North American Journal of Fisheries Management 22:1105–1123, 2002

Development of a Fish-Based Index of Biotic Integrity for Small Inland Lakes in Central Minnesota

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Abstract.—We developed a fish-based index of biotic integrity (IBI) for a set of Minnesota lakes having similar geophysical and chemical features. Fish data were collected by means of trap nets, gill nets, shoreline seines, and backpack electrofishing. Of 30 evaluated metrics, we identified 16 metrics of three types: species richness, community assemblage, and trophic composition. In contrast to lotic IBIs, where a single sampling gear is usually used, data from all four sampling gears were necessary for IBI development. We selected metrics based on responses to measures of human-induced stress based on watershed land use patterns and human population density. Species richness and community composition metrics describing intolerant or habitat specialist species were most sensitive to differences in human-induced stress. Because these species were found in the nearshore zone of lakes, effective sampling of the nearshore fish community was essential to the development and performance of the IBI. Trap-net- and gill-net-based metrics, however, were essential to the development of trophic composition metrics, the trap nets providing the best insectivore and omnivore metric and the gill nets providing the best top carnivore metrics. Lake IBI scores reflected differences in land use patterns, trophic state, and aquatic vegetation. Sensitivity analysis indicated that selected metrics contributed to IBI performance, but the relative contribution of individual metrics varied among human-induced stress categories. Additional work is needed to test the performance of this IBI on an independent group of lakes, to set the range of applicability, and to determine the effectiveness of the IBI as an assessment tool for lakes.

A standardized method for assessing the biotic integrity of lake ecosystems does not currently exist. Lake integrity was evaluated historically by using indirect physiochemical assessments (Karr and Dudley 1981). Chemical monitoring, however, fails to detect many human-induced perturbations, such as habitat destruction (Karr 1981, 1994). Indirect monitoring also ignores the fact that organisms inhabiting an aquatic ecosystem are the fundamental sensors responding to stress affecting the system (Loeb 1994).

A popular biologically based method for measuring the integrity of aquatic systems is the index of biotic integrity (IBI). The IBI was originally developed by Karr (1981) as a rapid, cost-effective, and standardized method for assessing environmental degradation in midwestern U.S. streams based on the characteristics of their fish communities. A multimetric approach, the IBI defines a group of measures or metrics that, when combined, indicate overall biological condition (Barbour et al. 1995). Each metric in an IBI should represent some aspect of biological assemblage structure, function, or other measurable characteristic that changes in some predictable way with increased human-induced stress (as cited in Barbour et al. 1995). This approach has been applied to streams across North American (Fausch et al. 1984; Karr et al. 1986; Miller et al. 1988; Lyons et al. 1995; Paller et al. 1996; Hughes et al. 1998; Yoder and Smith 1999). Attempts to apply the IBI approach to lentic systems (Minns et al. 1994; Harig and Bain 1998; Jennings et al. 1999b; Schulz et al. 1999; Whittier 1999; Lyons et al. 2000) have met with limited success.

Development of lake IBIs lags behind development of stream IBIs because of difficulties in classifying lakes into similar groups, predicting expected fish assemblages for similar lake classes, and sampling (Whittier 1999). Because IBI performance is based on expected characteristics of a particular assemblage type, in a specific size and type of water body, in a specific ecoregion or basin, IBIs must be developed for classes of reasonably comparable ecosystems (Plafkin et al. 1989). Classification of bodies of water into comparable

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Received May 11, 2001; accepted January 18, 2002

groups, however, is more complex for lakes than for streams because habitats in lakes are more multidimensional (Whittier 1999). Fish assemblages in lakes are also more difficult to characterize. For wadable streams similar to those used to develop the IBI, electrofishing provides appropriate data for IBI assessment (Whittier 1999). No single gear, however, can sufficiently sample all habitat types or all species present in a lake (Weaver et al. 1992; Magnuson et al. 1994; Jackson and Harvey 1997). To thoroughly sample a lake requires methods that are effective in both littoral and pelagic areas. This poses the questions of how and whether to combine data from different gears and what represents a unit of sampling effort (Weaver et al. 1992; Jackson and Harvey 1997; Whittier 1999).

Minnesota lakes cover a wide array of environmental conditions, ranging from relatively undisturbed lakes in forested northern Minnesota to highly urbanized lakes in the Twin Cities Metropolitan area to agriculturally influenced lakes in southern and western Minnesota. Over the past 50 years, species diversity (Radomski and Goeman 1995) and sizes of various species (Olson and Cunningham 1989) in Minnesota lakes have declined, suggesting a decline in biological integrity. In addition, Schupp (1992) and Cross and McInerny (1995), using standardized assessment data, successfully documented changes in fish assemblages along environmental gradients. The goal of this study was to develop a fish-based IBI for Minnesota lakes that reflects overall lake integrity.

Methods

Study sites.—We chose study lakes that minimized natural variation in physical and chemical lake characteristics and maximized the range of human-induced stresses. The Minnesota lake classification system (Schupp 1992) was used to select lakes with similar characteristics. This classification system is based on variables associated with lake size and depth, lake chemistry, and length of the growing season. To reduce potential lake size effects, we included only lakes between 48 and 200 ha surface area. Selected study lakes (Table 1) had similar alkalinity, maximum depth, percent littoral area (percent of lake area deeper than 4.6 m), and shoreline complexity (shoreline development index, SDI; Orth 1983). Aerated and minepit lakes were also excluded. Study lakes belonged to four major drainage basins (Upper Mississippi River, Red River, St. Croix River, and Minnesota River). All but three species (ciscoes, brook silversides, and flathead catfish) collected during this study are found in all four drainage basins (Hatch and Schmidt 2000).

TABLE 1.—Mean morphometric and chemical variables for Minnesota lakes used in the development of a fish-based index of biotic integrity (95% confidence limits are given in parentheses).

Variable	All study lakes	Subset
N	131	52
Area (ha)	118 (111–125)	102 (92–111)
Maximum depth (m)	18.1 (16.9–19.4)	17.4 (15.2–19.4)
Alkalinity (mg/L $CaCO_3$)	124 (114–134)	115 (101–130)
Percent littoral	40 (37–42)	41 (36–45)
Shoreline development index	1.67 (1.58–1.76)	1.60 (1.48–1.73)

Study lakes were located in two ecoregions: the Central Hardwood Forest Ecoregion and the Northern Lakes and Forest Ecoregion (Omernik 1987; Heiskary and Wilson 1989). Mean summer water chemistry characteristics for all lakes in these two ecoregions did not differ significantly (MNPCA 1999). Because of the prevalence of stocking in Minnesota waters, we included stocked lakes. Walleyes *Stizostedion vitreum*, northern pike *Esox lucius*, muskellunge *E. masquinongy*, and tiger muskellunge (northern pike × muskellunge) were the primary species stocked. One lake was stocked with rainbow trout *Oncorhynchus mykiss*, a nonnative.

Sampling.—We used trap nets, gill nets, shoreline seines, and backpack electrofishing to ensure that we sampled all lake habitats. Trap-net (N = 129) and gill-net (N = 131) data were obtained from standardized lake surveys (MNDNR 1993) conducted between June and late August from 1993 through 1997. Trap nets targeted inshore insectivorous species such as bluegills *Lepomis macrochirus*, whereas gill nets targeted open water carnivorous species such as walleyes. Both trap nets and gill nets targeted the most common omnivorous species, bullheads *Ameiurus* spp. The number of trap nets and gill nets set per lake depended on lake size, averaging six gill nets per lake and nine trap nets per lake. Net sites were chosen to represent available habitats. Trap nets had a 12.2-m lead approximately 1.1 m deep with two 1.8-m × 0.9-m frames and six 0.76-m hoops with a 13-cm diameter throat; all mesh was 19-mm bar nylon. Gill nets were 76 m × 1.8 m with six 15.2-m panels of 19-, 25-, 32-, 38-, and 51-

mm bar mesh. Nets were set overnight and emptied the next day. Species were identified, counted, and weighed.

We sampled a subset of the study lakes (N = 52), using methods suitable for small nongame species, because lake surveys focused primarily on game species and larger nongame species (Table 1). Nearshore fish communities were sampled from 1997 through 1999 with a combination of shoreline seining and backpack electrofishing. All sampling was conducted during the day in the spring (May and June) or fall (September and October). May sampling began when surface water temperatures reached 15°C; October sampling ceased when surface water temperatures fell below 15°C. Excessive lake conductivity ($>$500 μmho/cm) and algal turbidity in some lakes during the midsummer months (July and August) prevented effective sampling during that period. Seining and electrofishing were completed on the same day. The seine was 15.2 m × 1.5 m with a bag and all mesh was 6.4-mm nylon. In each lake, we selected 10 random, equally spaced sampling stations 30 m long. On average, this method sampled 6% of the total shoreline. Two shocking passes were conducted at each station, one near the shoreline and one at a depth of approximately 75–100 cm. At each station, one 30-m seine haul parallel to the shoreline and out to the length of the seine or to the maximum wadable depth (approximately 1.3 m) was completed. Species were identified and counted. Seining and electrofishing data at each station were combined, with the results for one station representing 1 unit of sampling effort. The combined nearshore seining and electrofishing data will be referred to as nearshore data.

Potential metrics.—We considered various potential fish-based metrics, including those used in other lake and stream IBIs (Karr 1981; Karr et al. 1986; Minns et al. 1994; Simon and Lyons 1995; Jennings et al. 1999b; Niemela et al. 1999; Schulz et al. 1999; Whittier 1999). We classified fish species collected in this study as to tolerance (intolerant, neutral, or tolerant), feeding (insectivore, omnivore, or top carnivore), habitat specialist (vegetation-dwelling, small benthic-dwelling, or other), family (centrarchid, cyprinid, or other), and origin (native or nonnative) groups, using information from the literature (Phillips et al. 1982; Becker 1983; Scott and Crossman 1985; Lyons 1992; Minns et al. 1994; Niemela et al. 1999) and personal observation. Because Whittier and Hughes (1998) reported discrepancies in tolerance classification between lentic and lotic systems for some fish species, we verified tolerance classifications with methods similar to those described in Whittier and Hughes (1998). Species classifications are listed in Table 2.

Richness metrics, defined as the number of species within tolerance, feeding, habitat, and family groups, were calculated by combining species-richness data from the 52 lakes sampled by nearshore sampling with the corresponding species-richness data obtained with trap nets and gill nets. Gear-specific metrics describing assemblage composition were expressed as the relative abundance or relative biomass of a specific group in either trap-net, gill-net, or nearshore samples. Evaluated gear-specific metrics were chosen on the basis of species vulnerability to a given gear. Nearshore sampling data were used for assemblage composition metrics describing small, nongame species and included the relative abundance of cyprinid, small benthic-dwelling, vegetation-dwelling, and intolerant fishes. Cyprinid-based metrics excluded common carp, a nonnative species. Trap-net data and gill-net data were used for composition metrics based on game fish and larger nongame species and were expressed as both relative abundance and relative biomass. Trap-net data were used for insectivore composition metrics, gill-net data for top carnivore composition metrics. Both trap-net and gill-net data were used to evaluate omnivore, intolerant, and tolerant composition metrics, because both gears targeted species found in these groups.

Lake characteristics and human-induced stress.—We used disturbance within a lake's watershed as a non–fish-based measure of human-induced stress. Disturbance was indexed by using percent forested land cover, cultivated land cover, and urban land cover within a lake's watershed (MNDNR 1999) and the population density of the county in which a lake was located (Minnesota Planning 2000). A lake's watershed was defined as an area of at least 12.95 km^2 (1,295 ha) enclosed by a continuous height of land drainage (MNDNR 1999). We chose forest, cultivated, and urban land use because they represented the extremes of potential land use categories (urban, cultivated, hay, brush, forest, water, bog, and mining). We used the population density of the county in which a lake was located because population data were not available by watershed for all lakes. For lakes in which both watershed and county population estimates were available, the two density estimates were highly correlated (Pearson's correlation, N = 29, $\rho = 0.88$, $P < 0.0001$). Percent land use for forest (3–87%), cultivated (0–72%), urban (0–87%) categories, and population density (3–1,228 people/

TABLE 2.—Family, tolerance, feeding, and habitat classifications for fish species collected in Minnesota lakes by trap nets, gill nets, shoreline seining, and backpack electrofishing. The following abbreviations are used: I = intolerant, T = tolerant; Fi = filter, He = herbivore, In = insectivore, Om = omnivore, Tc = top carnivore; Smb = small benthic dwelling, and Veg = vegetation dwelling. Occurrence is the percent of lakes from the 52-lake subset used to evaluate species richness that included the species. Species denoted by asterisks were sampled exclusively by seining or backpack electrofishing. Species denoted by ''ns'' were not found in the subset of lakes.

Species	Family	Tolerance	Feeding	Habitat	Occurrence (%)
Bowfin *Amia calva*	Amiidae		Tc	Veg	44.2
Cisco *Coregonus artedi*	Salmonidae	I	Fi		21.2
Rainbow trout *Oncorhynchus mykiss*	Salmonidae		Tc		1.9
Central mudminnow* *Umbra limi*	Umbridae		In	Veg	42.3
Northern pike *Esox lucius*	Esocidae		Tc	Veg	96.2
Muskellunge *Esox masquinongy*	Esocidae	I	Tc	Veg	
Tiger muskellunge[ns] (northern pike × muskellunge)	Esocidae		Tc		9.6
Common carp *Cyprinus carpio*	Cyprinidae	T	Om		28.9
Brassy minnow* *Hybognathus hankinsoni*	Cyprinidae		He		1.9
Hornyhead chub* *Nocomis biguttatus*	Cyprinidae	I	In		3.9
Golden shiner *Notemigonus crysoleucas*	Cyprinidae		In		51.9
Emerald shiner* *Notropis atherinoides*	Cyprinidae		In		1.9
Bigmouth shiner* *Notropis dorsalis*	Cyprinidae		In		1.9
Blackchin shiner* *Notropis heterodon*	Cyprinidae	I	In	Veg	36.5
Blacknose shiner* *Notropis heterolepis*	Cyprinidae	I	In	Veg	34.6
Spottail shiner* *Notropis hudsonius*	Cyprinidae		In		13.5
Spotfin shiner* *Cyprinella spiloptera*	Cyprinidae		In		21.2
Mimic shiner* *Notropis volucellus*	Cyprinidae	I	In	Veg	17.3
Common shiner* *Luxilus cornutus*	Cyprinidae		In		3.9
Northern redbelly dace *Phoxinus eos*	Cyprinidae		He	Veg	5.8
Bluntnose minnow* *Pimephales notatus*	Cyprinidae		Om		75.0
Fathead minnow* *Pimephales promelas*	Cyprinidae	T	Om		28.9
Creek chub* *Semotilus atromaculatus*	Cyprinidae	T	In		1.9
White sucker *Catostomus commersoni*	Catostomidae	T	Om		73.1
Bigmouth buffalo *Ictiobus cyprinellus*	Catostomidae		In		3.9
Shorthead redhorse *Moxostoma macrolepidotum*	Catostomide		In		3.9
Greater redhorse *Moxostoma valenciennesi*	Catostomide	I	In		3.9
Black bullhead *Ameiurus melas*	Ictaluridae	T	Om		61.5
Yellow bullhead *Ameiurus natalis*	Ictaluridae		Om		90.4
Brown bullhead *Ameiurus nebulosus*	Ictaluridae		Om		50.0
Tadpole madtom* *Noturus gyrinus*	Ictaluridae		In	Smb/Veg	32.7
Flathead catfish *Pylodictis olivaris*	Ictaluridae		Tc		1.9
Channel catfish[ns] *Ictalurus punctatus*	Ictaluridae		Tc		
Banded killifish* *Fundulus diaphanus*	Fundulidae	I	In		53.9
Brook silverside* *Labidesthes sicculus*	Atherinidae		In		3.9
Brook stickleback* *Culaea inconstans*	Gasterosteidae		In		15.4
Rock bass *Ambloplites rupestris*	Centrarchidae	I	Tc		32.7
Green sunfish *Lepomis cyanellus*	Centrarchidae		In		80.8
Pumpkinseed *Lepomis gibbosus*	Centrarchidae		In		92.3
Bluegill *Lepomis macrochirus*	Centrarchidae		In		100.0
Hybrid sunfish *Lepomis* spp.	Centrarchidae		In		90.4
Smallmouth bass *Micropterus dolomieu*	Centrarchidae	I	Tc		11.5
Largemouth bass *Micropterus salmoides*	Centrarchidae		Tc		98.1
White crappie *Pomoxis annularis*	Centrarchidae		Tc		19.2
Black crappie *Pomoxis nigromaculatus*	Centrarchidae		Tc		92.3
Rainbow darter* *Etheostoma caeruleum*	Percidae	I	In	Smb	1.9
Iowa darter* *Etheostoma exile*	Percidae	I	In	Smb	76.9
Johnny darter* *Etheostoma nigrum*	Percidae		In	Smb	65.4
Yellow perch *Perca flavescens*	Percidae		In		98.1
Log perch* *Percina caprodes*	Percidae		In	Smb	9.6
Walleye *Stizostedion vitreum*	Percidae		Tc		75.0
Sauger[ns] *Stizostedion canadense*	Percidae		Tc		
Mottled sculpin* *Cottus bairdi*	Cottidae	I	In	Smb	11.5

km^2) covered a broad range. We assumed these disturbance variables at least partially reflected the impact of more specific stressors, such as shoreline alterations, fishing pressure, and runoff, for which widespread information was unavailable. We used principal components analysis (PCA) to reduce the number of land use and population variables (SAS Institute 1999). Land use and population data were normalized by $\log_{10}(x + 1)$ transformation.

We tested for differences in lake characteristics and watershed land use among watershed disturbance categories, using general linear models (GLMs, $P \leq 0.05$; SAS Institute 1999). Measures of habitat complexity and physical or chemical lake characteristics included SDI (Orth 1983), percent littoral area (percent of lake area <4.6 m deep), maximum depth, and total alkalinity. Latitude was used to index regional climate effects. Lake connectivity was categorized into three classes (no connections, moderate connections, or well connected), based on stream inflows and outflows, connectivity to another lake, and proximity of a major river. Because total species richness is influenced by inherent lake characteristics (Rahel 1986; Matuszek and Beggs 1988; Minns 1989; Magnuson et al. 1994; Pierce et al. 1994), we also tested for effects of lake characteristics on native species richness by using linear regression analyses and GLMs ($P \leq 0.05$; SAS Institute 1999). This ensured that we were not comparing lakes that were naturally species-depauperate with lakes that were naturally more species-rich. If lake characteristics are similar across watershed disturbance categories and species richness is not influenced by lake characteristics, then metric responses probably result from differences in lake integrity and not from differences in underlying lake characteristics.

Metric selection and scoring.—We used an elimination process to select metrics for inclusion in the IBI. First, we used Spearman's rank correlation analysis to identify metrics correlated to land use (SAS Institute 1999). Metrics significantly correlated ($P \leq 0.05$) to land use were retained and scored. *P*-values were not Bonferroni-adjusted because we did not want to increase type II error. If a metric was not significantly correlated to at least one measure of land use, it was eliminated from further consideration. If the relative abundance and relative biomass of a given metric group were both correlated to land use, we retained the metric having stronger correlations to land use. If correlations were similar for both relative abundance and relative biomass, we retained both metrics for scoring. We also examined the distribution and species composition of each metric. If a metric had a narrow distribution, for example, only one or two species contributed to the metric, then the metric was excluded. Also, if a relative abundance or relative biomass metric was composed of only a single species, that metric was excluded.

Retained metrics were standardized by a continuous variable scoring method described by Minns et al. (1994). We chose continuous variable scoring over discrete scoring to allow a greater range of scores, avoid sequence gaps, and minimize bias (Fore et al. 1994). Each metric was standardized so that scores ranged between 0 and 10. Scores were assigned by using the following equation and conditions (Minns et al. 1994):

$$M_s = A + B \cdot M_r .$$

$$\text{If } M_s < M_{\min}, \text{ then } M_s = 0,$$

$$\text{if } M_r > M_{\max}, \text{ then } M_s = 10.$$

A standardized metric (M_s) was defined as a linear function of a raw metric (M_r). The minimum and maximum thresholds ($M_{\min} = 0$ and $M_{\max} = 10$) defined the upper and lower limits for the standardized metric. For metrics positively related to biotic integrity, the lower limit, $M_{\min}$, was set to zero and the upper limit was set at or near the 95th percentile of the cumulative frequency distribution of the raw metric values. For metrics negatively related to lake integrity, the lower limit was set close to the 95th cumulative percentile and the upper limit was set close to the 5th cumulative percentile. The relationship between the raw and standardized metric was assumed to be linear between the upper and lower bound.

Next we used GLMs to test ($P \leq 0.05$) the ability of metric scores to predict human-induced stress (SAS Institute 1999). Metric score was the response variable and watershed disturbance and lake size were main effects. Watershed disturbance category was chosen as a main effect because it provided a cumulative description of multiple human-induced stressors. Lake size was divided into three categories: less than 80 ha; between 81 and 120 ha; and more than 120 ha. Differences among category means were tested with Tukey's multiple comparison method (SAS Institute 1999). Only metrics with a significant watershed disturbance main effect were retained. Retained metrics were also tested for redundancy by using Pearson's correlation analysis. If two metrics were highly correlated ($\rho > 0.8$), only one of the metrics was retained.

IBI evaluation.—We calculated IBI scores for 52 lakes that had trap-net, gill-net, and nearshore data by summing the scores of the standardized metrics that were selected for inclusion in the final IBI. The highest possible IBI score was 160; the lowest possible was 0. IBI scores were tested ($P \leq 0.05$) against watershed disturbance categories and lake size by using GLMs and Tukey's multiple comparison method (SAS Institute 1999). We used Pearson's correlation analysis (SAS Institute 1999) to test individual metric and IBI scores against trophic state, as derived from summer water transparency (Carlson 1977), PCA1, land use within the watershed, land use within a 100-m zone around the perimeter of the lake, and richness of submerged vegetation. The effects of predator stocking on IBI scores were tested with GLMs ($P \leq 0.05$; SAS Institute 1999). Two different measures of stocking were tested: number of stocked species and intensity of stocking. Stocking was categorized as none, one species, or mixed species (usually two species). Intensity of stocking was categorized by dividing the gill-net catch rate of stocked species into quartiles. Gill-net catches were used because gill nets targeted the stocked predator species.

We assessed the sensitivity of the IBI to each metric by systematically removing a metric from the IBI, calculating a reduced IBI (scaled for the elimination of one metric), and then calculating the difference between the reduced and full IBI (Minns et al. 1994). This process was repeated for each of the 52 lakes. Next, we calculated the variance of the differences for each reduced IBI. The variance of the differences for a reduced IBI suggested the relative importance of an eliminated metric. The ratio of the variance of differences within a watershed disturbance category to the variance of the differences for all lakes provided a measure of a metric's range of sensitivity. Metrics with high ratios affected IBI scores in a particular watershed disturbance category more than metrics with low ratios. Metrics with ratios greater than the median for a category were considered potentially informative within that category.

Results

Sampling

We collected 52 species, of which 13 were intolerant species and 5 were tolerant species (Table 2). Insectivores were the most common feeding group (29 species), followed by top carnivores (11 species) and omnivores (7 species). For habitat specialists, we collected six small benthic-dwelling species and eight vegetation-dwelling species. Total species richness averaged 19 species per lake and ranged from 11 to 29 species. No single sampling method sampled the entire fish community adequately. Nearshore sampling collected a total of 41 species (mean = 12.6 species per lake; $N = 52$). Trap nets collected 23 species (mean = 10.6 species per lake; $N = 129$). Gill nets collected 26 species (mean = 9.7 species per lake; $N = 131$). Nearshore sampling collected 24 species not sampled by the other gears, most of which were small, nongame species such as darters and cyprinids (Table 2). Trap nets collected one species not sampled by the other gears (bigmouth buffalo), whereas gill nets collected five species not collected by the other gears (channel catfish, flathead catfish, rainbow trout, saugers, and ciscoes). For an average lake, trap nets and gill nets added six species not collected by nearshore sampling, most of which were top carnivores and omnivores.

Lake Characteristics and Human-Induced Stress

We identified four watershed disturbance categories, using principal components. Principal component 1 (PCA1) explained 60% of the variation with inverse loading between forested land cover and urban activity (urban land use and population density). Principal component 2 (PCA2) explained an additional 29% of the variation with inverse loading between cultivated land use and forested land use and urban activity (Table 3). We used each quadrant in the plot of PCA1 against PCA2 to identify watershed disturbance categories (Figure 1): forested, mixed forest and agricultural, agricultural, and urban. Land use and population density differed significantly among the four categories (Figure 2).

Inherent lake characteristics differed little among the watershed disturbance categories and had minimal influence on native species richness (Table 4). Mean lake area, maximum depth, percent littoral area, and total alkalinity did not differ significantly among the four watershed disturbance categories. Lakes in the forested category had greater shoreline complexity, as measured by the SDI, than did lakes in the agricultural category. Stocking occurred in more than half the study lakes in each watershed disturbance category. Native species richness was not significantly related to lake area, total alkalinity, percent littoral area, or maximum depth (Table 5). Native species richness

TABLE 3.—Results of principle components analysis on watershed land use and population density variables for lakes used in index of biotic integrity development.

Principle component	Eigenvalue	Proportion of variance explained	Cumulative variance explained	Coefficient eigenvectors			
				% Cultivated	% Forest	% Urban	Population density
PCA1	2.42	0.60	0.60	0.27	−0.53	0.55	0.59
PCA2	0.80	0.29	0.89	−0.81	0.31	0.44	0.24
PCA3	0.34	0.09	0.97	0.12	0.37	0.48	0.79

was positively related to SDI and latitude. Native species richness did not differ among the three connectivity categories ($N = 52$; $F = 2.95$; $P = 0.06$).

Metric Selection and Scoring

All 10 species-richness metrics were significantly correlated to land use and thus were retained for scoring (Table 6). The numbers of native, cyprinid, intolerant, small benthic-dwelling, and vegetation-dwelling species increased with increasing lake quality. In contrast, the numbers of tolerant and omnivore species decreased with increasing lake quality.

All four nearshore composition metrics were significantly correlated to land use and were retained for scoring (Table 6). The relative abundances of intolerant, cyprinid, small benthic-dwelling, and vegetation-dwelling fishes increased with increasing lake quality.

Four trap-net composition metrics were retained for scoring: insectivore relative biomass, omnivore relative biomass, tolerant relative abundance, and tolerant relative biomass. Insectivore relative abundance was eliminated because it was not correlated to land use, but insectivore relative biomass was positively correlated to cultivated land use. Omnivore relative biomass was retained for scoring instead of omnivore relative abundance because the former had stronger correlations to land use. Relative abundance and relative biomass of tolerant fishes displayed similar correlations to land use; as a result, they were both retained. The relative biomass of omnivores and the relative abundance and biomass of tolerant fishes decreased with increasing lake quality. Although the

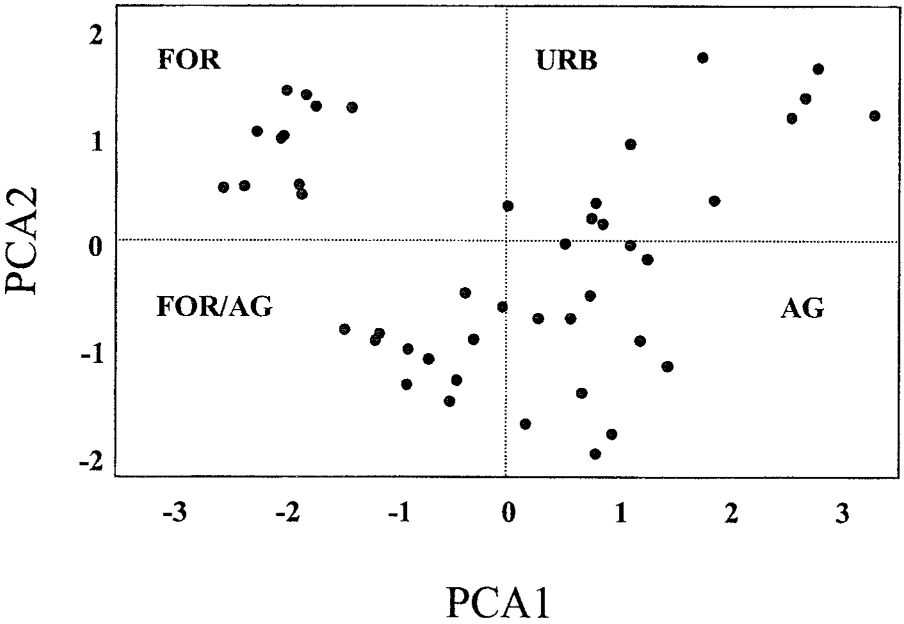

FIGURE 1.—Plot of principal component 1 (PCA1) versus principal component 2 (PCA2). Each quadrant represents a watershed disturbance category: FOR identifies lakes in watersheds with primarily forest cover, FOR/AG lakes in watersheds with mixed forest and agricultural land use, AG lakes in watersheds with primarily agricultural land use, and URB lakes with primarily urban land use.

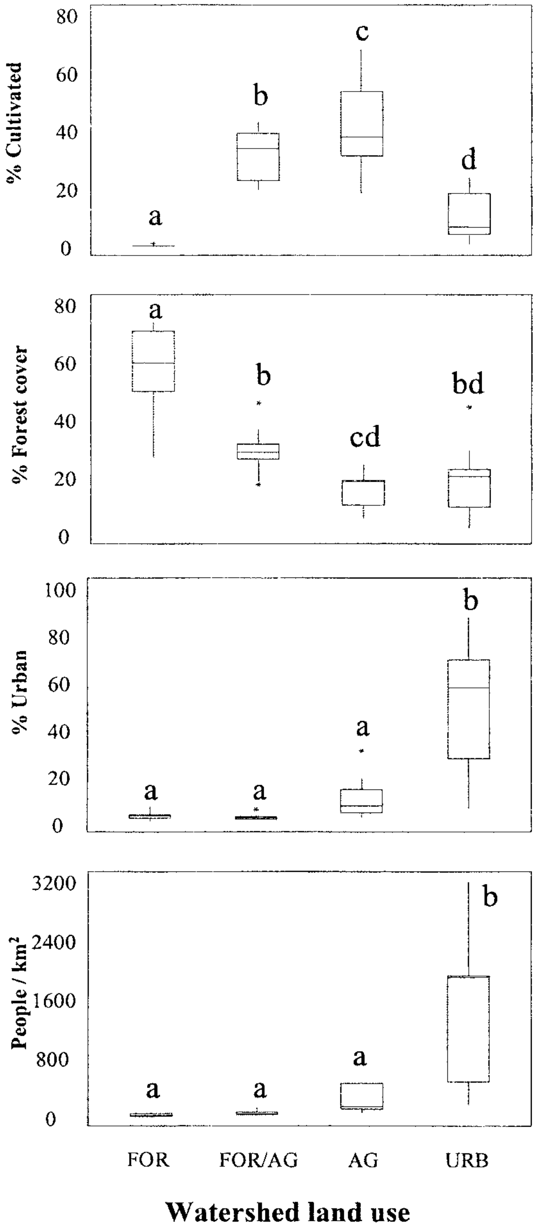

FIGURE 2.—Box-and-whisker plots for watershed land use and population density within each watershed disturbance category. Watershed land use or population density did not differ significantly ($P \leq 0.05$) between watershed disturbance categories where denoted by the same lowercase letters, according to general linear models and Tukey's multiple comparison test. See Table 4 for explanation of land use category abbreviations.

relative abundance and relative biomass of intolerant fishes were correlated to land use, we excluded these metrics because less than 1% of the trap-net samples contained more than one intolerant species.

Four gill-net composition metrics were retained for scoring: top carnivore relative abundance, top carnivore relative biomass, intolerant relative abundance, and intolerant relative biomass. Both relative abundance and relative biomass measures were retained for top carnivores and intolerant fishes because they had similar correlations to land use. The relative abundance and relative biomass of top carnivores and intolerants increased with increasing lake quality. Neither relative abundance metrics nor relative biomass metrics for tolerant fishes or omnivores were retained for scoring because the corresponding trap-net metrics had stronger correlations to land use.

Metrics describing tolerant and omnivorous species were negative metrics; that is, high metric scores correspond to low species richness or low relative abundance or biomass. All other metrics were positive metrics, and high scores indicate high species richness or high relative abundance or biomass.

On the basis of the GLM results, we selected eight species-richness metrics that predicted differences among watershed disturbance categories for inclusion in the IBI: native, intolerant, insectivore, omnivore, cyprinid, small benthic-dwelling, and vegetation-dwelling species richness (Tables 7, 8). Scores for native, insectivore, and cyprinid richness were lower for lakes in agricultural watersheds. Scores for small benthic dwellers and vegetation dwellers were highest for lakes in the least disturbed forested watersheds. Omnivore scores were lower, indicating more omnivores species, in lakes in urban watersheds. Intolerant and tolerant scores were lowest, indicating fewer intolerant species and more tolerant species, in lakes in agricultural and urban watersheds. The response of the top carnivore metric was unclear, scores being higher for lakes in the least disturbed forested watersheds and in the urban watersheds. Although centrarchid species richness was negatively correlated with cultivated land use, this metric, once scored, failed to predict watershed disturbance. As a result, we considered top carnivore and centrarchid species richness to be poor metrics and excluded them from the IBI. We detected no lake area effects.

We selected three nearshore relative abundance metrics for inclusion in the IBI: relative abundance

TABLE 4.—Mean lake characteristics by watershed disturbance category as estimated by general linear models for Minnesota lakes used in the development of a fish-based index of biotic integrity. Abbreviations are as follows: FOR = primarily forest cover, FOR/AG = mixed forest cover and agricultural use, AG = primarily agricultural use, and URB = primarily urban use.

	Watershed disturbance category						
Lake characteristic	FOR	FOR/AG	AG	URB	*N*	*F*	*P*-value
Area (ha)	103	110	83	113	52	2.22	0.10
Maximum depth (m)	20.6	16.7	16.3	15.8	52	1.09	0.36
Littoral area (%)	0.35	0.38	0.45	0.43	52	1.25	0.30
Alkalinity (mg/L $CaCO_3$)	92	133	120	121	37	1.70	0.19
Shoreline development index	1.83	1.74	1.38	1.52	52	3.92	0.01

of intolerant, relative abundance of small benthic-dwelling, and relative abundance of vegetation-dwelling fishes (Tables 7, 8). Intolerant scores were highest for lakes in forested watersheds and lowest for lakes in agricultural and urban watersheds. Vegetation-dweller scores were lowest for lakes in urban watersheds. Scores for small benthic dwellers were highest for lakes in forested watersheds. The response of the cyprinid metric was unclear, scores being higher for lakes in mixed agricultural and forest watersheds and in urban watersheds. As a result, we excluded this metric. No lake area effects were detected.

We selected three trap-net composition metrics for inclusion in the IBI: relative biomass of insectivores, relative biomass of omnivores, and relative biomass of tolerants (Tables 7, 8). Lakes in agricultural watersheds had lower insectivore scores than lakes in all other watershed disturbance groups. A significant area effect was detected for the insectivore biomass metric: Lakes smaller than 80 ha tended to have higher insectivore scores than did lakes larger 120 ha. Omnivore biomass scores were lower, indicating higher relative biomass, in lakes with agricultural and urban watersheds. Tolerant relative abundance and biomass scores predicted similar watershed disturbance with scores being lower, indicating higher relative abundance and biomass, in agricultural and urban watersheds. For consistency with other trap-net metrics, we selected the tolerant relative biomass metric for inclusion in the IBI. No significant area effects were detected for omnivore or tolerant metrics.

We selected two gill-net relative biomass metrics for inclusion in the IBI: relative biomass of top carnivores and relative biomass of intolerants (Tables 7, 8). Lakes in forested watersheds had higher scores for intolerants and top carnivores for both relative abundance and biomass metrics than did lakes in agricultural or urban watersheds. We selected the biomass metrics for inclusion in the IBI because biomass scores had a wider distribution. No lake area effects were detected.

IBI Evaluation

We detected significant differences in IBI scores among watershed disturbance categories (Figure 3). Lake IBI scores followed a disturbance gradient in which the least disturbed lakes (forested) had the highest scores, followed by moderately disturbed lakes (mixed forest and agriculture) and then highly disturbed lakes (agricultural or urban). IBI scores did not differ significantly between lakes in agricultural watersheds and those in urban watersheds. Individual metric values and IBI values were significantly correlated to several measures of human-induced stress (Table 9). Lake IBI scores increased as submerged vegetation richness and forested land use increased and decreased as trophic state, PCA1, cultivated land use, and urban land use increased (Figure 4). Neither the number of species stocked nor the intensity of stocking

TABLE 5.—Linear regression results for the effect of inherent lake characteristics on native species richness for Minnesota lakes used in the development of a fish-based index of biotic integrity.

Lake characteristic	*N*	R^2	*F*	*P*-value
Area (ha)	52	0.06	3.04	0.09
Maximum depth (m)	52	0.0001	0.00	0.96
Littoral area (%)	52	0.05	2.80	0.10
Alkalinity (mg/L $CaCO_3$)	37	0.06	2.36	0.13
Shoreline development index	52	0.09	4.74	0.03
Latitude	52	0.12	6.83	0.01

TABLE 6.—Spearman rank correlation coefficients between proposed fish assemblage metrics and watershed land use variables; $P \leq 0.05$*, $P \leq 0.005$**.

	Land use		
Metric	Cultivated	Forest	Urban
Species richness ($N = 52$)			
Native	−0.31*	0.35*	−0.15
Intolerant	−0.40**	0.66**	−0.52**
Tolerant	0.21	−0.43**	0.48**
Insectivore	−0.25	0.47**	−0.36*
Omnivore	0.19	−0.32*	0.33*
Top carnivore	−0.33*	0.10	0.04
Centrarchid	−0.30*	0.13	0.11
Cyprinid	−0.27*	0.25	−0.08
Small benthic dwellers	−0.35*	0.44**	−0.29*
Vegetation dwellers	−0.31*	0.47**	−0.47**
Nearshore composition ($N = 52$)			
Intolerants	−0.18	0.48**	−0.51**
Cyprinids	−0.22	0.31*	−0.11
Small benthic dwellers	−0.38*	0.48**	−0.33*
Vegetation dwellers	0.06	0.32*	−0.62**
Trap-net composition ($N = 129$)			
Insectivores			
Number	−0.09	−0.03	0.02
Biomass	−0.24**	0.17	−0.01
Omnivores			
Number	0.35**	−0.15	0.17
Biomass	0.40**	−0.31**	0.32**
Intolerants			
Number	−0.51**	0.60**	−0.51**
Biomass	−0.50**	0.60**	−0.49**
Tolerants			
Number	0.33**	−0.30**	0.36**
Biomass	0.30**	−0.34**	0.41**
Gill-net composition ($N = 131$)			
Omnivores			
Number	0.33**	−0.13	0.21
Biomass	0.37**	−0.22*	0.22*
Top carnivores			
Number	−0.19*	0.24**	−0.30**
Biomass	−0.24**	0.21*	−0.28**
Intolerants			
Number	−0.56**	0.61**	−0.43**
Biomass	−0.54**	0.59**	−0.43**
Tolerants			
Number	0.16	−0.13	0.24**
Biomass	0.20	−0.16	0.21*

affected IBI scores (Figure 5). Lake characteristics associated with higher IBI scores were low percent littoral area, high maximum depth, high Secchi depth transparency, and high latitude. Lake area, alkalinity, lake connectivity, and shoreline complexity (SDI) were not significantly related to the IBI scores.

Variances of the differences between total IBI scores and reduced IBI scores across all lakes ranged from 2.26 for the insectivore species richness to 9.02 for the relative abundance of vegetation dwellers in nearshore samples; the mean variance for all metrics was 6.04 (Table 10). High variance indicates greater sensitivity of the total IBI to an individual metric.

Sensitivity of the total IBI to individual metrics varied among watershed disturbance categories (Table 10). Metrics with variance ratios greater than the median for a category made a greater contribution to the IBI within that category. We could not identify clear patterns in the contribution of species-richness metrics among watershed disturbance categories. Indices for lakes in forested and mixed forest and agricultural watersheds were more sensitive to the relative abundance of intolerants, small benthic dwellers, and vegetation dwellers in nearshore samples than were indices for lakes in agricultural or urban watersheds. IBIs for lakes in urban watersheds were sensitive to all three trophic composition

TABLE 7.—Mean metric scores by watershed disturbance category estimated by general linear models. The model *P*-value is for the full model, including both watershed disturbance and lake area main effects; the watershed *P*-value is for the watershed disturbance main effect. Within rows, means with the same lowercase letter are not significantly different according to Tukey's multiple-comparisons test. See Table 4 for abbreviations.

	P-value		Watershed disturbance category			
Metric	Model	Watershed	FOR	FOR/AG	AG	URB
Species richness						
Native	0.02	0.01	8.4 z	7.5 yz	6.7 y	7.7 yz
Intolerant	0.0001	0.0001	9.5 z	7.0 z	3.2 y	3.7 y
Tolerant	0.0002	0.0001	6.4 z	3.8 yz	2.8 y	1.7 y
Insectivore	0.04	0.02	8.5 z	7.7 yz	6.5 y	7.1 yz
Omnivore	0.02	0.02	5.4 z	4.2 yz	3.5 xy	2.3 x
Top carnivore	0.02	0.008	8.0 z	6.8 y	6.2 xy	7.8 yz
Centrarchid	0.07	0.05	9.0	8.8	8.1	9.3
Cyprinid	0.008	0.004	6.8 z	6.2 z	3.8 y	6.9 z
Small benthic dwellers	0.001	0.0002	7.8 z	4.1 y	3.9 y	4.1 y
Vegetation dwellers	0.0005	0.0003	9.1 z	6.7 y	5.6 y	5.6 y
Nearshore composition						
Intolerants	0.0008	0.0002	4.7 z	5.6 z	1.2 y	1.1 y
Cyprinids	0.02	0.02	3.8 yz	5.0 z	1.4 y	5.1 z
Small benthic dwellers	0.0001	0.0001	5.9 z	1.9 y	1.3 y	1.4 y
Vegetation dwellers	0.005	0.001	3.0 z	4.7 z	1.8 yz	0.4 y
Trap-net composition						
Insectivores (biomass)	0.002	0.002	6.2 z	6.3 z	4.2 y	6.2 z
Omnivores (biomass)	0.0001	0.0001	8.1 z	6.7 yz	4.7 y	5.9 y
Tolerants						
Number	0.0001	0.0001	9.4 z	9.4 z	6.9 y	7.2 y
Biomass	0.0001	0.0001	9.4 z	9.6 z	5.9 y	6.1 y
Gill-net composition						
Top carnivores						
Number	0.006	0.004	6.2 z	5.0 yz	4.8 y	3.8 y
Biomass	0.01	0.002	8.2 z	7.4 yz	6.7 y	6.5 y
Intolerants						
Number	0.0001	0.0001	5.9 z	1.9 y	0.9 xy	0.0 x
Biomass	0.0001	0.0001	7.4 z	3.0 y	1.3 xy	0.1 x
Total IBI	0.0001	0.0001	114.1 z	91.3 y	63.8 x	66.8 x

TABLE 8.—Standardized scoring criteria for the 16 metrics included in the final fish-based index of biotic integrity for Minnesota lakes. Calculated scores that are less than 0 or greater than 10 are constrained to 0 and 10, respectively.

Metric	Scoring criterion
Species richness	
Native	0.4 × number of native species
Intolerant	2.0 × number of intolerant species
Tolerant	10 − 3.33 × number of tolerant species
Insectivore	0.77 × number of insectivore species
Omnivore	12 – 2 × number of omnivore species
Cyprinid	2.0 × number of cyprinid species
Small benthic dwellers	2.5 × number of small benthic-dwelling species
Vegetation dwellers	1.67 × number of vegetation-dwelling species
Nearshore composition	
Intolerants	18.94 × proportion of intolerant individuals
Small benthic dwellers	109.89 × proportion of small benthic-dwelling individuals
Vegetation dwellers	19.84 × proportion of vegetation-dwelling individuals
Trap-net composition	
Insectivores	12.35 × proportion of insectivores by biomass
Omnivores	10 − 16.39 × proportion of omnivores by biomass
Tolerants	10 − 25.64 × proportion of tolerants by biomass
Gill-net composition	
Top carnivores	11.0 × proportion of top carnivores by biomass
Intolerants	125 × proportion of intolerants by biomass

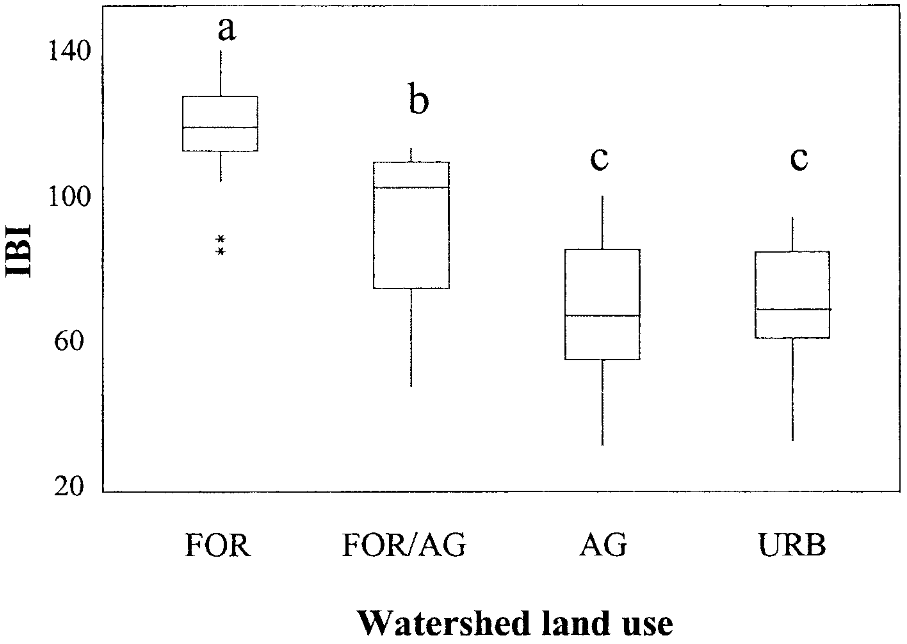

FIGURE 3.—Box-and-whisker plots of index of biotic integrity (IBI) scores for lakes in the four watershed disturbance categories (see caption to Table 4 for category explanations). Scores for watershed disturbance categories denoted by the same lowercase letter were not significantly ($P \leq 0.05$) different according to general linear models and Tukey's multiple comparison test.

TABLE 9.—Pearson correlation coefficients between metrics included in the index of biotic integrity (IBI) and the IBI and measures of human-induced stress for 52 Minnesota lakes; $P \leq 0.05$*, $P \leq 0.005$**.

Metric	Submerged vegetation	PCA1	Trophic state	Cultivated watershed	Forest watershed	Urban watershed
Species richness						
Native	0.53**	−0.26	−0.33*	−0.31*	0.40**	−0.05
Intolerant	0.74**	−0.69**	−0.73**	−0.32*	0.63**	−0.45**
Tolerant	0.33	−0.56**	−0.48**	−0.16	0.49**	−0.46**
Insectivore	0.62**	−0.43**	−0.49**	−0.22	0.46**	−0.28*
Omnivore	0.11	−0.41**	−0.29*	−0.07	0.34*	−0.36*
Cyprinid	0.38	−0.21	−0.37*	−0.30*	0.25	0.01
Small benthic dwellers	0.60**	−0.46**	−0.36*	−0.28*	0.57**	−0.26
Vegetation dwellers	0.71**	−0.54**	−0.47**	−0.24	0.48**	−0.39**
Nearshore composition						
Intolerants	0.50*	−0.54**	−0.62**	−0.09	0.37*	−0.40**
Small benthic dwellers	0.50*	−0.50**	−0.50**	−0.42**	0.57**	−0.21
Vegetation dwellers	0.54*	−0.39*	−0.55**	0.13	0.12	−0.38*
Trap-net composition						
Insectivores	0.17	−0.06	−0.14	−0.28*	0.11	0.13
Omnivores	0.49*	−0.24	−0.18	−0.24	0.22	0.01
Tolerants	0.73**	−0.38**	−0.45**	−0.09	0.31*	−0.25
Gill-net composition						
Top carnivores	0.31	−0.29*	−0.27*	−0.11	0.32*	−0.22
Intolerants	0.25	−0.55**	−0.51**	−0.32*	0.63**	−0.32*
IBI	0.72**	−0.69**	−0.71**	−0.33*	0.65**	−0.42**

metrics. Each metric made a relatively greater contribution to the IBI in at least one watershed disturbance category, indicating that all metrics influenced the IBI.

Discussion

Metrics used in an IBI should describe the structure, composition, and function of an ecosystem and display predicted responses to human-induced stress. In this study we identified 16 metrics that responded in a detectable, predictable, and biologically meaningful manner to differences in watershed land use, trophic state, and aquatic vegetation richness. These metrics described species richness, assemblage composition, and trophic composition of fish communities in lakes.

Of the 16 metrics included in our IBI, 10 had been identified as potentially useful metrics in at least one other lentic IBI study. The richness of total native species (Minns et al. 1994), intolerant species (Minns et al. 1994; Jennings et al. 1999b; Whittier 1999), cyprinid species (Minns et al. 1994), and small benthic-dwelling species (Jennings et al. 1999b) was positively related to lake integrity in this study and others. Richness of tolerant, insectivore, omnivore, and vegetation-dwelling species was not evaluated in the other lentic IBI studies. For assemblage composition metrics, Jennings et al. (1999b) also reported higher relative abundance of intolerant and vegetation-dwelling fishes in nearshore samples of less impacted lakes. Whittier (1999) identified the relative abundance of tolerant fish as a negative metric. Jennings et al. (1999b) did not find a correlation between the relative abundance of tolerant fish and environmental quality but reported that the metric was driven by the abundance of a single species. Minns et al. (1994) and Whittier (1999) found trophic composition responses similar to those found in this study. Bachmann et al. (1996) also reported a negative relationship between top carnivore relative biomass and lake productivity. Jennings et al. (1999b) found a positive correlation between the relative abundance of top carnivores and lake quality and a poor correlation between the relative abundance of omnivores and lake quality. Sampling biases, however, could have influenced the response of the top carnivore metric in Jennings et al. (1999b) because open water areas, which many carnivores inhabit, were not sampled.

TABLE 9.—Extended.

Metric	Cultivated riparian	Forest riparian	Urban riparian
Species richness			
Native	−0.42**	0.21	0.10
Intolerant	−0.44**	0.60**	−0.39**
Tolerant	−0.15	0.53**	−0.47**
Insectivore	−0.36*	0.48**	−0.18
Omnivore	−0.06	0.40**	−0.46**
Cyprinid	−0.30*	0.20	0.09
Small benthic dwellers	−0.30*	0.43**	−0.20
Vegetation dwellers	−0.41**	0.50**	−0.32*
Nearshore composition			
Intolerants	−0.15	0.48**	−0.44**
Small benthic dwellers	−0.34*	0.41**	−0.21
Vegetation dwellers	0.01	0.34*	−0.43**
Trap-net composition			
Insectivores	−0.25	0.09	0.03
Omnivores	−0.34*	0.18	−0.08
Tolerants	−0.20	0.41**	−0.35*
Gill-net composition			
Top carnivores	−0.15	0.23	−0.15
Intolerants	−0.36*	0.44**	−0.25
IBI	−0.42**	0.62**	−0.41**

In this study, we evaluated composition metrics based on both relative abundance and relative biomass. Jennings et al. (1999b) and Whittier (1999) evaluated composition metrics based on relative abundance, whereas Schulz et al. (1999) did not evaluate composition metrics. We found that both relative abundance and relative biomass composition metrics responded to lake integrity. Relative biomass metrics, however, generally showed a stronger response than relative abundance metrics to differences in lake integrity. Minns et al. (1994) used relative biomass–based composition metrics to accommodate for a large size range of fishes and to indicate energy flow in ecosystems by way of biomass (Odum 1969). Minns et al. (1994), Harig and Bain (1998), and Whittier (1999) reported a negative relationship between lake integrity and nonnative fish. We did not evaluate a nonnative fish metric because the only nonnative species (except in the one lake stocked with rainbow trout) was the common carp, and it was incorporated in the tolerant and omnivore metrics.

To be useful, a lake IBI must be able to differentiate between human-induced degradation and natural physical and chemical phenomena that structure resident fish communities. As has been shown, species richness in lakes increases with increasing lake size (Matuszek and Beggs 1988; Minns 1989; Magnuson et al. 1994; Pierce et al. 1994). Other variables found to influence richness are lake depth (Matuszek and Beggs 1988; Benson and Magnuson 1992), elevation and latitude (Matuszek and Beggs 1988), pH (Matuszek and Beggs 1988; Magnuson et al. 1994), and alkalinity (Rahel 1986). Similar lake classes, however, should re-

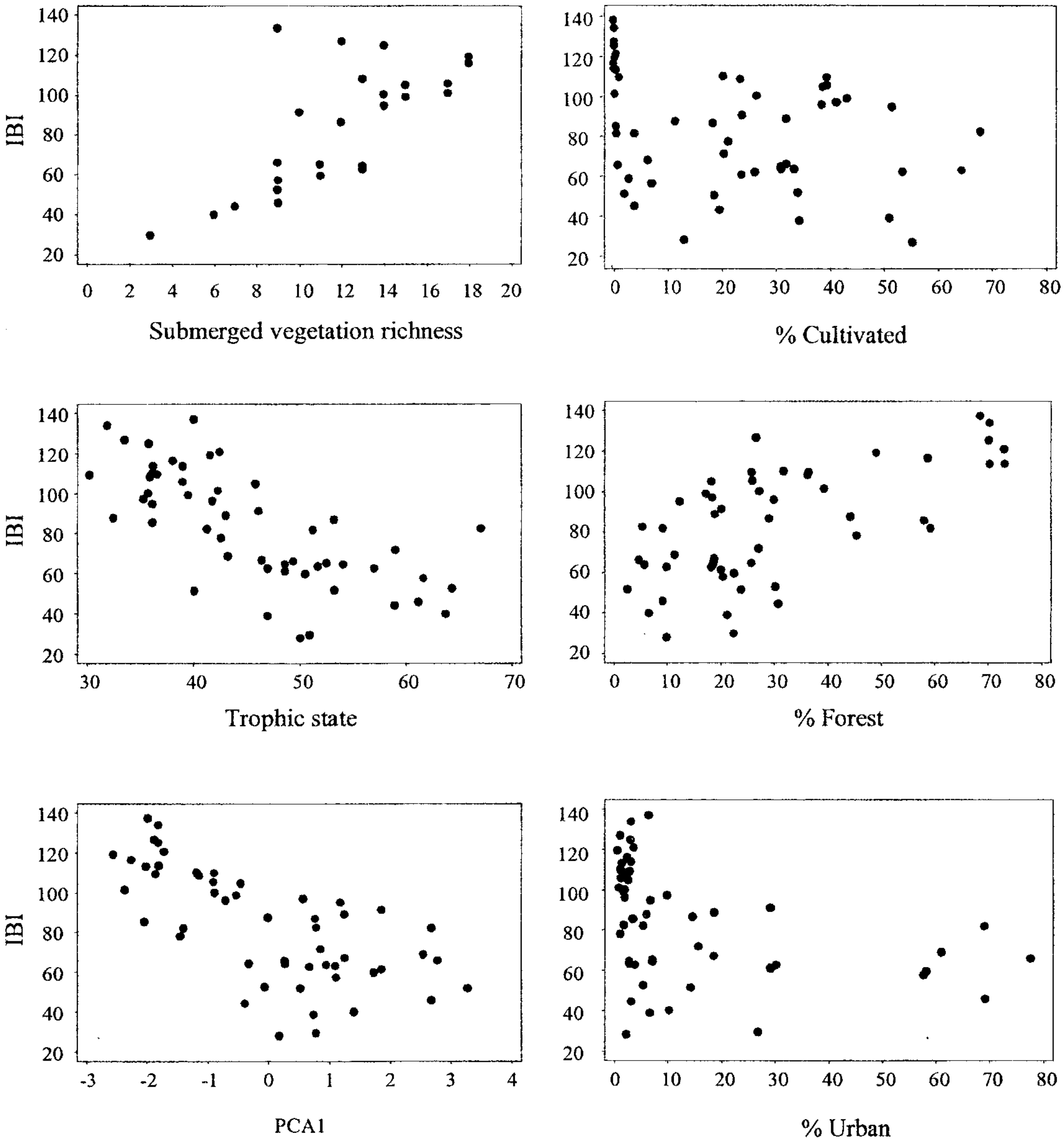

FIGURE 4.—Scatter plots of index of biotic integrity (IBI) scores versus submerged vegetation richness, trophic state, and watershed land use. The submerged vegetation plot contains data from only 25 lakes. Other plots represent all 52 lakes with calculated IBI scores; PCA1 = principal component analysis 1.

spond in a similar manner to anthropogenic stresses if the classification system accounts for ecologically meaningful variation (Emmons et al. 1999). Natural variability in physical and chemical lake characteristics may have dampened relationships between metrics and lake quality in other lentic IBI studies. Unlike this study, other lentic IBI studies did not limit study lakes to specific lake classes or lake sizes. For example, Schulz et al. (1999) suggested that inherent differences in the physical and chemical characteristics of study lakes may have impaired IBI performance in Florida lakes. In this study, we selected study lakes from three lake classes that had similar physical and chemical characteristics. As a result, we believe the observed differences in fish assemblages reflect true differences in lake biotic integrity.

Development of a successful IBI depends on

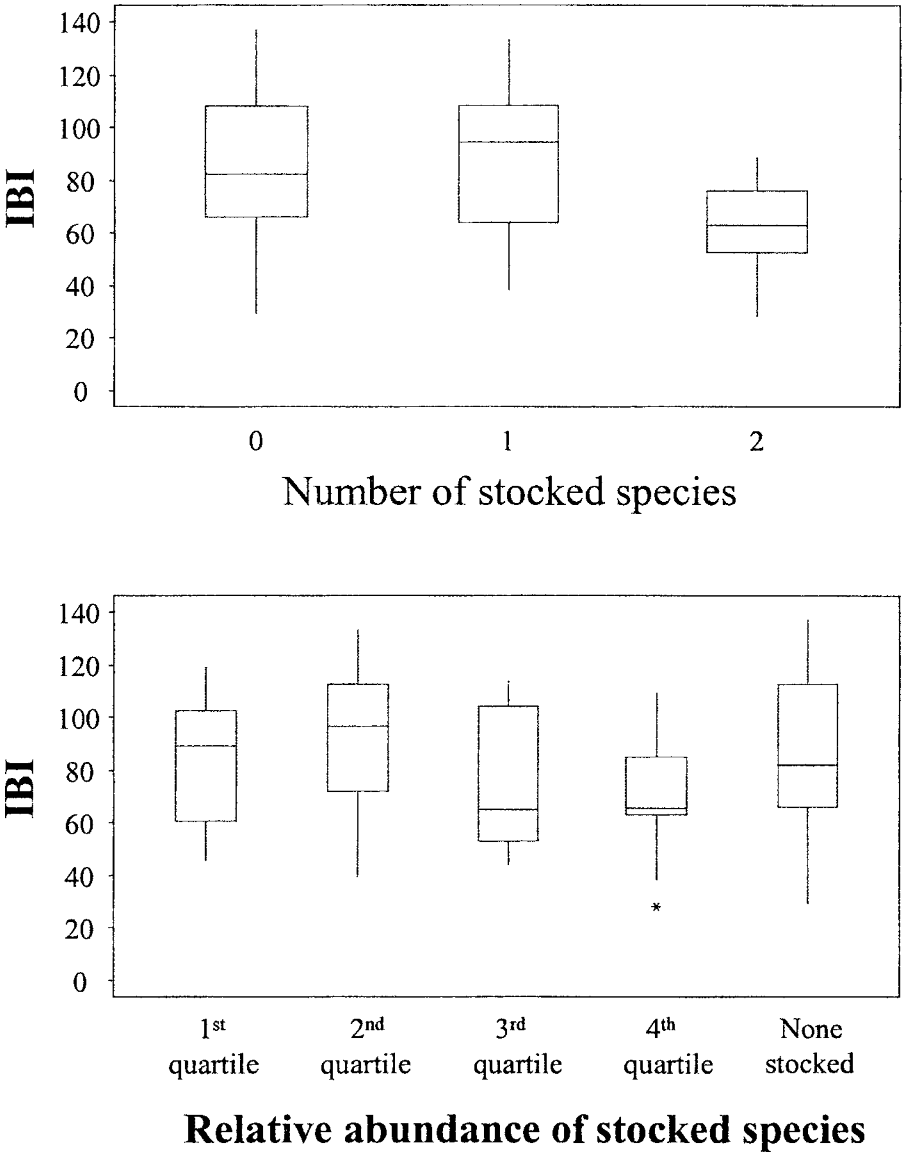

FIGURE 5.—Box-and-whisker plots of index of biotic integrity (IBI) scores for lakes stocked with none, one, or two species (upper panel) and for lakes with different relative abundances of stocked species based on gill-net catch (none, first quartile, second quartile, third quartile, and fourth quartile; lower panel). Lake IBI scores did not differ significantly ($P \leq 0.05$) according to general linear models among the number of species stocked categories or the relative abundance of stocked species categories.

thorough sampling of the fish community. Because fish assemblages in lakes are difficult to characterize, no single gear is sufficient to sample all habitat types or all species present in a lake (Weaver et al. 1992; Magnuson et al. 1994; Jackson and Harvey 1997). Like Harig and Bain (1998), Jennings et al. (1999b), Schulz et al. (1999), and Whittier (1999), we also used multiple sampling gears to estimate species-richness metrics. We found that nearshore sampling collected more species (approximately 70% of the species found in a lake) than did trap nets or gill nets, including more intolerant and habitat specialist species. Trap nets and gill nets, however, collected more top carnivores and omnivore species. Although trap-net and gill-net data were collected during different times,

TABLE 10.—Ratios of within-watershed-disturbance-category variance to the total variance of the difference between the full and reduced index of biotic integrity (IBI) scores for each metric for the 52 Minnesota lakes used to evaluate IBI performance. See Table 4 for abbreviations.

Metric	Variance ratios				Total variance
	FOR	FOR/AG	AG	URB	
Species richness					
Native	0.70	0.82	***0.87***	0.52	2.94
Intolerant	0.08	0.86	0.61	***1.11***	6.13
Tolerant	***0.93***	***1.20***	0.64	***0.75***	5.67
Insectivore	***1.07***	0.53	***1.18***	0.53	2.26
Omnivore	0.54	***1.33***	***1.20***	0.58	5.61
Cyprinid	0.49	0.73	***0.98***	0.59	6.37
Small benthic dwellers	***1.19***	***1.25***	0.58	***0.61***	5.27
Vegetation dwellers	***0.80***	0.74	***1.12***	***1.20***	3.77
Nearshore community composition					
Intolerants	***1.27***	***1.36***	0.37	0.16	7.56
Small benthic dwellers	***1.25***	0.87	***0.88***	0.52	6.65
Vegetation dwellers	***1.55***	***0.96***	0.58	0.12	9.02
Trap-net composition					
Insectivores	0.48	***1.04***	0.85	***1.06***	8.38
Omnivores	0.19	***0.93***	***1.18***	***1.66***	7.62
Tolerants	0.25	0.45	***1.46***	***1.62***	6.95
Gill-net composition					
Top carnivores	0.63	***0.96***	0.80	***1.30***	4.14
Intolerants	***1.45***	0.82	0.74	0.16	8.34

historical data show little temporal variability in species collected by either gear. Combined, the sampling gears used in this study should have provided adequate estimates of species richness.

We avoided problems associated with combining abundance or biomass data across gears (Weaver et al. 1992; Jackson and Harvey 1997) by developing gear-specific composition metrics. Composition metrics evaluated by Minns et al. (1994) and Jennings et al. (1999b) were also gear-specific. Whittier (1999) combined abundance data across gears, which could have dampened observed relationships between composition metrics and lake quality. Jackson and Harvey (1997) stated that simple approaches to combine catches from different gears were not appropriate because of different covariances between species and among gears. Although we combined abundance data from nearshore seining and electrofishing samples, we do not believe this was problematic because we sampled the same areas of the lake with each gear. In contrast, the gears for which we did not combine data–trap nets and gill nets–sampled different areas of a lake (littoral zone and pelagic zone, respectively).

Besides gear diversity, sampling effort for an IBI must be sufficient to minimize the influence of random sampling variation. Jennings et al. (1995) advised sampling effort be such that the addition of another unit of sampling effort does not substantially increase species richness or change proportional abundances. In a previous study, effort levels for gill nets and trap nets were determined to be adequate to reveal trends in fish populations (MNDNR 1993). For the nearshore sampling, we evaluated total species collected against increasing effort by using accumulation curves and Monte Carlo resampling techniques. Results indicated that for lake sizes between 48 and 200 ha, 10 sampling stations were sufficient (M. T. Drake, unpublished data). In addition, our effort level was within the ranges reported by others. Vaux et al. (2000) reported that for lakes as large as 900 ha, nine 4-min backpack electrofishing transects were sufficient to collect a reasonably complete sample of the available species. Fago (1998), who used a combination of electrofishing and a small-mesh seine, found that 15 stations adequately sampled nearshore species richness, but those stations were half as large as the stations used in this study.

Besides lake classification and sampling issues, effective IBI development is also subject to the independent measure of lake ecosystem integrity. We assumed that watershed land use and population density reflected lake biotic integrity because increased human activity is linked to such important factors as habitat alteration and cultural eutrophication. For example, Christensen et al. (1996) found significantly more coarse woody debris in undeveloped lakes than in developed lakes, and within developed lakes coarse woody debris was more abundant at forested sites than at cabin-occupied sites. Radomski and Goeman (2001) found that human activity significantly influenced the littoral area of small to moderate size Minnesota lakes, the developed shorelines having 66% less emergent vegetation coverage than the undeveloped shorelines. Poe et al. (1986) and Bryan and Scarnecchia (1992) reported that increased human activity led to reduced aquatic vegetation species richness and abundance. Also, lakes close to population centers in Minnesota were associated with greater fishing pressure (Cook and Younk 1998). Although watershed land use was a coarse measure of human impacts on lake integrity, species richness and community composition metrics responded to different land use patterns. This suggests that fish metrics are robust. In addition, the IBI responded in a predictable and biologically meaningful manner to two measures of human-induced stress, trophic state and aquatic vegetation richness, that were not used in the metric selection process.

Although our analysis focused primarily on the influence of large-scale land use patterns on IBI scores, we think it has considerable importance for understanding lake integrity and identifying more localized stressors. Categorizing lakes into distinct classes that integrate multiple land use patterns and population densities emphasizes that multiple stressors influence aquatic ecosystems. Rose (2000) states that fish populations face multiple stressors that cause simultaneous changes in environmental quality. Furthermore, the cumulative effects of multiple stressors can differ greatly from the sum of their independent effects. Simultaneous impacts by multiple stressors probably prevent the detection of clear relationships between individual metrics and individual stressors. For example, Jennings et al. (1999a) reported that local habitat modifications led to small changes in local species richness, but fish assemblage structure responded at a larger spatial scale, when many diverse incremental changes accumulated within a basin over time. Moyle and Randall (1998) noted that declines in biotic integrity have multiple causes, both local and regional in origin. Therefore, the influence of more localized stressors may be easier to detect within a watershed disturbance category. For example, an unusually low IBI score for a lake in a primarily forested watershed would suggest a localized disturbance. Also, detection of an unusually high score for a lake in a disturbed watershed could provide insight into factors that protect lakes from large-scale land use disturbances. Identification of the influence of large-scale land use patterns on fish communities, however, emphasizes that we need large-scale solutions (Moyle and Randall 1998). The local shoreline restoration efforts that have gained popularity in recent years may not improve lake integrity if we do not address the large-scale issues (Jennings 2001).

Acknowledgments

Thanks are extended to F. Henson, B. Ickes, P. Radomski, J. Stewart, and R. Walsh for assistance with data collection and Tim Cross for assistance with GIS land use data. This manuscript was critically reviewed by S. Niemela of the Minnesota Pollution Control Agency; C. Anderson, T. Cross, and J. Hiebert of the Minnesota Department of Natural Resources; S. Fischer of the Missouri Department of Conservation; Thom Whittier of Dynamac, Inc.; and two anonymous reviewers. This project was funded in part by the Federal Aid in Sport Fish Restoration (Dingell–Johnson) program.

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