Influence of Landscape Characteristics on Fish Species Richness Among Lakes of Glacier National Park, Montana

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Abstract

Studies suggest that abiotic factors at local and landscape scales partially influence patterns of occurrence of fish species in freshwaters. We examined the occurrence of fishes in relation to landscape characteristics and connectivity of habitat among 16 lakes west of the Continental Divide in Glacier National Park, Montana. Ten native and five nonnative species were observed among lakes, including catostomids, cottids, cyprinids, and salmonids. Estimated species richness (based on rarefaction) varied from 1.00 ± 0.00 to 10.22 ± 0.02 (mean $\pm$ 95% confidence interval) and estimated native species richness varied from 1.00 ± 0.00 to 7.85 ± 0.02 among lakes. Information-theoretic models indicated that the presence of dispersal barriers had a strong influence on estimated native species richness among lakes. To a lesser extent, lake maximum depth, lake surface area, and distance from study lakes to a common downstream branching point in the hydrographic network influenced estimated native species richness. Nonnative species, specifically lake trout (*Salvelinus namaycush*), have become widespread throughout the Flathead Drainage, but these data show that the upstream extent of their distribution is limited by the presence of barriers to fish dispersal. Our results indicated that habitat connectivity primarily influences, occurrence, and richness of native species in lakes of Glacier National Park.

Key words: fish species richness, landscape characteristics, barriers, native, nonnative

Introduction

Biogeography is the study of geographic patterns of species distribution and underlying processes that influence those patterns (Cox et al. 1976). At the coarsest scale, patterns of species distribution may be explained by the evolutionary history of species, tectonic activity, continental movement, and glacial events (Tonn 1990, Matthews 1998). At a finer scale, species distribution may be influenced by local environmental conditions, the biology of individual species, and interactions among species (Tonn 1990, Matthews 1998).

Large-scale patterns of native fish distribution in northern North America are largely influenced by glacial history. During the most recent glacial period, the Wisconsinan, with three major glacial expansions spanning ~ 120,000-10,000 years before present (Mathews 1998), glaciers and ice sheets covered much of North America. Glacier National Park, Montana, is located in an area associated with the Cordilleran Glacier Complex, which at its maximum was composed of interconnected valley and piedmont glaciers and an ice sheet centered in British Columbia, Canada (Flint 1957). As Wisconsinan glaciers retreated, fishes likely colonized northern latitudes from Cascadia glacial refugia (Crossman and McAllister 1986, McPhail and Lindsey 1986). Additionally, remnants of Glacial Lake Missoula, which was located directly south of Glacier National Park, may have provided a source of colonizing fishes. At its peak, Glacial Lake Missoula covered an area larger than Lake Erie and Lake Ontario combined, and was formed, drained, and reformed several times as massive ice dams ruptured (Alt 2001). Therefore, regional patterns of fish species distribution in Glacier National Park may be viewed as a legacy of post-glacial colonization. At a more localized scale, distribution of fishes in specific water bodies in this region may be the result of habitat availability, i.e., species area relationships (MacArthur and Wilson 1967, Tonn 1990) and suitability, barriers to movement and colonization, interactions among species, and stochastic events.

Although lakes in Glacier National Park have experienced past introductions and invasions of nonnative fishes, extirpations of native species as a direct result of establishment of nonnative species has not been documented, and the historic data necessary to evaluate assemblage level effects are not available. Additionally, information regarding the basic distribution patterns of fishes in Glacier National Park is not readily available with the exceptions of scientific literature related to species of special concern (e.g., Marnell 1987, Fredenberg 2002, Mogen and Kaeding 2005a, Mogen and Kaeding 2005b) and popular literature related to sport fishing (e.g., Schneider 2002). The first complete scientific account of the fishes of Glacier National Park was written by Schultz (1941), based on systematic sampling of Glacier National Park waters conducted by the U.S. Bureau of Fisheries in 1932 and 1934. Perhaps Morton (1968a, 1968b, 1968c), who summarized available information from 1916 through 1966, provided the most complete body of information available for fisheries of Glacier National Park.

Understanding patterns of species distribution underlies effective management and conservation of ecological communities, species assemblages, individual species, and local populations. The relatively unperturbed habitat of Glacier National Park makes it an ideal system to examine patterns of fish species distribution associated with landscape characteristics in an area that has received little attention in the fishery literature. Additionally, understanding factors affecting species distribution may elucidate the potential for future nonnative species invasions in this area.

We used a landscape ecological approach (see Turner et al. 2001) to examine the influence of landscape characteristics and heterogeneity on native fish species richness among lakes in Glacier National Park, west of the Continental Divide (Fig. 1). Within this framework, we consider lakes within the study area to represent suitable habitat patches within a background matrix of unsuitable habitat. Additionally, we consider these patches to be interconnected to varying degrees by way of the North Fork and Middle Fork Flathead rivers and their tributaries. Therefore, this study examines the influence of both categorical pattern, e.g., patch-level metrics such as lake size and elevation (Turner et al. 2001) and linear network pattern, e.g., stream network connectivity and discontinuity associated with dispersal barriers (Turner et al. 2001) on native fish species richness. Our specific objectives were to (1) examine the influence of landscape characteristics on native species distribution in lakes of Glacier National Park, located in the upper Flathead River Drainage, Montana, (2) summarize distributions of nonnative species, and (3) discuss potential for future invasions by nonnative fishes in this region based on patterns of native species distribution.

Methods and Materials

Study Area

Lakes within Glacier National Park, located in northwestern Montana (Fig. 1), represent portions of three major drainages; the Flathead Drainage (west of the Continental Divide), the Hudson Drainage (east of the Continental Divide in the northern portion of Glacier National Park), and the Missouri Drainage (east of the Continental Divide in the southern portion of Glacier National Park). The present study focused on 16 lakes within Glacier National Park west of the Continental Divide, which are part of the North Fork Flathead (U.S. Geological Survey Cataloging Unit:

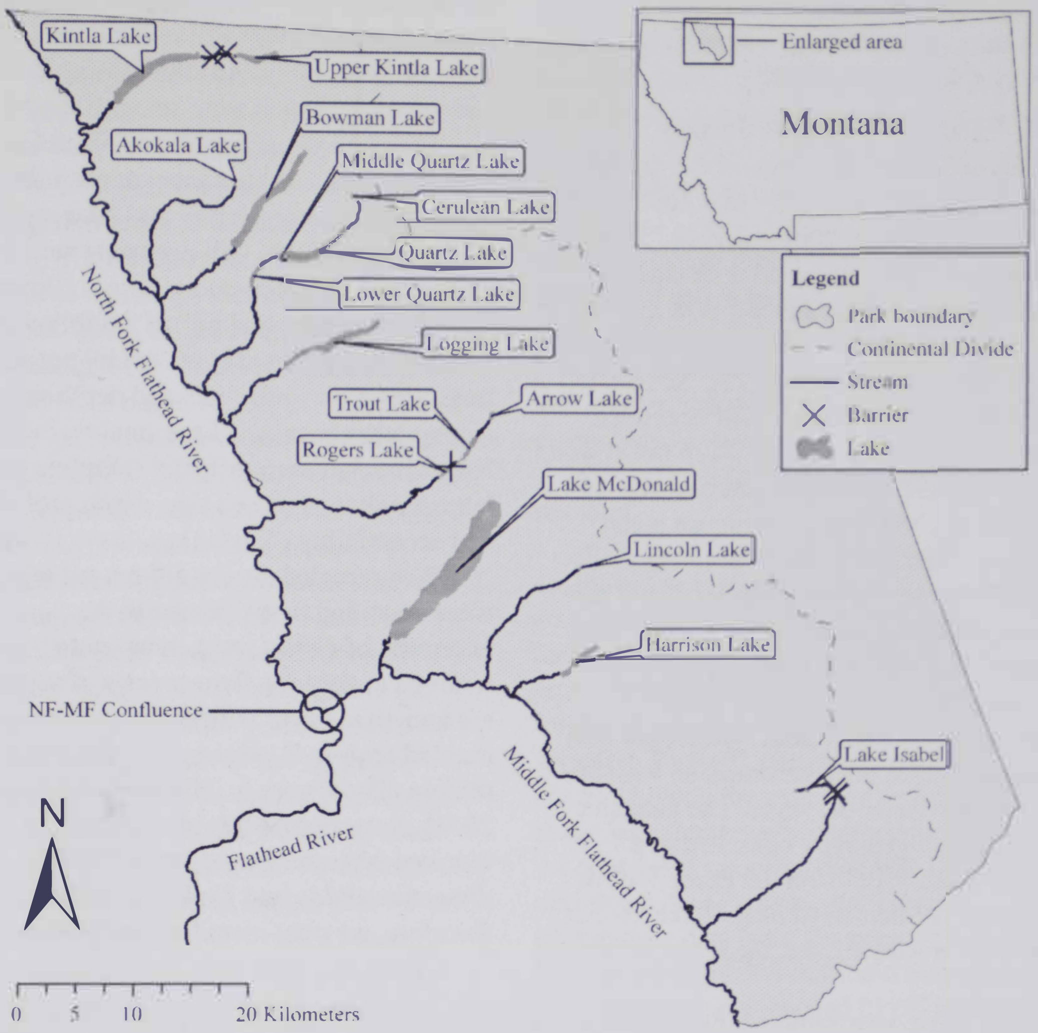

Figure 1. Study area, Glacier National Park, located in northwestern Montana. Sixteen study lakes are labeled, solid line represents the boundary of Glacier National Park, dashed line represents the Continental Divide, and solid bold lines represent the stream system made up of the North Fork and Middle Fork Flathead rivers and tributary streams associated with study lakes. An **X** represents the locations of a barrier.

17010206) and the Middle Fork Flathead (U.S. Geological Survey Cataloging Unit: 17010207) watersheds (U.S. Environmental Protection Agency 2006). Situated in glaciated valleys, lakes within Glacier National Park can generally be classified as cirque and moraine lakes (Gallagher 1999). These glacial lakes vary from round and deep to long and narrow, and are fed by headwater streams originating from glaciers and snowfields (Schneider 2002). Only 10 native fish species are known to occur in the Flathead Lake-River ecosystem, but at least 17 additional species have been introduced or currently inhabit portions of the watershed (Spencer et al. 1991). Fish assemblages within Glacier National Park lakes vary from monospecific to lakes containing intact native fish species assemblages and lakes containing complex fish assemblages marked by multiple nonnative species. Additionally, the study lakes represent the known distribution of adfluvial bull trout (*Salvelinus confluentus*), a species listed as threatened under the federal Endangered Species Act of 1973, in the Columbia River Basin headwaters of Glacier National Park, and a number of headwater populations of westslope cutthroat trout (*Oncorhynchus clarkii* *lewisi*), a species of special concern in all states throughout its native distribution in the U.S. (NatureServe 2007).

Fish Sampling Methodology

We conducted gill net surveys during the summers of 2004, 2005, and 2006 in 16 lakes within Glacier National Park (Table 1). Surveys were conducted with sinking experimental gill nets that were 38 m long, 2 m deep, and constructed of multifilament nylon with five panels; 19-, 25-, 32-, 38-, and 51-mm bar mesh. Gill nets were configured as either a single 38-m net or as a double net, i.e., two 38-m nets tied end-to-end such that the 51-mm bar mesh panel of one net was tied to the 19-mm bar mesh panel of the second net. Number of gill nets set varied among lakes (Table 1) according to scientific collection permit requirements; the collection permit allowed lethal sampling of ≤ 10 bull trout. We set gill nets perpendicular to the lake shoreline with one end anchored near the shore. The near shore end of the net generally consisted of a 19-mm bar mesh panel with the exceptions of three of seven nets in Akokala Lake, five of eight nets in Arrow Lake, three of four nets in Cerulean Lake, one of three nets in Lake Isabel, five of 12 nets in Lincoln Lake, and three of four nets in the 2006 Lower Quartz Lake sample, which were set with the 51-mm bar mesh panel near shore. We set gill nets from a float tube, canoe, or motorboat depending on accessibility and lake-specific boating regulations. Gill nets were set during late afternoon and evening, allowed to soak overnight, and pulled the following morning beginning at sunrise. Gill net set time, soak time, pull time, and depth varied among lakes because of seasonality, i.e., day length in relation to different sampling dates, lake morphometry, i.e., size, depth profile, and accessibility (Table 1).

Fish sampled during gill net surveys were identified to species (with the exception of *Cottid* spp.), enumerated, and returned to the lake. Two species of sculpins are known to occur within the study area—mottled sculpin (*Cottus bairdi*) and slimy sculpin (*C. cognatus*); (Holton and Johnson 2003). Accurate species identification required laboratory examination and dissection (Eddy and Underhill 1978); therefore, we only identified sculpins to

Table 1. Lake, year sampled, number of gill nets (*n*), gill net configuration (single = 38 m; double = 76 m), gill net soak time (hr; mean ± SD), and gill net depth (m; mean ± SD) at the inshore and offshore ends of the gill nets.

Lake	Month and year sampled	*n*	Configuration	Soak time (hr)	Depth (m) Inshore	Depth (m) Offshore
Akokala	July 2004	7	Single	9.4 ± 0.2	1.8 ± 0.4	4.5 ± 1.7
Arrow	June 2004	8	Single	9.3 ± 0.2	1.2 ± 0.7	10.7 ± 3.9
Bowman	August 2005	10	Double	14.1 ± 1.6	3.2 ± 1.7	34.4 ± 9.9
Cerulean	July 2004	4	Single	9.0 ± 1.1	0.5 ± 0.3	17.8 ± 6.1
Harrison	August 2005	10	Single	12.4 ± 0.9	5.0 ± 1.7	18.9 ± 6.4
Isabel	September 2004	3	Single	17.2 ± 1.9	2.6 ± 0.5	8.9 ± 1.0
Kintla	August 2005	10	Double	13.0 ± 1.8	2.1 ± 1.5	25.4 ± 15.2
Lincoln	August 2004	12	Single	10.8 ± 0.7	1.8 ± 1.1	12.3 ± 5.5
Logging	August 2005	10	Double	12.2 ± 1.7	2.7 ± 2.0	20.5 ± 12.0
Lower Quartz	August 2005	8	Single	12.8 ± 2.0	3.3 ± 1.9	13.5 ± 5.0
	June 2006	4	Single	15.0 ± 0.1	4.5 ± 2.4	6.6 ± 1.4
McDonald	September 2005	10	Double	16.1 ± 0.4	12.1 ± 16.4	31.3 ± 14.3
Middle Quartz	August 2005	6	Single	11.5 ± 0.2	4.4 ± 2.2	9.7 ± 1.0
Quartz	September 2005	6	Single	17.8 ± 1.4	2.1 ± 1.5	16.8 ± 4.7
	June 2006	2	Double	8.8 ± 0.0[1]	4.7 ± 3.5	14.2 ± 5.4
Rogers	July 2005	2	Single	11.5 ± 0.6	2.7 ± 0.6	3.5 ± 1.1
Trout	July 2005	4	Single	12.6 ± 1.2	1.5 ± 0.8	12.3 ± 2.7
Upper Kintla	July 2005	4	Single	9.0 ± 0.0[1]	0.8 ± 0.8	18.3 ± 5.4

[1]Standard deviation (SD) value less than 0.05

genera. Westslope cutthroat trout were historically the only native member of the genus *Oncorhynchus* present in the study area (Liknes and Graham 1988); however, rainbow trout (*O. mykiss*) and Yellowstone cutthroat trout (*O. c. bouvieri*) have been introduced to areas of the Flathead Drainage resulting in hybridization and introgression with native westslope cutthroat trout (Hitt et al. 2003, Boyer et al. 2008). Field identification of hybridized westslope cutthroat trout based on morphological and meristic characteristics alone is problematic (Gyllensten et al. 1985, Leary et al. 1987); therefore, we did not identify cutthroat trout based on hybrid status or to subspecies.

Electrofishing surveys were conducted in the summers of 2004, 2005, and 2006 at sites located in wadeable portions of the littoral zone of study lakes (Table 2). We selected electrofishing sites based on presence of large substrates, e.g., cobble and boulder, which was considered likely to provide fish cover. Electrofishing sites were open to movement, i.e., block nets were not used, 100-m in length, and ~ 3-m wide, and number of sites varied among lakes (Table 2); two sites were surveyed in Arrow Lake with site lengths of 106 and 173 m. Sites were sampled using a backpack electrofishing unit (model LR-24 Electrofisher, Smith-Root, Inc., Vancouver, Washington) using a single pass. The LR-24 Quick Setup option was used to produce a 30Hz, 12-percent duty cycle at 25 W power output with the exception of Arrow Lake where a 10-percent duty cycle was used. Output voltage was increased if fish were not exhibiting galvanotaxis and varied from 296 ± 17 V (mean ± SD) to 810 ± 0 V among lakes (Table 2). Electrofishing time varied among sites (Table 2) based on number of fish sampled and habitat complexity. Fish sampled during electrofishing surveys were identified to species (as above), enumerated, and released.

Electrofishing surveys were not conducted in Cerulean Lake due to logistical constraints associated with its remote location and at Rogers Lake because of an apparent fish kill prior to scheduled sampling. On the scheduled date for sampling Rogers Lake, dead fish were observed along the shoreline and floating in the lake. Lake surface temperature on the scheduled sampling date was 21 °C; mid-day 2 August 2006. Additionally, temperature data from the period 22 August 2006 to 13 July 2007 indicated that mean daily temperatures reached 21 °C in the inlet stream and 23 °C at the outlet stream of Rogers Lake (unpublished).

Table 2. Lake, year sampled, number of 100-m electrofishing sites (*n*), electrofisher voltage setting (V; mean ± SD), and electrofishing time (min; mean ± SD).

Lake	Month and year sampled	*n*	Voltage (V)	Electrofishing time (min)
Akokala	July 2004	4	547 ± 78	19.6 ± 5.1
Arrow[1]	June 2004	2	800 ± 0	23.0 ± 8.8
Bowman	June 2005	6	392 ± 21	23.2 ± 6.7
	June 2006	4	296 ± 17	22.3 ± 4.7
Harrison	August 2005	3	500 ± 0	13.2 ± 2.2
Isabel	September 2004	2	785 ± 35	18.0 ± 8.9
Kintla	June 2005	6	420 ± 0	31.0 ± 6.7
	June 2006	3	310 ± 0	25.4 ± 3.7
Lincoln	August 2004	4	685 ± 0	15.1 ± 2.2
Logging	August 2005	6	600 ± 0	15.1 ± 4.0
Lower Quartz	August 2005	6	550 ± 0	15.4 ± 4.3
McDonald	June 2006	5	327 ± 11	20.3 ± 3.8
Middle Quartz	August 2005	6	567 ± 26	10.7 ± 2.4
Quartz	June 2006	6	397 ± 40	18.4 ± 2.5
Trout	Juyl 2005	6	467 ± 26	13.7 ± 1.7
Upper Kintla	July 2005	6	545 ± 10	17.7 ± 3.5

[1]Electrofishing sites for Arrow Lake were 106 and 173 m in length.

Landscape Characteristics

Landscape characteristics, including lake morphometrics, i.e., patch-level metrics (Turner et al. 2001), were measured either on-site during the summers of 2004, 2005, and 2006, or determined from previously recorded data. Lake morphometrics included lake surface area, maximum length, and maximum depth. Other landscape characteristics included lake elevation, distance from the study lake to the confluence of the North Fork Flathead River and the Middle Fork Flathead River (hereafter referred to as NF-MF distance; Fig. 1), and presence of putative fish dispersal barriers (hereafter referred to as barriers) located within the drainage downstream of the study lake.

We determined lake surface area, maximum length, and elevation (Table 3) from a geographical information system (GIS) lake layer (simple polygon; NAD 1983 UTM projected coordinate system). Lake maximum depth (Table 3) was measured from available bathymetric maps (Bowman Lake, Harrison Lake, Kintla Lake, Lake McDonald, Logging Lake, Lower Quartz Lake, Quartz Lake, and Upper Kintla Lake; see USDI Fish and Wildlife Service 1977) or on-site (Akokala Lake, Arrow Lake, Cerulean Lake, Lake Isabel, Lincoln Lake, Middle Quartz Lake, Rogers Lake, and Trout Lake) using a handheld depth finder (model LPS-1, VEXILAR, Inc., Minneapolis, Minnesota). NF-MF distance (Table 3) was measured from a GIS stream layer (simple polyline; NAD 1983 UTM projected coordinate system). This metric represents the distance from individual study lakes to a common branching point in the contemporary hydrographic network (Fig. 1) and likely path of post-glacial colonization from Flathead Lake and Cascadia glacial refugia. Barriers were located by walking stream reaches between each study lake and either the North Fork Flathead River or the Middle Fork Flathead River. We measured barriers, defined by vertical drops of $\geq$ 1.8 m (Evans and Johnston 1980), for width and height and recorded their locations.

Statistical Analysis

To make comparisons among lakes where both gill net and electrofishing surveys were performed, we used a rarefaction method (Sanders 1968, Simberloff 1972) to estimate species richness that included nonnative species and native species richness excluding nonnative species. Rarefaction estimated expected

Table 3. Presence and absence of barriers downstream of lake, maximum lake depth (Depth; m), lake surface area (ha), distance from lake to the confluence of the North Fork Flathead River and the Middle Fork Flathead River (NF-MF; km), maximum lake length (Length; km), and elevation (m) for 16 study lakes in Glacier National Park, Montana.

Lake	Barrier	Depth (m)	Surface area (ha)	NF-MF (km)	Length (km)	Elevation (m)
Akokala	Absent	6.9	9.5	73.3	0.7	1443
Arrow	Present	16.5	23.9	55.1	0.8	1241
Bowman	Absent	77.1	697.5	63.9	10.5	1228
Cerulean	Absent	35.9	20.3	63.8	0.7	1423
Harrison	Absent	41.1	162.6	28.5	2.3	1126
Isabel	Present	16.0	18.3	82.2	0.6	1742
Kintla	Absent	118.9	694.1	84.3	6.8	1222
Lincoln	Absent	22.7	13.9	35.0	0.7	1401
Logging	Absent	60.4	450.6	48.3	7.9	1161
Lower Quartz	Absent	18.9	67.5	58.4	2.0	1277
McDonald	Absent	141.4	2780.9	11.6	15.2	961
Middle Quartz	Absent	12.5	19.0	60.3	0.7	1340
Quartz	Absent	83.2	351.8	60.7	4.8	1346
Rogers	Absent	4.3	34.5	51.7	1.0	1156
Trout	Present	49.8	87.4	52.7	2.8	1190
Upper Kintla	Present	55.8	189.5	88.0	3.7	1332

species richness standardized to the smallest sample size (Simberloff 1972) to make statistical comparisons among lakes where different numbers of fish were sampled. Although rarefaction methods are useful for comparing among samples of different sizes, we note that rarefaction-based species richness estimates may be sensitive to small sample sizes and to samples with highly variable species specific relative abundances (Hurlbert 1971).

Because species composition varied between gill net surveys (generally dominated by salmonid and sucker species; Table 4) and electrofishing surveys (generally dominated by minnow and sculpin species; Table 5), gill net and electrofishing data were rarefied separately. For each lake we drew a random subsample of 34 individuals from the total sample of individuals observed during gill net surveys and drew a random subsample of seven individuals from the total sample of individuals observed during electrofishing surveys. Based on this procedure, the species identity of randomly-drawn individuals was known, unlike methods that use rarefaction algorithms to predict species richness (see Hurlbert 1971, Kwak and Peterson 2007); therefore, two random subsamples, i.e., gill net and electrofishing, of individuals could be combined and number of species present could be determined. We repeated this procedure 10,000 times and used the mean value as an estimate of species richness for statistical comparisons.

We used simple linear and multiple linear regression (PROC REG; SAS Institute 2004) to model the effect of landscape characteristics on native species richness (rarefaction estimate). Lake surface area and maximum length were $\log_{10}$ transformed to normalize data; normality was determined based on a Kolmogorov-Smirnov test (Sokal and Rohlf 1995) for normal distributions (PROC UNIVARIATE; SAS Institute 2004). We used an indicator variable to represent the presence of a barrier located within the drainage downstream of the study lake. The three-lake morphometrics were highly correlated ($P < 0.0001$); therefore, no models were examined that contained a combination of these variables. Elevation and NF-MF distance were highly correlated ($P = 0.008$); therefore, no models were examined that contained both of these variables.

We examined three groups of models. The first group consisted of five simple linear regression models used to examine the influence of five individual landscape characteristics (excluding the presence of barriers) on native species richness. The second group consisted of five multiple linear regression models used to examine additive effects of barriers and (a) each of the three lake morphometrics individually, (b) lake elevation, and (c) NF-MF distance on native species richness. The third group consisted of three multiple linear regression models used to examine additive effect of barriers, NF-MF distance, and each of the three lake morphometrics individually on native species richness.

An information-theoretic approach using Akaike's Information Criterion adjusted for small sample sizes (AIC_c, Hurvich and Tsai 1989) in conjunction with Δ_i values was used to select appropriate approximating models supported by the empirical data (Burnham and Anderson 2002). We excluded models with Δ_i values > 10.00 from consideration (Burnham and Anderson 2002). The model likelihood given the data [$L(g_i|x)$]. Akaike weights (weight of evidence for a given model; w_i), and evidence ratios (w_1/w_j) were calculated to assist in comparisons among appropriate approximating models (Burnham and Anderson 2002). For appropriate approximating models with greater than one independent variable, we calculated reduction in error sums of squares associated with inclusion of each independent variable, i.e., the marginal contribution of each independent variable, in the model (Neter et al. 1996).

Results

Ten native and four nonnative fish species were sampled among 16 lakes during gill-net and electrofishing surveys in Glacier National Park (Tables 4 and 5).

Table 4. Sample size (n) and percent of sample made up of 14 species among 16 lakes sampled using gill nets in Glacier National Park, Montana. An asterisk (*) denotes nonnative species.

Lake	*n*	BLT	CUT	MWF	PWF	BRK*	KOK*	LKT*	LWF*	LNS	LSS	NPM	PEM	RSS	SCU
Akokala	103	12.6	3.9	83.5											
Arrow	73	19.2	30.8												
Bowman	543	3.1	4.2	74.8				9.6		6.8				0.9	0.6
Cerulean	54	11.1		88.9											
Harrison	424	2.1	2.8	79.7		0.2	0.9	2.1		12.0					
Isabel	150	38.0	62.0												
Kintla	626	1.9	7.5	60.5				5.4		17.7			5.6	1.3	
Lincoln	278	3.2	2.5	23.4		3.6				67.3					
Logging	984	0.7	4.2	50.0				2.5		17.8		24.3		0.5	
Lower Quartz	441	2.9	13.2	53.3				0.5		29.5				0.7	
McDonald	478	1.7	0.4	14.2	2.1		1.7	6.9	15.3	8.6	4.8	24.1	18.8	1.5	
Middle Quartz	210	5.2	5.7	66.7						20.0				2.4	
Quartz	493	11.0	5.7	67.3				0.2		12.6	1.8			1.4	
Rogers	130	0.8	6.9	59.2				0.8		28.5		3.8			
Trout	125	20.8	78.4												0.8
Upper Kintla	34	100.0													

BLT = bull trout, CUT = cutthroat trout, MWF = mountain whitefish, PWF = pygmy whitefish, BRK = brook trout, KOK = kokanee, LKT = lake trout, LWF = lake whitefish, LNS = longnose sucker, LSS = largescale sucker, NPM = northern pikeminnow, PEM = peamouth, RSS = redside shiner, SCU = sculpin *spp.*

Table 5. Sample size (*n*), and percent of sample made up of nine species among 14 lakes sampled using electrofishing gear in Glacier National Park, Montana. An asterisk (*) denotes nonnative species.

Lake	*n*	BLT	CUT	MWF	BRK*	LNS	NPM	PEM	RSS	SCU
Akokala	76	2.6								97.4
Arrow	39	46.2	53.8							
Bowman	212					8.5			10.4	81.1
Harrison	7		14.3		14.3	28.6				42.9
Isabel	12	75.0	25.0							
Kintla	259		0.4			88.8		7.5		79.8
Lincoln	20									100.0
Logging	46						45.7		21.7	32.6
Lower Quartz	76		2.6	1.3		26.3			43.4	30.3
McDonald	76					3.9	26.3	17.1	21.1	27.6
Middle Quartz	11					9.1			90.9	
Quartz	97					60.8			20.6	18.6
Trout	7									100.0
Upper Kintla	9	100.0								

BLT = bull trout, BRK = brook trout, CUT = cutthroat trout, LNS = longnose sucker, MWF = mountain whitefish, NPM = northern pikeminnow, PEM = peamouth, RSS = redside shiner, SCU = sculpin *spp*.

Native species included bull trout, cutthroat trout, mountain whitefish (*Prosopium williamsoni*), pygmy whitefish (*Prosopium coulterii*), largescale sucker (*Catostomus macrocheilus*), longnose sucker (*C. catostomus*), sculpin, northern pikeminnow (*Ptychocheilus oregonensis*), peamouth (*Mylocheilus caurinus*), and redside shiner (*Richardsonius balteatus*). Total number of species observed within lakes varied from one to 13, and number of native species varied from one to 10 (Table 6). Following rarefaction, estimated species richness varied from (mean ± 95% CI) 1.00 ± 0.00 to 10.22 ± 0.02 and estimated native species richness varied from 1.00 ± 0.00 to 7.85 ± 0.02 (Table 6). All nonnative species were in the family Salmonidae, including brook trout (*S. fontinalis*), kokanee (*O. nerka*), lake trout (*S. namaycush*), and lake whitefish (*Coregonus clupeaformis*).

Maximum lake depth varied from 4.3 to 141.4 m, lake surface area varied from 9.5 to 2780.9 ha, NF-MF distance varied from 11.6 to 88.0 km, maximum lake length varied from 0.6 to 15.2 km, and lake elevation varied from 961 to 1742 m (Table 3). Barriers were located in Camas Creek, Kintla Creek, and Park Creek (Table 3, Fig. 1). The barrier in Camas Creek was a waterfall measuring 7.2 m high and 23.2 m wide in a steep canyon. This waterfall was downstream of Trout Lake and therefore also influenced Arrow Lake located upstream of Trout Lake (Fig. 1). Multiple barriers were located in Kintla Creek downstream of Upper Kintla Lake (Fig. 1). The most substantial barriers in Kintla Creek were a waterfall within a bedrock constrained canyon measuring 2.8 m high and 2.7 m wide, and a waterfall measuring 6.7 m high and 14.3 m wide. Three waterfalls were located in Park Creek downstream of Lake Isabel measuring 2.7 m high and 3.0 m wide, 2.4 m high and 3.4 m wide, and 1.8 m high and 2.9 m wide.

Five simple linear regression models examining the influence of the individual landscape characteristics had no support given the data, i.e., $\Delta_i > 10.00$, and were therefore not presented. All supported models included presence of barriers (Table 7). The weight of evidence against alternative models relative to the top ranked model increased rapidly for models ranked 5 through 8 based on evidence ratios (Table 7). For models best supported by the empirical data (Δ_i values less than or equal to 2.00; Burnham and Anderson 2002), the top ranked model included presence of barriers and maximum lake depth (Table 7). For this model, inclusion of barriers reduced model error sums of squares by 76 percent and inclusion of maximum lake depth

Table 6. Study lake, observed native species richness and mean native species richness (± 95% CI) based on rarefaction, and observed species richness and mean species richness based on rarefaction. Richness estimates were based on samples from gill-net and electrofishing surveys.

Lake	Native species richness		Species richness	
	Observed	Mean (± 95% CI)	Observed	Mean (± 95% CI)
Akokala	4	3.80 ± 0.01	4	3.80 ± 0.01
Arrow	2	2.00 ± 0.00	2	2.00 ± 0.00
Bowman	6	5.18 ± 0.01	7	6.15 ± 0.02
Cerulean[1]	2		2	
Harrison	5	4.54 ± 0.01	8	5.44 ± 0.02
Isabel	2	2.00 ± 0.00	2	2.00 ± 0.00
Kintla	7	5.71 ± 0.01	8	6.58 ± 0.02
Lincoln	5	4.30 ± 0.01	6	5.04 ± 0.02
Logging	7	5.81 ± 0.01	8	6.39 ± 0.02
Lower Quartz	6	5.91 ± 0.01	7	6.10 ± 0.01
McDonald	10	7.85 ± 0.02	13	10.22 ± 0.02
Middle Quartz	5	4.76 ± 0.01	5	4.75 ± 0.01
Quartz	7	6.30 ± 0.01	8	6.40 ± 0.01
Rogers[1]	5		6	
Trout	3	3.00 ± 0.00	3	3.00 ± 0.00
Upper Kintla	1	1.00 ± 0.00	1	1.00 ± 0.00

[1]Incomplete data for Cerulean and Rogers lakes is a result of incomplete sampling, i.e., no electrofishing surveys.

Table 7. Model rank (Rank) based on Akaike's Information Criterion values adjusted for small sample size, variables entered into the mode, Akaike's Information Criterion values adjusted for small sample size (AIC_C), change in AICc (Δ_i), likelihood of the model given the data [$L(g_i|x)$], Akaike weights (w_i), the evidence ration (w_1/w_j) relative to the highest ranked model for models with ΔAIC_C values less than 10.00.

Rank	Variables in model	AIC_C	Δ_i	$L(g_i\|x)$	w_i	w_1/w_j
1	Barrier, depth	1.37	0.00	1.00	0.34	
2	Barrier, surface area	2.11	0.73	0.69	0.23	1.48
3	Barrier, depth, NF-MF distance	3.10	1.73	0.42	0.14	2.43
4	Barrier, length	3.41	2.04	0.36	0.12	2.83
5	Barrier, NF-MF distance, surface area	4.32	2.95	0.23	0.08	4.25
6	Barrier, NF-MF distance, length	5.12	3.74	0.15	0.05	6.80
7	Barrier, elevation	6.24	4.87	0.09	0.03	11.33
8	Barrier, NF-MF distance	7.94	6.57	0.04	0.01	34.00

reduced model error sums of squares by 49 percent in the linear model. The second highest ranked model included presence of barriers and lake surface area (Table 7). For this model, inclusion of the presence of barriers reduced model error sums of squares by 75 percent and inclusion of lake surface area reduced model error sums of squares by 46 percent in the linear model. The third highest ranked model included the presence of barriers, maximum lake depth, and NF-MF distance (Table 7). For this model, inclusion of the presence of barriers reduced model error sums of squares by 75 percent, inclusion of maximum lake depth reduced model error sums of squares by 51 percent, and inclusion of NF-MF distance reduced model error sums of squares by 21 percent in the linear model.

Discussion

Presence of barriers and some metric of habitat size, i.e., lake depth and lake surface area, best explained patterns of estimated native species richness in Glacier National Park. We did not detect cyprinids and catostomids in lakes located upstream of barriers (Arrow Lake, Lake Isabel, Trout Lake, and Upper Kintla Lake), and of lakes located upstream of barriers, we only detected cottids in Trout Lake. All regression models with Δ_i values less than 10.00 included the presence of barriers. Additionally, inclusion of barrier in the top three approximating models reduced error sums of square by 74-76 percent. Our combined results revealed that barriers limit dispersal of fishes in this system, but in the absence of barriers estimated native species richness generally increased with increasing habitat size, i.e., positive parameter estimates for lake depth and lake surface area.

The observed pattern of native fish distribution among study lakes may have occurred if the most successful, early post-glacial colonizers were primarily salmonids and, to a lesser extent, cottids. In this situation specific species assemblages may have colonized the study system prior to or during formation of dispersal barriers that we documented in this study. Alternatives to this hypothesis exist. For example, structures that we identified as migratory barriers may not be true barriers, but allow limited passage of fish that are powerful swimmers or that are capable of navigating complex or high-velocity habitat. However, absence of nonnative salmonids and native cyprinids and catostomids in all lakes located upstream of migratory barriers, despite their widespread presence in other study lakes, provided little support for this hypothesis. Structures identified as barriers in this study may not have been true barriers at all times in history, but may have allowed limited, sporadic, or seasonal passage during some past colonization. Additionally, the barriers may have been breached sometime in the past following colonization by fishes in downstream lakes. These alternatives are plausible; however, absence of native cyprinids and catostomids and nonnative salmonids would still suggest that native salmonids were early colonizers from downstream sources. Alternatively, local extirpations following colonization of more diverse fish assemblages may have occurred in lakes located upstream of barriers; however, no available historic data were available to provide insight into this hypothesis.

There are no known populations of nonnative cyprinids, catostomids, or cottids in the Flathead Lake-River ecosystem (Holton and Johnson 2003). Nonnative centrarchids and ictalurids were introduced early in the 20th century into the mainstem Flathead River and Flathead Lake (Spencer et al. 1991), and some were widespread in the lower systems, however, these warm-water species may not have found suitable habitat in the cirque and moraine lake systems we sampled. Yellow perch (*Perca flavescens*) and northern pike (*Esox lucius*), introduced into the Flathead ecosystem in 1910 and 1965, respectively (Spencer et al. 1991), are cool water species with great habitat tolerance and widespread distribution in the Flathead Lake/River ecosystem, but thus far neither species has been detected in Glacier National Park waters west of the Continental Divide.

All nonnative species detected in this study were salmonids. Spencer et al. (1991) documented the dates of first introductions into the Flathead Lake-River ecosystem: lake trout (1905), lake whitefish (1909), brook trout (1913), Yellowstone cutthroat trout (1913), Arctic grayling (*Thymallus arcticus*) (1913), rainbow trout (1914), kokanee (1916), and Chinook salmon (*O. tshawytscha*) (1916). More recent introductions of golden trout (*O. aguabonita*) (1938) and coho salmon (*O. kisutch*) (1969) also occurred (Spencer et al. 1991). The only nonnative salmonids Schultz (1941) documented in study lakes were brook trout in Harrison Lake, and kokanee and Arctic grayling in Lake McDonald.

No nonnative species were observed in lakes located upstream of barriers (Arrow Lake, Lake Isabel, Trout Lake, and Upper Kintla Lake). There is a paucity of information regarding early stocking efforts within Glacier National Park. The most complete data is summarized in Morton

(1968a, 1968b, 1968c) for the period of 1916 to 1966. Fish stocking in Glacier National Park lakes has seldom occurred since the 1960s. Along with fish stocking in lakes surveyed in this study, numerous stockings occurred in stream systems within Glacier National Park (Morton 1968a, 1968b, 1968c). The most commonly stocked fish in the lakes represented in this study was Yellowstone cutthroat trout. Yellowstone cutthroat trout were stocked at some time in the past in all study lakes with the exceptions of Cerulean Lake, Lake Isabel, Lincoln Lake, Rogers Lake (although they were stocked throughout the Camas Creek drainage where Rogers Lake is located), and Upper Kintla Lake. However, we did not discriminate between nonnative Yellowstone cutthroat trout, native westslope cutthroat trout, or their hybrids because of difficulty associated with identification based solely on morphology.

Brook trout were historically stocked in Harrison Lake, Lake McDonald, Lake Isabel, and Lake Ellen Wilson, which is located in the same drainage directly upstream of Lincoln Lake. Brook trout were observed in this study in Harrison Lake, but not in Lake McDonald or Lake Isabel. Dux and Guy (2004) recently documented brook trout in tributary streams to Lake McDonald. Based on this study, brook trout also now occur in Lincoln Lake. Brook trout stocked in Lake Isabel in 1927 (Morton 1968b) may not have established a self-sustaining population as we did not detect them, and previous creel surveys indicated only a small number of brook trout that Morton (1968b) considered to be misidentifications. All other intentional stocking efforts among lakes examined in this study occurred in Lake McDonald where Chinook salmon, rainbow trout, and steelhead were stocked in addition to brook trout and Yellowstone cutthroat trout as previously mentioned. Lake whitefish were not detected in Lake McDonald by Schultz (1941) although he mentioned they had been reported there. They now make up the largest share of fish biomass in that lake (Dux 2005).

We did not detect many of the nonnative species in this study previously reported in Glacier National Park (Morton 1968a, 1968b, 1968c) . Kokanee were reported in Bowman Lake, Harrison Lake, and in great abundance in Kintla Lake and Lake McDonald; however, kokanee were only present in samples from Harrison Lake and Lake McDonald in this study. The limited number of kokanee that we detected in Glacier National Park may be partially due to our sampling methods but more likely resulted from the major system-wide decline in kokanee abundance in the Flathead Lake/River ecosystem (see Spencer et al. 1991).

Ongoing and future invasion by nonnative fishes in Glacier National Park is a topic of conservation concern; specifically invasion by lake trout, rainbow trout, and rainbow trout X cutthroat trout hybrids. Although lake trout were introduced into the Flathead River system in 1905 (Spencer et al. 1991), they were not yet documented in Glacier National Park waters west of the Continental Divide in 1941 (see Schultz 1941). Currently lake trout have colonized all of the large moraine lakes in Glacier National Park west of the Continental Divide (Bowman Lake, Harrison Lake, Kintla Lake, Lake McDonald, Logging Lake, Lower Quartz Lake, and Quartz Lake). Fredenberg (2002) detected an increase in lake trout abundance in the four largest lakes in Glacier National Park west of the Continental Divide from 1969 to 2000. Dux (2005) provided documentation of how extensively the aquatic fauna of the largest lake in Glacier National Park, Lake McDonald, is now dominated by a nonnative lake trout – lake whitefish fish assemblage. This invasion has the potential to negatively impact populations of adfluvial bull trout through competitive interactions as both species are generally top-level predators in systems that they inhabit. Donald and Alger (1993) observed that where large-scale geographic distributions of these species do overlap, bull trout and lake trout were generally separated based on elevation. However, elevation did not limit distribution of either species, and Donald and Alger (1993) suggested that post-glacial colonization patterns and competitive interaction resulted in the observed separation. Additionally, bull trout and lake trout may segregate by habitat when sympatric within a stream-lake system. For example, bull trout may adopt a stream-dwelling life history whereas lake trout will occupy lake habitat, e.g., Saint Mary Drainage, Montana and Alberta.

In an analysis of hybridization between native westslope cutthroat trout and nonnative rainbow trout in the Flathead River system (including portions of Glacier National Park), Hitt et al. (2003) found that rainbow trout introgression was spreading rapidly and in an upstream direction from the mainstem Flathead River and that environmental factors alone would probably not restrict further spread of hybridization and introgression. Additionally, Boyer et al. (2008) found that spatial patterns of population admixture for rainbow trout X westslope cutthroat trout follow stepping stone and continent island models of dispersal. These data suggested that further invasion of rainbow trout and rainbow trout X westslope cutthroat hybrids might occur and likely increase the conservation priority of isolated headwater populations of westslope cutthroat trout populations (Allendorf et al. 2001).

Based on distribution of native species in lakes examined in this study, the presence of dispersal barriers apparently has had a powerful influence on limiting fish distribution. Therefore, these structures may also play an important role in limiting further spread of nonnative fishes. Neither lake trout nor rainbow trout were detected in any study lakes located upstream of barriers; however, both species have expanded their distribution to the edge of these barriers. For example, both species were observed in Rogers Lake located just downstream of the barrier isolating Arrow Lake and Trout Lake. Of the study lakes not isolated by barriers, lake trout were also not detected in Akokala Lake, Cerulean Lake, Lincoln Lake, and Middle Quartz Lake. These lakes are relatively shallow (with the exception of Cerulean Lake), have a small surface area, and are located a considerable distance from mainstem Flathead River habitat, which may be a surrogate variable associated with the distance from the study lakes to the confluence of the North Fork Flathead River and Middle Fork Flathead River. A qualitative assessment of lake trout distribution in the study lakes indicated that lake trout occurred in large, deep lakes located in close proximity to mainstem Flathead River habitat. Therefore, Akokala, Cerulean, Lincoln, and Middle Quartz lakes may represent less preferred habitat for lake trout, are inhabited by lake trout at low levels, or have not been colonized yet.

Middle Quartz Lake and Cerulean Lake are part of a chain of lakes in the Quartz Creek and Rainbow Creek drainages. Lake trout were first documented in Lower Quartz Lake (most downstream lake in chain) in 2003 and in Quartz Lake in 2005 (Meeuwig and Guy 2007); therefore, lake trout must have moved through Middle Quartz Lake and may be present in Middle Quartz Lake at levels below which were detectable based on our sampling. Alternatively, Middle Quartz Lake may represent less preferred habitat for lake trout compared to Quartz Lake, which is located in close proximity just 0.40 km upstream of Middle Quartz Lake. Although Cerulean Lake has a relatively small surface area, it is relatively deep; deeper than Lower Quartz Lake and comparable to Harrison Lake of which both contain lake trout. Additionally, lack of any structures believed to significantly reduce fish movement upstream from Quartz Lake to Cerulean Lake suggested that Cerulean Lake may be at risk of invasion by lake trout. Akokala Lake and Lincoln Lake are located a large distance from mainstem Flathead River habitat, which may limit the potential for colonization (Beisner et al. 2006). Additionally, Akokala Lake is relatively shallow and may not be preferred habitat for lake trout, which often, but not exclusively, inhabit deep, cool waters (Scott and Crossman 1973). Although we documented lake trout in Rogers Lake, the shallowest lake we sampled, a fish kill was observed coincident with peak summer temperatures at this lake suggesting that this lake may be subject to frequent local extirpations. Despite the relatively shallow depth of Akokala Lake and the distance of Akokala Lake and Lincoln Lake from mainstem Flathead River sources, potential for nonnative species invasion should not be dismissed.

We did not quantitatively examine the influence of landscape characteristics on distribution of nonnative species because potential interactions between intentional introductions and natural colonization could not be separated based on available data. Additionally, we cannot disregard an influence of nonnative species on native species richness. However, systematic baseline data for the lakes we examined are not available to make an accurate assessment of assemblage level effects of establishment by nonnative species. Therefore, these data provide a baseline for future sampling efforts within the study area.

This study provides information on landscape characteristics that have influenced distribution of native species in Glacier National Park lakes located west of the Continental Divide. The effect of barriers stands out as a dominant factor in shaping distribution of fishes in this system. Protection afforded by those barriers may also be the single most important factor preserving native bull trout and cutthroat trout assemblages on the west side of Glacier National Park. We believe that these data in conjunction with current distribution data on nonnative species can provide insight into the potential for future invasions within this system and help prioritize waters in need of special conservation concern.

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