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Fish Assemblages in Subarctic Lakes: Does Fire Affect Fish–Environment Relations in Northern Alberta?

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Abstract.—In 1995, a wildfire swept through a large area of the Caribou Mountains, a remote subarctic plateau of northern Alberta, Canada, containing numerous unstudied and unexploited small lakes. To assess near-term effects of fire and to establish information on assemblage–environment relations in this previously unstudied region, we sampled lakes in burned and unburned (reference) catchments within 2 years of the fire. To further understand species–environment relations in these small, subarctic lakes, we also compared aspects of their fish assemblages with those of assemblages in previously studied lakes of similar sizes in the boreal mixed-woods region to the south and in several large Caribou Mountain lakes. Correspondence analysis revealed three simple but distinct small-lake fish assemblages in the Caribou Mountains: those dominated by northern pike *Esox lucius*, suckers *Catostomus* spp., or Arctic grayling *Thymallus arcticus*. Canonical correspondence analysis revealed significant species–environment relations, but there was also some evidence that biotic interactions contributed to these assemblage types. Despite its extensiveness (84% of catchment area disturbed), fire did not appear to impact fish assemblages in burned lakes. Percentage disturbance accounted for less than 10% of the variation in fish assemblage structure among lakes, and reference and burned lakes were represented among all three assemblage types. However, burned lakes had fewer small northern pike than did reference lakes, suggesting possible effects of fire at the population level. Large Caribou Mountain lakes had a higher species richness and a distinctive species pool, reflecting important limnological differences with their neighboring small lakes. Despite a smaller regional species pool, the small Caribou Mountain lakes displayed local richness that was comparable to similarly sized lakes in the boreal mixed-woods region. Also comparable was the limited near-term effects that catchment-level disturbance had on the resident fish communities in small lakes of both regions. Population-level differences between disturbed and reference lakes, however, suggest that longer-term impacts are possible.

Aquatic systems are linked to their surrounding drainage basins through connections of hydrology, nutrients, light, and wind, and therefore can be sensitive to landscape disturbance. In boreal Canada, wildfire is an important natural disturbance on the landscape (Johnson 1992). Although some work has been conducted on the effects of this disturbance on stream ecosystems, studies of lake systems are comparatively sparse (Gresswell 1999), despite the abundance of lakes in boreal landscapes. Investigations of lakes on the nutrient-poor Canadian Shield have shown that impacts from forest fires can include nutrient pulses (Carignan et al. 2000; Planas et al. 2000; Scrimgeour et al. 2000) and accompanying increases in temperature (Krause 1982; Steedman et al. 2001), sediment transport (Beaty 1994; Steedman and France 2000), and water flow into lakes (Verry et al. 1983; Buttle and Metcalfe 2000). These effects, however, likely vary depending on the severity of the dis-

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turbance and on specific regional and local conditions, such as availability of nutrients or runoff from the catchment. Furthermore, the effects such changes have on fish communities and populations in northern lakes are largely unknown.

In streams, fire can cause direct mortality of fish (Gresswell 1999), even to the point of local extirpation (Rinne 1996; Rieman et al. 1997). Indirect routes of change, however, are more likely in lake systems. For example, nutrient enrichment that increases lake productivity could have a positive effect on fish through increased food supply (Grant and Tonn 2002), or a negative effect through increased risk of overwinter oxygen depletion (Danylchuk and Tonn 2003). Changes in water yield also create the potential for greater connectivity of lakes, increasing colonization opportunities for fishes within a drainage network that could lead to subsequent changes in community composition (Magnuson et al. 1998).

The few studies that have assessed the effects of fire on fish communities in lakes have produced limited evidence of strong, or even consistent, impacts. On the nutrient-rich Boreal Plains of Alberta, Tonn et al. (2003) found little support that landscape disturbance (forest harvesting or fire) affecting approximately 18% of catchment areas altered fish community–lake environment relationships, although a trend toward a greater abundance of white sucker *Catostomus commersoni* and a greater proportion of small-sized sucker in disturbed lakes than in reference lakes may have suggested a possible trophic enrichment. St-Onge and Magnan (2000), in contrast, found smaller proportions of small white sucker and yellow perch *Perca flavescens* in more heavily impacted lakes on the Boreal Shield of Québec (91% of catchment areas disturbed), suggesting increased mortality of young fishes. Clearly, effects of landscape disturbance are not uniform even for the same species, and may vary among regions due to differences in environmental conditions and biotic communities. Additional research in a variety of forested regions and on a variety of fish communities is necessary to further our understanding of the role of landscape disturbance in shaping lake communities.

A large wildfire, ignited by lightning, occurred in June 1995 in the Caribou Mountains, a subarctic plateau in northern Alberta that contained numerous but previously unstudied lakes. The primary goal of this research was to examine near-term effects of forest fire on Caribou Mountain fish assemblages by comparing small lakes (<160 ha) in burned catchments, sampled 1–2 years after the fire, to similar lakes without recent disturbance. Basic information on species–environment relationships is sparse for this remote and distinct region, and therefore the study presented an opportunity to describe the small-lake fish communities and compare them to those found in larger (>530 ha) lakes of the same region. The present study also provided a northern complement to the work of Tonn et al. (2003) on small lakes in Alberta's Boreal Plains mixed-wood forest. We therefore took advantage of these parallel data sets to compare aspects of fish assemblages in small lakes of the two regions.

Methods

Study area.—The 15 study lakes were located in the Caribou Mountains (approximately 59°N, 115°W), a large (10,000 km^2), subarctic plateau in northern Alberta, Canada (Figure 1). Temperatures in the region average 10°C during May–August, with an average of only 60 frost-free days per year. Winter temperatures reach −40°C, although they typically range from −15°C to −25°C. The region is semi-arid, with 400–450 mm of annual precipitation (Strong and Leggat 1992).

The plateau is approximately 800 m above sea level, rising 300–500 m above the nearby river valleys. It contains a large number of lakes and streams, which are headwaters of systems that flow either south to the Peace River or north to Great Slave Lake; all of the lakes that we sampled fall into the former category. Vegetation in the region is characterized by dense stands of black spruce *Picea mariana*, with carpets of *Sphagnum* spp. and other mosses and lichens in the understory. Over half of the area is covered by peatlands. The muskeg and organic soils are almost exclusively gray, wooded loams. Surficial geology consists of till, gravel, sand, and clay deposits, with zones of discontinuous permafrost overlying sedimentary bedrock (Strong and Leggat 1992).

A large (129,000 ha) and intense fire swept through the plateau in June 1995. Prior to 1995, a stand-replacing fire had likely not occurred in 90 years (McEachern et al. 2000). During the following two summers, we sampled six recently burned lakes, along with nine lakes with undisturbed watersheds that we treated as reference sites (two of the reference lake catchments had experienced forest fire previously, one in 1961 and one in 1982). Between 60% and 95% (mean = 84%) of the catchment area of burned lakes were affected by the 1995 fire. In addition, we sampled five nearby but substantially larger lakes (Figure

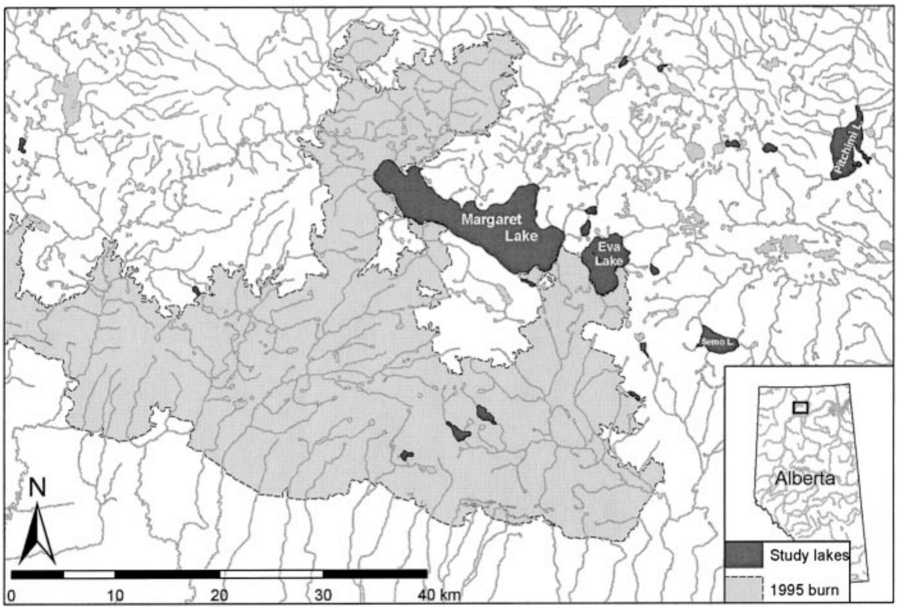

FIGURE 1.—Map of the Caribou Mountains study area in northern Alberta, indicating locations of study lakes and the 1995 wildfire. The named study lakes are four of five large lakes that were sampled; the fifth, Wentzel Lake, is located to the east of the mapped area.

1; Table 1) to compare their fish community attributes to the small lakes in this largely unstudied region. Lakes were accessible only by float plane.

Study site attributes and limnology.—Lake and catchment areas were derived from a geographic information systems database, and depth was measured by echosounding along 5–15 transects per lake. Catchment slope was calculated by dividing elevation gain by linear distance to lakeshore, based on 10–30 transects. Aerial photographs from 1996 were used to estimate the percentage of a drainage basin disturbed by fire. Water chemistry values (total phosphorus, chlorophyll *a*, color, pH, HCO_3, calcium, magnesium), collected via multiple hauls from the epilimnion with a weighted polyvinyl chloride tube, are means from samples taken in July, August, and September 1996 (see McEachern et al. [2000] for analytical methods).

Fish assemblages.—Fish surveys were conducted in July and August 1996 (nine reference,

TABLE 1.—Environmental characteristics of the Caribou Mountain study lakes, Alberta. Presented are means (±SE) for the reference and burned small lakes and for the large lakes (n = number of study lakes). Chemistry data were collected in 1996. Burned lakes had somewhat greater maximum depths than reference lakes (t-test, $P = 0.098$), but otherwise the two groups did not differ for any characteristic ($P > 0.13$); ND = no data.

	Small lakes		
Attribute	Reference (n = 9)	Burned (n = 6)	Large lakes (n = 5)
Drainage basin area (ha)	1,520 (869)	977 (246)	34,671 (17,565)
Lake area (ha)	61 (6)	80 (24)	3,110 (1,374)
Maximum depth (m)	2.9 (0.8)	8.5 (3.2)	38.7 (8.8)
Mean depth (m)	1.2 (0.3)	2.8 (0.9)	10.2 (2.3)
Catchment slope (%)	2.6 (0.3)	3.5 (0.6)	ND
Total phosphorus (μg/L)	85.6 (20.2)	115.7 (18.1)	19.8 (3.9)
Chlorophyll *a* (μg/L)	6.2 (1.1)	8.4 (3.8)	2.8 (1.3)
Color (mg Pt/L)	239 (47)	260 (59)	108 (25)
pH	6.6 (0.1)	6.8 (0.1)	8.2 (0.2)
HCO_3 (mg/L)	21.1 (4.1)	24.8 (3.0)	31.5 (3.8)
Ca + Mg (mg/L)	9.3 (1.2)	11.3 (1.5)	11.7 (1.2)
% of catchment burned	0	84.2 (5.7)	Low to none

five burned, and four large lakes) and from late June through July 1997 (one burned and five large lakes), with four of the large lakes sampled in both years.

Lundgren's benthic-survey gill nets (14 3.0-m-wide panels, 1.5 m deep, with square mesh sizes of 6.25–75 mm) were set overnight (14–16 h) at randomly chosen stations within three depth zones ($<$3 m, 3–6 m, $>$6 m), with effort adjusted for lake size (6–16 net sets made over one to two nights). All captured fish were identified, enumerated, and measured (total length [TL] $\pm$ 1 mm). Catches for each species were subsequently converted to catch per unit effort (CPUE, as number of individuals per net per hour).

Data analysis.—Prior to analyses, we examined a correlation matrix of the environmental variables to identify redundant variables. Because an excessive number of variables can compromise the stability and reliability of multivariate analysis, and because one of a pair of highly correlated variables can be dropped with little loss of information (Jolliffe 1972; King and Jackson 1999), we excluded mean depth and HCO_3 from subsequent analyses, since they were highly correlated ($r >$ 0.9) with maximum depth and calcium, respectively, yet had smaller eigenvectors on the first two axes of a preliminary principal components analysis (PCA). Calcium and magnesium values were added together for each lake to form a single water chemistry variable, used to describe the position of a lake within a groundwater flow system (e.g., Devito et al. 2000).

Data were either arcsine-square-root transformed (percentage data) or $\log_{10}(x + 1)$ transformed (CPUE and all other environmental variables, excluding pH) prior to analyses. Analyses of fish communities and community–environment relations were conducted by use of ordination, a group of graphical and statistical techniques that summarize multivariate data (e.g., a fish species-by-lakes matrix) into fewer dimensions while preserving as much of the original variation as possible (Gauch 1982). Where applicable, rare species were downweighted. The programs PC-ORD (version 3.2, MjM Software, Gleneden Beach, Oregon) and CANOCO (version 4.0, GLW-CPRO, Wageningen, Netherlands) were used for all ordination analyses.

Small Caribou Mountain lakes.—Preliminary detrended correspondence analyses showed gradient lengths of 2.9 or greater, indicating that unimodal methods were appropriate for all subsequent ordinations (ter Braak 1987). We used correspondence analysis (CA) ordination on the transformed CPUE data to examine the small-lake fish assemblages from the seven reference and five burned lakes in which fish were present. We then created a joint plot with selected environmental variables (based on their r^2 cutoff values) to graphically display the relationships among fish assemblage structure and environmental features (see McCune and Mefford [1995]).

We assessed the relative influence of fire, lake environment, and fire–lake interactions on fish assemblage structure by variance partitioning, which uses a series of partial canonical correspondence analyses (CCA; Borcard et al. 1992). The CCAs used three data sets: fish, disturbance, and environment. For fish, the transformed CPUE matrix was used, while the percentage of the drainage basin areas burned in 1995 was used as our measure of disturbance. To summarize the multivariate environment data into a few variables, more comparable in number to our single disturbance variable (see Borcard et al. [1992]), we used the first two axes' scores from a PCA of lake morphometry and catchment variables (slope, drainage basin area, maximum depth, and lake area) plus the first two axes' scores from a PCA of water chemistry variables (total phosphorus, pH, color, chlorophyll *a*, and calcium plus magnesium). Significance of the ordination was assessed via a Monte Carlo permutation test (1,999 permutations; see ter Braak and Šmilauer [1998]), while the amount of variation in the fish assemblage data explained by disturbance was determined with a partial CCA that used the environmental components as covariables. With the same approach, we also partitioned variance in the combined (burned plus reference lakes) fish assemblage data into the proportions explained by (a) morphometry and catchment characteristics, (b) water chemistry, and (c) the interaction between these two sets of variables, omitting the effect of fire.

To examine effects of fire at the population level, we compared length-frequency distributions between burned and reference lakes. The northern pike *Esox lucius* was the only species with enough individuals ($>$15 per lake) in enough lakes of both types (burned and reference) to allow analysis. Following St-Onge and Magnan (2000) and Tonn et al. (2003), we separated small ($<$280 mm) and large individuals based on a visual assessment of length distributions from reference and burned lakes, and then used a *t*-test to compare the proportion of the population composed of small individuals between reference and burned lakes.

TABLE 2.—Number of reference, burned, and large study lakes in the Caribou Mountains, Alberta, in which each fish species was captured.

Species and group	Small lakes: Reference (n = 9)	Small lakes: Burned (n = 6)	Large lakes (n = 5)	Total (n = 20)
Northern pike	5	3	5	13
Arctic grayling	4	5	1	10
Longnose sucker *Catostomus catostomus*	2	2	4	8
White sucker	1	1	4	6
Burbot *Lota lota*		2	4	6
Lake whitefish *Coregonus clupeaformis*			5	5
Lake trout *Salvelinus namaycush*			4	4
Cisco *Coregonus artedi*			4	4
Trout-perch *Percopsis omiscomaycus*			2	2
Ninespine stickleback *Pungitius pungitius*			2	2
Walleye *Stizostedion vitreum*			1	1
Slimy sculpin *Cottus cognatus*			1	1
Pearl dace *Margariscus margarita*		1		1
Total number of species	4	6	12	13
Mean number of species	1.3	2.3	7.4	3.2
Number of fishless lakes	2	1	0	3

Results

Lake Environment

Small lakes in the Caribou Mountains were mostly shallow, with slightly acidic and colored water that was also rich in phosphorus (Table 1). Drainage basins were quite variable, and catchment-area-to-lake-area ratios ranged from 1.7 to 135 (mean = 19). Burned lakes tended to be deeper than reference lakes (t-test on maximum depth, $P = 0.098$), but otherwise the two groups did not differ statistically in the measured traits ($P > 0.13$) (Table 1).

Small-Lake Fish Assemblages

Three small lakes (two reference and one burned) were fishless. Fishless lakes were similar in chemistry and morphometry to lakes with fish (t-tests, $P > 0.05$), although fishless lakes had over 2.5 times higher chlorophyll-*a* levels and were only two-thirds as deep as lakes with fish. Given the small sample size, however, these trends were not statistically significant (t-tests; $\log_{10}$(chlorophyll *a*), $P = 0.07$; $\log_{10}$(maximum depth), $P = 0.13$).

Only six species of fish were found in the 15 small lakes (Table 2). A Monte Carlo analysis revealed that this total is less than what would be obtained by sampling 15 lakes of the boreal mixed woods at random (mean = 8.4 ± 0.1 species, $t = 16.9$, $P < 0.0001$), based on the data of Tonn et al. (2003). Pearl dace occurred in only one lake and, as a rare species, was excluded from ordination analyses. White sucker occurred in a single burned lake and a single reference lake, and was therefore combined for analyses with the ecologically similar longnose sucker into a single taxon, ''suckers.''

The CA ordination of small Caribou Mountain lakes resulted in assemblages arranged as a triangle, with lakes dominated by northern pike, Arctic grayling, and ''suckers'' at the three corners (Figure 2; Table 3). The first axis (57% of the variation in species data) separated lakes dominated by northern pike from the others. This axis was positively correlated with calcium plus magnesium, and negatively correlated with water color and drainage basin area, thereby indicating that northern pike dominated in clear, hard-water (and alkaline) lakes with small catchments. Axis 2 (40% of the variation in species data) separated Arctic grayling lakes from sucker lakes. Arctic grayling dominated in lakes with steeper catchments and lower total phosphorus and chlorophyll-*a* levels. The CPUE data suggested negative (biotic) relationships between densities of northern pike and Arctic grayling ($r = -0.50$, $P = 0.10$) and between northern pike and suckers ($r = -0.80$, $P = 0.006$) in small lakes. Specifically, the only small lakes in which Arctic grayling or suckers achieved substantial catch rates (>0.5 fish per net per hour) were those lacking northern pike (Figure 3).

Lakes did not separate out as either burned or reference. Instead, these two lake types were well mixed, with both groups including lakes dominated by northern pike, Arctic grayling, and suckers (Figure 2). The CCA explained 64% of the variation in the fish CPUE data (Monte Carlo permutation test, $P = 0.042$). The variance partition-

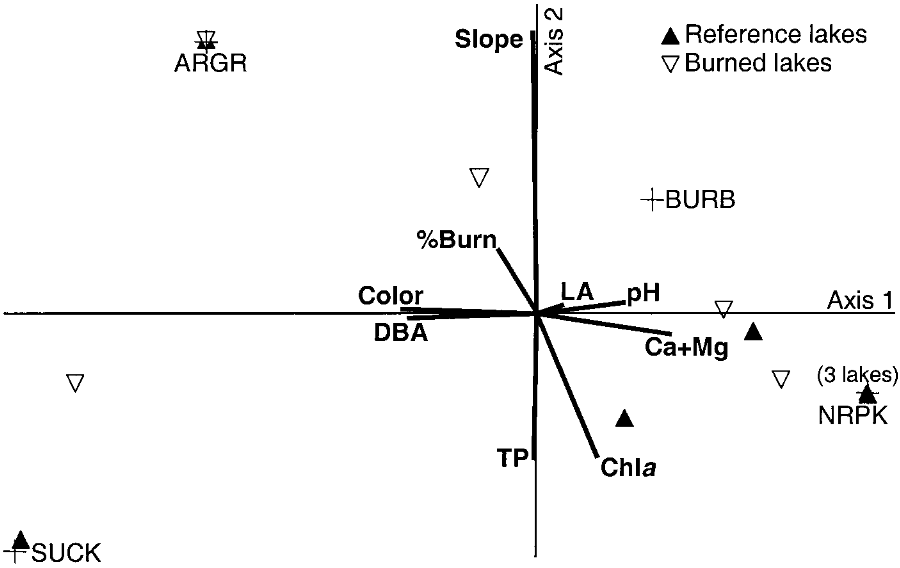

FIGURE 2.—Results of a correspondence analysis of fish catch per unit effort in small Caribou Mountain lakes, showing fish communities in reference (closed triangles) and burned (open triangles) lakes, fish species centroids (crosses), and environmental joint-plot vectors. Maximum depth had a very short vector and is not shown. Fish species are Arctic grayling (ARGR), burbot (BURB), northern pike (NRPK), and sucker species (SUCK). Environmental attributes are chlorophyll *a* (Chl*a*), drainage basin area (DBA), lake area (LA), total phosphorus (TP), and percentage of catchment burned (%Burn).

ing procedure showed that disturbance (percentage of drainage basin burned) contributed relatively little (15%) to the explained variation in the fish data. ''Environment'' (i.e., catchment characteristics, morphometry, and water chemistry) accounted for most (81%) of the explained variation, while only 4% was attributable to the interaction of disturbance and environment. The amount of variation explained by disturbance, after accounting for environment, was not significant (Monte Carlo permutation test, $P = 0.18$). Of the variance in fish assemblage data explained by the environmental principal components, 55% was explained by catchment and morphometry, 42% by water chemistry, and only 2.5% by their interaction.

Size structure of northern pike populations differed marginally between burned and reference lakes. A smaller percentage of small individuals (<280 mm) was found in burned lakes (4.3%, $n = 3$ lakes) compared to reference lakes (35.5%, $n = 5$ lakes) (Figure 4; one-tailed t-test, $P = 0.06$). Densities (CPUE) of these northern pike populations, however, did not differ between burned and references lakes (t-test, $P = 0.75$).

Large-Lake Fish Assemblages

Compared to the small lakes, the large Caribou Mountain lakes were exactly that: more than 40 times larger in surface area and 7.5 times deeper (Table 1). Drainage ratios (catchment area to sur-

TABLE 3.—Mean relative proportion of fish species (based on catch per unit effort) captured in assemblages dominated by northern pike, Arctic grayling, or sucker species in small lakes of the Caribou Mountains, Alberta.

Species and group	Northern pike ($n = 7$)	Arctic grayling ($n = 3$)	Suckers ($n = 2$)
Northern pike	0.886	0.123	
Arctic grayling	0.064	0.857	0.033
Longnose sucker	0.043		0.099
White sucker			0.471
Burbot	0.008	0.019	
Pearl dace			0.397
Total number of species	4	3	4
Mean number of species	2	1.67	3.5

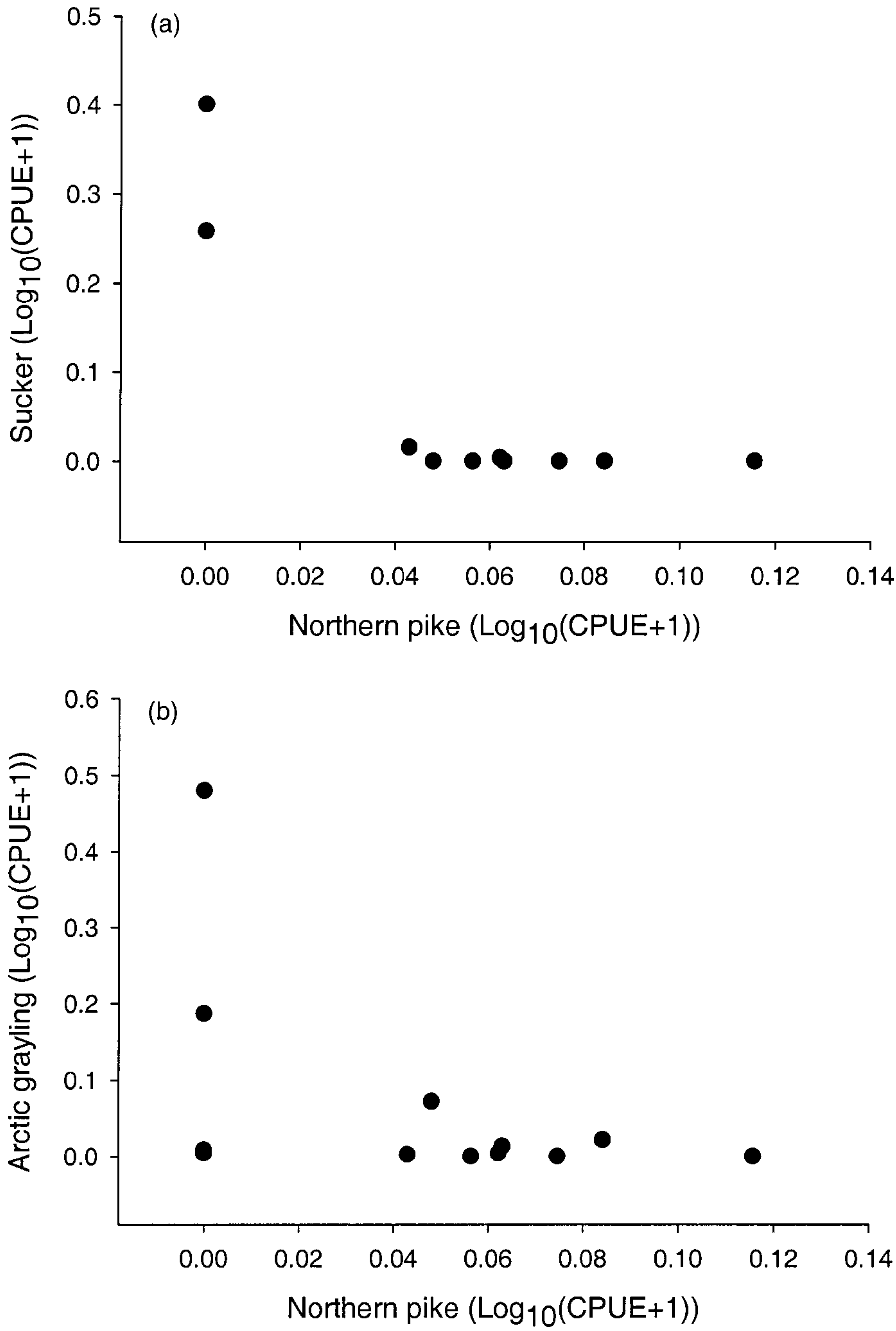

FIGURE 3.—Relations between northern pike catch per unit effort (CPUE) and (A) sucker CPUE or (B) Arctic grayling CPUE in small Caribou Mountain lakes.

face area) averaged just over 11. These large lakes were more oligotrophic, with lower levels of total phosphorus, chlorophyll *a*, and color, but higher pH compared to the small lakes of the region (Table 1).

Large-lake fish assemblages were compositionally distinct from small-lake assemblages: 12 species occurred in at least one of the five large lakes, compared to six species in the 15 small lakes. Only pearl dace, found in a single small lake, was absent

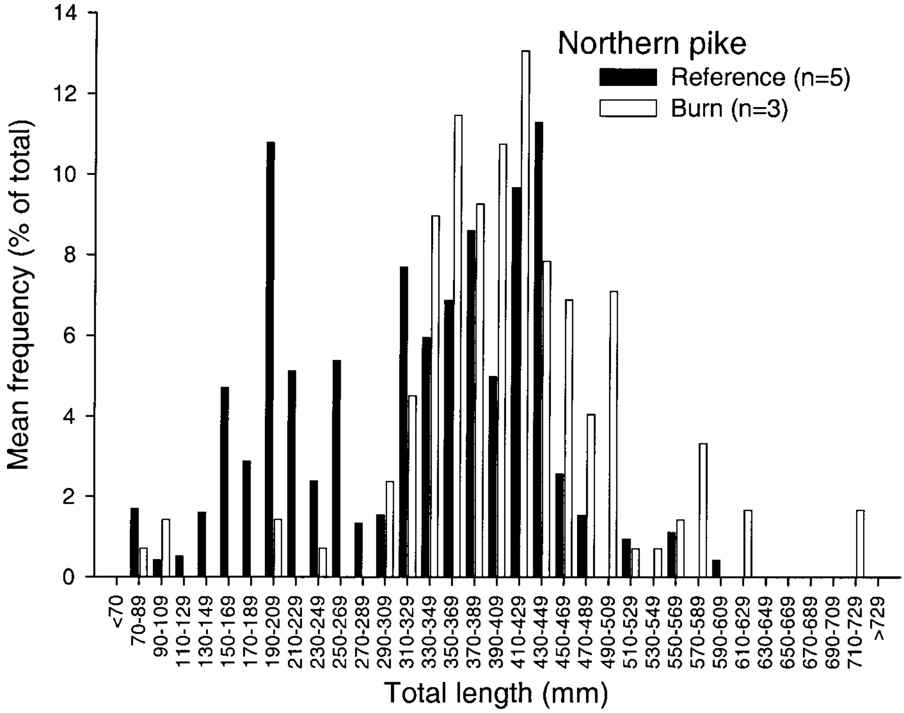

FIGURE 4.—Length-frequency distributions of northern pike from small Caribou Mountain lakes disturbed by forest fire ($n = 3$ lakes), and from undisturbed reference lakes ($n = 5$ lakes). Data are means of the frequencies from individual lakes, based on 15–47 individual fish.

from the large lakes. In contrast, seven species were restricted to large lakes, and four species occurred proportionately more frequently in large lakes than in small lakes. Among common species, only Arctic grayling was more commonly found in small lakes, occurring in 60% of small lakes but only 20% of large lakes. Large lakes had significantly more species (5–9, mean = 7.4) than small lakes (0–4, mean = 1.8) (t-test, $P < 0.0001$).

Discussion

General Description of the Lakes and their Fishes

Most small (≤160 ha) Caribou Mountain lakes are shallow (and likely unstratified), and their waters have rather high concentrations of nutrients, especially phosphorus. Because of the large amount of peatlands on the plateau, however, lake waters in the Caribou Mountains are slightly acidic and highly colored, and epilimnetic chlorophyll-*a* concentrations are low relative to phosphorus levels, likely due to light limitation caused by the stained water (McEachern et al. 2000; Prepas et al. 2001).

Fish assemblages in the small Caribou Mountain lakes were simple (1.8 species per lake; 2.2 if fishless lakes are excluded). Despite this fact, assemblages were not homogeneous. Three taxa were common (northern pike, Arctic grayling, and suckers), and lakes were found in which each of the taxa dominated, such that the ordination involving the small Caribou Mountain lakes was characterized by a triangle of northern pike lakes, Arctic grayling lakes, and sucker lakes.

Small samples sizes, particularly among the sucker and Arctic grayling lakes, allow only preliminary interpretations of community–environment relations, such as the tendency of Arctic grayling to be dominant in lakes with steep catchments and low phosphorus and chlorophyll-*a* concentrations. The CPUE data revealed negative relationships between the piscivorous northern pike and both Arctic grayling and suckers. In boreal mixed-woods lakes, predation effects are typically expressed not as negative density relations, but as mutually exclusive distributions between northern pike and small-bodied forage fish (minnows, sticklebacks) (Robinson and Tonn 1989; Paszkowski and Tonn 2000; Tonn et al. 2003). The co-occurrence of suckers and Arctic grayling with northern pike is not unexpected, however, given their larger adult body size, which affords them a size refuge from predation (Robinson and Tonn 1989). Nevertheless, the negative abundance relationships suggest that predation may also be an important ecological force in these subarctic lakes.

The tendency of the three fishless lakes to be shallower and to have higher chlorophyll-*a* concentrations than fish-bearing small lakes suggests that the fishless condition is associated with low concentrations of dissolved oxygen under the ice during the long subarctic winter (Schindler et al. 1974; Barica and Mathias 1979). Three fishless lakes out of 15 small lakes is comparable to the proportion of fishless lakes found in small lakes of Alberta's boreal mixed-woods region (Paszkowski and Tonn 2000; Tonn et al. 2003).

Effects of Fire

Burned lakes tended to be deeper than reference lakes, but otherwise the two groups showed no differences in morphometry or water chemistry. This contrasted with findings of McEachern et al. (2000), who found significant increases in color and total phosphorus in burned lakes over the 1996–1997 period. Though we lacked 1997 data, McEachern et al. (2000) lacked two reference lakes with high color and high total phosphorus. Thus, although we also observed a trend for higher total phosphorus in our burned lakes, large variation among our reference lakes likely resulted in nonsignificant differences. Regardless, McEachern et al. (2000), like us, found no differences in chlorophyll *a* between burned and reference lakes, suggesting little if any increase in planktonic production in lakes that experienced fire (but see Scrimgeour et al. [2001]).

All three fish assemblage types (northern pike, Arctic grayling, suckers) were encountered in both disturbed (burned) and reference lakes; therefore, as with phytoplankton assemblages (McEachern et al. 2002), there was no evidence for a disturbance-adapted fish assemblage. Furthermore, the areal extent to which a lake's catchment was burned explained little ($<10\%$) of the variation in fish assemblage structure among lakes. Instead, environmental factors unrelated to disturbance contributed over 80% of the explained variation in fish assemblages.

There was, however, some evidence that fire affected fish at the population level. A smaller percentage of small northern pike (<280 mm) were caught in burned versus reference lakes. This result was similar to that found for yellow perch and white sucker in small Boreal Shield lakes in Québec (St.-Onge and Magnan 2000), but contrasts with our findings for white sucker in small Boreal Plains lakes (Tonn et al. 2003). Interestingly, both St.-Onge and Magnan (2000) and the present Caribou Mountain study dealt with similar high levels of disturbance (91% and 84% of drainage basins burned, respectively), versus the much lower level of disturbance (18–19%) in the Boreal Plains study. St.-Onge and Magnan (2000) suggested that the reduced proportion of small fish in disturbed lakes could have resulted from increased mortality of age-0 fish due to lowered food availability. Northern pike in the underrepresented sizes of our study would have represented two age-classes, age-0 and age-1, when the June 1995 fire struck (P. Aku and W. Tonn, unpublished data). Juvenile northern pike feed extensively on macroinvertebrates in northern Alberta lakes (Beaudoin et al. 1999) and would be vulnerable to disruptions in this food resource (Rinne 1996). However, Scrimgeour et al. (2001) found greater biomass of littoral benthic macroinvertebrates in burned Caribou Mountain lakes, thus leaving the mechanism behind this population-level pattern unresolved. Nevertheless, the reduction in small northern pike, combined with the negative relationships between the abundance of northern pike and the other two dominant taxa (Arctic grayling and suckers), suggests that community-level effects of fire may occur after some time lag.

Comparisons with Other Systems

Large Caribou Mountain lakes averaged almost four times as many species as small lakes. The greater richness in the large lakes was most likely the result of the greater diversity of habitat types in the larger and deeper lakes than in smaller and shallower lakes (Barbour and Brown 1974; Magnuson 1976). Examples of habitats absent from the smaller lakes include well-oxygenated, deep, and cold bottom layers above rocky substrates, which support such bottom-feeding species as lake whitefish (e.g., Healey 1980), slimy sculpin, and trout-perch (Magnuson and Smith 1963). These benthic species are excluded from the shallow, unstratified small lakes, which instead support the coldwater, but often surface-feeding, Arctic grayling (Northcote 1995), as well as white and longnose suckers and northern pike. These latter three species were also found in the large lakes, but are not confined to cold, oligotrophic waters (Hokanson 1977). Also missing from the small lakes is a large, open-water pelagic zone that can support zooplankton-feeding species such as cisco (Aku et al. 1997;

Aku and Tonn 1997) and their predator, the lake trout (Vander Zanden et al. 1999). The large, deep lakes should also provide greater environmental stability against potential disturbances, such as winterkill (Barica and Mathias 1979).

In a parallel study, Tonn et al. (2003) surveyed 37 similarly sized small lakes in remote areas of Alberta's Boreal Plains mixed-wood forest (55–57°N, 110–117°W), approximately 400 km south of and approximately 200 m lower in elevation than the Caribou Mountains. Superficially, the capture of 13 species in 20 subarctic lakes (this study) compares very favorably with 10 species in 37 boreal mixed-woods lakes (Tonn et al. 2003). However, the Caribou Mountains total was inflated by the presence of the five large lakes; the 15 small lakes supported only six species, which is fewer than expected from 15 small boreal mixed-woods lakes (Tonn et al. 2003).

Local richness in fish assemblages of the small Caribou Mountain lakes (mean number of species per lake = 1.8, or 2.2 if fishless lakes are excluded) was slightly lower than levels found in the boreal mixed woods (2.5 and 2.7 with and without fishless lakes, respectively). Greater differences between regions were found in species composition. Over half of the 10 species from the boreal mixed-woods lakes were absent from the Caribou Mountains, including some of the most common and widespread species (e.g., brook stickleback *Culaea inconstans*, fathead minnow *Pimephales promelas*, and yellow perch). These are coolwater or warmwater fishes (Hokanson 1977) that approach their northern geographical limits in the boreal mixed woods of northern Alberta (Scott and Crossman 1973). The relatively sharp climatic and elevational gradient provided by the Caribou Mountains likely has prevented successful colonization by these species. In contrast, Arctic grayling and burbot, coldwater Caribou Mountain species, occur in the Boreal Plains ecoregion, but are not typically found in the shallow, soft-bottomed, and isolated systems that characterize small lakes of the latter region (Robinson and Tonn 1989; Paszkowski and Tonn 2000; Tonn et al. 2003).

Despite these differences in species composition between regions, the present study and Tonn et al. (2003) both indicated that catchment disturbances (fire and/or forest harvesting) have minimal community-level impacts in the short term, explaining only 3–9% of the variation among local fish assemblages. This is despite the fact that potential limnological effects of these disturbances, particularly increases in nutrient input or hydrological changes, could have important ecological consequences (Tonn et al. 2003). Although population-level differences, in terms of size distributions of individual species, were detected between reference and disturbed lakes in both regions, differences were not consistent between regions, and a clear ecological mechanism was not identified in either case (see also St.-Onge and Magnan [2000]). It appears that any population-level effects of landscape disturbance in these boreal and subarctic lakes are subtle; multi-lake surveys such as ours are useful for the detection of these effects, but not intensive enough to reveal the mechanism(s) behind them.

Conclusions

The small Caribou Mountain lakes and their fish assemblages share some general characteristics with morphometrically similar lakes in the boreal mixed-wood forest to the south: a similar low species richness per lake, apparent influences of winterkill and piscivory, and the lack of a community-level effect of fire, at least in the near term (1–2 years postfire). The limited overlap in species composition between the two regions, however, suggests that the exact operation of any common mechanisms that structure the fish assemblages will likely differ. Likewise, the differential responses of populations to landscape disturbance could reflect differences in the interactions between lakes and their catchments (McEachern et al. 2000) or the greater severity of the fire in the Caribou Mountains versus the fires that affected the boreal mixed-woods lakes (Tonn et al. 2003). Clearly, more intensive studies, as well as longer-term, community-level monitoring, are required to better understand the factors that structure fish assemblages in the Caribou Mountain lakes and the effects of disturbance on lake communities in general.

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