Impacts of road access on lake trout (*Salvelinus namaycush*) populations: regional scale effects of overexploitation and the introduction of smallmouth bass (*Micropterus dolomieu*)

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Abstract: In lake trout (*Salvelinus namaycush*) lakes of northeastern Ontario, Canada, aerial surveys of fishing activity on individual lakes (N = 589) and quantitative gillnet surveys (N = 65) were used to assess the effects of road access on angling effort and the presence of introduced smallmouth bass (*Micropterus dolomieu*). Angling effort, particularly during the open-water season, was highest and often exceeded estimated sustainable levels on lakes with good road access. Approximately 25% of the remote lakes also received excessive pressure during the winter season. Angler numerical responses to lake trout abundance were detected in remote lakes, but not in road-accessible lakes. Smallmouth bass were more prevalent in lakes with road access and human settlement (either cottages or lodges), supporting the theory that they were introduced into these lakes. Lake trout populations were depleted throughout much of the study range. Even without road access or smallmouth bass, lake trout abundance was still 47% lower than in unexploited reference lakes. When bass and (or) road access were present, lake trout abundance decreased by 77%. Remote lake trout populations in this area are clearly vulnerable to the negative impacts of improved access, a vector for both overexploitation and species introductions.

Résumé : Des inventaires aériens de l'activité de pêche sur des lacs individus (N = 589) et des inventaires quantitatifs au filet maillant (N = 65) nous ont servi à évaluer les effets de l'accès routier sur l'effort de pêche sportive et sur la présence d'achigans à petite bouche (*Micropterus dolomieu*) introduits dans des lacs à touladis (*Salvelinus namaycush*) du nord-est de l'Ontario, Canada. L'effort de pêche, particulièrement durant la période d'eau libre, est le plus élevé dans les lacs facilement accessibles par la route et il dépasse souvent le niveau admissible estimé. Environ 25 % des lacs éloignés subissent aussi une pression excessive durant la saison d'hiver. On remarque une relation entre le nombre de pêcheurs et l'abondance des touladis dans les lacs éloignés, mais pas dans les lacs accessibles par la route. Les achigans à petite bouche sont plus présents dans les lacs à accès routier et à présence humaine (chalets ou auberges), ce qui laisse croire qu'ils ont été introduits dans ces lacs. Les populations de touladis sont réduites dans presque toute la région d'étude. Même en l'absence d'accès routier et d'achigans à petite bouche, l'abondance des touladis est tout de même de 47 % inférieure à celle des lacs témoins non exploités. Quand il y un accès routier et (ou) présence d'achigans, l'abondance des touladis est réduite de 77 %. Les populations éloignées de touladis sont visiblement vulnérables aux impacts négatifs de l'amélioration de l'accès routier, un vecteur représentatif à la fois de la surexploitation et de l'introduction d'espèces.

[Traduit par la Rédaction]

Introduction

Many of Canada's recreational fisheries have shown the effects of overexploitation (Post et al. 2002) or the impacts of invasive or introduced species (Vander Zanden et al. 2004*b*). However, the rugged terrain and relatively low human settlement density in remote areas of the Boreal Shield region of Ontario give the impression that such areas would likely have many unexploited fish stocks and unaltered aquatic communities. In fact, little of northern Ontario can still be considered remote. All-terrain vehicles and a network of forestry and other roads now make all but a few protected areas accessible to anglers (fig. 1 in Gunn and Sein 2000). With improved access, widely distributed sportfish populations, such as lake trout (*Salvelinus namaycush*), a species that occurs in less than 1% of the lakes (Martin

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and Olver 1976), now appear to require management planning and action at a broad landscape level rather than at the traditional individual-lake level (Lester et al. 2003).

Several life history characteristics of lake trout, including its late maturity and low fecundity (Martin and Olver 1980), make this large-bodied sportfish highly vulnerable to overexploitation (Post et al. 2002). The high susceptibility of lake trout populations to overharvest has been demonstrated using life history based simulation models (Shuter et al. 1998). Direct observations of lake trout population decline in response to angling pressure have also been reported. Gunn and Sein (2000) estimated that over 70% of a population in one lake was harvested after only a few months in an open-access fishery. However, extrapolating from case histories to regional effects of exploitation is difficult because many factors contribute to an angler's choice of location (Aas et al. 2000; Beard et al. 2003). Moreover, lake trout fisheries are influenced by lake-specific biotic factors that affect angling catch rates, such as the presence or absence of other competitive fish species (Goddard et al. 1987).

In addition to excessive angling exploitation, the adverse impacts of invasive or introduced species are now threatening many indigenous fish populations (Rahel 2002). With respect to lake trout populations of northeastern Ontario, the introduction of centrarchids into inland lakes appears to be a potentially serious problem (Vander Zanden et al. 1999*a*, 1999*b*). For example, the introduction of smallmouth bass (*Micropterus dolomieu*) can significantly alter the abundance and availability of littoral zone prey fish species that are important seasonal forage for lake trout (MacRae and Jackson 2001; Jackson 2002). Although stocking of centrarchids has been conducted by management agencies to create alternate angling opportunities, many introductions are unplanned, occurring either by dispersal through connected waterways (Jackson and Mandrak 2002) or through introductions by anglers or lake residents (Lintermans 2004). Warm-water species such as smallmouth bass are also more likely to be successful in areas at the northern limit of their range because of climate warming (Jackson and Mandrak 2002; Sharma and Jackson 2008).

The objectives of our study were threefold: (*i*) to investigate the factors that influence angling effort for lake trout over a broad landscape scale, particularly in relation to road access, proximity to human settlement, and the abundance of trout in particular lakes; (*ii*) to assess if smallmouth bass had been introduced and how patterns of human usage, such as roads and cottages and lodges, have affected the distribution of smallmouth bass in our study area; and (*iii*) to assess how introduced bass combined with angling effort have affected lake trout abundance.

Materials and methods

Our study area encompassed northeastern Ontario, Canada, where over 900 lake trout lakes exist, representing approximately one-third of the total number of lake trout lakes in the province and approximately 8% of the global resource (Gunn et al. 2004; Selinger et al. 2006). We collected fishery-dependent (angling effort) and fishery-independent (index netting) data and assessed the native range of smallmouth bass in this region to address the objectives of this study.

Aerial surveys of angling effort

Estimates of angling effort were obtained by aerial surveys of 589 lakes (herein referred to as the effort lakes) across northeastern Ontario between 2001 and 2003 (Fig. 1). This cost-effective method compares favourably with traditional on-the-water or access-point creel surveys (Lockwood and Rakoczy 2005) and has been recommended for collecting angling effort data in Ontario (Lester and Dunlop 2004).

Effort surveys were stratified by season (open-water season and winter) and day type (weekday versus weekends and holidays). One midday flight between 1000 and 1400 was conducted each week, alternating between day types. Lakes were chosen based on flight lines that allowed for the maximum number of samples possible. Angling effort (E, h·year^{-1}) was calculated by season (j) for each water body as

$$(1) \qquad E_j = \frac{\mathrm{MAC}_j \cdot T_j \cdot p_j \cdot D_j}{K_{m,j}}$$

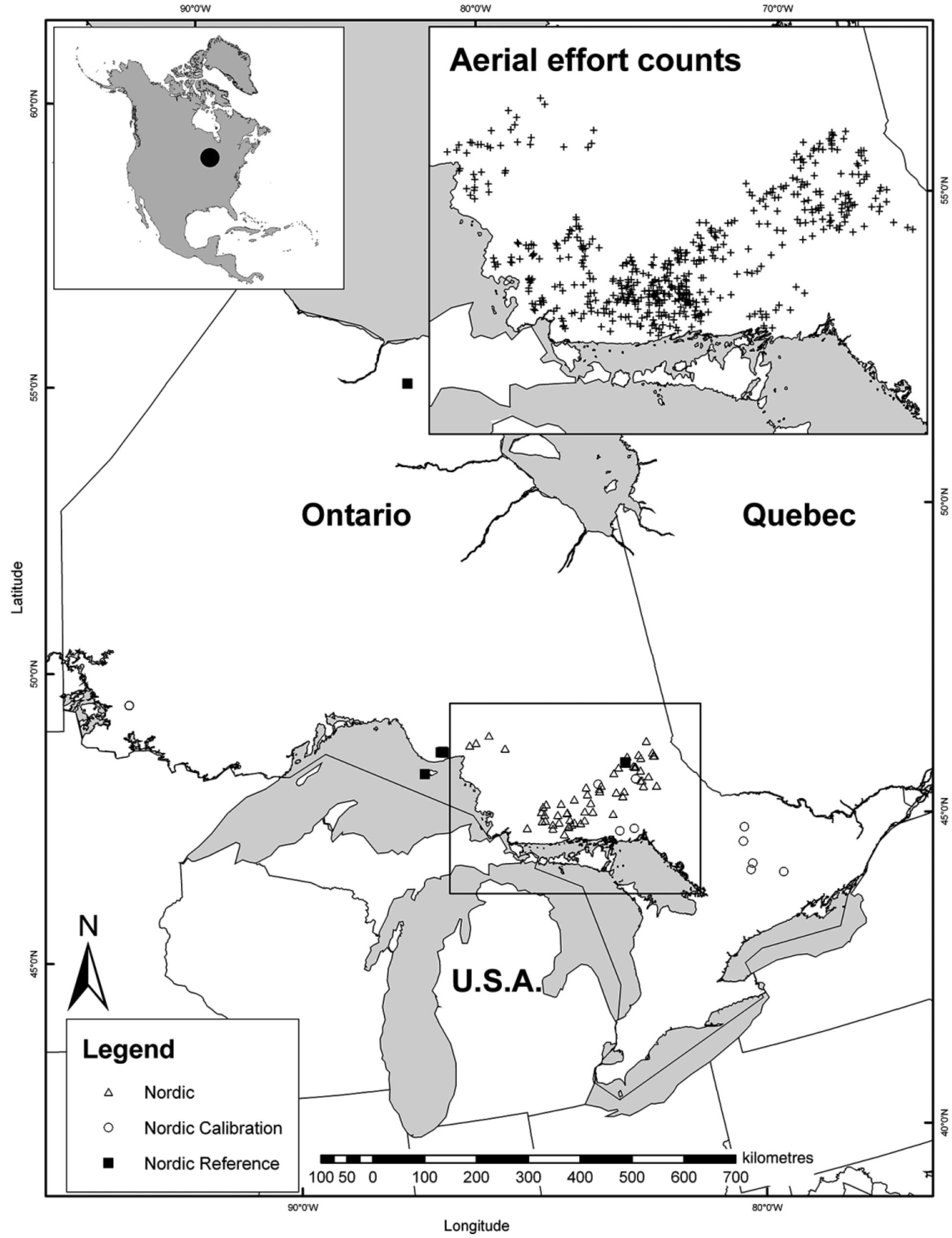
where MAC is mean midday activity count, T is the length of the angling day (assumed to be 14 and 10 h in the open-water season and winter, respectively), p is party size (correcting for instances in which parties were counted rather than individual anglers; occupied ice huts were assumed to have a party size of two), and D is the number of fishing days in the season. Season and day type specific correction factors (K_m) were developed from appropriately stratified roving creel data (Lester and Dunlop 2004; Parker et al. 2006) and applied to correct for changing fishing activity during the course of the day. During the open-water season, K_m values were 1.3 and 1.1 on weekdays and weekends–holidays, respectively. Winter correction factors were 1.5 and 1.2 on weekdays and weekend–holidays, respectively. Greater detail of aerial effort survey methods is provided in Selinger et al. (2006). Effort was then divided by lake surface area to obtain angling intensity (h·ha^{-1}). In addition, estimated angling intensity at maximum sustainable yield (E_{MSY}, h·ha^{-1}) was calculated as per Lester and Dunlop (2004), derived from the model presented in Shuter et al. (1998):

$$(2) \qquad E_{\mathrm{MSY}} = 10^{0.0054+\frac{1.892}{\mathrm{Area}^{0.16}}-0.222\cdot\log_{10}\mathrm{TDS}+0.073\cdot\log_{10}\mathrm{Area}\cdot\log_{10}\mathrm{TDS}}$$

where E_{MSY} is related to lake surface area (Area, ha) and total dissolved solids (TDS, mg·L^{-1}). All water quality parameters (including TDS) were measured between 2001 and 2004 by water sampling shortly after ice-out (April).

Each effort lake was classified as to the type of access. Access was defined as highway, primary road, secondary road, tertiary road, trail, remote (greater than 500 m from any type of road or trail access), or restricted (former forestry roads or trails with access blocked or bridges eliminated). The closest population centres of at least 5000 and 50 000 people were also determined for each lake. Using the combination of roads needed to access the lake and assigned travel speeds for each type of road (highway, 100 km·h^{-1}; primary, 80 km·h^{-1}; secondary, 40 km·h^{-1}; tertiary, 20 km·h^{-1}; trail, remote, and restricted, 2 km·h^{-1}), the amount of time needed to access the lake was calculated from each population centre.

Fig. 1. Map of Ontario, Canada, showing location of Nordic reference lakes, study lakes, and calibration lakes (see Appendix A). Enlarged section of northeastern Ontario shows locations of lakes surveyed for angling effort.



Fish community assessment

A subset of 59 of the effort lakes was chosen for fish community analyses (Fig. 1). Lakes were randomly selected from three surface-area categories (50–150 ha, 150–400 ha, 400–20000 ha) in proportion to the number of all known lake trout lakes by these same size categories within the region using the Ontario Ministry of Natural Resources Aquatic Habitat Inventory (AHI) database; see atlas of lakes in northeastern Ontario in Gunn et al. (2004). We avoided lakes that had any special angling regulations in place (base regulation: three fish of any size per day; 1 January to 30 September at the time of data collection) because both fish abundance and anglers' choice of locations to fish can be affected by regulations (Cox et al. 2003).

Between 2000 and 2004, whole-lake fish community assessments were conducted using the Nordic index netting method. The Nordic method is based on a depth-stratified, random-sampling design that takes place during the period of summer thermal stratification (Appleberg 2000; Morgan and Snucins 2005). The sampling effort in each depth stratum (<3 m, 3–5.9 m, 6–11.9 m, 12–19.9 m, 20–34.9 m, 35–49.9 m, and 50–75 m) is proportional to the volume of water in each stratum, thus providing a whole-lake, volume-weighted estimate of entire fish community relative abundance and relative biomass. Benthic gillnets (30 m long × 1.5 m high) with randomly arranged (but identical between nets) seamless panels of geometrically increasing mesh sizes (5, 6.25, 8, 10, 12.5, 15.5, 19.5, 24, 29, 35, 43, and 55 mm (square measure)) were set at random orientations to shore between 1800 and 2000 and lifted between 0600 and 0800 on the following morning. All fish were identified to species and measured for fork length (mm), total length (mm), and round weight (g). We used the Nordic results to determine the presence or absence of smallmouth bass and pelagic prey species (including rainbow smelt (*Osmerus mordax*), lake whitefish (*Coregonus clupeaformis*), and cisco (*Coregonus artedi*)) and to determine lake trout relative abundance (Appendix A). In addition, six reference lakes for which exploitation was considered either nil or minimal were surveyed (Fig. 1). Four of the reference lakes (Mishi, Mishibishu, Katzenbach, and Whitepine) were long-term fish sanctuaries (i.e., no fishing allowed for >10 years), and two lakes (Michi and Hawley) were extremely remote with very restricted access.

Assessment of smallmouth bass introduction

Historical presence or absence of smallmouth bass was determined for the netting assessment lakes that had smallmouth bass present. First, we used the AHI database consisting of lake survey information compiled from standard qualitative assessment methods conducted from the 1960s to the 1980s. These surveys used 120 m gangs of gillnets (38, 51, 64, 76, 89, 102, 114, and 127 mm (stretched measure)) and minnow traps set overnight (Dodge et al. 1985). The AHI surveys were a rapid assessment method usually involving only a single sampling effort per lake (duration 2–5 days) but were shown by Bowlby and Green (1987) to be very effective at detecting the presence of the larger, more common fish species. These authors showed that smallmouth bass were one of the species more easily captured with the AHI gear and reported a 85% effectiveness of detecting smallmouth bass when they are known to be present in a water body. Of the remaining lakes in our survey that had bass during the AHI surveys, lake elevation and broad geographical area were used to assess whether bass populations were native or non-native based on the study of Robbins and MacCrimmon (1974). They suggest that populations along the north shore of Lake Huron, north of Lake Wanapitei (Sudbury), or near Temagami would only be native in lakes below 237, 267, and 300 m above sea level, respectively.

Current information on the presence or absence of cottages or tourist lodges was also determined for these lakes using land-use permit and private land patent data from the AHI database and the Natural Resource Values Information System database, and in some cases, information was updated by field crews during netting assessments.

Statistical analyses

Analyses of variance (ANOVA) were used to test for differences in angling intensity (h·ha^{-1}, log-transformed) among access types. Post hoc comparisons were done using Tukey's tests.

We used multiple regression to determine the relative influence of lake surface area (log-transformed), access type, and travel time to each lake (log-transformed) from population centres of 5000 and 50 000 people on angling effort (h·year^{-1}). Travel time to each lake was weighted proportional to (i.e., multiplied by) the inverse of the number of residents of the specific population centre under consideration, because we assumed that a large population was likely to exert more pressure than a small population for a given travel time to a lake. Type III sums of squares were used to calculate partial F statistics to assess the significance of each variable above and beyond the other variables entered into the model (Spitvak et al. 2007). On the subset of effort lakes used for population assessments, we used ordinary linear regression to test the angler numerical response (E_j, log-transformed) to our Nordic index of lake trout abundance (catch per unit effort (CPUE, (log-transformed)); Appendix A). For this analysis, we excluded lakes with no effort because we were interested in lake trout abundances that actually attracted anglers. We assessed the power of nonsignificant statistical tests using the methods outlined in Zar (1999) and homogeneity of variances using Levene's test.

Analyses of contingency tables were done using chi-square statistics (Zar 1999). Specifically, we tested whether the proportion of lakes fished above or below E_{MSY} were more frequent in any given access type.

We also tested the hypothesis that the presence of smallmouth bass was affected by road access and the presence of cottages or lodges using log-linear methods (Zar 1999). Here, lakes with highway, primary, secondary, and tertiary road access were grouped as road-accessible lakes, whereas lakes with trail, remote, or restricted access were grouped as remote lakes.

Finally, we tested for differences in chemical, fish community, or habitat-related variables that may explain the presence of smallmouth bass or roads using ANOVA. We also tested how bass presence or absence and road access vs. remote access interacted to affect lake trout abundance using a factorial ANOVA. Again, access types were grouped into the more broad categories of road access and remote. Post hoc analysis was done with a Tukey's test. Quantification of the statistical power of additive effects of road access and bass was performed using analytical procedures outlined in Gerow (2007). All other statistical tests were performed using Statistica (version 6; StatSoft, Inc. 2001) and considered significant at $P < 0.05$.

Results

Factors affecting angling intensity and effort

Total angling intensity estimated from the aerial surveys ranged from 0 to 92 h·ha^{-1}; intensities ranged from 0 to 36 h·ha^{-1} during the winter and from 0 to 68 h·ha^{-1} during the open-water season (Table 1). Sample sizes of midday activity counts (i.e., the number of flights) for individual lakes ranged from 10 to 64.

There were significant differences in angling intensity among access types ($F_{[6,579]} = 5.27$, $P < 0.001$; Fig. 2) during the open-water season. Remote lakes received less pressure than primary and secondary road accessible lakes. During the winter, there was no difference in angling intensity among access types ($F_{[6,575]} = 1.17$, $P = 0.32$; Fig. 2). The proportion of lakes angled beyond the estimated sustainable levels (E_{MYS}) was higher for lakes with road access than without road access ($\chi^2_6 = 37.42$, $P < 0.001$). For example, 63% of highway-accessed lakes were angled at inten-

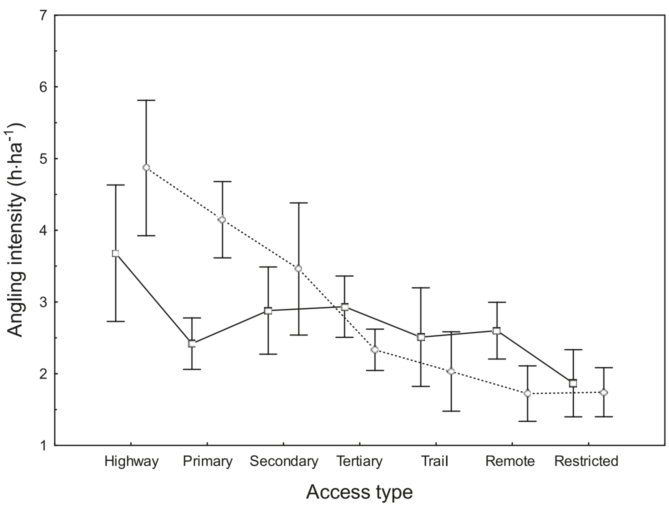
Table 1. Sample sizes (*N*), range in number of midday activity counts (MAC) from individual water bodies, and mean (range in parentheses) effort intensities (h·ha^{-1}) by surface area category from 589 lakes surveyed by aerial methods.

Surface area category	*N*	MAC range	Open-water season effort intensity (h·ha^{-1})	Winter effort intensity (h·ha^{-1})
<150	377	10–64	2.4 (0–68.2)	3.0 (0–36.3)
150–400	129	17–60	2.6 (0–18.5)	2.4 (0–17.0)
>400	83	17–40	3.8 (0–32.0)	1.9 (0–19.6)

Table 2. Multiple regression models predicting open-water season and winter angling effort (h·year^{-1}) from lake surface area, access type, and time to lake (TTL) from the closest population centres of 5000 (TTL 5000) and 50 000 (TTL 50 000) people.

Model	Variable	Partial *F*	*P*	Partial r^2
Open-water season	Surface area (ha)	303.04	<0.001	0.44
	Access type	14.71	0.001	0.02
	TTL 5000	12.57	<0.001	0.01
	TTL 50 000	4.69	0.03	<0.01
Winter	Surface area (ha)	92.27	<0.001	0.18
	TTL 50 000	15.27	0.001	0.05
	TTL 5000	5.38	0.02	0.01

Fig. 2. Open-water season (◇, dotted line) and winter (□, solid line) angling effort intensity (h·ha^{-1}) by access type. Error bars represent ± 1 standard error.



sities beyond E_{MSY}, whereas only 26% of remote lakes were angled beyond the estimated sustainable level.

Multiple regression revealed distinct seasonal patterns in angling effort (h·year^{-1}) related to road accessibility and proximity to population centres (Table 2). During the open-water season, surface area accounted for the majority of variation in angling effort (partial $F_{[1,452]}$ = 303.04, P < 0.001, partial r^2 = 0.44). The type of access was a significant term in the regression model, although it accounted for little additional variation (partial $F_{[1,452]}$ = 14.71, P = 0.001, partial r^2 = 0.02). Similarly, travel times to a lake from population centres of both 5000 and 50 000 people were significant in the model; however, they explained little further variation (5000, partial $F_{[1,452]}$ = 12.57, P < 0.001, partial r^2 = 0.01; 50 000, partial $F_{[1,452]}$ = 4.69, P = 0.03, partial r^2 < 0.01). Patterns differed slightly during the winter; surface area still accounted for the majority of explained variation in angling effort (partial $F_{[1,447]}$ = 92.27, P < 0.001, partial r^2 = 0.18). Time to a lake from the closest population of at least 50 000 explained a further 5% of the variation (partial $F_{[1,447]}$ = 15.27, P = 0.001, partial r^2 = 0.05), and an additional 1% was explained by the time to a lake from the closest population centre of 5000 people (partial $F_{[1,447]}$ = 5.38, P = 0.02, partial r^2 = 0.01).

Angler numerical responses to lake trout abundance only occurred in remote lakes (Figs. 3*a*, 3*b*). During the open-water season, angling intensity (h·ha^{-1}) was significantly related to lake trout abundance (r^2 = 0.30, P = 0.014) in remote lakes, but intensity and abundance were not significantly related in road-accessible lakes (r^2 = <0.01, P = 0.96; Fig. 3*a*). Similar results were observed during the winter, where angling intensity increased with lake trout abundance on remote lakes only (remote, r^2 = 0.31, P = 0.003, road-accessible, r^2 = 0.09, P = 0.28; Fig. 3*b*). Our statistical power to detect a significant angler numerical response in the open-water season and winter was 5% and 19%, respectively. Variances were homogenous among the models (P > 0.05).

Assessment of smallmouth bass introduction

In the subset of lakes where bass were present in the Nordic assessment (N = 16), historical survey records from the AHI program suggest that they had not been present in 50% (8) of these lakes during past decades. Of the remaining eight lakes, bass populations were found in lakes at elevations that were too high to be accounted for by natural postglacial colonization. In addition, there were no consistent confounding physical, chemical, or biotic factors that would explain bass presence in the study lakes. Lake trout lakes

Fig. 3. Angling intensity ($h \cdot ha^{-1}$) versus lake trout (*Salvelinus namaycush*) catch per unit effort (CPUE, number of $fish \cdot net^{-1}$) during (*a*) winter and (*b*) the open-water season. Fitted curves represent significant log–log relationships for remote lakes (○) only. Relationships for road-accessible lakes (■) were not significant.

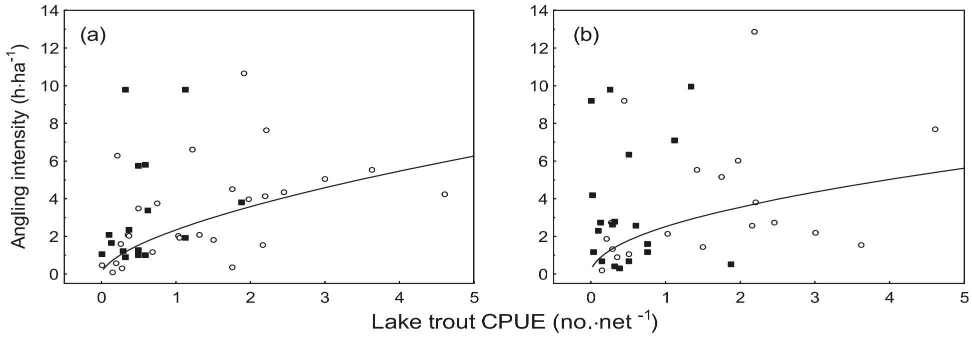


Table 3. Means (±95% confidence interval) of physical, productivity, fish community, and thermal variables from reference lakes and lakes without and with smallmouth bass (*Micropterus dolomeu*).

	Lakes				
Variables	Reference	Without bass	With bass	*F*	*P*
Physical variables					
Surface area (ha)	455 (45, 865) a (*n* = 6)	174 (19, 329) a (*n* = 42)	446 (216, 676) a (*n* = 16)	2.33	0.105
Maximum depth (m)	49.3 (37.1, 61.5) b (*n* = 6)	31.9 (27, 36.8) a (*n* = 38)	28.2 (21.3, 35.1) a (*n* = 16)	4.53	0.015
Elevation (m)	329 (273, 385) ab (*n* = 6)	375 (352, 398) b (*n* = 38)	324 (292, 356) a (*n* = 16)	3.79	0.028
Productivity variables					
Total dissolved solids ($\mu g \cdot L^{-1}$)	47.0 (–2.3, 96.3) a (*n* = 6)	36.8 (17.5, 56.1) a (*n* = 40)	21.4 (15.2, 27.6) a (*n* = 14)	0.52	0.599
Phosphorous ($\mu g \cdot L^{-1}$)	n/a	6.3 (5.3, 7.3) a (*n* = 39)	6.2 (4.7, 7.7) a (*n* = 14)	0.02	0.895
Secchi depth (m)	5.8 (1.2, 10.4) a (*n* = 6)	6.7 (5.6, 7.8) a (*n* = 29)	5.8 (4.3, 7.3) a (*n* = 14)	0.61	0.547
Fish community variables					
Species richness	9 (5, 13) ab (*n* = 6)	9 (8, 10) a (*n* = 42)	11 (9, 13) b (*n* = 16)	3.15	0.050
Relative fish community biomass ($g \cdot net^{-1}$)	2966 (2204, 3728) b (*n* = 6)	2167 (1738, 2596) ab (*n* = 42)	1915 (1627, 2203) a (*n* = 16)	3.44	0.038
Pelagic prey presence (%)	83 (*n* = 6)	33 (*n* = 42)	74 (*n* = 16)	—	—
Thermal variables					
Growing degree days	1408 (1307, 1509) b (*n* = 6)	1701 (1663, 1739) a (*n* = 42)	1696 (1640, 1752) a (*n* = 16)	15.27	<0.001
Thermocline depth (m)	4.3 (2.7, 5.9) a (*n* = 6)	4.3 (3.6, 5.0) a (*n* = 29)	4.9 (3.9, 5.9) a (*n* = 13)	0.47	0.629

Note: Species richness (defined as the number of species present) and relative fish community biomass were determined from Nordic surveys. Growing degree days were calculated from the year in which the Nordic survey was conducted (Terry Marshall, Northwest Science and Technology, Ontario Ministry of Natural Resources, Thunder Bay, Ontario, Canada, personal communication). Thermocline depth was the depth at the beginning of the thermocline measured during the Nordic survey. *F* statistics and *P* values are from analyses of variance comparing the groups. Statistically similar values are denoted by the same lowercase letter. n/a, not available.

with bass had similar surface areas, TDS, total P, Secchi depth, growing degree days, and thermocline depth as lakes without bass (Table 3). However, lakes with bass were at lower elevations (although still above the elevation restrictions to natural bass postglacial dispersal) and had, on average, two more species (one of which can be attributed to bass). In contrast, the presence of smallmouth bass was related to the presence of cottages and (or) lodges and road

Table 4. Number of lakes sampled with (present) and without (absent) smallmouth bass (*Micropterus dolomieu*) by road accessibility and presence or absence of cottages or lodges.

	Road accessible		Remote	
Smallmouth bass	Cottage or lodge present	Cottage or lodge absent	Cottage or lodge present	Cottage or lodge absent
Present	3 (0.63)	7 (–1.06)	3 (–0.25)	3 (–2.72)
Absent	1 (–0.63)	14 (1.06)	4 (0.25)	23 (2.72)

Note: Values in parentheses are standard residuals from log-linear analysis.

Table 5. Means (95% confidence interval) of physical, productivity, fish community, and thermal variables from reference, remote, and road-accessible lakes.

	Lakes				
Variables	Reference	Remote	Road-accessible	*F*	*P*
Physical variables					
Surface area (ha)	455 (45, 865) a (*n* = 6)	174 (105, 243) a (*n* = 33)	340 (26, 654) a (*n* = 25)	1.79	0.175
Maximum depth (m)	49.3 (37.1, 61.5) b (*n* = 6)	32.3 (25.6, 39.0) a (*n* = 29)	28.2 (24.3, 32.1) a (*n* = 25)	6.80	0.002
Elevation (m)	329 (273, 385) b (*n* = 6)	375 (356, 394) a (*n* = 29)	371 (348, 394) a (*n* = 25)	18.95	<0.001
Productivity variables					
Total dissolved solids ($\mu g \cdot L^{-1}$)	47.0 (–2.3, 96.3) a (*n* = 6)	19.2 (15.9, 22.5) a (*n* = 31)	51.7 (10.6, 92.8) a (*n* = 23)	3.16	0.050
Phosphorous ($\mu g \cdot L^{-1}$)	n/a	6.3 (5.3, 7.3) a (*n* = 31)	6.2 (4.7, 7.7) a (*n* = 22)	0.02	0.895
Secchi depth (m)	5.8 (1.2, 10.4) a (*n* = 6)	6.5 (4.9, 8.1) b (*n* = 22)	6.0 (5.1, 6.9) a (*n* = 21)	8.59	<0.001
Fish community variables					
Species richness	9 (5, 13) a (*n* = 6)	8 (7, 9) a (*n* = 33)	10 (8, 12) a (*n* = 25)	0.51	0.605
Relative fish community biomass ($g \cdot net^{-1}$)	2966 (2204, 3728) b (*n* = 6)	1946 (1674, 2218) a (*n* = 33)	2058 (1692, 2424) a (*n* = 25)	9.57	<0.001
Pelagic prey presence (% of lakes)	83 (*n* = 6)	42 (*n* = 33)	44 (*n* = 25)	—	—
Thermal variables					
Growing degree days	1408 (1307, 1509) b (*n* = 6)	1695 (1648, 1742) a (*n* = 33)	1696 (1658, 1734) a (*n* = 25)	14.35	<0.001
Thermocline depth (m)	4.3 (2.7, 5.9) a (*n* = 6)	4.5 (3.6, 5.4) a (*n* = 21)	4.5 (3.6, 5.4) a (*n* = 21)	0.02	0.979

Note: Species richness (defined as the number of species present) and relative fish community biomass were determined from Nordic surveys. Growing degree days were calculated from the year in which the Nordic survey was conducted (Terry Marshall, Northwest Science and Technology, Ontario Ministry of Natural Resources, Thunder Bay, Ontario, Canada, personal communication). Thermocline depth was the depth at the beginning of the thermocline measured during the Nordic survey. *F* statistics and *P* values are from analyses of variance comparing the groups. Statistically similar values are denoted by the same lowercase letter. n/a, not available.

access (χ^2_4 = 17.97, P = 0.001). Disproportionately more lakes that had both road access and cottages or lodges had smallmouth bass present. Fewer remote lakes that lacked cottages or lodges had bass (Table 4).

Effects of roads and smallmouth bass on lake trout

There were no obvious differences in lake characteristics among reference, remote, or road-accessible lakes. Reference, remote, and road-accessible lakes were similar in lake size, productivity (total P, TDS), thermocline depth, and fish species richness (Table 5). Even though reference lakes were deeper, at lower elevations, had cooler climate conditions (growing degree days), and had higher total fish biomass than remote and road-accessible lakes, the latter two lake types were still similar to each other in these characteristics.

Lake trout relative abundance differed significantly in relation to road access and smallmouth bass presence. In the six reference lakes (no road access, no bass, and no angling), the mean CPUE was 2.6 $fish \cdot net^{-1}$. There was a significant interaction between the presence of smallmouth bass and road access on lake trout CPUE (ANOVA, $F_{[1,55]}$ = 6.68, P = 0.012; Fig. 4; Table 6). In remote lakes without

Fig. 4. Lake trout (*Salvelinus namaycush*) catch per unit effort (CPUE, number of fish·net^{-1}) by access type in lakes with (hatched bars) and without (solid bars) smallmouth bass (*Micropterus dolomieu*). Reference lakes had no road access or smallmouth bass and minimal or no angling. Error bars represent ± 1 standard error.

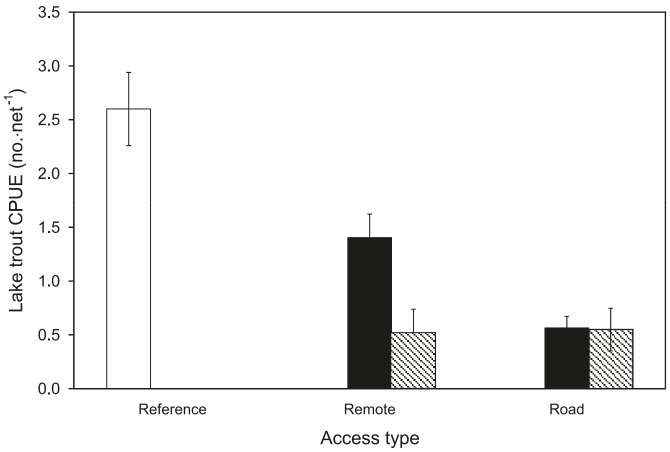


Table 6. Two-way analysis of variance (ANOVA) results of the effect of smallmouth bass presence and road access on lake trout abundance in 59 lakes in northeastern Ontario, Canada.

Effect	SS	df	MS	*F*	*P*
Smallmouth bass	16.76	1	16.76	14.02	<0.001
Access	0.69	1	0.69	0.58	0.449
Smallmouth bass × access	7.99	1	7.99	6.68	0.012
Error	65.75	55	1.20		

Note: SS, sum of squares; df, degrees of freedom; MS, mean squares; *F*, *F* statistic; *P*, probability.

smallmouth bass, lake trout CPUE was 47% (1.4 fish·net^{-1}) lower than in reference lakes, suggesting that this was the effect of general or background levels of exploitation in the region. In the presence of smallmouth bass, there was a significant further reduction to 77% fewer fish per net (0.6 fish·net^{-1}). Observed lake trout CPUE was similar in road-accessible lakes with (0.5 fish·net^{-1}) and without (0.6 fish·net^{-1}) smallmouth bass and statistically similar to remote lakes with bass. The power to detect the additive detrimental effect of road access and bass (i.e., the observed 17% reduction) in lake trout abundance was 3%.

Discussion

Factors affecting angling effort

Although case studies of specific lakes have shown that improved access drastically increases angling effort (Gunn and Sein 2000), our survey study demonstrates how extensive this effect is over a very broad study area, an area that includes >50% of the known lake trout lakes in northeastern Ontario. We found that fishing intensity increased with the quality or ease of the access (from paved highway to rough trails or no direct access), but this effect was only significant in the open-water season. During the winter angling season, there were no significant differences among access categories, showing that snowmobiles and all terrain vehicles have now made the entire region a readily accessible resource.

More than half of the easily accessed (e.g., highway) lakes were angled beyond estimated sustainable levels, but remote lakes were also heavily used, with more than 25% of them receiving angling effort above the estimated maximum sustainable level. Management strategies designed to limit access or maintain “remoteness” of these Boreal Shield ecosystems will therefore have only limited success in preventing overexploitation. Maintaining sustainability in other easily accessed salmonid fisheries has proved difficult despite restrictive harvest regulations (Parker et al. 2007). Limited-access fisheries (i.e., reducing total harvest) have been suggested as one of the only truly effective management solutions to limit overexploitation in such areas (e.g., Lester et al. 2003).

The quality of the fishery, in this case measured as the abundance of lake trout in the lake, did affect fishing effort expended by anglers, but angling effort tracked CPUE abundance only in remote areas. This finding suggests that improved access leads to a shift in the “predator–prey” response of anglers to fish abundance (Cox et al. 2003; Post et al. 2008). The increased ease of access (e.g., decreased time spent foraging) appeared to compensate for decreased fish abundance (e.g., lower quality food patch) in the readily accessible lakes. In contrast, when anglers must expend more energy to reach remote lakes, they deliberately balance this deficit by searching for the highest quality fisheries. Post et al. (2008) reported a similar finding from rainbow trout (*Oncorhynchus mykiss*) fisheries in the interior of British Columbia. An alternate explanation for our observations is that anglers in remote areas display self-regulation and simply move on to higher quality lakes once fish abundance declines by some detectible level in the fishery (Hansen et al. 2000). This situation would help in maintaining lake trout stocks in remote lakes by allowing time to recover before intensive fishing occurs again. In contrast, in the easily accessible lakes with high fishing pressure, self-regulation of the fishery is far less effective. Catch rates are often independent of the initial decline in lake trout populations (Shuter et al. 1998), allowing road-accessible lakes to rapidly approach and perhaps stay in a collapsed state (Gunn and Sein 2000).

Our results suggest that angling effort is strongly related to the type of access available, but only weakly related to the proximity of population centres. Other studies have suggested strong relationships between effort and distance to population centres (Post et al. 2002, 2008). In our region, linear distances are likely an inappropriate measure because forestry roads can be extremely convoluted and of varying quality along their lengths. We therefore chose to represent our measure of accessibility by the time spent traveling to a given lake. We also considered the influence of up to two different population centres on the effort applied to each lake, rather than the influence of one comparatively large population centre on each lake as in Post et al. (2008). Another confounding factor that we could not account for was influence of angler participation rates in cities or towns of differing population size. Based on the resource-based nature of the community types in northeastern Ontario, we would expect that the declining relationship in participation rates with population size derived in Post et al. (2008) would be less pronounced in our study. We attempted to account for this by weighting travel times in favour of large communities.

Assessment of smallmouth bass introduction

Although smallmouth bass are native to portions of the Shield area of Ontario (Hubbs and Lagler 2004), they have also been introduced widely throughout Ontario. Of the estimated 2421 smallmouth bass populations in Ontario, more than 800 were established through introductions, and bass now occupy lakes and rivers at least as far north as Timmins (Kerr and Grant 2000). Several recent studies show that bass introductions into new waters are still occurring (Snucins and Gunn 2003; Lippert et al. 2007). All of the lakes with bass in our study were found either where they were absent during the AHI surveys or in lakes at elevations that were above the levels that would have allowed natural postglacial colonization (Robbins and MacCrimmon 1974). Mean elevation of our lakes with bass was 300 m, whereas the highest elevation from Robbins and MacCrimmon (1974) where bass would occur naturally was 300 m. In addition, we have shown a strong association of the presence of bass with road accessibility and the presence of cottages and (or) lodges. Roads have been identified as major vectors for the inland spread of several exotic species (Bossenbroek et al. 2001; MacIsaac et al. 2004). More specifically, studies of factors affecting smallmouth bass introductions into other lake trout lakes in Ontario have identified road accessibility as a likely factor in explaining their current distribution (Vander Zanden et al. 2004*a*, 2004*b*). Other factors in the Vander Zanden et al. (2004*a*) model of bass distribution, such as lake surface area, were similar among our study lakes with and without bass.

Effect of angling effort and introduced smallmouth bass on lake trout abundance

In our study, road access was clearly associated with two stressors that impact lake trout populations: high angling effort and the presence of smallmouth bass. However, even in remote lakes without bass, lake trout abundance was still only half that of unfished reference lakes. Our aerial surveys also found that fishing effort exceeded sustainable levels in many of the remote lakes. In addition, no physical or chemical characteristics that may affect lake trout abundance (Trippel and Beamish 1993) could account for observed differences in CPUE among reference, road-accessible, or remote lakes. These findings therefore add to a growing body of evidence (Post et al. 2002; Lester et al. 2003) indicating that natural lake trout populations are depleted across much of the Boreal Shield of Ontario and that overexploitation is likely the main cause. Recent experimental studies have reduced concerns about habitat alterations (e.g., sedimentation) as a serious impact on small Shield lakes (Gunn and Sein 2000; Steedman and France 2000; Steedman and Kushneriuk 2000), and there is encouraging evidence that regional acidification is also declining (Gunn and Keller 1990). Earlier studies have also concluded that Ontario lake trout populations are also particularly sensitive to exploitation (Payne et al. 1990; Shuter et al. 1998). The Shuter et al. (1998) simulation model indicated that if a population is exploited beyond a “safe” level of effort, it could sustain itself at a lower equilibrium abundance.

Our results suggest that many of the road-accessible populations may be in a very depleted state, with heavily angled lakes having approximately one-fifth of the lake trout abundance found in reference lakes. The presence of smallmouth bass therefore appears to have an equivalent effect on lake trout as high rates of exploitation. Introduced bass are known to decimate littoral fish communities such as yellow perch (*Perca flavescens*) (Lippert et al. 2007) and cyprinids (Jackson 2002) that provide important seasonal forage for lake trout (Vander Zanden et al. 1999*a*). This effect is often exacerbated by nearshore habitat alterations brought about by human development (Jackson 2002). In these instances, lake trout are forced to consume energetically less profitable food such as zooplankton (Vander Zanden et al. 1999*b*). Vander Zanden et al. (2004*a*) suggest that pelagic forage species should buffer the effects of bass introductions on the trophic status of lake trout; however, our results show that lake trout abundance was still negatively affected even when pelagic prey (cisco, whitefish, or rainbow smelt) were present in the majority (73%) of lakes with bass. Other physical and chemical factors could not explain the differences among lakes with and without bass. The low abundance of lake trout in the presence of smallmouth bass was also not likely attributable to higher angler harvest, because observed angling effort in remote lakes with smallmouth bass was significantly lower than in remote lakes without smallmouth bass (mean without smallmouth bass = 5.6 $h{\cdot}ha^{-1}$, mean with smallmouth bass = 1.5 $h{\cdot}ha^{-1}$, t_{33} = 3.23, P = 0.003). We acknowledge that our single point in time sampling does not capture the effects of possible past exploitation and that the lower lake trout CPUE in the remote lakes with bass may be a function of this history. However, the food web alterations that accompany bass introductions could impede recovery if these were once heavily exploited trout populations.

The combined effects of these stressors (i.e., road-accessible lakes with bass) did not appear to result in a further decrease in lake trout abundance. However, we lacked the statistical power in our broad-scale survey approach to adequately address this question. At the observed level of among-lake variation, a sample size of lakes larger than the number of known lake trout lakes in the province would be needed to accurately detect an additive effect.

Our study indicates that lake trout fisheries over a large region of northeastern Ontario are depleted and that roads are an important vector for increased exploitation and the introduction of smallmouth bass, a species that adversely affects lake trout. Our findings concur with similar results or concerns expressed by other authors (Post et al. 2002; Lester et al. 2003; Browne 2007), but in this broad-scale survey, we have added considerable quantitative data to support our interpretation of these changes and trends. The expected expansion of the range of smallmouth bass under climate change and continued extension of road networks into wilderness areas demands that strong measures be taken to protect remaining lake trout populations.

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Appendix A. Nordic index netting calibration

Calibration of the Nordic method to lake trout density was performed between 1999 and 2002 on 10 lakes (see Fig. 1 in main text) where detailed population estimates were available, either by mark–recapture studies (N = 5) or by plantings of known numbers of lake trout in former trout lakes where native populations had been completely extirpated (N = 5) (Table A1). Hatchery-reared lake trout (both adult brood stock and 1- and 2-year-old juveniles) were released in the lakes 1–2 months before the netting was conducted. One lake (Broker) was surveyed in 2001 and 2002; known numbers of trout were planted each year but identified by unique fin clips. For each calibration lake, the CPUE was calculated only for the lake trout within the size range of fish used in the corresponding population estimate.

Calibration of the Nordic gear to lake trout density tested two models relating catch per unit effort (CPUE) to fish density. Generally, CPUE is related to density (N) by the equation

$$\text{(A1)} \quad \text{CPUE} = q \cdot N$$

where q is catchability (Ricker 1975). This assumes that catchability is density-independent; therefore, we also tested the model for density-dependent catchability:

$$\text{(A2)} \quad \text{CPUE} = q \cdot N^b$$

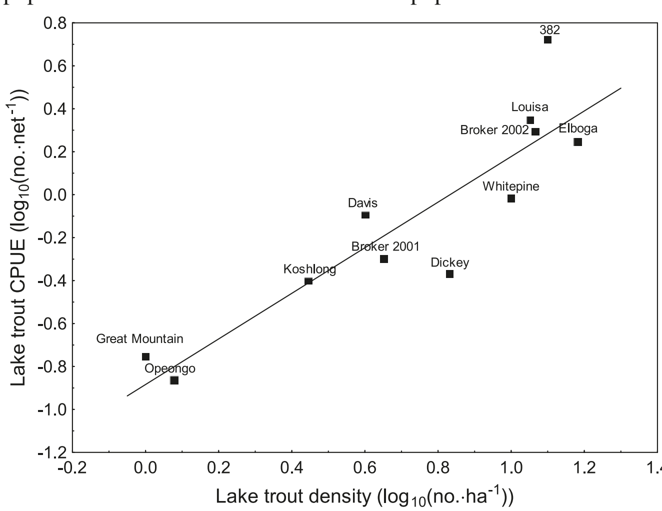
where b is the allometric slope of relationship between CPUE and density.

Table A1. Surface area (ha), lake trout (*Salvelinus namaycush*) size used in population estimate (mm), density (number·ha^{-1}), and source of population estimates for 11 lakes in Ontario, Canada, used in calibration of the Nordic method.

Lake	Surface area (ha)	Size (mm)	Lake trout density (no.·ha^{-1})	Source
Lake 382	37	>127	12.6	Mills et al. 2002
Louisa	567	>300	11.3	B. Munroe, Algonquin Fisheries Assessment Unit, Ontario Ministry of Natural Resources, Whitney, Ont., personal communication
Whitepine	67	>350	10	J. Gunn, Cooperative Freshwater Ecology Unit, Laurentian University, Sudbury, Ont., unpublished data
Davis	34	>370	4	Experimental stocking, E. Snucins and W. Selinger
Great Mountain	198	>560	1	Experimental stocking, E. Snucins and W. Selinger
Dickey	209	>275	6.8	D. Hughes, Haliburton–Hastings Fisheries Assessment Unit, Ontario Ministry of Natural Resources, Bancroft, Ont., personal communication
Koshlong	409	>200	2.8	D. Hughes, Haliburton–Hastings Fisheries Assessment Unit, Ontario Ministry of Natural Resources, Bancroft, Ont., personal communication
Opeongo[a]	1799	>450	1.2	T. Middel, Harkness Fisheries Laboratory, Ontario Ministry of Natural Resources, Algonquin Provincial Park, Ont.
Broker 2001	108	>174	4.5	Experimental stocking, E. Snucins and W. Selinger
Broker 2002	108	>140	11.7	Experimental stocking, E. Snucins and W. Selinger
Elboga	28	>470	15.2	Experimental stocking, E. Snucins and W. Selinger

[a]Only one arm of this lake was surveyed (total lake surface area = 5863 ha); netting results were assumed to be representative of the entire lake.

Fig. A1. Catch per unit effort (CPUE; no.·net^{-1}, log-transformed) from Nordic surveys versus known densities (no.· ha^{-1}, log-transformed) from 10 Ontario lake trout (*Salvelinus namaycush*) populations. See Table A1 for details on population estimates.



Calibration experiments showed a strong positive linear correlation between the log-transformed netting CPUE and known densities of lake trout (also log-transformed) in the test lakes. CPUE explained 81% of the variation in density ($P < 0.001$; Fig. A1). Furthermore, the slope of the allometric equation (1.06 ± 0.17 (standard error of the estimate)) was not significantly different from 1 (*t* test, $t_9 = 0.35$, $P > 0.50$). The final model was

$$\text{(A3)} \qquad \text{CPUE} = 0.13 \cdot N$$

where CPUE is the arithmetic mean CPUE (number per net) and *N* is the population density (number per hectare).

Reference

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