Consequences Of Human Lakeshore Development on Emergent and Floating-Leaf Vegetation Abundance

PAUL RADOMSKI* AND TIMOTHY J. GOEMAN

*Minnesota Department of Natural Resources, Division of Fisheries,
1601 Minnesota Drive, Brainerd, Minnesota 56401, USA*

Abstract.—Vegetation abundance along undeveloped and developed shorelines of Minnesota lakes was compared to test the hypothesis that development has not altered the abundance of emergent and floating-leaf vegetation. Aerial photographs of clear-water lakes dominated by centrarchids and walleyes *Stizostedion vitreum* were analyzed for vegetation. Vegetative coverage was estimated in 12 randomly selected 935-m^2 digitized photograph plots for both developed and undeveloped shorelines of 44 lakes representing a gradient of development. Vegetative cover in littoral areas adjacent to developed shores was less abundant than along undeveloped shorelines. On average, there was a 66% reduction in vegetation coverage with development. The estimated loss of emergent and floating-leaf coverage from human development for all Minnesota's clear-water centrarchid–walleye lakes was 20–28%. Significant correlations were detected between occurrence of emergent and floating-leaf plant species and relative biomass and mean size of northern pike *Esox lucius,* bluegill *Lepomis macrochirus,* and pumpkinseed *Lepomis gibbosus* (Spearman's rank correlation, $P < 0.05$). Current shoreline regulatory policies and landowner education programs may need to be changed to address the cumulative impacts to North American lakes.

Humans have destroyed many prairies, wetlands, and old growth forests, and only remnants of these habitats remain in relatively natural condition. North American lakeshores also are being rapidly developed and altered by humans, and many lakes are now surrounded by homes and seasonal cabins. Development pressures are increasing with more dwellings per lake each year (Kelly and Stinchfield 1998). In addition, many seasonal cabins are now being converted to sprawling lakeshore estates. This human habitation has a cumulative effect on the habitat, water quality, and biota of lake ecosystems (Engel and Pederson 1998).

Efforts to evaluate human influences on lake ecosystems have focused on increased nutrient loading (i.e., cultural eutrophication) and on reducing the resulting nuisance conditions of algal blooms and abundant aquatic macrophytes (Cooke et al. 1993). Most aquatic vegetation studies have focused on the adverse effects of abundant vegetation or exotic species (Pieterse and Murphy 1990) or on macrophyte removal to enhance fisheries (Cross et al. 1992; Olson et al. 1998). Few studies exist on the direct cumulative effects of human lakeshore habitation on littoral habitats.

Human activities along shorelines reduce the quality of littoral habitats and alter aquatic animal communities. These consequences have been difficult to document because of the cumulative effects of continued development. Incremental changes may be detected with comparative studies or when there is baseline data. Christensen et al. (1996) found significantly less riparian coarse woody debris along developed compared with undeveloped shorelines in Wisconsin and Michigan, and they predicted that recent losses in developed lakes will affect littoral communities for about 2 centuries. Meyer et al. (1997) surveyed vegetation, frog populations, and bird distribution and productivity on northern Wisconsin lakeshores, and concluded that housing development dramatically altered native vegetation, especially shrubs, and reduced frog populations. Ostendorp et al. (1995) summarized substantial emergent plant declines in central European lakes due to recreational activities and boat wakes.

The loss of native aquatic macrophytes can have consequences on the entire lake ecosystem (Wilcox and Meeker 1992). Aquatic plants provide fish and wildlife with food, spawning or nesting habitat, foraging substrates, and cover from sun and predators (Engel 1990). Early life stages of most fish depend on appropriate habitat in the littoral zone, where aquatic macrophytes are an important component. Many species, such as northern pike *Esox lucius,* have well-documented associations with aquatic macrophytes (Scott and Crossman 1973; Becker 1983), and we continue to gain

knowledge of the importance of aquatic vegetation for fish (e.g., Chapman and Mackay 1984; Gotceitas and Colgan 1987; Bruno et al. 1990; Conrow et al. 1990). In addition, aquatic plant density or growth form affects predator–prey interactions (e.g., Savino and Stein 1982, 1989; Dionne and Folt 1991).

Widespread lakeshore development has led some fisheries managers in central North America to believe there has been a degradation of important fish nursery and foraging habitat. The objective of this study was to determine if lakeshore development has had a substantial cumulative impact on the emergent and floating-leaf plant abundance of certain lakes. Because extensive historical inventories of vegetation were lacking, a comparative approach using developed and undeveloped shorelines from 44 lakes was employed. The whole-lake consequences of development on emergent and floating-leaf vegetation were also compared with those on submergent vegetation by using available survey data from 195 lakes. In addition, the consequences of development estimated in the 44 lakes were scaled to 531 related lakes to estimate cumulative effects regionally, and fisheries implications were made using available survey data from hundreds of lakes in the area.

Methods

We selected 24 northcentral Minnesota lakes predominated by centrarchids and walleyes *Stizostedion vitreum.* All lakes were from limnological lake class 23 of the Minnesota Department of Natural Resources (MDNR) lake classification system (Schupp 1992), a system based on lake size, water depth, and lake fertility. Class 23 lakes have a mean Secchi reading of 4.6 m, an average maximum depth of 26.2 m, a mean littoral area of 30.3% (percent of total area less than 4.6 m deep), and fish communities predominated by bluegill *Lepomis macrochirus,* pumpkinseed *Lepomis gibbosus,* largemouth bass *Micropterus salmoides,* black crappie *Pomoxis nigromaculatus,* walleye, yellow perch *Perca flavescens,* and northern pike. We chose this limnological lake class because many have been surveyed for aquatic plants and they are small to moderate in size (average 120 ha and, thus, easily photographed), have a gradient of human lakeshore development and emergent and floating-leaf vegetation abundance, and are representative of a cluster of lake classes that include 531 important Minnesota fishery lakes (lake classes 22–25 and 27). We chose lakes that had more than 12 homes or cabins and sufficient undevel-

oped shoreline to obtain vegetative coverage data from each shoreline type, developed and undeveloped. Common emergent and floating-leaf vegetation for these lakes include bulrushes *Scirpus* spp. (most notably hardstem bulrush *Scirpus acutus*), yellow water lily *Nuphar* spp., white water lily *Nymphaea odorata,* cattail *Typha* spp., arrowhead *Sagittaria* spp., sedges *Carex* spp., spikerushes *Eleocharis* spp., horsetail *Equisetum fluviatile,* common reed *Phragmites australis,* common burreed *Sparganium eurycarpum,* wild rice *Zizania palustris,* three-way sedge *Dulichium arundinaceum,* and watershield *Brasenia schreberi.*

Aerial photographs of each lake were obtained following the recommendations of Marshall (1994). Lakes were photographed with a wide-format aerial camera (23 cm) with a 15.24-cm focal length lens at a scale of 1:7,920, and color infrared positive-transparency film (Kodak Aerochrome Infrared 2443) was used in conjunction with a Kodak Wratten 12 and antivignetting filter. The entire surface area of each lake was photographed during the month of August 1996. We chose August because this corresponds to the peak biomass for most emergent and floating-leaf plants in Minnesota. Color infrared film was used because it is generally superior for interpreting emergent and floating-leaf vegetation; however, the lack of shadow penetration is a disadvantage. Photographs were taken when sun elevation and wind conditions produced minimal shadowing, glitter, and specular reflection on the water surface. By photographing with a minimum 30° sun elevation, we sought to balance two opposing problems: reflection or glitter and shadowing of nearshore water. These procedures had benefits and shortcomings, but the resulting photographs provided satisfactory images. Lakes were surveyed by boat in late summer to delineate emergent and floating-leaf stands to aid in image interpretation.

Photographs were digitized using a transparency film scanner, and images were processed and analyzed using image analysis software. Images were scanned at a density of 393.7 pixels/cm. At a 1:7,920 scale, this means an actual ground area covered per pixel was 405 cm^2. Twelve 30.6-m-square plots, each totaling 935 m^2, were randomly selected from both developed and undeveloped shorelines in each of 44 lakes (N = 1,056 plots). We defined developed shoreline plots as those including a boat dock within the center of the plot and an undeveloped shoreline plot as those without dwellings or docks nearby. We used docks as the indicator of human development because each

dwelling typically has a dock, and docks are often focal points for many human activities that may affect vegetation abundance. We randomly selected undeveloped shoreline plots from nonwetland-associated shoreline to allow unbiased comparisons with developed shoreline plots. Emergent and floating-leaf percent coverage and abundance (m^2) were estimated in each plot using Adobe Photoshop and MultiSpec. Each three-channel color (red, green, blue) pixel in a plot was classified within the MultiSpec software using the unsupervised classification ISODATA iterative clustering algorithm (Richards 1993). This algorithm classifies image pixels based on spectral properties using principal components and an iterative process that associates each pixel with a cluster center located at the smallest Euclidean distance to the pixel. The number of pixels classified as aquatic vegetation, both emergent and floating-leaf, were counted for each plot using either MultiSpec or Adobe Photoshop.

Statistical analysis.—First, we tested the null hypothesis that developed shoreline plots had the same chance of being devoid of emergent and floating-leaf aquatic vegetation as undeveloped shoreline plots using contingency table analysis and a chi-square test. Contingency table analysis was also used to test the null hypothesis that the presence of vegetation was independent of the extent of total lake development class (based on dwellings per shoreline kilometer). Lightly developed lakes were defined as having less than 6 dwellings/km for the entire shoreline, moderate developed lakes as having between 6 and 12 dwellings/km, and highly developed lakes as having more than 12 dwellings/km. In addition, a randomized one-factor analysis of variance (ANOVA) was performed to compare differences in plot vegetative abundance among structure size-classes of nonnatural structures (Manly 1991). Based on the total amount of areal coverage, we classified structures in the plots (i.e., docks, boat stations, boats, and swimming platforms) as small (<20 m^2), medium (20–35 m^2), or large (>35 m^2). We also tested, using a two-sample randomization test, whether the presence of a boat or boat station associated with a dock affected the amount of emergent and floating-leaf vegetation within plots.

Second, we used two approaches to model the occurrence of emergent and floating-leaf vegetation. A conventional approach in answering environmental questions often involves comparing averages from two or more groups, but here we also used a modeling approach to compare distributions of vegetative coverage from different groups. The first approach used survival analysis (Muenchow 1986). Using this approach, we could test the null hypothesis that there was homogeneity between the occurrence of emergent and floating-leaf vegetation based on shoreline type (i.e., developed and undeveloped). The product-limit method was used to estimate the occurrence functions for developed and undeveloped plots (survivorship function in failure analysis terminology; Kaplan and Meier 1958). The Wilcoxon chi-square test was used to test the null hypothesis. A two-parameter Weibull distribution model was applied to the cumulative percent of occurrence by plot vegetation abundance for each shoreline type for all vegetated plots. Good distributional fits were indicated by linearity in these Weibull plots, so a Weibull occurrence distribution model was used for further analysis. Weibull parameters are alpha (α) and beta (β), where alpha is the 63.2 percentile of the occurrence abundance distribution and beta corresponds to the slope of the line in the Weibull plot. Maximum likelihood estimates of the Weibull distribution parameters were made. Four Weibull model combinations were compared by using Akaike's information criteria to see if shoreline type aided in modeling vegetation distributions. White and Bennetts (1996) presented this approach with a negative binomial distribution example. If the inclusion of shoreline type aided in the simple modeling of vegetation distributions, then further modeling using additional information might provide insights into where vegetation probably occurred.

The second modeling approach we used was based on the observed frequency distributions of vegetation coverage across lakes. We compared gamma distribution functions fit to observed vegetative coverage frequency distributions for developed and undeveloped plots and for the total lake development class, that is,

$$f(x) = [\beta^{\alpha}/\Gamma(\alpha)] \, x^{\alpha-1} e^{-\beta x},$$

where $0 < x < \infty$ and alpha and beta are positive. If the models based on lightly, moderately, or highly developed lakes differed, then the degree of total lake development could be reasoned to be an important factor in the amount of vegetation present along both developed and undeveloped shorelines. Using the percent of each plot covered by emergent and floating-leaf vegetation, we created a frequency distribution of plant coverage by grouping plots in intervals of 3% and the last interval some-

times a plus group (e.g., 0–3%, 3–6%, . . . 42–45%, 45+%). Estimates of the gamma distribution alpha and beta parameters were calculated by performing a nonlinear regression using iteratively reweighted least squares (Dennis and Costantino 1988). The gamma distribution has a flexible form and can be used to generalize the negative binomial distribution to continuous variables (Hilborn and Mangel 1997). It has been shown that if the error term is assumed to have the distribution in the exponential family, this approach is equivalent to maximum likelihood estimation, and in this case it maximizes the multinomial likelihood (Jennrich and Moore 1975). Estimates of the gamma parameters and their confidence intervals were used to compare, among the three total lake development classes (lightly, moderate, and highly), emergent and floating-leaf distributions of plots for all shoreline plots and for developed and undeveloped shoreline plots. The alpha parameter reflects the shape of the frequency distribution or variation in vegetation abundance observations. The beta and alpha parameters together determine the mean of the distribution. The gamma distribution was assumed to model emergent and floating-leaf abundance better than other distributions because it has a long right tail that would take into account the occasional high plant abundances observed in shallow bays. Goodness-of-fit was tested using the Kolmogorov–Smirnov one-sample test (Zar 1974).

Third, we tested the null hypothesis that vegetation abundance for each shoreline type combination was from the same distribution. To test this hypothesis, we performed a randomized two-factor ANOVA to compare differences in vegetative abundance among lakes and between shoreline types (Manly 1991). To test for differences in vegetation abundance in developed and undeveloped plots as a function of development at the whole-lake scale, a split-plot ANOVA was used with the lake effect nested within the total development classes. This analysis allowed for a test of the effects of development at two scales, whole-lake and local.

Fourth, an estimate of emergent and floating-leaf coverage loss for Minnesota's 531 centrarchid–walleye lakes was made based on (1) recent dwelling counts for each of the 531 lakes and (2) the mean differences in vegetation between developed and undeveloped shorelines estimated for the 44 study lakes. The present and historical number of homes or dwellings was obtained from the MDNR, which has conducted periodic lake surveys on these 531 lakes since 1945 (MDNR 1993). A range of vegetation loss was calculated by varying, for each of the 531 lakes, an assumption addressing the percentage that a lake's shoreline was developable. We assumed that 70–100% of the shoreline could be developed, which seemed reasonable because some lakes have wetland areas that are not developable. In addition, the whole-lake consequences of development on emergent and floating-leaf vegetation were compared with those on submergent vegetation by using MDNR data from 195 clear-water centrarchid–walleye lakes collected in surveys from 1993 to 1997. For each lake survey, aquatic plants were sampled using 10–50 transects (depending on lake size); each transect ran perpendicular to the shore and extended to the maximum depth of vegetation growth. All aquatic plants observed within the transect were identified. The number of homes per shoreline kilometer was correlated with the percent of transects in which a given plant species occurred using Spearman's Rho. If the percent of transects with a particular species is significantly correlated with the number of homes per kilometer, then it suggests positive or negative development effects. This analysis attempted to determine whether emergent and floating-leaf vegetation and submergent vegetation were equally vulnerable to shoreline development. The five most typically found submergent plant species or genera in these lakes were muskgrass *Chara* spp., coontail *Ceratophyllum demersum,* flatstem pondweed *Potamogeton zosteriformis,* bushy pondweed *Najas flexilis,* and northern water milfoil *Myriophyllum sibiricum*; the five most common emergent and floating-leaf plant species or genera were hardstem bulrush, yellow water lily, white water lily, arrowhead, and broad-leaf cattail *Typha latifolia.* These 10 species were used in the correlation analysis.

Lastly, because the potential consequences of aquatic macrophyte losses to sport fish are of interest to fish managers, associations between the occurrence of emergent and floating-leaf plant species and the relative biomass and mean size of northern pike, bluegill, and pumpkinseed were explored. These fish species were selected because each has a life history that is dependent on some form aquatic macrophyte in the littoral zone (Becker 1983), and thus the amount of certain types of vegetation may determine the abundance or size of these fish. This analysis used MDNR lake survey data collected from 609 lakes from 1993 to 1997 (MDNR 1993). The percent of lake transects in which a given plant species occurred was correlated with the relative biomass (kg/net) and mean size (kg) of these three fish species using Spearman's Rho. The five most typical emergent

TABLE 1.—Frequency of emergent and floating-leaf presence and absence by total lake development class (and row percentages). Lightly developed lakes were defined as having less than 6 dwellings/km for the entire shoreline; moderately developed lakes had from 6 to 12 dwellings/km, and highly developed lakes had more than 12 dwellings/km.

Class	Vegetation absent	Vegetation present	Total
Lightly developed	63	249	312
	(20.2)	(79.8)	
Moderately developed	190	314	504
	(37.7)	(62.3)	
Highly developed	126	114	240
	(52.5)	(47.5)	
All classes	379	677	1,056

TABLE 2.—Median, mean, and standard deviation of emergent and floating-leaf vegetation coverage (m^2) by shoreline plot type and total lake development. Lightly developed lakes had less than 6 dwellings/km, moderately developed lakes from 6 to 12 dwellings/km, and highly developed lakes more than 12 dwellings/km.

Shoreline plot type	Total lake development class		
	Lightly	Moderately	Highly
Developed			
Median	11.47	0.14	0.00
Mean	43.07	26.35	23.42
Standard deviation	(73.87)	(66.82)	(61.44)
Sample (N)	156	252	120
Undeveloped			
Median	37.13	15.88	2.85
Mean	116.57	79.92	77.60
Standard deviation	(164.41)	(133.47)	(154.86)
Sample (N)	156	252	120

and floating-leaf plant species or genera (as noted above) were used in the correlation analysis. The estimate of relative biomass and mean size for each species by lake was determined from standard Minnesota summer gill-net surveys for northern pike and trap-net surveys for bluegill and pumpkinseed. Correlation analysis was conducted using all lakes and then only that subset classified as clear-water centrarchid–walleye lakes. Only lakes from which these species were collected were used.

Statistical analyses were performed with JMP software (SAS Institute 1995). All tests were considered significant at $\alpha = 0.05$.

Results

Significantly more undeveloped shoreline plots had emergent or floating-leaf vegetation present than developed shoreline plots, leading us to reject our first null hypothesis that developed and undeveloped shorelines are equally likely to contain aquatic vegetation (chi-square, $P < 0.0001$). Of the 528 plots for each shoreline type, 283 developed shoreline plots had vegetation present, whereas 393 undeveloped shoreline plots had vegetation present. We also rejected (contingency table analysis) the null hypothesis that the presence of vegetation was independent of the extent of total lake development (Table 1; chi-square, $P < 0.0001$). Vegetation was rarer along developed shorelines, especially moderately and highly developed shorelines versus undeveloped and lightly developed shorelines (Table 2; Figure 1).

Emergent and floating-leaf vegetation abundance was significantly different among plots with different amounts of structures (randomized ANOVA, $P < 0.004$). Vegetative coverage in lots with small structures averaged 45.0 m^2, whereas that in

plots with medium and large structures averaged 24.4 m^2 and 23.7 m^2, respectively. Smaller docks also were more likely to have vegetation nearby than larger docks (Table 3). Structures were significantly larger in lakes that were more developed (Figure 2; Tukey–Kramer HSD test, $P < 0.05$). However, the abundance of vegetation on developed shorelines did not differ between those with or without a boat or a boat station within the plot (two-sample randomization test, $P = 0.36$).

Survivorship analysis of vegetation abundance by shoreline type suggested that developed shorelines had less vegetation. Developed shorelines were consistently less likely to have emergent and floating-leaf plants occurring in nearshore littoral areas (Figure 3), and the occurrence functions by shoreline type were significantly different (Wilcoxon test, $P < 0.0001$). Weibull plots for all plots with vegetation suggest that shoreline type aided in modeling vegetation distributions (Table 4). Because smaller Akaike's Information Criteria (AIC) scores indicate more parsimonious models, we concluded that separate Weibull parameters, alpha and beta, for developed and undeveloped shorelines best modeled the data.

Developed shorelines had greater frequencies of plots with the lowest vegetative coverage and fewer plots with high vegetative coverage (i.e., a short-tailed distribution). Frequency distributions for emergent and floating-leaf vegetation were adequately approximated by a gamma distribution (Figure 4). Of the 12 frequency distributions classified by plot type and extent of lake development, we rejected the null hypotheses that the data fit the gamma distribution model 4 times (Kolmogorov–Smirnov goodness-of-fit test, $P < 0.0001$ to $P = 0.007$); 3 of the 4 involved
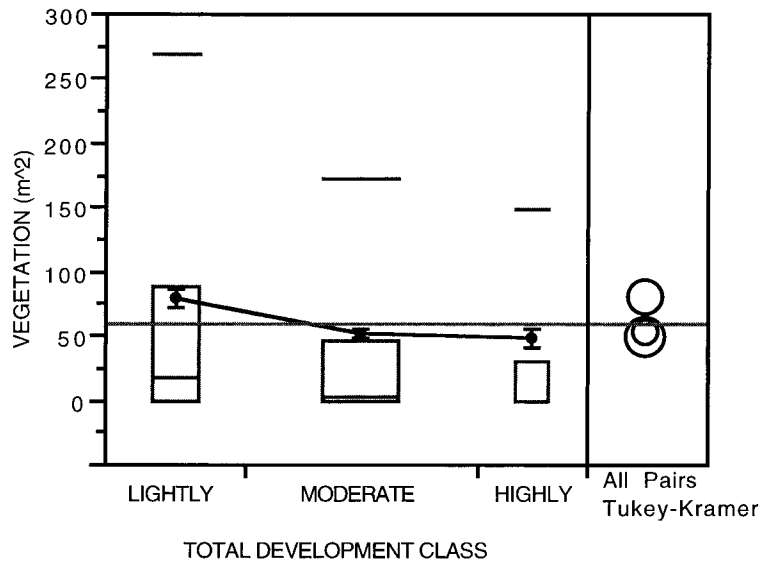
FIGURE 1.—Box plot of emergent and floating-leaf vegetation (m²) by total lake development class. Lightly developed lakes had less than 6 dwellings/km, moderately developed lakes 6–12 dwellings/km, and highly developed lakes more than 12 dwellings/km. The box represents the interquartile range, the line in the box the median, and lines above and below the box represent the 90% and 10% quantiles (the latter coinciding with the lower quartile lines). The means of each group, with 1 SE, are connected with lines. The horizontal line crossing the graph represents the overall mean. Significant differences between mean vegetation abundances were tested with the Tukey–Kramer HSD test; circles for means that are significantly different either do not intersect or intersect only slightly. Here, the mean vegetation abundance of plots from lightly developed lakes differed significantly from that of moderate and highly developed lakes.

developed and undeveloped shoreline plots combined. Thus, combining developed and undeveloped plots produced more complex frequency distributions that were not modeled well with the gamma distribution. Graphical estimation of the difference between gamma parameters suggests that alpha and beta parameter values depend on whether the shoreline plot was developed or not (Figure 5). Undeveloped plots produced lower alpha parameter estimates with less variability, indicating that these plots con-

TABLE 3.—Frequency (and row percentages) of emergent and floating-leaf presence and absence by size-class of nonnatural structures. Structures in the plots included docks, boat stations, boats, and swimming platforms. The structure size-classes were based on the amount of areal coverage, namely, small (<20 m²), medium (20–35 m²), and large (>35 m²).

Structure size-class	Vegetation absent	Vegetation present	Total
Small	65 (39.4)	100 (60.6)	165
Medium	103 (49.5)	105 (50.5)	208
Large	76 (49.0)	79 (51.0)	155

sistently had higher vegetative coverage. Alpha and beta estimates for developed plots from moderately and highly developed lakes were higher than those for lightly developed lakes, reflecting greater relative frequencies of low-vegetation-coverage intervals. Alpha and beta estimates for developed plots from lightly developed lakes were more similar to those of undeveloped plots. This suggests that when lakes have more than 6 dwellings/km vegetative loss along developed shorelines may be substantially greater than along developed shorelines in lightly developed lakes.

The amount of emergent and floating-leaf vegetation was significantly different based on shoreline type, developed shorelines having significantly less vegetation (randomized ANOVA, $P < 0.05$; Table 5). The interaction between shoreline type and lake was not significant (randomized ANOVA, $P > 0.05$), suggesting that development affected vegetation abundance similarly across lakes. The mean emergent and floating-leaf vegetation plot coverage was 31.1 m² (3.3% of plot) for developed shorelines and 90.2 m² (9.6% of plot) for undeveloped ones. The difference in the sample means of vegetation coverage between de-
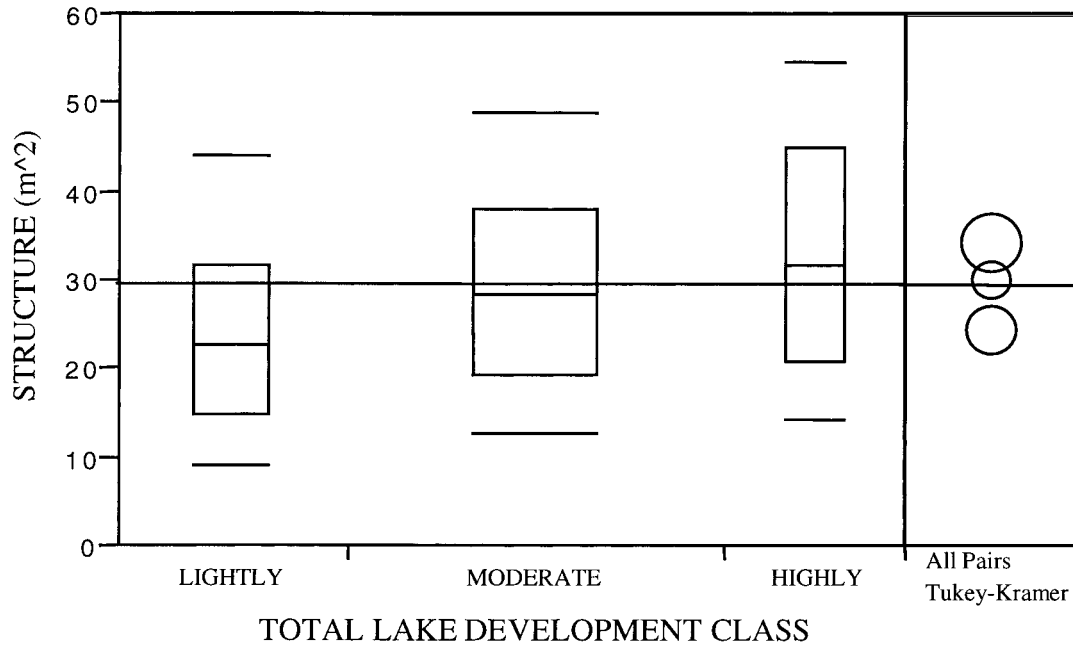
FIGURE 2.—Box plot of size of structures by total lake development class. Lightly developed lakes had less than 6 dwellings/km, moderately developed lakes 6–12 dwellings/km, and highly developed lakes more than 12 dwellings/km. The box represents the interquartile range, the line in the box the median, and the lines above and below the box the 90% and 10% quantiles. The horizontal line crossing the graph represents the overall mean. Significant differences between mean structure size were tested with the Tukey–Kramer HSD test; circles for means that are significantly different either do not intersect or intersect only slightly. Here, all pairs are significantly different.
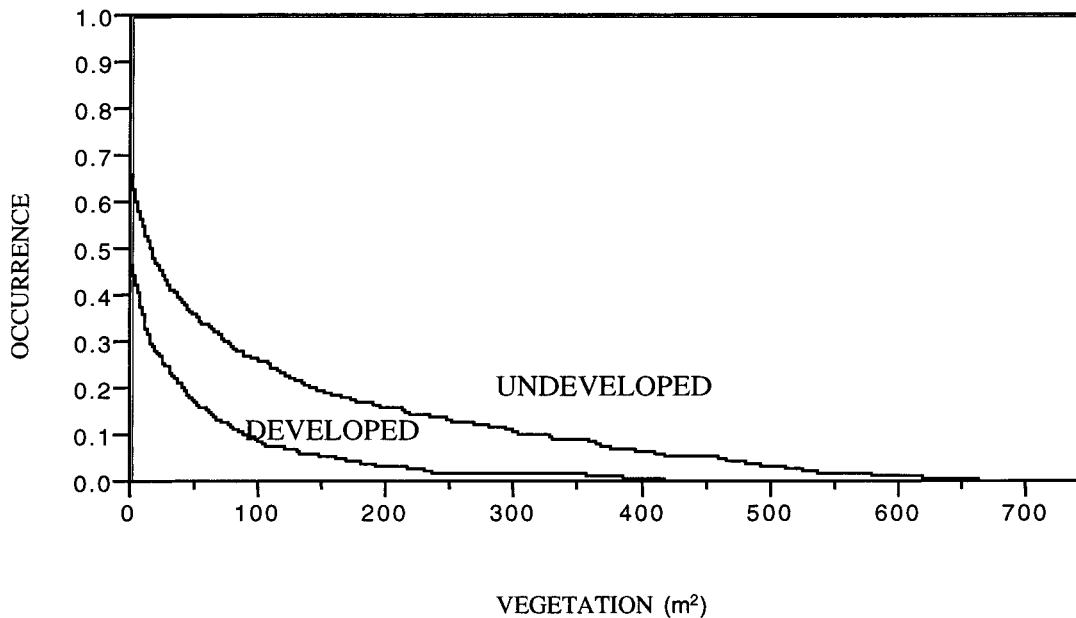

FIGURE 3.—Product-limit estimates of the occurrence function for vegetation abundance (m²) in developed and undeveloped shoreline plots. Occurrence is the probability that a plot would have a given level of vegetative coverage.

TABLE 4.—Sum of log likelihood, number of parameters, Akaike Information Criteria (AIC) score, and AIC score minus the minimum score (AIC − AIC$_{min}$) for four Weibull models. Weibull parameters are alpha and beta, where alpha is the 63.2 percentile of the occurrence distribution and beta corresponds to the slope of the line in the Weibull plot. The model with the lowest AIC score is the best one.

Model	Log-likelihood sum	Number of parameters	AIC score	AIC − AIC$_{min}$
General model alpha and beta do not vary by shoreline type	3,606.555	2	7,217.110	32.910
General model alpha, beta varies with shoreline type	3,602.745	3	7,211.490	27.290
General model beta, alpha varies by shoreline type	3,589.817	3	7,185.634	1.434
Alpha and beta vary by shoreline type	3,588.100	4	7,184.200	0.000

veloped and undeveloped plots was 59 m² (randomized 95% confidence interval, 45–74 m²), and vegetation coverage averaged 66% less with development.

The total lake development class effect on vegetation abundance was insignificant with respect to the variation from lake to lake (split-plot ANOVA, $P > 0.05$; Table 6). A major source of variability in vegetation abundance was the lake-to-lake variation within lake development classes. Our earlier analysis (contingency table analysis) failed to account for the total lake development effect being confounded with the lake effect. The shoreline type effect on vegetation abundance was significant with respect to the variation of vegetation abundance in developed and undeveloped plots within a lake ($P < 0.05$; Table 6). The interaction between total lake development class and shoreline type was not significant, suggesting that the difference between developed and undeveloped shorelines generally did not diminish in lakes with increasing total lake development. This analysis using split-plot ANOVA failed to reject the hypothesis that the cumulative impacts of shoreline development are greater than the sum of individual lakeshore resident impacts. However, this analysis had low power to test for significance of the interaction between development class and shoreline type $(1 - \beta = 0.2366)$ and for the total lake development class effect $(1 - \beta = 0.1977)$.

The estimated total loss of emergent and floating-leaf coverage from human development for Minnesota's 531 centrarchid–walleye lakes was 20–28%. This estimate of cumulative effect was based on recent home counts and the mean differences in vegetation between developed lake lots and undeveloped shoreline. The current estimated median density of dwellings for Minnesota's clear-water centrarchid–

walleye lakes is 8.7 homes/km, or six times the 1950s level (Figure 6).

The frequency of occurrence of the common emergent and floating-leaf species were negatively correlated to the number of homes per kilometer, all but arrowhead being significant (Spearman's Rho, $P < 0.05$, $N = 195$ lakes; Figure 7). No significant correlations were found for the common submergent plant species. Hardstem bulrush had the highest correlation between percent of transects in which a given plant species occurred and homes per kilometer (Spearman's Rho = -0.38, $P < 0.0001$). In more developed lakes the probability of observing emergent and floating-leaf vegetation decreased, but the probability of sampling the typical submergent plant species for these lakes did not. This suggests that emergent and floating-leaf species are more sensitive to human activities.

Significant correlations were detected between the occurrence of emergent and floating-leaf plant species and the relative biomass and mean size of northern pike, bluegill, and pumpkinseed (Spearman's Rho, $P < 0.05$; Table 7). Nine of the 15 plant and fish biomass correlations were significantly positive when all lakes were used in the analysis. Northern pike biomass was positively correlated with four of the five plant species. All three fish species had positive correlations with the lakewide occurrence of broad-leafed cattail and yellow water lily. Analysis of just the clear-water centrarchid–walleye lakes produced significant positive correlations for northern pike biomass with arrowhead and white water lily. Bluegill and pumpkinseed mean size was positively correlated with hardstem bulrush (Spearman's Rho, $P < 0.05$; Table 7). Northern pike mean size was negatively
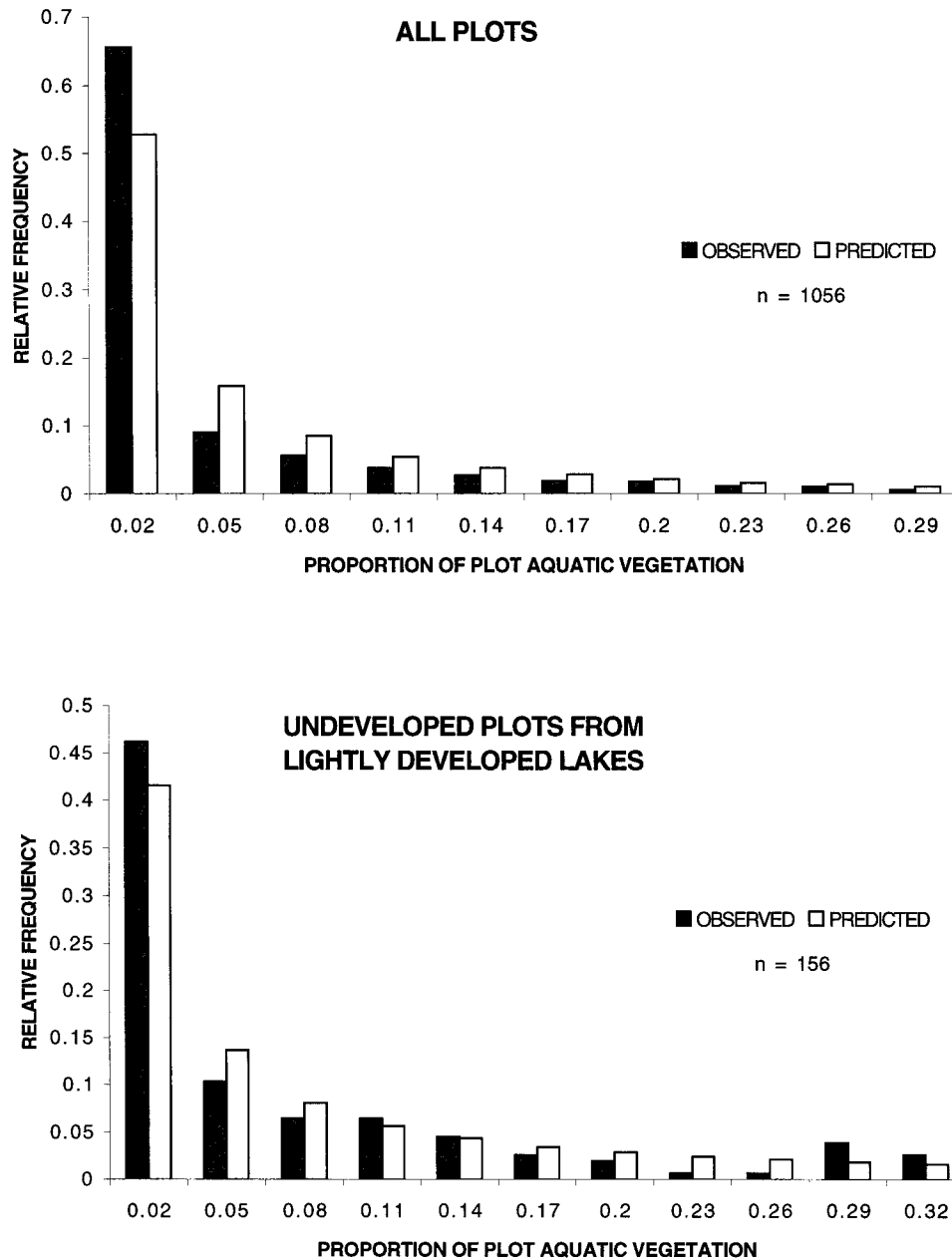
ALL PLOTS

RELATIVE FREQUENCY

■ OBSERVED □ PREDICTED

n = 1056

PROPORTION OF PLOT AQUATIC VEGETATION

UNDEVELOPED PLOTS FROM LIGHTLY DEVELOPED LAKES

RELATIVE FREQUENCY

■ OBSERVED □ PREDICTED

n = 156

PROPORTION OF PLOT AQUATIC VEGETATION

FIGURE 4.—Observed distributions of proportional coverage of emergent and floating-leaf vegetation in 935-m^2 shoreline plots compared with those predicted by the gamma distribution for all samples (upper panel) and for undeveloped plots in lightly developed lakes (lower panel).

correlated with hardstem bulrush occurrence in the lakes.

Discussion

The cumulative impact of human activities on aquatic vegetation in the littoral area of clear-water centrarchid–walleye lakes was significant. Devel-

oped shorelines had substantially less emergent and floating-leaf vegetation than undeveloped shorelines. For every developed shoreline plot, there was on average a 66% reduction in vegetative coverage relative to undeveloped conditions. Because aquatic vegetation is an important element of lake habitat, the substantial estimated loss of
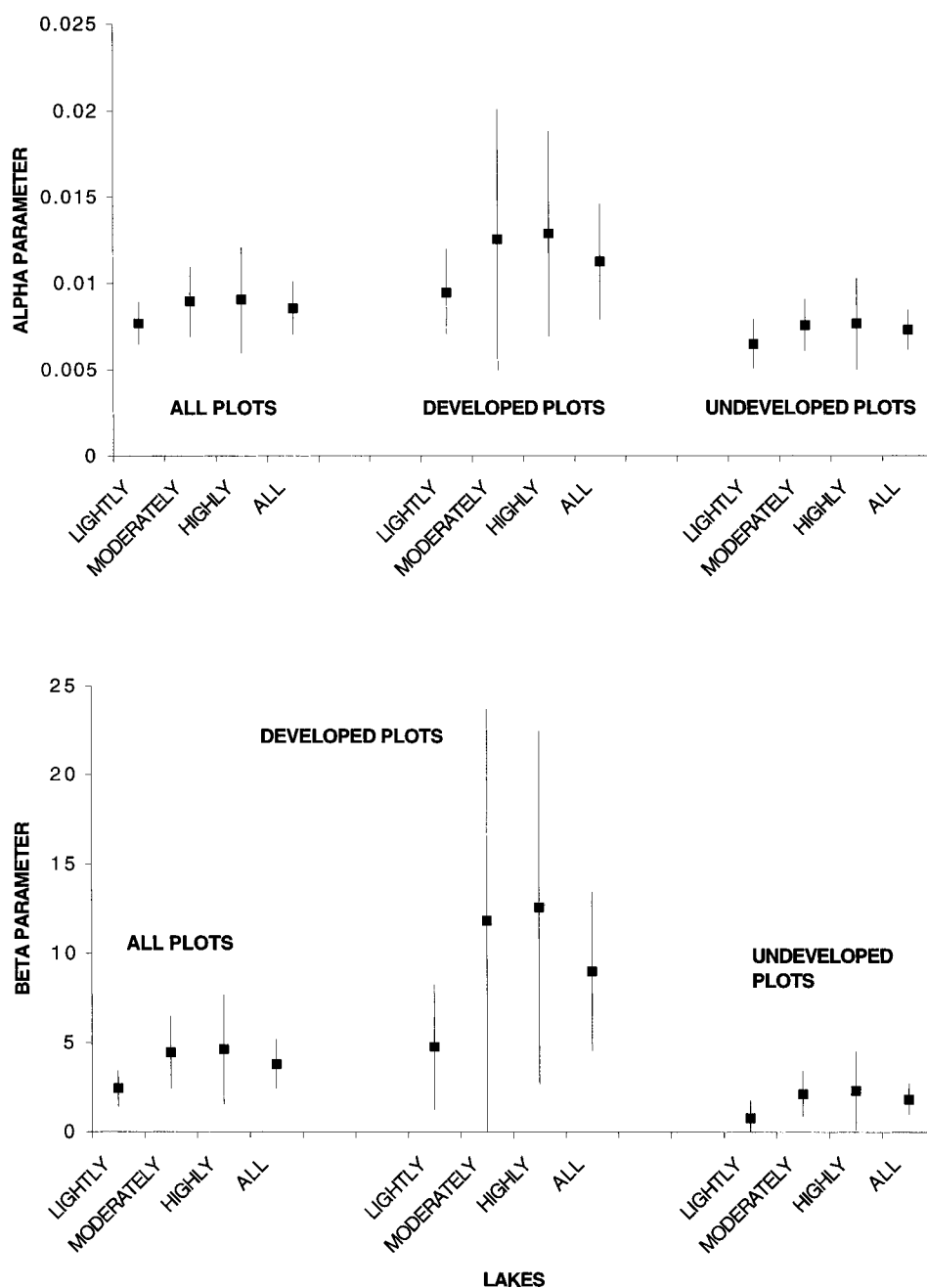
FIGURE 5.—Gamma distribution and approximate 95% confidence intervals of alpha (upper panel) and beta (lower panel) parameters for plots of all shorelines and developed and undeveloped shorelines for lakes with different levels of total lake development; lightly = less than 6 dwellings/km, moderately = 6–12 dwellings/km, and highly = more than 12 dwellings/km.

emergent and floating-leaf vegetative cover, 20–28%, in Minnesota's centrarchid–walleye lakes is a concern. With increasing development trends and growing human population, the continued domes-

tication of North American lakeshores will probably accelerate plant losses. For example, we predict that the loss of emergent and floating-leaf vegetative cover by 2010 may reach as high as 45%

TABLE 5.—An analysis of variance table summarizing the effect of shoreline type (developed and undeveloped) and lake on emergent and floating-leaf vegetation abundance. Significance levels (P) were determined from the proportion of randomization mean squares that exceeded the observed mean square.

Source of variation	df	Sum of squares	Mean square	F	P
Lake	43	3,954,568	91,967	9.62	<0.01
Shoreline type	1	924,068	924,068	96.63	<0.01
Lake × shoreline type	43	950,835	22,112	2.31	0.11
Error	968	9,256,787	9,563		

for this group of lakes (assuming the housing development rate observed since the 1950s and a 66% reduction in vegetation due to development).

Other investigations have documented substantial shoreline habitat modification by human activity, supporting the conclusions of this study. For a group of Wisconsin lakes, it was noted that developed shorelines had 92% less floating-leaf and 83% less emergent vegetative cover than undeveloped shorelines (Meyer et al. 1997). In addition, Jennings et al. (1996) noted changes in nearshore substrate composition in Wisconsin lakes due to human activity. In an Iowa lake, Byran and Scarnecchia (1992) found significant reductions in aquatic macrophyte abundance in developed compared with undeveloped shorelines. Many lakeshore home owners remove lake vegetation adjacent to their property to create beach conditions. The construction of piers and docks and alteration of shoreline with riprap, concrete, and seawalls destroy emergent vegetation, including rushes, bulrushes, and sedges (Beauchamp et al. 1994; Engel and Pederson 1998). Christensen et al. (1996) found that littoral woody debris was significantly less abundant in developed lakes. Szajnowski (1983) found a rapid loss of emergent plants in Polish lakes from 1958 to 1982 due to removal by humans. Boat and snowmobile traffic create openings and fragment emergent vegetation stands (Kahl 1993). Increased boating activity, including larger boats and personal watercraft, increases the number of boat–plant collisions and wave action,

both causing increased plant damage (Ostendorp et al. 1995). Because shoreline habitat is influenced by both natural and anthropogenic factors from both the lake and land, Crowder et al. (1996) concluded that ''shoreline habitats in general are subject to more profound and rapid change than open lake settings.'' However, assessing anthropogenic effects can be difficult.

This study had several shortcomings. For example, if riparian owners were heavily selecting lakeshore lots based on emergent or floating-leaf vegetation, comparisons of vegetation differences and calculation of habitat loss could be confounded. Riparian owners might have selected shorelines with less emergent vegetation in lightly developed lakes; i.e., both the alpha and beta gamma distribution parameters for frequency distributions of vegetative cover for undeveloped plots in lightly developed lakes were lower than those of moderately and highly developed lakes (Figure 5). If lightly vegetated shorelines were selected for development, the remaining undeveloped shore would be the heavily vegetated areas. However, this was not observed; the average emergent and floating-leaf vegetation abundance in undeveloped plots decreased with increasing total lake development (Table 2). Other factors, such as road location, lot elevation, and riparian or submerged vegetation are also known to be important in dwelling site selection.

Another shortcoming of this study was that riparian owners may have selected lakes that were

TABLE 6.—Split-plot analysis of variance table summarizing the effect of shoreline type (developed and undeveloped), lake within total lake development class (nested), and total lake development class on emergent and floating-leaf vegetation abundance.

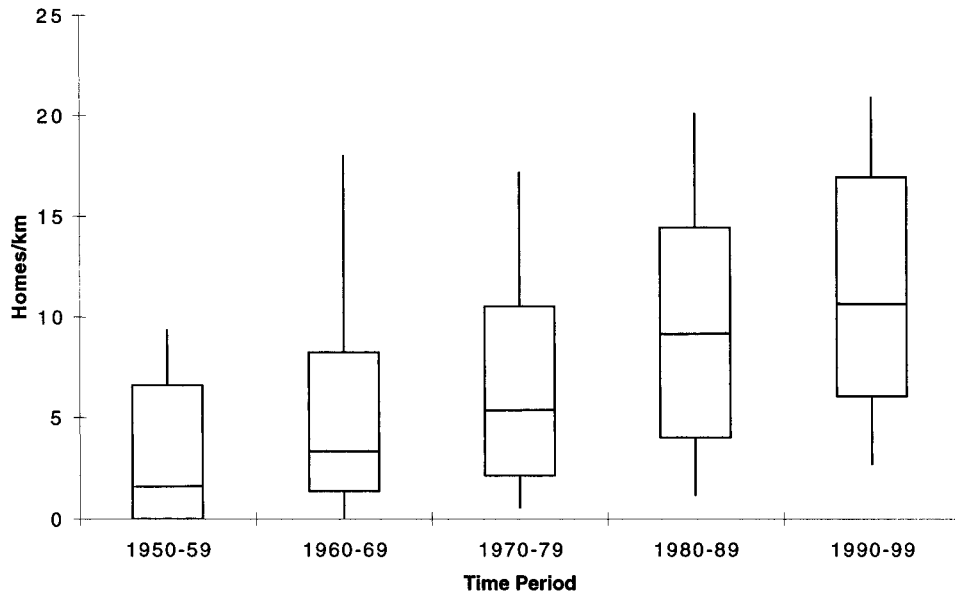| Source of variation	df	Sum of squares	Mean square	F	P
Development class	2	167,735	83,867	0.92	0.4075
Lake (development class)	41	3,746,658	91,382	9.05	<0.0001
Shoreline type	1	421,420	421,420	41.75	<0.0001
Development class × shore type	2	21,417	10,708	1.06	0.3465

FIGURE 6.—Shoreline development for 531 northcentral Minnesota centrarchid–walleye lakes based on dwellings or homes per kilometer for the period 1950 to 1999. The box represents the interquartile range, the vertical lines the 10% and 90% quantiles, and the line within the box the median.
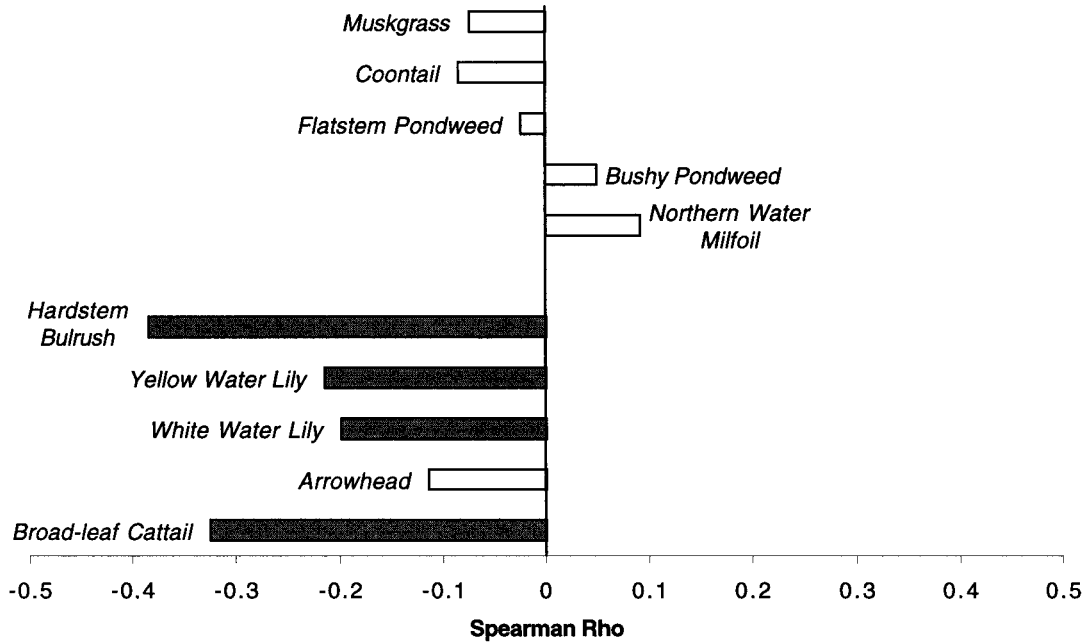

FIGURE 7.—Spearman's rank correlations between the percent of transects in which a given plant species occurred and homes per kilometer for 195 clear-water centrarchid–walleye lakes. The top five bars are the common submergent species and the bottom five bars are the common emergent and floating-leaf plants for these lakes. Significant correlations are shaded ($P < 0.05$).

TABLE 7.—Significant Spearman's rank correlations, based on Minnesota Department of Natural Resources lake survey data, between the percent of transects in which a given plant species occurred and the relative biomass and mean size of northern pike, bluegills, and pumpkinseeds for all lakes and clear-water centrarchid–walleye lakes ($P < 0.05$).

Species and lake group	Percent of lake transects in which plant occurred				
	Hardstem bulrush	Yellow lily	White water lily	Arrow-head	Broad-leaf cattail
Relative biomass (kg/net)					
Northern Pike					
All lakes ($N = 595$)		0.15	0.24	0.13	0.10
Clear-water lakes ($N = 181$)			0.17	0.21	
Bluegill					
All lakes ($N = 523$)		0.10	0.13		0.09
Clear-water lakes ($N = 178$)					
Pumpkinseed					
All lakes ($N = 423$)		0.10			0.19
Clear-water lakes ($N = 152$)					
Mean size (kg)					
Northern Pike					
All lakes ($N = 595$)		−0.12			
Clear-water lakes ($N = 181$)	−0.19				
Bluegill					
All lakes ($N = 523$)	0.11				
Clear-water lakes ($N = 178$)	0.16				
Pumpkinseed					
All lakes ($N = 423$)	0.17	0.13	0.12	0.13	0.20
Clear-water lakes ($N = 152$)	0.19				0.19

less vegetated. However, the comparison of consequences of development on the common species of submergent vegetation versus those to emergent and floating-leaf species indicate that riparian owners may not be selecting less vegetated clear-water lakes but rather that common nearshore emergent and floating-leaf species are more vulnerable and sensitive to human activities (Figure 7).

In this comparative study, the total lake development effects or whole-lake effects of development on nearshore emergent and floating-leaf vegetation evidence were not robust. The variation in vegetation between lakes was confounded with total lake development effects. Nonetheless, shoreline development probably has effects beyond the local site of human habitation. Analyses of emergent vegetative cover from historical photographs of several lakes in Minnesota dating from the 1940s to the 1990s have shown both substantial local and modest whole-lake development effects (i.e., vegetation reductions away from areas of shoreline development) on emergent vegetation (MDNR, unpublished data). Additional analyses using historical data from a larger set of lakes may provide greater insight on the whole-lake effects and fine-scale degradation of undeveloped regions within a lake.

Emergent and floating-leaf plants are important to fish, wildlife, and humans. Several papers have summarized the fish and wildlife value of these plants (Killgore et al. 1993; Meyer et al. 1997; Engel and Pederson 1998). We found that the abundance of northern pike, bluegill, and pumpkinseed was positively correlated with lakewide occurrence of emergent and floating-leaf aquatic plants. Although the correlation coefficients were low, this comparison study of multiple lakes suggests that declines in emergent and floating-leaf vegetation due to development may result in lower fish production. Hinch and Collins (1993) similarly concluded that aquatic macrophytes abundance was positively correlated with bluegill and pumpkinseed abundance in Ontario lakes, probably due to the importance of this habitat for the growth and survival of juveniles and adults. For northern pike, Minns et al. (1996) used simulation modeling to predict that northern pike biomass would decline and mean weight would increase with reductions in juvenile habitat. Those simulations are supported by our findings of positive correlations between northern pike biomass and emergent and floating-leaf plant occurrence and negative correlations between the mean size of pike and some species of aquatic plants. Humans also benefit from these plants because stands of emergent

plants and water lilies dampen the force of waves, reducing shoreline erosion. Humans and their culture benefit from the esthetic values of lakes with natural vegetation (Klessig 1995). People enjoy lakes for their natural beauty, and many people find developed shorelines unnatural and unattractive (Macbeth 1992; Korth 1994). Minnesota lake users cite vegetation removal in shoreland areas as a common factor degrading lake esthetics (Anderson et al. 1999).

Shoreline management, which is often conducted through regulations and permitting programs, should address the cumulative effects on aquatic habitats. For example, in Minnesota a permit is required to remove emergent vegetation, apply herbicides, remove floating-leaf vegetation from an area larger than a channel 4.6 m wide, or remove submergent vegetation in an area larger than 232.3 m^2. Annually, about 8,000 property owners are issued permits to destroy aquatic plants in lakes adjacent to their property. Although most permits are for chemical control of submerged macrophytes, 16% of the 1998 permit holders removed floating-leaf vegetation, and of the permits issued, 24% allowed destruction of emergent vegetation. The reported use of the herbicide 2,4-D in public lakes was about 21,000 kg in 1998; however, the majority of 2,4-D use in the state lakes is illegal and goes unreported (MDNR, unpublished data). Also, the commercialization of aquatic macrophyte removal has probably increased the amount of shoreline altered and may have decreased public concern over the consequences.

With increasing development and more full-time occupancy of lakeshore homes, habitat protection that depends solely on site-specific or individual property regulation will become more biologically insufficient and administratively impractical. The many regulation and permit programs address only a single impact at a single site with the focus on individual landowner considerations. Unfortunately, this scope results in resource degradation or losses that are inconsistent with policies designed to conserve public aquatic resources. This scope also does not factor in substantial noncompliance and modifications too small to require a permit (e.g., vegetation removal, sand blankets, riprap, log removal, and boat ramps). Few permits of aquatic vegetation removal had been issued for lakes in this study, yet we estimated substantial loss of vegetative cover. The existing regulatory framework, which is based primarily on individual riparian rights, allows the resource to be gradually lost even without illegal activity. Jennings et al.

(1999) note that permitting programs are designed to prevent radical alterations to lake ecosystems and that they have merit for conserving small habitat fragments, but that natural resource management agencies should address cumulative habitat alterations in their management programs. Because iterative small-scale changes can cumulatively produce large-scale effects, small modifications to habitat are becoming an issue of considerable concern (Burns 1991).

Natural resource management agencies should do more to discourage actions that cause small losses or alterations to aquatic habitat. Perhaps encouraging lake associations and local communities to allow the designation of some lakes as pesticide-free or as natural-landscape lakes would provide alternative messages and mechanisms to protect the natural character of some lakes. Another option might include the elimination of riparian owner rights to destroy aquatic plants and replacement with a regulatory system in which aquatic plant control is allowed only by lake associations or lake improvement districts. Community-based management of shorelines, like community control of commercial fishing or other property rights systems, may be effective legal processes for protecting these public or common property resources (Feeny et al. 1990). Creative solutions might include a mix of property tax incentives for shoreline management, acquisition of development rights, legal covenants for new development, and community planning. In addition, we recommend exploring the use of shoreline zoning rules to encourage natural habitat or undomesticated areas on the water's edge of lake lots as buffer strips to protect or enhance water quality and esthetics (Henderson et al. 1999). Regulated vegetated buffers are already a common and accepted tool used to protect stream resources from detrimental actions (e.g., logging) by riparian owners. A majority of the Minnesota lake users surveyed would support stricter regulations for shoreline development in order to maintain natural shoreline characteristics (Anderson et al. 1999).

The results of our study indicate that human activity has reduced aquatic plant abundance in important central North American lakes. Significant cumulative effects of localized emergent and floating-leaf vegetation loss were found. While it was not surprising that there has been an impact of development on aquatic vegetation, what is surprising is that the cumulative impact of human activity on these public resources has not received more attention. Although emergent and floating-

leaf vegetation removal is currently extensive and intensive, the permanence of the effects is highly dependent on the riparian owner collective. Natural resource management agencies need more effective regulations. However, government regulation by itself will not be enough. Agencies should also implement programs that change the attitudes and behavior of lakeshore property owners, who have been largely unaware that their actions have not been in their own best interest—i.e., protecting and promoting healthy and esthetic lake ecosystems. The damage to aquatic ecosystems could be mitigated or restored with a simple change in human attitudes toward plants in the water, either with a new dominant lakeshore ethic and lifestyle or, superficially, with a new lawn and garden fashion. Thus, MDNR has recently intensified its education program directed at lakeshore homeowners in the hope of generating beneficial cumulative effects by promoting the beauty of natural shorelines.

Acknowledgments

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