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Effects of restrictive harvest regulations on rehabilitation of coaster brook trout in Minnesota's portion of Lake Superior

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ABSTRACT

Adfluvial brook trout in Lake Superior, commonly referred to as coasters, were once widely distributed among tributaries and supported trophy fisheries. The Minnesota Department of Natural Resources recently enhanced efforts to rehabilitate brook trout in Minnesota waters by imposing restrictive harvest regulations intended to produce more large individuals adopting a coaster life-history. The agency evaluated effects of the regulation changes by conducting electrofishing stream surveys concurrently with changes and three additional times over the next 16 years. Catch per unit effort of brook trout across all streams was similar among sampling periods. Generalized linear mixed models indicated a greater proportional size structure (number ≥ 330 mm/number ≥ 200 mm) and proportion of older fish (≥ age 3) after the regulation change. Genetic analyses indicated that individuals from coaster hatchery strains, which were stocked in nearby jurisdictions, made up only 5.6% of all individuals in Minnesota streams and 12% of individuals ≥330 mm, although the two largest fish were hatchery strain. Our results indicated that conservative regulations can contribute to rehabilitation of coaster populations and that stocked coasters could not account for the improved size and age structure.

Introduction

Brook trout *Salvelinus fontinalis* are the only native salmonines to inhabit both tributary streams and the waters of Lake Superior in Minnesota. An adfluvial life history form of brook trout in Lake Superior, referred to as "coaster" brook trout, was renowned for achieving large size (MacCrimmon and Gots, 1980; Roosevelt, 1865). Coasters were once widely distributed among Lake Superior tributaries (Newman and DuBois, 1996), although their distribution in most Minnesota tributaries is restricted by natural barrier falls within a short distance of the lake. Anecdotal angling reports indicate that large coasters were frequently caught at stream mouths in Minnesota in the mid to late 1800s, prior to the establishment of railways and roads (Roosevelt, 1865; Smith and Moyle, 1944). Soon thereafter, coaster populations experienced precipitous declines due to overfishing, habitat degradation, barriers to migration, and competition with other salmonines (Horns et al., 2003; Newman et al., 2003; Schreiner et al., 2008). Despite adversities over the past 150 years, small numbers of coasters are still present in the Minnesota waters of Lake Superior and utilize spawning and nursery habitat in tributaries.

Early attempts to rehabilitate coasters in Minnesota consisted of stocking various life stages of brook trout from the mid to late 1900s (Schreiner et al., 2006). These efforts were unsuccessful, as were similar attempts by other Lake Superior fisheries management agencies (Newman et al., 2003; Schreiner et al., 2008). In the early 1990s, the Minnesota Department of Natural Resources (MNDNR) began taking a stepwise approach to coaster rehabilitation. In 1992, the agency, after a series of public meetings, developed recommendations for coaster rehabilitation in Minnesota waters. Many of these recommendations were included in the 1995 *Fisheries Management Plan for the Minnesota Waters of Lake Superior* (Schreiner, 1995). The stated goal for coasters in the 1995 plan was to determine if rehabilitation of self-sustaining coaster stocks was feasible in Minnesota's portion of Lake Superior. Recommendations included conducting a genetic assessment to determine the ancestry of existing brook trout before any stocking was to be

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considered. In 1997, an initial shore-wide survey was conducted to determine the distribution, relative abundance and ancestry of brook trout present along the Minnesota shore of Lake Superior (Tilma et al., 1999). The survey was conducted by electrofishing streams below barriers during the spawning period and found a number of streams with low brook trout abundance.

Given the encouraging results of the initial survey, and the desire to protect these stocks (Burnham-Curtis, 2000), the MNDNR responded by implementing conservative regulations in 1997 for the entire 240 km of Minnesota's portion of Lake Superior and the area in streams below barrier falls accessible to migratory fish from Lake Superior. The regulations included a change from a continuous season to a closed season from the day after Labor Day (early September) to mid-April, a reduction in possession limit from five fish in combination with brown trout *Salmo trutta* to only one brook trout, and a change in size limits from a minimum size of 10 in (254 mm) with no more than three fish over 16 in (406 mm) to a minimum size of 20 in (508 mm).

Management for coaster brook trout is complicated by the range of life histories the species exhibits, from lacustrine and lacustrine-adfluvial types to stream residents that may make occasional use of lake habitat, and by the uncertainty as to which factors lead individuals to adopt the different life histories (Huckins et al., 2008; Kusnierz et al., 2009; Robillard et al., 2011b). The MNDNR describes its management of brook trout below barriers in Lake Superior tributaries as management for coaster brook trout (Schreiner et al., 2006). This stems, in part, from Becker's (1983) broad definition of coasters as brook trout that spend part of their life in Lake Superior. The lifetime use of Lake Superior by Minnesota brook trout is unknown, but they must make use of the lake because conditions within streams are often unsuitable for parts of the year. A narrower definition of a coaster includes only the lacustrine and lacustrine-adfluvial life histories (Huckins et al., 2008). Regardless of the definition of a coaster, management actions targeting streams will necessarily affect adfluvial and resident brook trout, if present. The implementation of conservative regulations to enhance coaster brook trout populations and fisheries relies on two premises: 1) minimal exploitation of all brook trout will help maintain robust populations that may have a better chance of producing coasters, and 2) minimal exploitation of large coasters will provide them the chance to reproduce and to be captured multiple times to enhance recreational fishing.

The MNDNR has chosen to forego stocking in its current coaster rehabilitation efforts; yet, Minnesota populations may be affected by coasters originating outside of its jurisdiction. The Grand Portage Band of Chippewa stocks streams and in Lake Superior within reservation waters on the northernmost portion of Minnesota's Lake Superior shore (GLFC stocking database, www.glfc.org/fishstocking/; accessed May 14, 2015; Moore et al., 2006). Other agencies in Wisconsin and Michigan also stock brook trout in Lake Superior (GLFC stocking database, www.glfc.org/fishstocking/; accessed May 14, 2015; WIDNR and USFWS, 2005). Recently, these agencies have primarily stocked coaster hatchery strains derived from populations whose individuals achieve large size (Huckins et al., 2008). Wild coasters also can move long distances (e.g., an individual recaptured over 300 km from its tagging site; H. Quinlan, unpublished data). Thus, larger brook trout captured in Minnesota may result from straying hatchery-reared or wild fish as well as the response of local Minnesota populations to regulation changes.

In this paper, we present the results of stream surveys conducted to assess the status of brook trout along the Minnesota shore of Lake Superior. Our objectives are to: 1) describe the distribution of brook trout in streams below barriers during the spawning season, 2) determine if size and age distributions have increased following regulation changes, and 3) determine the extent to which stocked coasters from other management agencies contribute to Minnesota populations. Results presented in this paper may influence the decisions of management agencies with regard to management actions, e.g., restrictive harvest regulations or stocking programs, to rehabilitate self-sustaining coaster populations.

Methods

MNDNR field collections

The study area consisted of sections below barriers in 28 streams and a seasonal barrier on the Knife River along the Minnesota shore of Lake Superior between Duluth and the Grand Portage Reservation (Fig. 1, Electronic Supplementary material (ESM) Table S1). Fall electrofishing surveys were conducted in 1997, 2002, 2007, 2008, and 2013. Not all streams were sampled each of these years. In particular, several larger streams could not be sampled in 2007 due to high sustained flows and were instead sampled in 2008. Also, only 10 streams were sampled in 2002 due to limited staff availability. The sample in 1997 was concurrent with regulation changes and was considered pre-regulation for comparison to post-regulation samples. Data from 2007 and 2008 were combined and treated as one sample year for analysis. Streams were sampled from late-September through early-November. Multiple trips were made to the same stream in some years, resulting in 1–6 sampling events per stream. Sampling occurred from the lake to the first barrier falls, to the extent possible, on all streams (ESM Table S1). A single individual in 1997 was sampled in an adult trap 0.1 km from the lake on the French River. Water temperature was measured near the stream mouth on each sampling date.

Fish were sampled using a Smith Root model 11-A backpack electrofishing unit (300–400 V, 60 Hz) or an ETS Electrofishing ABP-3 unit. Sample crews consisted of 3–6 individuals depending on stream width. A splitter was placed on the electrofishing unit to allow two anodes, or for some larger streams, two units were used. Multiple passes were conducted if all brook trout observed on the first pass were not netted, and time allowed. Gear configurations, crew members and sampling intensity (time electroshocked per stream distance) varied across years. In contrast, station length of each stream did not change

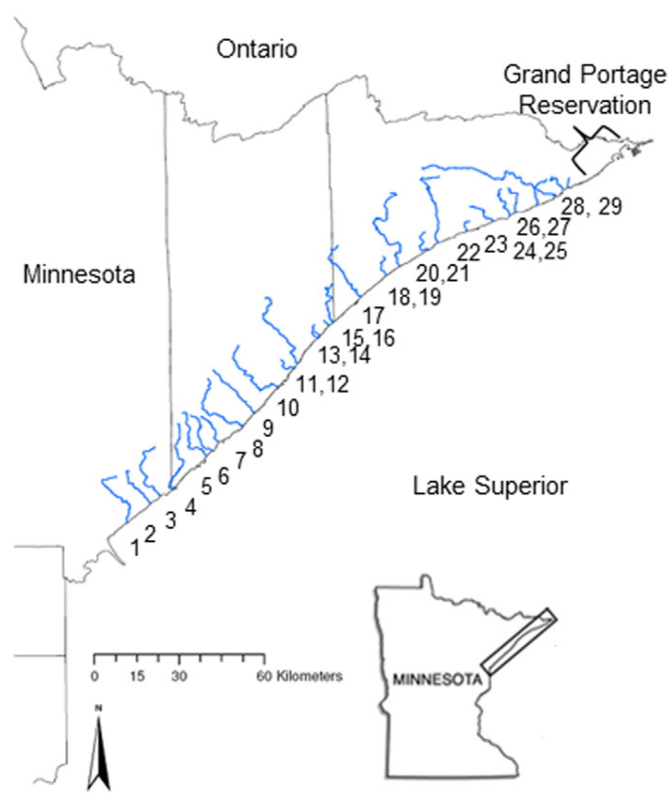

Fig. 1. Locations of streams sampled on the Minnesota shore of Lake Superior. Stream names are indicated in ESM Table S1.

throughout the surveys. Catch rates were therefore determined as the number of fish sampled per stream distance (fish/km), which likely better reflected fish abundance than fish per unit time. When multiple passes were conducted, catch rates were based on the number sampled on the first pass only.

All brook trout sampled were measured to the nearest millimeter (mm). Scale samples were collected for age determination and back-calculation of mean length at age using the biological intercept model (Isely and Grabowski, 2007). A small portion of a pelvic fin was placed in 95% ethanol or air dried in envelopes for genetic analysis.

Additional samples for genetic analysis

Genetic material or genotype data were provided by partner management agencies to represent the coaster brook trout hatchery populations that have been stocked in Lake Superior: Nipigon strain derived from Lake Nipigon, Ontario, populations and reared in Canadian and Red Cliff tribal hatcheries, and Tobin Harbor and Siskiwit Bay strains derived from Isle Royale, Michigan, populations and reared in U.S. Fish and Wildlife Service (USFWS) hatcheries. The USFWS provided adipose fin clips from 45 adults collected to obtain gametes to supplement captive broodstocks in fall 2008 from Tobin Harbor. Additional genotype data were provided by the United States Geological Survey (Wendylee Stott, Great Lakes Science Centre, Ann Arbor, MI) for samples from Siskiwit Bay and Lake Nipigon, and from six Minnesota tributaries to Lake Superior sampled in 1998 upstream of the barrier falls. The Grand Portage Band provided 31 scale samples collected from four streams along the northernmost section of Minnesota's Lake Superior shoreline in 2007 and 2008. Streams and nearshore waters of the reservation previously had been stocked with Nipigon strain brook trout and have continuously been stocked since 2004 with Siskiwit Bay or Tobin Harbor strain brook trout. Note that hereafter the term Minnesota streams refers to all Lake Superior tributaries in the state exclusive of the reservation streams.

Genotyping

Only samples from 2007 onward were evaluated for genetics because the stocking program using Isle Royale coaster strains in nearby Grand Portage streams had begun three years earlier and increases in size and age structure in Minnesota streams were first becoming apparent, leading managers to question whether hatchery strays were accounting for the larger fish. Tissue samples from 2007, 2008 and 2013 were prepared for polymerase chain reaction (PCR) amplification using a DNA extraction procedure. A piece of fin was placed in a 1.5 ml tube with 250 ml of 5% solution of chelating resin (Chelex®, Sigma Chemical, St. Louis, MO). Samples were incubated overnight in 56 °C water bath and boiled 8 min. Microsatellite amplification was performed in 15 μl reactions containing 1× polymerase buffer (10 mM Tris–HCl, 50 mM KCl, 0.1% Triton® X-100), 1.5 mM $MgCl_2$, 0.2 mM each dNTP, 0.5 μM of the forward and reverse primers, with the forward primer labeled with a fluorescent dye 6FAM, VIC, NED or PET, and 0.5 units Taq DNA polymerase (Promega, Madison, WI). Nine microsatellite DNA loci designed for brook trout were used in the survey: SfoC24, SfoC38, SfoC79, SfoC86, SfoC88, SfoC113, SfoC115, SfoC129, and SfoD75 (King et al., 2012). Each set of samples included a water blank as a negative control to detect possible contamination of PCR solutions. Amplification was carried out with 35 cycles at the following temperature profile: 95 °C for 30 s, 50 °C for 30 s, and 72 °C for 1 min; followed by a 20 min extension at 72 °C. PCR products were submitted to the Biomedical Genomics Center (University of Minnesota, St. Paul) for electrophoresis on an ABI Prism 3130xl Genetic Analyzer (Applied Biosystems, Foster City, CA). Alleles were scored using the software program Genemapper v.4.1 (Applied Biosystems).

Population data analysis

Although the goals of coaster management in Minnesota are to protect and maintain self-sustaining populations (Schreiner et al., 2006), it was recognized that limited nearshore and stream habitat may restrict abundance (Ostazeski and Schreiner, 2004; Tilma et al., 1999). In addition, abundance is difficult to measure with electrofishing as stream flows fluctuate widely and fish move between the lake and streams. Therefore, effects of conservative regulations may more readily be detected as changes in size and age structure than increases in abundance. Furthermore, from an angler's perspective, it was the large size of coasters that historically brought fame to the fisheries (MacCrimmon and Gots, 1980; Roosevelt, 1865), and is an important component of the desire to rehabilitate populations.

Changes in length and age distributions of Minnesota brook trout following regulation changes were of main interest. Brook trout sampled throughout this study are assumed to represent a random sample for each sampling year. Recaptured fish from multiple sampling events within the same year (recognized by clipped fins) were removed so that only unique individuals were included in analyses. To assess changes in length distributions among survey years, the proportional size structure (PSS_Q) was assessed using standards proposed for lake inhabiting brook trout:

$$\frac{\text{number of quality length fish} \geq 330\text{ mm}}{\text{number of stock length fish} \geq 200\text{ mm}}$$

(Anderson, 1980). Because all fish were captured in streams and their lifetime use of Lake Superior was unknown, no attempt was made to classify individuals as coasters. Instead, PSS_Q standards for lake-inhabiting brook trout were used to evaluate increases at the upper end of the length distribution, which would most likely reflect increases in fish adopting a coaster life history.

To assess changes in age distributions, the proportions of older fish (≥ age 3) were compared, excluding age 0 because of the ineffectiveness of sampling this age class. Reports on the utility of scales for aging brook trout vary widely (Cooper, 1951; Stolarski and Hartman, 2008; Bobrowksi et al., 2011). For example, Stolarski and Hartman (2008) found good agreement between ages assigned by scales and otoliths up to age 2, but scales tended to produce age estimates lower than those of otoliths among older individuals. Scales were used throughout the present study, therefore analyses based on age were presumed appropriate because bias, if present, should have similarly affected samples collected before and after regulation changes.

Generalized linear mixed-effect models with a logistic link function and binomial error distribution (Breslow and Clayton, 1993) were fit to estimate PSS_Q and proportions of fish ≥ age 3 for each sample year (2007 and 2008 combined as one sample year). The PSS_Q is equal to the conditional probability of a fish's length being ≥330 mm given that it is ≥200 mm; thus, a logistic model was fit for the Prob(length ≥ 330) in the subset of all individual fish data in which length ≥ 200 mm to estimate PSS_Q across the study region. A categorical Year variable was used as a fixed effect explanatory variable with the model contrasts set so that the pre-regulation year 1997 was compared to each of the other sample years. A Gaussian random stream effect with variance σ^2_{stream} was included to accommodate repeated measures in individual streams in different years; this adjusts for inherent differences among streams so the fixed year effects give an estimate of the average PSS_Q across all streams for each sample year (note that because the model was fit at the individual fish level, it explicitly adjusts for different sample size among streams). The model gave an estimate of among-stream variability in PSS_Q in the σ^2_{stream} parameter, and also allowed predictions of typical PSS_Q for each stream. Similarly, a mixed effect logistic model was fit for Prob(age ≥ 3) using the subset of data for which age > 0, and each of the sample year effect estimates of Prob(age ≥ 3) was compared to 1997. Models including Year were compared to a null intercept-only model (i.e., one that assumes no differences among sampling years) with Akaike information criterion (AIC) scores. Models provided evidence for yearly differences if they reduced AIC scores >2 compared with the null model (Burnham and Anderson, 2002).

Genotypic data analysis

Data were first tested for deviations from Hardy–Weinberg expectations and linkage equilibrium using the probability test (Raymond and Rousset, 1995) in the software GENEPOP v.4. Only the Tobin Harbor and Lake Nipigon populations and those from six Minnesota streams were tested due to small sizes of other samples.

The Bayesian clustering algorithm implemented in the program STRUCTURE (Pritchard et al., 2000) was used to identify coaster hatchery strain ancestry (i.e., strays or their descendants) in individuals from Minnesota and Grand Portage streams. STRUCTURE estimates the number of genetically distinct populations (K) contributing to a set of samples and the proportion of the genome (i.e., the ancestry) contributed to individuals by each of the K populations. Based on simulations described in ESM Appendix S1, analyses were run at $K = 4$. Using resulting ancestry proportion estimates and criteria established in the simulations, each individual was categorized as wild Minnesota, Isle Royale coaster hatchery strain (either Tobin Harbor or Siskiwit Bay), Nipigon coaster hatchery strain, or an admixed descendant of hatchery and wild Minnesota fish.

After assigning ancestry, ANOVA and post-hoc Tukey HSD tests were used to compare back-calculated lengths-at-age among wild Minnesota, coaster hatchery strain individuals in Minnesota streams, and admixed descendants. Back-calculated lengths-at-age for Isle Royale populations were also compared using means and standard errors from Slade (1994) (raw data were not available). Aging errors may have occurred; however, readers reported greatest difficulties in detecting annuli at the outer edge of scales from older fish. Back-calculated lengths to early ages would still be valid if early annuli were accurately identified.

Results

Population characteristics

A total of 29 streams were sampled by MNDNR, but the number varied each year: 22 (1997), 10 (2002), 25 (2007–08), and 26 (2013) (Table 1). Three streams were sampled just one year, 6 in two years, 13 in three years, and 7 streams were sampled in all four years. Due to multiple trips to some streams in a sampling year, the number of sampling events completed was 41 (1999), 24 (2002), 59 (2007–08), and 39 (2013). The high number of sampling events in 2007–08 was due to the survey being split between two years. Due to high water conditions only small to medium size streams were sampled in 2007. The larger rivers were then sampled in 2008 along with some of the more productive streams from 2007. Water temperatures ranged between 0 and 15 °C during sampling, but 67% of fish were captured while water temperatures were between 1.4 °C and 6.9 °C and 96% were captured at temperatures between 0 °C and 9.7 °C (Table 2). These data need to be interpreted cautiously because warmer temperatures were not encountered in all years (ESM Table S2), in part because they were avoided based on previous experience.

A total of 385, 126, 358, and 264 brook trout were sampled during the 1997, 2002, 2007–08 and 2013 surveys, respectively. Catches varied widely among streams, but also among years and sampling events within years for the same stream (Table 1, ESM Table S2). For example, only eight streams had more than 10 individuals sampled in a single event, but only Kimball Creek achieved this every year. Thirteen streams had no brook trout sampled at least one year, but Farquar Creek was the only stream sampled in multiple years without sampling a brook trout. Within the same year, 16 streams had brook trout sampled during at least one event, but no brook trout were sampled on another attempt.

Table 1
Number of brook trout sampled (N) in Minnesota tributaries of Lake Superior and mean catch per effort based on distance sampled (N/km) during 1–6 sampling events (S) per year for each stream in 1997, 2002, 2007, 2008 and 2013. Streams are numbered as shown on Fig. 1.

	1997			2002			2007			2008			2013		
Stream	N	S	N/km	N	S	N/km	N	S	N/km	N	S	N/km	N	S	N/km
1. Lester River	–	–	–	–	–	–	–	–	–	0	1	0	–	–	–
2. French River[a]	1	1	10	–	–	–	–	–	–	–	–	–	–	–	–
3. Sucker River	0	2	0	–	–	–	2	1	3	1	1	1	1	1	1
4. Knife River	–	–	–	–	–	–	–	–	–	–	–	–	9	1	10
5. Stewart River	3	2	1	–	–	–	0	2	0	–	–	–	0	1	0
6. Silver Creek	3	2	4	–	–	–	5	2	6	–	–	–	1	2	1
7. Encampment River	1	1	3	–	–	–	0	2	0	–	–	–	0	1	0
8. Gooseberry River	–	–	–	–	–	–	–	–	–	4	1	9	26	2	30
9. Split Rock River	12	4	2	–	–	–	–	–	–	1	2	0	0	1	0
10. Beaver River	0	1	0	–	–	–	1	2	3	–	–	–	0	1	0
11. Palisade Creek	–	–	–	–	–	–	0	2	0	–	–	–	1	1	1
12. Baptism River	3	2	1	–	–	–	–	–	–	0	1	0	3	1	3
13. Little Marais River	5	1	31	1	1	6	21	4	30	6	1	38	3	2	9
14. Dragon Creek	–	–	–	–	–	–	–	–	–	3	1	6	1	2	1
15. Little Manitou River	–	–	–	–	–	–	–	–	–	1	1	4	9	1	35
16. Caribou River	0	2	0	–	–	–	2	2	6	2	1	13	4	1	26
17. Cross River	47	6	17	5	3	4	–	–	–	2	2	2	9	2	10
18. Onion River	82	3	92	46	4	38	4	2	7	–	–	–	17	2	29
19. Poplar River	–	–	–	2	3	4	5	1	33	5	2	17	9	3	20
20. Spruce Creek	58	2	172	2	1	12	31	3	43	25	2	74	24	3	48
21. Cascade River	8	2	17	1	1	4	–	–	–	–	–	–	0	1	0
22. Fall River	–	–	–	–	–	–	3	3	14	–	–	–	1	1	14
23. Devil Track River	68	3	10	4	2	1	–	–	–	39	2	9	18	1	8
24. Kimball Creek	32	2	10	46	4	7	16	2	5	26	1	16	37	2	11
25. Kadunce Creek	58	2	68	19	4	11	84	4	30	55	1	86	88	2	103
26. Brule River	–	–	–	0	1	0	–	–	–	–	–	–	–	–	–
27. Flute Reed River	2	2	2	–	–	–	4	2	4	5	1	9	3	2	3
28. Carlson Creek	0	1	0	–	–	–	3	2	2	–	–	–	0	1	0
29. Farquar Creek	0	1	0	–	–	–	0	2	0	–	–	–	0	1	0

[a] A single individual >330 mm was sampled in an adult trap 0.1 km upstream of the stream mouth.

Table 2
Stream temperatures at the time of sampling for brook trout in Minnesota tributaries of Lake Superior during 1997, 2002, 2007, 2008 and 2013. Date from 2007 and 2008 were combined as one sampling period.

	1997		2002		2007–08		2013		Total	
Temperature (°C)	N	%	N	%	N	%	N	%	N	%
0.0–1.4	114	29.6	9	7.1	7	2.0	13	4.9	143	12.6
1.4–4.2	98	25.5	80	63.5	75	20.9	122	46.2	375	33.1
4.2–6.9	93	24.2	17	13.5	249	69.6	35	13.3	39	34.8
6.9–9.7	52	13.5	20	15.9	14	3.9	90	34.1	176	15.5
9.7–12.5	22	5.7	0	0.0	9	2.5	4	1.5	35	3.1
12.5–15.0	6	1.6	0	0.0	4	1.1	0	0.0	10	0.9

Shorewide catch rates based on fish/km were similar across years; although rates declined in the first two sampling periods following regulation changes, the rate was nearly identical to the pre-regulation rate in the final sampling period (Fig. 2). Based on fish of all sizes, there have not been consistent changes in overall abundance of brook trout; however, catch rates of individuals ≥330 mm suggest increases in larger individuals following the regulation change (Fig. 2).

The size structure (Fig. 3) and age structure (Fig. 4) across all populations varied considerably among years. Few fish overall attained quality size (≥330 mm), but more did so in later years (0.5%, 1.6%, 5.3% and 2.3% of individuals in the respective sampling years). Notably, no fish ≥350 mm or ≥ age 4 were sampled until after the regulation changes. The generalized linear mixed-effect models provided support for shorewide increases in proportions of larger and older fish following regulation changes (Table 3). Models of size structure with year effects lowered AIC scores 2.6 below the null model, with estimated PSS_Q increasing 4–6 times after regulation changes, although only 2007–08 showed a significant increase ($P = 0.01$) compared to the pre-regulation year. The random stream effects showed little variation in PSS_Q among streams, e.g., stream-specific PSS_Q estimates only ranged from 0.08 to 0.10 for the 2013 sample year (ESM Table S3). Models of age structure showed stronger evidence for change, with year effects lowering AIC scores 9.4 below the null model. Year coefficients indicated a slight decrease in the proportion of fish ≥ age 3 from pre-regulation to 2002, but 3–4 times increases in the last two sampling years. Among-stream variability in Prob(age ≥ 3) was estimated to be higher than that for PSSQ; stream-specific estimates for the proportion of fish ≥ age 3 ranged from 0.03 to 0.24 for the 2013 sample year (ESM Table S3). Aging error may have affected these data; but, if the bias was toward underestimating ages of older fish (Stolarski and Hartman, 2008), then our analysis should be conservative. If regulation changes did increase the number of older fish, then post-regulation samples would likely have had more fish with underestimated ages, thus reducing our ability to detect actual increases.

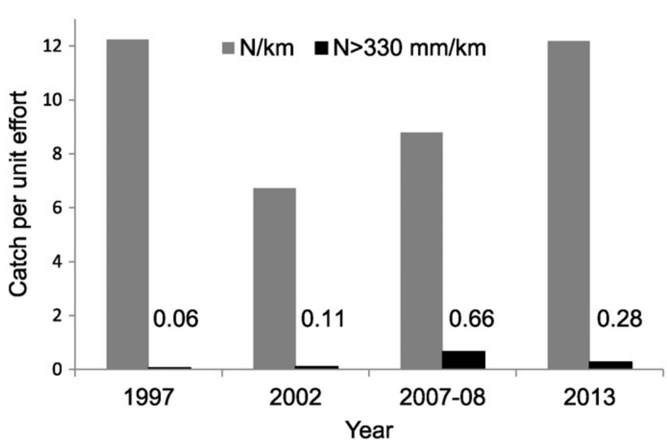

Fig. 2. Catch per unit effort of electrofishing for brook trout in Minnesota tributaries of Lake Superior measured as number per length of stream sampled (N/km) and number of fish ≥330 mm per length of stream sampled (N ≥ 330 mm/km). The latter values are displayed because some bars are difficult to discern on the graph. The data include one individual >330 mm sampled in an adult trap on the French River in 1997.

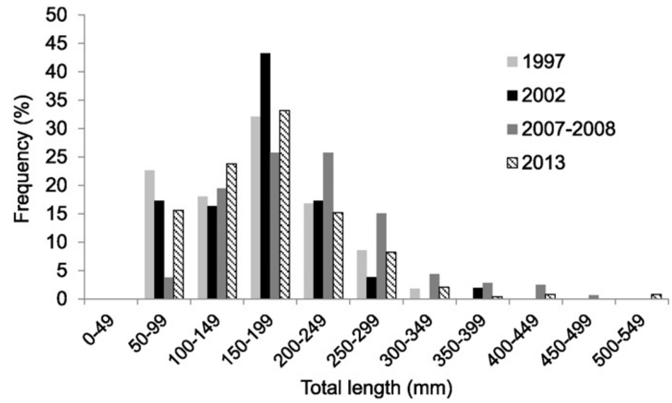

Fig. 3. Length frequency distributions of brook trout sampled in Minnesota tributaries of Lake Superior during 1997, 2002, 2007–2008 and 2013.

Coaster hatchery strain ancestry

Hardy–Weinberg tests were conducted for each locus in the Tobin Harbor and Lake Nipigon samples and the six Minnesota streams with samples size of at least 34. Of 68 tests for polymorphic loci, 15 resulted in P-values <0.05, but only one remained significant after sequential Bonferroni correction for multiple testing (Rice, 1989). Of 278 tests for linkage equilibrium, 35 resulted in P-values <0.05, but only two remained significant after correction for multiple testing. The loci were deemed to meet assumptions of genetic equilibrium for evaluating ancestry in STRUCTURE.

Excluding recaptures, 316 samples collected in Minnesota streams in 2007–08 and 222 collected in 2013 were processed for genetic analysis. Eleven samples from 2007 to 2008 and four from 2013 failed to amplify and four from 2007 to 2008 were identified as splake, which are hybrid crosses between male brook trout and female lake trout *Salvelinus namaycush*. The remaining 518 fish were predominantly (85.3%) of wild Minnesota ancestry and the percentage was similar during both sampling years (Table 4). Only 29 (5.6%) individuals were categorized as coaster hatchery strain. Of these, 16 were assigned to Isle Royale, 4 to Nipigon, and the remaining 9 had relatively high proportions of both Isle Royale and Nipigon ancestry. Finally, another 47 (9.1%) individuals had a mix of coaster hatchery strain and wild Minnesota ancestry.

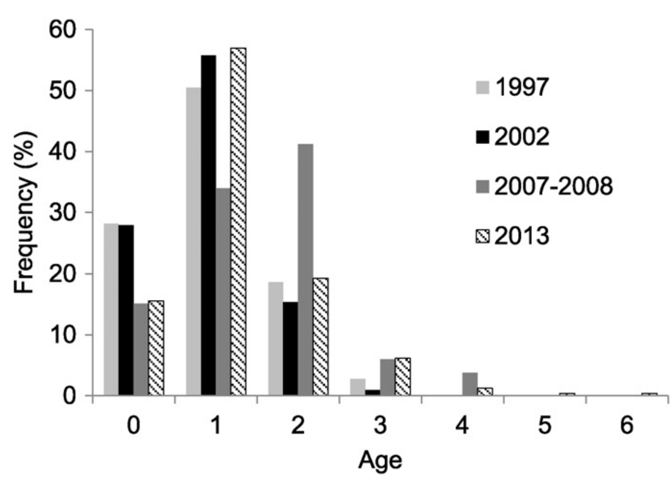

Fig. 4. Age frequency distributions of brook trout sampled in Minnesota tributaries of Lake Superior during 1997, 2002, 2007–2008 and 2013.

Table 3
Generalized linear mixed model estimates for size structure (PSS_Q; sample size = 338 fish from 24 streams) and age structure (proportion of fish ≥ age 3; sample size = 782 fish from 26 streams) before (1997) and after (2002, 2007–08, and 2013) regulation changes for brook trout across all study streams. Intercept values represent model estimates for the 1997 sample year, other model coefficient estimates are contrasts between 1997 estimates and those of post-regulation sample years. P-values represent Z-tests for differences in coefficient estimates from zero; estimated proportions are the model estimates back-transformed to proportions.

Model and year	Model estimate	SE	P-value	Estimated proportion
PSS_Q				
Intercept–1997	−3.78	0.74	3×10^{-7}	0.02
2002	1.39	1.06	0.19	0.08
2007–08	1.84	0.76	0.01	0.13
2013	1.46	0.84	0.08	0.09
Proportion ≥ age 3				
Intercept–1997	−3.45	0.43	4×10^{-15}	0.03
2002	−0.41	1.03	2×10^{-4}	0.02
2007–08	1.40	0.32	1×10^{-9}	0.11
2013	1.20	0.34	9×10^{-11}	0.10

An additional 31 samples from Grand Portage Reservation streams were processed for genetic analysis. Two of these failed and the rest had coaster hatchery strain ancestry: 22 assigned to Isle Royale, 3 to Nipigon and 4 had relatively high proportions of both Isle Royale and Nipigon ancestry. None assigned as wild Minnesota or admixed individuals.

Most fish from Minnesota streams that assigned to coaster hatchery strains occurred in streams close to the Grand Portage Reservation (Table 4). All three fish sampled from Carlson Creek (5 km from the reservation) were assigned to coaster hatchery strains. In 2007–08, all seven streams from Carlson Creek to Spruce Creek (58 km from the reservation) had at least one coaster hatchery strain fish while none were found farther away. In 2013, a lower percentage of coaster hatchery fish were identified and most were with sampled within 76 km of Grand Portage (Flute Reed to Onion River). The single exception was a fish sampled in the Knife River, an additional 100 km farther away. This individual slightly exceeded the assignment criterion for a hatchery strain individual and may be an incorrectly classified admixed individual. Low numbers of putative admixed fish were found in most Minnesota streams.

Table 4
Genetic ancestry assignment for brook trout sampled in Minnesota tributaries of Lake Superior under Minnesota Department of Natural Resources jurisdiction and four streams on the Grand Portage Reservation. Individuals were classified as having wild Minnesota (MN), coaster hatchery of Isle Royale or Nipigon strain (hatchery), or mixed ancestry between wild and hatchery strains (admixed). Streams are numbered as shown on Fig. 1.

	2007–08 ancestry				2013 ancestry			
Stream	N	MN	Hatchery	Admixed	N	MN	Hatchery	Admixed
Minnesota streams								
2. Sucker R	3	2	0	1	1	1	0	0
4. Knife R	2	1	0	1	9	6	1	2
6. Silver Cr	5	4	0	1	1	1	0	0
8. Gooseberry R	4	4	0	0	17	14	0	3
9. Split Rock R	1	1	0	0	–	–	–	–
10. Beaver Cr	1	1	0	0	–	–	–	–
11. Palisade Cr	–	–	–	–	1	1	0	0
12. Baptism R	–	–	–	–	3	3	0	0
13. Little Marais R	24	23	0	1	3	3	0	0
14. Dragon Cr	3	1	0	2	1	1	0	0
15. Little Manitou R	–	–	–	–	9	8	0	1
16. Caribou R	4	3	0	1	4	2	0	2
17. Cross R	2	2	0	0	9	9	0	0
18. Onion R	4	3	0	1	16	6	3	7
19. Poplar R	9	9	0	0	9	9	0	0
20. Spruce Cr	41	33	2	6	21	18	0	3
22. Fall R	3	2	1	0	1	1	0	0
23. Devil Track R	34	29	1	4	16	14	2	0
24. Kimball Cr	37	32	2	3	34	33	0	1
25. Kadunce Cr	112	102	7	3	61	56	1	3
27. Flute Reed R	8	2	5	1	3	2	1	0
28. Carlson Cr	3	0	3	0	–	–	–	–
Minnesota total	300	254	21	25	218	188	8	22
Grand Portage	29	0	29	0	–	–	–	–

Strays from coaster hatchery programs could not account for most of the increase in the number of larger fish. Of the 25 fish of quality length (≥330 mm), most had wild Minnesota ancestry: 17 (68%) assigned as wild Minnesota, 5 (20%) as admixed, and only 3 (12%) as coaster hatchery strains (Fig. 5). The two largest individuals sampled did, however, assign to coaster hatchery strains. These fish, a 536 mm fish assigned to Isle Royale and a 529 mm fish assigned to Nipigon, were the only individuals that exceeded the current minimum size limit of 508 mm for harvest.

Back-calculated lengths-at-age were compared among samples from 2007, 2008 and 2013 that also had genetic ancestry data, and data from Isle Royale coaster populations. Coasters from Isle Royale had the fastest average growth, while coaster hatchery strain individuals appeared to grow faster than wild Minnesota individuals in Minnesota streams (Fig. 6A). Mean back-calculated length-at-age 1 differed among all ancestry groups [$F(3, 462) = 8.23$, $P < 0.001$], but the post-hoc Tukey test indicated that this was attributable to the longer length of Isle Royale coasters ($P < 0.05$). Groups in Minnesota streams differed by at most 3.1 mm. By age 2, mean back-calculated lengths again differed [$F(3, 221) = 24.6$, $P < 0.001$] and Isle Royale coasters were the longest, but the mean length of coaster hatchery strain individuals (211.2 mm) also significantly exceeded that of wild Minnesota individuals (187.6 mm) ($P = 0.05$). Beyond age 2, hatchery strain individuals were longer than wild Minnesota and admixed individuals, but sample sizes were low and no significant differences were detected. Although mean back-calculated lengths were lower, some Minnesota and admixed individuals had growth histories similar to coaster hatchery strain individuals in Minnesota streams (Fig. 6B).

Discussion

Brook trout were consistently found, at least in small numbers, from most tributaries sampled in Minnesota's portion of Lake Superior. The number of larger and older individuals has increased, while overall abundance appears stable, following implementation of conservative regulations. Genetic data indicated that strays from coaster strain stocking programs could not account for most of the increased number of large fish, although the two largest individuals sampled assigned to

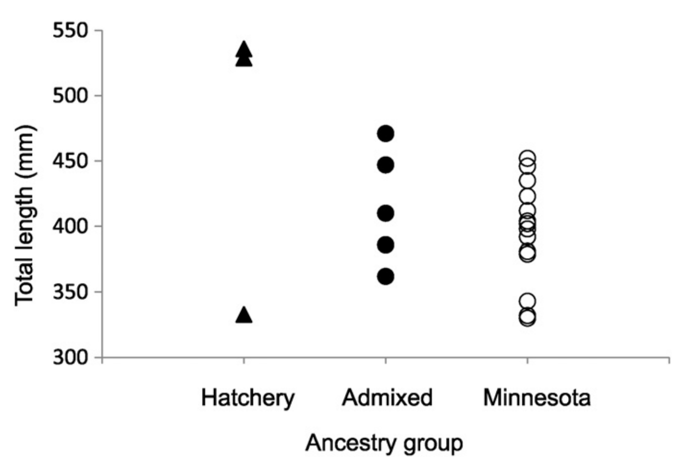

Fig. 5. Ancestry of all quality length fish (≥330 mm). Fish were assigned as wild Minnesota (N = 17), coaster hatchery strain (N = 3), or mixed ancestry between wild and hatchery strains (admixed; N = 5).

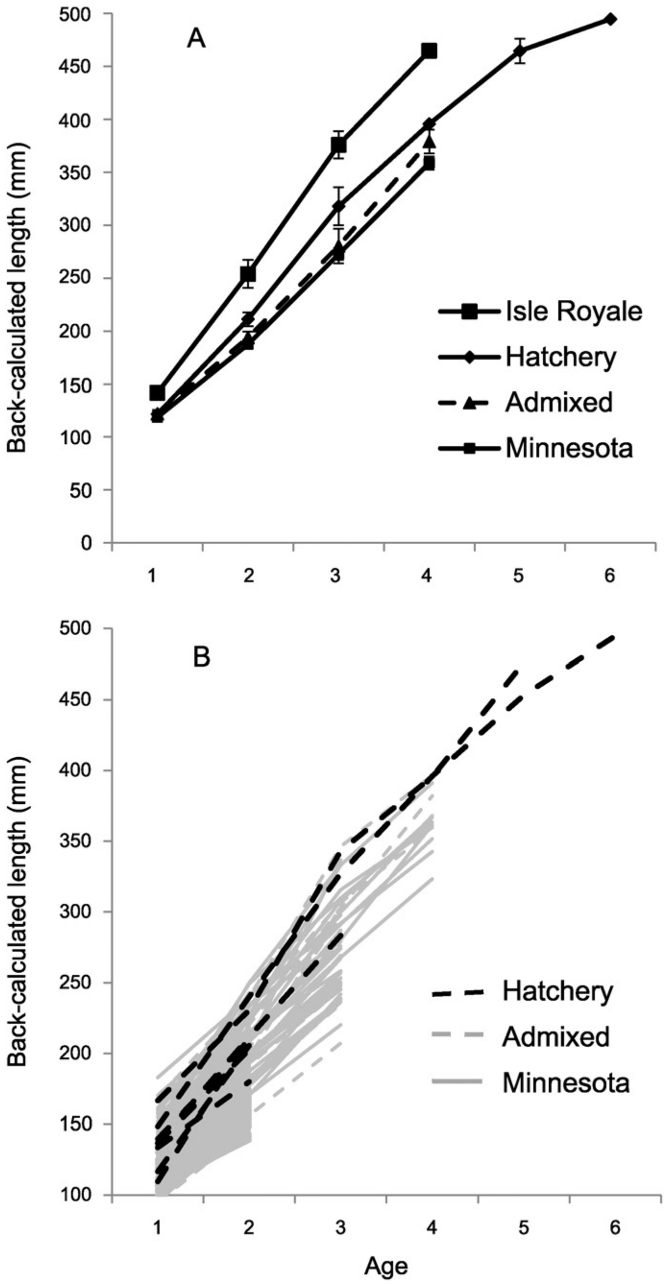

Fig. 6. Back-calculated lengths-at-age (+/−SE) for brook trout sampled in Minnesota streams during 2007, 2008 and 2013 having wild Minnesota, coaster hatchery strain, or mixed ancestry between wild and hatchery strains (admixed). Mean lengths-at-age (A) also include data for coasters from Tobin Harbor, on Isle Royale, Michigan, the source population for one of the hatchery strains (data from Slade, 1994). The figure for back-calculated lengths-at-age for individual brook trout (B) includes only fish ≥ age 2 for clarity.

coaster hatchery strains. Most Minnesota brook trout did not achieve the higher growth rates of the coaster hatchery strains nor the large sizes reached in other coaster populations. Both adequate growth and longevity will be needed to produce more quality-sized fish**.** If MNDNR and the public wish to continue managing for large size structure in Lake Superior brook trout populations, conservative regulations will likely have to remain in place.

Throughout this study, we did not know which individuals have or will make substantial use of Lake Superior habitat. Small numbers of brook trout have persisted in Minnesota streams below barriers with access to Lake Superior, but in recent decades individuals rarely achieved the large sizes characteristic of recognized coaster populations. Prior to the restrictive regulations, populations below barriers did have greater proportions of larger and older fish than did populations above barriers (Tilma et al., 1999), suggesting some use of Lake Superior resources (although seasonal and year differences in sampling may have influenced these findings). Whether brook trout below barriers in Minnesota streams are adfluvial or stream-lake generalists (Robillard et al., 2011b) is uncertain, but they must frequently use the lake as conditions within streams are often unsuitable for parts of the year. Annual electroshocking surveys for juvenile steelhead *Oncorhynchus mykiss* are conducted in late August to early September at many of the same locations sampled during this study. Few brook trout are sampled while targeting juvenile steelhead at these locations (MNDNR, unpublished data), while more brook trout were sampled on most streams during the fall spawning season. Highly variable catches among sampling events in the same year and stream also likely reflect the movement of fish from stream to lake. Several Minnesota or admixed individuals had growth histories similar to those of the coaster hatchery strain individuals, suggesting that they had also used lake habitat. In a similar situation, Scribner et al. (2012) suggested that the brook trout population below barrier falls on the Salmon Trout River, Michigan, was composed of coasters with no resident below-barrier population. The previous lack of large fish in Minnesota streams may have resulted from high mortality for a species vulnerable to angling (Huckins and Baker, 2008; Huckins et al., 2008), resulting in few fish older than age 3 prior to regulation changes. Given a chance to grow older, more fish may attain the large size for which coasters are known (Huckins et al., 2008; Robillard et al., 2011a).

Ontario also has implemented and evaluated conservative regulations for coasters (Bobrowski et al., 2011). In the 1990s, regulations varied for Lake Nipigon, the Nipigon River, and Nipigon Bay of Lake Superior, but bag limits were reduced, seasons were shortened, and relatively high minimum size limits were imposed. In 2005, a consistent regulation allowing just one coaster with a minimum length of 56 cm was implemented for all of these waters. In two bays of Lake Nipigon, the abundance of spawners increased following regulation changes in the 1990s and again following 2005. The mean length and proportion of larger fish (>46 cm) increased in post-2005 samples, although fish >56 cm increased slightly in just one bay. Managers deemed the results encouraging and maintenance of the regulation was recommended (Bobrowski et al., 2011). Ontario's length limit in relation to the size structure of their coaster populations differed greatly from that in Minnesota. In the two bays of Lake Nipigon, 12.5–22.9% of spawners exceeded the high minimum length limit of 56 cm at the time regulations were implemented. In comparison, no individuals sampled in Minnesota stream samples exceeded the length limit of 50 cm at the time of implementation in 1997 and the first to do so were not sampled until 2013. To date, Minnesota's length limits have essentially imposed a catch-and-release fishery.

Our data suggest that Minnesota brook trout do not grow as fast as individuals from several other recognized coaster populations. Back-calculated lengths-at-age were consistently shorter for Minnesota brook trout than they were for coasters from Isle Royale. Lengths at time of capture also support slower growth by Minnesota brook trout. We did not report details on these data because of different sampling times within the growing season across our study and in comparison with other studies (Huckins et al., 2008; Kusnierz et al., 2009). Excluding hatchery strain individuals, brook trout in Minnesota streams averaged 96, 162, 240, 315, and 420 mm at ages 0–4, respectively. These data suggest that a typical Minnesota brook trout grows slower than coasters in Tobin Harbor, the Salmon Trout River, Michigan, and especially Lake Nipigon (Huckins et al., 2008), although they grow faster than those in the Hurricane River, Michigan (Kusnierz et al., 2009). The causes of growth difference remain uncertain because the life history adopted by Minnesota brook trout is unknown. If many brook trout in Minnesota streams make only limited use of the lake, then average growth may be relatively low, but individuals that do use the lake may attain higher growth rates (e.g., Robillard et al., 2011a). However, no brook trout from Minnesota streams, including the coaster hatchery strain fish, had back-calculated lengths beyond age 1 that exceeded the mean lengths reported for Isle Royale coasters (Fig. 6A and B). The relatively low productivity, cold temperatures, and limited amount of shallow water (<7 m) habitat along the Minnesota shoreline likely contribute to slower growth rates.

The proximity to the Grand Portage Reservation of fish assigned to coaster hatchery strains suggests strays from reservation stocking as the likely source of many of these individuals in Minnesota streams. Most of these fish assigned to Isle Royale (Siskiwit Bay and Tobin Harbor), the strains stocked in reservation waters since 2004. Genetic data cannot distinguish hatchery strays from wild offspring of parents from the same strain, but the low number of hatchery strain fish outside of reservation streams makes it unlikely that two hatchery parents would mate in most Minnesota streams. Isle Royale itself is a potential source of natural migrants as it lies only 40 km from the closest Minnesota streams, although coasters must traverse deep water without contiguous coastal habitat that they favor (Mucha and Mackereth, 2008). For the Grand Portage Reservation, stocking has successfully produced some coasters and we found no evidence that populations outside of the reservation have provided migrants to reservation streams, although our sample sizes were low for reservation streams.

Nipigon strain ancestry was low in Minnesota populations, despite the stocking of this strain in the 1980s by the MNDNR, until the early 2000s by the Grand Portage Band, and the ongoing stocking of Nipigon strain or crosses by the Red Cliff Band of Lake Superior Chippewa on reservation waters in Wisconsin. Potential for some straying of wild fish from the Nipigon River area also exists. Only 26 fish had indications of Nipigon ancestry, usually at proportions <0.50. The Wisconsin DNR reports that previous stockings of Nipigon strain coasters have not restored either a resident stream population or provided a significant fishery (Wisconsin DNR, http://dnr.wi.gov/topic/fishing/lakesuperior/cbrktrout.html; accessed June 15, 2015). One fish sampled in 2007 and three in 2013 were assigned to Nipigon strain and were potentially stocked fish, which could have come from stocking waters on the Grand Portage Reservation, the Red Cliff Reservation in northern Wisconsin, or in Michigan. The origins of the four fish identified as splake are also unknown, but they are routinely stocked by the Wisconsin DNR and Michigan DNR into Lake Superior. However, splake are also stocked into a few headwater lakes of Minnesota Lake Superior tributaries and could have migrated downstream.

Admixed individuals were found in many streams, but in low numbers (9.1% of all samples). These individuals would result from natural reproduction between coaster hatchery strain and wild Minnesota individuals. The hatchery strain parents may have come from recent or past stocking of coaster strains in other jurisdictions, natural migrants from Isle Royale, or from past stocking of the Nipigon strain in Minnesota streams. Regardless of the source of hatchery strain ancestry, the low proportion of hatchery strain and admixed individuals indicates relatively little impact of past stocking of coaster hatchery strains on the genetic composition of Minnesota populations. This low impact may result from limited straying or low survival of stocked fish, or poor reproductive contributions when they compete with established populations, as has been observed for other brook trout populations (Wilson et al., 2008).

The extent to which brook trout from populations above barrier falls move downstream over barriers is unknown. Eddy and Underhill (1974) suggested that "the Lake was restocked" by fish passing down from above barriers. Genetic data are consistent with movement as there is relatively low genetic differentiation between above- and below-barrier samples within the same stream (F_{st} range 0.000–0.033; mean 0.015; unpublished data for six streams provided by Wendylee Stott, USGS — Ann Arbor). Scribner et al. (2012) found evidence of individuals from an above-barrier population in below-barrier samples from the Salmon Trout River, Michigan. D'Amelio and Wilson (2008) indicated that connectivity varied considerably between above- and below-barrier brook trout populations in the Nipigon Bay area of Lake Superior, as indicated by a wide range in F_{st} values (0.036–0.220). Regardless of the number of fish moving downstream, they are unlikely to account directly for many large fish below barriers in Minnesota streams. In a 1998 sampling above barriers in 7 streams, only 1 of 318 individuals exceeded 254 mm (Tilma et al., 1999) while 9.2% of the individuals sampled below barriers in 1997 exceeded this size. Above-barrier individuals that move downstream may help sustain below-barrier populations, and some may eventually attain large size due to the added protection of conservative regulations and access to the resources of Lake Superior.

Along with angling, the introduction of numerous other species of trout and salmon over the past century has likely affected brook trout populations (Huckins et al., 2008). The niche once occupied solely by brook trout is now shared by as many as six salmonines. Steelhead, the most frequently sampled salmonine in this study, were introduced into the Minnesota waters of Lake Superior in 1895 (Hassinger et al., 1974). Other salmonines introduced since the mid-1900s and sampled during this study included brown trout, pink salmon *Oncorhynchus gorbuscha*, Chinook salmon *Oncorhynchus tshawytscha*, and Coho salmon *Oncorhynchus kisutch*. Therefore, there is an increased likelihood that non-native salmonines have negatively affected brook trout feeding positions (Fausch and White, 1981), growth rates (Fausch and White, 1986; Rose, 1986), and spawning movements (Janetski et al., 2011), or have reduced some populations of brook trout (Moore et al., 1983; McKenna et al., 2013).

Anecdotal field observations and temperature data revealed lessons about the importance of flow, turbidity, time period and water temperature for determining when migratory brook trout were present in the streams. Streams on the Minnesota shore of Lake Superior are short in length, steep in gradient, and have little groundwater, which results in large fluctuations in flow after precipitation events (Detenbeck et al., 2005). Minimal groundwater contributions and wave action from the lake result in many stream mouths becoming blocked by gravel bars for most summer months (Trebitz et al., 2002). Precipitation events in the fall often restore access between the lake and streams and increase turbidity and flow, both of which have been associated with increased brook trout movements (Gradall and Swenson, 1982; Scruton et al., 2003). Brook trout (and other adult salmonines) were rarely observed in streams under base flow conditions. High water velocity and low visibility precluded effective sampling immediately after precipitation events; however, a sampling opportunity occurred while moderate flows persisted prior to streams returning to low and clear base flow conditions. Temperature also played a role. Most brook trout were sampled between mid and late October, a time period that corresponded with water temperature less than 7 °C. Movements peaked for coaster populations in other parts of the Lake Superior basin during this time and with low or declining water temperatures (Huckins and Baker, 2008; Kusnierz et al., 2009). Tools used to assess individuals' movements in other coaster populations [e.g., two-way fish traps, Huckins and Baker (2008); passive integrated transponder tag detectors, Kusnierz et al. (2009); isotopes, Robillard et al. (2011b)] will be needed to better understand seasonal and lifetime use of lake and stream habitats by Minnesota brook trout.

A number of factors were considered before MNDNR implemented harvest regulations. An initial survey determined which tributaries supported brook trout, their relative abundance, and the pre-regulation size structure. We were surprised to find spawning brook trout in tributaries where they were not expected based on summer electrofishing surveys and angler reports. In some cases, anglers and agencies have advocated for implementation of stocking programs before initial surveys have been conducted. Leonard et al. (2013), addressing an coaster rehabilitation effort in another part of Lake Superior, noted that prior information would have likely altered management decisions regarding stocking to better conserve local genetic diversity and consider the ecological context for the action. Post-regulation sampling called for in the management plan showed the value of monitoring populations. We documented increases in large fish, which will help maintain angler support for the regulations. Unfortunately, few fall creel survey data (which targeted a Chinook salmon fishery) were available to assess declines in fishing pressure resulting from regulation changes, but anecdotal reports to MNDNR suggest minimal harvest mortality.

We have shown that restrictive harvest regulations, when implemented across a large expanse of contiguous shoreline, can improve size and age structure of a coaster brook trout stock, although in Minnesota, shore-wide abundance has apparently remained relatively unchanged. Restrictive regulations were deemed necessary for coaster rehabilitation (Huckins et al., 2008) and other jurisdictions have implemented regulation changes, including Ontario, Michigan and Wisconsin, but few data are currently available to evaluate effectiveness in the latter two states (Bobrowski et al., 2011). Nearby jurisdictions have also stocked coaster hatchery strains as part of their rehabilitation efforts (WIDNR and USFWS, 2005; Moore et al., 2006; Leonard et al., 2013), but so far this has not led to substantial increases in coasters in American waters (Bobrowski et al., 2011). Although two fish in our study likely came from these stocking efforts, MNDNR intends to continue using restrictive regulations, along with habitat enhancement, as its primary brook trout management tools. Anglers must be informed that the purpose of the restrictive regulation is focused on preventing overharvest of brook trout before they are allowed to grow and reproduce, and that the traditional harvest-based fishery will no longer be available. Anglers must also have realistic expectations that after implementing restrictive harvest regulations it will take time before noticeable changes in size and age structure will occur.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.jglr.2016.05.006.

References

Anderson, R.O., 1980. Proportional stock density (PSD) and relative weight (Wr): interpretive indices for fish populations and communities. In: Gloss, S., Shupp, B. (Eds.), Practical Fisheries Management: More With Less in the 1980s. Proceedings of the 1st Annual Workshop of the New York Chapter American Fisheries Society, pp. 27–33.

Becker, G.C., 1983. Fishes of Wisconsin. University of Wisconsin Press, Madison.

Bobrowski, R., Chase, M., Swainson, R., Van Ogtrop, A., Bobrowicz, S., Cullis, K., Sobchuk, M., 2011. Update on brook trout rehabilitation in the Ontario waters of Lake Superior, Lake Nipigon, and the Nipigon River: Public Workshop Proceedings. Upper Great Lakes Management Unit Technical Report 11-02. Ontario Ministry of Natural Resources, Thunder Bay, ON (31 pp.).

Breslow, N.E., Clayton, D.G., 1993. Approximate inference in generalized linear mixed models. J. Am. Stat. Assoc. 88 (421), 9–25.

Burnham, K.P., Anderson, D.R., 2002. Model Selection and Multimodel Inference. Springer-Verlag, NY.

Burnham-Curtis, M.K., 2000. Genetic profiles of selected brook trout populations from Lake Superior. Research Completion Report Prepared for U.S. Department of the Interior, U.S. Fish and Wildlife Service, Ashland Fisheries Resource Office, Ashland, WI.

Cooper, E.L., 1951. Validation of the use of scales of brook trout, *Salvelinus fontinalis*, for age determination. Copeia 1951, 141–148.

D'Amelio, S., Wilson, C., 2008. Genetic population structure among source populations for coaster brook trout in Nipigon Bay, Lake Superior. Trans. Am. Fish. Soc. 137, 1213–1228.

Detenbeck, N.E., Brady, V.J., Taylor, D.L., Snarski, V.M., Batterman, S.L., 2005. Relationship of stream flow regime in the western Lake Superior basin to watershed type characteristics. J. Hydrol. 309, 258–276.

Eddy, S., Underhill, J.C., 1974. Northern Fishes, With Special Reference to the Upper Mississippi Valley. third ed. University of Minnesota Press, Minneapolis (414 pp.).

Fausch, K.D., White, R.J., 1981. Competition between brook trout and brown trout for positions in a Michigan stream. Can. J. Fish. Aquat. Sci. 38, 1220–1227.

Fausch, K.D., White, R.J., 1986. Competition among juveniles of Coho salmon, brook trout, and brown trout in a laboratory stream, and implications for Great Lakes tributaries. Trans. Am. Fish. Soc. 115, 363–381.

Gradall, K.S., Swenson, W.A., 1982. Responses of brook trout and creek chubs to turbidity. Trans. Am. Fish. Soc. 111, 392–395.

Hassinger, R.L., Hale, J.G., Woods, D.E., 1974. Steelhead of the Minnesota North Shore. Section of Fisheries Technical Bulletin 11. Minnesota Department of Natural Resources, St. Paul.

Horns, W.H., Bronte, C.R., Busiahn, T.R., Ebener, M.P., Eshenroder, R.L., Gorenflo, T., Kmiecik, N., Mattes, W., Peck, J.W., Petzold, M., Schreiner, D.R., 2003. Fish Community Objectives for Lake Superior. Great Lakes Fishery Commission, Ann Arbor, MI (Special Publication 03-01).

Huckins, C.J.F., Baker, E.A., 2008. Migrations and biological characteristics of adfluvial coaster brook trout in a south shore Lake Superior tributary. Trans. Am. Fish. Soc. 137, 1229–1243.

Huckins, C.J., Baker, E.A., Fausch, K.D., Leonard, J.B.K., 2008. Ecology and life history of coaster brook trout and potential bottlenecks in their rehabilitation. N. Am. J. Fish. Manag. 28, 1321–1342.

Isely, J.J., Grabowski, T.B., 2007. Age and growth. In: Guy, C.S., Brown, M.L. (Eds.), Analysis and Interpretation of Freshwater Fisheries Data. American Fisheries Society, Bethesda, MD, USA, pp. 187–232.

Janetski, D.J., Moerke, A.H., Chaloner, D.T., Lamberti, G.A., 2011. Spawning salmon increase brook trout movements in a Lake Michigan tributary. Ecol. Freshw. Fish 20, 209–219.

King, T.L., Lubinski, B.A., Burnham-Curtis, M.K., Stott, W., Morgan II, R.P., 2012. Tools for the management and conservation of genetic diversity in brook trout (*Salvelinus fontinalis*): tri- and tetranucleotide microsatellite markers for the assessment of genetic diversity, phylogeography, and historical demographics. Conserv. Genet. Resour. 4, 539–543.

Kusnierz, P.C., Stimmell, S.P., Leonard, J.B.K., 2009. Movement and growth indicators in resident and adfluvial coaster brook trout in the Hurricane River, Lake Superior, MI, USA. J. Great Lakes Res. 35, 385–391.

Leonard, J.B.K., Stott, W., Loope, D.M., Kusnierz, P.C., Sreenivasan, A., 2013. Biological consequences of the coaster brook trout restoration stocking program in Lake Superior tributaries within Pictured Rocks National Lakeshore. N. Am. J. Fish. Manag. 33, 359–372.

MacCrimmon, H.R., Gots, B.L., 1980. Fisheries for charrs. In: Balon, E.K. (Ed.), Charrs: Salmonid Fishes of the Genus Salvelinus. Dr W. Junk, The Hague, The Netherlands, pp. 797–839.

McKenna Jr., J.E., Slattery, M.T., Clifford, K.M., 2013. Broad-scale patterns of brook trout responses to introduced brown trout in New York. N. Am. J. Fish. Manag. 33, 1221–1235.

Moore, S.E., Bromfield, R., Larson, G.L., 1983. Standing crops of brook trout concurrent with removal of rainbow trout from selected streams in Great Smoky Mountains National Park. N. Am. J. Fish. Manag. 3, 72–80.

Moore, S., Whiting, B., Newman, L., 2006. A Coaster Brook Trout Rehabilitation Plan for the Grand Portage Reservation. Grand Portage Band of Chippawas, Natural Resource Management, Grand Portage, MN.

Mucha, J.M., Mackereth, R.W., 2008. Habitat use and movement patterns of brook trout in Nipigon Bay, Lake Superior. Trans. Am. Fish. Soc. 137, 1203–1212.

Newman, L.E., DuBois, R.B., 1996. Status of brook trout in Lake Superior. Prepared for the Lake Superior Technical Committee by the Brook Trout Subcommittee. Great Lakes Fishery Commission, Ann Arbor, Michigan.

Newman, L.E., DuBois, R.B., Halpern, T.N. (Eds.), 2003. A Brook Trout Rehabilitation Plan for Lake Superior. Great Lakes Fishery Commission Miscellaneous Publication 2003-03.

Ostazeski, J.J., Schreiner, D.S., 2004. Identification of ground water intrusion areas on the Lake Superior shoreline and selected tributaries in Minnesota. Lake Superior Area Completion Report. Minnesota Department of Natural Resources, St. Paul, MN.

Pritchard, J.K., Stephens, M., Donnelly, P., 2000. Inference of population structure using multilocus genotype data. Genetics 155, 945–959.

Raymond, M., Rousset, F., 1995. An exact test for population differentiation. Evolution 49, 1280–1283.

Rice, W.R., 1989. Analyzing tables of statistical tests. Evolution 43, 223–225.

Robillard, M.M., Casselman, J.M., McLaughlin, R.L., Mackereth, R.W., 2011a. Alternative growth histories in populations of Lake Superior brook trout: critical support for partial migration. Biol. Conserv. 144, 1931–1939.

Robillard, M.M., McLaughlin, R.L., Mackereth, R.W., 2011b. Diversity in habitat use and trophic ecology of brook trout in Lake Superior and tributary streams revealed through stable isotopes. Trans. Am. Fish. Soc. 140, 943–953.

Roosevelt, R.B., 1865. Superior Fishing: the Striped Bass, Trout, and Black Bass of the Northern States Reprint 1985 Minnesota Historical Society Press, St. Paul.

Rose, G.A., 1986. Growth decline in sub-yearling brook trout after emergence of rainbow trout. Can. J. Fish. Aquat. Sci. 43, 187–193.

Schreiner, D.R. (Ed.), 1995. Fisheries Management Plan for the Minnesota Waters of Lake Superior. Minnesota Department of Natural Resources, St. Paul (Special Publication 149).

Schreiner, D.R., Ostazeski, J.J., Halpern, T.N., Geving, S.A., 2006h. Fisheries Management Plan for the Minnesota Waters of Lake Superior. Section of Fisheries Special Publication 163. Minnesota Department of Natural Resources, St. Paul.

Schreiner, D.R., Cullis, K.I., Donofrio, M.C., Fischer, G.J., Hewitt, L., Mumford, K.G., Pratt, D.M., Quinlan, H.R., Scott, S.J., 2008. Management perspectives on coaster brook trout rehabilitation in the Lake Superior Basin. N. Am. J. Fish. Manag. 28, 1350–1364.

Scribner, K., Huckins, C., Baker, E., Kanefsky, J., 2012. Genetic relationships and gene flow between resident and migratory brook trout in the Salmon Trout River. J. Great Lakes Res. 38, 152–158.

Scruton, D.A., Ollerhead, L.M.N., Clarke, K.D., Pennell, C., Alfredsen, K., Harby, A., Kelley, D., 2003. The behavioral response of juvenile Atlantic salmon and brook trout to experimental hydropeaking on a Newfoundland (Canada) River. River Res. Appl. 19, 577–587.

Slade, J.W., 1994. A Pilot Study on the Status of Coaster Brook Trout in the Waters of Isle Royale National Park, Lake Superior. U.S. Fish and Wildlife Service, Ashland, WI (19 pp.).

Smith Jr., L.L., Moyle, J.B., 1944. A Biological Survey and Fishery Management Plan for the Streams of the Lake Superior North Shore Watershed. Minnesota Department of Conservation (Technical Bulletin Number 1. 288 pp.).

Stolarski, J.T., Hartman, K.J., 2008. An evaluation of the precision of fin ray, otolith, and scale age determinations for brook trout. N. Am. J. Fish. Manag. 28, 1790–1795.

Tilma, J.S., Ostazeski, J.J., Morse, S.D., 1999. Completion Report: Coaster Brook Trout Study in Lake Superior and Its North Shore Tributaries Above and Below Barriers. Minnesota Department of Natural Resources, Division of Fish and Wildlife, Section of Fisheries (Study 4, Job 458).

Trebitz, A.S., Morrice, J.A., Cotter, A.M., 2002. Relative role of lake and tributary in hydrology of Lake Superior coastal wetlands. J. Great Lakes Res. 28, 212–227.

Wilson, C.C., Stott, W., Miller, L., D'Amelio, D., Jennings, M., Cooper, A., 2008. Conservation genetics of Lake Superior brook trout: issues, questions, and directions. N. Am. J. Fish. Manag. 28, 1307–1320.

Wisconsin Department of Natural Resources (WIDNR), United States Fish and Wildlife Service (USFWS), 2005d. Wisconsin Lake Superior Basin Brook Trout Plan. United States Fish and Wildlife Service, Ashland Fish and Wildlife Conservation Office, Ashland, WI.