

Linking the occurrence of brook trout with isolation and extinction in small Boreal Shield lakes

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SUMMARY

1. We surveyed 62 Canadian Shield lakes (<50 ha) to determine the relationship between factors related to isolation and extinction and the occurrence of brook trout (BT) (*Salvelinus fontinalis*), for which local extinctions have been documented over the last century in half of the lakes.
2. Logistic regression and information–theoretic model selection were used to determine the importance for the occupancy of BT of (i) isolation factors (degree of lake connectivity and the proximity of source populations of BT in neighbouring bodies of water) and (ii) extinction factors (lake morphometry and trophic status, as proxies of the risk of lake anoxia; predation and competition; and flooding caused by beaver (*Castor canadensis*) dams, which could potentially increase the risk of anoxia).
3. Isolation factors were the best predictors of the absence of BT in these lakes. Among extinction factors, only the impact of beaver dams (as measured by an index of increased water level and mortality of shrubs and trees in the littoral zone) improved model fits. Beaver dams were present at the outlets of all study lakes, but extensive mortality of riparian trees and shrubs was more common in lakes where BT populations were extinct.
4. Taken together, these results suggest that recolonization is a major factor determining the occurrence of BT while flooding caused by beaver dams might contribute to BT extinction by increasing the likelihood of winterkill in these small lakes.

Keywords: beaver dam, connectivity, local extinction, recolonization, *Salvelinus fontinalis*

Introduction

Large-scale studies have shown that biogeographic variation and physical/chemical gradients are responsible for many patterns in fish species presence/absence (Johnson *et al.*, 1977; Tonn & Magnuson, 1982; Rahel, 1984; van Zyll de Jong, Cowx & Scruton, 2005). Since the balance between colonization and extinction events is responsible for such patterns, it is important to assess the relative importance of these phenomena in order to understand the dynamic nature of fish

assemblages (Tonn, Vandebos & Pazkowski, 1995; Magnuson *et al.*, 1998). While connectivity among bodies of water is important (Olden, Jackson & Peres-Neto, 2001), it has been suggested that factors related with extinction could be better predictors of fish species richness and community composition than the isolation of lakes (Magnuson *et al.*, 1998). Habitat loss, chemical alteration, pollution, genetic introgression and overexploitation are among the most commonly reported anthropogenic factors causing fish extinction (Miller, Williams & Williams, 1989). Biotic interactions, such as predation by introduced piscivores, are other potential causes of extinction in temperate lakes (Chapleau, Findlay & Szenasy, 1997; Findlay, Bert & Zheng, 2000). Natural catastrophes, such as winter anoxia, have also been reported to explain local

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extinction in fish (Nürnberg, 1995a). This could explain the absence of salmonids or large-bodied predators in lakes, with potential indirect consequences for the more tolerant prey (Tonn & Magnuson, 1982; Nürnberg, 1995a).

Local extinctions of brook trout (BTE) (*Salvelinus fontinalis* Mitchill) have been documented during the last century in La Mauricie National Park of Canada (LMNPC), Québec, Canada, potentially explained by anoxia. Differences in the ratio of lake area (LA) to depth and trophic status might relate to differences in the risk of anoxia, as has been shown in boreal lakes similar to ours (Nürnberg, 1995a). Fish introductions could also have contributed to local BTE through their effect as predators or competitors. Logging, which was a major perturbation in the territory until 1970 (Pelletier, 1996), is another factor that may affect brook trout (BT) in Canadian Shield lakes (Bérubé & Levesque, 1998). Nearly half of the BTE were documented after the creation of the park, however, an event that coincided with the reduction of fish introductions and the end of logging. This also coincided with the end of beaver (*Castor canadensis* Kuhl) trapping (Plante, 1996a,b), which was followed by the rapid spread of beavers through the park (Masse & Bordeleau, 1988; Masson *et al.*, 2001).

Despite an increasing literature on the effects of beavers on ecosystem processes and fish communities in streams (Naiman *et al.*, 1994; Gurnell, 1998; Snodgrass & Meffe, 1998; Collen & Gibson, 2001; Rosell *et al.*, 2005), little is known of their effects on lake ecosystems (France, 1997). By increasing water level, beavers increase both microbial respiration in the flooded soils (Sonster-Alpin & Klotz, 1995) and the inputs to aquatic systems of allochthonous organic matter (Pollock *et al.*, 1995). These effects might eventually increase the risk of anoxia, a phenomenon commonly observed in beaver ponds (Fox & Keast, 1990; Collen & Gibson, 2001). Since the BT is sensitive to habitat alterations and low oxygen concentration (e.g. Baldigo & Lawrence, 2001), we expected to find a relationship between the impact of beaver dams and the local BTE populations.

Most lakes in the park are well connected through the hydrographic network, although the degree of connectivity probably varies among them. If isolation is an important factor in these systems, therefore, variables, such as drainage density (DD), the total length of streams in the catchment and the presence of

BT in neighbouring waterbodies (lakes or streams) should be good predictors of BT occurrence. Beaver dams at lake outlets also constitute a semi-permeable barrier to fish movements (Schlosser, 1995; Ray, Ray & Rebertus, 2004). Since they were present in all the study lakes (but with different effects on littoral vegetation), however, we cannot analyse their role on connectivity. We thus assumed that their effect on fish recolonization is similar for all the study lakes.

The objective of the present study was to assess the relative importance of factors associated with isolation and extinction in determining lake occupancy by BT. We analysed a set of 62 lakes, in half of which local extinction has been documented. We tested the hypotheses that BT occurrence is related with (i) isolation factors, such as the degree of lake connectivity and the proximity of source populations (SRC) and (ii) extinction factors, such as lake morphometry and trophic status (as proxies of the risk of anoxia), biotic interactions (i.e. predation and competition), and flooding caused by beaver dams (a factor potentially increasing the risk of anoxia). We used logistic regression and information-theoretic (I-T) model selection (Burnham & Anderson, 2002) to rank the importance of these factors in explaining BTE. Given that the creation of the La Mauricie National Park of Canada in 1970 changed the relative roles of anthropogenic versus natural factors affecting lakes, we analysed the pre- and post-park periods separately to identify the factors responsible for BTE.

Methods

Study area

La Mauricie National Park of Canada is located in south-central Québec (46°46'N, 73°00'W; Fig. 1). It covers an area of 536.5 km², includes 139 lakes and is part of the St-Maurice catchment. The lakes are generally shallow (4.6 ± 3.5 m; mean ± 1 SD) and small (28.0 ± 76.1 ha; 88.9% are <50 ha), with an average altitude of 289 ± 60 m. Here, we analysed a set of 62 lakes <50 ha, for which we had historical data about the presence of BT (Table 1; Fig. 1).

Before the creation of the park in 1970, the study area was heavily exploited by foresters (Pelletier, 1996). Beavers were present, but their numbers were controlled by trapping (Masse & Bordeleau, 1988; Plante, 1996a). These human activities ceased with the

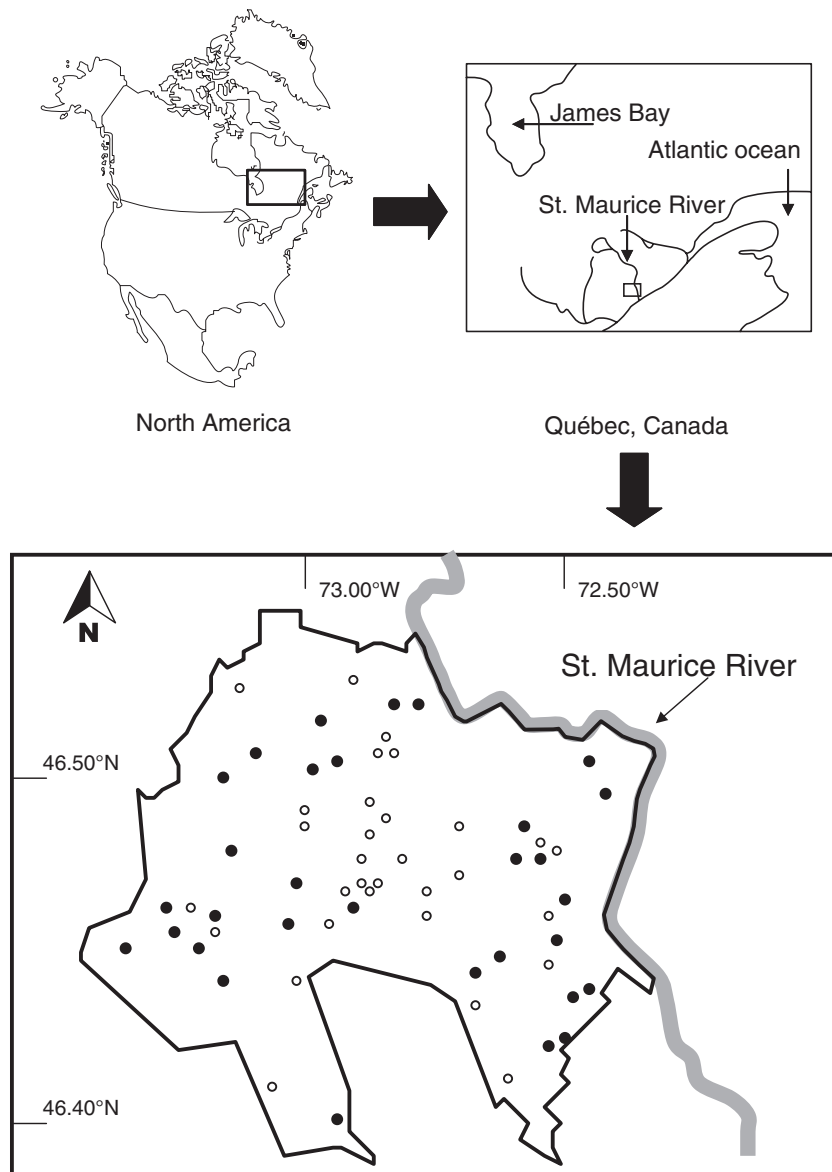


Fig. 1 Location of the 62 study lakes. The close-up shows the locations of the sampling sites within La Mauricie National Park of Canada. Open and solid circles indicate lakes with current or extinct populations of brook trout, respectively.

creation of the park. Therefore, the direct impacts of forestry were reduced while the occurrence of beaver damming on both lakes and streams rose rapidly (Pelletier, 1996; Plante, 1996a). By 1985, beaver had colonized most of the lakes (Masse & Bordeleau, 1988); by 1995, almost all of the lake outlets had beaver dams (Masson *et al.*, 2001). Such a rapid increase in beaver population density could be explained by reduced mortality due to trapping and predation (Villemure, 2003).

Most BT populations were exploited before the creation of the park. In contrast, angling was subsequently confined to the most productive and accessible lakes. However, it is not possible to compare current and historical levels of exploitation in these lakes. While angling was conducted in most of our study lakes before the creation of the park, only 18 have been fished since its creation. None of the lakes that experienced BTE has been fished since the creation of the national park.

Table 1 Main characteristics of the study lakes

	Brook trout present (<i>n</i> = 31)		Brook trout extinct (<i>n</i> = 31)		<i>P</i> -value	Transformation
	Mean ± SD	Range (min.–max.)	Mean ± SD	Range (min.–max.)		
Lake area (ha)	13.2 ± 11.4	2.6–46.8	12.7 ± 11.3	1.0–40.3	0.5461	log
Maximum depth (m)	13.2 ± 8.4	2.1–39.6	12.7 ± 8.0	3.0–30.4	0.8014	log
Mean depth (m)	4.6 ± 3.7	0.8–19.4	4.1 ± 2.5	0.7–9.2	0.8035	log
Altitude (m)	289.3 ± 48.6	199.0–379.0	282.7 ± 67.7	176.0–404.0	0.6604	–
Catchment area (km ²)	2.6 ± 1.9	0.5–8.3	1.7 ± 1.4	0.2–7.3	0.0088	log
TP (µg L ⁻¹)	12.7 ± 14.5	4.4–88.8	12.1 ± 4.7	6.4–5.2	0.1337	K–W
TN (µg L ⁻¹)	308.7 ± 153.6	191.6–901.7	294.0 ± 77.3	151.3–518.7	0.4947	K–W
DOC (mg L ⁻¹)	5.5 ± 1.8	2.8–9.4	5.5 ± 2.2	2.4–0.4	0.8451	log
pH	5.9 ± 0.3	5.4–6.5	6.1 ± 0.4	5.1–6.8	0.0314	–
Conductivity (µS cm ⁻¹)	20.8 ± 6.5	14.1–50.3	23.7 ± 13.4	15.4–83.3	0.4555	K–W
SL (km)	14.1 ± 20.9	<0.1–80.7	3.1 ± 4.5	0.0–22.7	0.0003*	K–W
DD (km ⁻¹)	1.3 ± 0.6	<0.1–2.7	1.0 ± 0.5	0.0–2.2	0.0192	–
BIF (0–3)	2.3 ± 0.5	2–3	2.6 ± 0.5	2–3	0.0107	χ ²
Number of fish species [†]	2.1 ± 2.0	0–7	1.3 ± 1.7	0–6	0.0281	K–W

TP, total phosphorus; TN, total nitrogen; DOC, dissolved organic carbon; SL, total length of streams in the catchments located upstream of the lake; DD, drainage density; BIF, beaver impact factor (see text).

Neighbouring brook trout populations (SRC) were found in lakes or streams adjacent to 30 lakes with brook trout and 22 lakes without brook trout (see text). Transformation, data transformation; K–W, the Kruskal–Wallis test was applied; χ², a χ² test was applied given that BIF only had two values (2 and 3); *P*-values for the ANOVA are also shown.

*Significant after the sequential Bonferroni correction.

[†]Brook trout excluded.

Background on the fish communities

After the last Wisconsin glaciation, most lakes in the park were probably colonized by BT while only a few were colonized by arctic charr *Salvelinus alpinus* (L.), ninespine stickleback *Pungitius pungitius* (L.) and spoonhead sculpin *Cottus ricei* (Nelson) (based on Lacasse & Magnan, 1994; Plante, 1996b). Historical documents and fishing club reports allowed us to confirm that nearly all park lakes supported BT at the end of the 19th century (Plante, 1996b). Fishing clubs that exploited lakes in this territory before the creation of the park in 1970 were responsible for several fish introductions (Magnan, 1988; Lacasse & Magnan, 1994; Plante, 1996b). Fish introductions thus occurred mostly before the creation of the park, with 19 new species recorded between 1850 and 1977 and only one during the subsequent two decades (Plante, 1996b). This represents a large increase in fish species richness considering that only four species were probably to have been present in the park's inland bodies of water before 1850 (Plante, 1996b). Of our study lakes, 79% contain at least one introduced species, whereas only two species can be considered as having naturally colonized the lakes (i.e. BT and arctic charr; Table 2).

A combination of historical data, fishing club reports, and interviews with club members or people having worked in the clubs until the end of the 1960s was used to validate the status of BT populations when the park was created (Plante, 1996b). Because information on the impacts of beaver dams before 1970 is not available and information on BTE for that period is also less reliable, we ran separate statistical analyses for the pre- and post-park periods. Data on fish communities were not available for all the lakes before the creation of the park (Plante, 1996b). Therefore, fish community data for the period following the creation of the park were used for both pre- and post-park data sets. These data were obtained by pooling information from different surveys made between 1971 and 1977 and between 1993 and 1995 (Masson *et al.*, 2001). The first surveys (1971–77) were conducted to establish the occurrence of species important for sport fishing. All lakes were sampled with gillnets and most with minnow traps. The second survey (1993–95) assessed the presence/absence of fish in lakes that had been less intensively sampled in 1971–77. Fish were captured between July and September with (i) multifilament gillnets (1.8 m deep × 38 m long with stretched mesh of 25, 32, 38,

	Brook trout*	
	Present (n = 31)	Extinct (n = 31)
Predators		
Lake trout [<i>Salvelinus namaycush</i> (Walbaum)]	1	0
Rock bass [<i>Ambloplites rupestris</i> (Rafinesque)]	0	2
Smallmouth bass [<i>Micropterus dolomieu</i> Lacepède]	2	1
Competitors		
Arctic charr [<i>Salvelinus alpinus</i> (L.)]*	0	1
Blacknose shiner (<i>Notropis heterolepis</i> Eigenmann & Eigenmann)	0	2
Brook stickleback [<i>Culaea inconstans</i> (Kirtland)]	5	3
Brown bullhead [<i>Ameiurus nebulosus</i> (Lesueur)]	3	0
Common shiner [<i>Luxilus cornutus</i> (Mitchill)]	6	1
Creek chub [<i>Semotilus atromaculatus</i> (Mitchill)]	6	7
Fathead minnow [<i>Pimephales promelas</i> Rafinesque]	3	1
Golden shiner [<i>Notemigonus crysoleucas</i> (Mitchill)]	0	1
Longnose dace [<i>Rhinichthys cataractae</i> (Valenciennes)]	1	1
Northern redbelly dace [<i>Phoxinus eos</i> (Cope)]	8	2
Pearl dace [<i>Semotilus margarita</i> (Cope)]	26	15
Rainbow smelt [<i>Osmerus mordax mordax</i> (Mitchill)]	2	0
Yellow perch [<i>Perca flavescens</i> (Mitchill)]	1	3
White sucker [<i>Catostomus commersonii</i> (Lacepède)]	1	2

*Present in the study lakes before 1850 (Plante, 1996b). The other species were considered as introduced (see text).

51, 64 and 76 mm and 1.8 m deep × 7.6 m long with stretched mesh panels of 25 and 12.5 mm; Plante, 1996b) and (ii) commercial baited minnow traps. When possible, seine nets, trap nets and electrofishing were also used. Angling and visual observations yielded additional information about the presence of species.

The presence of BT was reported in all 62 study lakes until the 1930s (Plante, 1996b). The comparison of experimental studies with historical data (documents available at the national park; Plante, 1996b) allowed us to classify the lakes into two categories: (i) lakes supporting BT populations ($n = 31$) and (ii) lakes formerly supporting BT ($n = 31$; i.e. populations reported in historical records but absent during experimental fishing). BTE were confirmed for 16 of the lakes before the creation of LMNPC (i.e. between the 1930s and the 1970s; Plante, 1996b), which corresponds to an extinction rate of four extinctions per decade. The other 15 extinctions have occurred since the creation of the park (i.e. 1970–95; Plante, 1996b), increasing the extinction rate to six extinctions per decade. Given that the pre-park period considered here spans 40 years (1930–70) and the post-park 25 years (1970–95), this number of extinctions corre-

Table 2 Fish assemblages in the study lakes in relation with potential predators and competitors

sponds to a 50% increase in the extinction rate after the creation of the park. This is a conservative estimation of the change, since extinction rates were close to zero between the end of the 19th century and 1930 (Plante, 1996b). Lakes without documented historical information on BT, or those reported to have been stocked with BT, were not included in the analysis. BT was found in sympatry with other fish species in 29 of the 31 BT lakes whereas 11 of the 31 BTE lakes were completely fishless.

Among the other 17 fish species found in the study lakes, three were considered as potential predators while 14 were considered as potential competitors of BT (Table 2). Lake trout, rock bass and smallmouth bass are recognized as piscivores (see Scott & Crossman, 1973) and thus were considered as potential predators of BT. Species such as arctic charr, yellow perch, creek chub and white sucker have been shown to compete with and depress BT populations (Fraser, 1978; Magnan, 1988; Tremblay & Magnan, 1991; Lacasse & Magnan, 1992; Magnan, Proulx & Plante, 2005; O'Connell, Dempson & Power, 2005). The remaining species were also considered as potential competitors because they are probably to share prey (benthic organisms and zooplankton) with BT (Scott &

Crossman, 1973). Statistical analyses were run both with and without these latter species included in the 'competitor' category (see Statistical analyses, below). Since the results of the analyses were similar, we only report the results related to the former analysis (i.e. with all non-piscivores species considered as competitors). Because detailed historical information about introduced species is not available for all the lakes, it was not possible to model their extinction patterns.

Physicochemical parameters

At the end of May 1997, integrated water samples were taken in the top 5 m of the water column in the deepest part of each lake. For lakes shallower than 5 m, the integrated sample excluded the deepest 1 m layer. Samples were filtered within 12 h and stored at 4 °C until analysed (within 72 h). Samples for dissolved organic carbon (DOC) determination were filtered on washed Gelman Supor 0.45- μ m membranes (Pall Corporation, East Hills, NY, U.S.A.) and kept at 4 °C. DOC was measured (Shimadzu TOC-5000, GMI Inc., Ramsey, MN, U.S.A.) within 72 h by infrared gas analysis after sample acidification and He sparging followed by Pt-catalysed oxidation at 700 °C (Carignan, D'Arcy & Lamontagne, 2000). Total phosphorus (TP) was measured using the molybdenum blue method (Stainton, Capel & Armstrong, 1977) after autoclaving 50-mL samples with 0.5 g of potassium persulphate for 1 h at 120 °C. Total nitrogen (TN) was measured as NO₃ – after alkaline persulphate digestion of 50-mL samples at 120 °C (D'Elia, Steudler & Corwin, 1977). Nitrate was measured on filtered samples by automated flow injection analysis (Lachat methods 10-107-04-1-B and 10-107-06-1-F).

Lake and catchment morphometric data (Table 1) were obtained from surveys made during the 1970s (Environnement Canada-Parcs, 1992).

Beaver impact

To investigate the potential impact of beaver on BT habitat, we defined a 'beaver impact factor' (BIF) based on the maximum effects of beaver damming on the lakes observed during an independent survey conducted between 1985 and 1995 (Masse & Bordeleau, 1988; Masson *et al.*, 2001). The presence and the impact of beaver dams were assessed by direct observations of the whole lake perimeter. Most of the

lakes were visited with a small boat, while less accessible ones were inspected on foot. In all cases, these observations were confirmed by one or more observation sessions by plane or helicopter. The BIF ranged from 0 to 3, where 0 = no beaver dam at the lake outlet; 1 = beaver dam present but no effects on the water level; 2 = beaver dam present and increased water level (in this case, dead trees were only rarely observed on the lake perimeter, mostly close to the lake outlet); 3 = beaver dam present and increased water level with extensive mortality of shrubs and trees at least within the first few metres of the whole lake perimeter. In this latter case, a continuous strip of dead and fallen trees (trunk diameters >20 cm) was observed. Moreover, signs of shore erosion occurred over the whole perimeter of these lakes. Given that the extent of flooding was not quantified in this study, we used the above-mentioned patterns in littoral tree mortality as proxies for the impact of beaver on forest soil and lake water quality. A sharp, albeit temporary, increase in water colour was observed in many lakes with BIF = 3 following the increased water level (M. Plante, pers. obs.). BIF is probably partly related with features of the littoral zone (e.g. slope) or the outlet (e.g. presence of boulders to stabilize the dam) that have not varied much over the last century. Therefore, BIF (which was measured only in the post-1970 period) might be regarded as a proxy of potential beaver dam impacts in the pre-1970 period. However, we expect that this variable is a poor predictor of extinctions for this period because of the supposed low densities of beaver before the creation of the park. Only lakes >50 ha had BIF \leq 1.

Statistical analyses

Differences between BT and BTE lakes were first examined by a univariate approach on the whole data set. We used ANOVA to compare the two groups of lakes. When necessary, data were log-transformed to normalize the residuals. If this procedure was unsuccessful, the nonparametric Kruskal-Wallis test was applied. We applied a sequential Bonferroni correction to control for the table-wise inflation of type I error (see text and table captions). However, we carefully considered *P*-values falling between the standard (0.05) and the corrected alpha level because it is recognized that sequential Bonferroni correction is too conservative (Moran, 2003).

We tested a set of 11 candidate logistic regression models (see below) based on different *a priori* hypotheses to identify factors predicting the patterns of presence/absence and thus of local BTE. In accordance with the I–T approach, we assumed that all candidate models had equal prior probabilities (Burnham & Anderson, 2002). The Akaike Information Criterion corrected for small sample sizes (AICc) was used to compare and rank the models (Burnham & Anderson, 2002). In some studies using small sample sizes, AICc has been shown to be outperformed by its uncorrected version (i.e. AIC) (Richards, 2005). We thus ran all analyses on both AICc and AIC. Since the main results did not differ qualitatively between the two approaches, we show only results based on AICc.

Akaike Information Criterion corrected is based on the principle of parsimony, helping to identify the model that accounts for the most variation with the fewest variables. A model selection method like this requires the calculation of the AICc differences (Δ_i) for all candidate models in the set as:

$$\Delta_i = \text{AICc}_i - \min \text{AICc}$$

where $\min \text{AICc}$ is the smallest AICc value within a given set of models (Burnham & Anderson, 2002). The larger the Δ_i , the less plausible the model: models with $\Delta_i < 2$ have substantial support, those where $4 < \Delta_i < 7$ have considerably less support, while those with $\Delta_i > 10$ have essentially no support (Burnham & Anderson, 2002). Similarly, the inclusion of an additional variable in a given model is recognized as improving its plausibility only when associated with a reduction of more than two units of the AICc (Burnham & Anderson, 2002).

The plausibility of each model as the best model was estimated by calculating the Akaike weights (w_i) (*sensu* Burnham & Anderson, 2002). The Akaike weights allow one to obtain the relative plausibility of each fitted model and can be interpreted as the weight of evidence in favour of a particular model being the actual best model for the situation at hand (i.e. given the data available and the *a priori* set of models defined) (Burnham & Anderson, 2002).

Finally, by analogy with the concept of confidence intervals (CI) used in parameter estimation, Burnham & Anderson (2002) suggested that a ‘confidence set of models’ can be determined among the available set of *a priori* defined models. This means that a subset of

plausible models, and not only the best model, could be retained for inference. A practical way to assess which models should be included in the confidence set is to sum the Akaike weights from largest to smallest until the sum is ≥ 0.95 (Burnham & Anderson, 2002). This procedure allows one to acknowledge model uncertainty and focus on more than one plausible hypothesis to explain a given phenomenon.

Within a given model, the strength of the relationship between each independent variable and the dependent variable was assessed based on the odds ratios. Positive and negative relationships are indicated by odds ratios, >1 or <1 respectively. When the unit value is not included within the odds ratios CI for the parameter of a given variable, the relationship is considered as significant (Quinn & Keough, 2002).

Akaike weights are not only useful for ranking models and obtaining their relative plausibility, but can also be used to rank the relative importance of a given predictor variable in the set of models. Such information is obtained by summing the Akaike weights over the subset of models which include that particular variable. To get unbiased results, it is recommended that each variable appears in a similar number of models in the *a priori* set of models.

Bootstrapping was used to confirm the results of the above analyses. The entire process described above was conducted 10 000 times on the same numbers of samplings with replacement. Bootstrapped estimates the 95% CI associated with Δ_i and w_i (Δ_i^* and w_i^*) were estimated by assessing the 2.5% and 97.5% quantiles for the distribution of these two values. We also estimated selection frequencies (π_i^*) for each model, i.e. the frequency with which a given model was selected as the ‘best’ model in the data set, which could be interpreted as a bootstrap estimate of w_i (Burnham & Anderson, 2002). Therefore, π_i^* values were used to obtain bootstrap estimates of the 95% confidence set of models and w_i for single variables.

As required by the I–T approach, we verified that the full model (i.e. model ABCD; see *A priori* hypotheses and related models), which we included in the model set for comparison, fitted the data correctly (Burnham & Anderson, 2002). However, since model ABCD showed a quasi-complete separation of the data in most of the bootstrapped samples, it was not possible to get a correct estimate of the maximum

likelihood for the logistic regression model. Therefore, it was not possible to calculate I–T statistics including model ABCD. To overcome this problem, I–T statistics based on the bootstrap results were obtained excluding this model and thus cannot be compared directly to the results based on the original data (i.e. no bootstrap applied). Comparisons between the original and bootstrap results were used only to corroborate the main conclusions. For the post-1970 data, we encountered the same problem with those models including the number of large piscivorous species (SP) variable (see below), which was thus excluded before bootstrapping.

In addition to the I–T approach, we compared the fit of the different models by examining the residuals and computing the generalized coefficient of determination (maximum-rescaled R^2 ; Nagelkerke, 1991). We also compared the ability of models to discriminate between BT and BTE lakes with the coefficient of classification accuracy (c) (Hosmer & Lemeshow, 2000). The c coefficient does not give the rate of correct classification for a given cut-off value but rather gives a measure of the trade off between sensitivity and specificity for every possible cut-off value used to make predictions (Hosmer & Lemeshow, 2000). It is important to note here that a model should not be judged only on the basis of its classification accuracy (c coefficient), but also on its goodness-of-fit (I–T parameters): a model with a high c coefficient does not necessarily have a good fit (Hosmer & Lemeshow, 2000).

A priori hypotheses and related models

We used our knowledge about small Canadian Boreal Shield lakes to develop a set of 11 candidate logistic models to predict the local BTE patterns in the study lakes. Therefore, our models were used to predict separately the absence (i.e. documented extinction) of BT before and after the creation of the national park.

Hypothesis A: Nürnberg (1995b) established empirical relationships to predict the duration of anoxia in lakes based on mean depth (Z_{mean}), LA, TN, TP and DOC. Assuming that there is a link between the duration of hypoxia/anoxia and winterkill (Nürnberg, 1995a), we used these variables to build a model to predict the occurrence of local BTE (Table 3). Given that Nürnberg (1995b) used the ratio Z_{mean}/LA in her models as an estimator of lake shape, we also included the interaction between Z_{mean} and LA in the model. However, given that Z_{mean} is mathematically derived from the ratio between lake volume and area, the use of both variables in a regression can lead to artificial collinearity (Jackson, Harvey & Somers, 1990). To avoid this potential bias, we replaced Z_{mean} by maximum depth (Z_{max}) in our models, which was measured independently from LA (Table 3).

Hypothesis B: Predation by large piscivorous fish may affect the species richness of prey fish in temperate lakes (Chapleau *et al.*, 1997). Even though predation by piscivorous fish on BT has rarely been reported (Scott & Crossman, 1973), BT recruitment might be affected by predation on juveniles, which in

Table 3 Set of candidate logistic models based on eleven hypotheses defined *a priori* to explain the extinction of brook trout in the study lakes. See text for details

Hypothesis	Model
A	$a + b.LA + c.Z_{\text{max}} + d.LA.Z_{\text{max}} + e.DOC + f.TP + g.TN$
B	$a + b.SP + c.SC$
C	$a + b.SRC + c.SL + d.DD$
D	$a + b.BIF$
AB	$a + b.LA + c.Z_{\text{max}} + d.LA.Z_{\text{max}} + e.DOC + f.TP + g.TN + h.SP + i.SC$
AC	$a + b.LA + c.Z_{\text{max}} + d.LA.Z_{\text{max}} + e.DOC + f.TP + g.TN + h.SRC + i.SL + l.DD$
AD	$a + b.LA + c.Z_{\text{max}} + d.LA.Z_{\text{max}} + e.DOC + f.TP + g.TN + h.BIF$
BC	$a + b.SP + c.SC + d.SRC + e.SL + f.DD$
BD	$a + b.SP + c.SC + d.BIF$
CD	$a + b.SRC + c.SL + d.DD + e.BIF$
ABCD	$a + b.LA + c.Z_{\text{max}} + d.LA.Z_{\text{max}} + e.DOC + f.TP + g.TN + h.SP + i.SC + l.SRC + m.SL + n.DD + o.BIF$

LA, lake area; Z_{max} , maximum depth; DOC, dissolved organic carbon; TP, total phosphorus; TN, total nitrogen; BIF, beaver impact factor (see text); SP, number of large piscivorous species; SC, number of potential competitor species; SRC, presence of a brook trout source population (see text); SL, total length (km) of streams in the catchments located upstream of the lake; DD, drainage density (km^{-1}).

turn might contribute to an increased risk of extinction. Furthermore, the presence of other non-piscivorous fish might negatively affect both the numbers and the biomass of BT by competing for zooplankton and benthic invertebrates (Magnan, 1988; Tremblay & Magnan, 1991; Lacasse & Magnan, 1992). Thus, we assumed that the number of both predator (SP) and competitor species (SC) could increase the risk of BTE through their potential effects on populations of this species (Table 3).

Hypothesis C: The degree of connectivity is an important factor allowing the recolonization of lakes after extinction events or providing temporary access to refuge areas (Tonn & Magnuson, 1982). Since detailed information about the inter-lake connections *via* the hydrographic network was not available for this study, we used the following isolation variables as proxies for the likelihood of recolonization:

1 Presence of SRC: A dummy variable describing the presence of BT populations in the closest lake or stream connected to the lake (either up- or downstream). We determined the presence of SRC using data from surveys of waterbodies in the park (Masson *et al.*, 2001).

2 Total length (km) of streams (SL) in the catchments upstream of the lake.

3 Drainage density (km^{-1}): The ratio between SL and catchment area.

Since SRC does not take into account important factors, such as the size of the SRC or distance from the lake, it cannot fully represent the likelihood of recolonization. However, since SRC might play a critical role in determining the likelihood of successful fish colonization (Schlosser & Kallemeyn, 2000), we considered that this variable contained sufficient information to be included in the model. Furthermore, both SL and DD are potentially linked to the magnitude of seasonal floods, and could thus be important in establishing temporary recolonization routes in otherwise poorly connected systems (Ray *et al.*, 2004) (Table 3). In fact, floods could be related with an increase in the use of shallow streams by dispersing fish and to an increase of the permeability of beaver dams to fish migration. SL was significantly correlated with catchment area ($R = 0.48$; $P < 0.0001$), which could also be seen as a proxy of isolation. However, given the high collinearity between these two variables, catchment area was excluded from the analyses. Since SRC could change over the scale of the century,

SL and DD should be considered *a priori* as more reliable proxies of the likelihood of recolonization by BT over this temporal scale. Therefore, we consider that these three variables (i.e. SRC, SL and DD) are complementary and are worth including in the model. Since these variables might also be related with the access to refuge areas (such as well-oxygenated streams) or reduce residence time (and thus lower the risk of anoxia), they could also be considered as partly related with extinction. However, for the sake of simplicity, we treated them as isolation factors only, considering that the access to refuge areas is a property embedded within the concept of isolation.

Hypothesis D: We assumed the effects of beaver dams on the likelihood of recolonization by BT to be fairly similar for all the study lakes since every lake outlet was dammed. In addition, we assumed that the among-lake differences in the impact of beaver dams were more important upstream (i.e. on lake shores) than downstream (i.e. on the outlet) of the dam itself. Therefore, we considered the observed variation of BIF as potentially related more with local extinction factors than to isolation ones. We thus expect BIF, which could potentially increase the risk of anoxia, to be a good predictor of BTE (Table 3).

Hypotheses AB, AC, AD, BC, BD, CD: We considered all possible pair-wise combinations of hypotheses A–D as separate hypotheses.

Hypothesis ABCD: Since both extinction and recolonization events may have shaped the present occurrence of BT in the LMNPC area, we included all the variables used to build models A–D in a single model (Table 3).

Since each variable used in the elaboration of the 11 *a priori* models appears in five models, it is possible to make direct, unbiased comparisons of their relative Akaike weights (Burnham & Anderson, 2002). Since all the variables but the BIF always occur grouped in a model (e.g. SP and SC; see Table 3), this approach allows us to compare the relative Akaike weights of groups of variables rather than of single ones.

As stated before, this approach was used to model separately extinctions that occurred before 1970 and those that occurred after the creation of the park. Since the relative importance of factors related with extinction is probably to have changed with the creation of the park, we expected that the two analyses would highlight different patterns. In particular, since fish introductions decreased sharply with the creation of

the park, we expected that models including hypothesis B would predict better BTE that occurred before 1970. In contrast, since beaver activity increased after the creation of the park, we expected that models including hypothesis D would predict better BTE that occurred after 1970. Finally, we have no *a priori* reason to expect that the relative importance of hypotheses A and C would have changed with the period considered.

The impact of collinearity among the independent variables was checked by calculating the variance inflation factor. This factor was <3 for all the variables used in the models, indicating that our analyses were not affected by collinearity (Quinn & Keough, 2002).

Results

Univariate comparisons

Catchment area, pH, the SL in the catchment, DD, BIF and fish species richness (not including BT) were significantly different between BT and BTE lakes (Table 1). Even though only SL was significant after a sequential Bonferroni correction, these results suggest that other factors might be linked to brook occurrence patterns: SL, DD and catchment area, which can be considered as proxies of lake connectivity, were smaller in BTE than in BT lakes. Both pH and BIF were significantly higher in BTE lakes, whereas species richness (not including BT) was lower in BTE than in BT lakes. Differences in mean pH were small between the two groups of lakes, with BTE lakes being slightly less acidic. Beaver dams were recorded in all the study lakes, and none had an impact <2: BIF was two in 34 lakes and three in the 28 others. None of the variables shown in Table 1 were significantly different ($P < 0.5$) between lakes with BIF = 2 and BIF = 3 (results not shown).

Multiple logistic regression and model inference

Pre-1970 period

The sum of the Akaike weights suggests that models CD, C, BC, BD and D (ranked by their w_i) should be included in the 95% confidence set of models for predicting BTE for the period before 1970. Model selection based on AICc ranked models CD and C as the two best (Table 4a). Model C included only

isolation-related factors (SRC, SL and DD), whereas model CD also included BIF. Classification accuracy was >0.80 for both models, indicating excellent discrimination (Table 5a) (Hosmer & Lemeshow, 2000). These two models have w_i values of 0.36 and 0.46, respectively, and together they represent 82% of the confidence set of the models. However, the AICc difference between the two models is <2 units, indicating that the inclusion of BIF in model CD produced a model that added only slightly more information to model C in terms of improving its plausibility, only because of the increased number of parameters. Both models C and CD were significant after the sequential Bonferroni correction, but the CI of the odds ratios relative to single variables suggests that none of the independent variables was clearly associated with the pattern of BT occurrence (Table 5a). Compared with models C and CD, the three others included in the 95% confidence set have relatively low plausibility ($w_i < 0.07$ in all cases). However, two of these models included hypothesis B, suggesting a potential role for competition and predation in the local BTE. All other models had a $w_i < 0.015$, suggesting very low plausibility.

Akaike weights for the single variables confirm the importance of variables related with recolonization (i.e. S, SL and DD), which had a combined weight of 0.885. Beaver impact and inter-specific interactions (SP and SC) had weights of 0.563 and 0.140 respectively. In contrast, the relative importance of lake morphometry and physicochemical variables (LA, Z_{\max} , $LA.Z_{\max}$, DOC, TP and TN) was much lower, with w_i of <0.001.

Bootstrapping estimates Based on the sum of π_i^* , bootstrapping indicated that seven models should be included in the 95% confidence set (Table 4a). Models A, B and D were thus excluded. CD was the model with the highest relative plausibility, but the absolute value of its selection frequency (π_i^*) gave only moderate support (i.e. 0.29). The lowest π_i^* values within the confidence set were obtained for models AB, AD and BC (0.09, 0.06 and 0.06, respectively), whereas models C, AC and BD had intermediate values (0.17, 0.16 and 0.13, respectively). The large CI for both Δ_i^* and w_i^* confirmed a relatively high uncertainty for this set of models, which postulated that extinctions occurred before the creation of the national park (Table 4a).

Table 4 Results of the model selection based on the Akaike information criterion corrected for small samples (AICc). Analyses were performed by including brook trout extinctions that occurred (a) before or (b) after 1970

Model	K	AIC _c	Δ_i	w_i	Δ_i^* 95% CI	w_i^* 95% CI	π_i^*
(a)							
A	7	74.6	19.7	0.00002	4.8–44.2	0.0000–0.0400	0.0013
B	3	62.2	7.3	0.01169	0.7–40.9	0.0000–0.2442	0.0165
C	4	55.4	0.5	0.35752	0.0–29.2	0.0000–0.5109	0.1672
D	2	59.7	4.8	0.04250	0.7–41.1	0.0000–0.2527	0.0279
AB	9	74.0	19.1	0.00003	0.0–37.7	0.0000–0.9857	0.0869
AC	10	70.2	15.3	0.00022	0.0–24.4	0.0000–0.9997	0.1576
AD	8	73.0	18.1	0.00005	0.0–42.9	0.0000–0.6977	0.0574
BC	6	58.7	3.9	0.06708	0.0–28.5	0.0000–0.9841	0.0597
BD	4	58.9	4	0.06087	0.0–36.5	0.0000–0.7816	0.1323
CD	5	54.9	0	0.45997	0.0–27.9	0.0000–0.9048	0.2932
ABCD [†]	13	73.2	18.3	0.00005	–	–	–
(b)							
A	7	70.6	23.9	0.00000	8.7–45.9	0.0000–0.0082	0.0005
B	3	61.2	14.6	0.00049	11.2–45.3	0.0000–0.0021	0.0000
C	4	50.6	3.9	0.09821	0.1–30.6	0.0000–0.3788	0.0301
D	2	58.3	11.7	0.00289	5.3–42.0	0.0000–0.0472	0.0032
AB	9	73.4	26.8	0.00000	10.9–49.1	0.0000–0.0028	0.0002
AC	10	55.9	9.3	0.00974	0.0–16.8	0.0002–0.9999	0.3704
AD	8	70.3	23.6	0.00001	3.7–45.5	0.0000–0.0958	0.0113
BC	6	53.1	6.5	0.02787	3.8–33.8	0.0000–0.0799	0.0031
BD	4	58.3	11.7	0.00207	4.9–43.7	0.0000–0.0532	0.0058
CD	5	46.6	0	0.70623	0.0–26.3	0.0000–0.9973	0.5753
ABCD [†]	13	49.6	3.0	0.15620	–	–	–

The number of parameters used in the model (K), AIC_c differences (Δ_i), Akaike weights (w_i), bootstrapped estimates of the 95% confidence intervals (95% CI) for both Δ_i (Δ_i^*) and w_i (w_i^*) and model selection frequencies (π_i^*) are shown (based on 10 000 bootstrap samples) (see text for details of statistical analyses). Bold indicates those models included in the 95% confidence set of models (based on either w_i or π_i^* ; see text).

[†]Not included in the bootstrap because of a quasi-complete separation of data points in a large number of bootstrapped samples (see text).

Variables related with recolonization (i.e. SRC, SL and DD) had a relatively high weight (i.e. 0.678), whereas variables related with beaver impact (BIF), inter-specific interactions (SP and SC) and risk of anoxia (LA, Z_{\max} , LA. Z_{\max} , DOC, TP and TN) had moderate-to-low weights (0.511, 0.399 and 0.303, respectively).

Post-1970 period

The sum of the Akaike weights suggests that models CD, C and ABCD (ranked by their w_i) should be included in the 95% confidence set of models for predicting BTE for the period after 1970. The P -values of these three models were significant after the sequential Bonferroni correction for multiple comparisons (Table 5b). Model CD (which included SRC, SL, DD and BIF) was the best, with a w_i of 0.71, suggesting that there was only moderate selection uncertainty in

this set of models. Classification accuracy was >0.8 for all three models, indicating excellent discrimination (Table 5b) (Hosmer & Lemeshow, 2000). However, model CD was found to be (i) more parsimonious than model ABCD, which had eight more parameters, a Δ_i of 3, and a w_i of 0.16 and (ii) more plausible than model C, which had a Δ_i of 3.9 and a w_i of only 0.10, even though model C had one less parameter than model CD. Therefore, Δ_i values indicated that the inclusion of BIF in model CD produced a model that added information and did not simply have a better fit because of the increased number of parameters. The $\Delta_i < 4$ indicated that models ABCD and C could be considered plausible even though they were less probable than model CD. The CI of the odds ratios relative to the variables included in model CD suggested that SRC and BIF were the best candidate variables for explaining the occurrence of BT in park lakes after 1970 (Table 5b). In model CD, only these

Table 5 Details of models to predict local extinction patterns of brook trout included in the 95% confidence set of models. Analyses were performed by including brook trout extinctions that occurred (a) before (47 lakes) or (b) after (46 lakes) 1970

Model	Variable	Estimate (\pm SE)	<i>P</i> -value	Odds ratio (CI)	<i>R</i> ²	Model <i>P</i> -value	<i>c</i>
(a)							
C	SRC	-0.9876 \pm 0.5996	0.1661	0.14 (0.01–1.46)	0.35	0.0031*	0.81
	SL	-0.0752 \pm 0.0588	0.0567	0.93 (0.83–1.04)			
	DD	-0.81 \pm 0.6096	0.0662	0.45 (0.14–1.47)			
D	BIF	0.7023 \pm 0.3253	0.0268	4.07 (1.14–14.58)	0.14	0.0268	0.67
BC	SP	0.3151 \pm 1.2084	0.7943	1.37 (0.13–14.63)	0.39	0.0079	0.84
	SC	-0.3721 \pm 0.3141	0.1814	0.69 (0.37–1.28)			
	SRC	-1.1219 \pm 0.6504	0.0469	0.11 (0.01–1.36)			
	SL	-0.0532 \pm 0.0587	0.2559	0.95 (0.85–1.06)			
BD	DD	-0.7963 \pm 0.6297	0.1875	0.45 (0.13–1.55)	0.27	0.0162	0.76
	SP	-0.4743 \pm 0.2483	0.1690	4.41 (0.50–38.68)			
	SC	1.4837 \pm 1.108	0.0276	0.62 (0.38–1.01)			
	BIF	0.8094 \pm 0.353	0.0170	5.05 (1.26–20.14)			
CD	SRC	-1.1134 \pm 0.6339	0.0502	0.11 (0.01–1.30)	0.42	0.0021*	0.83
	SL	-0.0609 \pm 0.0557	0.1065	0.94 (0.84–1.05)			
	DD	-0.749 \pm 0.6543	0.2386	0.47 (0.13–1.71)			
	BIF	0.8094 \pm 0.353	0.0825	3.69 (0.82–16.60)			
(b)							
C	SRC	-1.3553 \pm 0.6604	0.0172	0.07 (0.01–0.90)	0.42	0.0009*	0.83
	SL	-0.2878 \pm 0.1804	0.0033	0.75 (0.53–1.07)			
	DD	-0.3023 \pm 0.6741	0.6531	0.74 (0.20–2.77)			
CD	SRC	-2.0766 \pm 0.8308	0.0023	0.02 (<0.01–0.41)	0.55	0.0001*	0.89
	SL	-0.3837 \pm 0.2299	0.0040	0.68 (0.43–1.07)			
	DD	-0.2763 \pm 0.8002	0.7290	0.76 (0.16–3.64)			
	BIF	1.1113 \pm 0.4837	0.0110	9.23 (1.39–61.48)			
ABCD	LA	-0.4222 \pm 0.3184	0.1264	–	0.83	<0.0001*	0.95
	<i>Z</i> _{max}	-1.6595 \pm 1.0394	0.0051	–			
	LA. <i>Z</i> _{max}	0.0562 \pm 0.0361	0.0226	–			
	DOC	3.5109 \pm 2.2014	0.0006	33.48 (0.45–999.99)			
	TP	0.1931 \pm 0.3199	0.5387	1.21 (0.65–2.27)			
	TN	0.0356 \pm 0.0364	0.2344	1.04 (0.97–1.11)			
	SP [†]	–	–	–			
	SC	1.5915 \pm 1.3656	0.0843	4.91 (0.34–71.38)			
	SRC	-13.9275 \pm 8.3396	<0.0001	<0.01 (<0.01–125.94)			
	SL	-3.703 \pm 2.3207	<0.0001	0.03 (<0.01–2.33)			
DD	5.1978 \pm 4.0306	0.1011	180.87 (0.07–999.99)				
BIF	7.1476 \pm 4.2284	0.0010	999.9 (0.10–999.99)				

LA, lake area; *Z*_{max}, maximum depth; DOC, dissolved organic carbon; TP, total phosphorus; TN, total nitrogen; BIF, beaver impact factor (see text); SP, number of large piscivorous species; SC, number of potential competitor species; SRC, presence of a brook trout source population (see text); SL, total length (km) of streams in the catchments located upstream of the lake; DD, drainage density (km⁻¹).

Parameter estimates (\pm SE) and their associated *P*-values, odds ratios with confidence intervals (CI) for variables that are not involved in any interaction terms, coefficients of determination (*R*²), model *P*-values, and the *c* statistic are shown. *P*-values were obtained by likelihood ratio tests. Bold indicates significant odds ratios. See Table 3 for variable definitions.

c, measure of classification accuracy that varies from 0.5 (no apparent accuracy) to 1.0 (perfect accuracy). *c* corresponds to the area under the receiver operating characteristic (ROC) curve (Hosmer & Lemeshow, 2000).

*R*², computed as a generalized coefficient of determination scaled to 1, or 'maximum-rescaled *R*²' (Nagelkerke, 1991).

*Significant after the sequential Bonferroni correction.

[†]Not included in the analyses on the post-1970 data because of a quasi-complete separation of data points detected when this variable was included (see text).

two variables had an odds ratio CI value that did not include the value 1, suggesting that (i) SRC was significantly related with BT presence (odds ratio = 0.02; CI = <0.01–0.41) while (ii) BIF was significantly related with BT absence (odds ratio = 9.23; CI = 1.39–61.48). BIF improved the predicted values only for

lakes with a SL < 10 km (result not shown), suggesting that lakes located downstream in a large hydrographic network are less probably to be influenced by beaver. BT was always present in lakes with a SL > 10 km, and both models C and CD predicted extremely low extinction probabilities in these cases. Besides models BC and AC, which had relatively low plausibility (Δ_i equal to 6.5 and 9.3, respectively), all the other models had a $\Delta_i > 10$, suggesting very low plausibility (Burnham & Anderson, 2002).

Akaike weights for the single variables confirm these results: variables related with recolonization (i.e. S, SL and DD) and beaver impact had weights of 0.995 and 0.867 respectively. In contrast, the relative importance of the other variables was much lower, with the variables for inter-specific interactions (SP and SC) and risk of anoxia (LA, Z_{\max} , LA. Z_{\max} , DOC, TP and TN) having weights of 0.187 and 0.163 respectively.

Bootstrapping estimates Based on the sum of π_i^* , bootstrapping indicated that seven models should be included in the 95% confidence set (Table 4b). Models A, B and AB were thus excluded. CD had the highest relative plausibility, with $\pi_i^* = 0.57$. Model AC was relatively plausible, with $\pi_i^* = 0.37$, whereas all the other models had $\pi_i^* < 0.05$. The CI for both Δ_i^* and w_i^* were relatively large for models CD, AC and C. However, based on their 95% CI, the other models only rarely had $\Delta_i^* < 3$, and their w_i^* CI were very small, with the upper values only rarely above 0.1. This suggests that a certain degree of selection uncertainty exists among models CD, AC and C, but not between these three models and the others.

Variables related with recolonization (i.e. S, SL and DD) and the impact of beaver had weights of 0.979 and 0.596, respectively, whereas variables related to the risk of anoxia (LA, Z_{\max} , LA. Z_{\max} , DOC, TP and TN) and inter-specific interactions (SP and SC) had weights of 0.382 and 0.009 respectively. Besides confirming the importance of recolonization and BIF, these results give relatively more importance to variables related with the risk of anoxia and less to beaver impact and inter-specific interactions than do the results based on the original data.

Discussion

Our results indicate that isolation is key to explaining the distribution of BT in small Canadian Shield lakes.

Variables associated with isolation were relatively important predictors for both the pre- and post-1970 periods. Moreover, our study identified a possible link between the ecological engineering by beavers and the local risk of BTE, which appears to be fairly high in the small lakes of our study region. The BIF was less important than isolation variables in predicting the occurrence of BT in both periods. However, the relative importance of BIF increased after the creation of the park, which corresponded to the increase in beaver abundance.

The inclusion of BIF only moderately improved the already very good classification accuracy of the model with isolation factors (i.e. CD versus C) for the post-1970 period, but it improved sufficiently the fit of this model to increase its plausibility, as shown by the higher Akaike weight of model CD compared with model C. Considering that model performance should not be assessed only on the basis of its ability of correctly classify the data, but also on goodness-of-fit (a model with a good classification accuracy does not necessarily have a good fit; Hosmer & Lemeshow, 2000), we can conclude that it is worth including the effects of beavers in the model. Even if the original and the bootstrapped results cannot be compared directly (e.g. model ABCD was not included in the bootstrapping), the importance of isolation factors and beaver impact was corroborated by bootstrapping. Besides confirming the higher plausibility of model CD compared with the others, the bootstrap approach also revealed a higher degree of uncertainty in model selection, with a total of seven models included in the 95% CI of models. More specifically, bootstrapping suggested that other potential extinction factors, such as inter-specific interactions, lake morphometry, nutrients and DOC, despite their low weight in the original analyses, also deserve some consideration. These variables appeared in models AC, AD, BC and BD, which had non-negligible π_i^* values, but also in model ABCD, which had a moderate w_i .

The most striking difference between the original and the bootstrapped results of the post-1970 period is relative to model AC, which had a relatively high bootstrapped π_i^* value despite its low Akaike weight. This difference could partly be explained by the absence of model ABCD from the bootstrapping (model AC is included in model ABCD) and by the relatively small sample size used in this study, which could have changed the influence of the results based

on the original and the bootstrapped data. The results of the bootstrapping suggest that variables related with anoxia could have affected BTE rates in isolated lakes. Nevertheless, estimates of Akaike weights for independent variables from both original and bootstrapped data (respectively w_i and π_i^*) revealed that the most important factors among those considered in this study for the period after 1970 are recolonization and BIF. Taken together, these results support the hypothesis of a potential role for recolonization and beaver impact. However, given the differences between original and bootstrapped data, the results also indicate that the role of variables related with anoxia should be scrutinized more carefully in the future.

Besides changes in the frequencies of fish introductions and beaver dams, other factors might have contributed to differences in the degree of uncertainty in model selection between the pre- and post-1970 periods. First, logging and fishing pressure, which were not quantified in this study, might have affected BT populations mainly before the creation of the park. Secondly, the data are probably less reliable for the pre-1970 period.

Magnuson *et al.* (1998) compared the relative roles of isolation and extinction in determining fish assemblages in both Finnish and Wisconsin lakes. Their approach showed that extinction rather than isolation variables were more important in predicting richness and composition in both groups of lakes. They suggested that 'immigration rates of new species in a lake are low (decades to millennia), but that a local extinction can occur relatively quickly, from months to a few years to a few decades after an invasion'. This conclusion is in agreement with the large number of local BTE observed in small lakes in the park over a relatively short period (50% of the populations were lost in less than a century). However, in contrast to Magnuson *et al.* (1998), the isolation factors used in our analysis, though approximate, are better predictors of the occurrence patterns of BT than extinction factors. This could be only partly explained by differences in the length of the gradient of extinction factors, since the ranges in LA, lake depth, pH and conductivity (the four extinction factors considered by Magnuson *et al.*, 1998) were roughly similar between the two studies, albeit slightly shorter in our case. Besides suggesting that we have probably neglected some other potential extinction factors (e.g. diseases), this difference might be partly related with the fact

that we considered recolonization by a species that is very common in the study area rather than recolonization by new species invading local communities. Since our best predictor of BT presence is the presence of SRC in the neighbouring bodies of water, our results suggest that BT movements within the catchment are important in determining its presence in a given body of water. This holds true even if we consider that the presence of SRC might also reflect the possibility that lakes with BT serve as a source of individuals for other waterbodies. This conclusion is in agreement with a genetic study on BT populations conducted by Angers *et al.* (1999) in the park. They showed, using microsatellite markers, that BT populations were genetically more similar within than among the catchments, suggesting that recolonization by individuals from different catchments is a rarer event.

Documented local extinction patterns are more informative than presence/absence data because the latter gives no information on whether an absence is due to an extinction event or because the species never colonized the site. However, as in our case, if local extinction patterns are obtained by comparing samples taken at different times, it is possible that some extinction events could have been followed by recolonization, thus potentially leading to underestimates in the number of extinctions. Therefore, our approach is conservative with respect to the potential role of extinction factors. This could partly explain the relatively low predictive power of the extinction variables in our study. At the same time; however, it supports the hypothesis of a potential relationship between BTE and BIF, which should be given more attention in the future. Given the large number of extinctions that have occurred in the park since its creation, the potential link with beavers (the only extinction factor indicated by our results) is worth further consideration. Based on fishing statistics, BT are present in almost all the lakes of the Mastigouche Reserve (P. Magnan, pers. obs.), an area adjacent to the national park with comparable hydrology and where beaver populations and damming are still controlled. This gives additional support to the view that there could be a link between beaver activity and local BTE. However, even though the BTE rate clearly rose in the park area after the increase of beaver abundance (from four to six extinctions per decade, i.e. a 50% increase in the extinction rate), the relatively

high extinction rate observed before 1970 cannot be explained by the effects of beaver damming.

Given their morphometry, our study lakes may experience anoxia during the ice-covered period (Nürnberg, 1995a), which on average extends from December to May in the area. Anoxia might have occurred during the initial phase of flooding, particularly in lakes with BIF = 3, when large amounts of organic matter, in the form of forest litter, soil and fallen trees, could have temporarily boosted microbial respiration (Sonster-Alpin & Klotz, 1995). The clear signs of shore erosion and the temporary changes in water colour observed in most lakes with BIF = 3 are probably related with such an increase in the amount of allochthonous organic matter. In summary, we suggest that the impact of beaver might create transient anoxic conditions, which apparently were not taken into account by other predictors of anoxia such as those suggested by Nürnberg (1995a). Admittedly, our results are correlative and BIF is a rather crude descriptor of the potential effects of beavers on lake habitats. However, the magnitude of the extinctions observed after the creation of the park, and the marked effects of beaver on the littoral habitat, are striking. Given the increase in beaver populations in both North America and Europe (Rosell *et al.*, 2005), we hope this study will stimulate new research on the effects of these mammals over a broader context.

Lakes without BT were either completely fishless (11 lakes) or hosted species more tolerant than salmonids to hypoxia and other environmental stressors (20 lakes) (Whittier & Hughes, 1998 and references therein). Only one population of a hypoxia-intolerant species (i.e. arctic charr) was found in a lake without brook charr (Table 2). Furthermore, fish species richness was lower in BTE than in BT lakes, even though the BT was not included in the analyses. Since fish introductions were anthropogenic, and mostly occurred independently of the hydrographic network, these differences in fish species richness are probably not the result of differences in lake connectivity. Taken together, these results suggest that environmental conditions were harsher in BTE than in BT lakes, and even harsher in those BTE lakes that were fishless. This suggests that a gradient of temporary hypoxia/anoxia could underlie such a pattern.

Even though univariate tests showed that there was a slight difference in pH between BT and BTE lakes

(Table 1), there was no evidence that acidification could explain the pattern of local BTE. The pH of the study lakes is within the range of Canadian Shield lakes (Carignan *et al.*, 2000; Perez-Fuentetaja *et al.*, 2000) and is within the tolerance range for BT (Power, 1980). Finally, the mean pH of BTE lakes was slightly higher than that of BT lakes (Table 1).

It is not surprising that the R^2 values of the best-ranked models were relatively low since the available variables were only indirect proxies and rough descriptors of the likelihood of local extinction and recolonization events. For example, BIF does not take into account the extent or the duration of flooding events, and reference sites with no beaver dams were lacking. In addition, climatic and/or hydrological events occurring just after the damming might have alleviated or worsened the negative effects of the impoundment. Finally, we do not have estimates of population size, a factor that can affect local extinction risks (Dunham *et al.*, 1999). However, given the relatively small sizes of the lakes studied, BT populations are probably small and thus more vulnerable to stochastic events that could lead to extinction (Dunham *et al.*, 1999).

Coupled with the genetic studies by Angers *et al.* (1999), our study suggests that recolonization by BT, at least at the catchment scale, is rather common in this area. What remains unknown is at what temporal scale these habitats could be recolonized. The BT is a good colonizer (Lacasse & Magnan, 1994) and its non-anadromous form is 'exceptionally mobile relative to other salmonids' (Rodriguez, 2002). This supports the view that recolonization is probable at the within-catchment scale in the park. The high mobility of BT might explain the within-catchment genetic similarity among different populations, as shown by microsatellite analysis (Angers *et al.*, 1999).

By revealing the relationship between both isolation (lake connectivity) and extinction (beaver impact on riparian vegetation) factors and the occurrence of BT, our results show how characteristics of the landscape can affect lacustrine fish populations. They also show the importance of considering the ecosystem level in conservation efforts rather than focussing only on a few target species. Recognizing the indirect effects that some species can have on others could certainly contribute to our viewing conservation actions in a broader perspective.

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