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Effects of Forest Harvesting and Fire on Fish Assemblages in Boreal Plains Lakes: A Reference Condition Approach

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Abstract.—To assess the impacts of forest harvesting and fires on lentic fish assemblages in the Boreal Plains ecoregion (Alberta, Canada), we applied a reference condition approach to 37 lakes in burned, logged, or undisturbed catchments. Fish assemblages in the reference lakes were classified into two types: those dominated by large-bodied piscivores and those dominated by small-bodied fishes. A discriminant function analysis with only two environmental descriptors (lake maximum depth and average slope of the catchment) could correctly predict assemblage type in 84% of reference lakes. Depth likely reflects the influence that winter oxygen concentrations have on fish assemblage type, whereas catchment slope is correlated with a variety of landscape-level features. Although potential effects of forest harvesting and fire can increase the susceptibility of lakes to winter hypoxia (via nutrient enrichment) and alter connectivity to the regional drainage network (via altered hydrology), fish assemblages in 93% of the disturbed lakes did not deviate from the discriminant function predictions, suggesting little, if any, assemblage-level effects of the disturbances over the 1–2-year time period of our study. Indeed, the level of disturbance in a catchment could explain less than 3% of the variation in assemblage structure, although a slight increase in the catches of white sucker *Catostomus commersoni* and a greater proportion of small individuals in white sucker populations may have reflected a modest enrichment effect in burned lakes. Current levels of landscape disturbance on the Boreal Plains appear to have minimal effects on lake fish assemblages but, because of the susceptibility of these lakes to winterkill, higher levels of terrestrial disturbance could prove detrimental.

Natural disturbances such as wildfire have recently been promoted as models for forest harvesting in boreal regions (e.g., Payette 1992; Harvey et al. 2002). If we are to manage such forested landscapes in ways that emulate natural disturbances, we need to understand the effects of both fire and forestry on the various components of the landscape, including aquatic habitats. Compared with flowing-water systems, however, effects of landscape disturbances on lakes are poorly known (Gibbons and Salo 1973; Gresswell 1999). Furthermore, studies have largely been limited to nutrient-poor lakes in regions underlain by granitic bedrock, such as Canada's Boreal Shield (Carignan et al. 2000; Steedman and Kushneriuk 2000) and Fennoscandia (Rask et al. 1998). Very few studies have examined effects on lakes in more nutrient-rich landscapes, such as the Boreal Plains ecoregion of western Canada (Rowe 1972).

Wildfire is an essential component of the landscape in the mixed-wood forest of the Boreal Plains (Johnson 1992), affecting 0.4–2.2% of the region annually (Murphy 1985; Cumming 1997). Such fires likely produce nutrient pulses that ''reset'' trophic conditions in lakes (Carignan et al. 2000; Scrimgeour et al. 2001). Extrapolating from the better-known responses of lotic and Boreal Shield systems, we might expect increases in water flow to lakes (Verry et al. 1983; Buttle and Metcalfe 2000) and increases in temperature (Krause 1982; Steedman et al. 2001) and turbidity (Beaty 1994; Steedman and France 2000) within lakes to accompany those nutrient pulses, at least in certain topographic settings. The size and persistence of these effects, however, and the responses of lake biota are largely unknown.

Because of their economic value and important

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trophic roles, fishes have received some attention in studies assessing the impacts of landscape disturbances on freshwater ecosystems. Effects of wildfire, reviewed by Gresswell (1999), can include mortality of adults, reduced recruitment, and population extirpation. As suggested above, however, Gresswell's review revealed that effects of fire on fishes in lakes are poorly studied. In a recent study of 38 lakes in Québec, St-Onge and Magnan (2000) found that the abundance of important fish species and the growth of yellow perch *Perca flavescens* did not differ among lakes in reference, harvested, and burned catchments. Catches of juvenile yellow perch and white sucker *Catostomus commersoni*, however, were lower in lakes with disturbed catchments, suggesting that increases in mortality of young fish may have occurred.

While effects of forest harvesting and fire remain poorly studied for lakes in general and largely unknown for the Boreal Plains, a second natural disturbance, winterkill, is known to be an important structuring force for fish populations and assemblages in the region's lakes due to their naturally eutrophic state, shallow depth, and often poor connectivity to larger drainage networks (Robinson and Tonn 1989; Paszkowski and Tonn 2000; Danylchuk and Tonn 2003). Winter hypoxia can quickly and selectively reduce or eliminate populations of large piscivorous species that are vulnerable to low oxygen concentrations (e.g., northern pike *Esox lucius* [Casselman and Harvey 1975]) and, in extreme cases, can render lakes fishless (Beaudoin et al. 2001; W. Tonn and coworkers, unpublished data). In lakes that do not experience regular hypoxia, however, large-bodied, piscivorous fishes can extirpate populations of small-bodied fishes (Harvey 1981; Robinson and Tonn 1989; Paszkowski and Tonn 2000). If landscape disturbances alter winter oxygen regimes, fish assemblages could change dramatically.

Because our understanding of landscape disturbance as a factor that shapes fish populations and assemblages in lakes is poor, our capacity to formulate management strategies for fisheries resources in forested landscapes is limited. To help address this deficiency, we applied a multivariate reference condition approach (e.g., Reynoldson et al. 1997; Bailey et al. 1998; see below) to the fishes in 37 Boreal Plains lakes of north-central Alberta, addressing the following questions:

(1) Do the characteristics of fish assemblages and populations in lakes affected by fire or forest harvesting differ from what would be expected if those lakes remained undisturbed?
(2) Do disturbances interact with the landscape, morphometric, and chemical features of lakes to shape fish assemblages?
(3) Do the effects on fish assemblages depend on the form of disturbance (wildfire versus forest harvesting)?

The Reference Condition Approach

In a reference condition approach, the structure of assemblages at disturbed sites is compared with that at reference sites to determine whether the former fall outside the range of expected conditions based on the latter. If environmental variables explain a substantial part of the variation in assemblage structure at reference sites, empirical models can be constructed to predict the structure of assemblages expected at disturbed sites. Deviations from the predicted assemblages can then be used to assess effects of the disturbance. By identifying different assemblage types among the reference sites via multivariate community analysis techniques (Legendre and Legendre 1998), we can refine assemblage-level predictions, thus making the approach more sensitive (Bailey et al. 1998). Such an approach is the basis for several aquatic macroinvertebrate biomonitoring programs (e.g., Parsons and Norris 1996; Reynoldson et al. 2001); a conceptually similar approach was developed by Tonn et al. (1983) to classify and predict fish assemblages in lakes. These multivariate approaches differ from those based on computing an additive index from a set of derived metrics (Karr 1991; Gerritsen 1995), but both involve comparisons of disturbed sites to the range of scores represented by reference sites. The depauperate nature of the region's fish fauna and the eurytopic nature of the species that are present likely reduces the effectiveness of a multimetric index substantially (Joy and Death 2000).

Methods

Study sites.—The 37 study lakes were located in remote areas of Alberta's Boreal Plains mixedwood forest (55°–57°N, 110°–117°W). The region is semiarid (mean annual precipitation = 380 mm; Strong and Leggat 1992), and wildfires are important disturbances that shape vegetation and other landscape patterns (Johnson 1992). In the spring of 1995, wildfires affected 8.1–44.2% (median = 17.9%) of the catchments of 10 of the 37 study lakes. Fires tended to affect low-lying catchments dominated by black spruce *Picea mariana*. Although small-scale harvesting of conifers *Picea* spp. has occurred for decades in boreal Alberta, large-scale harvesting of poplars *Populus* spp. for pulp production began only in the 1990s and is concentrated in upland-dominated catchments. Forest harvesting occurred in the catchment of six study lakes in the winter of 1995–1996, affecting 15.0–27.3% (median = 18.8%) of the catchments. Management guidelines stipulate an uncut buffer of at least 100 m from lake edges; thus these lakes experienced no shoreline disturbance as a result. Harvesting occurs in the winter on frozen ground, which minimizes other disturbances associated with forestry activities. The remaining 21 study lakes were minimally affected by harvesting or fires for at least 50 years (<5% of catchment area disturbed), with virtually no disturbance within 800 m of lake margins. Study lakes were accessible only by float plane or all-terrain vehicle.

Limnology.—Vertically integrated euphotic-zone water samples were collected monthly from each lake in July–September 1996 and were used to determine summer mean water quality values (see Prepas et al. [2001b] for analytical details). Depth measurements were made by an echosounder along transects during fish sampling; recorded depths were digitized as binary point vector files. Bathymetric and contour lines were created with SYSTAT (SPSS 1996). Lake and catchment areas and percentages of catchments covered by wetland and upland vegetation (subdivided into coniferous and deciduous) were estimated from 1:20,000 or 1:15,000 aerial photographs. Mean catchment slopes were estimated from 10 to 18 transects extending from the catchment boundary to the shoreline, on 1:50,000 topographic maps.

Fish assemblages.—Fishes were sampled in July–August of 1995 (seven reference lakes), 1996 (11 reference, 5 burned, and 3 harvested lakes), and 1997 (three reference, five burned, and three harvested lakes). Time constraints (limiting sampling to a common two-month period) and travel costs (due to limited accessibility) required the distribution of fish sampling across three different years. Lundgren's benthic survey gill nets (fourteen 3-m-wide panels 1.5 m deep, with square mesh sizes of 6.25, 8, 10, 12.5, 16.5, 22, 25, 30, 33, 38, 43, 50, 60, and 75 mm) were set overnight (14–16 h) at randomly chosen stations within three depth zones (<3 m, 3–6 m, and >6 m), with effort adjusted for lake size (6–16 net sets made over 1–2 nights). All captured fish were identified and measured (total length [TL] ± 1 mm), and up to 200 individuals of each species were weighed (wet mass ± 1 g). Catches were subsequently converted to catch per unit effort (CPUE, as number of individuals per net per hour) and biomass per unit effort (BPUE, as grams per net per hour). Biomass of fish that were measured but not weighed was estimated from population-specific mass–length regressions (W. Tonn, unpublished data).

Data analysis.—Canonical correspondence analysis (CCA; ter Braak and Verdonschot 1995) was used to uncover underlying patterns in fish community composition and their relationship to environmental characteristics among the reference lakes. We performed CCA on fish assemblage data from all reference lakes that contained fish. Fish data consisted of CPUE for each species. With the reference condition approach, environmental variables that can be affected by the disturbance(s) are excluded prior to analysis (Reynoldson et al. 1997, 2001). Based on previous studies of forest harvesting and fire (e.g., Gresswell 1999; Carignan et al. 2000), we excluded most water chemistry variables: nutrients (N, P), anions and cations, alkalinity, dissolved oxygen concentration, color, and chlorophyll *a*. The nine remaining variables (area, maximum depth, catchment slope, percent upland vegetation in catchment, percent deciduous trees, percent coniferous trees, percent wetland area, number of inlets and outlets, and pH) were subjected to the forward selection procedure ($P < 0.05$) in the CANOCO 4 package (ter Braak and Smilauer 1998). Percentage data (e.g., catchment slope) were arcsine-square-root transformed, whereas CPUE and other environmental variables (except for pH and number of inlets and outlets) were transformed as $\log_{10}(x + 1)$.

Following the identification of fish assemblage types in reference lakes, we used discriminant function analysis (DFA; Minitab 1996) with cross validation to predict fish assemblage type based only on environmental data. As above, environmental variables available to the DFA were limited to those that should have been unaffected by catchment disturbance. The best model (based on percentage of lakes correctly classified) was then applied to the disturbed lakes to determine if their fish assemblages conformed with the expected (reference) fish–environment relations; departures from the reference pattern (incorrect predictions) would suggest community-level effects of disturbance. Following the approach of Borcard et al. (1992), we also performed a series of partial CCAs on data from the 35 lakes that contained fish to partition the variance in fish assemblage composition between that which could be explained by

TABLE 1.—Characteristics of reference, burned and harvested study lakes. Presented are medians and ranges (in parentheses). Data are from Prepas et al. (2001a, 2001b) and the Sustainable Forest Management Network (unpublished). The three groups did not differ for any characteristic (ANOVA, $P > 0.05$ following Bonferroni correction), except the percentage of deciduous trees, where harvested catchments were higher than burned catchments (Tukey's multiple comparison test, $P < 0.05$).

Characteristic	Reference (n = 21)	Burned (n = 10)	Harvested (n = 6)
Area (ha)	65.0 (14.0–200.0)	65.9 (38.8–205.9)	52.4 (23.1–114.8)
Maximum depth (m)	4.1 (1.8–11.2)	2.0 (1.5–11.6)	3.3 (1.9–7.6)
Catchment slope (%)	3.5 (0.3–8.0)	0.9 (0.3–4.6)	1.9 (0.7–4.8)
No. of Inlets and outlets	2 (0–4)	1 (0–3)	2 (0–4)
Upland vegetation in catchment (%)	76.7 (6.9–94.7)	37.1 (0–78.0)	77.1 (50.2–94.8)
Deciduous trees in catchment (%)	59.5 (0–85.3)	3.0 (0–38.6)	44.0 (18.2–72.7)
Color (mg Pt/L)	43.7 (16.8–358.0)	102.4 (30.3–388.0)	76.4 (43.6–267.0)
pH	7.6 (4.9–9.4)	7.0 (6.4–7.3)	7.4 (6.5–7.6)
Alkalinity (mg $CaCO_3$/L)	85.0 (2.9–158.3)	38.2 (12.4–83.4)	62.9 (18.8–151.3)
Ca^{2+} plus Mg^{2+} (mg/L)	29.5 (1.2–64.0)	16.0 (6.8–43.0)	29.6 (11.0–46.6)
Total phosphorus (μg/L)	43.6 (23.8–115.8)	51.5 (27.0–79.1)	31.7 (19.1–138.9)
Fish species richness	2.5 (0–4)	3 (1–6)	1 (0–3)

the degree of disturbance (as measured by percentage of catchment disturbed) versus the environmental features of the lakes that best discriminated between fish assemblage types (as determined by the earlier DFA).

To uncover population-level effects of catchment disturbances, we used t-tests to compare the abundances (CPUE and BPUE) of the five most widely distributed species (or species group, see below) between reference and disturbed lakes; similarly, one-way analyses of variance (ANOVAs) were used to compare abundances across the three lake types (reference, burned, or harvested catchments). For inclusion in the analyses, a species had to be present in at least two reference lakes and two disturbed lakes. If abundance measures were not normally distributed (Ryan–Joiner test, $P < 0.05$), values were transformed ($\log_{10}$[CPUE + 1], $\log_{10}$[(1,000 × BPUE) + 1]) for analysis. After transformations, variances (within species) were found to be homogeneous (Levene's test, $P > 0.05$).

To determine whether the size structure of fish populations differed between reference and disturbed lakes, we plotted the size distributions of the four most widely distributed species (see below) for lakes where 15 or more individuals were caught in gill nets. Following St-Onge and Magnan (2000), we established TL values that operationally separated small and large individuals for each species based on visual assessment of size distributions and our knowledge of species' regional growth and life history patterns. For each of the four species, we compared the proportion composed of small individuals for reference versus disturbed lakes with t-tests (if data were distributed normally) or Mann–Whitney tests.

Results

Although lakes smaller than 10 ha were not sampled due to float plane restrictions, the study lakes and their catchments proved typical of smaller lakes in the boreal mixed-wood forest of Alberta (e.g., Prepas et al. 1988) in that the lakes were shallow, circumneutral, and productive. Given the distribution of forest harvesting and fires on the boreal Alberta landscape (see Methods), burned catchments tended to have less upland habitat and deciduous trees and their lakes were more colored than harvested catchments and lakes, although only percent deciduous trees differed significantly (Table 1). Most importantly for the reference condition approach, however, environmental characteristics of disturbed lakes (burned or harvested) fell within the ranges displayed by reference lakes, and none differed significantly from reference systems (ANOVA with Bonferroni correction, $P > 0.05$; Table 1).

Our fish surveys encountered 10 species. Brook stickleback *Culaea inconstans* (25 lakes in total, including 12 reference lakes), fathead minnow *Pimephales promelas* (12 lakes, 6 reference), and northern pike *Esox lucius* (11 lakes, 5 reference) were the most widespread. Two lakes (1 reference, 1 burned) were fishless. Among the remaining lakes, richness ranged from 1 to 6 species (mean = 2.3). Fish analyses involved six taxa, including the above plus yellow perch. For multivariate analyses, white sucker and longnose sucker *Catostomus catostomus* were combined into a single taxon, ''suckers''; similarly, pearl dace *Margariscus margarita*, finescale dace *Phoxinus neogaeus*, northern redbelly dace *Phoxinus eos*, and their hybrids were designated ''dace.'' These combined taxa were created to accommodate the relative rarity of the individual species and identification difficulty in the field. Iowa darter *Etheostoma exile* was collected in only one lake and was excluded as a rare species. One reference lake (containing fathead minnow) was excluded from fish–environment analyses as an outlier because it was partially meromictic, which confounded key environmental relationships.

In the CCA, catchment slope, lake area, and pH were chosen by forward selection ($P < 0.05$) for inclusion in the analysis. The CCA triplot of reference lakes indicated two distinct fish assemblage types (Figure 1). Similar analyses that used BPUE or presence/absence data clearly revealed this same fish-assemblage dichotomy, indicating its robustness. One set of 12 reference lakes was dominated by small-bodied fishes and a second set (7 lakes) was dominated by large-bodied fishes, including one or more piscivorous species (northern pike and yellow perch). Small-fish assemblages were shallower and had catchments with gentler slopes and less upland vegetation than lakes containing the large-fish assemblage type (*t*-tests; $P < 0.05$).

With the recognition of distinct assemblage types among the reference lakes, the next step was to select environmental variables that would be included in a DFA model to predict the expected assemblage type in disturbed lakes. After excluding water chemistry variables that could be affected by fire or forest harvesting, and dropping others due to colinearity, a DFA model that included a set of only two variables, maximum depth and catchment slope, offered maximum discriminatory power. Classification with cross-validation assigned 16 of the 19 reference lakes (84%) to their correct groups.

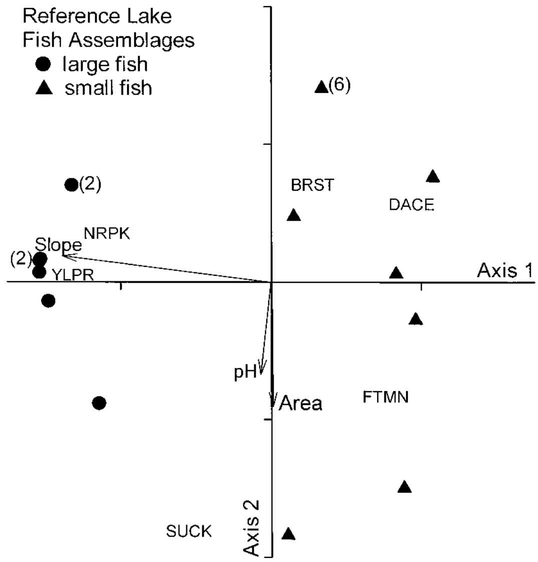

FIGURE 1.—Canonical correspondence analysis triplot of 19 reference lakes based on the catch per unit effort (individuals per net per hour) of six fish taxa. Two fish assemblages, one characterized by the piscivorous northern pike and other large-bodied species and one by small-bodied species, are distinguished along axis 1. Three environmental variables chosen by a forward selection procedure ($P < 0.05$) are indicated by arrows. The numbers of lakes represented by single points are indicated in parentheses. The following species or species groups are plotted: brook stickleback (BRST); pearl, finescale, and northern redbelly dace (DACE); fathead minnow (FTMN); northern pike (NRPK); yellow perch (YLPR); and white and longnose suckers (SUCK).

The reference lake discriminant model was then applied to the disturbed lakes to determine the extent to which fish–environment relations derived from reference lakes could predict fish assemblage types in disturbed lakes. To assess the DFA predictions, a correspondence analysis of both reference and disturbed lakes identified disturbed-lake assemblages as belonging unambiguously to either the large-fish or small-fish assemblage type (Figure 2). Based on these classifications, the reference-lake discriminant model predicted correctly the fish assemblage type for 14 of the 15 disturbed lakes (93.3%), of which 11 were small-fish lakes and 4 were large-bodied piscivore lakes. The single incorrect assignment was a harvested

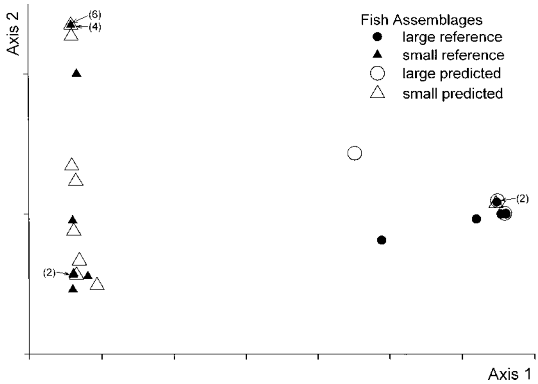

FIGURE 2.—Correspondence analysis based on catch per unit effort of six fish taxa for 19 reference lakes and 15 lakes disturbed by forest harvesting or fire. For burned and harvested lakes, symbols reflect the fish assemblage type predicted by a discriminant function model based on environmental variables from the reference lakes. The numbers of lakes represented by single points are indicated in parentheses.

lake that contained only northern pike, but was predicted to contain a small-fish assemblage.

The variance-partitioning procedure indicated that for lakes with fish (19 reference and 15 disturbed lakes), 23.3% of the variance in assemblage composition was explained by the two environmental variables used in the discriminant model (maximum depth and catchment slope) but that only 2.6% of the variance could be explained by disturbance (percentage of catchment burned or harvested). There was no interaction of disturbance and environmental variables.

Abundance (by CPUE or BPUE) of five widespread taxa examined (brook stickleback, fathead minnow, northern pike, white sucker, and dace) did not differ significantly between reference and disturbed lakes or among the three lake types when burned and harvested lakes were tested separately (Table 2). White sucker exhibited marginally higher CPUE, but not BPUE, in burned versus reference lakes (Table 2). Both white sucker and dace were absent from the six harvested lakes; zero catches, however, precluded statistical comparisons due to serious violations of test assumptions.

The proportion of small fish in the populations did not differ between reference and disturbed lakes for brook stickleback (small fish [<62 mm]; *t*-test, $P = 0.18$), fathead minnow (<62 mm; *t*-test, $P = 0.58$), or northern pike (<225 mm; Mann–Whitney, $P = 1.00$). Only populations of white sucker showed differences in size structure with disturbance (Figure 3), with a marginally larger proportion of small individuals (<220 mm) found in burned lakes as compared to reference lakes (*t*-test; $P = 0.06$).

Discussion

Our investigation, focusing initially on undisturbed reference lakes, indicated that two distinct fish assemblage types in lakes of boreal Alberta are remarkably predictable from just a few environmental variables. Maximum depth and catchment slope are sufficient to characterize the primary physical environments of the two types of lakes, wherein other biotic and abiotic factors act to shape the extant fish assemblages. Previous studies of other small lakes within the general study area indicated that the type of assemblage in a given lake is largely determined by the presence or absence of piscivory by northern pike and, to a lesser extent, yellow perch (Robinson and Tonn 1989; Paszkowski and Tonn 2000). The presence of these species in a lake is, in turn, strongly

TABLE 2.—Catch per unit effort (fish per net per hour; mean ± SE, with number of lakes in parentheses) for fish taxa in lakes from reference and disturbed (burned and harvested) catchments. The *P*-values are for comparisons between (i.e., *t*-test: reference versus disturbed) or among (i.e., ANOVA: reference versus burned versus harvested) lake types. For all species except northern pike, data were $\log_{10}(x + 1)$ transformed. Due to the absence of white suckers and dace from harvested lakes, ANOVA could not formally test for differences among the three lake types without seriously violating test assumptions.

		Disturbed		*P*-values	
Species	Reference	Burned	Harvested	*t*-test	ANOVA
Brook stickleback	0.7 ± 0.3 (13)	0.6 ± 0.2 (9)	0.2 ± 0.2 (3)	0.80	0.70
Fathead minnow	3.0 ± 1.8 (7)	2.1 ± 0.9 (4)	0.03 ± 0.03 (2)	0.55	0.31
Northern pike	0.3 ± 0.05 (6)	0.2 ± 0.0 (2)	0.4 ± 0.2 (3)	0.85	0.39
White sucker	0.2 ± 0.1 (9)	0.9 ± 0.6 (5)		0.09	
Dace spp.[a]	2.3 ± 1.2 (4)	3.2 ± 2.4 (6)		0.91	

[a] Combined catches of finescale, northern redbelly and pearl dace.

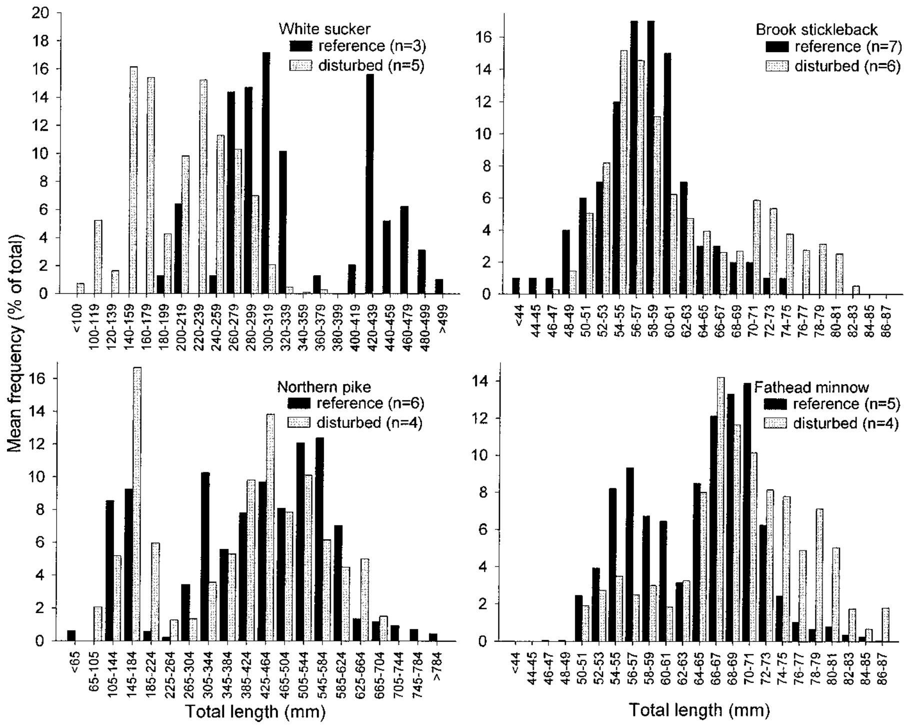

FIGURE 3.—Size-frequency distributions of four fish species from lakes disturbed by forest harvesting and fire and undisturbed reference lakes. Data are means of the frequencies from individual lakes (i.e., sample sizes refer to the number of lakes contributing to a mean). White suckers were absent from lakes with forest harvesting, so the disturbed distribution for this species represents only populations from burned catchments.

affected by its propensity to winterkill (strongly correlated with depth; Babin and Prepas 1985) or by the ability of fish to recolonize following a winterkill (Tonn and Magnuson 1982; Magnuson et al. 1998).

Therefore, if landscape disturbance could alter conditions in a lake such that piscivores were either eliminated or became established, one might expect a change in fish assemblage type. Although harvested catchments had a greater percentage of deciduous trees than did burned catchments, due to the nonrandom distributions of these disturbances, reference systems did not differ from either disturbance type in any of the measured landscape or limnological characteristics. Increases in nutrient concentrations following harvesting or burning (Carignan et al. 2000; Prepas et al. 2001a) would offer the most likely mechanism for altering fish assemblages in western boreal lakes, as any resulting increase in primary production could lead to greater winter oxygen depletion rates (Babin and Prepas 1985) and an increase in the frequency or severity of winterkill. Indeed, Prepas et al. (2001a) found that increases in total phosphorus and chlorophyll-*a* concentrations following harvesting were strongest in shallow, poorly stratified lakes, which are more susceptible to winterkill and, if isolated, often lack northern pike (Tonn and Magnuson 1982).

If disturbance routinely increased the frequency or severity of winterkill via nutrient enrichment, we might expect misclassifications whereby lakes predicted to hold northern pike-dominated assemblages actually contained small-fish assemblages (or were fishless). For example, Beaudoin et al. (2001) documented the transformation of a lake in boreal Alberta from being dominated by northern pike and yellow perch to a fishless state following a severe winterkill. Alternatively, if higher surface water flow occurred following disturbance (e.g., Keenan and Kimmins 1993; Sahin and Hall 1996), we might expect the opposite direction of misclassification, that is, lakes predicted to have only small-bodied species would regularly contain northern pike due to improved access of piscivores to winterkill-prone lakes (Tonn and Magnuson 1982). One harvested lake was indeed misclassified in this latter way.

The 93% correct prediction of assemblage type in disturbed lakes, however, suggested that forest fire or harvesting did not (with one possible exception) result in either change. Furthermore, variance partitioning indicated that the extent of landscape disturbance added little information to explain fish assemblage structure in a lake. Thus, although mechanisms exist that could cause changes in fish assemblage type (Prepas et al. 2001a), our failure to detect changes suggests that these mechanisms were not strong enough to affect fish, at least over the time scale (1–2 years post-disturbance) of our study. Indeed, no evidence of changes in lake water levels, residence times, or local runoff could be linked directly to forest harvesting in hydrological studies involving the same lakes used in our study (Devito et al. 2000; K. Devito, University of Alberta, personal communication). Rather, any changes in hydrology were better explained by long- and short-term patterns of precipitation. Similarly, some postharvest increases in nutrients in these lakes (Prepas et al. 2001a) were likely confounded, in part, by interannual variation in weather conditions. Although sample sizes among all combinations of fish assemblages and disturbance types were sometimes limited, we found that fish assemblages in harvested and burned lakes were comparable, suggesting that the two forms of disturbance have similar (although not always identical) impacts on lakes in the Boreal Plains (see also St-Onge and Magnan 2000).

Changes in the populations of individual species are necessary precursors of changes in whole assemblages. We found few differences in the abundance or size distribution of populations between reference and disturbed lakes. Most notably, unaffected populations included the dominant piscivore, northern pike. Interestingly, the one species that did display differences, white sucker, also responded to disturbance (fire and forest harvesting) in Boreal Shield lakes (St-Onge and Magnan 2000). The difference we found in Alberta lakes, however, was opposite of that reported in Québec lakes, with burned lakes in Alberta supporting more individuals and a greater proportion of small fish than did reference lakes, leaving the potential mechanism(s) of change unresolved. Such differences between regions in responses of lake ecosystems to disturbance is not surprising given that even within a single region, underlying nutrient relations in undisturbed waterbodies are affected by landscape features, such as the proportion of the catchment occupied by wetlands (Prepas et al. 2001b). Incidentally, although white sucker and dace were absent from all six harvested lakes in our study, we have observed them elsewhere in harvested lakes. Indeed, several of our reference lakes containing one or both of these taxa were subsequently harvested, and these taxa persisted post-harvest at similar densities (Tonn and coworkers, unpublished data).

We found the reference condition approach, which has been used mostly to assess benthic invertebrate communities in streams, to be a useful tool for assessing fish assemblage responses (or lack thereof) in our lakes. Our success rate (84%) at predicting fish assemblage type based on a limited number of environmental variables was high compared to the range reported elsewhere (e.g., 55.9%–79.8% in Reynoldson et al. 2001). Reynoldson et al. (2001) noted that high rates of successful predictions were more likely with few sites or diverse faunas. Our study was characterized by a relatively small number of sites, which should increase the likelihood that discrete assemblages will be identified (Wright 1995). However, our predictive success involved only six fish taxa (versus the 124 invertebrate taxa used by Reynoldson et al. 2001), suggesting that the analytical approach can be quite robust.

With respect to lake management in the boreal mixed-wood forest, our study suggests that a relatively small amount of information about the morphometry and surrounding landscape of a lake provides good predictive power regarding the presence or absence of piscivorous game fish. Current levels of natural landscape disturbance do not seem to be endangering fisheries resources or threatening nongame species, at least in the short term. The within-lake natural disturbance of winter hypoxia appears more important than catchment disturbance in shaping the fish assemblages of lakes in the western boreal forest. We must recognize, however, that limnological mechanisms associated with winterkill can be affected by catchment disturbance and may simply require greater accumulation of disturbed areas, more time, or both to produce a biologically significant effect. If our survey was expanded in space, and especially in time, as forest harvesting continues, our perception of linkages between fish assemblages, lake environments, and terrestrial disturbances might be different (Paterson et al. 1998; Scully et al. 2000).

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