impact native lake fish genetic diversity, populations, and communities (Eby et al. 2006); and (c) alter ecosystem properties (Ogutu-Ohwayo 1989; Ogutu-Ohwayo & Hecky 1991; Kaufman 1992; Witte et al. 1992; Pace et al. 1999; Simon et al. 2003; Findlay et al. 2001). Small temperate lake fish communities are expected to be extremely susceptible to non-native piscivore introductions due in part to their insular nature, small size and low habitat heterogeneity, relatively low species diversity and the fact that most fish in such communities are dominated by small-bodied species such as minnows (family Cyprinidae), darters (family Percidae) and sticklebacks (family Gasterosteidae (Schindler 1990; Tonn & Paszkowski 1986; Tonn et al. 1992).

In northeastern North America, many small lakes have been stocked with piscivores including smallmouth and largemouth bass [*Micropterus dolomieu* and M. *salmoides*], northern pike [*Esox lucius*], yellow perch [*Perca flavescens*], and walleye [*Sander vitreus*]) to create new recreational fishing opportunities. Evidence for the impacts of these and other species on fish communities of small temperate lakes comes from two different methodological approaches. In correlational (non-manipulative) studies, the effects of introduced piscivores are inferred from spatiotemporal covariation between piscivore density, abundance or richness and fish community attributes such as richness or abundance (Chapleau et al. 1997; Whittier & Kincaid 1999; Whittier et al. 1997; Findlay et al. 2001; MacRae & Jackson 2001; Jackson 2002; Whittier et al. 2002). In experimental approaches, systems (e.g. small lakes) are experimentally manipulated. In an experimental system, fish community structure is ascertained, piscivore populations are then manipulated by augmentation or removal with fish community structure and composition subsequently monitored to infer piscivore effects (i.e., He & Kitchell 1990; He & Wright 1992; Lepak et al. 2006; Weidel et al. 2007). Both methods have their limitations. Non-manipulative methods have lower inferential strength owing to the inability to completely control for potentially confounding factors (Quinn & Keough 2002). On the other hand, the combination of the spatial scale of the phenomena under study, limited resources (McGarigal & Cushman 2002), and the reluctance to allow introduction of novel predators into (previously) uninfected systems means that experimental manipulations are usually highly limited in scope, raising the question of the generality of observed effects.

Here I use a modified Control/Impact (CI- Green (1979)) design to test the hypothesis that introduction of an exotic top piscivore (pike or bass) into small temperate lakes results in declines in minnow and small fish diversity in small temperate lakes, by using a fish community survey database that extends over a thirty-eight year (1970-2007) period in Gatineau Park, Québec. In the CI design, control lakes are those for which there was no evidence of piscivore presence in 1970, and none today. By contrast, impact lakes are those which, in 1970, already had introduced piscivores, or had piscivores introduced sometime during this period. Adding the time dimension to the standard control-impact design allows us to test two predictions: (1) minnow and small fish species richness will be lower in experimental lakes than control lakes; and (2) the difference between control and impact lakes should increase over time, as native small bodied-species are extirpated over time.

In addition to testing for the effects of introduced piscivores on small temperate lake fish diversity, I investigated if piscivore introduction affected two distinct ecological relationships, the Species-Area (SAR) (MacArthur & Wilson 1967; He & Legendre 1996) and Species-Elevation (SER) (Rahbek 1995) relationships. I used a signal-to-noise ratio estimated from these two ecological relationships to assess support for one prediction: (1) that the signal-noise ratio will be smaller in experimental lakes as compared to control lakes in all time periods.

Methods

Fish sampling

Gatineau Park has 55 recognized lakes, ranging in size from under one to 700 hectares (Rother 1983). Historical fish community data for a subset of these lakes were obtained from two previously published studies (Rubec 1975; Chapleau et al. 1997). Rubec (1975) sampled 29 lakes in the summers of 1970 and 1971(for simplicity, henceforth referred to as 1971 data), utilizing a 10 X 2.5m seine (0.64cm mesh, 0.32cm bag), or a 4.5m (0.64cm mesh) seine when the lake bottom prevented the use of the larger net. Chapleau et al. (1997) surveyed 20 lakes in the summers of 1990 and 1991 (henceforth referred to as 1991 data) using two experimental gill nets (40 X 1.8m with 13, 19, 25, 31, and 38mm mesh sizes); a trammel net (37 X 1.2m with outer wall mesh of 20cm and inner wall mesh of 25mm); two trap nets (9.1 X 0.9m lead, 6mm mesh size, and rings 76cm in diameter); a 10 m beach seine where the bottom permitted; and 9 pairs of unbaited minnow traps (44.5cm long, 23cm in diameter with a 1.1cm opening). Minnow traps, gill, trammel and trap nets were set for approximately 48 hours, and were checked and reset at another location within the lake after 24 hours.

In addition to historical fish community data, in the summer of 2006 and 2007 (here on referred to as 2006 data), I re-sampled 25 lakes previously surveyed in 1971 and

1991. Sampling order was randomly selected for 2006/2007 lakes using a random number generator in R Version 2.6.2 (R Core Development Team 2007). A total of 20 lakes were visited between May and September 2006, and an additional five between June and September 2007. To ensure all lakes were adequately sampled, most lakes, including all piscivore lakes were resampled in 2007.

2006/2007 sampling was completed using identical gear to Chapleau et al. (1997), including: two experimental gill nets (40 X 1.8m with 13, 19, 25, 31, and 38mm mesh sizes); a trammel net (37 X 1.2m with outer wall mesh of 20cm and inner wall mesh of 25mm); two trap nets (9.1 X 0.9m lead, 6mm mesh size, and rings 76 cm in diameter); a 10 m beach seine; and 9 pairs of unbaited minnow traps (44.5cm long, 23cm in diameter with a 1.1cm opening). Small lakes and those lakes known to have very few or only small fish species were sampled minus one experimental gill net and both trap nets. All sampling device locations were randomly chosen and spaced ≥20m from each other, using Hawth Tools Version 3.27 (Beyer 2004). Experimental gill and trammel nets, and three minnow traps were randomly located, treating the entire lake as the sampling area, whereas the trap and seine nets, and six minnow traps were randomly located within 30 m of the shoreline. All stationary nets and traps were set at a randomly selected depth and orientation from the shoreline ranging from 48 hours for smaller lakes to 120 hours (5 nights) for larger lakes. Sampling devices were checked after 24 hours, moved and reset at another randomly selected location within the lake. All caught fish were measured for total length, identified to species, and occasionally photographed. When, on occasion, identification was uncertain, specimens were preserved in 10% formalin, labeled and returned to the laboratory for proper identification.

Introduced piscivores were considered present if one or more individuals of yellow perch (*Perca flavescens*), largemouth bass (*Micropterus dolomieu*), smallmouth bass (*Micropterus salmoides*), or northern pike (*Esox lucius*) were detected in a lake. I restricted my analysis to three different but overlapping samples. Sample 1 ($n = 14$) includes all lakes sampled in 1971, 1991 and 2006. Sample 2 includes all lakes sampled in both 1971 and 2006 ($n = 21$), irrespective of whether they were sampled in 1991. Sample 3 includes all lakes sampled in both 1991 and 2006 ($n = 17$), irrespective of whether they were sampled in 1971. In each of these samples, a non-piscivore lake is one for which no piscivores were detected at both the beginning and end of the sampling interval (e.g. in 1971 and 2006 for samples 1 and 2). By contrast, a piscivore lake was considered to be one for which (a) piscivores were present at the beginning and end of the interval; or (b) piscivores were not detected at the beginning of the interval, but there is independent evidence of their presence fairly soon after the initial sample and before the last sampling period. This latter condition applies only to Ramsay Lake, for which no piscivores were detected in 1971 or 1991, but substantial numbers of northern pike were detected in 1995 and again on subsequent sampling in 2001 (Vachon 2006). Ramsay is thus considered as belonging to the piscivore class for the 1991-2006 (sample 3) analysis, but is not considered in the 1971-1991-2006 or 1971-2006 analyses.

Morphometric Factors

Lake area (AREA) was extracted from 1:20,000 topographic data layers (Ministère des Ressources naturelles et de la Faune du Québec 1999), while elevation (ELEV) was estimated using a 30m resolution Digital Elevation Model (DEM) (Centre for Topographic

Information 2004). Both physical factors were estimated for all lakes using ArcInfo Version 9.1 software (ESRI 2004).

Statistical Methods

For my investigation, I used one-way repeated measures analysis of variance (RM ANOVA), treating lakes as subjects, to assess temporal changes in mean minnow, small fish and total fish species richness in piscivore and no-piscivore lakes. Post hoc effect sizes (r) for RM ANOVA were calculated as outlined in Field (2005).

RM ANOVA assumptions including, normality of residuals, homogeneity of variance and sphericity were assessed. All RM ANOVA analyses, associated effect size calculations, and assumption diagnostics were conducted using SPSS release 17.0 (SPSS 2008). To ensure residual homoscedasticity and normality, minnow and small fish species richness were transformed using the equation $\log_{10}(y + 1)$, while total fish species richness was $\log_{10}$ transformed.

In addition to assessing temporal changes in fish diversity in piscivore and no-piscivore lakes, using data from sample two (1971-2006), I used linear regression to investigate the effect of piscivore introduction on total fish species richness-area and -elevation relationships. To accomplish this, I first fit a set of nested models which included a null model with only the intercept, and all combinations of lake area (AREA), elevation (ELEV), and/or piscivore status (PISC), for both 1971 and 2006 (Table 3).

The information theoretic method was then used to choose among competing models (Burnham and Anderson, 2002). Akaike's Information Criterion corrected for small sample size (AICc) was used to compare competing models, and was calculated as

$$\mathrm{AICc} = -2\,loglikelihood + 2k + \frac{2K(K+1)}{(n-K-1)}$$

where K is the number of parameters that have been fit. To rank each model, I rescaled AICc values so that the model with the minimum AICc had a value of 0, using the equation

$$\Delta_i = \mathrm{AICc}_i - \mathrm{minAICc}$$

Further, Δ_i was then used to calculate w_i (or AICc weights), the approximate probability that model i is the best model in the set r, as

$$w_i = \frac{\exp\left(-\frac{1}{2}\Delta_i\right)}{\sum_{r=1}^{R} \exp\left(-\frac{1}{2}\Delta_r\right)}$$

Next, I used the variable (area or elevation) with the most support based on model selection using AICc, to fit for each time period (1971 and 2006), three models: one to lakes with a piscivore, one to lakes without a piscivore, and one to all lakes (all piscivore and no piscivore lakes combined). If piscivores were affecting these relationships, I expected to observe a weaker species-area or -elevation signal in piscivore lakes (Tittensor et al. 2007; White & Kerr 2007). To assess this, I defined the signal-to-noise ratio as the t-value calculated for β as

$$\beta / \mathrm{SE}_\beta$$

where β is the estimated parameter value for the selected coefficient (i.e., area or elevation), and SE_β is the standard error of the mean for the coefficient β.

Using t, were piscivores to be affecting the species-area/-elevation relationship, I expected this signal-to-noise ratio to be lower in piscivore lakes, which can be written as

$t(\mathrm{NP}) > t(\mathrm{P})$ for both 1971 and 2006

For linear regressions, diagnostic plots and tests of residuals were evaluated to ensure all underlying statistical assumptions were met. To ascertain homoscedastic and normalized residuals lake area, elevation and total fish species richness was $\log_{10}$ transformed. All linear regression analyses were conducted using R 2.8.1 (R Development Core Team, 2008).

Results

Fish community data were obtained for Gatineau Park, Québec lakes, surveyed by Rubec (1975) (29 lakes) in the summers of 1970 and 1971, Chapleau et al. (1997) (20 lakes) in the summers of 1990 and 1991, and Aiken (25 lakes) in the summers of 2006 and 2007 (Table 1.1). A combined total of 32 fish species were sampled from these lakes, including four piscivore species, 13 minnow species and 19 small-bodied fish species. While the 2006-2007 survey yielded no unrecorded species, it did show northern pike were present in four lakes that had no record of occurrence in 1970/71. Two species detected in 1970/71 - lake trout (*Salvelinus namaycush*) (present in Meech Lake) and margined madtom (*Noturus insignis*) (present in Loutre Lake) were not detected in any lakes sampled in 2006/2007.

Piscivore Effects on Species Richness

For samples 1 and 2, but not sample 3, average minnow species richness was significantly lower in introduced piscivore lakes (sample 1 (1971-1991-2006): $p = 0.002$, $r = 0.58$; sample 2 (1971-2006): $p = 0.002$, $r = 0.40$; sample 3 (1991-2006): $p = 0.06$, $r = 0.24$) (Table 1.2; Figure 1.1 and 1.2), while average small fish species richness was significantly lower using sample 1 and 3, but not sample 2 (sample 1: $p = 0.002$, $r = 0.54$;

sample 2: $p = 0.0002$, $r = 0.41$; sample 3: $p = 0.07$, $r = 0.21$) (Table 1.2; Figure 1.1 and 1.2). There was no evidence that overall mean minnow or small fish species richness changed over time (Table 2). For minnow species richness, an interaction between piscivore and year was observed for all samples (sample 1: $p = 0.02$, $r = 0.29$; sample 2: $p = 0.003$, $r = 0.38$; sample 3: $p = 0.05$, $r = 0.23$). There was evidence of a similar Year × Piscivore effect for small fish species richness when sample 2 was used ($p = 0.005$, $r = 0.34$), however no interaction was observed for sample 1 or 3.

Mean total fish species richness, for all samples, did not: (a) differ between piscivore and no piscivore lakes, nor (b) change over time (Table 1.2, Figure 1.1 and 1.2). There was an interaction between piscivore and year when analyzing sample 3 ($p = 0.01$; $r = 0.35$), however the same was not observed for sample 1 or 2.

Piscivore Effects on Species-Area and Species-Elevation Relationships

A set of 10 nested models were fit, which included all combinations of lake area, elevation, and piscivore status (Table 1.3). The top five models based on model selection using AICc all included elevation (Table 1.4). In both years, the most supported model was: ELEV×PISC ($AICc_{1971} = 3.8$; $AICc_{2006} = -7.3$), followed by ELEV, ELEV+PISC, AREA+ELEV, and AREA+ELEV+PISC. Together, all five of these models had a summed AICc weight (w_i) of 0.88. Area and elevation were weakly correlated (Pearson's $r = 0.34$), meaning that distinguishing between these two effects may be somewhat difficult.

However, it is important to note that in both 1971 and 2006 elevation was the best predictor of total fish species richness, with the best fit model (ELEV×PISC) explaining 63 and 41 percent of the variation in total fish species richness. Assessing this model when fit to the 1971 data and when PISC = 0, the model reduced to: LTOT = 8.92 - 3.45 × ELEV, and when PISC = 1: LTOT = 2.78 - 0.86 × ELEV. Similarly, upon being fit to the 2006 data and when PISC = 0: LTOT = 5.05 - 1.78 × ELEV, and when PISC = 1: LTOT = 1.96 - 0.52 × ELEV. For both time periods, elevation was significantly negatively related to total fish species richness. The intercept for piscivore lakes was 6.14 and 3.10 units lower than no piscivore lakes in 1971 and 2006, while, the slope of the best fit line was shallower for piscivore lakes by 2.58 and 1.26 units in 1971 and 2006.

Given the overwhelming support for lake elevation, I then fit total species richness-elevation regressions to all lake status by time period combinations to further explore the impact of piscivore introduction on SER (Table 1.5, Figure 1.3). Results indicated that the intercept and slope were lower for piscivore lakes as compared to no piscivore lakes for both time periods. Using the signal to noise ratio (t); the data supported my prediction that t(NP) > t(P) for both 1971 and 2006.

Discussion

Introduced Piscivore Effects

Similar to Chapleau et al (1997), and MacRae and Jackson (2001), total species richness was found to be almost identical in both piscivore and no piscivore lakes, and across all time periods. The same cannot be said for minnow and small fish species richness. For example, using sample two (1991-2006), piscivore lakes had on average two or 43% less minnow species and three or 50% less small fish species than lakes without an introduced piscivore.

My results strongly support the hypothesis that introduced piscivores negatively affect minnow and small fish species richness over time; a finding consistent with previous observational studies. Prior work in Gatineau Park done by Chapleau et al. (1997) found minnow and small fish species richness to be lower in lakes with introduced piscivores. Similarly, in the northeastern United States, a number of studies have demonstrated minnow species richness to be substantially lower in lakes with piscivorous fish (Whittier et al. 1997; Findlay et al. 2001) compared to those without, and in central Ontario, MacRae and Jackson (2001) showed minnow and small fish species richness and relative species abundance to be lower in lakes with smallmouth bass.

These observational studies are consistent with manipulative experiments examining the effects of either deliberate piscivore introduction or removal. In a study where a non-native piscivore (northern pike) was introduced into a small lake, He and Kitchell (1990) observed declines in small fish biomass, and suggested that northern redbelly/finescale dace and fathead/brassy minnow were most affected by piscivore introduction. These findings were attributed to direct consumption and indirect emigration (He &Kitchell 1990; He & Wright 1992). More recent manipulative experiments have examined the effects of piscivore removal. Weidel et al. (2007) found that both native littoral species abundance increased and relative predation risk decreased, while Lepak et al. (2006) observed the reestablishment of native fish food web linkages following non-native piscivore removal through electrofishing.

Though sampling error is important to consider for longitudinal studies assessing highly mobile animals such as fish, it does not appear to have biased my results. Two main sources of sampling error could lead us to erroneously infer a piscivore effect when:

(1) sampling methods were inconsistent across time, and (2) sampling effort was different across time. If sampling error biased my results, I would expect all species richness estimates to be biased consistently high or low (i.e., inaccurate); this was not the case. With regards to (1) and (2), differences in sampling method and effort were not apparent for this study. Rubec (1975) only used a seine net, while Chapleau et al. (1997) used a seine net plus nine minnow trap pairs, two gill nets, a trammel net and two trap nets. To account for these differences between sampling protocols used in 1971 and 1991/2006, in addition to the 1971-1991-2006 (sample 1) comparison, I also included a 1991-2006 comparison (sample 2). My sampling protocol was very similar to Chapleau et al. (1997), but I increased the number of seine net and minnow trap replicates since both were found to be most effective at catching minnows. Given that both Chapleau et al. (1997) and this study sampled with more sampling devices, and with at least the same amount of effort, I would expect all species richness variables to increase consistently over time in both introduced piscivore and no introduced piscivore lakes; this was not observed.

Elevation was a strong predictor of fish species richness in both 1971 and 2006, but was considerably stronger when presence of an introduced piscivore, and a piscivore by elevation interaction term were also included. Plenty of evidence suggests elevation influences fish communities to some extent in streams (Carter & Hubert 1995; Jowett & Richardson 2003; Santoul et al. 2004; Jowett; Oberdorff et al. 2007) and lakes (Chapleau et al. 1997; Baldigo & Lawrence 2000; Irz et al. 2004; Bertolo & Magnan 2006). Other well known ecological signals such as SAR (Tittensor et al. 2007; Drumbrell et al. 2008), the species-energy relationship (White & Kerr 2007), and species accumulation functions

(Flather 1996) have been demonstrated to be disrupted by anthropogenic stress. Little evidence, however, suggests anthropogenic stress alters SER.

For both time periods, the slope of the SER was shallower in piscivore lakes as compared to no piscivore lakes, providing evidence that introduced piscivores disrupt traditional ecological signals. These findings are consistent with prior studies which found a shallower slope for both SAR (Tittensor et al. 2007; Drumbrell et al. 2008) and the species-energy relationship (White & Kerr 2007) in habitats modified by human anthropogenic stress. A shallower slope for SAR has been attributed to differences in patch occupancy, species-richness, and relative species abundance (Tittensor et al. 2007), while White & Kerr (2007) attributed a shallower butterfly species-energy slope in human dominated environments to biotic homogenization via rare species extinction and common species range expansion.

In my first set of analyses total species richness did not differ between lakes with and without an introduced piscivore. This implies that biotic homogenization may be the underlying process (es) responsible for the shallower SER fit to piscivore lakes. As was also seen in my first set of analyses both minnow and small fish species richness declined drastically over time in piscivore lakes. This observation suggests that broad declines in minnow and small fish species richness coupled with a potentially compensatory introduction of other species may contribute to a weaker SER in piscivore lakes.

I observed the consistent decline of minnow and small fish species richness over time in lakes with an introduced piscivore. In this case, however, long term datasets were important to detecting these effects. By comparing piscivore and no piscivore lakes using only 1971 data, I would have dramatically underestimated the effects of exotic piscivores (see Figure 1). Only by accumulating data from multiple time periods was I able to establish a substantial observable decline in the variables under study.

Figures and Tables

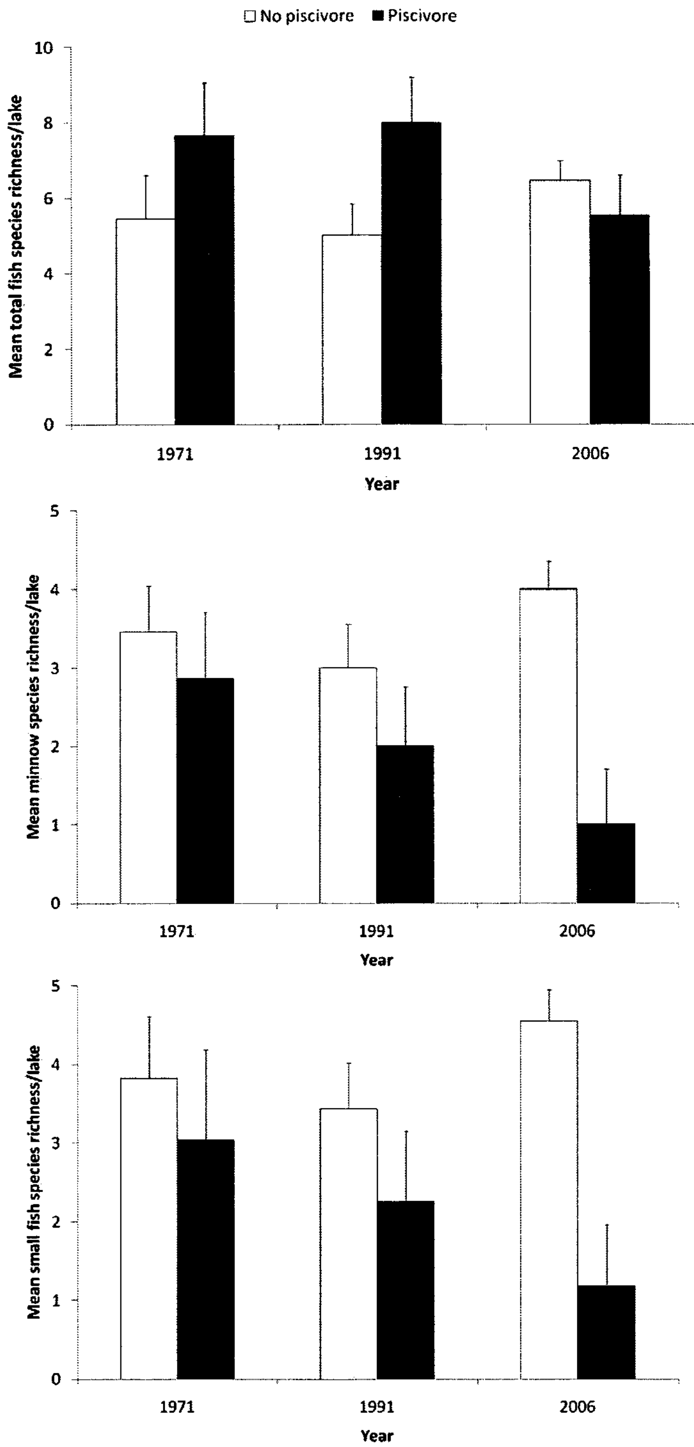

Figure 1.1. Mean total fish, minnow, and small fish species richness (± 1 SE) in no introduced piscivore and introduced piscivore lakes. For 1971 data are from 26 lakes (n_p = 15; n_{np} = 11), for 1991 - 19 lakes (n_p = 12; n_{np} = 7), and 2006 - 22 lakes (n_p = 11; n_{np} = 11). Data were collected by Rubec (1975) in 1970/1971, Chapleau et al. (1997) in 1990/1991, and Aiken (this study) in 2006/2007.

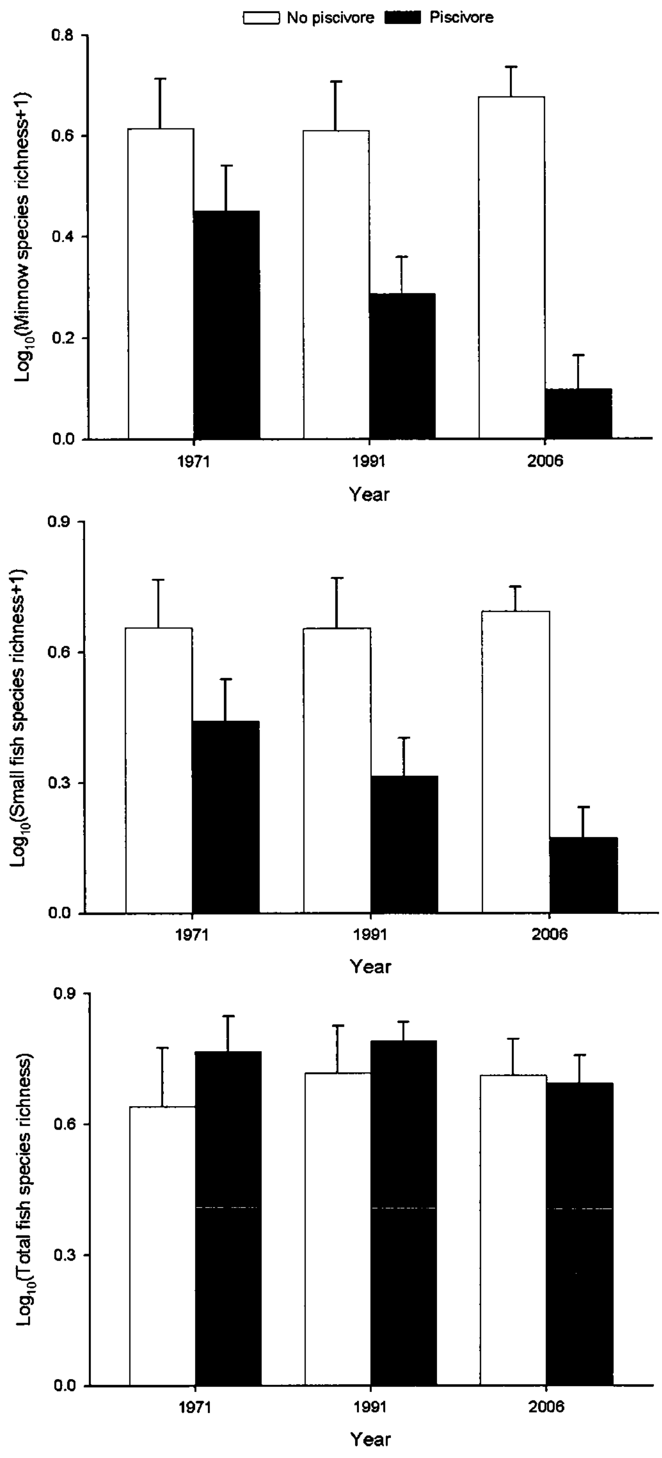

Figure 1.2. Mean minnow, small fish, and total fish species richness (± 95% CI) in introduced piscivore (n = 8) and no introduced piscivore lakes (n = 6). Data are from 14 Gatineau Park lakes, and were collected by Rubec (1975) in 1970/1971, Chapleau et al. (1997) in 1990/1991, and Aiken (this study) in 2006/2007.

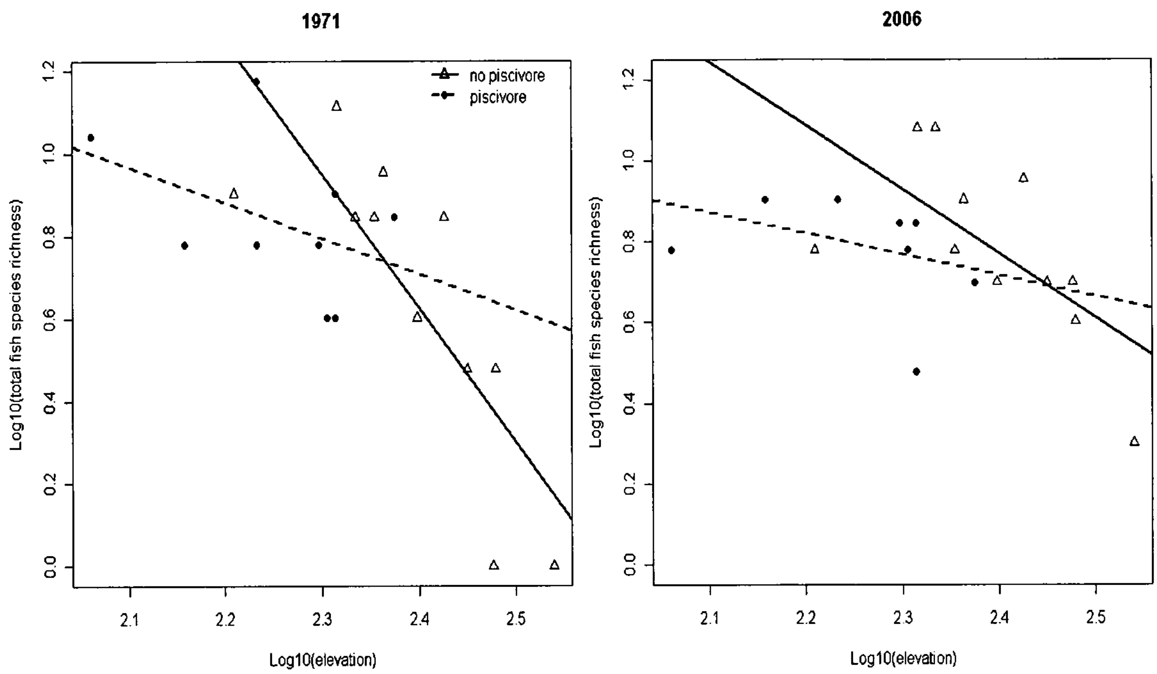

Figure 1.3. 1971 and 2006 bivariate plots of total fish species richness versus lake elevation. Straight lines were fit using models found in Table 5. Data sources are the same as in Figure 1.

Table 1.1. Summary of fish species detected in Gatineau Park, Québec lakes in 1970/1971 ($n = 29$), 1990/1991 ($n = 20$) and 2006/2007 ($n = 25$); where detected = 1, not detected = 0, and lake(s) where species historically detected but not sampled = blank. Data were collected by Rubec (1975) in 1970/1971, Chapleau et al. (1997) in 1990/1991, and Aiken (this study) in 2006/2007.

Common Name	Scientific Name	Code	1971	1991	2006
blackchin shiner**	*Notropis heterolepis*	bcsh	1		
blacknose shiner**	*Notropis heterodon*	blsh	1	1	1
bluegill	*Lepomis macrochirus*	blgl	0	1	
bluntnose minnow**	*Pimphales notatus*	blmn	1	1	1
banded killifish***	*Fundulus diaphanus*	bnkl	1	1	1
brown bullhead	*Ameiurus nebulosus*	brbl	1	1	1
brassy minnow**	*Hybognathus hankinsoni*	brmn	1	1	1
brook stickleback***	*Culaea inconstans*	brst	1	1	1
brook trout	*Salvelinus fontinalis*	brtr	1	1	1
cisco	*Coregonus artedi*	cisc	1	1	
central mudminnow***	*Umbra limi*	mdmn	1	1	1
common shiner*	*Luxilus cornutus*	cmsh	1	1	1
creek chub*	*Semotilus atromaculatus*	crch	1	1	1
finescale dace*	*Phoxinus neogaeus*	fndc	1	1	1
fathead minnow*	*Pimphales promelas*	ftmn	1	1	1
goldenshiner*	*Notemigonus crysoleucas*	glsh	1	1	1
iowa darter***	*Etheostoma exile*	iwdr	1	1	1
lake trout	*Salvelinus namaycush*	lktr	1	0	0
longnose dace**	*Notropis heterodon*	lndc	1	0	
largemouth bass*	*Micropterus salmoides*	lrbs	0	1	1
margined madtom***	*Noturus insignis*	mrmd	1	0	0
northern redbelly dace*	*Phoxinus eos*	nrdc	1	1	1
northern pike*	*Esox lucius*	nrpk	1	1	1
pearl dace**	*Margariscus margarita*	prdc	1	1	1
pumpkinseed	*Lepomis gibbosus*	pump	1	1	1
rainbow smelt	*Osmerus mordax*	rnsm	1	1	1
smallmouth bass*	*Micropterus dolomieu*	smbs	1	1	1
spottail shiner**	*Notropis hudsonius*	spsh	1	0	
threespine stickleback***	*Gasterosteus aculeatus*	tsst	1	1	1
walleye	*Sander vitreus*	wall	0	1	
white sucker	*Catostomus commersoni*	whsc	1	1	1
yellow perch*	*Perca flavescens*	ylpr	1	1	1

*Piscivore species

**Minnow and small fish species

***Small fish species

Table 1.2. Summary of one-way repeated measures analyses of variance comparing mean minnow, small fish, and total fish species richness in introduced piscivore and no introduced piscivore lakes. For sample 1 (1971-1991-2006) 14 lakes ($n_p = 8$; $n_{np} = 6$), sample 2 (1971-2006) 21 lakes ($n_p = 9$; $n_{np} = 12$), and sample 3 (1991-2006) 17 lakes ($n_p = 9$; $n_{np} = 8$). Data were collected by Rubec (1975) in 1970/1971, Chapleau et al. (1997) in 1990/1991, and Aiken (this study) in 2006/2007. Minnow and small fish species richness were $\log_{10} + 1$ transformed, while, total fish species richness was $\log_{10}$ transformed.

Sample	Richness	Piscivore (MS; *F*; *p*; *r*)	Year (MS; *F*; *p*; *r*)	Piscivore × Year (MS; *F*; *p*; *r*)
1971-91-2006	minnow	1.17; 16.36; 0.002; 0.58	0.08; 2.47; 0.11; 0.17	0.16; 4.94; 0.02; 0.29
	small	1.14; 13.88; 0.003; 0.54	0.06; 1.36; 0.28; 0.10	0.09; 2.27; 0.13; 0.16
	total	0.08; 0.69; 0.42; 0.05	0.001; 0.04; 0.96; 0.004	0.03; 1.75; 0.20; 0.13
1971-2006	minnow	1.13; 12.62; 0.002; 0.40	0.09; 2.29; 0.15; 0.11	0.43; 11.40; 0.003; 0.38
	small	1.36; 12.94; 0.002; 0.41	0.08; 2.38; 0.14; 0.11	0.34; 9.88; 0.005; 0.34
	total	0.04; 0.36; 0.56; 0.02	0.02; 0.82; 0.38; 0.04	0.07; 3.32; 0.08; 0.15
1991-2006	minnow	0.58; 4.02; 0.06; 0.21	0.03; 0.98; 0.34; 0.06	0.12; 4.50; 0.05; 0.23
	small	0.55; 3.42; 0.08; 0.19	0.02; 0.60; 0.45; 0.04	0.11; 3.39; 0.09; 0.18
	total	0.16; 2.13; 0.17; 0.12	0.005; 0.82; 0.38; 0.05	0.04; 6.64; 0.02; 0.31

Note: For each model term (piscivore, year and piscivore × year), reported are Mean Square (MS); *F*-ratio (*F*); *p*-value (*p*) and effect size (*r*) respectively.

Table 1.3. Summary of the set of nested candidate models including one null model where only an intercept was fit, and 10 models which included every possible combination of lake area (AREA), elevation (ELEV), and piscivore status (PISC) regressed against total fish species richness. Fish data are from 21 Gatineau Park lakes (sample 2: $n_p = 9$; $n_{np} = 12$), and were collected by Rubec (1975) in 1970/1971 and Aiken (this study) in 2006/2007. Lake total fish species richness, area and elevation were $\log_{10}$ transformed.

Model
NULL
AREA
ELEV
PISC
AREA+ELEV
AREA+PISC
ELEV+PISC
AREA+ELEV+PISC
AREA×PISC
ELEV×PISC
AREA×ELEV×PISC

Table 1.4. Results of model selection using Akaike's Information Criterion corrected for small sample size (AICc). The models with the most support (lowest AICc value) from each time period are denoted with bold text. Data sources are the same as in Table 2 (sample 2). Lake total fish species richness and elevation were $\log_{10}$ transformed.

	1971			2006		
Model	AICc	ΔAICc	w_i	AICc	ΔAICc	w_i
NULL	15.37	11.57	0.0017	-2.62	4.68	0.02859
AREA	16.98	13.18	0.0008	-1.67	5.64	0.01771
ELEV	5.44	1.64	0.2414	-6.61	0.69	0.21008
PISC	16.94	13.14	0.0008	-2.16	5.15	0.02266
AREA+ELEV	8.53	4.73	0.0515	-4.96	2.35	0.09183
AREA+PISC	19.69	15.89	0.0002	3.35	10.66	0.00144
ELEV+PISC	6.84	3.04	0.1197	-6.45	0.85	0.19392
AREA+ELEV+PISC	9.93	6.13	0.0256	-4.86	2.44	0.08757
AREA×PISC	20.62	16.82	0.0001	10.23	17.54	0.00005
ELEV×PISC	**3.8**	**0**	**0.5481**	**-7.3**	**0**	**0.29692**
AREA×ELEV×PISC	17.09	13.29	0.0007	-0.03	7.28	0.00781

Table 1.5. Summary of linear regressions comparing 1971 and 2006 total fish species richness with lake elevation in no piscivore lakes (np), piscivore lakes (p), and all lakes combined (all). Data sources are the same as in Table 2 (sample 2). Lake total fish species richness and elevation were $\log_{10}$ transformed.

Year	Lk	$\alpha(\pm SE)$	$\beta(\pm SE)$	$t;t_1$	ε	R^2	$p;p_1$
1971	np	8.91(1.63)	-3.45(0.68)	4.99; -4.61	0.23	0.68	0; 0
	p	2.78(1.32)	-0.86(0.59)	1.85; -1.30	0.18	0.19	0.11; 0.24
2006	np	5.05(1.41)	-1.78(0.59)	3.59; -3.01	0.18	0.48	0.005; 0.01
	p	1.96(1.14)	-0.52(0.51)	1.72; -1.02	0.14	0.13	0.13; 0.34

Note: Models are of the form $y = \alpha + \beta x$, where, α = intercept, β = slope or rate of change in the dependent variable y ($\log_{10}$ total fish species richness) as the independent variable x ($\log_{10}$ elevation) increases, 95%CI = 95% confidence interval, t; t_1 = t-values for α and β calculated as α/α standard error and β/β standard error, ε = residual standard error, r^2 = coefficient of determination, and p; p_1 = p-values for α and β respectively.

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Chapter 2 Estimating piscivore invasion risk for small temperate lakes

Introduction

A lake's biota has been argued to be susceptible to species introductions, often resulting in significant alterations of community structure (Magnuson 1976). For example, in northeastern North America, the stocking of small lakes with invasive piscivores (i.e., smallmouth and largemouth bass [*Micropterus dolomieu* and *M. salmoides*, respectively], northern pike [*Esox lucius*], yellow perch [*Perca flavescens*], and walleye [*Sander vitreus*]) has been implicated in the decline of native minnow (family Cyprinidae) and small fish biodiversity (Chapleau et al. 1997; Whittier et al. 1997; Whittier & Kincaid 1999; Findlay et al. 2001; Whittier et al. 2002). These observations are consistent with widespread evidence supporting the contention that aquatic predators, whether endogenous or anthropogenically introduced, have strong effects on fish communities (Zaret & Paine 1973; Robinson & Tonn 1989; He & Kitchell 1990; He & Wright 1992; Crivelli 1995; Jackson et al. 2001; Bonar et al. 2005; Bystrom et al. 2007), aquatic food-webs (Carpenter & Kitchell 1993; Carpenter et al. 1985), and ecosystem processes (Eby et al. 2006).

Predicting where and when invasive species such as introduced piscivores will colonize a novel lake is a prudent conservation and management strategy for mitigating future losses of biodiversity (MacIsaac et al. 2004; Vander Zanden et al. 2004). One common approach is to consider invasion susceptibility to be related to the extent to which the physiochemical and biotic properties of waterbodies from which the species of concern is currently absent match those of waterbodies within the species' historical and/or current distribution (Moyle & Light 1996; Harig & Fausch 2002). This approach has been employed to assess invasion risk for a number of invasive fish species, including rainbow smelt [*Osmerus mordax*] (Drake & Lodge 2006; Mercado-Silva et al. 2006), Eurasian ruffe [Gymnocephalus cernauus] (Drake & Lodge 2006), and smallmouth bass (Vander Zanden et al. 2004).

In addition to physiochemical and biotic characteristics that typically define a species' niche, landscape attributes, including those associated with anthropogenic activities, have considerable potential to influence invasion susceptibility (Cowie & Werner 1993; Lonsdale & Lane 1994). For example, roads may influence susceptibility by increasing angler access, a major source of introductions into small temperate lakes (Magnuson 1976) as well an important factor structuring fish populations and communities (Thompson & Lee, 2000; Steel et al. 2004; Wall et al. 2004; Ripley et al. 2005; Rieman & McIntyre 1995; Gunn & Sein 2000). The role road access plays in the invasion process is especially important because it represents a primary pathway through which exotic species invade new lakes (Magnuson 1976; Hrabik & Magnuson 1999; MacIsaac et al. 2004). Particularly for small temperate lakes, anglers have been historically and to a lesser extent still are an important vector for fish introductions into small temperate lakes, often facilitating invasions purposefully via unauthorized introductions or accidentally via bait bucket transfers (Litvak & Mandrak 1993; Hrabik & Magnuson 1999; Vander Zanden et al. 2004).

A second landscape feature that is likely to influence invasion susceptibility is the stream network. There is ample evidence that fish community composition and abundance is associated with the degree of spatial isolation afforded by the stream network (Snodegrass et al. 1996; Lonzarich 1998; Hershey et al. 1999; Olden et al. 2001). Yet spatial isolation has not traditionally been considered extensively for predicting fish invasions of aquatic ecosystems (Jackson et al. 2001). With the growing widespread use of Geographic Information Systems (GIS) in fisheries science this is changing. Studies have begun creating lake landscape position and isolation metrics to attempt to explain lake water chemistry (D'Arcy & Carignan 1997; Kratz et al. 1997; Soranno et al. 1999; Quinlan et al. 2003; Martin & Soranno 2006), plankton populations and species richness (Michels et al. 2001; Cottenie & Meester 2003), molluscan assemblages (Lewis & Magnuson 2000; Heino & Muotka 2006), fish distributions (Dunham & Rieman 1999; Hershey et al. 2006; Spens et al. 2007), and lake community structure (Olden et al. 2001; Beisner et al. 2006; Bertolo & Magnan 2006).

For this chapter, I estimated piscivore invasion risk for a set of small lakes located in Gatineau Park, Québec using previously published and newly collected fish data. More specifically, I aimed to: (1) evaluate the influence of anthropogenic and spatial factors on piscivore invasion, and (2) compare two analyses aimed at estimating piscivore invasion risk. For the first analysis, I created a time series for each lake sampled on two or more occasions using data collected in 1971 (Rubec 1975), 1981 (Brunet 1982), 1991 (Chapleau et al. 1997) and 2006 (this study). For each time interval (i.e., 1971 to 1981) I determined whether or not a piscivore species invaded a lake. I then modeled invaded/not invaded lakes using predictor variables that included lake anthropogenic and spatial factors, morphometry, and small fish species richness. For the second analysis, I used data from each lakes first sampling event, and determined whether a piscivore species was detected or not detected at that time. I then assumed susceptibility to be related to the extent to which the anthropogenic, spatial, morphometric and biological properties of waterbodies from which a piscivore species was detected match those of waterbodies within the species' distribution across Gatineau Park. The resulting validated susceptibility models from each analysis were then used to: (1) assess what underlying lake characteristics best explain historical piscivore distribution and invasion; (2) identify lakes at greatest risk for future invasion, and (3) make informed management recommendations designed to mitigate risk.

Methods

Fish Data

Gatineau Park has 55 recognized lakes, ranging in size from under one to 700 hectares (Rother 1983). Historical fish community data for a subset of these lakes were obtained from three previous studies (Rubec 1975; Brunet 1983; Chapleau et al. 1997). Rubec (1975) sampled 29 lakes in the summers of 1970 and 1971(for simplicity, here on referred to as 1971 data), Brunet (1983) sampled 16 lakes in the summers of 1980 and 1981 (for simplicity, here on referred to as 1981 data) using two experimental gill nets (40 × 1.8m with 13, 19, 25, 31, and 38mm mesh sizes) and 6 unbaited minnow traps (44.5cm long, 23cm in diameter with a 1.1cm opening), while, Chapleau et al. (1997) surveyed 20 lakes in the summers of 1990 and 1991 (here on referred to as 1991 data). Detailed fish sampling methodologies for each of these studies, with the exception of Brunet's (1983), are described in chapter 1.In addition to historical fish community data, in the summer of 2006 and 2007 (here on referred to as 2006 data), I re-sampled 25 lakes previously surveyed in one or more of 1971, 1981 and/or 1991. Detailed sampling methods used for the 2006 and 2007 survey are again outlined in chapter 1.

Predictor Variables

Spatial Isolation

Spatial isolation variables (Table1) were extracted from a hydro network generated using Geographic Information System (GIS) hydrographic data obtained from the Canadian 1:50,000 National Topographic Database (NTDB) (Centre for Topographic Information 2005), projected to Universal Transversal Mercator (UTM), zone 18, North American Datum 1983 (NAD83). A hydro network can be defined as, "a simplified representation of the blue lines on maps defining streams, rivers and water bodies, in which centerlines can be drawn through all areal features (any river or waterbody represented by a polygon in a GIS) to create a continuous, single-line network throughout the river system (Maidment 2002)." Generating a hydro network for Gatineau Park involved first defining the drainage area to process, and then using the hydrographic data (i.e., stream [polyline], river [polygon] and waterbody [polygon] data) to generate a hydro network with no breaks or gaps. This required delineating centerlines for all areal features, and performing a number of GIS functions to create a clean, continuous hydro network. Finally, flow direction for the network was set so that water flowed in the proper direction (i.e., downhill). All hydro network generation and processing was completed in ArcInfo Version 9.2 (ESRI 2007).

Once the hydro network was constructed, any number of spatial attributes could then be created (see Theobald et al. 2006 for examples). The first spatial factor extracted was instream distance (DIST), estimated as the instream distance from a lake to the nearest occupied waterbody. An occupied waterbody was defined as a lake or mainstem river containing one or more of northern pike, largemouth bass, smallmouth bass, walleye, and/or yellow perch. Both the Gatineau, Rideau and Ottawa rivers were considered mainstem rivers as all piscivore species are endemic to these rivers (McAllister & Coad 1974; Coad 2007). All stream distances were estimated using the Network Analyst extension for ArcInfo 9.1 (ESRI 2005).

Lake elevation (ELEV) was estimated using a 30m resolution Digital Elevation Model (DEM) (Centre for Topographic Information 2004). In addition, using this DEM and the hydro network, stream slope (SSLP) was calculated as the stream gradient between a lake and the nearest occupied waterbody as

$$\frac{\text{upstream ELEV} - \text{downstream ELEV}}{\text{DIST}} \times 100$$

Whether or not a fish can reach a target lake from a nearby-occupied waterbody is likely to depend on the size of the stream(s) connecting the two waterbodies. I therefore used minimum Strahler stream order (STRAH), defined, as the order of the smallest stream a fish must use to move between the potential donor and target lakes. Strahler stream order (Strahler 1952, 1957) was selected as it measures a stream's position in the hierarchy of tributaries, its size and watershed area (Leopold et al. 1964).

Anthropogenic

Two anthropogenic variables (Table 1) were extracted from 1:25,000 topographic data layers collated between 1988 and 1995 (Ministère des Ressources naturelles et de la Faune du Québec 1999). One is simply the distance to nearest public road, in kilometers, calculated by estimating the straight line distance from a lake's edge to the nearest public road, using the nearest features tool (Jenness 2004) in Arcview 3.2 (ESRI 2005). Public roads were defined as those roads accessible by car to the public, and for example, did not include roads only accessible to hikers, bikers, horse back riders, park personnel or private land owners.

The second index was obtained by first summing the length (in km) of roads and official recreational trails within each lakes watershed using Hawth Tools (Beyer 2004) in ArcInfo 9.2 (ESRI 2007). Summed road lengths for each watershed were then divided by the area of the watershed (km^2) minus waterbody area (defined as all waterbodies - excluding streams) to obtain a watershed road and trail density measure for each lake.

Species-Area

Lake area (AREA) was extracted from 1:20,000 topographic data layers (Ministère des Ressources naturelles et de la Faune du Québec 1999) using ArcInfo 9.2 (ESRI 2007). In addition,and the number of small bodied fish species detected during the first sampling occasion was also included as these small species are exceptionally prone to gape limited piscivores (Tonn & Paszkowski 1986).Invasion Analysis 1

Using data collected in 1971, 1981, 1991, and 2006, I compiled data for only those lakes surveyed in two or more time periods. This resulted in the inclusion of 29 lakes, with 10 lakes sampled in two time periods (1971 and 1991; 1971 and 2006; 1991 and 2006), 15 in three time periods (1971 and 1981 and 2006; 1971 and 1991 and 2006), and 4 in all time periods (1971 and 1981 and 1991 and 2006). For each lake, a time interval was then defined as time 1 to time 2. For example, Kidder Lake was sampled in all sampling periods (1971, 1981, 1991, and 2006), and thus had three time intervals (1971 to 1981, 1981 to 1991, and 1991 to 2006), whereas Philippe Lake was only sampled in two sampling periods (1971 and 1991), and thus had one time interval (1971 to 1991).

For each time interval three observations were possible: northern pike, small and largemouth bass, yellow perch and walleye could either (a) go extinct (i.e., present at time 1 and absent at time 2), (b) colonize a lake (i.e., absent at time 1 and present at time 2), or (c) status not have changed (i.e., present or absent at time 1 and 2). I combined all extinction and no status change lakes as there was only one case where a piscivore species apparently went extinct (yellow perch from Clair Lake), and assigned each of theses lakes a value of zero. All colonization observations were assigned a value of 1. Lakes with one, two or three observations, henceforth, will be denoted, n1, 2n(2), or 3n(3), with sample size equal to

$$N = n1 + 2n(2) + 3n(3)$$

Two inherent characteristics of the data were considered in the selection of an appropriate statistical model. First, given that a portion of the lakes had multiple observations, non-independence due to repeated measurements was possible. Second, the number of observations ranged per lake from one to three; this meant that n(1) lakes were missing data relative to $2n(2)$ and $3n(3)$ lakes. To account for these two inherent characteristics, I pursued a bootstrap analysis as follows.

(*i*) I used all $n(1)$ lakes, plus for each $2n(2)$ and $3n(3)$ lake one observation was selected at random resulting in a sample size of

$$n = n(1) + n(2) + n(3)$$

(*ii*) using sample *n*, I fit 11 candidate logistic regression models using the base, spatial, anthropogenic and establishment predictor variables (Table 2). The two base predictor variables were not used in the first invasion analysis, and were simply the time between sampling periods and the number of piscivore species already present in the lake. Four of these candidate models were developed using *a priori* knowledge, while the remaining seven were simply all possible combinations of these four models (i.e., model1+model2, model+model3, model1+model4...and so forth). The first *a priori* model was defined as the base model as the predictors were expected to be highly correlated with piscivore invasion, irrespective of any environmental or isolation factor(s), and included the number of piscviore species present at time 1, and the number of years between sampling periods. The second and third models were defined as access models because they were composed of road access and spatial isolation (access via the stream network) variables only. An establishment model was also developed, which consisted of lake area and small fish species richness. In addition, all possible combinations of these four models were also fit, including a full model which included all predictor variables to ensure the model fit the data correctly (Burnham & Anderson 2002).

AICc, was used to compare competing models, and was calculated as outlined in Chapter 1.

How well the model fit the data was assessed using an unweighted sum-of-squares goodness of fit test (Hosmer et al. 1997), while, parameter values for each predictor variable were estimated and evaluated by calculating their odds ratios and 95% confidence intervals. Model predictive ability was assessed using the area under the ROC (receiver operating characteristic) curve (*c*), a plot of model sensitivity (ability of the model to predict invaded) on the *y* axis against 1-specificity (ability of the model to predict not invaded) on the *x* axis (Zweig & Campbell 1993).

(*iii*) Steps 1 and 2 were repeated 100 times, sampling with replacement, to generate average (bootstrapped) AICc values, parameter estimates (and associated odds ratios), goodness of fit test statistics, area under the ROC curves (*c*), probability of invasion and each of these statistics associated 95% confidence intervals (CI).

All bootstrapping, graphing and logistic regression analyses were conducted using R 2.8.0 (R Development Core Team, 2008). The unweighted sum-of-squares goodness of-fit statistics were calculated using the Design package for R, Version 2.1-1 (Harrell 1997).

Invasion Analysis 2

The second invasion analysis involved determining which lake characteristics were associated with Gatineau Park lakes historically occupied by one or more piscivore species, and then using these characteristics to identify unoccupied Gatineau Park lakes potentially at risk for invasion. To do this, I first compiled a sample of lakes for which fish data were collected. Once compiled, I then included only those data collected on the first sampling event for each lake, and determined whether or not a piscivore species was detected or not detected. This resulted in the inclusion of 42 lakes, each of which was sampled between 1970 and 2007.

Using this sample of lakes, I then fit eight candidate logistic regression models: one null model with only an intercept, and a set of seven nested models using spatial, anthropogenic and species-area predictor variables (Table 2). Three of the candidate models were developed using *a priori* knowledge, while the remaining four were simply all possible combinations of these three models (i.e., model2+model3, model3+model4, model2+model4, model2+model3+model4). The first model was the null model, and included only an intercept. The second and third models were defined *a priori* and were termed access models because they were composed of road access and spatial isolation (access via the stream network) variables only. A species-area model was also defined a priori, and consisted of lake area and small fish species richness. In addition, all possible combinations of these latter three models were also fit, including a full model which included all predictor variables to ensure the model fit the data correctly (Burnham & Anderson 2002).

The information theoretic method (employing AICc, rescaled AICc, and w_i) was once again used to identify the most parsimonious model (Burnham & Anderson 2002). Identical to invasion analysis one, how well the most supported model (based on AICc) fit the data was assessed using the unweighted sum-of-squares goodness of fit test (Hosmer et al. 1997), parameter values for each predictor variable were estimated and evaluated by calculating their odds ratios and 95% confidence intervals, while, model predictive ability was assessed using the area under the ROC (receiver operating characteristic) curve (*c*). For invasion analysis two, all graphing and logistic regression analyses were conducted using R 2.8.0 (R Development Core Team, 2008). The unweighted sum-of-squares goodness of-fit statistics and area under the ROC curve were calculated using the Design package for R, Version 2.1-1 (Harrell 1997).

Estimating Lake Invasion Risk

For both invasion analyses, the overall classification success of the most supported model based on AICc was summarized in a confusion matrix (Fielding & Bell 1997). Rather than using an arbitrary value to classify lakes, the ROC (Receiver Operating

Characteristic) curve was used to determine a classifier threshold value. The probability at which sensitivity (ability of the model to predict invaded) equals specificity (ability of the model to predict not invaded) was used to determine the threshold value. Lakes classified as false positive (i.e., observed not invaded, predicted invaded) were considered "vulnerable" to piscivore invasion. Lakes classified as true positive (observed invaded, predicted invaded) or false negative (observed invaded, predicted not invaded) were considered "invaded", while those lakes classified as true negative (observed not invaded, predicted not invaded) were considered "not vulnerable" to piscivore invasion. For visualization purposes, each lake and its assigned category (vulnerable, invaded, and not vulnerable) were mapped in a GIS.

Results

Invasion Analysis 1

The sample used for invasion analysis one consisted of 29 lakes, all of which had a total of 52 observations. Of these 52 observations, 13 piscivore invasions occurred, with northern pike invading seven lakes, largemouth bass four, yellow perch two, walleye one, and smallmouth bass no lakes.

Based on model selection using AICc, model 4 (species-area) had the most support; having the lowest bootstrapped AICc value (Table 3). Model 4 included small fish species richness (SM) and lake area (AREA) only, and had a calculated AICc value and w_i of 27.57 and 0.51. The next three best performing models were models 7, 8, and 9, each of which had a bootstrapped w_i value = 0.14, 0.15, and 0.11. Model 8's AICc value was inflated because the model did not converge 19 times due to overfitting. Without these 19

AICc values, model 8 had a calculated $w_i = 0.05$ as opposed to the reported 0.15. In addition to model 8, model 10 did not converge 8 times, while model 11 did not converge at all. If I excluded model 8, model 7 was the next most supported model behind model 4, followed by model 9. All three of these models (7, 4, and 9) included SM and AREA, while model 7 also included years between samples (T) and number of piscivores present at time 1 (NPISC), and model 9 the anthropogenic variables distance to nearest road (RDIST), watershed road density (RDENS) and man-made barrier presence or absence (BAR).

Focusing on the most supported model 4, the unweighted sum-of squares goodness-of-fit statistic lent further support to the model selection results, indicating that the model was a good fit to the data ($p = 0.48$). The overall predictive ability of the model was also excellent, as the average area under the receiver operating characteristic curve (c) was = 0.87. Piscivore invasion risk increased with increasing small fish species richness and lake area (odds ratios (95% CI) = 107.13(46.05, 249.30) and 37.00(25.07, 54.62). The weight of evidence further supported these two variables, with the sum of w_i for all models which included area and small fish species richness = 0.82, the highest amount of support for any variable.

Invasion Analysis 2

The sample used for invasion analysis two consisted of 42 lakes, and of these 42 observations, a piscivore species was detected in 17 lakes. Based on model selection using AICc, model 7 (species-area+spatial) had the most support; having the lowest AICc value (Table 3). Model 7 included small fish species richness (SM), lake area(AREA) distance to nearest source population (DIST), stream slope (SSLP), elevation (ELEV), and minimum Strahler stream order (STRAH), and had a calculated AICc value and w_i of 43.38 and 0.65. The next four best performing models were models 8, 3, 6, and 4, each of which had a w_i value = 0.14, 0.12, 0.05, and 0.04. All four of these models included either species-area and/or spatial isolation variables. Focusing on the most supported model 7, the unweighted sum-of squares goodness-of-fit statistic lent further support to the model selection results, indicating that the model was a good fit to the data ($p = 0.63$). The overall predictive ability of the model was also excellent, as the area under the receiver operating characteristic curve (c) = 0.94. Piscivore invasion risk increased with increasing small fish species richness, lake area, and minimum Strahler stream order, and decreased with increasing lake elevation, distance to nearest source population, and stream slope.

Estimating Lake Invasion Risk

Using invasion analysis one's confusion matrix, a total of one lake (Renaud) was classified as "vulnerable" to piscivore invasion. A total of thirteen lakes were classified as invaded, meaning one or more piscivores invaded these lakes in the past 58 years. This left 15 lakes which were classified as not vulnerable to piscivore invasion.

For invasion analysis two, a total of three lakes (Pink, Richard, and Trudel) were classified as vulnerable, 22 not vulnerable, and 17 invaded.

Discussion

Invasive species are an increasing dilemma for both ecosystems and human economies (Pimentel 2000). As a result, it is imperative that predictive tools are developed to identify where invasions will happen next, when (if possible) they might happen, and the ramifications if and when such events do occur (National Invasive Species Council

2001). Due to their ability to alter native ecosystems (Byström et al. 2007), it is especially important that introduced predators are given utmost consideration. Piscivores such as walleye, yellow perch, northern pike and smallmouth/largemouth bass play an important role in structuring small lake fish communities, often completely eliminating small fish species (Robinson & Tonn 1989; Magnuson et al. 1998). This has been supported by both observational (Chapleau et al. 1997; Findlay et al. 2001) and manipulative studies (He & Kitchell 1990; He & Wright 1992; He et al. 1993). Given their pervasiveness, a quantitative and probabilistic approach coupled with a strong management strategy is needed to protect lakes where these piscivorous species will access and establish populations next (Mercado-Silva et al. 2006).

Here, using two risk analysis frameworks to suit small temperate lake ecosystems (Figure 1); I attempted to do exactly this. Using these frameworks, I developed sets of competing models for predicting piscivore invasion using historical invasion events, and historical distribution. First, two models were developed with the expectation that piscivores can access small temperate lakes through two potential pathways: (1) the stream network; and/or (2) anthropogenically via accessible recreational trails and/or roads. Second, an "establishment" model was developed with the expectation that piscivore invasion could be explained by lake environmental characteristics.

Results from invasion analysis one using historical invasion events from the previous 57 years, indicated that two lake establishment factors: lake area and small fish species richness are strong predictors (for small temperate Gatineau Park lakes) for discerning between a lake invaded or not invaded by a piscivore. Small species richness increased with increasing probability of piscivore invasion. One potential explanation for this is that, as the number of species increases so does the number of individuals (Gotelli & Colwell 2001), and as a result, lakes with higher numbers of species provide a higher number of resources for piscivores to exploit. It is likely that small fish species richness covaries with lake size (i.e., the species-area relationship), but I found no evidence of this in my sample, nor was their support for including an area × small fish species richness interaction term in the model. In comparison to small species richness, lake area's inclusion in my most supported model was not surprising given that both immigration and population persistence generally increases with increasing patch size (Tonn et al. 1990; Fahrig & Merriam 1994; Hanski 1994; Matter et al. 2005). A number of mechanisms could potentially explain this observation. First, larger lakes act as oxygen refuges during winter months, which is potentially important to the persistence of piscivore populations (Tonn & Magnuson 1982). Were long term dissolved oxygen data available, I would have included them in my candidate models. Secondly, in North America and Wisconsin, colonization rates are generally higher for large lakes due to increased human influences and connectivity to the stream network (Magnuson et al. 1998). Lake area was not correlated with any spatial isolation or anthropogenic factors, and my modeling results showed little support for the inclusion of my spatial isolation variables, however, some support was lent to model 9 which included anthropogenic access variables.

Invasion analysis two results were qualitatively similar to one's in that the establishment factors were included in the most supported model, but spatial isolation factors were by far the best predictors of piscivore presence/absence in analysis two. Larger/lower elevation lakes such as Meech, Carman, La Peche and a number of other lakes were stocked in the 1930's with species such as smallmouth bass and northern pike.

Over time these species (pike primarily) have spread throughout the watershed to higher elevation lakes such as Richard, Loutre, Hawley and Ramsay. If I were to have fit a model to more current data, because piscivores now currently occur in both lower and higher elevation/more isolated lakes, this spatial isolation effect may not have been as pronounced.

It has been acknowledged that spatial isolation might play an important role in forecasting the dispersal and colonization of top predators (Olden & Jackson 2001), though some recent studies suggest that past colonization routes (represented by lake geographic coordinates and elevation) are relatively more important than current hydrologic connections (represented by numerous lake spatial isolation metrics) in structuring fish communities (Bertolo & Magnan 2006). Few studies have used spatial factors to estimate piscivore invasion, but the few studies which have, generally show support for the role spatial isolation plays in explaining population processes. As an example, Spens et al. (2007) developed an upstream conductivity model to model the distribution of northern pike. They found that pike distribution was best predicted using the minimum distance between 5m elevation intervals (= maximum stream slope) and a downstream source population. Further, my two spatial isolation variables: distance to nearest source population and downstream stream slope have been shown to be excellent predictors of highly mobile species such as northern pike (Moen & Henegar 1971; Schlosser & Kallemeyn 2000; Ovidio & Philippart 2002). This was somewhat evident in invasion analysis two as distance to nearest source population was a strong predictor, but not in invasion analysis one.

Though my results had little support for anthropogenic variables, modelling piscivore invasion typically focuses exclusively on lake morphometric and biological characteristics, and often ignores the role anthropogenic access plays in the invasion process. This has been done even though the degree of road access has been acknowledged to be a vector of, for example: bass movement (Litvak & Mandrak 1993; Vander Zanden et al. 2004; Kaufman et al. 2009) and other introduced species (Copp et al. 2005; Von der Lippe & Kowarik 2007; Jodoin et al. 2008). One possible explanation for this lack of observable effect is the limited range of access values, a direct result of the relatively small scale at which my study was conducted.

My results have important implications for the conservation and management of small lake ecosystems. These ecosystems house a diverse number of organisms that are under continuous pressure from numerous anthropogenic sources including introduced piscivores. As a result, decisive conservation and management actions are required to ensure that the future state of these ecosystems is not compromised. A primary message from invasion analysis one (using historical invasion events) is that lake establishment factors (also called extinction factors by Magnuson et al 1998) appear to be the primary predictor of exotic piscivore invasion. From analysis two, spatial isolation factors in addition to the two lake establishment factors were good predictors of piscivore presence/absence. These findings, however, are probabilistic and, and as a result, need be interpreted with caution.

Figures and Tables

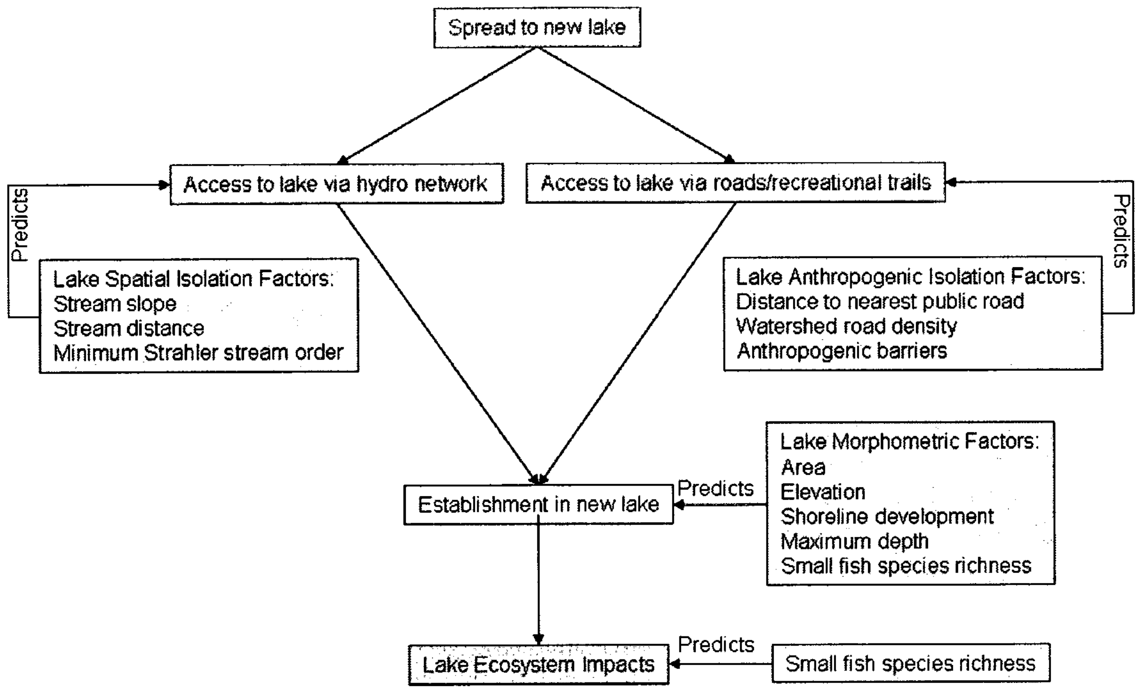
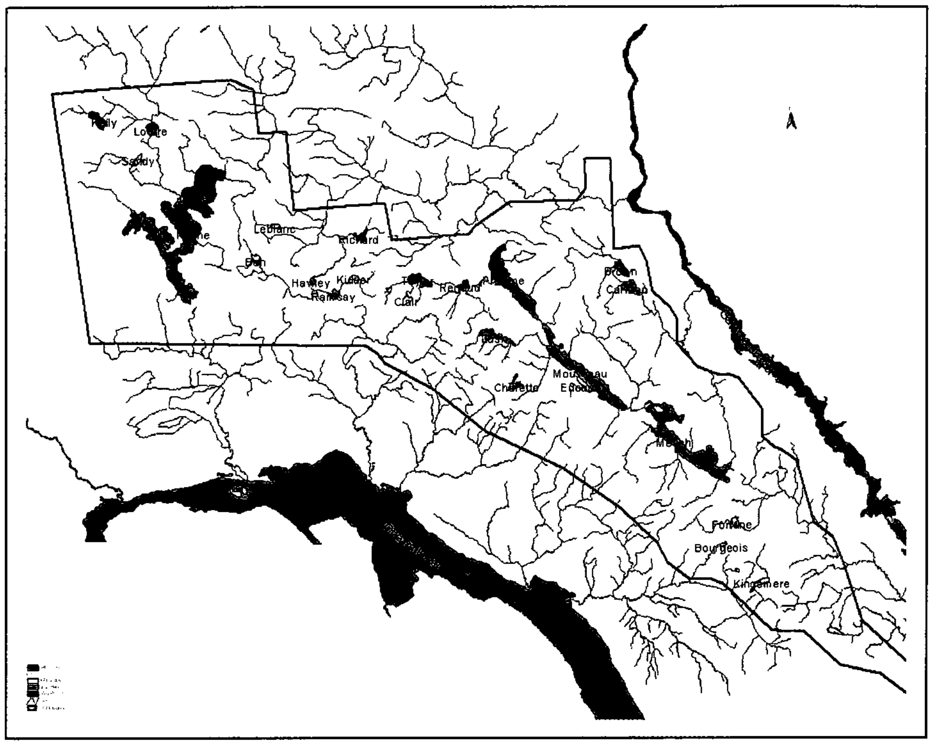


Figure 2.1. Flow chart demonstrating stage 5 of the invasion process (adapted from Lockwood et al. 2007). Stage 5 is the spread of the already introduced species (i.e., smallmouth bass) to new lakes within the geographic area (i.e., Gatineau Park), and occurs after a species has already been transported to the new geographic area (i.e., smallmouth bass were transported to Gatineau Park in 1908).

(a)



(b)

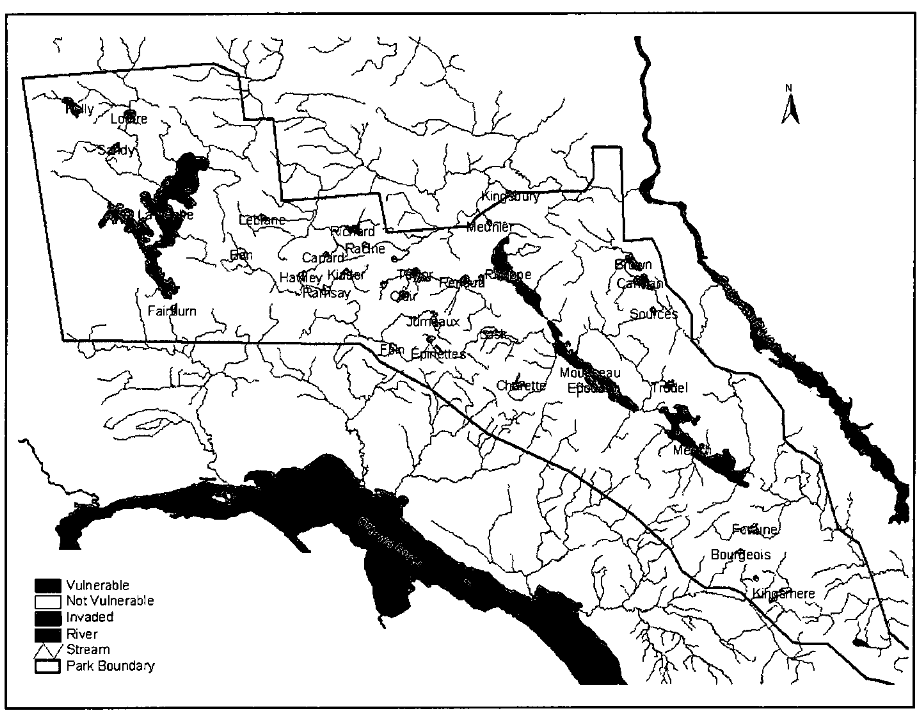


Figure 2.2. Map depicting piscivore invasion risk for (a) 29 Gatineau Park lakes calculated using model 4 (invasion analysis one) and (b) 42 Gatineau Park lakes calculated using model 7 (invasion analysis two). Lakes were classified as "not vulnerable" (green), "invaded" (yellow), and "vulnerable (red).

Table 2.1. Code and description of spatial, anthropogenic, morphometric and biological predictor variable(s) used to estimate piscivore colonization.

Code	Variable	Description	Units
Temporal			
N	Number of Piscivores	Number of piscivores present at time 1	
T	Time	Time between samples	yrs
Spatial			
ELEV	Elevation	Lake elevation above sea level	m
SSLP	Stream slope	Stream slope between target lake and nearest source population (US ELEV – DS ELEV / stream length × 100%) at time 1	%
DIST	Instream distance	Instream distance from lake to nearest occupied lake at time 1	km
Anthropogenic			
DPUB	Distance to nearest public road	Distance from lake to nearest public road	km
RDENS	Watershed road/trail density	Length of roads/trails in watershed / watershed area – waterbody area	km/km^2
BARR	Anthropogenic barrier	Presence (1) or absence (0) of a man-made barrier at lake outlet	
Morphometric			
AREA	$\log_{10}$(Area)	Total surface area of lake	km^2
Biological			
SM	Log_{10}(small fish species richness + 1)	Number of small fish species at time 1	

Table 2.2. Summary of invasion analysis one candidate models (models 1 to 4) and all possible candidate model combinations (models 5 to 11) fit to estimate piscivore invasion risk, and invasion analysis two candidate models (models 1 to 3) and all possible candidate model combinations (models 4 to 8) fit to estimate piscivore invasion risk. Variable codes are explained in Table 1.

Model	Predictor variables	Description
Invasion analysis 1		
1	NPISC+TIME	Base
2	RDIST+RDENS+BAR	Anthropogenic
3	DIST+SSLP+STRAH+ELEV	Spatial
4	AREA+SM	Species-Area
5	NPISC+TIME+RDIST+RDENS+BAR	Base+Anthropogenic
6	NPISC+TIME+ DIST+SSLP+STRAH+ELEV	Base+Spatial
7	NPISC+TIME+SM+AREA	Base+Species-Area
8	RDIST+RDENS+BAR+ DIST+SSLP+STRAH+ELEV	Access(Anthropogenic+Spatial)
9	RDIST+RDENS+BAR+ AREA+SM	Anthropogenic+Species-Area
10	DIST+SSLP+STRAH+ELEV+SM+AREA	Spatial+Species-Area
11	NPISC+TIME+ RDIST+RDENS+BAR+ DIST+SSLP+STRAH+ELEV+ AREA+SM	Full
Invasion analysis 2		
1	NULL	
2	RDIST+RDENS+BAR	Anthropogenic
3	DIST+SSLP+STRAH+ELEV	Spatial
4	AREA+SM	Species-Area
5	RDIST+RDENS+BAR+ DIST+SSLP+STRAH+ELEV	Access(Anthropogenic+Spatial)
6	RDIST+RDENS+BAR+ AREA+SM	Anthropogenic+Species-Area
7	DIST+SSLP+STRAH+ELEV+SM+AREA	Spatial+Species-Area
8	RDIST+RDENS+BAR+DIST+SSLP+STRAH+ELEV+ AREA+SM	Full

Table 2.3. Results of invasion analysis one model selection using average (bootstrapped) Akaike's Information Criterion corrected for small sample size (AICc), and invasion analysis two model selection using Akaike's Information Criterion corrected for small sample size (AICc).

Model	AICc	ΔAICc (±95%CI)	w_i (±95%CI)
Invasion analysis 1			
1	37.56	11.702(0.859)	0.0085(0.0029)
2	41.11	15.252(0.749)	0.0011(0.0003)
3	37.76	11.905(0.933)	0.0114(0.0065)
4	**27.57**	**1.71(0.65)**	**0.5126(0.0558)**
5	42.14	16.28(0.88)	0.0011(0.0005)
6	42.70	16.85(0.89)	0.0007(0.0003)
7	30.60	4.74(0.71)	0.1386(0.0234)
8	40.01	14.15(1.74)	0.1534(0.0650)
9	34.63	8.77(5.40)	0.1121(0.0355)
10	34.52	8.66(0.65)	0.0599(0.0359)
11	43.5	17.643(0.90)	0.0005(0.0002)
Invasion analysis 2			
1	58.79	15.41	0.0003
2	60.72	17.34	0.0001
3	46.77	3.39	0.1188
4	48.81	5.42	0.0429
5	54.20	10.82	0.0029
6	48.54	5.16	0.0490
7	**43.38**	**0**	**0.6461**
8	46.44	3.06	0.1399

Note: For invasion analysis 1values are average (bootstrapped) AICc differences (ΔAICc), and Akaike weights (w_i). Bold indicates the most supported model.

Table 2.4. Summary of the invasion analysis one (average (bootstrapped) parameter estimates and overall model performance), and the invasion analysis two (parameter estimates and overall model performance) logistic regression model with highest support based on model selection using AICc.

Predictor	β(±95%CI)	e^{β}(95%CIs)	*c*	*p*
Invasion analysis 1				
Model 4			0.87	0.48
Intercept	-1.40(0.62)			
SM	4.67(0.84)	107.13(46.04, 249.30)		
AREA	3.61(1.98)	37.00(25.07, 54.62)		
Invasion analysis 2				
Model 7				
Intercept	13.20(10.42)		0.94	0.63
DIST	-0.24(0.26)	0.79(0.61, 1.03)		
SSLP	0.13(0.86)	1.14(0.48, 2.71)		
STRAH	-0.58(1.95)	0.56(0.08, 3.94)		
ELEV	-0.04(0.04)	0.97(0.93, 1.00)		
SM	-1.76(3.11)	0.17(0.008, 3.86)		
AREA	2.90(3.05)	18.23(0.86, 384.96)		

Note: Parameter estimates (β±95%CI), odds ratios (e^{β} with 95% CIs), and area under the Receiver Operating Characteristic curves (*c*). *P*-values were obtained from an unweighted sum-of-squares, goodness-of-fit statistic (Hosmer et al. 1997) – the larger the p-value, the better the model fits the data. In addition, all statistics from invasion analysis one are average (bootstrapped) estimates, while statistics from invasion analysis two are point estimates.

Table 2.5. The observed and predicted frequencies of piscivore invasion, as predicted by model 4 (invasion analysis one) and model 7 (invasion analysis two), the logistic regression models with the highest support based on model selection using AICc.

		Predicted		
Model	Observed	0	1	Total
Invasion analysis 1				
4	0	15	1	16
	1	5	8	13
	Total	20	9	
Invasion analysis 2				
7	0	22	3	25
	1	3	14	17
	Total	25	17	

Note: The cutoff value was set as the point at which specificity equals sensitivity, and was calculated as 0.307 for invasion analysis one (model 4) and 0.495 for invasion analysis two (model7).

Table 2.6. Summary of probability of piscivore invasion (P) per lake as calculated by model4 (invasion analysis one), and 7 (invasion analysis two) the logistic regression models with the highest support based on model selection using AICc.

Lake	P(invasion|model4)	P(invasion|model7)
Ben	0.29	0.12
Black	0.02	0.001
Bourgeois	0.05	0.03
Brown	0.28	0.99
Canard		0.06
Carman	0.27	0.99
Charette	0.02	0.04
Clair	0.14	0.57
Edouard	0.09	0.97
Epinettes		0.001
Fairburn		0.50
Foin		0.07
Fortune	0.09	0.003
Hawley	0.28	0.13
Jumeaux		0.004
Kelly	0.38	0.60
Kidder	0.21	0.06
Kingsbury		0.24
Kingsmere	0.18	0.07
La Peche	0.99	1.00
LeBlanc	0.03	0.13
Loutre	0.21	0.78
Lusk	0.44	0.42
McLean		0
Meech	0.74	0.99
Meunier		0.04
Monette		0.05
Mousseau	0.91	1.00
Mudpout		0.78
Mulvihill	0.01	0.007
Petit Renaud	0.01	0.04
Philippe	0.83	0.99
Pink	0.26	0.52
Racine		0.19
Ramsay	0.57	0.19
Renaud	0.41	0.44
Richard	0.30	0.60
Sandy	0.02	0.75
Sources		0.75
Taylor	0.22	0.86
Trudel		0.89
Vase	0.04	0.12

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General Conclusion

Managing for Piscivores in Small Lake Ecosystems

Given that protected areas have been unable to decrease the anthropogenic impact of introduced fish on freshwater biodiversity (Chapleau et al. 1997; Knapp & Matthews 2000; Parker et al. 2001; Pilliod& Peterson 2001), devising a proper management strategy to reduce the impacts of invasive top predators is crucial to the long-term conservation of native fish biodiversity and Gatineau Park lake ecosystems.

A first step towards devising such a management strategy was the release of a Gatineau Park ecosystem conservation plan (Del Degan, Massé et Associés Inc. 2008). Aside from some very brief recommendations, this plan was not specifically designed to target aquatic environments, but rather to establish priorities and objectives for all park ecosystems. Possibly as a result of this, the ecosystem conservation plan ignored a number of important issues relating to aquatic environments (i.e., fish biodiversity losses caused by piscivore introduction). Aside from this negative, Del Degan, Massé et Associés Inc. (2008) did outline eight general priorities for park ecosystems:

(1) Reduce the impact of anthropogenic pressures on ecosystems;

(2) Maintain or restore the natural processes and balances needed for ecosystems to function properly;

(3) Ensure the viability of indigenous animal and plant species diversity;

(4) Maintain or restore biodiversity;

(5) Increase habitat availability, quality and connectivity;

(6) Conserve or restore the park's valued ecosystems

(7) Ensure that visitor services and activities are respectful of ecosystem support capacity;

(8) Raise public awareness about ecosystem-related issues and management practices.

Almost all of these priorities are relevant to the plight of small lake ecosystems in Gatineau Park. As my work has demonstrated, smallmouth bass and a number of other introduced invasive piscivore species (anthropogenic stressors) have been purposefully introduced and have spread to numerous park lakes, possibly: disrupting small lake ecosystem function; limiting the viability of indigenous fish species and as a result reducing fish biodiversity; and impacting some of the parks valued lake ecosystems. To mitigate these impacts, management actions to rectify these impacts should include:

- exploring an introduced piscivore eradication program;
- promoting and increasing recreational fishing pressure in the park to mitigate introduced piscivore (all popular sport fish) impacts;
- limiting the spread of invasive piscivores;
- limiting anthropogenic access to small lakes;
- education - raising public awareness about aquatic ecosystems and the perils of native species introductions; posting signage at lake recreational access points and/or sensitive lakes prohibiting illegal introductions;
- creating an aquatic biodiversity and/or invasive species information system, tracking the location and potential spread of aquatic species and/or introduced pests;
- drafting an invasive species management plan

Here, I will discuss the preceding list of proposed piscivore management actions; make recommendations pertaining to these actions based on work presented in Chapters 1 and 2; and finally, make suggestions on how to best implement these actions.

Piscivore Eradication

Implementing an eradication program is potentially the only course of action that can restore piscivore occupied lakes back to their original state prior to piscivore invasion. Eradication refers to the removal of every individual of an invasive species or the reduction of their population density below sustainable levels (Myers et al. 2000). Public perception coupled with a lack of political will, however, may not allow for the culling of thousands of sport fish, and further, eradication programs are not always successful. As a result, it is important that any type of eradication program is well planned, and specific objectives outlined (Mueller 2005). Specific objectives must address difficult questions such as: What level of treatment (piscivore removal) is necessary for success? and alternatively, how does one define success – an increase in native or small fish species - abundance? - biodiversity?

In addition to clear objectives, according to Myers et al. (2000), for an eradication program to be successful six essential requirements are needed:

(1) Sufficient resources;

(2) Lines of authority must be clear and must allow an individual or agency to take all necessary actions;

(3) Biology of organism must make it susceptible to removal (i.e., dispersal ability, reproductive biology, life history…);

(4) Reinvasion must be prevented;

(5) Pest must be detectable at low densities;

(6) Must watch for ecosystem effects.

Further, before eradication can begin, the feasibility of such a program must be considered. An initial decision making model outlined by Beamesderfer (2000) asks three questions that might help determine whether or not an eradication program is feasible for any individual lake; these include:

(1) Is predation significant?

(2) Is predator removal affectable? And

(3) Would the public accept it?

Question number one is relatively straight forward; all that is required is a definition of "significant predation". Defining this term might include any number of predator population metrics (i.e., density, relative abundance, etc.), or an estimate of the magnitude of impact on an aquatic community (i.e., number of extirpated species, predation risk, etc.). In chapter one, I demonstrated a set of piscivore occupied lakes with significant reductions in minnow and small fish diversity over time. These results could be used to answer question one and further identify lakes to focus eradication and restoration efforts.

Important factors to consider when answering question two (will predator removal be affectable?) include such issues as: How many resources are available? How large and isolated is the lake? – larger/less isolated lakes are more difficult to restore than smaller/more isolated lakes (Pacey and Marsh 1998); How many predators must be removed to have a positive effect (if any) on fish biodiversity? Is the biology of the target organism conducive to eradication? Is reinvasion preventable? And finally, will native fish species recolonize the lake in the future?

Recent work in a small Adirondack lake (~271 ha) revealed how invasive smallmouth bass can become, and also provided evidence that extensive mechanical removal (*via* electrofishing, netting, and angling) of an introduced piscivore can benefit small lake fish populations and ecosystem processes (Weidel et al. 2007; Lepak et al.

2006). These promising results, however, required the removal of approximately 47,682 individuals (>90% of the population) over a five year period, and undoubtedly extensive resources (Weidel et al. 2007). Other studies have demonstrated that for small isolated habitats or headwaters where physical barriers can be installed required an 80% reduction in the target population to be successful (Pacey and Marsh 1998 *in* Mueller 2005), while other studies suggest even more removal effort is required (i.e., Lydeard and Belk 1993; Dudley and Matter 2000).

The work in the Adirondacks, which has similar fish communities to Gatineau Park lakes, demonstrates that a removal program can potentially work in Gatineau Park. First, smallmouth bass was targeted in the Adirondacks (Weidel et al. 2007; Lepak et al. 2006), while studies in other geographic locales have also targeted northern pike (Jolley et al. 2008). Targeting smallmouth bass as opposed to northern pike or yellow perch makes more sense in Gatineau Park because smallmouth bass has not yet spread to new lakes since their introduction in the 1930's, and smallmouth bass eradication programs have been successful elsewhere (i.e., in an Adirondack Lake). In comparison, northern pike has proliferated across the park over time, meaning it is more likely they can re-establish in the future. For these reasons, a single lake experimental smallmouth bass removal program needs to be seriously considered, while, the spread of northern pike and all other piscivores to new lakes must be mitigated.

In deciding on a lake to pursue a piscivore removal program, I have come up with a series of filters to further help with the selection process. Most of these filters are from studies which suggest certain lake factors are indicative of eradication success (i.e., Pacey and Marsh 1998 *in* Mueller 2005) and have been modified to suit Gatineau lakes, these include:

Observable decline in small/minnow/total fish species richness?

One piscivore species?

High piscivore density?

Small lake?

Isolated lake?

High small/minnow/total fish diversity prior to piscivore introduction?

Based on these criteria, Leblanc, Ramsay and Sandy lakes are the most suitable candidates for an experimental eradication program.

Once question one and two have been answered question number three (would the public accept it?) can then be considered. The answer to this question is ultimately linked to how well the individual or agency responsible for the eradication program communicates and works with local stakeholders. Given that sport fishing is overseen by the Government of Québec in the park, yet the NCC oversees the conservation and management of park ecosystems makes for a difficult situation.

Public support is important to the success or failure of an eradication program because without it pursuing such a management initiative becomes difficult. If a lake is a popular recreational fishing destination, or used for other recreational purposes (i.e., campground, boating, swimming, etc.) then conducting a removal program might be difficult. Alternatively, if a lake is relatively isolated from human use and infrequently visited then it might be a more suitable candidate. An excellent way to ensure success is to involve local users right from the start of the decision making process, ensure that both the

Government of Québec and the NCC share the same objectives for eradication and restoration, and finally explicitly detail the purpose and reasoning for creating such a program.

One way to help gain public support is to promote recreational fishing, possibly in addition to a mechanical removal program. By promoting recreational fishing in the park, and in turn, increasing fishing pressure on piscivore populations, it may be possible to at the very least lower piscivore populations to levels where extirpated species are able to recolonize. Further, when the direct user of the targeted fish populations is included in the eradication program, success becomes more realistic.

Piscivore Invasion Mitigation

If the direct manipulation of invasive populations is not possible, then identifying lakes at risk of invasion (as was done in Chapter 2) becomes more pressing. Even if an eradication program is undertaken, identifying lakes at significant risk of invasion and implementing a program to mitigate the spread of these invasive species is still prudent. This might include quantifying ecological and anthropogenic interactions between non-native's and their ecosystems, and setting levels of risk for non-invaded lakes (Vander Zanden et al., 2004). This type of analysis is exactly what I attempted to accomplish in Chapter 2. The next step after identifying non-invaded lakes at high risk is to implement policies and programs designed to slow or eliminate the spread of piscivores into these susceptible environments (i.e., eradication).

As discussed in Chapter two, there are two routes by which an invasive species can invade a new lake: roads/recreational trails and/or the stream-network. As a result, any management action(s) aimed at slowing spread must concentrate on these two potential pathways. It is important to note that many studies have identified propagule pressure (a measure of the number of individuals released into a lake to which they are not native (Carlton 1996) as the best predictor of invasion success (Lockwood et al. 2005). This lends further support to eradication as a primary management option, maybe not to extinction, but to the point where emigration from one lake to another becomes less probable. Reducing piscivore populations in strategic lakes (i.e., lakes connected to lakes at high risk of invasion) coupled with other management strategies that are intended to slow or stop the spread of invasive piscivores would be beneficial.

For anthropogenic access there are a number of policies and actions that must be taken to limit potential illegal/accidental introductions. First, a park wide no stocking/introduction and no live bait policy must be established. In order for this to be effective, informing the general public and especially recreational fishers is recommended through educational campaigns, leaflets/pamphlets distributed at the park office or with provincial fishing licenses, posters, signage at lakes, etc. A second approach is to further limit anthropogenic access to park lakes. For important tourist lakes (i.e., Meech, La Peche, Philippe) this will not be feasible, but a focused educational campaign at these busy lakes in addition to further restricting access to smaller more remote lakes that have not already been invaded might be beneficial. For those remote lakes that have already been invaded by a piscivore species, eradication and potentially increasing both access and bag limits for recreational fishing might be considered to reduce piscivore populations. Currently more remote lakes (i.e., Edouard, Sandy, Carman, Brown) are seemingly rarely visited by recreational fishers, meaning piscivore populations are allowed to proliferate unfettered, while small fish species are extirpated.

Limiting spread via the stream network entails creating a physical barrier that dissuades piscivore movement. Man-made physical barriers such as weirs and low head dams generally do not agree with the parks promotion of ecological integrity. Alternatively, more natural physical barriers could be constructed such as waterfalls, cascades, bedrock chutes and highly sloped stretches of stream as they have been found to limit pike dispersal, for example (Spens et al. 2007). What is important is that current barriers that act or may potentially act as barriers to piscivore dispersal are left in tact. Removing these barriers for whatever reason is irresponsible, and will further lead to the spread of invasive predators throughout the park, and the continued decline of small lake fish biodiversity.

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Appendices

Appendix 1. Fish species detected in 25 Gatineau Park lakes in the summers of 2006 and 2007.

Lake	S.f.	O.m.	E.l.	U.l.	H.h.	N.cr.	L.c.	N.hl	P.e.	P.n.	Pi.n	Pi.p.	S.a.	M.m.	C.c.	A.n.	F.d.	L.g.	M.d.	M.s.	E.e.	P.f.	C.i.	G.a.
Ben	0	0	0	1	0	1	1	1	0	1	1	1	0	0	1	1	0	1	0	0	0	0	1	0
Black	0	0	0	0	0	1	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Bourgeois	0	0	0	0	0	1	0	0	1	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0
Brown	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	1	0	0	1	0	0
Carman	0	0	1	0	0	0	0	0	0	0	1	0	0	0	1	1	0	1	1	0	0	1	0	0
Clair	1	0	0	0	0	0	0	0	1	0	1	1	0	0	1	0	0	0	0	0	0	0	0	0
Edouard	0	0	0	0	0	1	0	0	0	0	1	0	0	0	1	1	0	1	1	0	0	1	0	0
Fortune	0	0	0	0	0	0	0	0	1	1	0	1	0	0	1	0	0	0	0	0	0	0	0	0
Hawley	0	0	0	1	0	1	1	1	1	1	1	1	0	1	1	1	0	1	0	0	1	0	0	0
Kelly	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	1	0	0	0	1	0	0
Kidder	0	0	0	0	1	1	1	1	1	1	0	1	1	0	1	1	0	1	0	0	0	0	0	0
Kingsmere	1	0	0	0	0	0	1	1	0	0	0	1	1	0	1	0	0	1	0	0	0	0	0	0
LeBlanc	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	1	1	0	0	0	0	0
Loutre	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	0	0	1	0	0
Lusk	0	0	0	0	0	1	1	0	1	1	0	1	0	1	0	1	0	0	0	0	0	1	0	0
Meech	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	1	1	1	0	1	0	0
Mulvihill	0	0	0	0	0	1	0	1	0	0	0	1	0	0	1	0	0	1	0	0	0	0	0	0
Petit Renaud	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	1	0	1	0	0	0	0	0	0
Pink	0	0	0	0	0	0	0	0	1	0	0	1	0	0	1	0	0	1	0	0	0	0	0	1
Ramsay	0	0	1	1	1	1	1	1	1	1	1	1	1	0	1	1	0	1	0	0	1	0	0	0
Renaud	0	0	0	1	0	1	1	1	0	0	0	0	0	0	1	1	0	1	0	0	0	1	0	0
Richard	0	0	1	0	0	0	1	1	1	1	0	1	1	0	1	1	0	0	0	0	1	0	0	0
Sandy	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0
Taylor	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	1	1	1	0	1	0	0
Vase	0	0	0	1	0	0	0	0	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0

Appendix 2. Averaged water chemistry covariates collected from the surface of 25 Gatineau Park lakes in the summers of 2006 and 2007.

Lake	pH	Conductivity	TDS	DO	Temp	Secchi
Ben	4.9	30.7	17.0	6.1	15.6	2.2
Black	6.7	60.0	33.0	7.4	23.3	1.0
Bourgeois	7.1	85.0	42.1	7.0	16.4	1.8
Brown	7.8	59.3	29.3	6.1	17.2	3.1
Carman	8.0	42.8	23.6	10.8	15.7	2.7
Clair	7.3	28.5	14.5	2.4	13.0	4.8
Edouard	6.8	16.7	8.0	3.8	23.5	3.3
Fortune	6.1	60.5	34.0	9.4	20.7	2.0
Hawley	6.7	55.8	27.0	7.0	14.7	1.7
Kelly	7.5	101.0	57.0	10.9	21.6	5.7
Kidder	9.8	72.6	38.7	8.0	14.7	5.0
Kingsmere	8.3	132.3	65.3	11.6	19.2	3.5
Leblanc	7.3	35.5	18.5	5.3	15.5	3.6
Loutre	7.8	133.5	66.5	2.8	20.2	2.2
Lusk	6.2	19.7	10.7	6.6	18.4	3.0
Meech	5.8	72.0	31.0	10.4	9.9	4.3
Mulvihill	7.5	134.7	75.3	7.2	21.7	2.4
Petit Renaud	9.8	69.5	38.5	6.4	19.9	1.2
Pink	8.0	222.5	125.0	10.1	19.0	5.4
Ramsay	7.2	40.3	20.3	5.1	10.7	1.9
Renaud	7.0	66.3	36.8	10.4	19.3	2.1
Richard	7.0	71.5	52.0	11.7	15.6	2.6
Sandy	7.2	26.5	13.0	4.3	13.0	2.7
Taylor	8.2	133.3	66.3	8.1	22.0	6.0
Vase	6.1	45.8	25.3	10.8	17.7	2.5

Note: Conductivity was measured in µs, TDS = Total Dissolved Solids measured in mg/L, DO = Dissolved Oxygen measure in mg/L, Temp = Temperature measured in ˚C, and Secchi disc depth, a surrogate for productivity, was measured in m.