Determining Aquatic Macrophyte Response to Human Perturbation in Watersheds and along Lakeshores of Wisconsin Lakes and the Tolerance Levels of Individual Species to Environmental Gradients.

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ABSTRACT

Variation in aquatic plant communities across lakes has been attributed to environmental gradients of water chemistry and more recently, human perturbations including agriculture, urban development, and direct removal of plants. However, more research is needed to understand specifically how human perturbation affects macrophyte communities and how individual macrophyte species respond to perturbations as a function of species tolerance levels to water chemistry attributes. The objectives of this study were (1) to determine what effects human perturbations at both the watershed and lakeshore levels have on aquatic macrophyte species richness and relative occurrence in Wisconsin lakes and (2) to quantify water chemistry attributes in selected Wisconsin lakes, assess the tolerance levels of individual macrophyte species growing within those lakes, and to determine relations of aquatic plant communities to environmental gradients across Wisconsin. Macrophyte communities in 53 Wisconsin lakes were surveyed to determine species richness and relative occurrence of individual species in the littoral zone of each lake. To determine the extent of regional variation, lakes were chosen from two different ecoregions: the Northern Lakes and Forests ecoregion and the Southeastern Till Plains ecoregion. Within these ecoregions, lakes were selected along two gradients of development: at the watershed scale, ranging from undeveloped (i.e., forested) to high agricultural or urban development, and at the lakeshore scale along a gradient of house densities. Occurrence of individual aquatic macrophyte species was sampled using snorkel and SCUBA within 18 0.25 m^2 quadrats along 14 randomly placed transects in each lake. Effects of watershed development (e.g., agriculture or urban land use) and lakeshore residential development were tested at whole lake (littoral zone) and near-shore scales using regression analyses. To determine sensitivity of individual species to water chemistry attributes across lakes and ecoregions, relative occurrences of macrophytes were compared to water quality data (alkalinity, conductivity, calcium, magnesium, pH, nitrogen, and phosphorus concentrations) using regression, range of occurrence, and canonical correspondence analysis (CCA). Species richness was negatively related to watershed and riparian development while individual species differed in levels of response. Species richness also declined in relation to concentrations of alkalinity, conductivity, calcium, magnesium, pH and nitrogen. Each individual species occurred within a specific range of tolerance to water chemistry attributes (such as nitrogen, alkalinity, pH, etc.). Some species such *Calla palustris* and *Najas gracillima* demonstrated narrow ranges of tolerance and only occurred in lakes with very low concentrations of alkalinity and nitrogen, while other species such as *Najas marina* and *Potamogeton crispus* were limited to narrow ranges of high concentrations of water chemistry attributes. Species with narrow ranges of tolerance at either end of the ecological gradient may be better for bioindication. Further management such as protection of undeveloped shorelines and reductions in aquatic plant removal is needed to protect and maintain healthy macrophyte communities.

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LITERATURE REVIEW

Macrophytes are an important element of healthy aquatic ecosystems. Aquatic vegetation provides critical habitat and food for waterfowl, fish, and other aquatic organisms (Davis and Brinson 1980). Macrophyte communities also influence water turbidity (Scheffer 1990, Rooney *et al.* 2003), the rate of shoreline erosion (Bhowmik 1978, van Nes *et al.* 2002), and may retain and reduce contaminants and excess nutrients entering from terrestrial systems (Moreira *et al.* 1999) and are influenced by these same features. In order to better protect macrophyte communities and conserve healthy lake ecosystems, biologists, land managers, and riparian landowners need to understand the relationship between watershed development, water chemistry, and aquatic macrophytes in lakes.

PLANTS AS CRITICAL HABITAT

INVERTEBRATES

Submerged macrophytes support a rich variety of invertebrate fauna ranging from Turbellarians and other benthic invertebrates that burrow into the soft substrate accumulated in macrophyte beds (Beckett *et al.* 1992), to crayfish that directly consume plant material (Olson *et al.* 1995). In the United Kingdom, Daldorph and Thomas (1995) documented snails as a predominant predator of periphyton growing on macrophytes in spring-fed drainage channels. While some macroinvertebrates feed on epiphyton found on submerged plants, others consume the plant tissue directly (Smith 2001). For example, Hanson and Chambers (1995) reviewed the effects of crayfish on macrophytes and found that these invertebrates preferred the soft material of submersed plants over the coarser plant matter of emergent species. Particularly in Wisconsin, the exotic rusty crayfish (*Orconectes rusticus*) is known to feed extensively on aquatic vegetation and can negatively impact macrophyte abundances because they clip the plants at base of the stems, hindering re-growth (Wilson 2002).

Aquatic macrophytes are also used by invertebrates as habitat. The abundance of invertebrate fauna associated with macrophyte stands is directly related to the amount of leafy substrate provided for colonization and protection from predators (Diehl 1988, Beckett *et al.* 1992). Beckett *et al.* (1992) found a drastic decrease in the diversity and density of invertebrate species in areas lacking macrophyte growth. In addition, the bottom sediment in these patches also contained fewer interstitial invertebrates. Diehl (1988) found that attack frequency for predators of invertebrates such as yellow perch (*Perca flavescens*), roach (*Rutilus rutilus*) and bream (*Abramis brama*) decreased when macrophyte complexity increased (also, Crowder and Cooper 1982). In the same study, extremely dense plants such as *Chara* beds provided complete protection for invertebrates because fish were unable to enter dense stands (Diehl 1998).

FISH

Aquatic vegetation is critical to many fishes because it provides refuge from predation, creates foraging areas, and provides spawning habitat for some fish. For example, macrophytes affect predator-prey interactions providing refuge for smaller fishes from predation by larger fishes (Savino and Stein 1982). In aquaria experiments, Valley and Bremigan (2002) found that healthy macrophyte stands promote largemouth bass (*Micropterus salmoides*) predation success rates on bluegill (*Lepomis macrochirus*). However, when macrophyte communities are invaded by aggressive species such as Eurasian watermilfoil (*Myriophyllum spicatum*) and coontail (*Ceratophyllum demersum*), plant stands become so dense that predatory fish are unable to maneuver through them to find prey items, which disrupts the food web; skewing prey species toward a smaller size structure (Keast 1984, Lillie and Budd 1992). In Fish Lake, Wisconsin, Olson *et al.* (1998) found that plant die-offs and strip harvesting of dense Eurasian watermilfoil stands increases size structure and growth rates for both largemouth bass and bluegill. Moving down the food chain, Crowder and Cooper (1982), using experimental ponds, found that the array of invertebrate diversity in bluegill diets is greatest at intermediate macrophyte densities and that diets are compromised when the macrophyte habitat is altered: either increases or decreases in density affected diets.

While most fishes simply prey on invertebrates and smaller fishes living among macrophytes, other fish directly consume the vegetation. Grass carp (*Ctenopharyngodon idella*) are known to actively browse on aquatic vegetation (Petr 2000). In addition, roach and rudd (*Scardinius erythrophthalmus*) have also been found to feed on soft, submerged macrophytes in Europe (Petr 2000). Another study indicates that bluegill may intentionally consume vegetation to help digest invertebrates (Gerking 1962).

Macrophytes also provide spawning habitat for some species of fishes (Becker 1983, Beauchamp *et al.* 1992, Petr 2000). Fishes including cyprinids, yellow perch and northern pike (*Esox lucius*) have adhesive eggs that stick to macrophytes after spawning and during incubation (Casselman and Lewis 1996, Petr 2000). In the Wolf River, Wisconsin, walleye (*Sander vitreus*) spawn on cattail (*Typha* spp.) beds and inundated marsh grasses, which differs from the cobble substrate commonly used in lakes and rivers (Kitchell *et al.* 1977). Other fishes, such as carps and catfishes (*Ictalurus* spp.), simply scatter their eggs amongst submergent vegetation (Petr 2000). And lake trout (*Salvelinus* *namaycush*), not known to usually use macrophyte habitats for spawning in the Great Lakes (Dorr *et al.* 1981), spawn over deep-water macrophyte beds in Lake Tahoe: it was suggested that the macrophytes provided adequate dissolved oxygen and protection from predation for the eggs that settled into the vegetation (Beauchamp *et al.* 1992).

WATERFOWL

Aquatic macrophyte communities are a major component of waterfowl production. Increased biodiversity of waterfowl and other avian species has been associated with healthy communities of aquatic vegetation (Krull 1970). Waterfowl such as ducks and geese feed on leaves, stems, tubers, and seeds of aquatic macrophytes (Krull 1970, Perrow *et al.* 1997, Petr 2000). Some plants such as water celery (*Vallisneria americana*) and pondweeds (*Potamogeton* spp.) are preferred as food sources over other aquatic macrophytes by many species of waterfowl (Engel 1990, Petr 2000). While geese and swans (*Cygnus* spp.) are true herbivores, feeding primarily on aquatic vegetation (Conover and Kania 1994), dabbling ducks (*Anas* spp.) and coot (*Fulica americana*) also feed on the invertebrates living on macrophytes as well as the plants themselves (Perrow *et al.* 1997). Juvenile waterfowl generally eat invertebrates that inhabit macrophytes, but will switch to seeds, tubers, and shoots of macrophytes when available (Engel 1990).

PLANT ECOLOGY

Aquatic macrophytes are integral components of aquatic ecosystems. While macrophytes are affected (e.g., growth, survival, diversity) by a suite of factors including water chemistry and nutrient concentrations, the plants also alter the chemical and physical properties of their aquatic surroundings. When human perturbations interfere with lake dynamics, and specifically macrophyte communities, important components of the ecosystem are compromised and may be lost.

HOW MACROPHYTE S EFFECT THE AQUATIC ENVIRONMENT

Macrophytes affect light penetration, sediment movement, nutrient dynamics, dissolved oxygen (DO) levels and other chemical properties of aquatic environments (Jaynes and Carpenter 1986, Rooney *et al.* 2003). Carpenter and Lodge (1986) state that while light is quickly attenuated through uninhabited water, the amount of light available to species growing in the understory declines exponentially within macrophyte canopies. Titus and Adams (1979) looked specifically at two macrophyte species in Lake Wingra and University Bay, Lake Mendota, Madison, Wisconsin and found that canopy forming plants (e.g., Eurasian watermilfoil) attenuate more light than rosulate species (e.g., water celery).

Macrophytes can also increase the amount of light available in the water column by preventing sediment resuspension and lowering nutrient levels. For example, in Lake Memphremagog, Quebec, Canada, Rooney *et al.* (2003) found that macrophyte communities stabilized the sediments, thereby increasing light penetration by decreasing turbidity in the water. Macrophytes prevent sediment resuspension by reducing littoral wave energy and stabilizing sediments with root structure (Davis and Brinson 1980, Carpenter and Lodge 1986). Rooney *et al.* (2003) found that as a result, sediment accumulation was greatest in the middle of macrophyte beds where macrophyte biomass was most dense and wave energy was reduced.

Macrophytes lower nutrient levels in the water and sediments by retaining nutrients in their biomass. A review by Carpenter and Lodge (1986) found that submerged macrophytes remove nutrients from the water and sediment during periods of growth and release nutrients back into the system during senescence. Yet not all macrophyte beds cycle nutrients at the same level. Carpenter and Lodge (1986) found that during decay, nitrogen is released from macrophyte biomass faster than phosphorous. In addition, they found low annual nutrient cycling in macrophyte stands in oligotrophic systems and high cycling in stands growing eutrophic systems. Because more nutrients are available in eutrophic systems, increased cycling is expected as explained by Ratray *et al.* (1991), who suggested that in eutrophic systems, macrophytes are able to sequester nutrients directly from the water column as well as from the sediment, therefore increasing the amount of nutrients in their biomass (which then are released during senescence).

Macrophyte communities also change the chemical properties of the sediment in which they grow (Jaynes and Carpenter 1986, Wigand *et al.* 1997). For example, in oligotrophic systems, phosphorous (P) is bound in the sediment to iron (Fe) and manganese (Mn) in precipitate form. Plants are able to remove P by increasing the redox potential by releasing oxygen into the substrate from their roots (Barko *et al.* 1991). For example, in Roach Lake, Vilas County, Wisconsin, Jaynes and Carpenter (1986) found that transplanted quillwort (*Isoetes* spp.) and milfoil species oxidized new sediments, lowering the pH, and unbinding sediment phosphorous from the iron-phosphorous precipitate. Wigand *et al.* (1997) found that in the Chesapeake Bay, Maryland, water celery did a better job of oxidizing the substrate than Eurasian watermilfoil and hydrilla (*Hydrilla verticillata*). They also suggested that while plants in both oligotrophic and eutrophic systems release oxygen from their roots, these effects are not seen in eutrophic systems because the redox potential is already so high that plants cannot release enough oxygen to overcome the redox deficit.

Photosynthesis, respiration and decomposition of macrophytes can result in large seasonal and diurnal fluctuations of dissolved oxygen (DO) levels. Photosynthesis by macrophytes in the littoral zone causes DO to "spike" during the day, whereas at night, high respiration rates of dense macrophyte stands reduce DO levels (Carpenter and Gasith 1978, Ondok *et al.* 1984, Wetzel 2001). Ondok *et al.* (1984) produced a model for common waterweed (*Elodea* canadensis) stands in a shallow pond that suggested respiration rates could reduce DO as much as 8 mg/L, depending on temperature of the water and biomass of the plants. Similarly, in Lake Wingra, Wisconsin, Carpenter and Gasith (1978) found that diurnal DO flux in beds of Eurasian watermilfoil was twice as great as that of areas with no weed growth. Decomposition of macrophytes at the end of the growing season and through the winter can also create DO deficits below tolerance thresholds of fish (Wetzel 2001). Wetzel (2001) stated that decomposition of senesced plant material and respiration of plants under the ice decreases the levels of DO during the winter. This is true in Wisconsin lakes because when lakes freeze and snow accumulates on the ice, macrophytes may not receive enough light for photosynthesis, causing the plants to increase respiration levels.

Environmental effects on Macrophytes

Environmental factors that affect aquatic plants include light, seasonal temperature fluctuations, sediment composition, exotic species invasion and nutrient concentrations (primarily nitrogen and phosphorous) (Barko *et al.* 1986, Madsen and Breinholt 1995). Light is an important factor limiting the depth of aquatic plant growth

(Sheldon and Boylen 1977, Nichols 1992). Fifty percent of available light is absorbed within the first meter of water, and adapting to this, aquatic macrophytes have become more efficient at absorbing lower levels of light than terrestrial plants (Wetzel 2001). For example, Sheldon and Boylen (1977) found aquatic plants growing at depths of water that receive only 1% of the light intensity available to terrestrial plants. Moreover, when light is reduced in an aquatic system (by turbidity, algal blooms, or shading from other plants) macrophyte communities may change in response (Boylen *et al.* 1999, Hauxwell and Valiela 2004). The change could be a shift from submerged species to floating-leaf and emergent species (Egertson *et al.* 2004) or to canopy-forming species that create a mat of vegetation at the surface of the water (Madsen *et al.* 1991).

The species that decline or disappear may be less photosynthetically efficient (Boylen *et al.* 1999). For example, Sand-Jensen *et al.* (2000) and Egertson *et al.* (2004) found that pondweeds are among the first taxa to decline in a system when water clarity is reduced. In Cape Cod estuaries, Hauxwell *et al.* (2003) found a drastic decline in eelgrass (*Zostera marina*) due to algal shading caused by anthropogenic nutrient loading. Other species, such as Eurasian watermilfoil adapt to shading through the elongation of stems, thinner leaves and canopy formation at the surface (Goldsborough and Kemp 1988).

Seasonal chronologies of temperate plants are significantly affected by the growing season (Nichols 1997). Frost affects emergent and floating-leaf species in the fall, and while submersed species may not be subjected to extreme temperature fluctuations, growth is limited by decreased light penetration in late summer and later when the lake is covered with ice and snow (Davis and Brinson 1980). Spence (1967) suggested the role temperature plays in seasonal plant dynamics is secondary and that light is still the most important factor, while Rooney and Kalff (2000) found that differences in growth of plants in Quebec, Canada was due to light-temperature interactions. This was also suggested by Nichols (1997) who found greater seasonal variation in macrophyte communities of Wisconsin lakes that had Secchi depths less than two meters. In general, temperature effects on plant growth are poorly understood and warrant further study.

Sediment composition of bottom substrates can influence the distribution, morphology, and productivity of aquatic macrophytes. For example, Nichols (1992) surveyed 68 Wisconsin lakes and found a preference for hard substrate (e.g., rocks and gravel) in 26 species whereas 14 species preferred soft substrate (e.g., organic material). These substrate 'preferences' may be due to how sediment provides or limits the amount of nutrients available to different plants. Barko and Smart (1986) found that the nutrient content within substrates of 17 different North American lakes was inversely related to the amount of sand in the sediment (i.e., very sandy sediments tend to have lower nutrient content), but interestingly, nutrient concentration in the sediment was unrelated to organic content. Relating this to macrophytes, Barko *et al.* (1991) found that Eurasian watermilfoil grew poorly on fine organic and sandy sediments (i.e., sediments with low nutrient content). Improved growth after adding fertilizer to these sediments suggested that poor growth was due to lower amounts of nitrogen and phosphorous (Barko *et al.* 1991). Mantai and Newton (1982) also looked at milfoil and found that the length of roots increased as nutrients became limiting. It should be noted that macrophytes may also draw nutrients from the water column when available, making the influences of sediment composition less clear. For example, research by Rattray *et al.* (1991) suggests no relation between sediment types and the growth of African elodea (*Lagarosiphon major*) and a milfoil (*Myriophyllum triphyllum*) when grown in eutrophic waters, but also found increased growth when plants were grown on eutrophic sediments in oligotrophic water.

Another factor eliciting change in macrophyte communities is the introduction of exotic plants. Exotic species invasions often result in macrophyte monocultures (concurrent with a decline in native macrophyte diversity) (Bayley *et al.* 1978, Boylen *et al.* 1999). The most common invasive species in Wisconsin are Eurasian watermilfoil and curly-leaf pondweed (*Potamogeton crispus*) (Bolduan *et al.* 1994, Nicholson 1981); and both are becoming increasingly more problematic (Madsen *et al.* 1991). Both plants reproduce vegetatively and fragments are transported across land easily on boats and trailers, which increases their likelihood to invade lakes where they then often out-compete native species (Asplund 2000).

Eurasian watermilfoil in a lake can severely impact native macrophyte communities. For example, Bayley *et al.* (1978) noted a decline in all native species, except common waterweed, in the Chesapeake Bay after the establishment of Eurasian watermilfoil. Eurasian watermilfoil is known to create dense canopies at the water surface which in turn, shades out native species (Bayley *et al.* 1978, Nichols 1994). Boylen *et al.* (1999) also documented that 13 of 20 species became extirpated from Lake George, New York because of shading caused by Eurasian watermilfoil. Interestingly, Madsen *et al.* (1991) found that not only do Eurasian watermilfoil canopies shade out native vegetation, but this milfoil is also intolerant of its own shade, sloughing its lower leaves under the canopy.

Curly-leaf pondweed may be equally detrimental to native plant species. It was introduced into the United States in the 1800's and quickly spread across the nation, though the vector is unknown (Nichols and Shaw 1986). It is capable of growing under ice cover during winter (when other plants are senesced) and quickly creates intense vegetative mats at the surface of the water in early spring, possibly shading out native species that are just starting to grow (Bolduan *et al.* 1994). But, because curly-leaf pondweed senesces early in the summer, it may be possible that this species does not complete with established native plants (that peak later in the summer) at the same level that Eurasian watermilfoil does (Nichols and Shaw 1986).

Increased nutrient input (i.e., 'eutrophication'), specifically nitrogen and phosphorous, is possibly the most significant cause of change in macrophyte communities (Scheffer 1990, Hauxwell and Valiela 2004, Edgerton *et al.* 2004). Eutrophication has been documented in estuaries, streams, rivers, and lakes across the world (Smith 2003). Effects of eutrophication may include increased productivity, simplification of biotic diversity, and increased prevalence of noxious algal blooms (Wetzel 2001). And eutrophication is often the result of human perturbation of terrestrial landscapes, primarily agricultural and urban land practices which in succession, affects aquatic environments (Bowen and Valiela 2001, Hauxwell and Valiela 2004, Egertson *et al.* 2004). For example, the algal shading that Hauxwell *et al.* (2003) documented in Cape Cod caused declines in native macrophyte beds. In Wisconsin, eutrophication of northern, oligotrophic systems and increased human movement among lakes has allowed many adventive macrophytes to expand their geographic range or abundance within that ecoregion (Nichols 1994); both curly-leaf pondweed and Eurasian watermilfoil are often associated with elevated nutrient levels (Nichols and Shaw 1986).

HUMAN IMPACTS ON AQUATIC MACROPHYTES

Aquatic plants can be affected by anthropogenic perturbations at different scales and locations including watershed (e.g., agricultural and urban) development, riparian development, and the direct removal of plants (e.g., near-shore effects) (Nichols and Lathrop 1994, Radomski and Goeman 2001, Egertson *et al.* 2004). Watershed development in Wisconsin largely can be categorized as conversion of native prairies and forests into agricultural or urban land uses (Omernik *et al.* 2000). Agriculture is widely known to negatively impact aquatic plant communities (Carpenter *et al.* 1998, Lougheed *et al.* 2001, Egertson *et al.* 2004). And as urban land uses encroach upon the shoreline interface of lakes, the effects of recreation and directly removing the plants also may cause declines in macrophyte communities (Liddle and Scorgie 1980).

Agricultural runoff is often blamed for much of the eutrophication in Midwestern U.S. water bodies (Smith *et al.* 1987, Crosbie and Chow-Frasier 1999, Egertson *et al.* 2004). Nutrient runoff can come from manure seepage (Sharpley and Moyer 2000) as well as field cultivation (Egertson *et al.* 2004). For example, Sharpley and Moyer (2000) tested the differences between the amount of nutrient runoff from manure versus compost, and found that phosphorous leachate from manure was 14-40 mg/L greater than that from compost. In addition, Sharpley and Moyer (2000) also found that 58% of the phosphorous in manure spread on fields is washed away by the first rainfall.

Declines in water quality can often be linked to increased nutrient inputs from agricultural practices (Carpenter *et al.* 1998, Bennett *et al.* 2001). Crosbie and Chow-Frasier (1999) found that nutrient loading in 22 marshes of the Great Lakes Region was attributed to agricultural development. Agricultural eutrophication of an Iowa lake that had previously oscillated between turbid and clear-water stable states may have contributed to a shift in the macrophyte community from a primarily submergent community to an emergent-dominated community (Egertson *et al.* 2004). Yet, as Wisconsin is progressively changing from an agriculturally-dominated landscape to more urban land use, macrophyte community changes are also being attributed to urban effects.

Urban development has been linked to eutrophication of water bodies worldwide (Carpenter *et al.* 1998, Sand-Jensen *et al.* 2000, Bowen and Valiela 2001), and urban sources of nutrient input are more diverse than are sources from agriculture. A review by Carpenter *et al.* (1998) lists urban sources of nitrogen and phosphorous as wastewater runoff, leachate from waste disposal sites, storm sewer outfalls, overflows of sewers and runoff from construction sites, golf courses and lawns. And they state that non-point urban sources may be more substantial than point sources (i.e., sewage or effluent), accounting for over 80 percent of the nutrient input into some lakes (Carpenter *et al.* 1998). Whether from point or non-point sources, urban eutrophication clearly affects macrophyte communities. In New England, a significant increase in nitrogen runoff to Waquoit Bay from urban sprawl (Bowen and Valiela 2001) resulted in decline in eel grass stands (Hauxwell *et al.* 2003). Findlay and Houlahan (1997) related a decrease in species richness to urban development (measured by road density) in Ontario wetlands. And in 34 northern Wisconsin lakes, Jennings *et al.* (2003) found a significant negative relation between urban development in watersheds and abundance of submergent, floating-leaf and emergent macrophytes.

Problems associated with lakeshore (i.e., riparian) development are similar to those associated with general watershed development but also include additional problems such as septic leachate, lawn fertilizer runoff, shoreline interface modifications (e.g., rip rap or seawalls) and the direct removal of plants. Often lakeshores are developed before a watershed is urbanized, and the septic systems of residential housing along lakeshores can fail after a few years of use, leaching nitrogen and phosphorous into the lake (Dillon *et al.* 1994, Moore *et al.* 2003). And in effort to add that 'personal touch', many lake-side lawns are manicured, mowed and fertilized. This fertilizer provides a direct source of eutrophication (Woodard and Rock 1995, Carpenter *et al.* 1998).

In addition, lakeshore owners may modify the shoreline interface by adding rip-rap, seawalls, and docks and/or directly remove macrophytes from the littoral zone and along the shoreline (Engel and Pederson 1998, Jennings *et al.* 1999). Rip-rap and seawalls prevent the growth of near-shore species such as emergents and preatophytes (Engel and Pederson 1998). And Jennings *et al.* (1999) found that sites with man-made structures such as rip-rap or seawalls had fewer floating-leaf macrophytes than those without. Macrophytes are also indirectly affected by docks and piers; Garrison *et al.* (2005) documented a 10-fold reduction in light availability under docks and piers in Rock and Ripley Lakes, Wisconsin and a subsequent reduction in macrophyte growth. In Minnesota, Radomski and Goeman (2001) found a 66 percent decline in floating-leaf and emergent vegetation relative to lakeshore residential development. And, Jennings *et al.* (2003) found similar results in 34 Wisconsin lakes.

In addition to the coincidental loss of macrophytes due to human activity, riparian land owners and lake associations often directly remove plants. Aquatic plant management (often implemented in eutrophic lakes with dense macrophyte communities) may be one of the most significant sources of decline in native species and increase in invasive species within macrophyte communities (Murphy *et al.* 1987, Fox and Murphy 1990). Aquatic plant management can include hand removal, raking, biomanagement, mechanical harvesting, and chemical application of herbicides (Bode 1997). Management practices are often extremely effective for removing target species, but often also negatively affect other, often less offensive species. Research by Fox and Murphy (1990) suggested than applications of chemical herbicides target specific species and therefore have fewer negative effects that mechanical harvesting. Nevertheless, any type of plant removal creates disturbed areas that are prone to re-colonization more so by invasive species than by native plants (Murphy *et al.* 1987). A review by Liddle and Scorgie (1980) suggests that this is an area in need of more extensive research.

BIOINDICATORS

HISTORY

Biotic indices where first created using diatoms to statistically quantify levels of disturbance in rivers and streams of the Conestoga basin, Pennsylvania (Patrick and Strawbridge 1963). Patrick and Strawbridge (1963) found diatoms from undegraded rivers and streams did not vary when compared across similar water types, but changed as pollution in a system increased. From this, they were able to characterize the level of pollution occurring in running water. Since then, environmental quality has been assessed with biotic indices using a variety of organisms including invertebrates (Hilsenhoff 1982, Weigel *et al* 2002), fish (Karr 1981, Lyons *et al.* 2001), and aquatic macrophytes (Grasmuck *et al.* 1995, Nichols 1999a). Specifically in Wisconsin, Hilsenhoff (1982) established an index for stream quality using insects, amphipods and isopods. Lyons (1992) has done extensive work using fish to index warm water streams, cold water streams (Lyons *et al.* 1996) and large rivers (Lyons *et al.* 2001) of Wisconsin. And Nichols (1999a) has proposed the floristic quality index (FQI) for aquatic macrophytes in Wisconsin lakes, which is currently used to assess aquatic macrophyte communities and lake health.

Biotic indices use a system of metrics or measures that reflect environmental quality in the community structure or the morphology of surveyed organisms (Kohler and Schneider 2003). Because biotic organisms integrate effects from a suite of perturbations into their structure, morphology, or ecology, these organisms or communities often reflect the overall quality of the aquatic environment they inhabit. Biotic indices can also be used to gauge the ecological integrity of aquatic systems by comparing communities in perturbed systems to those in areas without environmental degradation (Karr and Chu 1999). For instance, Karr (1981) developed a biotic index using fish community composition to assess the integrity of water resources in Illinois by comparing fish communities in protected, un-dammed rivers to community composition in rivers with more degradation.

Biotic indices are useful because conducting a complete assessment of an ecosystem would be time-consuming and costly. It would require sampling many organisms including bacteria, invertebrates, fish, and plants as well as nutrient, metal and chemical measurements. While the results from a complete study would be very detailed, the amount of time and money required to conduct such an assessment is often not feasible for managers (Hilsenhoff 1982). Less time (and therefore less cost) is needed to conduct a survey using a biotic index than is needed for complete assessment, which makes the use of these indices attractive to managers (Bernthal 2003). Not only does using a biotic index save time and money, it also provides a standardized way to compare data across systems. Standardized sampling methods can be used to detect trends over time, thus allowing evaluation of restoration or management projects (Karr and Chu 1999). In addition to this, indices can also be applied to previously collected data for comparison and assessment of past and present surveys.

While many advantages to biological indices exist, like all scientific approaches, there are also weaknesses. The disadvantages of biotic indices are that they assess only one taxa or community type (e.g., fish are surveyed for an IBI but macrophytes are not), often lack validation, and may lack general applicability due to regional variation in community patterns or taxa distribution (Karr and Chu 1999). Because an index only requires a survey of one community type in an ecosystem, other effects of degradation may remain undetected. For example, Hatzenbeler *et al.* (2004) compared an index based on aquatic macrophytes and one based on fishes, and found that macrophytes were more sensitive to riparian development than fish. If only fish had been surveyed, the effects of development on macrophytes would not have been detected. Therefore, when using a biotic index, it is advantageous to be aware of the limitations of the index and its applicability to other biota.

Another problem concerning biotic indices that should be addressed is that communities vary regionally and spatially, so caution should be taken when comparing results across systems. In some regions, lakes may have naturally low numbers of macrophytes (e.g., dystrophic systems) which may give the impression that a system is degraded by human perturbations, when in fact it is healthy (Bernthal 2003). For example, Nichols (2000) found that in Franklin Lake, Wisconsin (an oligotrophic lake with a naturally low number of species), an increase in the number of macrophyte species caused a better floristic quality index (FQI) score, indicating better water quality; while in actuality, the increased number of species was due to anthropogenic-increased nutrient levels. Often, what aquatic macrophyte indices actually indicate is the trophic status of a system and therefore generalization of biotic index requires regional calibration (Tremp and Kohler 1995).

MACROPHYTES AS BIOINDICATORS

Nichols (2000) stated that a macrophyte index, if successful, could provide a tool to study ecological processes, especially long-term trends and changes in macrophyte communities and littoral zones. Macrophytes are suitable and desirable as bioindicators due to several factors: most aquatic plants are stationary and easily identified therefore they are easily surveyed (Small *et al.* 1996) and because individual plant species have different tolerance levels for various water chemistry attributes, macrophyte community structure can reflect long-term changes in the environment (Robach *et al.* 1996, Melzer 1999, Kohler and Schneider 2003). In Wisconsin lakes, Hatzenbeler *et al.* (2004) compared aquatic plants to fish in their ability to bioindicate, and found that in lakes less than 80 hectares, plant communities provided a more sensitive indication of riparian development (i.e., lake health) than do fish communities.

Macrophyte communities (i.e., guilds) may be better indicators than individual plant species. Seddon (1972) found that because tolerances of individual species vary and overlap, plants do not fall into specific groups, but rather represent a continuum over a gradient of environmental factors. This suggests that looking at whole community types may provide a better index for aquatic systems. Supporting this, Grasmuck *et al.* (1995) confirmed that only a few species were sensitive enough to indicate change (e.g., river water crowfoot (*Ranunculus fluitans*) and sago pondweed (*Stuckenia pectinata*)) but suggested five macrophyte community guilds that indicate the chemical and morphometrical characteristics of rivers in France. Also in France, Robach *et al.* (1996) found that macrophyte communities of acidic and alkaline waters shared some similar species, but plant communities in each lake type responded differently to eutrophication, resulting in different indicator guilds for acidic and alkaline waters. And using 100 Bavarian lakes, Melzer (1999) described nine macrophyte community types indicative of nutrient gradients across oligotrophic to eutrophic glacial lakes.

WISCONSIN LAKES

Shifts in macrophyte communities of Wisconsin lakes (loss of some species and invasions of others) have been documented by Nichols and Lathrop (1994, also Nichols 2000). Nichols and Lathrop (1994) attributed changes in the Yahara Lake chain, Madison, Wisconsin since the 1800's to anthropogenic perturbations. And Jennings *et al.* (2003) documented declines in floating leaf and emergent vegetation relative to shoreline development in 53 Wisconsin lakes. Assessment of how macrophyte communities change in Wisconsin lakes in response to development at the watershed, shoreline and near-shore levels will provide insight into the effects of human perturbation on lotic systems. In addition, learning how plant communities respond to perturbations in Wisconsin lakes will allow for better predictions of future change.

THESIS OVERVIEW

Aquatic macrophytes are dynamic and variable by nature. Changes in communities may be attributed to natural variation in ecosystems along chemical and nutrient gradients and to impacts from anthropogenic perturbations such as agricultural and urban development. This project attempts to address the response of aquatic macrophytes to development at watershed and riparian levels and the distribution of macrophytes as determined by tolerance levels of individual species to ecological gradients of water chemistry attributes. The thesis is structured into two chapters. The first chapter addresses the response of aquatic macrophytes to development in the watersheds and along the lakeshores of Wisconsin lakes. Regression analyses are used to determine the response of species richness and the relative occurrence of individual species to anthropogenic development: agriculture, urban and total development at the watershed scale and house density (houses/km of shoreline) at the riparian scale. The second chapter describes the distribution of aquatic macrophytes along ecological gradients. Regression analyses are used to determine the response of individual species relative occurrence to water chemistry attributes, and canonical correspondence analysis is used to determine community compositions along environmental gradients of water chemistry attributes.

OBJECTIVES

Chapter I: Relations between anthropogenic development and macrophyte communities

Knowing how human development affects aquatic macrophyte communities is essential to the management and protection of aquatic ecosystems. Macrophytes are only one piece of the ecosystem puzzle, and when they are degraded, many other habitats and fauna are affected as well. The ability to predict change in macrophyte communities as development increases will provide managers with insight on how to prepare for changes or to prevent degradation through regulation and smart development practices.

While the distribution and diversity of aquatic macrophytes are often surveyed and documented, changes in aquatic communities are not often linked to development pressures in the watersheds or along lakeshores. Quantifying this link in Wisconsin will define the effects of anthropogenic perturbations and thereby provide managers with grounds to regulate development.

Transect survey data were used to explore the relations between development and macrophyte community structure. Macrophyte and development data were collected from 53 Wisconsin lakes; 27 southeastern lakes and 26 northern lakes. These data were analyzed as northern and southeastern ecoregion subsets and with ecoregions combined for a statewide dataset. In addition, all three analyses were truncated to include only the first four near-shore quadrats (within 7 m from shore) to assess effects on just proximal land-water interface plant communities. Species that occurred ≥ 5 percent of the quadrats in each dataset were used in the respective analyses. Specifically the objective of chapter one was to determine what effects human perturbations at both the watershed and lakeshore levels have on aquatic macrophyte species richness and relative occurrence in Wisconsin lakes.

Chapter II: Environmental gradients and tolerance levels of individual macrophyte species

Apart from development pressures, distribution of individual macrophyte species is often determined by environmental factors specific to each particular lake. Lakes in

Wisconsin occur along a gradient such that northern lakes often have lower levels of alkalinity, conductivity, pH, calcium, magnesium, nitrogen and phosphorous. southeastern lakes occur at the other end of the spectrum; being more calcareous and more eutrophic. Each aquatic macrophyte species occurs in lakes along this gradient relative to its individual range of tolerance to the water chemistry attributes. Some plants are flexible, occurring in lakes along the entire gradient, while other species are tolerant to only a small range of high or low concentrations of water chemistry.

Analysis of species occurrence along environmental gradients of water chemistry attributes will provide insight into the classification of lakes using aquatic macrophytes and allow for determination of a lake's location along ecological gradients by surveying the macrophyte community. Identification of less tolerant species will provide a means to detect pristine vs. degraded lakes for bioindication. This research will supplement the floristic quality index (FQI) currently used in Wisconsin for aquatic plant community assessment (Nichols 1999a).

Transect survey data were used to explore occurrence of macrophytes in lakes along environmental gradients of water chemistry. Macrophyte and water chemistry data were collected from 53 Wisconsin lakes; 27 southeastern lakes and 26 northern lakes. Specifically the objective of chapter two was to quantify water chemistry attributes in selected Wisconsin lakes, assess the tolerance levels of individual macrophyte species growing within those lakes, and to determine relations of aquatic plant communities to environmental gradients across Wisconsin.

CHAPTER I:

THE RESPONSE OF AQUATIC MACROPHYTES TO HUMAN PERTURBATIONS IN THE WATERSHEDS AND ALONG LAKESHORES OF WISCONSIN LAKES

ABSTRACT. Development of watersheds and riparian areas has negatively affected aquatic biodiversity and ecosystem processes. In particular, changes to aquatic plant communities have been attributed to agricultural and urban development in watersheds, and direct removal of plants by riparian landowners. The objective of this study was to determine what effects human perturbations at both the watershed and lakeshore levels have on aquatic macrophyte species richness and relative occurrence in Wisconsin lakes. Macrophyte communities in 53 Wisconsin lakes were surveyed to determine species richness and occurrence in the littoral zone of each lake. To address regional variation, lakes from two different ecoregions were surveyed: the Northern Lakes and Forests ecoregion and the Southeastern Till Plains ecoregion. Within ecoregions, lakes were selected along a gradient of development ranging from undeveloped (i.e., forested), to agricultural, urban and total development at the watershed scale; and riparian house density at the lakeshore scale. Snorkel and SCUBA were used to survey aquatic macrophyte species in 18 $0.25m^2$ quadrats along 14 randomly placed transects in each lake. Effects of watershed development (e.g., agriculture and/or urban) and riparian residential development were tested at whole-lake (littoral zone) and near-shore scales using regression analyses. Overall, species richness was negatively related to watershed and riparian development, while individual species differed in level of response to different perturbations. In lakes with greater watershed development, exotic

macrophyte species, particularly *Myriophyllum spicatum,* increased in abundance and native species, especially *Potamogeton* spp., basal species, and floating-leaf plants declined. In lakes with increased riparian development, reductions were seen in floating-leaf plants such as *Potamogeton* spp. and lily pads (i.e., *Nuphar* spp., *Nymphaea* spp., *Brasenia schreberi*), and specifically in northern lakes, basal species also declined. In general, aquatic macrophyte communities were negatively affected by development in watersheds and along lake shorelines in Wisconsin lakes with specific taxa affected differently. Further management, such as protection of undeveloped shorelines and reductions in aquatic plant removal, is needed to protect and maintain healthy macrophyte communities.

INTRODUCTION

Increasing watershed development, including agricultural and urban land uses, has been linked to many changes observed in aquatic ecosystems (Crosbie and Chow-Frasier 1999, Egertson *et al.* 2004). Runoff from agricultural land use is often a cause of cultural eutrophication of water bodies, and has been linked to a decline in submersed aquatic plants and shifts in aquatic macrophyte communities toward predominately floating-leaf and emergent species (Chambers 1987, Egertson *et al.* 2004). Crosbie and Chow-Frasier (1999) also found similar declines in aquatic macrophyte occurrence in 22 marshes of the Great Lakes ecoregion and related this to excess nutrient loading from agricultural land use.

Urban development has also been implicated in changes to aquatic macrophytes in water bodies world-wide (Crowder *et al.* 1996, Findlay and Houlahan 1997, Hauxwell and Valiela 2004). Findlay and Houlahan (1997) linked declines in aquatic macrophyte species richness to roads bisecting Ontario wetlands, and Hauxwell *et al.* (2003) linked loss of *Zostera marina* in Cape Cod to anthropogenic nitrogen loading. Urbanization may affect water bodies more than agriculture because impervious surfaces (i.e., roads, parking lots, and rooftops) do not allow precipitation to soak into the ground; therefore unfiltered runoff is transported directly to water bodies at a faster pace (Wang *et al.* 2003).

In addition to effects of overall watershed development on macrophyte communities, riparian development can also affect macrophyte communities more directly (Radomski and Goeman 2001, Jennings *et al.* 2003, Moore *et al.* 2003, Hatzenbeler *et al.* 2004). In Minnesota lakes, Radomski and Goeman (2001) found a

66% decline in floating-leaf and emergent macrophyte cover along developed shorelines relative to undeveloped shorelines. Jennings *et al.* (2003) surveyed 34 Wisconsin lakes and found a 20% decline in emergent and floating-leaf vegetation where a building (i.e., house or cottage) was present on shore and an overall negative correlation between macrophyte abundance and house density. In addition, Jennings *et al.* (1999) found sites with man-made structures such as rip-rap or seawalls had fewer floating-leaf macrophytes in the adjacent littoral zone. Hatzenbeler *et al.* (2004) found a linear decrease in species richness with increasing shoreline development in 16 northern Wisconsin lakes. Finally, Garrison *et al.* (2005) documented a 10-fold reduction in light availability under docks in Rock and Ripley Lakes, Wisconsin and a subsequent reduction in macrophyte growth in these areas.

The state of Wisconsin has considerable land use perturbations and associated impacts to aquatic plant communities. Impacts on Wisconsin lakes include agricultural land uses such as dairy farming and row cropping, and urban developments in the watersheds and along the shorelines of most lakes in the state. Nichols and Lathrop (1994) have attributed entire community shifts in lakes near Madison, Wisconsin, to cultural impacts, stating that the original vegetation in Lake Wingra was destroyed as early as the 1920's. Original macrophyte communities were also lost from Lake Waubesa by the 1930's and from Lakes Mendota and Monona by the 1950's. The objective of this study was to determine what effects human perturbations at both the watershed and lakeshore levels have on aquatic macrophyte species richness and relative occurrence in Wisconsin lakes.

STUDY AREA

Fifty-three lakes in two ecoregions of Wisconsin: 26 in the Southeastern Wisconsin Till Plain ecoregion (herein referred to as the southeastern ecoregion) and 27 in the Northern Lakes and Forests ecoregion (herein referred to as the northern ecoregion), were sampled to assess effects of development on macrophyte communities (Figure 1, Appendix A) (Omernik *et al.* 2000). Two lakes fell just outside the border of the southeastern ecoregion, but were sampled to increase the number of sampled lakes in this area and because conditions were similar to lakes in the southeastern ecoregion. The Northern Lakes and Forests ecoregion provided an area with lakes having lower nutrient levels, while the Southeastern Wisconsin Till Plain ecoregion provided lakes with higher nutrient and bicarbonate concentrations (Omernik *et al.* 2000). Both areas had lakes that varied along limnological and development gradients for assessing anthropogenic effects. Selected lakes ranged in surface area from 20-136 ha with watersheds ranging from 27-2,200 ha (Table 1, Appendix B). All lakes had a maximum depth of 5.5 m or greater, with the exception of Silver Lake in Vilas County, and Person Lake in Douglas County, Wisconsin, which were 3.7 m and 3.1 m deep, respectively.

Selected lakes spanned a continuum of development ranging from a completely undeveloped watershed and shoreline, to a watershed over 97% developed and a lakeshore with 42 houses per km of shoreline (Table 1). Overall, lakes in the northern ecoregion were less developed than southeastern lakes at both the watershed and riparian levels. Several lakes in the northern ecoregion and two lakes in the southeastern ecoregion had no agricultural development in the watershed, yet most lakes had at least some urban and riparian development (Appendix B). Lawrence Lake in Langlade

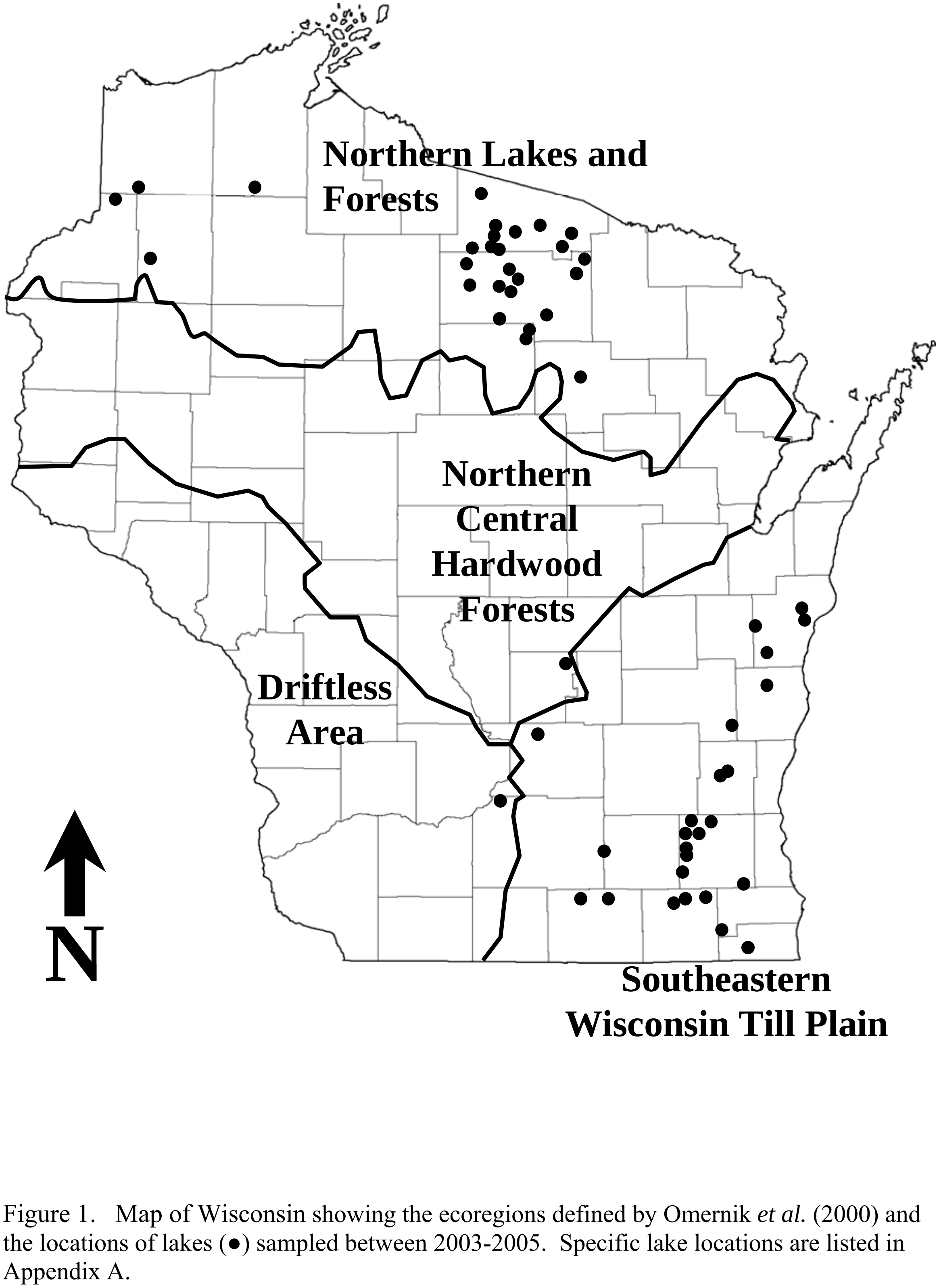

Figure 1. Map of Wisconsin showing the ecoregions defined by Omernik *et al.* (2000) and the locations of lakes (●) sampled between 2003-2005. Specific lake locations are listed in Appendix A.

Table 1. Mean, standard error (S. E.) about the mean, and range of lake characteristics for the 53 Wisconsin study lakes (26 southeastern and 27 northern). Variable descriptions are listed in Appendix K. Bold values represent variables that were significantly different between ecoregions (Mann-Whitney U-test).

	Southeastern Ecoregion		Northern Ecoregion			
Variable	Mean (±S.E.)	Range	Mean (±S.E.)	Range	U-stat	P
			General			
Lake area (hectares)	**46.2 (4.48)**	**19.4-99.3**	**67.0 (6.63)**	**20.3-136.4**	**467.0**	**0.018**
Max depth of lake (m)	12.0 (0.93)	6.1-27.4	9.4 (0.94)	3.1-21.6	236.5	0.063
Watershed area (hectares)	**259.6 (41.10)**	**27.1-942.7**	**570.9 (98.21)**	**58.8-2205.3**	**495.0**	**0.004**
Watershed area : Lake area	5.9 (0.88)	0.7-20.1	11.2 (2.72)	1.8-64.3	395.0	0.297
Lake perimeter (km)	**3.3 (0.28)**	**1.5-8.5**	**4.7 (0.32)**	**2.2-7.7**	**514.0**	**0.001**
			Development			
Agriculture development (proportion of watershed)	**31.6 (4.79)**	**0.0-73.4**	**3.6 (0.96)**	**0.0-15.6**	**68.5**	**<0.001**
Urban development (proportion of watershed)	**31.6 (4.23)**	**0.0-81.9**	**12.5 (2.45)**	**0.0-62.3**	**140.0**	**<0.001**
Total development (proportion of watershed)	**63.2 (3.86)**	**15.1-97.4**	**16.1 (2.75)**	**0.0-62.3**	**23.0**	**<0.001**
House density (# Houses/Lake perimeter)	**23.0 (2.07)**	**2.9-42.0**	**12.8 (1.07)**	**0.0-22.8**	**154.0**	**0.001**
Number of houses	75 (8.7)	6-203	58 (6.0)	0-107	286.5	0.251

Table 1 (continued). Mean, standard error (S. E.) about the mean, and range of lake characteristics for the 53 Wisconsin study lakes (26 southeastern and 27 northern). Variable descriptions are listed in Appendix K. Bold values represent variables that were significantly different between ecoregions (Mann-Whitney U-test).

	Southeastern Ecoregion		Northern Ecoregion			
Variable	Mean (±S.E.)	Range	Mean (±S.E.)	Range	U-stat	P
			Water Chemistry			
Alkalinity (mg/L)	**141.7 (6.88)**	**58-203**	**29.6 (3.06)**	**4-64**	**1.0**	**<0.001**
Conductivity (µmhos/cm)	**388.3 (24.38)**	**125-647**	**83.0 (9.13)**	**14-179**	**5.0**	**<0.001**
pH (Su)	**8.70 (0.05)**	**8.09-9.23**	**7.75 (0.11)**	**6.45-8.61**	**38.0**	**<0.001**
Calcium (mg/L)	**26.57 (1.26)**	**13.1-40.1**	**8.11 (0.92)**	**1.3-18.0**	**10.0**	**<0.001**
Magnesium (mg/L)	**25.47 (1.74)**	**6.9-41.1**	**2.8 (0.30)**	**0.4-7.6**	**2.0**	**<0.001**
Chlorophyll-*a* (mg/L)	5.72 (0.89)	2.11-20.70	6.41 (1.23)	1.12-26.91	326.0	0.656
Color (units)	**7.8 (0.88)**	**5-20**	**12.5 (1.39)**	**5-30**	**516.0**	**0.002**
Secchi (m)	2.72 (0.21)	1.20-5.03	2.42 (0.18)	0.91-3.81	302.0	0.383
Total Phosphorous (mg/L)	0.029 (0.005)	0.006-0.141	0.019 (0.002)	0.006-0.071	589.0	0.068
Total Nitrogen (mg/L)	**0.98 (0.06)**	**0.56-1.63**	**0.52 (0.03)**	**0.32-1.06**	**398.5**	**<0.001**

County, Wisconsin (northern ecoregion) was the only lake with no lakeshore or watershed development.

Lakes generally followed a latitudinal gradient statewide of increasing nutrient levels from north to south which parallels changes in geology from silica based granitic soils in the north to calcareous based soils in the south. Northern lakes on average had much lower alkalinity, calcium, and magnesium concentrations and lower conductivity and pH levels than southeastern lakes (Table 1, Appendix B).

METHODS

Macrophyte communities from 53 Wisconsin lakes were surveyed from June to early September over a span of three years (2003-2005); each lake was sampled only once. Within each lake, macrophytes were sampled at fourteen random-stratified sites (Appendix C). Development type (i.e., developed or undeveloped) was used as the strata; seven developed and seven undeveloped (natural) sites were chosen. Developed sites were defined as sections of shoreline at least 30 m wide that had a house within 50 m of the shoreline interface. Undeveloped sites were defined as sections of shoreline at least 50 m wide with no visible human influences. Human influences were defined as any building, structure, dock, boat, or landscape manicuring. In instances where a lake did not have either seven developed or natural sites, more of the non-limiting sites were chosen *in situ* so that 14 total sites were still sampled (Appendix C).

Certain areas of lakes were intentionally avoided. Obvious wetlands (i.e., extensive monotypic cattail beds or bog mats) were omitted from sampling during this study because wetlands were not considered land directly available for development and thus less likely subjected to the perturbations assessed. Moreover, wetlands had a different plant community composition than more hard-bottomed sites; this helped standardize comparisons across lakes. In this study, wetlands were defined as sites with a slope near zero and vegetation usually composed of either an extensive bed of emergent species or bog mats. Public beaches and mowed parks were also not sampled because these areas did not fit the criteria of developed (house within 50 m) or undeveloped (no perturbation), and were most likely subjected to active plant management activities which was beyond the scope of this study.

A transect was placed at the center of each site and set perpendicular to shore, out to a distance of 45 m. Snorkeling and SCUBA were used to assess plants found in 0.25 m^2 quadrats along the transect. Quadrats were placed every 2 m for the first 12 m of the transect from shore and then every 3 m to 45 m thereafter (Appendix D). Species richness was calculated as the total number of aquatic macrophyte species observed in the littoral zone of each lake. Relative occurrence was calculated as the number of quadrats in which a particular species occurred, divided by the total number of quadrats sampled in the littoral zone of that lake (Appendix E). Individual species were also grouped into guilds (Appendices F and G). Relative occurrence for each guild was calculated as the number of quadrats in which any species included in the respective guild occurred divided by the total number of quadrats in the littoral zone of that lake (Appendix H). Each quadrat was counted only once regardless of the number of species occurring in that quadrat, and quadrats that fell beyond the maximum depth of plant growth were not included in the total number of quadrats in the littoral zone (if a quadrat in the littoral zone had zero plant growth, it was included in the calculation of relative occurrence).

Macrophyte data were assessed using all quadrats in the littoral zone for whole-lake effects on the entire plant community and also using only the first four, near-shore quadrats for effects of development on species growing near shore. The first four quadrats were chosen because they fall within the first 7 m from shore, which corresponds to the length of 90% of the docks observed in this study; areas likely to be directly affected by human disturbances.

Species richness and relative occurrences of species and guilds were analyzed using simple and multiple regression to test for relations between terrestrial development and aquatic plant metrics. Species richness was used to determine the effects of development on the diversity of plants communities (species richness) across lakes, whereas relative occurrence of individual species was used to determine effects on specific plants. While only species occurring in ≥ 5 % of the quadrats were used in individual species analyses, all species were considered for guilds and species richness analyses. Guilds were used because they represent functional groupings of plants. Many species were not present at high relative occurrences, which is also not conducive to robust regression analyses. Therefore, combining species into guilds increased the likelihood of having taxonomic or functional representatives in every lake and also provided insight into effects of development types on specific groups of species. A total of nine guilds were analyzed: seven guilds were chosen based on plant morphology, one on taxonomy (*Potamogeton* spp.) and one on ecological invasiveness (exotic species) (Appendix F). Morphological guilds were created to determine how plant morphology affects a plant's susceptibility to specific types of perturbation such as direct removal of plants. Species were included in multiple guilds if they fit the criteria of more than one guild (Appendix G). The exotic species guild was not analyzed in regression analyses of the northern ecoregion data subset because representative species of that guild occurred in only 3 of the 26 lakes.

The effects of human perturbations were analyzed at watershed and lakeshore levels. Watershed level perturbations were analyzed as a particular land use occurring as a proportion of the total watershed area. Proportion of agricultural, urban, and total (ag + urban combined) land uses within each watershed were determined using the most current (yrs)1:12,000 digital orthophotography images (obtained through the University of Wisconsin-Stevens Point Advanced Computer Lab) in Arc View 3.x (ESRI 2003) (Appendix I). Aerial surveys were taken at different dates from 1986-2001 (Appendix J). Lakeshore-level perturbations were measured as the number of houses per km of shoreline for the entire perimeter of the lake (house density).

Statistical analyses were performed with SPSS 14.0 for Windows (SPSS Inc. 2005). To test the assumption of normality, Shapiro-Wilk tests were run on all independent (Appendix K) and dependent (Appendices E and H) variables. Transformations ($\log_{10}$, $\log_e$, and square root) were done on all variables and were usually unsuccessful in attempts to better normalize residual error in regression analyses. All independent variables were compared by ecoregion using the non-parametric Mann-Whitney U-test, as well as a selected number of species (Appendix E) and all guilds (Appendix K). In addition, species and guilds in northern and southeastern ecoregion near-shore data subsets were also compared (Appendix L and M, respectively).

In regression analyses, northern and southeastern ecoregions were analyzed separately and combined (i.e., statewide). Because the characteristics of lakes in both ecoregions were fundamentally different (e.g., different water chemistry and levels of development) and the occurrence of species was also different, species and communities had the potential to exhibit different regional responses to perturbations. Therefore, ecoregions were analyzed separately to examine whether species relative occurrence and community composition were affected by regional differences. And while the levels of many limnological features were significantly different between northern and southeastern ecoregions, lakes occurred along ecological and development gradients across the two ecoregions. Lakes in the northern and southeastern ecoregions represented opposite ends of the gradient; for that reason the data were combined to determine the response of species richness and individual species to perturbations along this gradient. Only species occurring in 5% or more of the total quadrats within an ecoregion were analyzed individually. But very few species occurred in $\geq 5\%$ of the quadrats of both ecoregions; therefore criteria for including species in the statewide analyses were set at occurrence in $\geq 5\%$ of the quadrats in at least one of the ecoregions (Table 2, Appendix E).

Simple linear and multiple regression were used to assess relations between macrophytes (species and guilds) and independent development variables (Appendix K):

$$y = mx + b$$

where:
y = dependent variable (macrophyte or guild)
x = independent variable (development variable)
b = intercept
m = parameter estimate

Alpha was considered significant at $P \leq 0.05$. Variables were transformed using $\log_{10}$, ln, and square root and evaluated to assess improvement in linearity and normalize residual error.

Table 2. Relative occurrences of aquatic macrophyte species used directly as dependent variables in regression analyses. Species were included in north and southeastern ecoregion analyses if they occurred in ≥ 5% of the quadrats (dash if not included) in the lakes sampled in the respective ecoregion. Species for the statewide analyses (marked by an X) occurred in ≥ 5% of the quadrats in at least one ecoregion. A relative occurrence is not listed in both ecoregions for all species used in the statewide analyses because species were chosen based on occurrence in both regions (not just combined occurrence). Bold indicates species were also used in the near-shore analyses (not all species were used because many did not occur ≥ 5% of the respective near-shore quadrats). Mean, standard error (S. E.) about the mean, and range for species in the littoral zone and near shore are listed in Appendices E and L, respectively.

	Regions Combined	Northern Ecoregion	Southeastern Ecoregion
Brasenia schreberi	-	0.05	-
Ceratophyllum demersum	X	0.07	**0.14**
Chara spp.	**X**	**0.12**	**0.50**
Elatine minima	-	**0.09**	**-**
Eleocharis acicularis	-	**0.14**	**-**
Elodea canadensis	X	0.18	**-**
Isoetes spp.	-	**0.16**	**-**
Juncus pelocarpus	-	**0.12**	**-**
Lemna trisulca	-	**-**	**0.05**
Lobelia dortmanna	-	**0.05**	-
Myriophyllum sibiricum	X	0.06	**0.08**
Myriophyllum spicatum	-	-	**0.26**
Myriophyllum tenellum	-	**0.11**	-
Najas flexilis	**X**	**0.28**	**0.27**
Najas marina	-	-	0.07
Nitella spp.	-	0.06	-
Nymphaea spp.	X	-	**0.05**
Potamogeton amplifolius	X	0.08	-
Potamogeton gramineus	**X**	**0.13**	0.05
Potamogeton illinoensis	-	-	0.10
Potamogeton pusillus	-	0.05	-
Potamogeton richardsonii	-	0.05	-
Potamogeton robbinsii	-	0.18	-
Potamogeton spirillus	-	0.05	-
Potamogeton zosteriformis	X	0.07	-
Stuckenia pectinata	-	-	**0.10**
Vallisneria americana	**X**	**0.28**	**0.10**

In watershed analyses, multiple regression was used on dependent variables (species or guilds) that occurred in two or more significant simple regressions in the respective ecoregions (northern, southeastern, or regions combined). Two approaches were implemented using forward selection of multiple regression. First, all seven independent watershed variables (listed in Table 3) were considered in each multiple regression. In this approach, one transformation was chosen for each species/guild analyzed and was kept consistent for all variables in each respective multiple regression analysis. The transformation was chosen based on which simple regression (including the dependent variable and urban, agriculture or total development as the independent variable) had the highest r^2 and best distribution of error. The second approach included only the independent variables that were significantly related to the dependent variable in the univariate regression analyses. In this approach, the best original transformation (i.e., the transformation of the univariate regression with the highest r^2) of each reported univariate regression (of the dependant variable v. the independent variable) was kept for each respective independent variable, with the exception of the watershed development variables. Because the watershed variables are comparable (i.e., have the same units), the transformation was kept consistent for these variables in each analysis: the transformation of the watershed development regression (i.e., dependent v. agriculture, urban or total development) with the highest r^2 was used for all watershed development variables in the respective multiple regression. This transformation was also used for the dependent variable. Akaike information criteria (AIC) weights were considered but due to the absence of competing multiple regression models found, not reported.

Table 3. Independent watershed level variables used in multiple regression analyses.

Variable	Description
Lake area	Surface area of the lake (ha)
Watershed area	Area of watershed (ha)
Watershed area : Lake area	Ratio of watershed area to lake area
Lake perimeter	Perimeter of shoreline around the lake (km)
Agriculture development	Proportion of the total watershed area in Agriculture: corn, forage crops, primary row crops, other row crops, and cranberry bog (Appendix I)
Urban development	Proportion of the total watershed area in Urban/developed: high and low intensity (Appendix I)
Total development	Agricultural and urban development summed

RESULTS

WATERSHED AND LAKESHORE DEVELOPMENT

Lakes and their corresponding watersheds were slightly larger in the northern ecoregion, whereas development (both urban and agriculture) was higher in southeastern watersheds (Table 1). Agricultural land use was low in northern watersheds, ranging from 0-16% (Appendix N), and much higher in the south, ranging from 0-73% of any watersheds (Appendix O). Urban development was more extensive than agricultural land in watersheds of both ecoregions; ranging from 0-6l% and 3-82% in northern and southeastern watersheds, respectively. And, agricultural and urban development combined (total development) ranged from 0-62% in northern watersheds and 15-97% in southeastern watersheds. Riparian development, expressed as house density (houses/km of shoreline), was much lower for northern lakes than southeastern lakes, ranging from 0-23 houses/km of shoreline and 3-42 houses/km, respectively (Table 1).

MACROPHYTE DISTRIBUTION

Species richness and relative occurrence of aquatic macrophytes varied between ecoregions. Northern lakes possessed greater species richness than southeastern lakes; on average, 27 species occurred per lake in the northern ecoregion, while southeastern lakes averaged 18 species per lake (Table 4). Overall, 103 macrophyte species were recorded in the 53 lakes sampled; 91 species were found in the northern lakes and 71 species in the southeastern lakes. Greater species richness was observed in the northern lakes, but relative occurrence (i.e., plant abundance) was lower on average for plants in lakes of this ecoregion, compared to the southeastern ecoregion.

Table 4. Mean, standard error (S.E.) about the mean, and range of macrophyte characteristics observed from the 53 Wisconsin study lakes (26 southeastern and 27 northern) sampled. Relative occurrence is the number of quadrats in which a plant occurred divided by the total number of quadrats in the littoral zone (quadrats past the maximum depth of plant growth were not included in analyses). Bold values represent variables that were found to be significantly different between regions (Mann-Whitney U-test).

	Southeastern Ecoregion		Northern Ecoregion			
Variable	Mean (±S.E.)	Range	Mean (±S.E.)	Range	U-stat	P
Species richness	**17.9 (1.18)**	5-27	**27.6 (1.54)**	9-47	586.0	<0.001
Total relative occurrence	**0.99 (0.00)**	0.92-1.00	**0.86 (0.02)**	0.52-0.99	9.0	<0.001
Maximum depth of plant growth (m)	5.34 (0.37)	2.4-9.2	4.29 (0.19)	2.5-6.5	236.5	0.063

Many individual species occurred in both ecoregions, but at often at different abundance levels (Appendix E). While many plants occurred in both ecoregions at different abundances, only 21 species occurred in ≥ 5% of northern quadrats and 12 species in ≥ 5% of the southeastern quadrats (Table 2, Appendix E). In northern lakes, species such as *Potamogeton robbinsii, Isoetes* spp., and *Juncus pelocarpus* were more common in occurrence, whereas in southern lakes, *Myriophyllum spicatum, Stuckenia pectinata*, and *Potamogeton illinoensis* occurred more often. Overall, the most commonly occurring species observed statewide were *Chara* spp., *Najas flexilis, Vallisneria americana,* and *Ceratophyllum demersum* (Appendix E). Most aquatic plants observed were native to Wisconsin with the exception of *M. spicatum, Lythrum salicaria, Phalaris arundinacea,* and *Potamogeton crispus* (Nichols 1999b). Exotic species also occurred more often in southeastern lakes than in northern lakes; only three lakes were found with exotic species (*M. spicatum*) in the northern ecoregion.

When only the first four near-shore quadrats of each lake were examined, the number of species that occurred ≥ 5% of the total quadrats of each region was fewer than the number used in the whole lake analyses (Table 2, Appendix L). In the northern analyses, 10 species occurred in ≥ 5% of the near-shore quadrats, and in the southeastern analyses, 9 species were found ≥ 5% relative occurrence. In addition, only 4 of the 10 species that had been included in the combined whole-lake analysis occurred at abundances high enough to be analyzed near shore. Though it did not occur in ≥ 5% of the quadrats at the whole-lake scale, *Eriocaulon aquaticum* in the northern ecoregion did occur in ≥ 5% of the near-shore quadrats; therefore it was also included in northern lakes near-shore analyses. In general, small, basal-growing species were higher in relative occurrence and larger, leafy species were found less often near shore than in the whole littoral zone of a lake.

Guilds included in the near-shore analyses were found at relative occurrences similar to the general distributions of the aquatic macrophytes included in each guild (Appendix M). For example, plants expected to grow near shore and in shallower water, such as emergents and floating-leaf plants with no roots (FL_NRT) were generally found at higher occurrences in the near-shore analyses relative to the whole-lake analyses in both ecoregions. In contrast to this, plants with the tendency or ability to grow in deeper water, such as the exotic species guild, *Potamogeton* spp., suspended species (NFL_NRT), and rooted plants without floating leaves (NFL_RT), were found at lower occurrences in the near-shore analyses relative to the whole-lake analyses in both ecoregions. Three guilds were not found at similar occurrences in both regions. The lily pad and rooted plants with floating leaves (FL_RT) guilds were found at higher occurrences near shore in the south, but at lower occurrences near shore in the north; while near-shore basal species occurrence was lower in the south and higher in the north.

MACROPHYTE RESPONSE

EFFECT OF WATERSHED DEVELOPMENT

As watershed development increased, species richness declined at both the whole-lake and near-shore scales of analyses. Statewide, at the whole-lake scale, the degree of total development (agriculture + urban) in the watershed was negatively correlated with macrophyte species richness (Figure 2): separately, agriculture land use (Figure 3) was more related to a decline in species richness than urban land use (Figure 4). But while

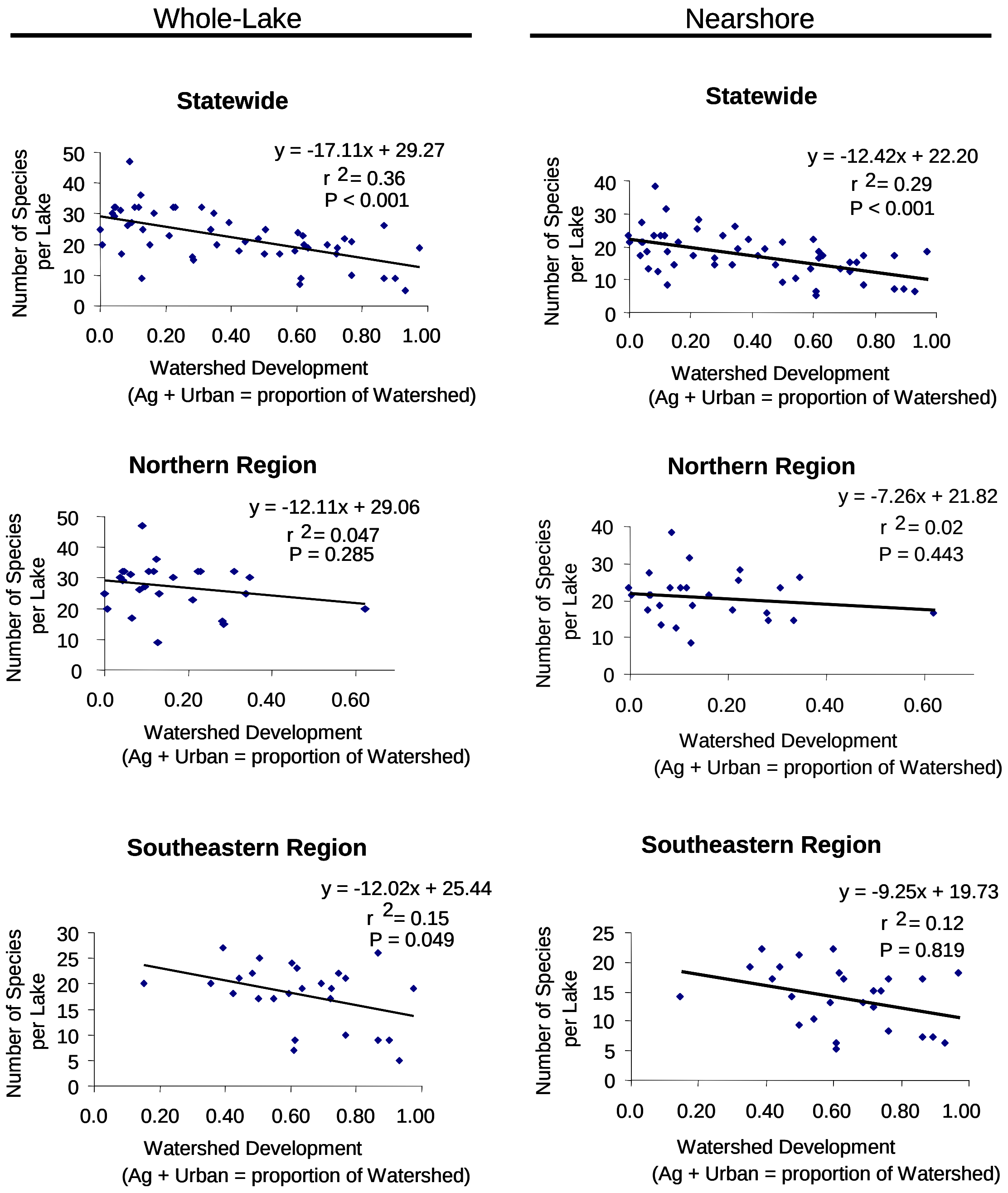

Figure 2. Linear regression models of species richness response to watershed development (agriculture + urban). Species richness is defined by the number of species found in a lake. The figure is organized such that the response of species richness in the entire lake is listed in the left-hand column, and the response of species richness in only the near-shore quadrats is listed in the right-hand column. Data in all regressions are not transformed. Models contain all species present in each lake.

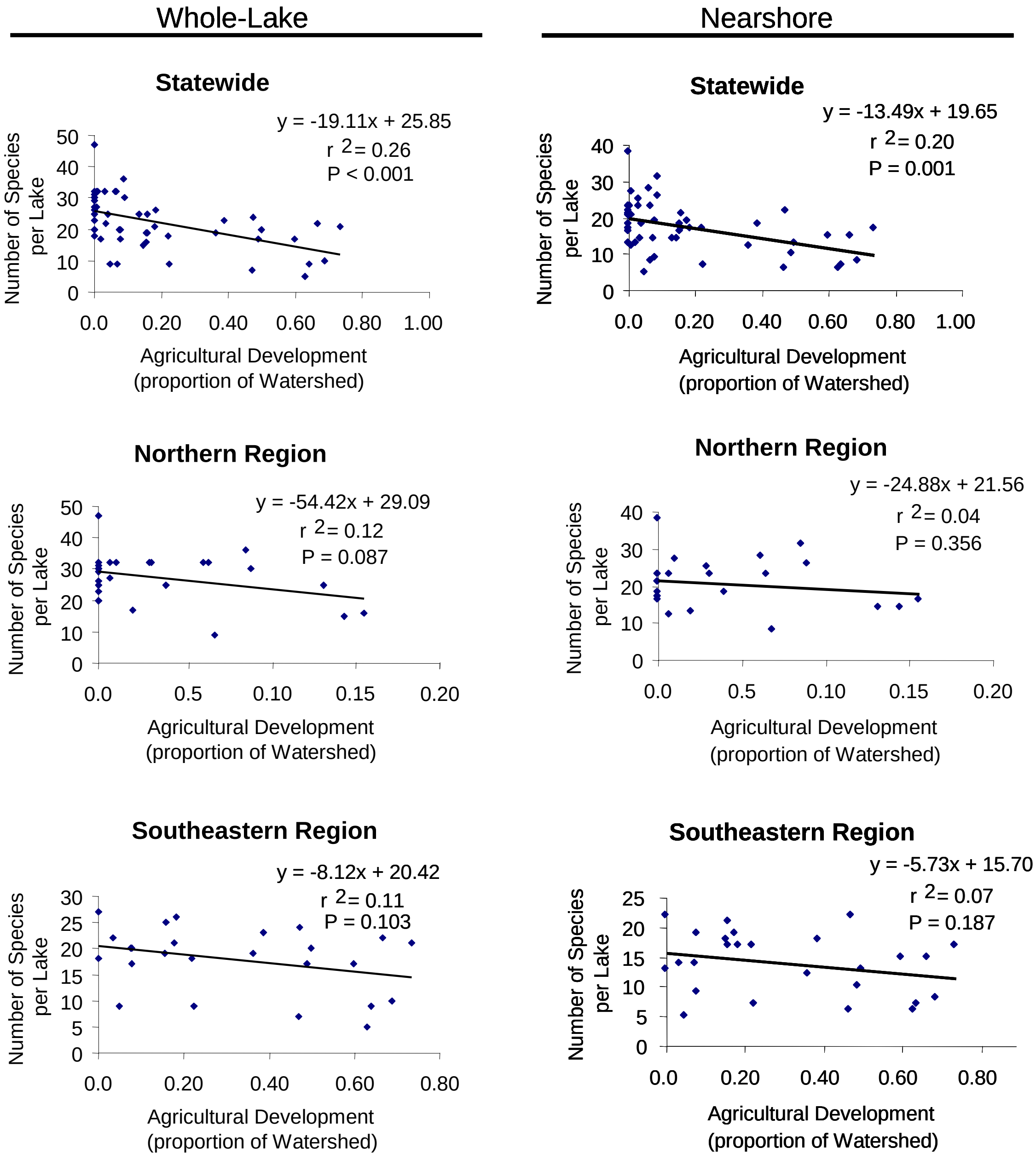

Figure 3. Linear regression models of species richness response to agricultural development. Species richness is defined by the number of species found in a lake. The figure is organized such that the response of species richness in the entire lake is listed in the left-hand column, and the response of species richness in only the near-shore quadrats is listed in the right-hand column. Data in all regressions are not transformed. Models contain all species present in each lake.

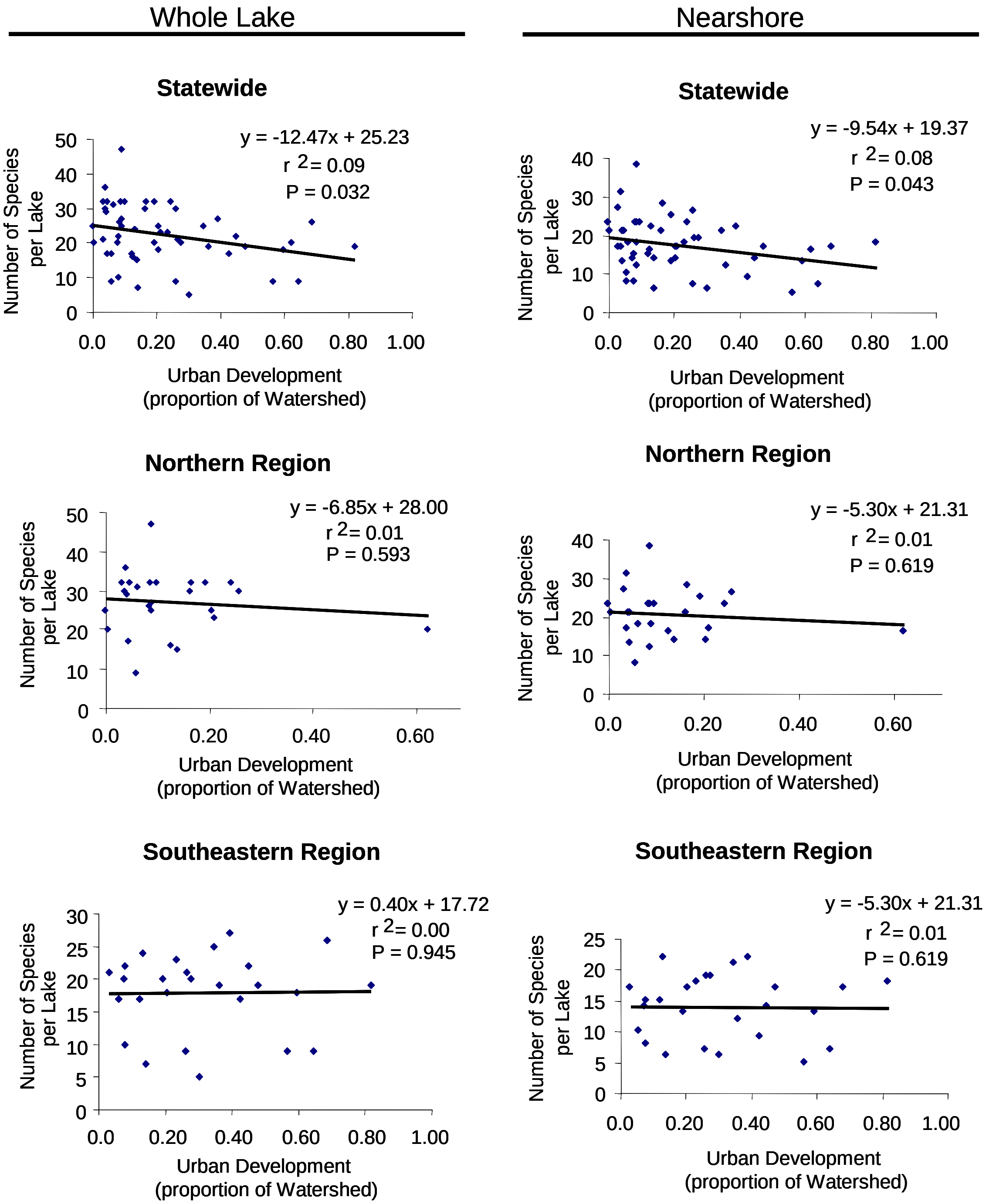

Figure 4. Linear regression models of species richness response to urban development. Species richness is defined by the number of species found in a lake. The figure is organized such that the response of species richness in the entire lake is listed in the left-hand column, and the response of species richness in only the near-shore quadrats is listed in the right-hand column. Data in all regressions are not transformed. Models contain all species present in each lake.

agricultural land use was more related to species richness decline than urban development in the statewide analysis, when regions were separated, relations between species richness and agriculture were not significant. The relation of species richness to total watershed development was significant in the southeastern ecoregion analysis when ecoregions were separated, but the relation was not significant in northern lakes. In general, relations of species richness to development in the near-shore analyses mirrored the relations found with the whole-lake analyses (Appendix Q).

When relative occurrence of individual species and guilds were considered, urban development did not affect plants as much as agricultural development or urban and agricultural development combined. Only 2 of 10 species analyzed responded significantly to urban development: *Chara* spp. increased with urban development, while *Potamogeton amplifolius* declined (Table 5, Appendix P). Four of the nine guilds were also significantly related to urban development in regions combined: exotic species increased, while lily pads, basal species, and floating-leaf, rooted species (FL_RT) declined with increasing urban development (Appendix P). When ecoregions were analyzed separately, two of the 21 species and one guild responded to urban development in northern lakes and only *C. demersum* was related to urban development in southeastern lakes.

When near-shore analyses were conducted, fewer relations between urban development and species or guilds were significant compared to the whole-lake analyses. Statewide (regions combined), the positive relation of urban development and *Chara* spp. remained significant, and the negative correlation of urban land use with basal species had a higher coefficient of determination, but the increase in exotic species was lower

Table 5. Significant relations between the level of watershed development and macrophyte species and guilds at the whole-lake scale. Macrophyte species are indicated by bold italics; guilds are not. Guilds are defined in Appendix F. Alpha was considered significant at P ≤ 0.05. Regression equations are listed in Appendix P.

Region	Macrophyte Species	r^2	P
	Proportion Urban Development		
Regions Combined	***Chara* spp.**	0.16	0.003
	Potamogeton amplifolius	-0.08	0.038
	Exotic Species	0.13	0.008
	Lily Pads	-0.17	0.003
	Basal Species	-0.16	0.004
	FL_RT	-0.12	0.013
Northern Ecoregion	***Myriophyllum tenellum***	0.21	0.018
	Brasenia schreberi	-0.15	0.050
	Lily pads	-0.17	0.036
Southeastern Ecoregion	***Ceratophyllum demersum***	-0.17	0.036
	Proportion Agricultural Development		
Regions Combined	***Ceratophyllum demersum***	0.17	0.002
	***Chara* spp.**	0.11	0.018
	Elodea canadensis	-0.26	<0.001
	Potamogeton amplifolius	-0.12	0.013
	Potamogeton gramineus	-0.17	0.003
	Vallisneria americana	-0.17	0.003
	FL_NRT	0.12	0.014
	Exotic Species	0.41	<0.001
	NFL_NRT	0.20	0.001
	Potamogeton spp.	-0.14	0.006
	Basal Species	-0.38	<0.001
	FL_RT	-0.12	0.010
Northern Ecoregion	***Elodea canadensis***	-0.17	0.038
	***Nitella* spp.**	-0.17	0.039
Southeastern Ecoregion	***Ceratophyllum demersum***	0.20	0.023
	Potamogeton gramineus	-0.15	0.050
	NFL_RT	0.21	0.022

Table 5 (continued). Significant relations between the level of watershed development and macrophyte species and guilds at the whole lake scale. Macrophyte species are indicated by bold italics; guilds are not. Guilds are defined in Appendix F. Alpha was considered significant at P ≤ 0.05. Regression equations are listed in Appendix P.

Region	Macrophyte Species	r^2	P
	Total Watershed Development (Agriculture + Urban)		
Regions Combined	***Chara* spp.**	0.26	<0.001
	Elodea canadensis	-0.21	0.001
	Potamogeton amplifolius	-0.17	0.002
	Potamogeton gramineus	-0.21	0.001
	Vallisneria americana	-0.12	0.011
	Exotic Species	0.48	<0.001
	NFL_NRT	0.27	<0.001
	Lily pads	-0.13	0.009
	Potamogeton spp.	-0.19	0.001
	Basal Species	-0.47	<0.001
	FL_RT	-0.20	0.001
Northern Ecoregion	***Myriophyllum tenellum***	0.23	0.012
	Lily pads	-0.20	0.024
Southeastern Ecoregion	***Potamogeton gramineus***	-0.18	0.031

than with the whole-lake analysis (Table 6, Appendix Q). When analyses were separated by ecoregion, no relations to urban development remained significant in northern lakes and only *C. demersum* remained related to urban land use in southeastern lakes; this relation had a higher coefficient of variation in the near-shore analyses.

While urban development was weakly related to species variables, agricultural land use affected many species and guilds. Six of the 10 species analyzed were significantly related to agricultural development at the statewide scale (Table 5, Appendix P). Of these six, only *C. demersum* and *Chara* spp. increased with increased agricultural land use; *Elodea canadensis, P. amplifolius, Potamogeton gramineus,* and *V. americana* were negatively affected. In addition, six of the nine guilds analyzed were also affected by agricultural land use; several groups of rooted species (including *Potamogeton* spp., basal species, and floating leaf, rooted (FL_RT) species) declined, but exotic species and non-rooted species (NFL_NRT and FL_NRT) increased when ecoregions were combined. When ecoregions were analyzed separately, two species in the north (*E. canadensis* and *Nitella* spp.) and one species in southeastern lakes (*P. gramineus*) declined with increased agriculture; only *C. demersum* in southeastern lakes increased. And while guilds in northern lakes showed no response; submersed, rooted species (NFL_RT) increased with agricultural development in southeastern lakes.

With near-shore analyses, the number individual macrophyte species related to agriculture was fewer than the number of guilds (Table 6, Appendix Q). The relative occurrence of *Chara* spp. near shore declined and *P. gramineus* increased relative to agriculture in the combined-region analysis. In addition, seven of the nine guilds responded significantly to agricultural land use; submersed species (NFL_NRT and

Table 6. Significant relations between the level of watershed development and near-shore macrophyte species and guilds. Only the first four near-shore quadrats (out to 7 m from shore) were analyzed. Macrophyte species are indicated by bold italics; guilds are not. Guilds are defined in Appendix F. Alpha was considered significant at $P \leq 0.05$. Regression equations are listed in Appendix Q.

Region	Macrophyte Species	r^2	P
	Proportion Urban Development		
Regions Combined	***Chara* spp.**	-0.16	0.003
	Exotic Species	0.09	0.029
	Basal Species	-0.22	<0.001
Southeastern Ecoregion	***Ceratophyllum demersum***	-0.18	0.034
	Proportion Agricultural Development		
Regions Combined	***Potamogeton gramineus***	0.08	0.046
	***Chara* spp.**	-0.17	0.002
	Basal Species	-0.45	<0.001
	Emergent Species	-0.09	0.031
	Potamogeton spp.	-0.09	0.032
	FL_RT	-0.11	0.017
	NFL_RT	0.09	0.031
	NFL_NRT	0.26	<0.001
Northern Ecoregion	***Isoetes* spp.**	-0.19	0.024
	NFL_NRT	-0.28	0.006
Southeastern Ecoregion	***Ceratophyllum demersum***	0.18	0.029
	Potamogeton spp.	-0.20	0.020
	Total Watershed Development (Agriculture + Urban)		
Regions Combined	***Chara* spp.**	-0.30	<0.001
	Potamogeton gramineus	-0.15	0.005
	Basal Species	-0.58	<0.001
	Emergent Species	-0.08	0.043
	Exotic Species	0.39	<0.001
	Potamogeton spp.	-0.10	0.021
	FL_RT	-0.12	0.011
	NFL_NRT	0.32	<0.001

Table 6 (continued). Significant relations between the level of watershed development and near-shore macrophyte species and guilds. Only the first four near-shore quadrats (out to 7 m from shore) were analyzed. Macrophyte species are indicated by bold italics; guilds are not. Guilds are defined in Appendix F. Alpha was considered significant at P ≤ 0.05. Regression equations are listed in Appendix Q.

Region	Macrophyte Species	r^2	P
Northern Ecoregion	NFL_NRT	-0.16	0.045
Southeastern Ecoregion	*Potamogeton* spp.	-0.30	0.004

NFL_RT) increased, and *Potamogeton* spp., emergent species, basal species, and FL_RT declined. When regions were separated in the analyses, *Isoetes* spp. and NFL_NRT species declined near shore in northern lakes, and *Potamogeton* spp. declined near shore in southeastern lakes. Similar to the whole-lake analysis, *C. demersum* increased near shore with agriculture in southeastern lakes.

Combining agriculture and urban land use for total development produced several regressions that were similar to those found when agriculture was addressed without considering the influences of urbanization (Table 5, Appendix P), suggesting that agricultural affects drive the effects of total development, and the effects of urban development played a lesser role. Overall, individual species including *E. canadensis, P. amplifolius, P. gramineus,* and *V. americana*, declined and *Chara* spp. increased. With the exception of *C. demersum*, which was not related to total development in either ecoregion or with regions combined (but was related to agriculture alone), these responses mirrored what was found with only agricultural affects. Guilds also responded to total development when regions were combined: six of the nine guilds analyzed (exotic species, lily pads, basal species, *Potamogeton* spp., suspended species (NFL_NRT) and floating leaved, rooted species (FL_RT)) were significantly related to total development when regions were combined, whereas only lily pads were related to total development in the northern ecoregion and no guilds showed significant relation total development in southeastern lakes. In contrast to analyses only considering agricultural land use, lily pads significantly responded to total development, whereas floating, non-rooted (FL_NRT) plants did not. When ecoregions were analyzed separately, *Myriophyllum tenellum* increased with total development and the lily pad guild declined in the Northern ecoregion. In southeastern lakes, only *P. gramineus* responded; declining with increasing development.

When near-shore quadrats were analyzed with ecoregions combined *Chara* spp., *P. gramineus*, and four guilds including *Potamogeton* spp., emergent species, basal species, and floating leaved, rooted species (FL_RT), declined with increasing development. And two guilds, exotic species and suspended species (NFL_NRT) increased with development. When regions were analyzed separately, suspended species decreased in the northern ecoregion and *Potamogeton* spp. declined in southeastern lakes (Table 6, Appendix Q).

EFFECT OF LAKESHORE DEVELOPMENT

Overall, a decline in species richness was related to riparian development (number of houses/km of shoreline) when regions were combined (Figure 5). Riparian development also negatively affected *Nymphaea* spp. and was positively related to *Chara* spp. (Table 7, Appendix R). Five guilds also a responded with house density; suspended species (NFL_NRT) and exotic species increased whereas lily pads, basal species, and floating leaved, rooted (FL_RT) species declined statewide. At the regional scale, lily pads declined with increased riparian development in both ecoregions. In addition, when regions were analyzed separately, *P. amplifolius*, and *V. americana* responded positively to house density in northern lakes, and *Brasenia schreberi* declined. And in southeastern lakes, *Nymphaea* spp. and floating, not rooted plants (FL_NRT) declined with increased house density.

When near-shore analyses were conducted, results were similar to that of the whole lake analyses (Appendix S). Statewide, *Chara* spp., exotic species and suspended

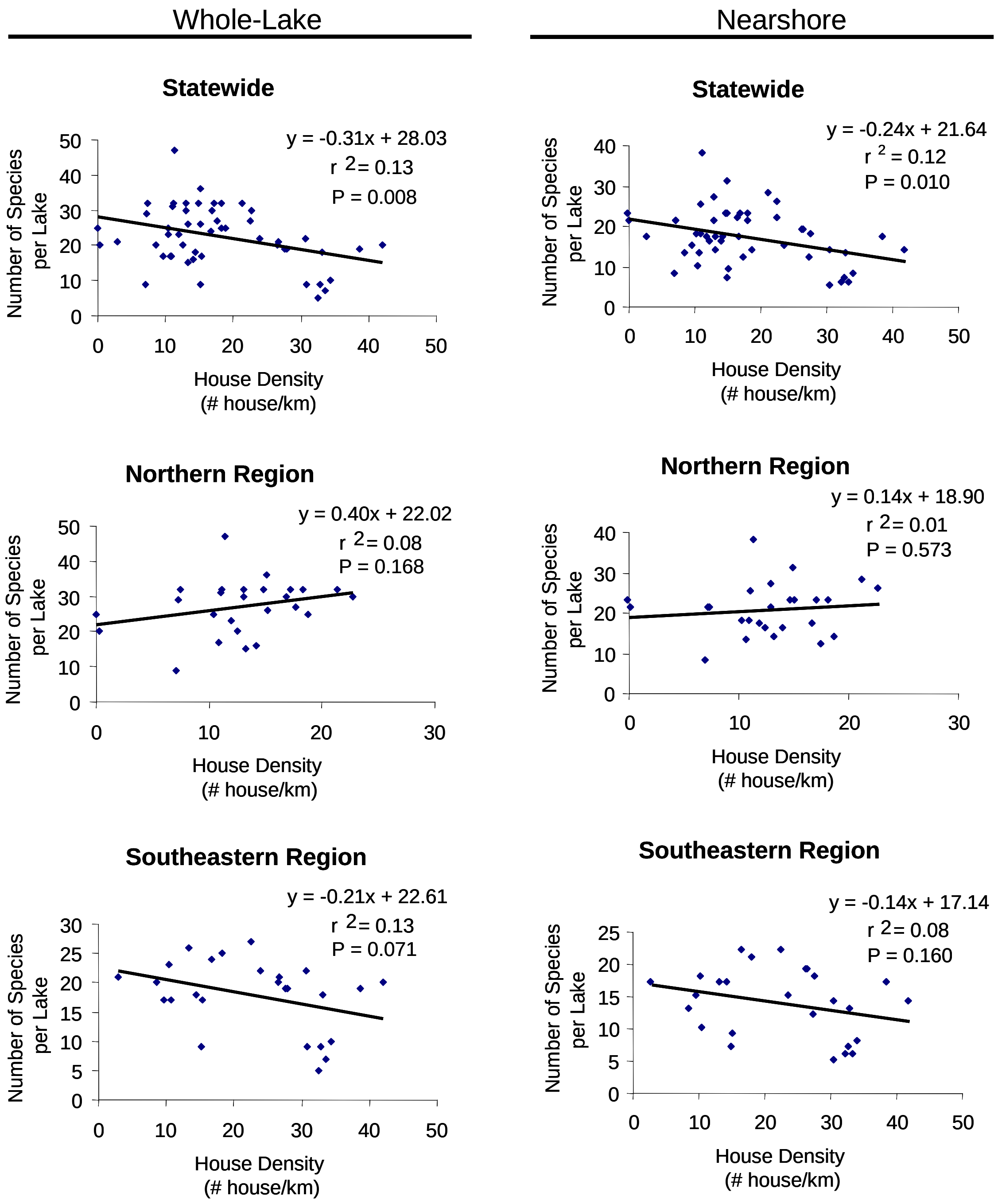

Figure 5. Linear regression models of species richness response to riparian development. Species richness is defined by the number of species found in a lake. The figure is organized such that the response of species richness in the entire lake is listed in the left-hand column, and the response of species richness in only the near-shore quadrats is listed in the right-hand column. Data in all regressions are not transformed. Models contain all species present in each lake.

Table 7. Significant relations between the level of riparian development and macrophyte species and guilds at the whole lake scale. Macrophyte species are indicated by bold italics; guilds are not. Guilds are defined in Appendix E. Riparian development is defined as the number of houses/km of shoreline in each lake. Alpha was considered significant at P ≤ 0.05. Regression equations are listed in Appendix R.

Macrophyte variable	r^2	P
Regions Combined		
***Chara* spp.**	0.18	0.002
***Nymphaea* spp.**	-0.13	0.009
Basal Species	-0.22	<0.001
Exotic Species	0.10	0.022
Lily Pads	-0.33	<0.001
FL_RT	-0.12	0.012
NFL_NRT	0.11	0.015
Northern Ecoregion		
Brasenia schreberi	-0.30	0.004
Potamogeton amplifolius	0.20	0.021
Vallisneria americana	0.15	0.049
Lily Pads	-0.24	0.011
Southeastern Ecoregion		
***Nymphaea* spp.**	-0.39	0.001
Lily Pads	-0.42	<0.001
FL_NRT	-0.24	0.012

species (NFL_NRT) increased, whereas three guilds; lily pads, basal species and floating leaf, rooted plants (FL_RT) declined in relative occurrence relative to increased riparian development. When ecoregions were analyzed separately, *B. schreberi, E. aquaticum* and basal species declined in the northern ecoregion, and in southeastern lakes *C. demersum, Nymphaea* spp., lily pads, floating leaf, non-rooted (FL_NRT) and floating leaf, rooted (FL_RT) species declined.

Multiple regression models demonstrated few significant relations. When regions were combined, lily pads were found to decline with increased urban development and decreased watershed area: lake area ratio at the whole-lake scale (Appendix T). Also with regions combined, *E. canadensis* was positively correlated at the whole-lake scale with increased agriculture and a decrease in watershed size, and *V. americana* was negatively correlated with agriculture concurrent with a decline in watershed area. In northern lakes, multiple regression revealed that increasing total development and decreasing watershed area caused an increase in *M. tenellum* (Appendix T). No multiple regressions were found in the southeastern ecoregion or at the near-shore scale.

DISCUSSION

The effect of human development at the watershed and lakeshore scales on aquatic macrophytes in this study was significant. At the watershed scale, agriculture and overall development had more effect on macrophyte communities in study lakes than did urban land use. In general, as watershed and riparian development increased, native pondweeds (*Potamogeton* spp.), floating-leaf plants, and several individual rooted, submerged species declined while the relative occurrence of suspended (NFL_NRT) and exotic species such as *C. demersum* and *M. spicatum* respectively increased. In Clear

Lake, Iowa, Egertson *et al.* (2004) documented shifts in the macrophyte composition from a community dominated by submerged species to a community of floating-leaf to emergent plants; attributing this shift to the affects of agricultural eutrophication. On the contrary, results of this study indicate a decline in all types of rooted species (submerged, emergent and floating-leaf) and an increase in suspended (NFL_NRT) species such as *Chara* spp. and *C. demersum*.

Habitat changes that are associated with the eutrophication of lakes may partially explain the observed decline of rooted species and increase of non-rooted and suspended species such as *Chara* spp. and *C. demersum* in this study. Eutrophic lakes have a higher prevalence of loose detritus and silt which could be detrimental for rooted macrophytes that are less able to anchor in the unstable substrate. In contrast, shifts in substrate may benefit suspended species that are able to partially bury themselves in loose substrate and thereby gain nutrients (Egertson *et al.* 2004). Species, such as *Chara* spp. and *C. demersum* have been documented to prefer softer substrates and higher nutrient levels in the water (Nichols 1999a).

Urban development in the watersheds of both ecoregions primarily affected only two groups of aquatic plants: those that produce floating leaves (negatively) and exotic species (positively). Perhaps the negative effects on floating-leaf plants can be attributed to increased recreational lake use (often concurrent with increased urban development), which impacts floating-leaf plants as they are more susceptible than submerged species to wave damage and cutting from boat motors, and to direct removal by lakeshore landowners (Asplund and Cook 1997). In contrast to the negative effects on native species, recreational lake use is a likely vector for the rapid spread of exotic species because many of these plants can reproduce vegetatively and are transported over land to new lakes via boat trailers (Nichols and Shaw 1986). These species, especially *M. spicatum*, have been shown to create dense monotypic stands that shade out native plants (Boylen *et al.* 1999) and interfere with boating and other recreation, which in turn enhances the socioeconomic dislike of aquatic plants (van Nes *et al.* 2002). Dense stands of macrophytes also increase the likelihood of aquatic plant management on a lake which is increasingly detrimental to the already-impacted native macrophyte communities. Current regulation and management is focusing on the education of boaters and lakeshore land owners to slow the spread of exotic species and to encourage ecologically safe alternatives to aquatic plant management (van Nes *et al.* 1999).

One must also keep in mind that many lakes in Wisconsin that are now impacted by urban development were first subjected to the effects of agricultural land use. With the transition of agriculture to urban land uses, a shift in aquatic macrophyte communities may also be observed. While this has not been documented to my knowledge, the effects of urban development (i.e., direct removal, increased boat traffic) are very different than those of agriculture (i.e., nutrient and soil run off) therefore a shift in species composition (e.g. loss of floating leaved plants but a gain of exotic species) may account for the apparent lack of species richness response to urban development.

Contrary to expectations, two macrophyte species increased with urban development: *Chara* spp. increased statewide and *M. tenellum* increased in northern lakes. While no research to my knowledge provides a mechanism for this response, *M. tenellum* may be more opportunistic than other basal-growing species; colonizing areas left open when other plants decline or disturbances (natural or anthropogenic) create an open area in the substrate. However, *M. tenellum* is still more sensitive than many species; as it does not occur in the more eutrophic southeastern lakes. The increase in *Chara* spp. contradicts Lougheed *et al.* (2001) who listed *Chara* spp. as intolerant to changes in water quality (also Vandeberg *et al.* 1999). However, in this study, *Chara* spp. were analyzed by genus only, and some species of *Chara* may be more resilient to water quality changes that result from development pressures than are other *Chara* species (Spence 1967). Interestingly, *Chara* spp. also increased with agricultural and total development at the whole-lake scale, but declined in the near-shore analyses at all watershed development levels. Though not rooted, *Chara* spp. grow on the bottom of the lake, below the leaves and stalks of other species; therefore it may be that as these species decline, more light is available for *Chara* spp. to grow. Near shore, *Chara* spp. may decline due to increased wave action that was previously reduced by other submerged and floating leaf macrophytes. Because *Chara* spp. do not produce roots, waves would more easily wash these species out into the lake or up onto shore where they would die. It is also possible that the increase of *Chara* spp. and *M. tenellum* may be for reasons other that urbanization and therefore, correlations could be spurious.

Analyses focusing on effects of development to plants in near-shore areas of lakes produced similar results to those found with whole lake analyses, suggesting that many species occur at similar abundances proportionately throughout the littoral zone and perturbations are not affecting these species more near shore where human activities should be greatest compared to the entire littoral zone. This shallow water region (out to 7 m from shore and generally less than 1.75 m in depth) is the area of lakes where watershed and lakeshore land uses are expected to directly transfer impacts to aquatic systems. Therefore, near-shore analyses were expected to produce more significant results than were found for species growing proximal to the land-water interface (i.e., emergents, floating leaf plants, lily pads, and basal-growing species). It may be that the expected declines were not seen because species generally inhabiting this zone in Wisconsin lakes (especially in the southeastern ecoregion) are already affected by perturbations (i.e., direct removal) to the extent that they no longer exist or the plants occur at densities too low to analyze (Jennings *et al.* 2003).

Near-shore analyses also revealed an interesting plant community dynamic. In this study, *C. demersum* was a deeper-growing species, but the coefficient of determination in southeastern lakes was higher for the relation to agricultural development in the near-shore analysis compared to the overall littoral zone when deeper water gradients were evaluated. Occurrence of *C. demersum* also increased near shore in response to increasing urban development (but did not at the whole-lake scale). This would suggest that *C. demersum* grows, or is more responsive, in near-shore habitats in southeastern lakes. An explanation may be that southeastern lakes are generally more eutrophic and more turbid, therefore shallow water provides better habitat with light and nutrients for *C. demersum* to grow. Also, *C. demersum* does not often anchor into the substrate therefore the location of this plant in the lake may only be due to the prevailing wave direction.

This study suggests that riparian development, like overall watershed development, was also detrimental to macrophyte communities—although effects differed. In relation to riparian development, *Chara* spp., exotic species and suspended species (NFL_NRT) increased while lily pads and floating-leafed species (FL_RT) decreased. In lakes with no riparian development, plants with floating leaves are expected to grow within the first two meters of depth and completely submersed plants are expected to grow to one percent light availability levels. As a result, submerged species would be expected to decrease before floating–leaf plants decline in response to eutrophication that causes algal blooms and increasing turbidity which reduces light availability (Egertson *et al.* 2004). In this study, the increase in plants without floating leaves and decline of plants with floating leaves as riparian development increased around the lakes supports the hypothesis that the floating-leaf characteristic of these plants' morphology increases susceptibility to development pressures (i.e., direct removal) because they are visually obvious and so lakeshore owners may be prone to want to remove them, and the floating leaves are more susceptible to cutting by boat motors that deeper growing species (Asplund and Cook 1997, Radomski and Goeman 2001). Radomski and Goeman (2001) documented a decline in floating leaf plants when riparian development increased in Minnesota lakes and Jennings *et al.* (2003) related similar declines in response to riparian development in Wisconsin lakes. The concurrent increase in submerged plants suggest that decline of floating-leaf plants may be selective. And while house density on northern lakeshores was much lower than along southeastern shorelines, macrophyte species declined in both ecoregions, suggesting that the negative effects of shoreline development are seen at very low levels of perturbation. Therefore observations in this study may indicate that the effect of human perturbations on rooted species is two-fold: while the processes affecting light limitation (i.e., shading, turbidity, etc.) at the watershed scale are being imposed on submerged species, the pressures of riparian development are also limiting the persistence of emergent and rooted floating-leaf (FL_RT) species.

Many relations, while significant, had low coefficients of determination (r^2 = 0.07-0.70), but these results were expected and are consistent with others' research (Radomski and Goeman 2001, Hrabik *et al.* 2005). Ecological data are often inherently non-linear, but transformations only increased the coefficient of determination for some regressions. Regardless, when working with ecological data, low goodness-of-fit is often expected because of the complex array of sources of variation due to unexplained environmental impacts affecting biotic communities. This may be especially true in this study since we are determining the relation of species relative occurrence in relation to anthropogenic perturbations (and not accounting for many ecological variables that are indubitably affecting the macrophyte communities).

Overall, response levels of many individual macrophyte species relative to development were not conclusive. Because elevated development levels in the southeastern ecoregion have already degraded many lake habitats and the narrow range of development pressures in the northern region, the detection of species response to development effects may only be possible at a statewide level. Moreover, another problem arises with rare species, which may be the most sensitive to affects of watershed and riparian development. Their rarity makes analysis less conducive to conventional analytical approaches. And without prior data, it is impossible to rule out the possibility that rare species naturally occur at low abundances (or are naturally non-existent). Natural variation in aquatic plant communities may still explain a large portion of species distribution in Wisconsin lakes.

Macrophyte communities can vary naturally in response to conservative environmental gradients that are not directly affected by anthropogenic perturbations (Lougheed *et al.* 2001). Lakes occur across Wisconsin along a natural ecological gradient such that concentrations of dissolved minerals including calcium, magnesium, alkalinity, conductivity, pH, nitrogen, and phosphorus increases from northeast to southwest (Moyle 1945, Omernik *et al.* 2000). Many studies have been published explaining the response and tolerance thresholds of aquatic macrophytes to gradients of environmental variables (Moyle 1945, Swindale and Curtis 1957, Seddon 1972, Nichols 1999b, Hrabik *et al.* 2005). And this aspect of aquatic macrophyte life history may be a major explanation for the natural rarity of many species. Plants such as *Lobelia dortmanna, Isoetes* spp., and *Utricularia minor* are plants found in northern lakes of this study that were listed as intolerant to high levels of conductivity by Toivonen and Huttunen (1995).

Future paleolimnological work with lake sediments may provide insight into historic macrophyte assemblages and abundances in Wisconsin lakes. Methods have been developed to reconstruct historic concentrations of water chemistry variables in lakes and the ability to determine effects of runoff from development and atmospheric deposition (Anderson 1993). Known historic concentrations (and macrophyte occurrence) may provide insight into the separation of the effects of anthropogenic perturbations from natural variation in macrophyte communities (Anderson 1993). Research in Musky Bay, Lac Courte Oreilles, Wisconsin, USA has demonstrated the potential of this type of research: attributing increased calcium, magnesium and nutrient concentration levels to local cranberry farming and riparian development (Garrison and

Fitzgerald 2005). More paleolimnological studies may provide managers and researches with scientific basis for the protection of watersheds and lakeshores to protect and maintain healthy macrophyte communities.

MANAGEMENT IMPLICATIONS

Previous studies assessing the effects of human development on macrophytes have focused on either the effects of riparian development or overall watershed development of individual lakes (Radomski and Goeman 2001, Egertson *et al.* 2004). This study addressed affects of both watershed and riparian development simultaneously in 53 lakes at a statewide scale as opposed to only individual lakes or relatively few lakes within an ecoregion. The data from this study show that the effects of human perturbation are occurring across regions and lake types.

These data may be used to support further research on the effects of aquatic plant management. Data collected for this project can be used to index the quality of Wisconsin lakes regionally and statewide. Collection of baseline data in multiple lakes provides a mean of comparison of these lakes over time. In addition, increasing the amount of information collected on Wisconsin lakes and macrophyte communities provides essential references for future research and management. For example, use of this research as baseline data will provide insight into the effects of development on northern lakes in Wisconsin as they continue to be developed.

Finally, my study can be used to educate the public to foster stewardship of Wisconsin lakes. Because many Wisconsin lakes are already highly developed, the protection of lake quality lies in the hands of riparian land owners and recreational lake users. Private interest groups and lake associations might use these data to assess and protect their water bodies. Sound education of these user groups will increase the ability of managers to effectively protect lakes and aquatic macrophyte communities in the lakes.

CHAPTER II

COMPOSITION OF AQUATIC MACROPHYTE COMMUNITIES AS DETERMINED BY THE TOLERANCE LEVELS OF MACROPHYTE SPECIES TO ENVIRONMENTAL GRADIENTS

ABSTRACT. Differences in aquatic plant communities among lakes may be attributed to the response levels of individual aquatic macrophyte species relative to variation in environmental gradients. The objective of this study was to quantify water chemistry attributes in selected Wisconsin lakes, assess the tolerance levels to water chemistry concentrations of individual macrophyte species growing within those lakes, and to determine relations of aquatic plant communities to environmental gradients across Wisconsin. Macrophyte communities in 53 Wisconsin lakes were surveyed to determine species richness and relative occurrence of individual species in the littoral zone of each lake. To assess the extent of regional variation, lakes were chosen from two different ecoregions: the Northern Lakes and Forests ecoregion and the Southeastern Till Plains ecoregion. Within these ecoregions, lakes were selected along two gradients of development: at the watershed scale, ranging from undeveloped (i.e., forested) to high agricultural or urban development, and at the lakeshore scale using a gradient of house densities. Relative occurrence of each aquatic macrophyte species was sampled using snorkeling and SCUBA within 18, 0.25 m^2 quadrats along 14 randomly-placed transects. Water chemistry including alkalinity, conductivity, calcium, magnesium, phosphorus, nitrogen, color, chlorophyll-*a*, pH and Secchi depth, was measured in each lake at turnover (spring or fall). Macrophyte species richness and occurrences were evaluated relative to water chemistry characteristics of lakes using regression analyses to assess

environmental tolerance levels of individual species across lakes, and canonical correspondence analysis (CCA) was used to determine the distribution of macrophyte assemblages as constrained by environmental attributes. Results indicate that aquatic macrophyte communities are influenced by the concentration levels of water chemistry attributes in a lake. Environmental gradients of alkalinity, conductivity, magnesium and pH influenced macrophyte communities such that species richness and occurrence of many individual species declined along a north to south distribution. Northern lakes were generally oligotrophic, and macrophyte communities had greater species richness and more basal growing species. Southeastern lakes showed higher levels of alkalinity, conductivity, nitrogen and phosphorous. *Ceratophyllum demersum, Chara* spp*.,* *Myriophyllum spicatum,* and *Stuckenia pectinata* appeared more tolerant of, and increased with higher levels of alkalinity and conductivity while less tolerant species such as *Lobelia dortmanna* and *Elatine minima* occurred only at low concentrations of dissolved minerals.

INTRODUCTION

Aquatic macrophyte community composition is structured by the response of individual species to biological, physical, and chemical factors that determine ability of plants to survive and thrive in a lake (Moyle 1945, Sculthorpe 1967, Heegaard *et al.* 2001, Hrabik *et al.* 2005). Heegaard *et al.* (2001) suggest that aquatic macrophytes are easily dispersed therefore the presence and persistence of plants in an aquatic community are primarily determined by the environmental factors of the lake (also Sculthorpe 1967). Environmental variables that may play a role in determining the distribution of aquatic macrophytes include pH (Titus 1992), alkalinity and conductivity (Moyle 1945, Vestergaard and Sand-Jensen 2000), and calcium and magnesium (Spence 1967, Seddon 1972, Heegaard *et al.* 2001). Nutrients such as phosphorous and nitrogen have also been considered with more recent emphasis due to cultural eutrophication processes and their overall negative effects on aquatic ecosystems (Toivonen and Huttunen 1995, Hauxwell and Valiela 2004).

The distribution of aquatic macrophytes has long been researched in relation to water chemistry (Moyle 1945, Spence 1967, Seddon 1972, Toivonen and Huttunen 1995, Nichols 1999a, b, Heegaard *et al.* 2001). As early as 1945, Moyle had recognized that each aquatic plant species has its own range of chemical tolerance and a range of optimal growth. And overlap of the unique response of each aquatic plant species to environmental variation is what creates different community types in relation to the physical and chemical attributes of any specific lake along an environmental continuum (Riis *et al.* 2000). Spence (1967) described aquatic macrophytes in Scottish lakes that were confined to rich waters defined by ranges in alkalinity and conductivity such as

Ceratophyllum demersum, Myriophyllum spicatum, Potamogeton praelongus, and *Stuckenia pectinata*, poor waters (*Isoetes lacustris, Ranunculus flammula*, and *Lobelia dortmanna*), and some as ubiquitous species (*Littorella uniflora*, and *Potamogeton gramineus*); all of which also occur in Wisconsin lakes. Similar characterizations of aquatic plant tolerances have been done across Europe and Canada, but less work has been done in the United States, especially in the more recent years (Spence 1967, Seddon 1972, Toivonen and Huttunen 1995, Nichols 1999b, Riis *et al.* 2000, Heegaard *et al.* 2001).

The most recent descriptions of aquatic macrophyte communities have combined responses of individual species with the variation of multiple environmental variables using canonical correspondence analysis (CCA). Toivonen and Huttunen (1995) used CCA to describe the relations of aquatic macrophytes to environmental characteristics in Finland. While they primarily used physical attributes of the lakes (i.e., altitude, area, maximum depth, and water color), they also addressed conductivity and stated this as the principle determinate of aquatic macrophyte species occurrence. In Northern Ireland, Heegaard *et al.* (2001) included chemical variables such as calcium, magnesium, pH, silica, potassium, sulphate and chloride in addition to physical features of their study lakes in a CCA. They also found that many aquatic plant species are constrained by high or low ionic concentrations while other plants are generalists; tolerant of a wide range of chemical concentrations. While Nichols (1999b) has described the distribution and habitats of aquatic plants in Wisconsin lakes, a community based analysis of environmental variables and species has not yet been undertaken.

The objective of this study was to quantify environmental gradients in selected Wisconsin lakes, assess response levels of individual macrophyte species growing within those lakes, and to determine relations of aquatic plant communities to environmental gradients. Wisconsin provides a unique landscape in which to do this research because the state has tens of thousands of lakes that are separated geographically and occur along gradients of environmental variation.

STUDY AREA

Fifty-three lakes in two ecoregions of Wisconsin: 26 in the Southeastern Wisconsin Till Plain ecoregion (herein referred to as the southeastern ecoregion) and 27 in the Northern Lakes and Forests ecoregion (herein referred to as the northern ecoregion), were surveyed for aquatic macrophytes (Figure 1, Appendix A) (Omernik *et al.* 2000). Two lakes fell just outside the border of the southeastern ecoregion, but were sampled to increase the number of sampled lakes in this region and because conditions were similar to lakes in the southeastern ecoregion. Selected lakes ranged in surface area from 20-136 ha with watersheds ranging from 27-2,200 ha (Table 1). All lakes had a maximum depth of 5.5 m or greater, with the exception of Silver Lake in Vilas County, and Person Lake in Douglas County, Wisconsin, which were 3.7 m and 3.1 m deep, respectively.

Both regions had lakes that varied along limnological and riparian and watershed development gradients. Selected lakes spanned a continuum of development ranging from a completely undeveloped watershed and shoreline, to watersheds over 97% developed and lakeshores with 42 houses per km of shoreline (Table 1, Appendix B).

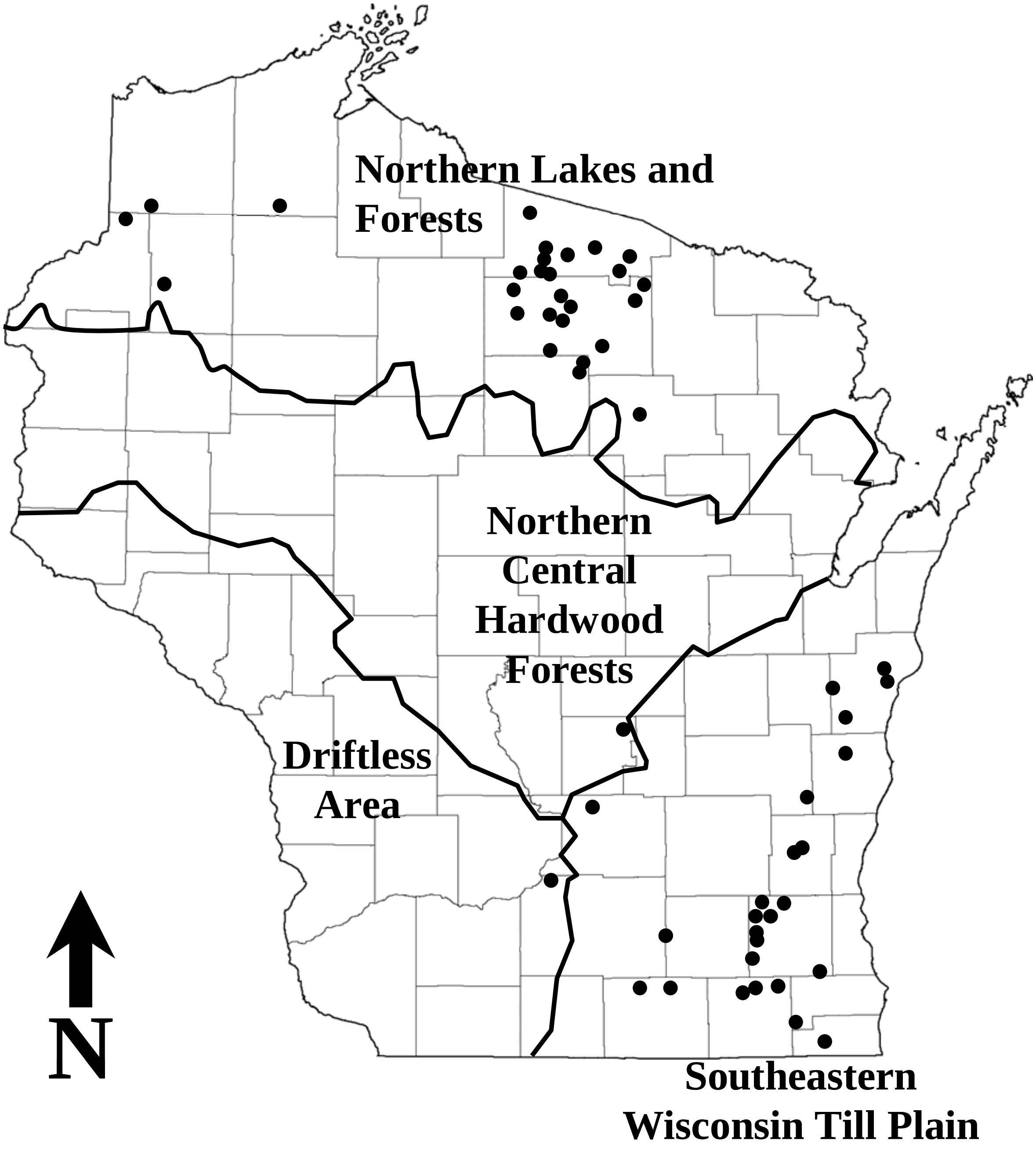

Figure 1. Map of Wisconsin showing the ecoregions defined by Omernik *et al.* (2000) and the locations of lakes (●) sampled between 2003-2005. Specific lake locations are listed in Appendix A.

Table 1. Mean, standard error (S. E.) about the mean, and range of lake characteristics for the 53 Wisconsin study lakes (26 southeastern and 27 northern). Variable descriptions are listed in Appendix K. Bold values represent variables that were significantly different between ecoregions (Mann-Whitney U-test).

	Southeastern Ecoregion		Northern Ecoregion			
Variable	Mean (±S.E.)	Range	Mean (±S.E.)	Range	U-stat	P
			General			
Lake area (hectares)	**46.2 (4.48)**	**19.4-99.3**	**67.0 (6.63)**	**20.3-136.4**	**467.0**	**0.018**
Max depth of lake (m)	12.0 (0.93)	6.1-27.4	9.4 (0.94)	3.1-21.6	236.5	0.063
Watershed area (hectares)	**259.6 (41.10)**	**27.1-942.7**	**570.9 (98.21)**	**58.8-2205.3**	**495.0**	**0.004**
Watershed area : Lake area	5.9 (0.88)	0.7-20.1	11.2 (2.72)	1.8-64.3	395.0	0.297
Lake perimeter (km)	**3.3 (0.28)**	**1.5-8.5**	**4.7 (0.32)**	**2.2-7.7**	**514.0**	**0.001**
			Development			
Agriculture development (proportion of watershed)	**31.6 (4.79)**	**0.0-73.4**	**3.6 (0.96)**	**0.0-15.6**	**68.5**	**<0.001**
Urban development (proportion of watershed)	**31.6 (4.23)**	**0.0-81.9**	**12.5 (2.45)**	**0.0-62.3**	**140.0**	**<0.001**
Total development (proportion of watershed)	**63.2 (3.86)**	**15.1-97.4**	**16.1 (2.75)**	**0.0-62.3**	**23.0**	**<0.001**
House density (# Houses/Lake perimeter)	**23.0 (2.07)**	**2.9-42.0**	**12.8 (1.07)**	**0.0-22.8**	**154.0**	**0.001**
Number of houses	75 (8.7)	6-203	58 (6.0)	0-107	286.5	0.251

Table 1 (continued). Mean, standard error (S. E.) about the mean, and range of lake characteristics for the 53 Wisconsin study lakes (26 southeastern and 27 northern). Variable descriptions are listed in Appendix K. Bold values represent variables that were significantly different between ecoregions (Mann-Whitney U-test).

	Southeastern Ecoregion		Northern Ecoregion			
Variable	Mean (±S.E.)	Range	Mean (±S.E.)	Range	U-stat	P
Water Chemistry						
Alkalinity (mg/L)	**141.7 (6.88)**	**58-203**	**29.6 (3.06)**	**4-64**	**1.0**	**<0.001**
Conductivity (µmhos/cm)	**388.3 (24.38)**	**125-647**	**83.0 (9.13)**	**14-179**	**5.0**	**<0.001**
pH (Su)	**8.70 (0.05)**	**8.09-9.23**	**7.75 (0.11)**	**6.45-8.61**	**38.0**	**<0.001**
Calcium (mg/L)	**26.57 (1.26)**	**13.1-40.1**	**8.11 (0.92)**	**1.3-18.0**	**10.0**	**<0.001**
Magnesium (mg/L)	**25.47 (1.74)**	**6.9-41.1**	**2.8 (0.30)**	**0.4-7.6**	**2.0**	**<0.001**
Chlorophyll-*a* (mg/L)	5.72 (0.89)	**2.11-20.70**	**6.41 (1.23)**	**1.12-26.91**	**326.0**	**0.656**
Color (units)	**7.8 (0.88)**	**5-20**	**12.5 (1.39)**	**5-30**	**516.0**	**0.002**
Secchi (m)	2.72 (0.21)	1.20-5.03	2.42 (0.18)	0.91-3.81	302.0	0.383
Total Phosphorous (mg/L)	0.029 (0.005)	0.006-0.141	0.019 (0.002)	0.006-0.071	589.0	0.068
Total Nitrogen (mg/L)	**0.98 (0.06)**	**0.56-1.63**	**0.52 (0.03)**	**0.32-1.06**	**398.5**	**<0.001**

Overall, lakes in the northern ecoregion were less developed than southeastern lakes at both the watershed and riparian levels. Lakes also followed a latitudinal gradient of increasing nutrient levels from northwest to southeast (Table 1). The northern ecoregion provided an area with lakes with lower alkalinity, calcium, and magnesium concentrations and lower conductivity and pH levels while the southeastern ecoregion provided lakes with higher nutrient and bicarbonate concentrations (Omernik *et al.* 2000).

METHODS

Macrophyte data were collected from the 53 Wisconsin lakes from June to September over a span of three years (2003-2005). Each lake was sampled only once. The entire shoreline was considered available for data collection except wetland and beach areas, which were omitted from sampling. For the purpose of this study, wetlands were defined as areas with a littoral zone slope near zero and vegetation primarily composed of extensive cattail beds or bog mats; beaches were defined as areas with sand substrate that did not appear to be natural (i.e., not consistent with the substrate of the rest of the lake) or areas directly roped off and labeled for swimming and most likely affected by active plant removal.

Within each lake, macrophytes were sampled at fourteen stratified-random sites (Appendix C). Sites chosen were a minimum of 30 m wide and defined as a segment of shoreline owned by a single resident (dwelling) or an undeveloped 30 m section of shore; generally riparian land ownership approximates 30 m of shoreline length. A transect was placed at the center of each site and set perpendicular to shore, out to a distance of 45 m or the maximum depth of plant growth, whichever was shallower. Snorkeling and SCUBA were used to assess plants in 18, 0.25 m^2 quadrats along the transect. Quadrats were placed every 2 m for the first 12 m of the transect and every 3 m out to 45 m (Appendix D). Relative occurrence of each species was calculated as the number of quadrats in which a species occurred, divided by the total number of quadrats sampled in the littoral zone of that lake (quadrats that fell beyond the maximum depth of plant growth were not included in the calculation of relative occurrence).

The protocol for collecting water chemistry and nutrient data collection and analyses were provided by the Water and Environmental Analyses Lab (University of Wisconsin - Stevens Point). Bottles were rinsed three times with lake water before a sample was collected, and the sample was taken at 0.5 m below the surface of the water. Chlorophyll-*a* sample bottles were wrapped in aluminum foil to keep the water sample in the dark and transported on ice. Calcium and magnesium samples were acidified with nitric acid, and nutrient samples were acidified with sulfuric acid; both to a $pH < 2.0$. All samples were kept on ice until delivered to the lab for analysis. Data were collected at turnover for each lake (spring or fall) to ensure accurate measurement of nutrient levels available for plant growth. For each lake, water samples for total phosphorous, nitrogen, alkalinity, conductivity, calcium, magnesium, pH, color, and chlorophyll-*a* were collected, and Secchi depth was recorded (Appendix K).

Most statistical analyses were performed using SPSS 14.0 for Windows (SPSS Inc. 2005). Canonical correspondence analysis (CCA) was performed using PC-ORD version 4.26 (McCune and Mefford 1999). To test the assumption of normality, Shapiro-Wilks tests were run on all independent and dependent variables (Appendix K). Simple linear regression was used to assess relations between individual macrophyte species and environmental variables. Alpha was considered significant at $P \leq 0.05$. Variables within each regression were transformed using $\log_{10}$, $\log_e$, and square root transformations to improve linearity and examined as needed to maximize the coefficient of determination (r^2) and normalize residual error.

Canonical correspondence analysis (CCA) was used to assess species distributions along environmental gradients of water chemistry attributes (Ter Braak 1986). This method disperses the weighted average of each species along linear trends of the environmental variables and has been used in several similar studies (Toivonen and Huttunen 1995, Heegaard *et al.* 2001, Lougheed *et al.* 2001). This multivariate approach provides a means to address patterns in community variation (i.e., multiple species distributions) as explained by multiple environmental variables simultaneously by combining correlation and regression techniques (Kent and Coker 1992). Water chemistry variables including calcium, magnesium, nitrogen, phosphorous, alkalinity, conductivity, pH, Secchi depth and latitude were used to represent the environmental conditions occurring in the study lakes. Due to low variation, color and chlorophyll-*a* were excluded in the final CCA analysis. Thirty-nine species occurred in ≥ 1% of the quadrats statewide and were considered for the CCA; twenty-two species (occurring in ≥ 3% of the quadrats) were included in the final CCA (Table 2). The inclusion of less common species and removal of environmental variables did not change the output significantly, therefore the model was assumed to be relatively stable. More species were used in the CCA than in regression analyses to analyze a more complete community distribution of plants across environmental gradients. Emergent species were not represented in the CCA due to low abundances, primarily because the sampling technique targeted more submersed taxa.

Table 2. Aquatic macrophyte species used as dependent variables in regression analyses and canonical correspondence analysis (CCA). Relative occurrence of individual species was used in both regression and CCA analyses as dependent variables. Ten species were chosen for regression analyses. More species were used in the CCA to analyze a more complete community distribution of plants across environmental gradients. Mean, standard error about the mean, and range for each species is listed in Appendix E.

	Regression	CCA
Ceratophyllum demersum	X	X
Chara spp.	X	X
Elatine minima		X
Eleocharis acicularis		X
Elodea canadensis	X	X
Heteranthera dubia		X
Isoetes spp.		X
Juncus pelocarpus		X
Myriophyllum sibiricum	X	X
Myriophyllum spicatum		X
Myriophyllum tenellum		X
Najas flexilis	X	X
Najas marina		X
Nitella spp.		X
Nymphaea spp.	X	X
Potamogeton amplifolius	X	X
Potamogeton gramineus	X	X
Potamogeton illinoensis		X
Potamogeton robbinsii		X
Potamogeton zosteriformis	X	X
Stuckenia pectinata		X
Vallisneria americana	X	X

RESULTS

The 53 lakes sampled in this study occurred along an ecological continuum of environmental variation that was highly correlated with latitude, such that lakes occurring in the northern ecoregion had different water chemistry than lakes in the southeastern ecoregion of Wisconsin (Table 1, Appendix U). Northern lakes were more oligotrophic and southeastern lakes were more eutrophic based on bicarbonate and nutrient concentrations. The greatest environmental gradients observed in this study were in alkalinity, conductivity, calcium, and magnesium, which were much higher and more variable in southeastern lakes compared to northern Wisconsin lakes (Figure 2). In contrast, Secchi depth and chlorophyll-*a* did not vary across ecoregions, and while nutrient concentrations were higher in southeastern lakes than in the north, the difference in phosphorous between regions was negligible.

Aquatic macrophytes species richness and relative occurrences varied regionally. On average, 27 macrophyte species were found per lake in the northern ecoregion, but southeastern lakes averaged only 18 species per lake. While many plants were present statewide, only 10 species occurred in ≥ 5% of the total quadrats sampled when both ecoregions were considered. Regionally, 21 species occurred in ≥ 5% of northern quadrats and 12 species in ≥ 5% of the southeastern quadrats (Appendix E). Greater species diversity was observed in the northern lakes, but total relative occurrence was lower on average for this ecoregion and plants did not grow as deep as in the southeastern ecoregion.

The distribution of aquatic plants relative to water chemistry variables showed a gradient of plant-water chemistry associations. Overall, macrophyte species richness per

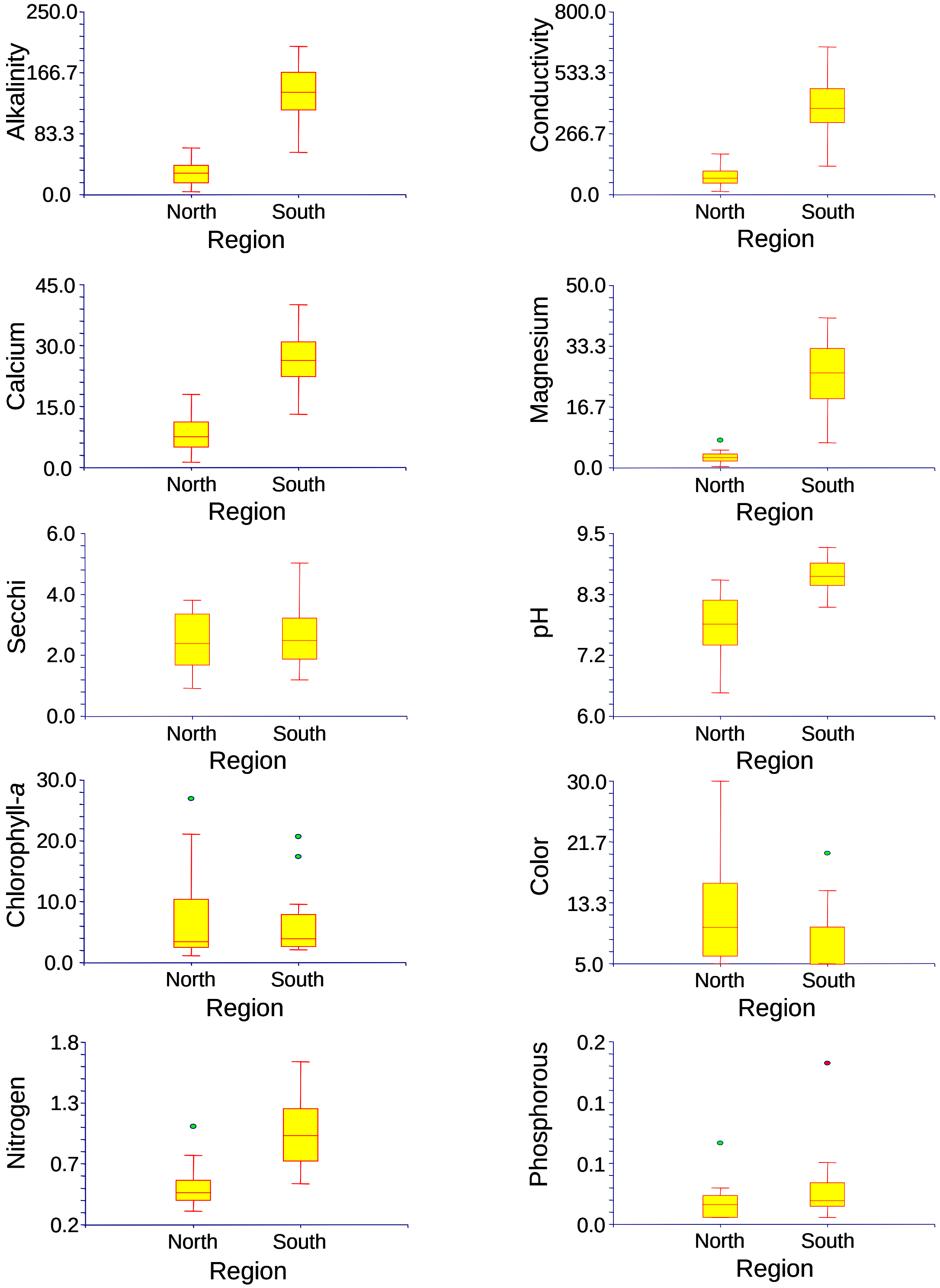

Figure 2. Range of water chemistry attributes for the 53 northern and southeastern Wisconsin lakes sampled. The horizontal center bar represents the mean, the box represents 25% quartiles about the mean, and the vertical bars represent 1.5 times the inter-quartile range. Outliers at lease three standard deviations from the mean and are depicted by a dot (●).

lake was negatively correlated with alkalinity, conductivity, calcium, magnesium, and nitrogen (Figure 3). Individual species showing similar responses included *Elodea canadensis, Potamogeton amplifolius,* and *Vallisneria americana* while others such as, *Chara* spp., *Myriophyllum sibiricum*, and *C. demersum* increased with higher nutrient concentrations (Table 3, Figure 4, Appendices V and W). *Nymphaea* spp., *Potamogeton zosteriformis*, and *Najas flexilis* showed no significant relation to any of the measured water chemistry levels.

Aquatic plants showed a wide variety of distributional responses relative to environmental factors of lakes (Figures 5-8). Species such as *Utricularia resupinata, L. dortmanna,* and *Sagittaria rigida* occurred were limited to low concentrations of alkalinity, conductivity, nitrogen and pH levels, suggesting that these plants are not tolerant of higher concentrations (Figures 5-8, Appendix X). Some species, such as *Najas marina* and *Potamogeton crispus, S. pectinata, M. spicatum* and *Potamogeton illinoensis* were found in lakes with higher concentrations of alkalinity, conductivity, and nitrogen and more basic pH levels (approx. 8-10). Other macrophytes such as *Spirodela polyrrhiza* and *Utricularia vulgaris* demonstrated relatively wide ranges of tolerance across several chemical gradients considered. Finally, some species were limited to narrow ranges of specific conditions while other limnological conditions do not seem to affect growth. For example, *Najas gracillima* was confined to lakes with low alkalinity (<30 mg/L) and conductivity (<105 µmhos/m), but was not confined to low nitrogen levels (0.4-0.7 mg/L). Another species, *Riccia fluitans*, was tolerant of very wide alkalinity and conductivity concentrations, but preferred lakes with higher nitrogen content (0.6-1.3 mg/L). Latitude, Secchi depth, and phosphorous concentration were also

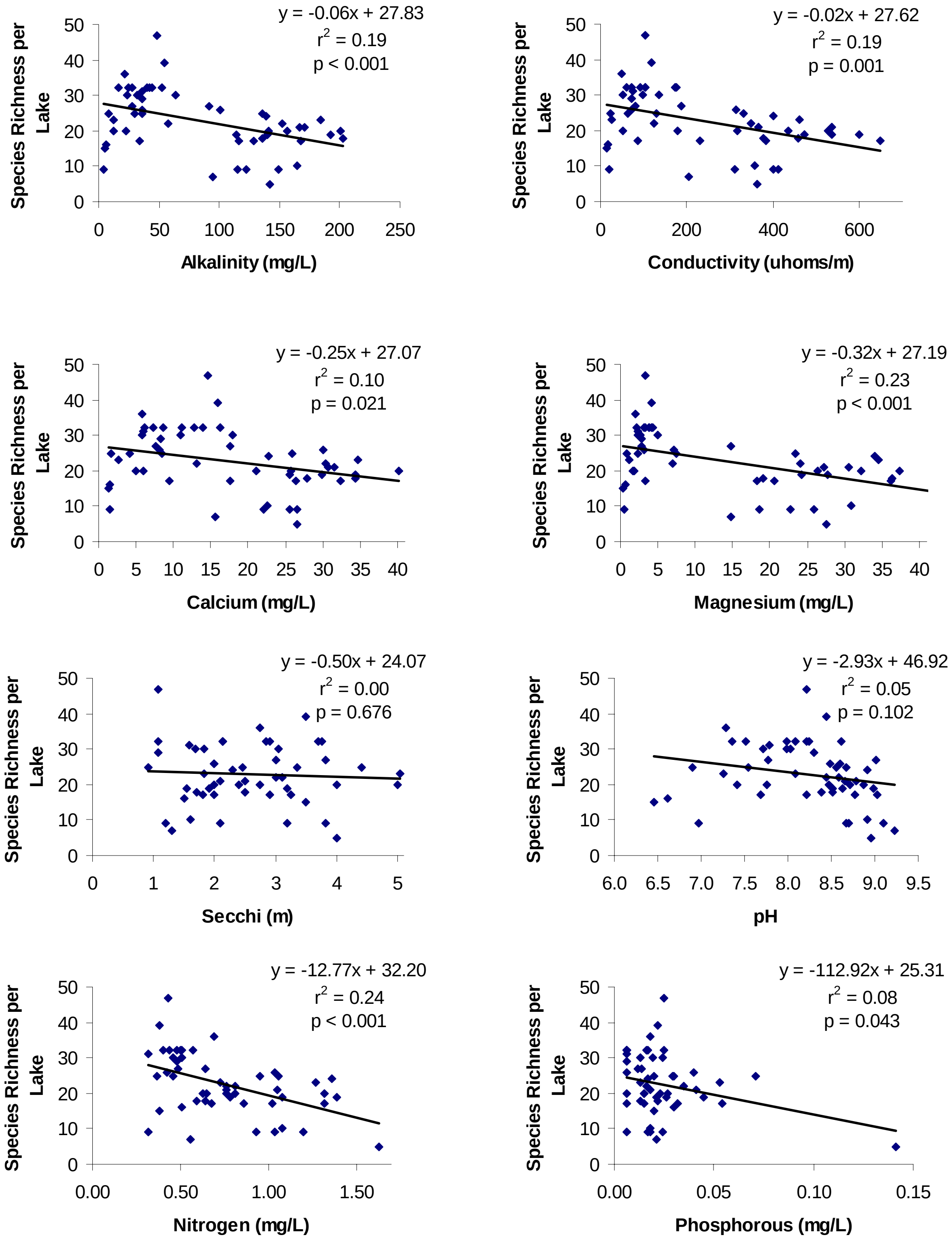

Figure 3. Linear regression models of species richness response to water chemistry attributes. Species richness is defined by the number of species found in a lake. Data in all regressions are not transformed. Models contain all species present in each lake.

Table 3. Significant relations between water chemistry levels and macrophyte species relative occurrence in the 53 Wisconsin lakes sampled. Species included in this analysis are listed in Table 2. Water chemistry variables are explained in Appendix K. Regression equations are listed in Appendix V.

	Macrophyte Species	r^2	P
Alkalinity	*Chara* spp.	0.62	<0.001
	Myriophyllum sibiricum	0.09	0.034
	Elodea canadensis	-0.24	<0.001
	Potamogeton amplifolius	-0.11	0.015
	Vallisneria americana	-0.13	0.009
Conductivity	*Chara* spp.	0.61	<0.001
	Myriophyllum sibiricum	0.10	0.020
	Elodea canadensis	-0.15	0.004
	Potamogeton amplifolius	-0.12	0.011
	Vallisneria americana	-0.14	0.007
pH	*Ceratophyllum demersum*	0.15	0.005
	Chara spp.	0.23	<0.001
	Myriophyllum sibiricum	0.10	0.020
	Elodea canadensis	-0.09	0.027
Calcium	*Ceratophyllum demersum*	0.08	0.044
	Chara spp.	0.56	<0.001
	Myriophyllum sibiricum	0.14	0.007
	Elodea canadensis	-0.16	0.003
	Vallisneria americana	-0.09	0.027
Magnesium	*Chara* spp.	0.65	<0.001
	Elodea canadensis	-0.26	<0.001
	Potamogeton amplifolius	-0.15	0.004
	Vallisneria americana	-0.13	0.008
Chlorophyll-*a*	*Ceratophyllum demersum*	0.12	0.012
Color	*Elodea canadensis*	0.18	0.001
	Potamogeton amplifolius	0.08	0.043
	Chara spp.	-0.13	0.008

Table 3 (continued). Significant relations between water chemistry levels and macrophyte species relative occurrence in the 53 Wisconsin lakes sampled. Species included in this analysis are listed in Table 2. Water chemistry variables are explained in Appendix K. Regression equations are listed in Appendix V.

	Macrophyte Species	r^2	P
Nitrogen	*Chara* spp.	0.20	0.001
	Elodea canadensis	-0.26	<0.001
	Potamogeton amplifolius	-0.18	0.001
	Potamogeton gramineus	-0.10	0.023
	Vallisneria americana	-0.09	0.030
Phosphorous	*Potamogeton gramineus*	-0.09	0.036

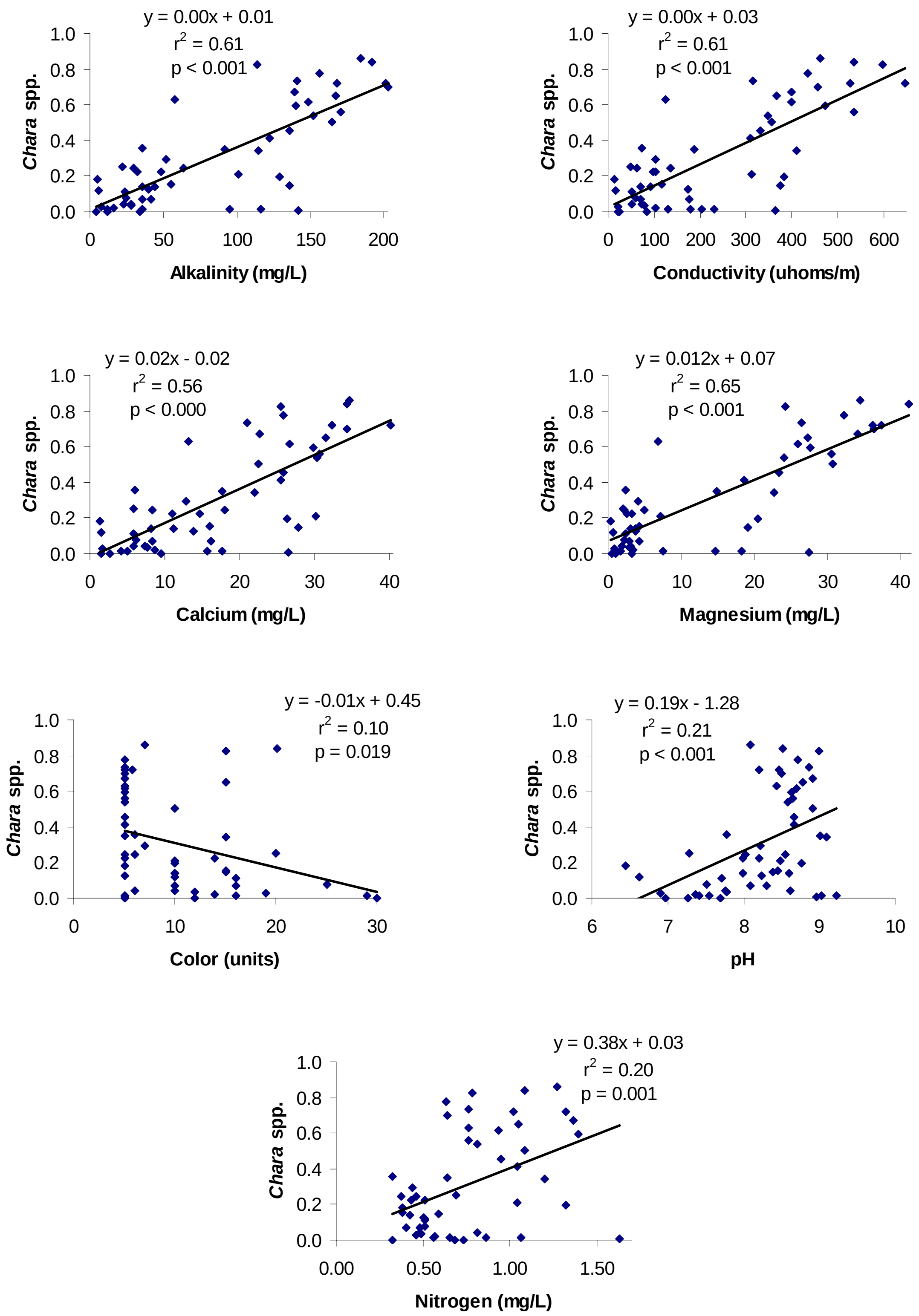

Figure 4. Linear regression models of *Chara* spp. relative occurrence response to water chemistry attributes in 50 Wisconsin lakes. Data in all regressions are not transformed.

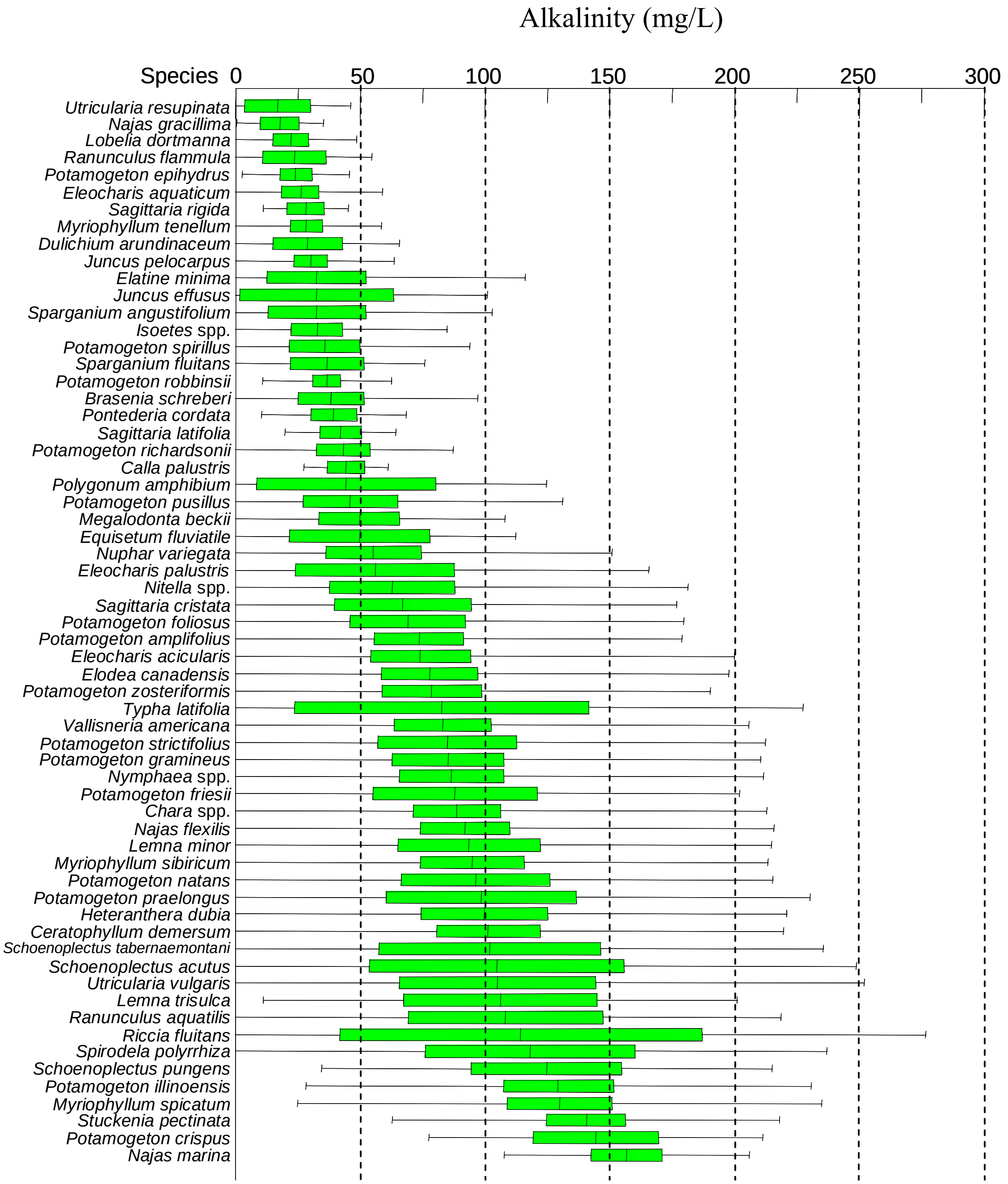

Figure 5. Specific alkalinity (mg/L) tolerances of individual macrophyte species occurring in five or more of the 53 Wisconsin lakes sampled. The center vertical bar in each box represents the mean. Boxes around the mean represent two standard errors about the mean and horizontal lines represent two standard deviations about the mean.

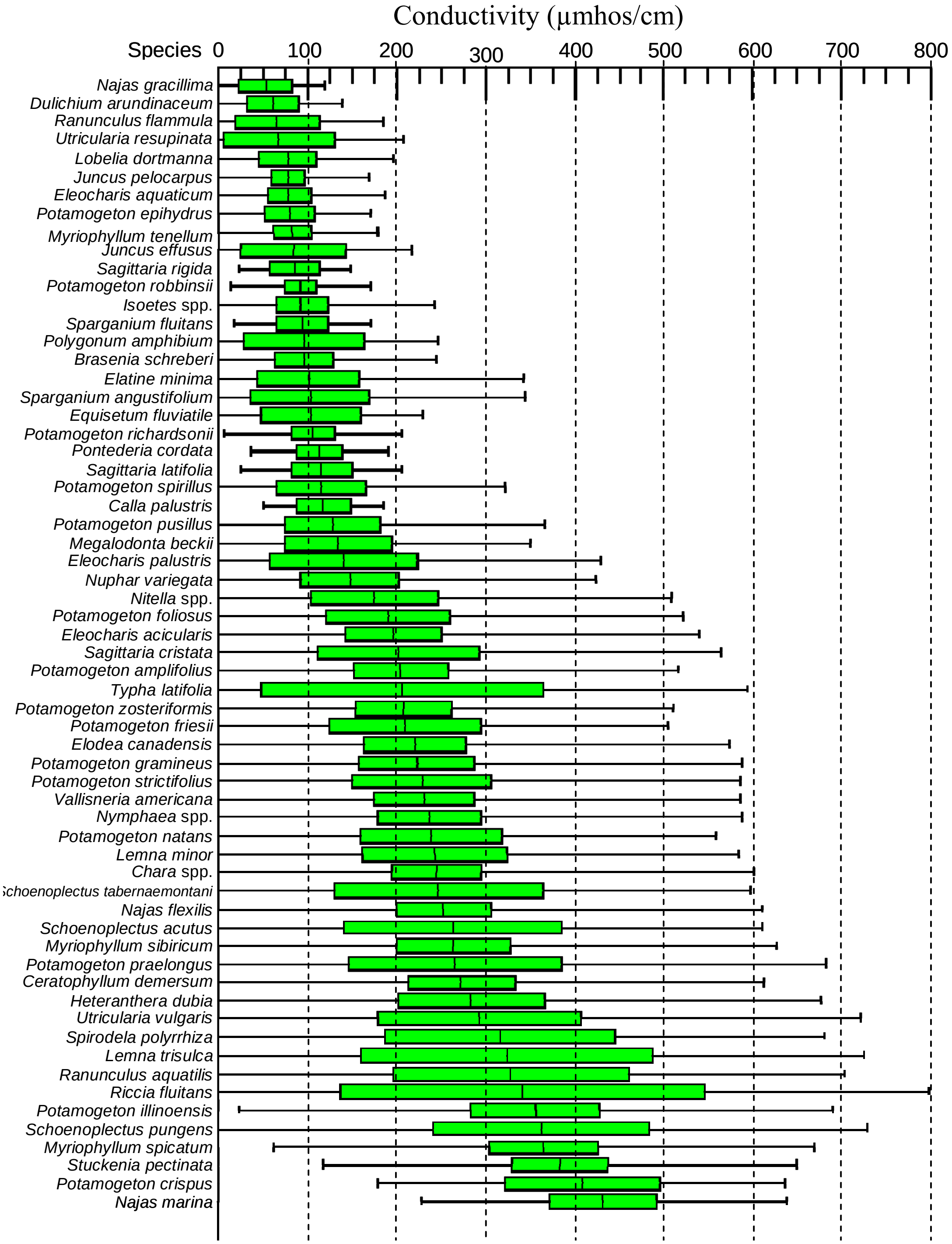

Figure 6. Specific conductivity (µmhos/cm) tolerances of individual macrophyte species occurring in five or more of the 53 Wisconsin lakes sampled. The center vertical bar in each box represents the mean. Boxes around the mean represent two standard errors about the mean and horizontal lines represent two standard deviations about the mean.

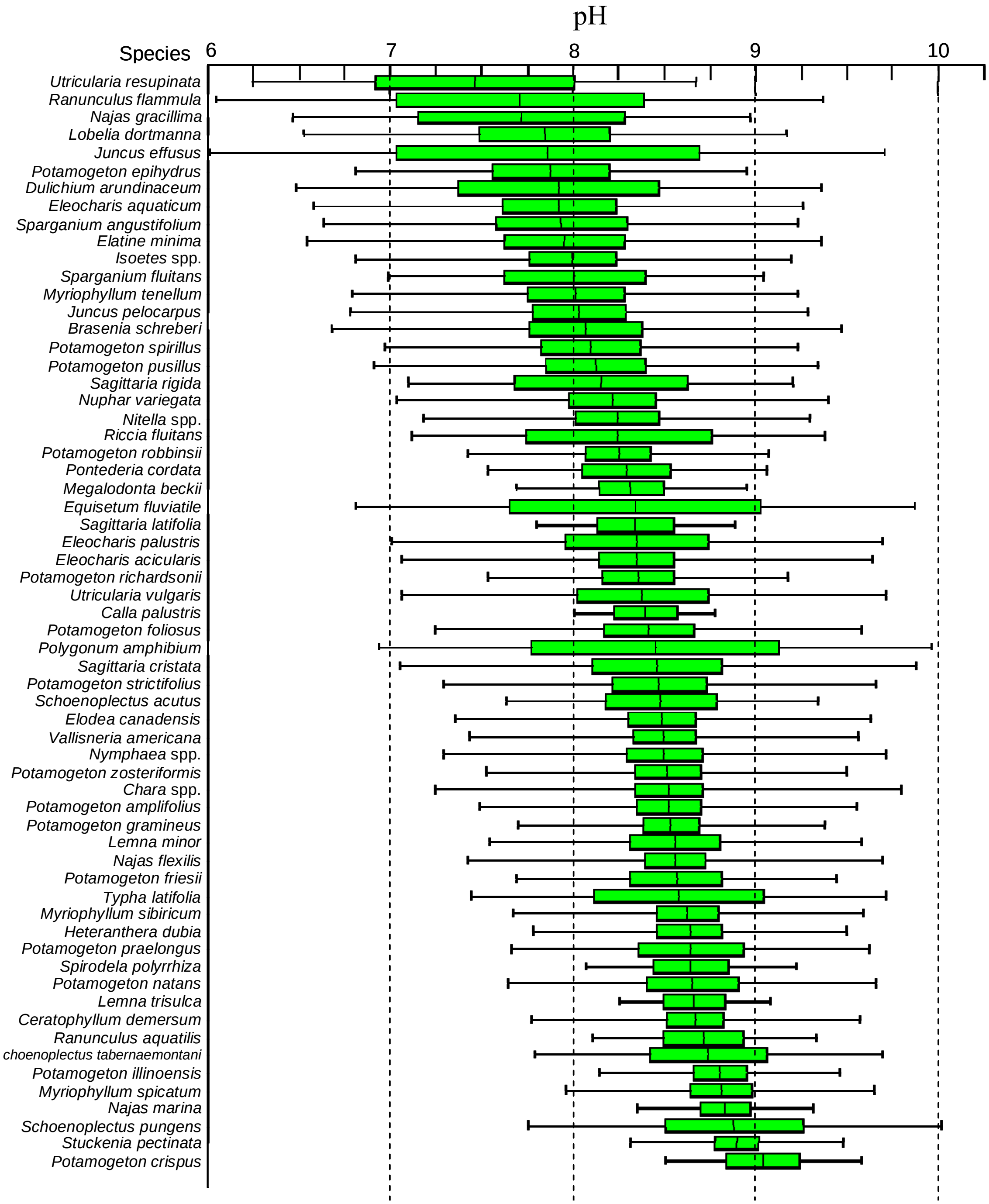

Figure 7. Specific pH tolerances of individual macrophyte species occurring in five or more of the 53 Wisconsin lakes sampled. The center vertical bar in each box represents the mean. Boxes around the mean represent two standard errors about the mean and horizontal lines represent two standard deviations about the mean.

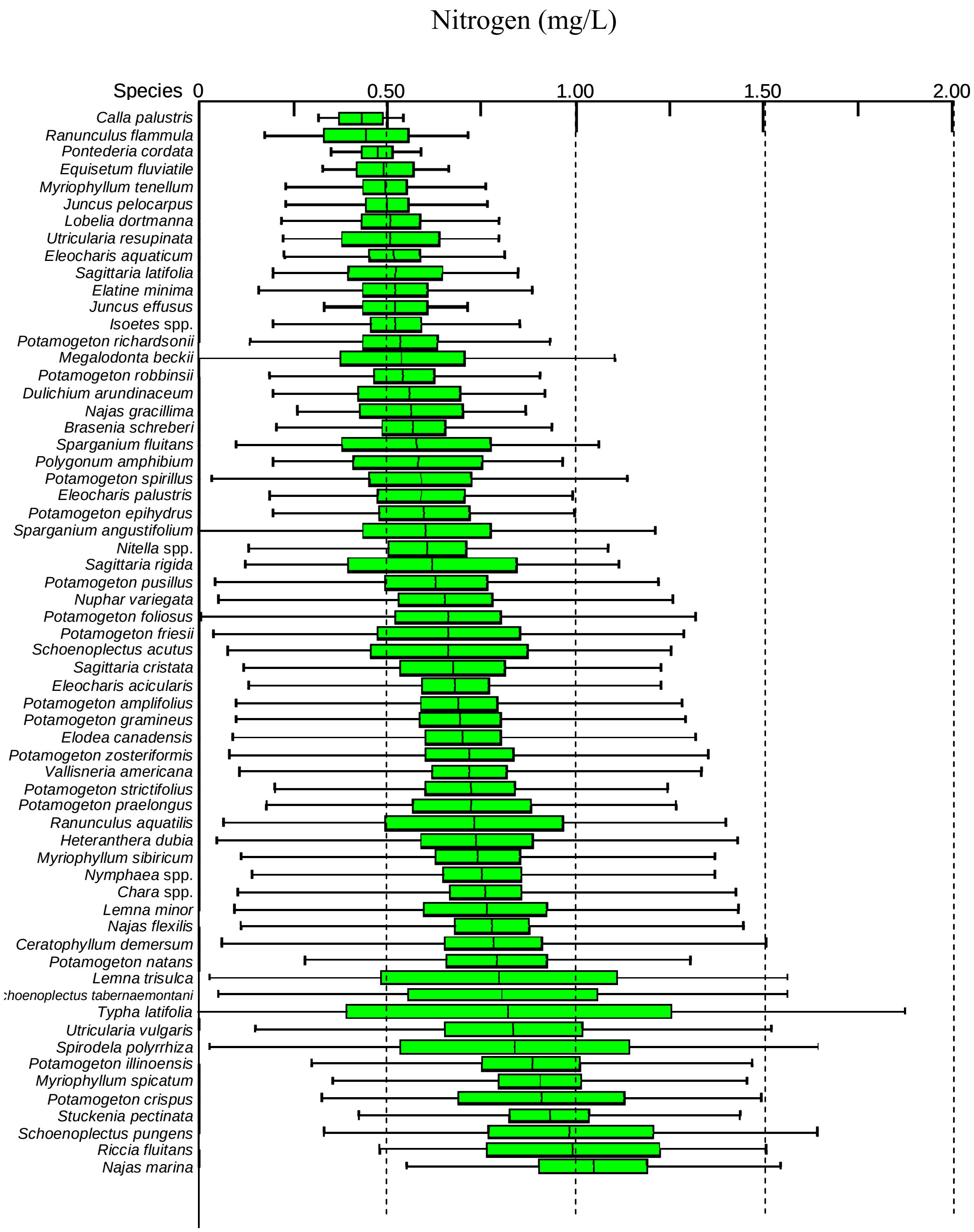

Figure 8. Specific nitrogen tolerances of individual macrophyte species occurring in five or more of the 53 Wisconsin lakes sampled. The center vertical bar in each box represents the mean. Boxes around the mean represent two standard errors about the mean, and horizontal lines represent two standard deviations about the mean.

considered, but the range of these measures across lakes was less variable and most species had similar ranges of occurrence (Appendices Y, Z, and AA).

Canonical correspondence analysis revealed distinct distributions of macrophyte species relative water chemistry characteristics of Wisconsin lakes (Figure 9, Appendix AB). Gradients of most water chemistry characteristics were correlated to and inversely related to latitude. The first two axes of the final CCA explained 32.7% of the variance in species-environment relations (Table 4). The most important predictors of macrophyte distribution were highly correlated with axis one and were latitude and concentrations of calcium, alkalinity, conductivity, nitrogen and magnesium. The second axis was primarily correlated with Secchi depth, and phosphorous and pH were moderately correlated with both axes. Macrophytes located to the upper left of the origin in the biplot occur in clear lakes with higher concentrations of alkalinity, conductivity, calcium, magnesium and nitrogen (Figure 9). Taxa plotted here are all submerged species including *N. marina, Chara* spp.*, S. pectinata,* and *P. illinoensis.* Species located in the lower left, including submerged species *M. spicatum, M. sibiricum, C. demersum, N. flexilis,* and *Heteranthera dubia,* and the floating-leaf *Nymphaea* spp., are more tolerant of turbid or stained (as indicated by Secchi depth), productive waters. Submerged species that tolerated lower water clarity but required lower concentrations of calcium, magnesium, alkalinity and conductivity included *E. canadensis, Potamogeton robbinsii, V. americana, P. amplifolius, and P. zosteriformis*. Taxa least tolerant of high nutrient concentrations and decreased water clarity included basal-growing plants such as *Elatine minima, Juncus pelocarpus, Eleocharis acicularis, Isoetes* spp., *Myriophyllum tenellum,* and also *Nitella* spp.; which tended to grow much deeper than other species.

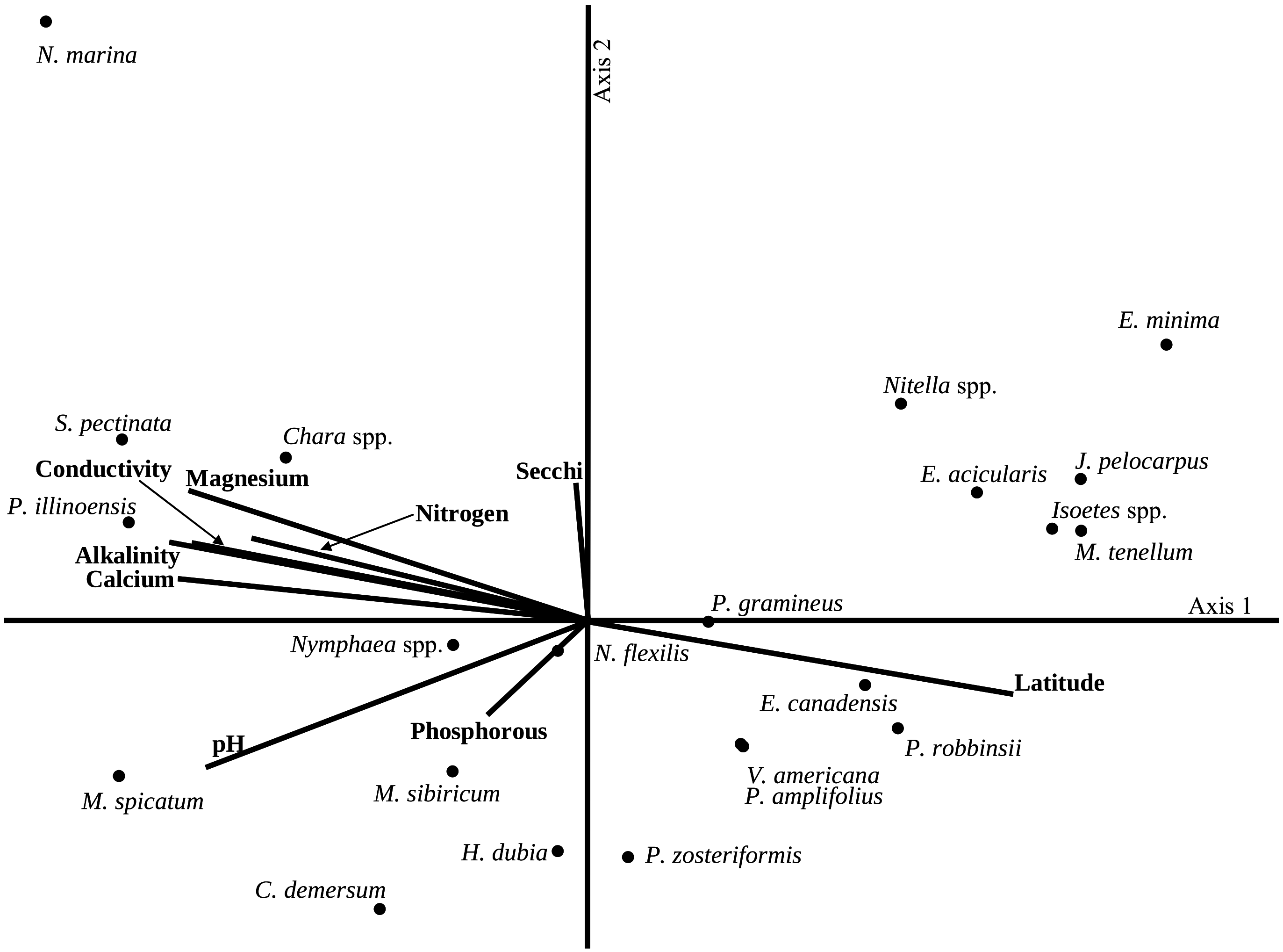

Figure 9. Canonical correspondence analysis biplot of aquatic macrophyte species occurring in ≥ 3% of statewide quadrats relative to environmental factors on CCA axes 1 and 2.

Table 4. Correlations of environmental variables with aquatic macrophyte species axes as determined by canonical correspondence analysis of the 53 Wisconsin lakes sampled.

Variable	Axis 1	Axis 2	Axis 3
Latitude	0.904	-0.156	0.145
Alkalinity	-0.896	0.169	0.073
Conductivity	-0.843	0.165	0.053
pH	-0.809	-0.314	0.094
Nitrogen	-0.719	0.180	0.083
Phosphorous	-0.213	-0.202	0.059
Calcium	-0.875	0.088	0.178
Magnesium	-0.855	0.279	0.064
Secchi depth	-0.027	0.292	0.285
Eigenvalues	0.476	0.191	0.123
% of variance explained	23.3	9.3	6.0
Cumulative % explained	23.3	32.7	38.7
Pearson Correlation	0.962	0.809	0.731

DISCUSSION

Aquatic macrophyte distributions are strongly linked to water chemistry (Moyle 1945, Swindale and Curtis 1957, Spence 1967, Seddon 1972). Bicarbonate concentrations often affect the composition of macrophyte communities (Toivonen and Huttunen 1995, Vestergaard and Sand-Jensen 2000). In addition, increasing nutrient levels in a lake can cause a shift in the macrophyte communities from submerged species to floating-leaf and emergent species (Egertson *et al.* 2004). Beyond the water chemistry gradient, other ecological factors such as competition, substrate type, anthropogenic perturbation, and predation likely play a role in the aquatic macrophyte community composition of any given lake.

OVERALL SPECIES RESPONSE TO WATER CHEMISTRY ATTRIBUTES

Bicarbonate concentrations (directly linked to alkalinity and conductivity in Wisconsin lakes (Spence 1967)) largely influenced the distribution of aquatic macrophytes across Wisconsin lakes in this study. Many species demonstrated specific ranges of tolerance and occurrence relative to these attributes. Vestergaard and Sand-Jensen (2000) suggested that bicarbonate should be considered the main determinant of aquatic macrophyte distributions because bicarbonate concentrations are closely and linearly related to alkalinity, conductivity, and pH in most fresh waters. This is also true in Wisconsin lakes (Spence 1967, Lillie and Mason 1983); species richness and relative occurrences of aquatic plants in this study were related to alkalinity, conductivity and pH, which was consistent with the findings of Vestergaard and Sand-Jensen (2000) and Toivonen and Huttunen (1995). However, Vestergaard and Sand-Jensen (2000) confirmed a correlation between macrophyte composition and alkalinity and pH, while

Toivonen and Huttunen (1995) stated that conductivity was more stable than pH in Finnish lakes and therefore a better indicator of trophic status and species richness. In this study, alkalinity and conductivity were highly correlated and both were very important to species richness and relative occurrence (Table 3, Appendices V and W). Specifically, *R. fluitans, Typha latifolia,* and *U. vulgaris* occurred in lakes with a wide range of alkalinity and conductivity concentrations, while smaller isoetids (i.e., small rosette species) such as *S. rigida, Calla palustris*, and *L. dortmanna* showed very narrow ranges of tolerance (Figures 5 and 6).

Bicarbonate concentration (e.g., alkalinity) was a better predictor of aquatic plant distribution than nutrient levels (e.g., nitrogen and phosphorus) in this study. In this study, nutrient concentrations were found at levels lower than previously reported for Wisconsin lakes in general (Juday and Birge 1931, Lillie and Mason 1983). Statewide, the mean phosphorus concentration (0.024 mg/L) was slightly lower than what Lillie and Mason (1983) found (0.031 mg/L), and in northern lakes, phosphorus concentrations (0.019 mg/L) were lower than results from Juday and Birge (1931) who found a mean of 0.023 mg/L. Our nitrogen levels (0.75 mg/L) were also lower than the mean concentration (0.86 mg/L) found by Lillie and Mason (1983). In addition species responses in this study were not completely consistent with those found in other studies, such as Blindow (1992) and Sand-Jensen *et al.* (2000), who documented a negative correlation between *Chara* spp. and eutrophication. In contrast, in this study *Chara* spp. was positively correlated with nitrogen, alkalinity, conductivity, pH, calcium, and magnesium levels. These findings may be partially explained by the fact that *Chara* was addressed as a whole genus; some species in the genus may be more tolerant of nitrogen levels than others (Spence 1967, Blindow 1992). In addition, Swindale and Curtis (1957) did find abundant *Chara* spp. in Wisconsin lakes with high conductivity.

Plant species richness in Wisconsin lakes was negatively correlated with nutrient status; species richness was greater in oligotrophic lakes than in mesotrophic lakes. This is contrary to the findings of Sand-Jensen *et al.* (2000) and Toivonen and Huttunen (1995), who found a unimodal response of plant species richness relative to eutrophication. The negative, linear response of macrophyte species richness with trophic status may be explained by the higher lakeshore residential development pressures associated with mesotrophic and eutrophic lakes in Wisconsin (Jennings *et al.* 2003). Development pressures may reduce species richness in these lakes via direct removal of plants, increase boat traffic or non-point runoff, which is supported by the findings of previous studies showing decline in aquatic macrophytes with lakeshore residential development (Bowen and Valiela 2001, Radomski and Goeman 2001, Jennings *et al.* 2003, Hatzenbeler *et al.* 2004). Often, the effects of lakeshore residential development may be species (or genus) specific or targeted towards particular plant morphologies. For example, plants that produce floating leaves or grow near the shoreline may be more prone to human removal or wave damage from storm events and recreational boating. As a result, vulnerable species may not have shown significant relations to increased water chemistry parameters because they were already absent because they may have been removed or destroyed.

INDIVIDUAL SPECIES OCCURRENCE IN RESPONSE TO WATER CHEMISTRY ATTRIBUTES

The trophic gradient of lakes in Wisconsin follows a latitudinal gradient such that mesotrophic and eutrophic lakes occur more frequently in southeastern Wisconsin, and many plant species are limited to specific ranges of these water chemistry parameters. For example, species such as *S. pectinata, M. spicatum, P. crispus* and *C. demersum* are generally restricted to mesotrophic and eutrophic waters (Seddon 1972, Blindow 1992, Vestergaard and Sand-Jensen 2000). Blindow (1992) documented abundant *S. pectinata, M. spicatum, P. crispus* and *C. demersum* in lakes with high nutrient levels. And Seddon (1972) also described these species as “obligate eutrophic” and confined to waters with conductivity >200 µmhos, but suggested that *C. demersum* is more tolerant of lower concentrations of bicarbonate than the other three species. While these species are considered generalists by other researchers and in the findings of this study (Seddon 1972, Nichols 1999b, Heegaard *et al.* 2001), the responses of these species to water chemistry attributes (e.g. nitrogen, alkalinity, pH, etc.) would indicate that even “tolerant” aquatic plants are at least somewhat constrained (Figures 5-8). Species not included in this analysis due to low relative occurrence may be even more sensitive to water chemistry than plants that were included.

Potamogeton spp. are strongly influenced by eutrophication. The response of native *Potamogeton* spp. to nutrient concentrations, in this study was consistent with prior research (Moyle 1945, Jackson and Charles 1987, Nichols 1999a, b, Riis and Sand-Jensen 2001, Egertson *et al.* 2004). In Danish streams, Riis and Sand-Jensen (2001) documented a large decline in *Potamogeton* spp. with an increase in eutrophication. Individual species including *P. gramineus, P. pusillus, P. friesii, P. praelongus*, and *P. natans* declined or were lost in their study due to increased water chemistry attributes. *Potamogeton*’s in this study were restricted to alkalinities <250 mg/L and nitrogen levels <1.5 mg/L. In addition, Egertson *et al.* (2004) found several species to decline due to increased nutrients in their study that were also documented in our research lakes (*P. praelongus, P. friesii, P. richardsonii, P. natans, P. filiformis, P. obtusifolius, P. pusillus,* and *Myriophyllum heterophyllum,*), but at abundances less than 5% (Egertson *et al.* 2004). Our results may indicate that these rare species have already been impacted in more eutrophic lakes to a point that they only occur at minimal levels if at all.

While the tolerance ranges observed for individual species in Wisconsin lakes were generally consistent with other research, a few relations contradicted previous observations. Prior observations suggested that *P. gramineus* and *Chara* spp. were intolerant to increased alkalinity and conductivity concentrations (Sand-Jensen *et al.* 2000, Vestergaard and Sand-Jensen 2000). This study indicated that these species occurred in lakes spanning a fairly wide range of ecological conditions (though relative occurrences of both species declined with increasing nutrients). And the CCA suggests that *Chara* spp. is quite tolerant of these attributes.

Other species in our study responded similarly to prior observations. According to Sand-Jensen *et al.* (2000) and Egertson *et al.* (2004), a decline in *P. zosteriformis* and an increase in *Nymphaea* spp. and *S. pectinata* were expected with an increase in nutrient concentrations. The CCA suggests that *P. zosteriformis* grows best in lakes with lower nutrient levels, and *S. pectinata* was more associated with higher levels. *Nymphaea* spp. were also associated with higher levels of nutrient concentrations, but were more apt to be tolerant of reduced water clarity.

AN EXPLANATION OF WATER CHEMISTRY IN WISCONSIN LAKES

Water chemistry of Wisconsin lakes is strongly linked to geological and anthropogenic factors. Chemical gradients of alkalinity, conductivity, calcium, magnesium, and pH found across Wisconsin lakes can be explained by bedrock geology and the land use history of the state (Kenoyer and Anderson 1989, Omernik *et al.* 2000). Northern Wisconsin bedrock is predominantly granite, rhyolitic, and metavolcanic rock (Mudrey *et al.* 1982). Therefore, soils and groundwater in the northern ecoregion does not carry high levels of calcium carbonate like groundwater in southeastern Wisconsin. Southeastern Wisconsin bedrock is predominately dolomite with some limestone and shale. Sedimentary dolomite is easily eroded and has high amounts of calcium carbonate, which in turn, provides a buffer to pH changes in lakes occurring in this area. Land in southeastern Wisconsin is also much more agricultural, fertile, and less wooded relative to northern Wisconsin. Runoff from such areas may provide increased nutrient inputs into the southeastern lakes (Carpenter *et al.* 1998).

Lentic water chemistry plays an integral role in the structure of aquatic plant communities. This study presents a description of the distribution of aquatic plant taxa in relation to the water chemistry of Wisconsin lakes. This study clearly shows aquatic macrophytes do not delineate into distinct tolerance groups, but rather occur along continuous series of ecological gradients that follow natural and anthropogenic patterns. Where a lake falls along this gradient may provide the best indication of species occurrence across lakes.

Aquatic macrophyte distributions in Wisconsin lakes are increasingly affected by eutrophication. Heegaard *et al.* (2001) suggested that, "The strong negative correlation of many species to high ionic content may be due to their intolerance, but it may also be influenced by the potential increase in competition during eutrophication". For example, basal-growing plants are more likely to be shaded out by larger, leafy plants, but may have an advantage over the larger plants in areas with certain substrate types or increased wave action. Eutrophication is something that is not likely to end in the foreseeable future. Therefore, studies such as this one are imperative to not only gain knowledge on the response of aquatic macrophytes to eutrophication, but also to provide baseline data for studies in the future.

MANAGEMENT IMPLICATIONS

Characterization of macrophyte species tolerance to water chemistry is essential in understanding the structure aquatic plant communities. Data collected for this project can be used to compare to previous work and predict partial change in aquatic macrophyte community composition as Wisconsin lakes evolve over time. These data can be compared to prior research by Wilson (1939), Swindale and Curtis (1957), and Nichols (1999b) to index the quality of aquatic macrophyte communities in Wisconsin lakes regionally and statewide, to determine lists of expected species for ecoregions in Wisconsin, and to understand how aquatic macrophyte communities are changing as watersheds become more developed.

Sculthorpe's (1967) paper raises the concern that studies showing a wide range of tolerance for many aquatic species are addressing the issue with too gross and ill-defined independent variables such as total hardness. This project includes specific measures of calcium and magnesium which may help managers know where to target efforts for conservation. In addition, this project provides insight into how species respond across latitude and inter-related water chemistry attributes including alkalinity, conductivity, calcium, magnesium, phosphorus, nitrogen, pH, and Secchi. This approach may account for not having finer criteria by incorporating more of the variation that effect plant distribution and species composition.

Increasing the amount of information collected on Wisconsin lakes and macrophyte communities provides essential reference material for future research and management. While each aquatic macrophyte species has its own range of tolerance to water chemistry attributes, Lougheed *et al.* (2001) suggested that community type may be a better indicator of quality than the presence of individual species. The results of this study are consistent with the findings of Nichols (1999a), who developed a quality assessment index for aquatic macrophytes in Wisconsin lakes. My research supplements the work of Nichols (1999a, b) and can be used to categorize macrophytes by tolerances and Wisconsin lakes by macrophyte community type.

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APPENDIX A. Physical locations of 53 Wisconsin lakes sampled (26 southeastern and 27 northern).

Lake	County	Township	Range	Section	Latitude
		Northern Ecoregion			
Arrowhead	Vilas	40N	06E	35	50.87145
Bear	Oneida	43N	06E	25	50.71872
Big Carr	Oneida	38N	07E	9	50.74082
Booth	Oneida	39N	05E	6	50.85880
Brandy	Vilas	40N	06E	35	50.87253
Cyclone	Washburn	39N	13W	26	50.75614
Deer	Burnett	41N	14W	7	50.99138
Deerskin	Vilas	41N	11E	31	50.93603
Erickson	Vilas	40N	07E	16	50.91536
Found	Vilas	40N	08E	14	50.91624
Gunlock	Vilas	40N	05E	36	50.88276
Hilts	Lincoln	35N	08E	15	50.44329
Horsehead	Oneida	37N	07E	16	50.64035
Johnson	Oneida/Vilas	40N	06E	34	50.86483
Julia	Oneida	36N	08E	12	50.54047
Lawrence	Langlade	32N	12E	15	50.13755
Lone Stone	Oneida	39N	11E	11	50.81164
Manson	Oneida	36N	07E	32	50.48811
Muskellunge	Oneida	38N	08E	3	50.74717
Person	Douglas	43N	13W	22	51.15662
Round	Vilas	43N	06E	35	51.16712
Silver	Vilas	40N	10E	27	50.87748

APPENDIX A (continued). Physical locations of 53 Wisconsin lakes sampled (26 southeastern and 27 northern).

Lake	County	Township	Range	Section	Latitude
Squaw	Lincoln	35N	08E	10	50.45251
Tahkodah	Bayfield	44N	07W	34	51.22646
Tom Doyle	Oneida	38N	08E	28	50.70871
Towanda	Vilas	40N	06E	23	50.90693
Townline	Oneida	39N	11E	31	50.75615
		Southeastern Ecoregion			
Ashippun	Waukesha	08N	17E	15	47.79321
Bohner	Racine	02N	19E	17	47.20255
Booth	Walworth	04N	17E	13	47.39671
Bullhead	Manitowoc	19N	21E	19	48.83854
Clear	Rock	04N	13E	20	47.40417
Denoon	Racine	04N	20E	5	47.44466
English	Manitowoc	18N	23E	7	48.77221
Fish	Dane	09N	07E	3	47.96163
Forest	Fond Du Lac	13N	19E	12	48.28942
Gibbs	Rock	04N	11E	27	47.38920
Keesus	Waukesha	08N	18E	14	47.80080
Little Elkhart	Sheboygan	16N	21E	34	48.51032
Lower Genesee	Waukesha	07N	17E	27	47.66779
Middle Genesee	Waukesha	07N	17E	22	47.67515
Moose	Waukesha	08N	18E	19	47.76753
Paddock	Kenosha	01N	20E	2	47.13986
Pleasant	Walworth	04N	16E	24	47.38399
Potter	Walworth	04N	18E	11	47.41383
Pretty	Waukesha	06N	17E	28	47.56880

APPENDIX A (continued). Physical locations of 53 Wisconsin lakes sampled (26 southeastern and 27 northern).

Lake	County	Township	Range	Section	Latitude
Silver	Columbia	12N	09E	6	48.25122
Silver	Waukesha	07N	17E	9	47.70461
Silver	Washington	11N	19E	27	48.04622
Tuttle	Marquette	17N	10E	22	48.66626
Upper Nashotah	Waukesha	07N	17E	12	47.71314
Wallace	Washington	11N	20E	6	48.11540
Wilke	Manitowoc	17N	21E	2	48.68974

APPENDIX B. Physical characteristics of 53 Wisconsin lakes sampled (26 southeastern and 27 northern). N.C. represents data that were not collected.

Lake	Watershed Area (ha)	Surface Area (ha)	Perimeter (km)	House Density	Proportion Agriculture	Proportion Urban	Maximum Depth (m)
Northern Ecoregion							
Arrowhead	788.44	39.15	3.21	22.76	0.09	0.26	13.11
Bear	294.06	119.58	7.06	15.15	0.00	0.08	9.14
Big Carr	504.76	84.53	6.07	7.09	0.07	0.06	21.64
Booth	381.03	82.62	6.26	13.09	0.00	0.16	10.36
Brandy	1659.10	45.64	3.47	21.33	0.06	0.17	13.41
Cyclone	62.67	34.75	2.45	15.13	0.09	0.04	5.49
Deer	216.04	65.26	4.92	10.36	0.04	0.09	5.49
Deerskin	553.79	121.87	6.47	14.84	0.01	0.10	5.49
Erickson	796.90	44.41	3.57	0.28	0.00	0.00	5.49
Found	1214.35	136.42	6.13	16.81	0.00	0.04	6.40
Gunlock	458.49	106.77	7.71	11.41	0.00	0.09	7.92
Hilts	68.04	24.64	2.42	7.43	0.00	0.05	21.34
Horsehead	230.19	58.79	4.87	18.29	0.03	0.09	7.92
Johnson	2205.32	34.29	3.55	17.20	0.06	0.24	12.80
Julia	276.17	97.54	6.01	11.14	0.03	0.19	5.79
Lawrence	367.63	20.27	2.79	0.00	0.00	0.00	14.33
Lone Stone	262.90	69.11	3.45	11.02	0.00	0.06	8.84
Manson	402.69	95.68	6.06	17.66	0.01	0.09	16.46
Muskellunge	540.08	116.05	6.87	7.28	0.00	0.04	7.32
Person	223.16	70.47	4.44	14.18	0.16	0.13	3.05
Round	N.C.	N.C.	N.C.	N.C.	N.C.	N.C.	7.62
Silver (Vilas County)	58.83	23.27	2.15	12.55	0.00	0.62	3.66

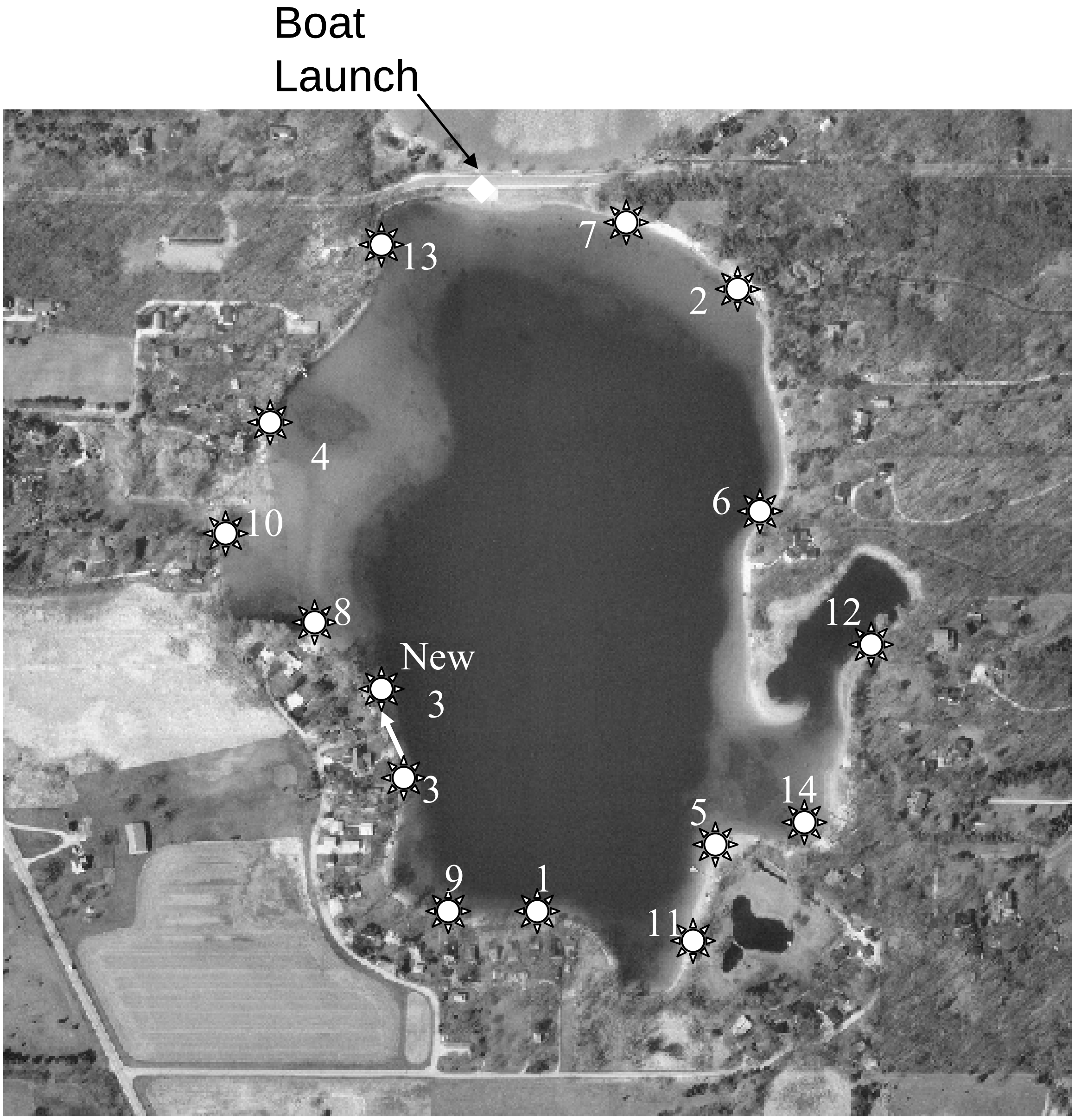
Appendix B (continued). Physical characteristics of 53 Wisconsin lakes sampled (26 southeastern and 27 northern). N.C. represents data that were not collected.

Lake	Watershed Area (ha)	Surface Area (ha)	Perimeter (km)	House Density	Proportion Agriculture	Proportion Urban	Maximum Depth (m)
Squaw	804.11	33.63	4.34	10.82	0.02	0.05	12.80
Tahkodah	227.99	59.82	4.21	13.29	0.14	0.14	5.49
Tom Doyle	867.79	44.34	3.75	13.07	0.01	0.03	9.14
Towanda	472.48	56.49	5.85	11.97	0.00	0.21	8.23
Townline	907.13	57.57	3.67	18.82	0.13	0.21	5.79
Southeastern Ecoregion							
Ashippun	204.99	38.13	3.50	8.57	0.50	0.19	12.19
Bohner	387.24	54.76	3.16	38.60	0.16	0.48	9.14
Booth	60.60	48.67	2.60	30.77	0.05	0.56	7.32
Bullhead	98.62	28.13	2.06	9.72	0.60	0.12	12.19
Clear	433.89	31.33	2.29	33.61	0.47	0.14	6.10
Denoon	276.63	68.01	3.99	27.55	0.36	0.36	16.76
English	61.52	19.40	1.76	32.46	0.63	0.30	27.43
Fish	413.24	99.29	4.86	10.71	0.49	0.06	18.90
Forest	38.34	20.51	2.17	22.58	0.00	0.39	9.75
Gibbs	592.42	29.46	2.09	2.87	0.73	0.03	7.01
Keesus	942.71	95.23	8.51	23.85	0.67	0.08	12.80
Little Elkhart	276.90	23.35	3.47	14.41	0.22	0.21	7.62
Lower Genesee	40.31	25.54	2.31	18.21	0.16	0.35	13.72
Middle Genesee	148.65	40.76	2.51	15.13	0.64	0.26	12.19
Moose	245.88	33.86	4.03	26.54	0.08	0.28	18.59
Paddock	115.56	52.28	1.54	27.88	0.16	0.82	9.75
Pleasant	286.13	58.75	4.24	16.76	0.47	0.13	8.84
Potter	198.52	62.68	4.21	32.79	0.22	0.64	7.92

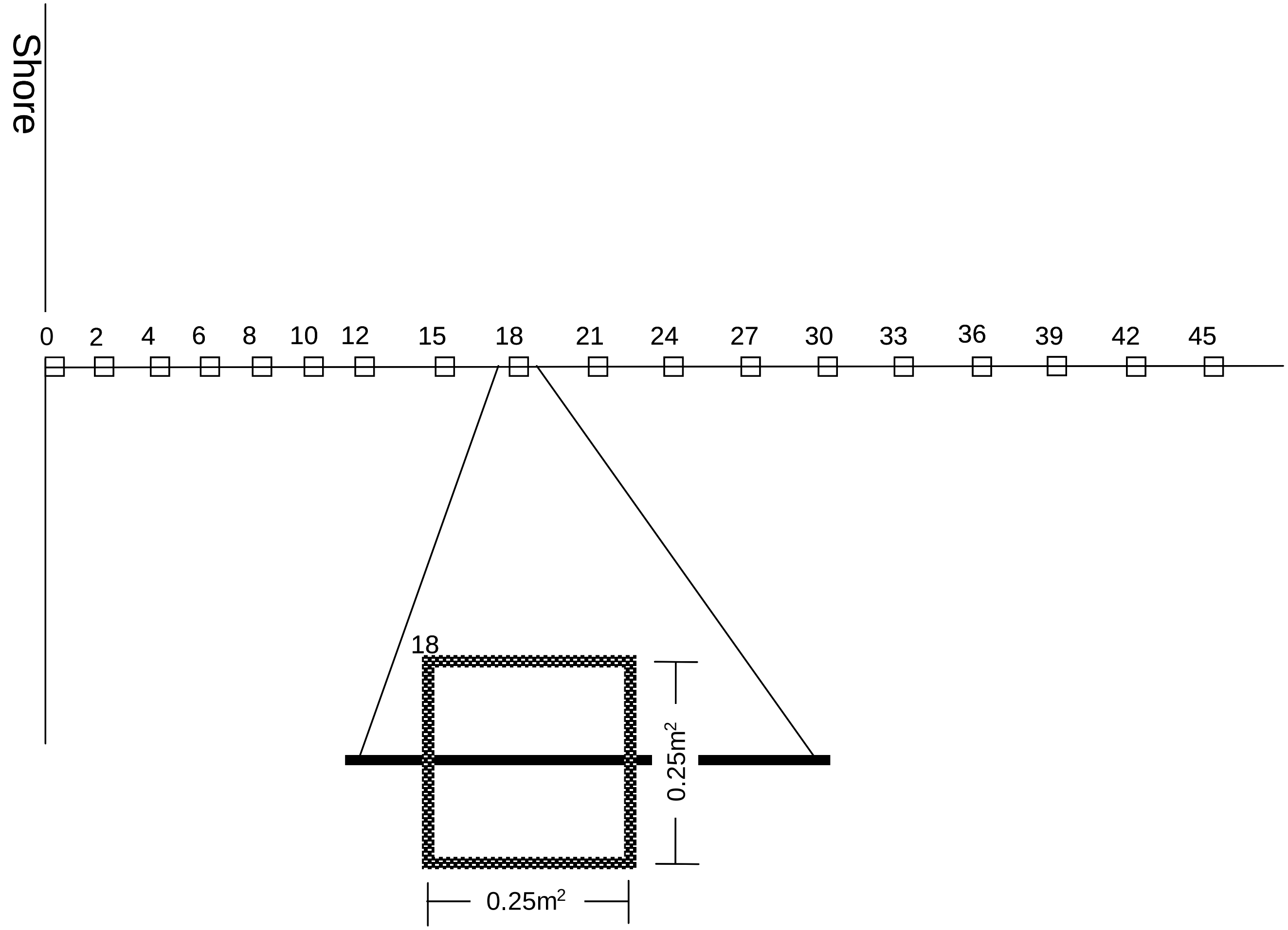
Appendix B (continued). Physical characteristics of 53 Wisconsin lakes sampled (26 southeastern and 27 northern). N.C. represents data that were not collected.

Lake	Watershed Area (ha)	Surface Area (ha)	Perimeter (km)	House Density	Proportion Agriculture	Proportion Urban	Maximum Depth (m)
Pretty	27.14	26.24	2.12	42.02	0.08	0.08	10.67
Silver (Columbia County)	514.90	87.84	3.42	13.30	0.18	0.68	12.80
Silver (Washington County)	183.28	29.92	4.51	33.05	0.00	0.60	14.33
Silver (Waukesha County)	230.22	49.54	4.81	15.38	0.08	0.43	13.41
Tuttle	44.49	63.16	3.23	30.64	0.03	0.45	10.06
Upper Nashotah	443.50	53.10	3.66	10.38	0.39	0.23	16.15
Wallace	225.73	22.52	2.40	26.68	0.18	0.27	10.67
Wilke	257.28	37.74	2.70	34.31	0.69	0.08	6.40

APPENDIX C. Digital Orthophoto (DOP) of Lower Genesee Lake, Wisconsin (T7N R17E S27) outlining sample site collection protocols. Fourteen random stratified terrestrial sites were selected. Two strata were chosen: developed (7) (even numbered) and undeveloped (7) (odd numbered) sites. If one stratum was completely filled during the selection process (i.e., less than seven sites could be found lake-wide), more sites of the remaining stratum were sampled to total 14. In the field, if a site did not correspond with the stratum assigned, the next available site found in a clockwise rotation was sampled. For example, see site 3 in diagram, if site 3 was not undeveloped, the location was moved to the next possible undeveloped site (same for developed sites).



APPENDIX D. Schematic of sampling design showing the placement of each 0.25m^2 quadrat. Transects were placed perpendicular to shore out to a distance of 45 meters. A sampling quadrat was placed every 2 meters for the first 12 meters, then every 3 meters out to 45 meters from shore. Each quadrat was placed on the transect with the near-shore edge centered on the appropriate meter mark.



APPENDIX E. Mean, standard error (S.E.) about the mean, and range of relative occurrences of macrophyte species selected for analysis in 53 Wisconsin lakes (26 southeastern and 27 northern). Relative occurrence is the proportion of total quadrats in a lake in which each species occurred. Bold values represent plant occurrence in ≥ 5 percent of the total quadrats in that ecoregion. If there is no value for a species, it did not occur in any lakes in that ecoregion. Mann-Whitney U-stats and P-values (P) are reported for species that are included in the statewide analyses (southeastern and northern ecoregions combined).

Macrophyte	Southeastern Ecoregion		Northern Ecoregion			
Species	Mean (±S.E.)	Range	Mean (±S.E.)	Range	U-stat	P
Brasenia schreberi	0.00 (0.00)	0.00-0.01	**0.05 (0.02)**	**0.00-0.41**	-	-
Ceratophyllum demersum	**0.14 (0.05)**	**0.00-0.77**	**0.07 (0.02)**	**0.00-0.32**	292.0	0.281
Chara spp.	**0.50 (0.05)**	**0.01-0.86**	**0.12 (0.02)**	**0.00-0.35**	97.0	<0.001
Elatine minima	0.00 (0.00)	0.00-0.02	**0.09 (0.03)**	**0.00-.049**	-	-
Eleocharis acicularis	0.02 (0.01)	0.00-0.28	**0.14 (0.02)**	**0.00-0.46**	-	-
Eleocharis palustris	0.00 (0.00)	0.00-0.05	0.01 (0.00)	0.00-0.04	-	-
Elodea canadensis	0.02 (0.01)	0.00-0.14	**0.18 (0.03)**	**0.00-0.50**	567.5	<0.001
Isoetes spp.	0.00 (0.00)	0.00-0.01	**0.16 (0.03)**	**0.00-0.61**	-	-
Juncus pelocarpus	0.00 (0.00)	0.00-0.01	**0.12 (0.02)**	**0.00-0.49**	-	-
Lemna trisulca	**0.05 (0.04)**	**0.00-0.85**	0.00 (0.00)	0.00-0.06	-	-
Lobelia dortmanna	-	-	**0.05 (0.02)**	**0.00-0.44**	-	-
Myriophyllum sibiricum	**0.08 (0.02)**	**0.00-0.31**	**0.06 (0.02)**	**0.00-0.37**	284.0	0.218
Myriophyllum spicatum	**0.26 (0.06)**	**0.00-0.87**	0.01 (0.00)	0.00-0.10	-	-
Myriophyllum tenellum	-	-	**0.11 (0.03)**	**0.00-0.50**	-	-
Najas flexilis	**0.27 (0.04)**	**0.00-0.65**	**0.28 (0.04)**	**0.00-0.60**	374.5	0.676
Najas marina	**0.07 (0.03)**	**0.00-0.52**	-	-	-	-
Nitella spp.	0.01 (0.01)	0.00-0.15	**0.06 (0.02)**	**0.00-0.34**	-	-
Nymphaea spp.	**0.05 (0.02)**	**0.00-0.39**	0.04 (0.01)	0.00-0.20	363.5	0.821
Potamogeton amplifolius	0.03 (0.01)	0.00-0.22	**0.08 (0.01)**	**0.00-0.24**	514.5	0.003
Potamogeton gramineus	**0.05 (0.02)**	**0.00-0.30**	**0.13 (0.03)**	**0.00-0.45**	461.0	0.043
Potamogeton illinoensis	**0.10 (0.02)**	**0.00-0.35**	0.00 (0.00)	0.00-0.03	-	-
Potamogeton pusillus	0.00 (0.00)	0.00-0.05	**0.05 (0.01)**	**0.00-0.24**	-	-
Potamogeton richardsonii	0.00 (0.00)	0.00-0.01	**0.05 (0.01)**	**0.00-0.16**	-	-

APPENDIX E (continued). Mean, standard error (S.E.) about the mean, and range of relative occurrences of macrophyte species selected for analysis in 53 Wisconsin lakes (26 southeastern and 27 northern). Relative occurrence is the proportion of total quadrats in a lake in which each species occurred. Bold values represent plant occurrence in ≥ 5 percent of the total quadrats in that ecoregion. If there is no value for a species, it did not occur in any lakes in that ecoregion. Mann-Whitney U-stats and P-values (P) are reported for species that are included in the statewide analyses (southeastern and northern ecoregions combined).

Macrophyte	Southeastern Ecoregion		Northern Ecoregion			
Species	Mean (±S.E.)	Range	Mean (±S.E.)	Range	U-stat	P
Potamogeton robbinsii	0.00 (0.00)	0.00-0.03	**0.18 (0.03)**	**0.00-0.53**	-	-
Potamogeton spirillus	0.00 (0.00)	0.00-0.02	**0.05 (0.02)**	**0.00-0.42**	-	-
Potamogeton zosteriformis	0.04 (0.02)	0.00-0.42	**0.07 (0.02)**	**0.00-0.25**	467.5	0.031
Stuckenia pectinata	**0.10 (0.02)**	**0.00-0.35**	0.00 (0.00)	0.00-0.06	-	-
Typha latifolia	0.00 (0.00)	0.00-0.01	0.00 (0.00)	0.00-0.03	-	-
Vallisneria americana	**0.10 (0.03)**	**0.00-0.58**	**0.28 (0.04)**	**0.00-0.60**	527.5	0.002

APPENDIX F. Guilds chosen for analysis: definition and example species. Species included in each guild are listed in Appendix G.

Guild	Criteria	Example species
Basal Species	Rooted, submerged plants that grow in basal rosette form and do not produce floating leaves.	*Eriocaulon aquaticum*
Emergent Species	Plants that grow in the shoreline-interface zone.	*Carex* spp.
Exotic Species	All non-natives	*Myriophyllum spicatum*
Lily Pads	Rooted plants that produce floating leaves but have minimal submerged leafy structure below the surface of the water.	*Nuphar variegata*
Potamogeton spp.	All species in the *Potamogeton* genus.	*Potamogeton amplifolius*
FL_RT	All rooted plants that produce floating leaves (some with submerged leafy structure).	*Potamogeton epihydrus*
FL_NRT	Plants not rooted, that produce floating leaves (duckweeds)	*Lemna minor*
NFL_RT	Rooted plants that do not produce floating leaves	*Vallisneria americana*
NFL_NRT	Plants not rooted and do not produce floating leaves (suspended in water column or settled on the bottom)	*Ceratophyllum demersum*

APPENDIX G. List of macrophyte species included in each guild chosen for analysis. All observed species were considered for guilds. Guilds were analyzed as dependent variables.

Lily Pads

Brasenia schreberi
Nuphar advena
Nuphar variegata
Nymphaea odorata

Emergent Species

Calla palustris
Carex comosa
Carex viridula
Cicuta bulbifera
Decodon verticillatus
Dulichium arundinaceum
Eleocharis palustris
Equisetum spp.
Equisetum fluviatile
Eupatorium spp.
Glyceria borealis
Hypericum perforatum
Impatiens capensis
Iris spp.
Juncus effuses
Leersia oryzoides
Lythrum spp.
Phalaris arundinacea
Pontederia cordata
Sagittaria latifolia
Schoenoplectus acutus
Schoenoplectus pungens
Schoenoplectus tabernaemontani
Scirpus pallidus
Scirpus spp.
Sium suave
Sparganium americanum
Sparganium androcladum
Sparganium eurycarpum
Triadenum spp.
Typha angustifolia
Typha latifolia
Veronica anagallis-aquatica
Zizania spp.

Floating-leaved, not rooted (FL_NRT)

Lemna minor
Lemna trisulca
Spirodela polyrrhiza
Wolffia Columbiana

***Potamogeton* spp.**

P. alpinus
P. amplifolius
P. bicupulatus
P. crispus
P. diversifolius
P. epihydrus
P. foliosus
P. friesii
P. gramineus
P. illinoensis
P. natans
P. praelongus
P. pusillus
P. richardsonii
P. robbinsii
P. spirillus
P. strictifolius
P. vaseyi
P. zosteriformis

Exotic Species

Myriophyllum spicatum
Najas marina
Phalaris arundinacea
Potamogeton crispus
Typha angustifolia

Suspended Species (NFL_NRT)

Ceratophyllum demersum
Chara spp.
Fissidens (*moss*)
Nitella spp.
Utricularia gibba
Utricularia purpurea
Utricularia vulgaris

APPENDIX G (continued). List of macrophyte species included in each guild chosen for analysis. All observed species were considered for guilds. Guilds were analyzed as dependent variables.

Submerged Species (NFL_RT)

Elodea canadensis
Elodea nuttallii
Heteranthera dubia
Megalodonta beckii
Myriophyllum alterniflorum
Myriophyllum heterophyllum
Myriophyllum sibiricum
Myriophyllum spicatum
Najas flexilis
Najas gracillima
Najas guadalupensis
Najas marina
Potamogeton alpinus
Potamogeton amplifolius
Potamogeton bicupulatus
Potamogeton crispus
Potamogeton diversifolius
Potamogeton epihydrus
Potamogeton foliosus
Potamogeton friesii
Potamogeton gramineus
Potamogeton illinoensis
Potamogeton praelongus
Potamogeton pusillus
Potamogeton robbinsii
Potamogeton spirillus
Potamogeton strictifolius
Potamogeton vaseyi
Potamogeton zosteriformis
Ranunculus spp.
Ranunculus aquatilis
Ranunculus flammula
Ruppia cirrhosa
Schoenoplectus subterminalis
Stuckenia pectinata
Vallisneria americana
Zannichellia palustris

Basal Species

Elatine minima
Eleocharis acicularis
Eriocaulon aquaticum
Gratiola aurea
Isoetes spp.
Juncus pelocarpus
Lobelia dortmanna
Myriophyllum tenellum
Riccia fluitans
Sagittaria cristata/graminea
Sagittaria rigida
Sagittaria spp.
Utricularia resupinata

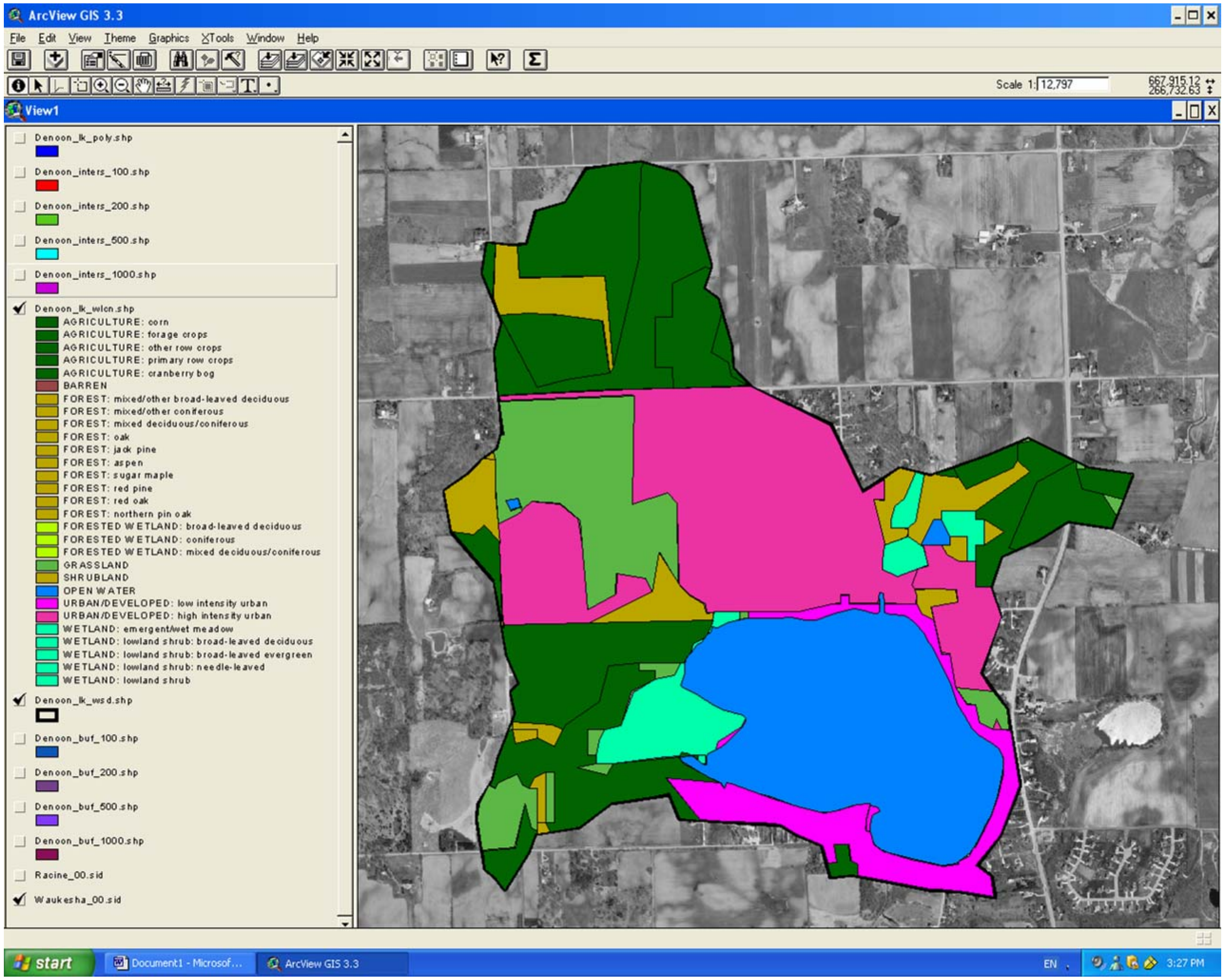
Floating-leaved, rooted Species (FL_RT)

Brasenia schreberi
Nuphar advena
Nuphar variegate
Nymphaea spp.
Polygonum amphibium
Potamogeton amplifolius
Potamogeton bicupulatus
Potamogeton epihydrus
Potamogeton gramineus
Potamogeton illinoensis
Potamogeton natans
Potamogeton spirillus
Potamogeton vaseyi
Sagittaria cuneata
Sparganium angustifolium
Sparganium fluctuans

APPENDIX H. Mean, standard error (S.E.) about the mean, and range of relative occurrences of guilds selected for analyses in 53 Wisconsin lakes (26 southeastern and 27 northern). Relative occurrence is the proportion of total quadrats in a lake in which a species included in that guild occurred. Guilds are defined in Appendix F. Bold values represent guilds that were found to be significantly different between ecoregions (Mann-Whitney U-test).

Macrophyte	Southeastern Ecoregion		Northern Ecoregion			
Guild	Mean (±S.E.)	Range	Mean (±S.E.)	Range	U-stat	P
Basal Species	**0.04 (0.02)**	0.00-0.37	**0.38 (0.04)**	0.03-0.81	676.0	<0.001
Emergent Species	0.02 (0.01)	0.00-0.15	0.04 (0.01)	0.00-0.24	417.5	0.235
Exotic Species	**0.34 (0.06)**	0.00-0.87	**0.01 (0.00)**	0.00-0.10	30.0	<0.001
Lily Pads	0.05 (0.02)	0.00-0.39	0.09 (0.02)	0.00-0.53	489.0	0.014
Potamogeton spp.	**0.26 (0.03)**	0.02-0.71	**0.45 (0.05)**	0.00-0.84	517.5	0.003
FL_RT	**0.22 (0.02)**	0.00-0.40	**0.35 (0.03)**	0.04-0.68	508.0	0.005
FL_NRT	0.07 (0.04)	0.00-0.85	0.01 (0.01)	0.00-0.11	293.0	0.249
NFL_RT	0.68 (0.04)	0.26-0.92	0.65 (0.05)	0.00-0.89	347.5	0.950
NFL_NRT	**0.63 (0.04)**	0.11-0.90	**0.24 (0.03)**	0.00-0.56	68.0	<0.001

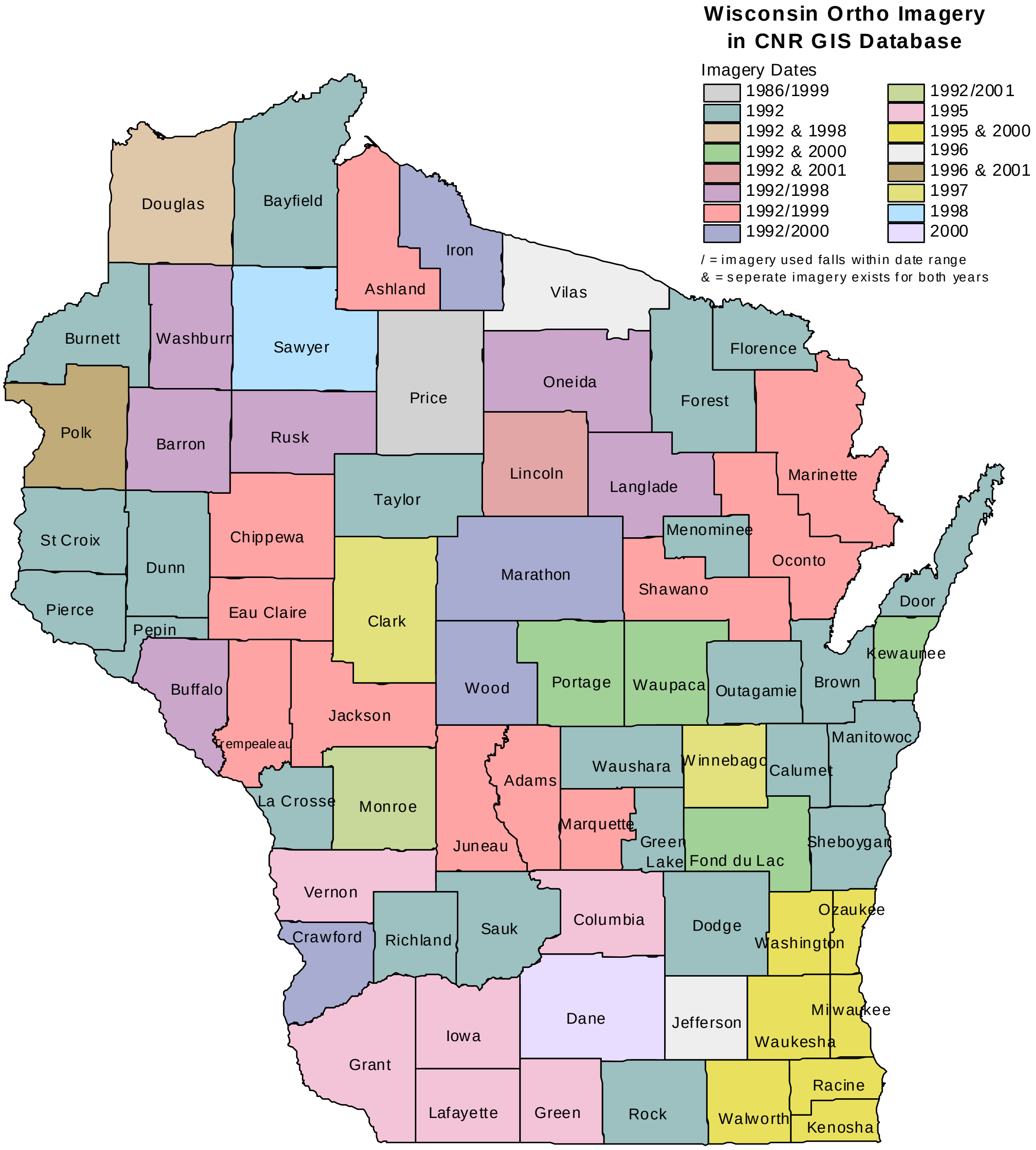
APPENDIX I. Watershed land use boundaries delineated for Denoon Lake, Wisconsin (T5N R20E S31-32). Land uses were categorized in ArcView 3.x using digital orthophoto (DOP) and 1:24,000 Wisconsin land cover (WLC) layers. This picture shows the different land cover delineations as estimated from the DOP. Land uses are defined in Appendix J.



Scale 1:12,797

667,915.12 ↔
266,732.63 ↕

APPENDIX J. Wisconsin Digital Orthophoto Imagery was provided by the University of Wisconsin Stevens Point. Counties are color coded according to the year of the most recent digital orthophoto images available.



APPENDIX K. List of variables analyzed and how they were calculated. Macrophyte data (species and guilds) were used only as dependent variables, development data were used only as independent variables. Water chemistry data were used as either; depending on the analysis.

Variable	Description
	General
Lake area	Surface area of the lake (ha)
Max depth of lake	Deepest point of the lake (m)
Watershed area	Area of watershed (ha)
Watershed area : Lake area	Ratio of watershed area to lake area
Lake perimeter	Perimeter of shoreline around the lake (km)
	Macrophyte Data
Species richness	Total number of taxa in a lake
Total relative occurrence	# quadrats with a plant in it/ total # quadrats in the littoral zone
Max depth of plant growth	Depth of water at deepest plant growth (m)
Number of species in each guild/lake	Total # of taxa in lake analyzed by guild
Relative occurrence of individual species	# quadrats occurred/total # quadrats in littoral zone (quadrats containing multiple species in one guild were counted only once)
Relative occurrence of guilds	# quadrats any species in that guild occurred/ total # quadrats in littoral zone
Relative occurrence of near-shore species	Dataset truncated to first four quadrats from shore in lake
Relative occurrence of near-shore guilds	Dataset truncated to first four quadrats from shore in lake
	Lakeshore Development
Number of houses	*In situ* count of houses around the lakeshore
House density	Number of houses / lake perimeter (km)

APPENDIX K (continued). List of variables analyzed and how they were calculated. Macrophyte data (species and guilds) were used only as dependent variables, development data were used only as independent variables. Water chemistry data were used as either; depending on the analysis.

Variable	Description
	Watershed Development
Agriculture development	Proportion of the total watershed area in Agriculture: corn, forage crops, primary row crops, other row crops, and cranberry bog
Urban development	Proportion of the total watershed area in Urban/developed: high and low intensity
Total development	Agricultural and urban development summed
	Water Chemistry
Alkalinity	total $CaCO_3$ mg/L
Conductivity	µmhos/cm
pH	negative log of the Hydrogen ion concentration
Calcium	mg/L
Magnesium	mg/L
Chlorophyll-*a*	mg/L
Color	units
Secchi depth	collected *in situ* m
Phosphorous	total phosphorus mg/L
Nitrogen	total (NO^{3-} + NO^{2-} +Kjeldahl) mg/L

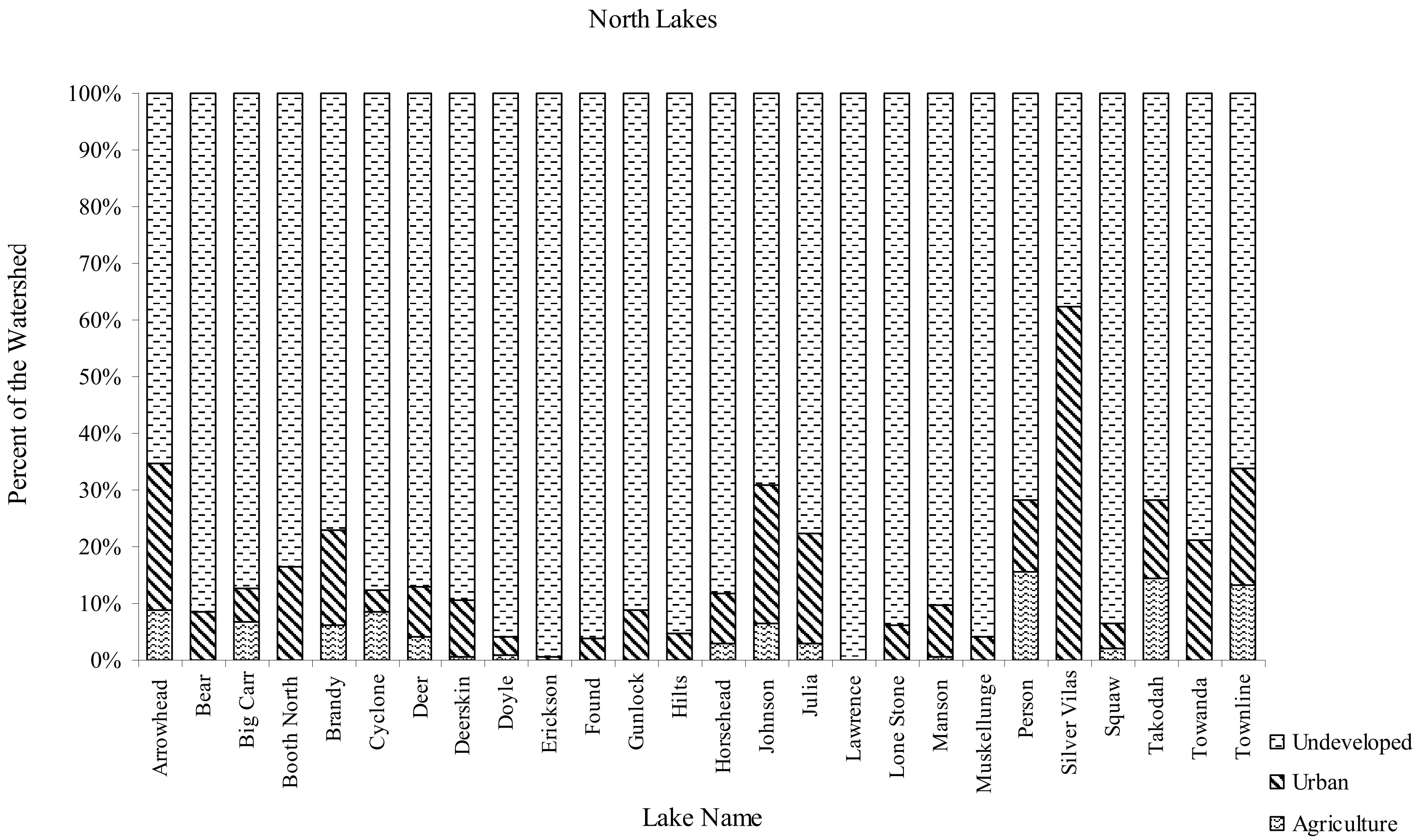
APPENDIX L. Mean, standard error (S.E.) about the mean, and range of relative occurrences of macrophyte species selected for near-shore analysis in 53 Wisconsin lakes (26 southeastern and 27 northern). Data from only the first four quadrats was used in these analyses. Relative occurrence is the proportion of total near-shore quadrats (within 7 m from shore) in a lake in which each species occurred. Bold values represent occurrence in ≥ 5 percent of the total near-shore quadrats in that ecoregion. If there is no value for a species, it did not occur in any near-shore quadrats in that ecoregion. It should be noted that this species list is a subset of the species chosen for the whole-lake analysis with the exception of *Eriocaulon aquaticum* being added to the list.

Macrophyte	Southeastern Ecoregion		Northern Ecoregion			
Species	Mean (±S.E.)	Range	Mean (±S.E.)	Range	U-stat	P
Ceratophyllum demersum	**0.12 (0.04)**	**0.00-0.70**	0.02 (0.00)	0.00-0.13	-	-
Chara spp.	**0.38 (0.05)**	**0.00-0.73**	**0.06 (0.02)**	**0.00-0.41**	72.0	<0.001
Elatine minima	-	-	**0.13 (0.03)**	**0.00-0.54**	-	-
Eleocharis acicularis	0.03 (0.01)	0.00-0.21	**0.14 (0.02)**	**0.00-0.31**	-	-
Eriocaulon aquaticum	0.00 (0.00)	0.00-0.04	**0.09 (0.03)**	**0.00-0.52**	-	-
Isoetes spp.	0.00 (0.00)	0.00-0.04	**0.21 (0.04)**	**0.00-0.61**	-	-
Juncus pelocarpus	0.00 (0.00)	0.00-0.04	**0.16 (0.02)**	**0.00-0.41**	-	-
Lemna trisulca	**0.06 (0.04)**	**0.00-0.98**	0.01 (0.00)	0.00-0.07	-	-
Lobelia dortmanna	-	-	**0.06 (0.02)**	**0.00-0.32**	-	-
Myriophyllum sibiricum	**0.05 (0.02)**	**0.00-0.29**	0.01 (0.01)	0.00-0.13	-	-
Myriophyllum spicatum	**0.21 (0.05)**	**0.00-0.68**	0.00 (0.00)	0.00-0.02	-	-
Myriophyllum tenellum	-	-	**0.09 (0.02)**	**0.00-0.34**	-	-
Najas flexilis	**0.24 (0.03)**	**0.00-0.61**	**0.21 (0.04)**	**0.00-0.68**	315.0	0.521
Nymphaea spp.	**0.07 (0.02)**	**0.00-0.45**	0.04 (0.01)	0.00-0.16	-	-
Potamogeton gramineus	0.04 (0.01)	0.00-0.32	**0.11 (0.03)**	**0.00-0.50**	459.0	0.041
Stuckenia pectinata	**0.07 (0.01)**	**0.00-0.16**	0.00 (0.00)	0.00-0.11	-	-
Vallisneria americana	**0.07 (0.02)**	**0.00-0.38**	**0.12 (0.02)**	**0.00-0.46**	463.5	0.039

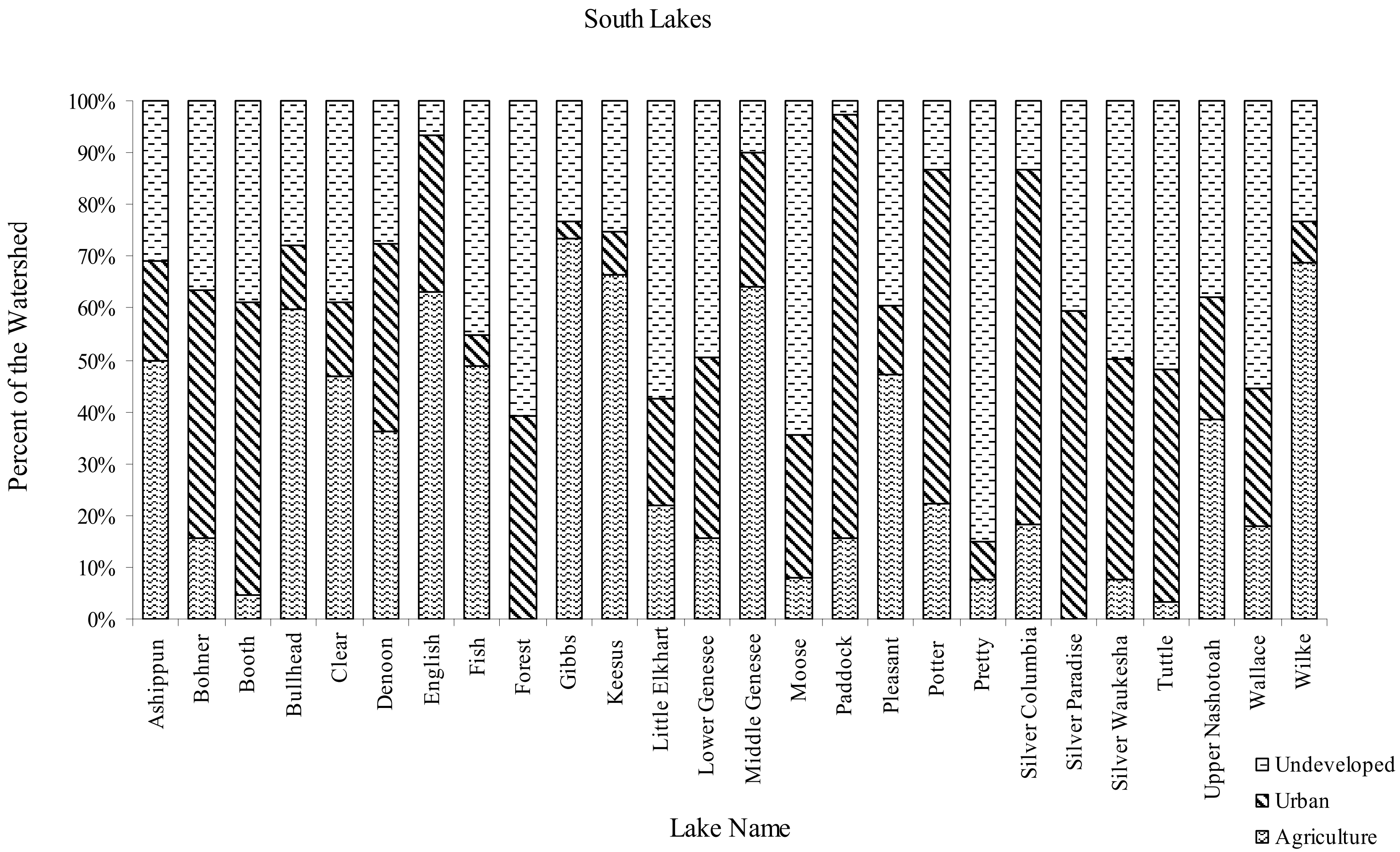
APPENDIX M. Mean, standard error (S.E.) about the mean, and range of relative occurrences of selected guilds observed near-shore in 53 Wisconsin lakes (26 southeastern and 27 northern). Data from only the first four quadrats was used in these analyses. Relative occurrence is the proportion of total near-shore quadrats (within 7 m from shore) in a lake in which a species included in that guild occurred. Guilds are defined in Appendix E. Bold values represent guilds that were found to be significantly different between ecoregions (Mann-Whitney U-test).

Macrophyte Guild	Southeastern Ecoregion		Northern Ecoregion			
	Mean (±S.E.)	Range	Mean (±S.E.)	Range	U-stat	P
Basal Species	**0.05 (0.01)**	0.00-0.29	**0.46 (0.04)**	0.04-0.89	684.5	<0.001
Emergent Species	0.06 (0.02)	0.00-0.34	0.11 (0.02)	0.00-0.55	437.5	0.120
Exotic Species	**0.26 (0.05)**	0.00-0.79	**0.00 (0.00)**	0.00-0.02	71.5	<0.001
Lily Pads	0.07 (0.02)	0.00-0.45	0.07 (0.01)	0.00-0.23	415.5	0.245
Potamogeton spp.	0.16 (0.02)	0.02-0.45	0.21 (0.03)	0.00-0.68	382.5	0.574
FL_RT	0.17 (0.03)	0.00-0.54	0.24 (0.03)	0.03-0.64	452.0	0.072
FL_NRT	0.09 (0.05)	0.00-0.98	0.02 (0.01)	0.00-0.23	306.5	0.363
NFL_RT	**0.55 (0.03)**	0.25-0.80	**0.39 (0.04)**	0.00-0.75	199.5	0.007
NFL_NRT	**0.50 (0.04)**	0.04-0.79	**0.10 (0.02)**	0.00-0.41	45.5	<0.001

APPENDIX N. Proportions of land use types in watersheds of northern lakes. Land use delineation is explained in Appendix H.



APPENDIX O. Proportions of land use types in watersheds of southeastern lakes. Land use delineation is explained in Appendix H.



Appendix P. Regression results of significant species (italics and boldface) and guild—watershed development relations at the whole lake scale in 53 Wisconsin lakes (26 southeastern and 27 northern). The equations listed represent the best model for each relation. Regressions of species listed are those of species that occur in $\geq 5\%$ of the quadrats in the respective ecoregion. Guilds are defined in Appendix E. Independent variables are explained in Appendix K.

Macrophyte Species Relative Occurrence	Independent Variable	Equation	r^2	P
		Regions Combined		
***Chara* spp.**	Watershed Area	$(y+1)^{1/2} = -0.0115(x+1)^{1/2} + 0.6922$	0.13	0.010
Elodea canadensis	Watershed Area	$(y+1)^{1/2} = 0.007(x+1)^{1/2} + 0.1021$	0.08	0.045
***Nymphaea* spp.**	Watershed Area	$(y+1)^{1/2} = 0.0057(x+1)^{1/2} + 0.043$	0.12	0.014
Vallisneria americana	Watershed Area	$y = 0.0002x + 0.1087$	0.18	0.002
Lily Pads	Watershed Area	$(y+1)^{1/2} = 0.0071(x+1)^{1/2} + 0.0785$	0.14	0.006
Basal Species	Lake Area	$(y+1)^{1/2} = 0.046(x+1)^{1/2} + 0.0301$	0.10	0.026
NFL_NRT	Lake Area	$(y+1)^{1/2} = -0.0335(x+1)^{1/2} + 0.8595$	0.08	0.047
***Chara* spp.**	Watershed : Lake	$(y+1)^{1/2} = -0.0579(x+1)^{1/2} + 0.6319$	0.08	0.050
Myriophyllum sibiricum	Watershed : Lake	$y = 0.0028x + 0.0404$	0.09	0.031
***Nymphaea* spp.**	Watershed : Lake	$(y+1)^{1/2} = 0.0429(x+1)^{1/2} + 0.0355$	0.16	0.004
Lily Pads	Watershed : Lake	$(y+1)^{1/2} = 0.0506(x+1)^{1/2} + 0.0781$	0.17	0.002
***Chara* spp.**	Perimeter	$\mathrm{Log}_{10}(y+1) = -0.1762(\mathrm{Log}_{10}(x+1)) + 0.2274$	0.08	0.048
Vallisneria americana	Perimeter	$y = 0.0424x + 0.0206$	0.13	0.008
Basal Species	Perimeter	$(y+1)^{1/2} = 0.239(x+1)^{1/2} - 0.1038$	0.11	0.017
Exotic Species	Perimeter	$(y+1)^{1/2} = -0.2281(x+1)^{1/2} + 0.7129$	0.08	0.040
NFL_NRT	Perimeter	$(y+1)^{1/2} = -0.1884(x+1)^{1/2} + 0.9853$	0.10	0.020
***Chara* spp.**	Proportion Urban	$\mathrm{Log}_{10}(y+1) = 0.5469(\mathrm{Log}_{10}(x+1)) + 0.0637$	0.16	0.003
Potamogeton amplifolius	Proportion Urban	$\mathrm{Log}_{10}(y+1) = -0.1159(\mathrm{Log}_{10}(x+1)) + 0.0307$	0.08	0.038
Basal Species	Proportion Urban	$(y+1)^{1/2} = -0.5604(x+1)^{1/2} + 0.6011$	0.16	0.004
Exotic Species	Proportion Urban	$(y+1)^{1/2} = 0.5735(x+1)^{1/2} + 0.0239$	0.13	0.008
Lily Pads	Proportion Urban	$(y+1)^{1/2} = -0.3248(x+1)^{1/2} + 0.3471$	0.17	0.003

APPENDIX P (continued). Regression results of significant species (italics and boldface) and guild—watershed development relations at the whole lake scale in 53 Wisconsin lakes (26 southeastern and 27 northern). The equations listed represent the best model for each relation. Regressions of species listed are those of species that occur in ≥ 5% of the quadrats in the respective ecoregion. Guilds are defined in Appendix E. Independent variables are explained in Appendix K.

Macrophyte Species Relative Occurrence	Independent Variable	Equation	r^2	P
FL_RT	Proportion Urban	$\mathrm{Log}_{10}(y+1) = -0.2851(\mathrm{Log}_{10}(x+1)) + 0.1281$	0.12	0.013
Ceratophyllum demersum	Proportion Agriculture	$y = 0.3432x + 0.0403$	0.17	0.002
***Chara* spp.**	Proportion Agriculture	$(y+1)^{1/2} = 0.3343(x+1)^{1/2} + 0.3748$	0.11	0.018
Elodea canadensis	Proportion Agriculture	$(y+1)^{1/2} = -0.4038(x+1)^{1/2} + 0.36$	0.26	<0.001
Potamogeton amplifolius	Proportion Agriculture	$(y+1)^{1/2} = -0.1929(x+1)^{1/2} + 0.2289$	0.12	0.013
Potamogeton gramineus	Proportion Agriculture	$(y+1)^{1/2} = -0.3153(x+1)^{1/2} + 0.3134$	0.17	0.003
Vallisneria americana	Proportion Agriculture	$(y+1)^{1/2} = -0.3957(x+1)^{1/2} + 0.4714$	0.17	0.003
Potamogeton spp.	Proportion Agriculture	$(y+1)^{1/2} = -0.3039(x+1)^{1/2} + 0.6474$	0.14	0.006
Basal Species	Proportion Agriculture	$(y+1)^{1/2} = -0.6551(x+1)^{1/2} + 0.5727$	0.38	<0.001
Exotic Species	Proportion Agriculture	$(y+1)^{1/2} = 0.7485(x+1)^{1/2} + 0.0281$	0.41	<0.001
FL_RT	Proportion Agriculture	$(y+1)^{1/2} = -0.2352(x+1)^{1/2} + 0.5746$	0.12	0.010
FL_NRT	Proportion Agriculture	$(y+1)^{1/2} = 0.2206(x+1)^{1/2} + 0.0177$	0.12	0.014
NFL_NRT	Proportion Agriculture	$y = 0.5542x + 0.337$	0.20	0.001
***Chara* spp.**	Proportion Ag + Urban	$\mathrm{Log}_{10}(y+1) = 0.5101(\mathrm{Log}_{10}(x+1)) + 0.0389$	0.26	<0.001
Elodea canadensis	Proportion Ag + Urban	$(y+1)^{1/2} = -0.3849(x+1)^{1/2} + 0.4523$	0.21	0.001
Potamogeton amplifolius	Proportion Ag + Urban	$\mathrm{Log}_{10}(y+1) = -0.1204(\mathrm{Log}_{10}(x+1)) + 0.0376$	0.17	0.002
Potamogeton gramineus	Proportion Ag + Urban	$\mathrm{Log}_{10}(y+1) = -0.2223(\mathrm{Log}_{10}(x+1)) + 0.0657$	0.21	0.001
Vallisneria americana	Proportion Ag + Urban	$\mathrm{Log}_{10}(y+1) = -0.2647(\mathrm{Log}_{10}(x+1)) + 0.1063$	0.12	0.011
Basal Species	Proportion Ag + Urban	$(y+1)^{1/2} = -0.7619(x+1)^{1/2} + 0.8013$	0.47	<0.001
Exotic Species	Proportion Ag + Urban	$(y+1)^{1/2} = 0.8528(x+1)^{1/2} – 0.2229$	0.48	<0.001
Lily pads	Proportion Ag + Urban	$(y+1)^{1/2} = -0.226(x+1)^{1/2} + 0.3395$	0.13	0.009
Potamogeton spp.	Proportion Ag + Urban	$\mathrm{Log}_{10}(y+1) = -0.3551(\mathrm{Log}_{10}(x+1)) + 0.1732$	0.19	0.001
FL_RT	Proportion Ag + Urban	$\mathrm{Log}_{10}(y+1) = -0.2717(\mathrm{Log}_{10}(x+1)) + 0.1418$	0.20	0.001
NFL_NRT	Proportion Ag + Urban	$\mathrm{Log}_{10}(y+1) = 0.4807(\mathrm{Log}_{10}(x+1)) + 0.0835$	0.27	<0.001

APPENDIX P (continued). Regression results of significant species (italics and boldface) and guild—watershed development relations at the whole lake scale in 53 Wisconsin lakes (26 southeastern and 27 northern). The equations listed represent the best model for each relation. Regressions of species listed are those of species that occur in ≥ 5% of the quadrats in the respective ecoregion. Guilds are defined in Appendix E. Independent variables are explained in Appendix K.

Macrophyte Species Relative Occurrence	Independent Variable	Equation	r^2	P
		<u>Northern Ecoregion</u>		
Ceratophyllum demersum	Watershed Area	$(y+1)^{1/2} = 0.008(x+1)^{1/2} - 0.0153$	0.15	0.049
Eleocharis acicularis	Watershed Area	$(y+1)^{1/2} = -0.0133(x+1)^{1/2} + 0.6059$	0.42	<0.001
Myriophyllum sibiricum	Watershed Area	$(y+1)^{1/2} = 0.0097(x+1)^{1/2} - 0.086$	0.27	0.007
Myriophyllum tenellum	Watershed Area	$\mathrm{Log}_{10}(y+1) = -0.0679(\mathrm{Log}_{10}(x+1)) + 0.2202$	0.31	0.003
Potamogeton pusillus	Watershed Area	$\mathrm{Log}_{10}(y+1) = -0.0312(\mathrm{Log}_{10}(x+1)) + 0.1014$	0.20	0.022
Basal Species	Watershed Area	$\mathrm{Log}_{10}(y+1) = -0.0797(\mathrm{Log}_{10}(x+1)) + 0.3469$	0.22	0.017
Juncus pelocarpus	Lake Area	$(y+1)^{1/2} = 0.0459(x+1)^{1/2} – 0.0704$	0.24	0.011
Potamogeton richardsonii	Lake Area	$(y+1)^{1/2} = 0.034(x+1)^{1/2} - 0.1192$	0.22	0.017
Eleocharis acicularis	Watershed : Lake	$(y+1)^{1/2} = -0.0755(x+1)^{1/2} + 0.5353$	0.40	0.001
Myriophyllum sibiricum	Watershed : Lake	$y = 0.0031x + 0.013$	0.20	0.021
Myriophyllum tenellum	Watershed : Lake	$\mathrm{Log}_{10}(y+1) = -0.0583(\mathrm{Log}_{10}(x+1)) + 0.0966$	0.20	0.023
Basal Species	Watershed : Lake	$\mathrm{Log}_{10}(y+1) = -0.0808(\mathrm{Log}_{10}(x+1)) + 0.2129$	0.19	0.026
Potamogeton richardsonii	Perimeter	$y = 0.0136x - 0.0185$	0.16	0.041
Brasenia schreberi	Proportion Urban	$(y+1)^{1/2} = -0.38(x+1)^{1/2} + 0.2765$	0.15	0.050
Myriophyllum tenellum	Proportion Urban	$y = 0.4882x + 0.0513$	0.21	0.018
Lily pads	Proportion Urban	$(y+1)^{1/2} = -0.4087(x+1)^{1/2} + 0.3846$	0.17	0.036
Elodea canadensis	Proportion Agriculture	$(y+1)^{1/2} = -0.6586(x+1)^{1/2} + 0.4338$	0.17	0.038
***Nitella* spp.**	Proportion Agriculture	$(y+1)^{1/2} = -0.5355(x+1)^{1/2} + 0.2288$	0.17	0.039
Myriophyllum tenellum	Proportion Ag + Urban	$y = 0.4578x + 0.0385$	0.23	0.012
Lily pads	Proportion Ag + Urban	$(y+1)^{1/2} = -0.3948(x+1)^{1/2} + 0.398$	0.20	0.024

APPENDIX P (continued). Regression results of significant species (italics and boldface) and guild—watershed development relations at the whole lake scale in 53 Wisconsin lakes (26 southeastern and 27 northern). The equations listed represent the best model for each relation. Regressions of species listed are those of species that occur in ≥ 5% of the quadrats in the respective ecoregion. Guilds are defined in Appendix E. Independent variables are explained in Appendix K.

Macrophyte Species Relative Occurrence	Independent Variable	Equation	r^2	P
		Southeastern Ecoregion		
Myriophyllum spicatum	Watershed Area	$(y+1)^{1/2} = 0.0261(x+1)^{1/2} + 0.0078$	0.25	0.010
Emergent Species	Watershed Area	$\text{Log}_{10}(y+1) = -0.0153(\text{Log}_{10}(x+1)) + 0.0446$	0.23	0.013
Exotic Species	Watershed Area	$(y+1)^{1/2} = 0.025(x+1)^{1/2} + 0.1336$	0.28	0.005
Myriophyllum spicatum	Lake Area	$y = 0.0056x + 0.0063$	0.17	0.038
Exotic Species	Lake Area	$y = 0.0059x + 0.0667$	0.21	0.019
Ceratophyllum demersum	Watershed : Lake	$(y+1)^{1/2} = 0.1375(x+1)^{1/2} – 0.0581$	0.19	0.027
***Nymphaea* spp.**	Watershed : Lake	$y = 0.0124x - 0.0239$	0.42	<0.001
Emergent Species	Watershed : Lake	$(y+1)^{1/2} = -0.0472(x+1)^{1/2} + 0.2268$	0.18	0.030
Lily Pads	Watershed : Lake	$y = 0.0124x - 0.0198$	0.41	<0.001
Ceratophyllum demersum	Proportion Urban	$(y+1)^{1/2} = -0.5793(x+1)^{1/2} + 0.5589$	0.17	0.036
Ceratophyllum demersum	Proportion Agriculture	$\text{Log}_{10}(y+1) = 0.4362(\text{Log}_{10}(x+1)) - 0.0002$	0.20	0.023
Potamogeton gramineus	Proportion Agriculture	$(y+1)^{1/2} = -0.2724(x+1)^{1/2} + 0.2857$	0.15	0.050
NFL_RT	Proportion Agriculture	$y = 0.3415x + 0.5598$	0.21	0.022
Potamogeton gramineus	Proportion Ag + Urban	$(y+1)^{1/2} = -0.5671(x+1)^{1/2} + 0.5933$	0.18	0.031

APPENDIX Q. Regression results of significant near-shore species (italics and boldface) and guild—watershed development relations in 53 Wisconsin lakes (26 southeastern and 27 northern). Data from only the first four quadrats was used in these analyses. The equations listed represent the best model for each relation. Regressions of species listed are those of species that occur in ≥ 5% of the near-shore quadrats (within 7 m from shore) in the respective ecoregion. Guilds are defined in Appendix E. Independent variables are defined in Appendix K.

Macrophyte Species Relative Occurrence	Independent Variable	Equation	r^2	P
		Regions Combined		
Chara spp.	Watershed Area	$y = -0.0002x + 0.2877$	0.08	0.046
Basal Species	Watershed Area	$(y+1)^{1/2} = 0.0108(x+1)^{1/2} + 0.2139$	0.10	0.023
Lily Pads	Watershed Area	$(y+1)^{1/2} = 0.0086(x+1)^{1/2} + 0.0482$	0.18	0.002
NFL_NRT	Watershed Area	$y = -0.0002x + 0.3724$	0.08	0.050
Chara spp.	Lake Area	$y = -0.0024x + 0.3547$	0.09	0.030
Potamogeton gramineus	Lake Area	$\mathrm{Log}_{10}(y+1) = -0.0674(\mathrm{Log}_{10}(x+1)) + 0.1455$	0.12	0.014
Basal Species	Lake Area	$(y+1)^{1/2} = 0.0428(x+1)^{1/2} + 0.102$	0.08	0.046
Lily Pads	Watershed : Lake	$\mathrm{Log}_{10}(y+1) = 0.0533(\mathrm{Log}_{10}(x+1)) - 0.0152$	0.23	<0.001
FL_RT	Watershed : Lake	$\mathrm{Log}_{10}(y+1) = 0.0477(\mathrm{Log}_{10}(x+1)) + 0.0399$	0.09	0.031
Chara spp.	Perimeter	$y = -0.0396x + 0.3785$	0.08	0.050
Potamogeton gramineus	Perimeter	$(y+1)^{1/2} = -0.1562(x+1)^{1/2} + 0.4898$	0.09	0.035
Basal Species	Perimeter	$(y+1)^{1/2} = 0.2668(x+1)^{1/2} - 0.1096$	0.13	0.009
Exotic Species	Perimeter	$(y+1)^{1/2} = -0.2064(x+1)^{1/2} + 0.6137$	0.08	0.041
NFL_RT	Perimeter	$(y+1)^{1/2} = -0.1394(x+1)^{1/2} + 0.9345$	0.10	0.025
NFL_NRT	Perimeter	$\mathrm{Log}_{10}(y+1) = -0.1958(\mathrm{Log}_{10}(x+1)) + 0.2377$	0.10	0.021
Chara spp.	Proportion Urban	$(y+1)^{1/2} = -0.5535(x+1)^{1/2} + 0.5984$	0.16	0.003
Basal Species	Proportion Urban	$(y+1)^{1/2} = -0.6901(x+1)^{1/2} + 0.7046$	0.22	<0.001
Exotic Species	Proportion Urban	$(y+1)^{1/2} = 0.4311(x+1)^{1/2} + 0.0274$	0.09	0.029
Chara spp.	Proportion Agriculture	$\mathrm{Log}_{10}(y+1) = -0.4408(\mathrm{Log}_{10}(x+1)) + 0.1039$	0.17	0.002
Potamogeton gramineus	Proportion Agriculture	$\mathrm{Log}_{10}(y+1) = 0.1254(\mathrm{Log}_{10}(x+1)) + 0.0229$	0.08	0.046

APPENDIX Q (continued). Regression results of significant near-shore species (italics and boldface) and guild—watershed development relations in 53 Wisconsin lakes (26 southeastern and 27 northern). Data from only the first four quadrats was used in these analyses. The equations listed represent the best model for each relation. Regressions of species listed are those of species that occur in ≥ 5% of the near-shore quadrats (within 7 m from shore) in the respective ecoregion. Guilds are defined in Appendix E. Independent variables are defined in Appendix K.

Macrophyte Species Relative Occurrence	Independent Variable	Equation	r^2	P
Basal Species	Proportion Agriculture	$(y+1)^{1/2} = -0.7298(x+1)^{1/2} + 0.6451$	0.45	<0.001
Emergent Species	Proportion Agriculture	$(y+1)^{1/2} = -0.188(x+1)^{1/2} + 0.2839$	0.09	0.031
Exotic Species	Proportion Agriculture	$(y+1)^{1/2} = 0.6485(x+1)^{1/2} + 0.0033$	0.37	<0.001
Potamogeton spp.	Proportion Agriculture	$y = -0.1991x + 0.2225$	0.09	0.032
FL_RT	Proportion Agriculture	$(y+1)^{1/2} = -0.2262(x+1)^{1/2} + 0.4903$	0.11	0.017
FL_NRT	Proportion Agriculture	$\mathrm{Log}_{10}(y+1) = 0.2194(\mathrm{Log}_{10}(x+1)) + 0.0053$	0.10	0.024
NFL_RT	Proportion Agriculture	$\mathrm{Log}_{10}(y+1) = 0.2502(\mathrm{Log}_{10}(x+1)) + 0.147$	0.09	0.031
NFL_NRT	Proportion Agriculture	$\mathrm{Log}_{10}(y+1) = 0.573(\mathrm{Log}_{10}(x+1)) + 0.0688$	0.26	<0.001
***Chara* spp.**	Proportion Ag + Urban	$(y+1)^{1/2} = -0.5911(x+1)^{1/2} + 0.7035$	0.30	<0.001
Potamogeton gramineus	Proportion Ag + Urban	$y = -0.1603x + 0.1439$	0.15	0.005
Basal Species	Proportion Ag + Urban	$(y+1)^{1/2} = -0.8753(x+1)^{1/2} + 0.915$	0.58	<0.001
Emergent Species	Proportion Ag + Urban	$(y+1)^{1/2} = -0.186(x+1)^{1/2} + 0.3308$	0.08	0.043
Exotic Species	Proportion Ag + Urban	$(y+1)^{1/2} = 0.6975(x+1)^{1/2} - 0.1904$	0.39	<0.001
Potamogeton spp.	Proportion Ag + Urban	$y = -0.1639x + 0.2524$	0.10	0.021
FL_RT	Proportion Ag + Urban	$(y+1)^{1/2} = -0.2515(x+1)^{1/2} + 0.5625$	0.12	0.011
NFL_NRT	Proportion Ag + Urban	$\mathrm{Log}_{10}(y+1) = 0.5376(\mathrm{Log}_{10}(x+1)) + 0.0323$	0.32	<0.001
Northern Ecoregion				
Eleocharis acicularis	Watershed Area	$(y+1)^{1/2} = -0.0112(x+1)^{1/2} + 0.5809$	0.36	0.001
Myriophyllum tenellum	Watershed Area	$\mathrm{Log}_{10}(y+1) = -0.037(\mathrm{Log}_{10}(x+1)) + 0.1349$	0.15	0.048
Lily Pads	Watershed Area	$\mathrm{Log}_{10}(y+1) = 0.0271(\mathrm{Log}_{10}(x+1)) - 0.0408$	0.15	0.050

APPENDIX Q (continued). Regression results of significant near-shore species (italics and boldface) and guild—watershed development relations in 53 Wisconsin lakes (26 southeastern and 27 northern). Data from only the first four quadrats was used in these analyses. The equations listed represent the best model for each relation. Regressions of species listed are those of species that occur in ≥ 5% of the near-shore quadrats (within 7 m from shore) in the respective ecoregion. Guilds are defined in Appendix E. Independent variables are defined in Appendix K.

Macrophyte Species Relative Occurrence	Independent Variable	Equation	r^2	P
Juncus pelocarpus	Lake Area	$(y+1)^{1/2} = 0.0421(x+1)^{1/2} + 0.0183$	0.19	0.028
Eleocharis acicularis	Watershed : Lake	$\mathrm{Log}_{10}(y+1) = -0.0696(\mathrm{Log}_{10}(x+1)) + 0.1204$	0.37	0.001
Lily Pads	Watershed : Lake	$\mathrm{Log}_{10}(y+1) = 0.0324(\mathrm{Log}_{10}(x+1)) + 0.0002$	0.18	0.029
***Isoetes* spp.**	Proportion Agriculture	$(y+1)^{1/2} = -0.744(x+1)^{1/2} + 0.5086$	0.19	0.024
NFL_NRT	Proportion Agriculture	$(y+1)^{1/2} = -0.6378(x+1)^{1/2} + 0.3494$	0.28	0.006
NFL_NRT	Proportion Ag + Urban	$(y+1)^{1/2} = -0.3816(x+1)^{1/2} + 0.4033$	0.16	0.045
		Southeastern Ecoregion		
Ceratophyllum demersum	Watershed Area	$(y+1)^{1/2} = 0.0164(x+1)^{1/2} - 0.0099$	0.15	0.049
Myriophyllum spicatum	Watershed Area	$(y+1)^{1/2} = 0.0253(x+1)^{1/2} - 0.0317$	0.27	0.007
***Nymphaea* spp.**	Watershed Area	$(y+1)^{1/2} = 0.0166(x+1)^{1/2} - 0.0636$	0.30	0.004
Emergent Species	Watershed Area	$\mathrm{Log}_{10}(y+1) = -0.0352(\mathrm{Log}_{10}(x+1)) + 0.1048$	0.22	0.017
Exotic Species	Watershed Area	$(y+1)^{1/2} = 0.0239(x+1)^{1/2} + 0.0583$	0.26	0.008
Lily pads	Watershed Area	$(y+1)^{1/2} = 0.0168(x+1)^{1/2} - 0.059$	0.29	0.005
Exotic Species	Lake Area	$y = 0.0042x + 0.0607$	0.16	0.043
Ceratophyllum demersum	Watershed : Lake	$y = 0.0183x + 0.0164$	0.51	0.048
Najas flexilis	Watershed : Lake	$(y+1)^{1/2} = -0.0929(x+1)^{1/2} + 0.6575$	0.15	0.049
***Nymphaea* spp.**	Watershed : Lake	$y = 0.0184x - 0.0388$	0.50	<0.001
Lily pads	Watershed : Lake	$y = 0.0192x - 0.0385$	0.49	<0.001
FL_RT	Watershed : Lake	$y = 0.0156x + 0.0805$	0.23	0.014

APPENDIX Q (continued). Regression results of significant near-shore species (italics and boldface) and guild—watershed development relations in 53 Wisconsin lakes (26 southeastern and 27 northern). Data from only the first four quadrats was used in these analyses. The equations listed represent the best model for each relation. Regressions of species listed are those of species that occur in ≥ 5% of the near-shore quadrats (within 7 m from shore) in the respective ecoregion. Guilds are defined in Appendix E. Independent variables are defined in Appendix K.

Macrophyte Species Relative Occurrence	Independent Variable	Equation	r^2	P
Vallisneria americana	Lake Perimeter	$y = 0.031x - 0.0355$	0.16	0.046
Ceratophyllum demersum	Proportion Urban	$(y+1)^{1/2} = -0.5627(x+1)^{1/2} + 0.5313$	0.18	0.034
Ceratophyllum demersum	Proportion Agriculture	$\mathrm{Log}_{10}(y+1) = 0.3795(\mathrm{Log}_{10}(x+1)) + 0.002$	0.18	0.029
Potamogeton spp.	Proportion Agriculture	$y = -0.2169x + 0.2334$	0.20	0.020
Potamogeton spp.	Proportion Ag + Urban	$y = -0.3268x + 0.3714$	0.30	0.004

Appendix R. Regression results of significant species (in italics and boldface) and guild—riparian development relations at the whole lake scale in 53 Wisconsin lakes (26 southeastern and 27 northern). The equations listed represent the best model for each relation. Regressions of species listed are those of species that occur in ≥ 5% of the quadrats in the respective ecoregion. Guilds are defined in Appendix E. Independent variables are defined in Appendix K.

Macrophyte Species Relative Occurrence	Independent Variable	Equation	r^2	P
		Regions Combined		
***Nymphaea* spp.**	# Houses	$\text{Log}_{10}(y+1) = -0.0178(\text{Log}_{10}(x+1)) + 0.0476$	0.09	0.033
Lily Pads	# Houses	$\text{Log}_{10}(y+1) = -0.0428(\text{Log}_{10}(x+1)) + 0.1019$	0.27	<0.001
***Chara* spp.**	Houses/km	$y = 0.012x + 0.0958$	0.18	0.002
***Nymphaea* spp.**	Houses/km	$\text{Log}_{10}(y+1) = -0.0309(\text{Log}_{10}(x+1)) + 0.0543$	0.13	0.009
Basal Species	Houses/km	$(y+1)^{1/2} = -0.1057(x+1)^{1/2} + 0.7911$	0.22	<0.001
Exotic Species	Houses/km	$(y+1)^{1/2} = 0.0796(x+1)^{1/2} – 0.0549$	0.10	0.022
Lily Pads	Houses/km	$\text{Log}_{10}(y+1) = -0.0663(\text{Log}_{10}(x+1)) + 0.1076$	0.33	<0.001
FL_RT	Houses/km	$y = -0.0057x + 0.3861$	0.12	0.012
NFL_NRT	Houses/km	$y = 0.0095x + 0.2638$	0.11	0.015
		Northern Ecoregion		
Brasenia schreberi	# Houses	$\text{Log}_{10}(y+1) = -0.0298(\text{Log}_{10}(x+1)) + 0.0676$	0.26	0.006
Lily Pads	# Houses	$\text{Log}_{10}(y+1) = -0.0337(\text{Log}_{10}(x+1)) + 0.0906$	0.22	0.015
Brasenia schreberi	Houses/km	$\text{Log}_{10}(y+1) = -0.0522(\text{Log}_{10}(x+1)) + 0.0748$	0.30	0.004
Potamogeton amplifolius	Houses/km	$\text{Log}_{10}(y+1) = 0.0277(\text{Log}_{10}(x+1)) - 0.0008$	0.20	0.021
Vallisneria americana	Houses/km	$\text{Log}_{10}(y+1) = 0.0793(\text{Log}_{10}(x+1)) + 0.0172$	0.15	0.049
Lily Pads	Houses/km	$\text{Log}_{10}(y+1) = -0.0583(\text{Log}_{10}(x+1)) + 0.0975$	0.24	0.011

APPENDIX R (continued). Regression results of significant species (in italics and boldface) and guild—riparian development relations at the whole lake scale in 53 Wisconsin lakes (26 southeastern and 27 northern). The equations listed represent the best model for each relation. Regressions of species listed are those of species that occur in ≥ 5% of the quadrats in the respective ecoregion. Guilds are defined in Appendix E. Independent variables are defined in Appendix K.

Macrophyte Species Relative Occurrence	Independent Variable	Equation	r^2	P
		Southeastern Ecoregion		
Ceratophyllum demersum	# Houses	$\mathrm{Log}_{10}(y+1) = -0.1017(\mathrm{Log}_{10}(x+1)) + 0.2316$	0.15	0.050
Myriophyllum sibiricum	# Houses	$\mathrm{Log}_{10}(y+1) = -0.0518(\mathrm{Log}_{10}(x+1)) + 0.1253$	0.16	0.040
***Nymphaea* spp.**	# Houses	$\mathrm{Log}_{10}(y+1) = -0.0601(\mathrm{Log}_{10}(x+1)) + 0.1276$	0.31	0.003
Lily Pads	# Houses	$\mathrm{Log}_{10}(y+1) = -0.0642(\mathrm{Log}_{10}(x+1)) + 0.1367$	0.35	0.002
FL_NRT	# Houses	$(y+1)^{1/2} = -0.039(x+1)^{1/2} + 0.4585$	0.18	0.032
***Nymphaea* spp.**	Houses/km	$\mathrm{Log}_{10}(y+1) = -0.0823(\mathrm{Log}_{10}(x+1)) + 0.1288$	0.39	0.001
Lily Pads	Houses/km	$\mathrm{Log}_{10}(y+1) = -0.0873(\mathrm{Log}_{10}(x+1)) + 0.1371$	0.42	<0.001
FL_NRT	Houses/km	$(y+1)^{1/2} = -0.0957(x+1)^{1/2} + 0.5809$	0.24	0.012

Appendix S. Regression results of significant near-shore species (in italics and boldface) and guild—riparian development relations in 53 Wisconsin lakes (26 southeastern and 27 northern). Data from only the first four quadrats was used in these analyses. The equations listed represent the best model for each relation. Regressions of species listed are those of species that occur in ≥ 5% of the near-shore quadrats (within 7 m from shore) in the respective ecoregion. Guilds are defined in Appendix E. Independent variables are defined in Appendix K.

Macrophyte Species Relative Occurrence	Independent Variable	Equation	r^2	P
		Regions Combined		
Basal Species	# Houses	$\mathrm{Log}_{10}(y+1) = -0.0567(\mathrm{Log}_{10}(x+1)) + 0.1875$	0.08	0.036
Lily Pads	# Houses	$\mathrm{Log}_{10}(y+1) = -0.0238(\mathrm{Log}_{10}(x+1)) + 0.0701$	0.08	0.039
FL_RT	# Houses	$\mathrm{Log}_{10}(y+1) = -0.0329(\mathrm{Log}_{10}(x+1)) + 0.1352$	0.07	0.048
***Chara* spp.**	Houses/km	$y = 0.0107x + 0.0284$	0.19	0.001
Basal Species	Houses/km	$(y+1)^{1/2} = -0.1292(x+1)^{1/2} + 0.9346$	0.31	<0.001
Exotic Species	Houses/km	$(y+1)^{1/2} = 0.0699(x+1)^{1/2} - 0.0724$	0.09	0.027
Lily Pads	Houses/km	$\mathrm{Log}_{10}(y+1) = -0.0439(\mathrm{Log}_{10}(x+1)) + 0.0819$	0.14	0.006
FL_RT	Houses/km	$(y+1)^{1/2} = -0.0643(x+1)^{1/2} + 0.6779$	0.19	0.001
NFL_NRT	Houses/km	$y = 0.0085x + 0.1478$	0.10	0.024
		Northern Ecoregion		
Brasenia schreberi	# Houses	$y = -0.0005x + 0.0584$	0.18	0.026
Eriocaulon aquaticum	# Houses	$\mathrm{Log}_{10}(y+1) = -0.0662(\mathrm{Log}_{10}(x+1)) + 0.1418$	0.49	<0.001
Brasenia schreberi	Houses/km	$y = -0.0041x + 0.0809$	0.35	0.002
Eriocaulon aquaticum	Houses/km	$\mathrm{Log}_{10}(y+1) = -0.1179(\mathrm{Log}_{10}(x+1)) + 0.1617$	0.58	<0.001
Basal Species	Houses/km	$\mathrm{Log}_{10}(y+1) = -0.0895(\mathrm{Log}_{10}(x+1)) + 0.2594$	0.24	0.011

APPENDIX S (continued). Regression results of significant near-shore species (in italics and boldface) and guild—riparian development relations in 53 Wisconsin lakes (26 southeastern and 27 northern). Data from only the first four quadrats was used in these analyses. The equations listed represent the best model for each relation. Regressions of species listed are those of species that occur in ≥ 5% of the near-shore quadrats (within 7 m from shore) in the respective ecoregion. Guilds are defined in Appendix E. Independent variables are defined in Appendix K.

Macrophyte Species Relative Occurrence	Independent Variable	Equation	r^2	P
		Southeastern Ecoregion		
Ceratophyllum demersum	# Houses	$Log_{10}(y+1) = -0.1107(Log_{10}(x+1)) + 0.2435$	0.22	0.015
Myriophyllum sibiricum	# Houses	$Log_{10}(y+1) = -0.0399(Log_{10}(x+1)) + 0.0926$	0.16	0.046
***Nymphaea* spp.**	# Houses	$Log_{10}(y+1) = -0.0568(Log_{10}(x+1)) + 0.1291$	0.16	0.043
Lily Pads	# Houses	$Log_{10}(y+1) = -0.0598(Log_{10}(x+1)) + 0.1362$	0.16	0.041
FL_NRT	# Houses	$Log_{10}(y+1) = -0.1065(Log_{10}(x+1)) + 0.2232$	0.20	0.024
Ceratophyllum demersum	Houses/km	$Log_{10}(y+1) = -0.133(Log_{10}(x+1)) + 0.221$	0.21	0.018
***Nymphaea* spp.**	Houses/km	$Log_{10}(y+1) = -0.0954(Log_{10}(x+1)) + 0.1535$	0.30	0.004
Lily Pads	Houses/km	$Log_{10}(y+1) = -0.1006(Log_{10}(x+1)) + 0.1622$	0.30	0.003
FL_RT	Houses/km	$(y+1)^{1/2} = -0.067(x+1)^{1/2} + 0.6736$	0.15	0.047
FL_NRT	Houses/km	$(y+1)^{1/2} = -0.1037(x+1)^{1/2} + 0.6428$	0.22	0.015

APPENDIX T. Multiple regression results of significant species (boldface and italics) and guild—watershed development relations in 53 Wisconsin lakes (26 southeastern and 27 northern) in multiple regressions. Regressions listed are those of species that occur in ≥ 5% of the quadrats in the respective ecoregion. The value reported for r^2 is the adjusted r^2 value.

Macrophyte Species Relative Occurrence	Independent Variable	Equation	r^2	P
		Regions Combined		
Elodea canadensis	x=Proportion Agriculture z=Watershed : Lake	$(y+1)^{1/2} = 0.407(x+1)^{1/2}+0.040(z+1)^{1/2}+0.256$	0.29	<0.001
Elodea canadensis	x=Proportion Agriculture z=Watershed Area	$(y+1)^{1/2} = -0.388(x+1)^{1/2}+0.006(z+1)^{1/2}+0.244$	0.29	<0.001
Vallisneria americana	x=Proportion Agriculture z=Watershed Area	$(y+1)^{1/2} = -0.366(x+1)^{1/2}+2.04E^{-004}z+0.377$	0.23	0.001
Vallisneria americana	x=Proportion Agriculture z=Watershed Area	$(y+1)^{1/2} = -0.375(x+1)^{1/2}+0.008(z+1)^{1/2}+0.317$	0.20	0.001
Lily Pads	x=Proportion Urban z=Watershed : Lake	$(y+1)^{1/2} = -0.258(x+1)^{1/2}+0.41(z+1)^{1/2}+0.213$	0.24	<0.001
		Northern Ecoregion		
Myriophyllum tenellum	x=Proportion Ag + Urban z=Watershed Area	$y = 0.480x-9.68E^{-005}z+0.090$	0.31	0.005
Myriophyllum tenellum	x=Proportion Ag + Urban z=Watershed Area	$y = 0.382x-0.171(\log_{10}(z+1))+0.496$	0.45	<0.001

APPENDIX U. Water quality attributes of 53 Wisconsin lakes sampled (26 southeastern and 27 northern). N.C. represents data that were not collected.

Lake	Alkalinity (mg/L)	Conductivity (µmhos/m)	Calcium (mg/L)	Magnesium (mg/L)	pH	Secchi (m)	Phosphorus (mg/L)	Nitrogen (mg/L)
Northern Ecoregion								
Arrowhead	32	98	11.0	2.6	7.99	3.05	0.013	0.51
Bear	36	71	8.1	3.1	8.60	1.98	0.006	0.42
Big Carr	4	21	1.5	0.5	6.97	3.81	0.006	0.32
Booth	64	136	18.0	4.9	8.03	1.83	0.024	0.46
Brandy	42	176	16.2	4.3	8.09	3.75	0.006	0.40
Cyclone	22	50	5.8	2.0	7.28	2.75	0.018	0.69
Deer	30	63	8.4	2.3	8.55	2.45	0.020	0.37
Deerskin	28	73	7.3	3.1	8.61	2.13	0.006	0.48
Tom Doyle	25	60	6.1	2.2	7.52	2.85	0.016	0.51
Erickson	23	51	5.9	1.9	7.76	2.40	0.006	0.81
Found	24	51	5.8	2.4	7.71	1.68	0.019	0.51
Gunlock	48	103	14.6	3.3	8.21	1.07	0.025	0.43
Hilts	52	103	12.8	4.1	8.22	2.90	0.006	0.44
Horsehead	44	93	11.2	3.8	7.99	1.07	N.C.	N.C.
Johnson	40	174	13.9	3.8	8.24	3.70	0.025	0.50
Julia	16	103	8.6	3.4	7.36	2.13	0.017	0.57
Lawrence	8	22	1.7	0.9	6.90	3.35	0.030	0.46
Lone Stone	36	74	6.0	2.4	7.78	1.58	0.006	0.32
Manson	28	74	7.7	2.9	7.77	3.81	0.014	0.49
Muskellunge	36	71	8.3	2.9	8.30	1.07	0.006	0.48
Person	6	17	1.5	0.7	6.62	1.50	0.030	0.51
Round	55	117	16.0	4.2	8.45	3.50	0.022	0.38

APPENDIX U (continued). Water quality attributes of 53 Wisconsin lakes sampled (26 southeastern and 27 northern). N.C. represents data that were not collected.

Lake	Alkalinity (mg/L)	Conductivity (μmhos/m)	Calcium (mg/L)	Magnesium (mg/L)	pH	Secchi (m)	Phosphorus (mg/L)	Nitrogen (mg/L)
Silver(Vilas County)	12	179	5.0	1.70	7.41	2.74	0.027	0.65
Squaw	34	85	9.5	3.30	7.69	2.00	0.032	0.68
Tahkodah	5	14	1.3	0.40	6.45	3.50	0.020	0.38
Towanda	12	25	2.6	1.10	7.26	1.83	0.013	0.73
Townline	36	131	4.2	7.55	7.55	0.91	0.071	1.06
				Southeastern Ecoregion				
Ashippun	201	528	40.1	37.4	8.47	4.00	0.015	1.32
Bohner	192	536	34.3	41.1	8.52	1.90	0.026	1.08
Booth	122	311	25.5	18.6	8.67	3.20	0.018	1.04
Bullhead	129	384	26.4	20.5	8.77	3.25	0.054	1.32
Clear	95	205	15.6	14.7	9.23	1.30	0.021	0.56
Denoon	140	472	29.9	27.7	8.63	3.20	0.045	1.39
English	142	364	26.5	27.5	8.96	4.00	0.141	1.63
Fish	116	230	17.6	18.2	9.03	1.80	0.015	0.86
Forest	92	188	17.6	14.8	9.02	3.00	0.012	0.64
Gibbs	167	367	31.5	27.3	8.79	2.10	0.041	1.05
Keesus	152	348	30.4	24.0	8.58	3.00	0.035	0.81
Little Elkhart	136	376	27.9	19.1	8.38	1.70	0.022	0.59
Lower Genesee	136	331	25.9	23.4	8.67	4.40	0.029	0.95
Middle Genesee	149	399	26.6	25.9	8.70	2.10	0.017	0.93
Moose	156	436	25.8	32.2	8.72	5.00	0.015	0.63
Paddock	114	599	25.5	24.2	8.99	1.55	0.021	0.78
Pleasant	139	399	22.7	34.1	8.92	2.30	0.017	1.36
Potter	115	412	22.0	22.7	9.10	1.20	0.024	1.20

APPENDIX U (continued). Water quality attributes of 53 Wisconsin lakes sampled (26 southeastern and 27 northern). N.C. represents data that were not collected.

Lake	Alkalinity (mg/L)	Conductivity (µmhos/m)	Calcium (mg/L)	Magnesium (mg/L)	pH	Secchi (m)	Phosphorus (mg/L)	Nitrogen (mg/L)
Pretty	141	316	21.0	26.4	8.87	2.00	0.023	0.76
Silver(Columbia County)	101	313	30.1	7.2	8.49	2.00	0.040	1.04
Silver(Washington County)	203	457	34.4	36.3	8.51	2.50	0.013	0.64
Silver(Waukesha County)	168	647	32.4	36.2	8.21	2.90	0.006	1.02
Tuttle	58	125	13.1	6.9	8.44	3.10	0.016	0.76
Upper Nashotah	184	461	34.7	34.5	8.09	5.03	0.053	1.27
Wallace	171	535	30.7	30.5	8.65	2.50	0.018	0.76
Wilke	165	357	22.5	30.8	8.91	1.60	0.018	1.08

Appendix V. Regression results of significant species (italics and boldface) and guild—water chemistry relations at the whole lake scale in 53 Wisconsin lakes (26 southeastern and 27 northern). The equations listed represent the best model for each relation. Regressions listed are those of species that occur in ≥ 5% of the quadrats in the respective ecoregion. Guilds are defined in Appendix E. Water chemistry variables are defined in Appendix K.

Macrophyte Species Relative Occurrence	Water Chemistry Variable	Equation	r^2	P
		Regions Combined		
***Chara* spp.**	Alkalinity	$y = 0.0035x + 0.0137$	0.62	<0.001
Elodea canadensis	Alkalinity	$y = -0.001x + 0.1855$	0.24	<0.001
Myriophyllum sibiricum	Alkalinity	$\mathrm{Log}_{10}(y+1) = 0.0266(\mathrm{Log}_{10}(x+1)) - 0.0196$	0.09	0.034
Potamogeton amplifolius	Alkalinity	$y = -0.0003x + 0.0818$	0.11	0.015
Vallisneria americana	Alkalinity	$y = -0.0011x + 0.2871$	0.13	0.009
Basal Species	Alkalinity	$\mathrm{Log}_{10}(y+1) = -0.1593(\mathrm{Log}_{10}(x+1)) + 0.3579$	0.74	<0.001
Exotic Species	Alkalinity	$(y+1)^{1/2} = 0.0601(x+1)^{1/2} - 0.2461$	0.47	<0.001
Potamogeton spp.	Alkalinity	$y = -0.0011x + 0.4531$	0.10	0.025
FL_RT	Alkalinity	$y = -0.0008x + 0.3523$	0.10	0.023
FL_NRT	Alkalinity	$(y+1)^{1/2} = 0.0151(x+1)^{1/2} - 0.035$	0.09	0.026
NFL_RT	Alkalinity	$\mathrm{Log}_{10}(y+1) = 0.0467(\mathrm{Log}_{10}(x+1)) + 0.1352$	0.11	0.015
NFL_NRT	Alkalinity	$y = 0.0033x + 0.1522$	0.58	<0.001
***Chara* spp.**	Conductivity	$y = 0.0012x + 0.0279$	0.61	<0.001
Elodea canadensis	Conductivity	$y = -0.0003x + 0.1653$	0.15	0.004
Myriophyllum sibiricum	Conductivity	$\mathrm{Log}_{10}(y+1) = 0.029(\mathrm{Log}_{10}(x+1)) – 0.0363$	0.10	0.020
Potamogeton amplifolius	Conductivity	$y = -0.0001x + 0.082$	0.12	0.011
Vallisneria americana	Conductivity	$y = -0.0004x + 0.2866$	0.14	0.007
Potamogeton spp.	Conductivity	$y = -0.0004x + 0.4463$	0.09	0.030
Basal Species	Conductivity	$\mathrm{Log}_{10}(y+1) = -0.1502 (\mathrm{Log}_{10}(x+1)) + 0.4065$	0.66	<0.001
Exotic Species	Conductivity	$(y+1)^{1/2} = 0.0367(x+1)^{1/2} - 0.2514$	0.50	<0.001
FL_RT	Conductivity	$y = -0.0003x + 0.352$	0.11	0.018

APPENDIX V (continued). Regression results of significant species (italics and boldface) and guild—water chemistry relations at the whole lake scale in 53 Wisconsin lakes (26 southeastern and 27 northern). The equations listed represent the best model for each relation. Regressions listed are those of species that occur in ≥ 5% of the quadrats in the respective ecoregion. Guilds are defined in Appendix E. Water chemistry variables are defined in Appendix K.

Macrophyte Species Relative Occurrence	Water Chemistry Variable	Equation	r^2	P
FL_NRT	Conductivity	$(y+1)^{1/2} = 0.0087(x+1)^{1/2} - 0.029$	0.09	0.031
NFL_RT	Conductivity	$\mathrm{Log}_{10}(y+1) = 0.0412(\mathrm{Log}_{10}(x+1)) + 0.1273$	0.09	0.033
NFL_NRT	Conductivity	$y = 0.0011x + 0.1795$	0.52	<0.001
Ceratophyllum demersum	pH	$(y+1)^{1/2} = 0.7869(x+1)^{1/2} - 2.0417$	0.15	0.005
***Chara* spp.**	pH	$(y+1)^{1/2} = 1.137(x+1)^{1/2} – 2.7775$	0.23	<0.001
Elodea canadensis	pH	$y = -0.0605x + 0.5956$	0.09	0.027
Myriophyllum sibiricum	pH	$(y+1)^{1/2} = 0.5343(x+1)^{1/2} - 1.3537$	0.10	0.020
Basal Species	pH	$y = -0.2854x + 2.5603$	0.61	<0.001
Exotic Species	pH	$(y+1)^{1/2} = 1.5725(x+1)^{1/2} - 4.2436$	0.33	<0.001
NFL_RT	pH	$(y+1)^{1/2} = 0.6438(x+1)^{1/2} - 1.0471$	0.19	0.001
NFL_NRT	pH	$(y+1)^{1/2} = 1.0647(x+1)^{1/2} - 2.4333$	0.29	<0.001
Ceratophyllum demersum	Calcium	$(y+1)^{1/2} = 0.0469(x+1)^{1/2} + 0.03$	0.08	0.044
***Chara* spp.**	Calcium	$y = 0.0191x - 0.0204$	0.56	<0.001
Elodea canadensis	Calcium	$y = -0.0049x + 0.1824$	0.16	0.003
Myriophyllum sibiricum	Calcium	$(y+1)^{1/2} = 0.0503(x+1)^{1/2} - 0.0187$	0.14	0.007
Vallisneria americana	Calcium	$y = -0.0054x + 0.2868$	0.09	0.027
Basal Species	Calcium	$\mathrm{Log}_{10}(y+1) = -0.1961(\mathrm{Log}_{10}(x+1)) + 0.303$	0.68	<0.001
Exotic Species	Calcium	$(y+1)^{1/2} = 0.1433(x+1)^{1/2} - 0.2962$	0.41	<0.001
FL_RT	Calcium	$y = -0.0042x + 0.3561$	0.08	0.041
FL_NRT	Calcium	$(y+1)^{1/2} = 0.0459(x+1)^{1/2} - 0.0863$	0.13	0.007
NFL_RT	Calcium	$\mathrm{Log}_{10}(y+1) = 0.057(\mathrm{Log}_{10}(x+1)) + 0.152$	0.10	0.022
NFL_NRT	Calcium	$y = 0.0179x + 0.1276$	0.50	<0.001
***Chara* spp.**	Magnesium	$y = 0.0172x + 0.0683$	0.65	<0.001
Elodea canadensis	Magnesium	$(y+1)^{1/2} = -0.0601(x+1)^{1/2} + 0.4305$	0.26	<0.001

APPENDIX V (continued). Regression results of significant species (italics and boldface) and guild—water chemistry relations at the whole lake scale in 53 Wisconsin lakes (26 southeastern and 27 northern). The equations listed represent the best model for each relation. Regressions listed are those of species that occur in ≥ 5% of the quadrats in the respective ecoregion. Guilds are defined in Appendix E. Water chemistry variables are defined in Appendix K.

Macrophyte Species Relative Occurrence	Water Chemistry Variable	Equation	r^2	P
Potamogeton amplifolius	Magnesium	$y = -0.0019x + 0.0794$	0.15	0.004
Vallisneria americana	Magnesium	$y = -0.0053x + 0.2685$	0.13	0.008
Basal Species	Magnesium	$\mathrm{Log}_{10}(y+1) = -0.1456(\mathrm{Log}_{10}(x+1)) + 0.2165$	0.70	<0.001
Exotic Species	Magnesium	$(y+1)^{1/2} = 0.1201(x+1)^{1/2} - 0.1294$	0.48	<0.001
Potamogeton spp.	Magnesium	$y = -0.0064x + 0.4466$	0.13	0.008
FL_RT	Magnesium	$y = -0.0042x + 0.343$	0.12	0.012
NFL_NRT	Magnesium	$y = 0.016x + 0.2114$	0.58	<0.001
Ceratophyllum demersum	Chlorophyll-*a*	$\mathrm{Log}_{10}(y+1) = 0.0789(\mathrm{Log}_{10}(x+1)) - 0.0218$	0.12	0.012
NFL_RT	Chlorophyll-*a*	$y = 0.0114x + 0.5967$	0.09	0.031
***Chara* spp.**	Color	$(y+1)^{1/2} = -0.1106(x+1)^{1/2} + 0.8181$	0.13	0.008
Elodea canadensis	Color	$(y+1)^{1/2} = 0.1016(x+1)^{1/2} - 0.0758$	0.18	0.001
Potamogeton amplifolius	Color	$\mathrm{Log}_{10}(y+1) = 0.0342(\mathrm{Log}_{10}(x+1)) - 0.0116$	0.08	0.043
Lily Pads	Color	$(y+1)^{1/2} = 0.0605(x+1)^{1/2} + 0.0282$	0.11	0.014
NFL_RT	Secchi	$\mathrm{Log}_{10}(y+1) = -0.1548(\mathrm{Log}_{10}(x+1)) + 0.3005$	0.10	0.023
***Chara* spp.**	Nitrogen	$\mathrm{Ln}(y+1) = 0.5187(\mathrm{Ln}(x+1)) - 0.0326$	0.20	0.001
Elodea canadensis	Nitrogen	$(y+1)^{1/2} = -0.9309(x+1)^{1/2} + 1.4614$	0.26	<0.001
Potamogeton amplifolius	Nitrogen	$(y+1)^{1/2} = -0.5667(x+1)^{1/2} + 0.9162$	0.18	0.001
Potamogeton gramineus	Nitrogen	$(y+1)^{1/2} = -0.557(x+1)^{1/2} + 0.9447$	0.10	0.023
Vallisneria americana	Nitrogen	$(y+1)^{1/2} = -0.6735(x+1)^{1/2} + 1.2339$	0.09	0.030
Basal Species	Nitrogen	$(y+1)^{1/2} = -1.6588(x+1)^{1/2} + 2.547$	0.47	<0.001
Exotic Species	Nitrogen	$(y+1)^{1/2} = 1.4505(x+1)^{1/2} - 1.6452$	0.29	<0.001
Potamogeton spp.	Nitrogen	$y = -0.2616x + 0.5464$	0.14	0.006
FL_RT	Nitrogen	$(y+1)^{1/2} = -0.5171(x+1)^{1/2} + 1.1823$	0.11	0.014

APPENDIX V (continued). Regression results of significant species (italics and boldface) and guild—water chemistry relations at the whole lake scale in 53 Wisconsin lakes (26 southeastern and 27 northern). The equations listed represent the best model for each relation. Regressions listed are those of species that occur in ≥ 5% of the quadrats in the respective ecoregion. Guilds are defined in Appendix E. Water chemistry variables are defined in Appendix K.

Macrophyte Species Relative Occurrence	Water Chemistry Variable	Equation	r^2	P
FL_NRT	Nitrogen	$(y+1)^{1/2} = 0.4268(x+1)^{1/2} - 0.4705$	0.08	0.044
NFL_NRT	Nitrogen	$\mathrm{Log}_{10}(y+1) = 0.4598(\mathrm{Log}_{10}(x+1)) + 0.0415$	0.18	0.002
Potamogeton gramineus	Phosphorous	$(y+1)^{1/2} = -6.01(x+1)^{1/2} + 6.2916$	0.09	0.036
Basal Species	Phosphorous	$(y+1)^{1/2} = -8.7614(x+1)^{1/2} + 9.226$	0.10	0.025
FL_RT	Phosphorous	$(y+1)^{1/2} = -6.5628(x+1)^{1/2} + 7.1411$	0.14	0.007
		Northern Ecoregion		
Ceratophyllum demersum	Alkalinity	$(y+1)^{1/2} = 0.0877(x+1)^{1/2} - 0.2826$	0.49	<0.001
***Chara* spp.**	Alkalinity	$y = 0.0031x + 0.0297$	0.23	0.012
Elatine minima	Alkalinity	$\mathrm{Log}_{10}(y+1) = -0.1068(\mathrm{Log}_{10}(x+1)) + 0.185$	0.41	<0.001
Eleocharis acicularis	Alkalinity	$\mathrm{Log}_{10}(y+1) = -0.0689(\mathrm{Log}_{10}(x+1)) + 0.148$	0.20	0.018
Juncus pelocarpus	Alkalinity	$\mathrm{Log}_{10}(y+1) = -0.0655(\mathrm{Log}_{10}(x+1)) + 0.1382$	0.19	0.021
Lobelia dortmanna	Alkalinity	$(y+1)^{1/2} = -0.053(x+1)^{1/2} + 0.4045$	0.24	0.009
Myriophyllum sibiricum	Alkalinity	$y = 0.0046x - 0.0762$	0.44	<0.001
Myriophyllum tenellum	Alkalinity	$y = -0.0032x + 0.2035$	0.15	0.045
Najas flexilis	Alkalinity	$(y+1)^{1/2} = 0.0823(x+1)^{1/2} + 0.0411$	0.27	0.005
Potamogeton amplifolius	Alkalinity	$(y+1)^{1/2} = 0.0565(x+1)^{1/2} - 0.0651$	0.36	0.001
Potamogeton gramineus	Alkalinity	$(y+1)^{1/2} = 0.0801(x+1)^{1/2} - 0.1396$	0.33	0.002
Potamogeton richardsonii	Alkalinity	$(y+1)^{1/2} = 0.0682(x+1)^{1/2} - 0.1966$	0.52	<0.001
Potamogeton robbinsii	Alkalinity	$(y+1)^{1/2} = 0.1135(x+1)^{1/2} - 0.2518$	0.53	<0.001
Potamogeton zosteriformis	Alkalinity	$(y+1)^{1/2} = 0.0855(x+1)^{1/2} - 0.2511$	0.62	<0.001
Vallisneria americana	Alkalinity	$(y+1)^{1/2} = 0.0999(x+1)^{1/2} - 0.0511$	0.40	<0.001
Basal Species	Alkalinity	$\mathrm{Log}_{10}(y+1) = -0.1583(\mathrm{Log}_{10}(x+1)) + 0.3579$	0.48	<0.001

Appendix V (continued). Regression results of significant species (italics and boldface) and guild—water chemistry relations at the whole lake scale in 53 Wisconsin lakes (26 southeastern and 27 northern). The equations listed represent the best model for each relation. Regressions listed are those of species that occur in ≥ 5% of the quadrats in the respective ecoregion. Guilds are defined in Appendix E. Water chemistry variables are defined in Appendix K.

Macrophyte Species Relative Occurrence	Water Chemistry Variable	Equation	r^2	P
Emergent Species	Alkalinity	$y = 0.0016x - 0.0045$	0.17	0.031
Potamogeton spp.	Alkalinity	$\text{Log}_{10}(y+1) = 0.2076(\text{Log}_{10}(x+1)) - 0.1356$	0.69	<0.001
FL_RT	Alkalinity	$(y+1)^{1/2} = 0.0409(x+1)^{1/2} + 0.3554$	0.17	0.030
FL_NRT	Alkalinity	$(y+1)^{1/2} = 0.0263(x+1)^{1/2} - 0.0861$	0.23	0.012
NFL_RT	Alkalinity	$\text{Log}_{10}(y+1) = 0.1674(\text{Log}_{10}(x+1)) - 0.0223$	0.50	<0.001
NFL_NRT	Alkalinity	$y = 0.0047x + 0.106$	0.22	0.014
Ceratophyllum demersum	Conductivity	$(y+1)^{1/2} = 0.0397(x+1)^{1/2} - 0.1725$	0.29	0.004
Elatine minima	Conductivity	$\text{Log}_{10}(y+1) = -0.0979(\text{Log}_{10}(x+1)) + 0.2152$	0.34	0.001
Elodea canadensis	Conductivity	$(y+1)^{1/2} = 0.0331(x+1)^{1/2} + 0.0611$	0.17	0.034
Eleocharis acicularis	Conductivity	$\text{Log}_{10}(y+1) = -0.0744(\text{Log}_{10}(x+1)) + 0.188$	0.24	0.010
Juncus pelocarpus	Conductivity	$\text{Log}_{10}(y+1) = -0.0766(\text{Log}_{10}(x+1)) + 0.1871$	0.26	0.006
Myriophyllum sibiricum	Conductivity	$(y+1)^{1/2} = 0.0432(x+1)^{1/2} - 0.2309$	0.36	0.001
Potamogeton amplifolius	Conductivity	$(y+1)^{1/2} = 0.0276(x+1)^{1/2} - 0.0114$	0.24	0.009
Potamogeton robbinsii	Conductivity	$\text{Log}_{10}(y+1) = 0.0897(\text{Log}_{10}(x+1)) - 0.0994$	0.18	0.026
Potamogeton richardsonii	Conductivity	$(y+1)^{1/2} = 0.0283(x+1)^{1/2} - 0.0879$	0.25	0.008
Potamogeton zosteriformis	Conductivity	$(y+1)^{1/2} = 0.0343(x+1)^{1/2} - 0.1055$	0.29	0.004
Vallisneria americana	Conductivity	$(y+1)^{1/2} = 0.0601(x+1)^{1/2} - 0.0552$	0.41	<0.001
Basal Species	Conductivity	$\text{Log}_{10}(y+1) = -0.1294(\text{Log}_{10}(x+1)) + 0.3737$	0.32	0.002
Potamogeton spp.	Conductivity	$\text{Log}_{10}(y+1) = 0.1641(\text{Log}_{10}(x+1)) - 0.1459$	0.43	<0.001
NFL_RT	Conductivity	$\text{Log}_{10}(y+1) = 0.1485(\text{Log}_{10}(x+1)) - 0.0603$	0.39	0.001
Ceratophyllum demersum	pH	$(y+1)^{1/2} = 0.8737(x+1)^{1/2} - 2.2577$	0.21	0.016
Elatine minima	pH	$\text{Log}_{10}(y+1) = -0.9037(\text{Log}_{10}(x+1)) + 0.8856$	0.28	0.004
Eleocharis acicularis	pH	$y = -0.0991x + 0.8999$	0.22	0.014
Lobelia dortmanna	pH	$(y+1)^{1/2} = -0.6707(x+1)^{1/2} + 1.9949$	0.17	0.034

APPENDIX V (continued). Regression results of significant species (italics and boldface) and guild—water chemistry relations at the whole lake scale in 53 Wisconsin lakes (26 southeastern and 27 northern). The equations listed represent the best model for each relation. Regressions listed are those of species that occur in ≥ 5% of the quadrats in the respective ecoregion. Guilds are defined in Appendix E. Water chemistry variables are defined in Appendix K.

Macrophyte Species Relative Occurrence	Water Chemistry Variable	Equation	r^2	P
Myriophyllum sibiricum	pH	$(y+1)^{1/2} = 0.7891(x+1)^{1/2} - 2.0503$	0.18	0.026
Najas flexilis	pH	$(y+1)^{1/2} = 1.108(x+1)^{1/2} - 2.614$	0.21	0.015
Potamogeton amplifolius	pH	$(y+1)^{1/2} = 0.8862(x+1)^{1/2} - 2.237$	0.38	0.001
Potamogeton gramineus	pH	$(y+1)^{1/2} = 1.1677(x+1)^{1/2} - 2.9721$	0.30	0.003
Potamogeton richardsonii	pH	$(y+1)^{1/2} = 0.9068(x+1)^{1/2} - 2.3649$	0.40	<0.001
Potamogeton robbinsii	pH	$(y+1)^{1/2} = 1.4269(x+1)^{1/2} - 3.6318$	0.37	0.001
Potamogeton zosteriformis	pH	$(y+1)^{1/2} = 1.0424(x+1)^{1/2} - 2.7068$	0.40	<0.001
Vallisneria americana	pH	$(y+1)^{1/2} = 1.4165(x+1)^{1/2} - 3.4729$	0.35	0.001
Basal Species	pH	$y = -0.2155x + 2.0547$	0.32	0.002
Potamogeton spp.	pH	$(y+1)^{1/2} = 1.5406(x+1)^{1/2} - 3.6545$	0.49	<0.001
FL_RT	pH	$(y+1)^{1/2} = 0.7018(x+1)^{1/2} - 1.3847$	0.23	0.013
NFL_RT	pH	$\mathrm{Log}_{10}(y+1) = 1.2981(\mathrm{Log}_{10}(x+1)) - 1.0089$	0.29	0.004
Ceratophyllum demersum	Calcium	$(y+1)^{1/2} = 0.1581(x+1)^{1/2} - 0.255$	0.49	<0.001
***Chara* spp.**	Calcium	$(y+1)^{1/2} = 0.0804(x+1)^{1/2} + 0.0841$	0.17	0.030
Elatine minima	Calcium	$\mathrm{Log}_{10}(y+1) = -0.1152(\mathrm{Log}_{10}(x+1)) + 0.1376$	0.38	0.001
Eleocharis acicularis	Calcium	$\mathrm{Log}_{10}(y+1) = -0.0806(\mathrm{Log}_{10}(x+1)) + 0.1229$	0.22	0.014
Elodea canadensis	Calcium	$(y+1)^{1/2} = 0.1124(x+1)^{1/2} + 0.0447$	0.21	0.017
Juncus pelocarpus	Calcium	$\mathrm{Ln}(y+1) = -0.0751(\mathrm{Ln}(x+1)) + 0.2602$	0.20	0.019
Lobelia dortmanna	Calcium	$\mathrm{Log}_{10}(y+1) = -0.0593(\mathrm{Log}_{10}(x+1)) + 0.0709$	0.21	0.017
Myriophyllum sibiricum	Calcium	$y = 0.017x - 0.0797$	0.56	<0.001
Potamogeton amplifolius	Calcium	$(y+1)^{1/2} = 0.1075(x+1)^{1/2} - 0.0624$	0.40	<0.001
Potamogeton gramineus	Calcium	$(y+1)^{1/2} = 0.1359(x+1)^{1/2} - 0.0914$	0.29	0.004
Potamogeton richardsonii	Calcium	$(y+1)^{1/2} = 0.0942(x+1)^{1/2} - 0.0972$	0.30	0.003
Potamogeton robbinsii	Calcium	$(y+1)^{1/2} = 0.1927(x+1)^{1/2} - 0.1837$	0.47	<0.001

APPENDIX V (continued). Regression results of significant species (italics and boldface) and guild—water chemistry relations at the whole lake scale in 53 Wisconsin lakes (26 southeastern and 27 northern). The equations listed represent the best model for each relation. Regressions listed are those of species that occur in ≥ 5% of the quadrats in the respective ecoregion. Guilds are defined in Appendix E. Water chemistry variables are defined in Appendix K.

Macrophyte Species Relative Occurrence	Water Chemistry Variable	Equation	r^2	P
Potamogeton zosteriformis	Calcium	$(y+1)^{1/2} = 0.1576(x+1)^{1/2} - 0.2333$	0.65	<0.001
Vallisneria americana	Calcium	$(y+1)^{1/2} = 0.1708(x+1)^{1/2} + 0.0058$	0.35	0.001
Basal Species	Calcium	$\mathrm{Log}_{10}(y+1) = -0.1613(\mathrm{Log}_{10}(x+1)) + 0.2792$	0.39	<0.001
Emergent Species	Calcium	$y = 0.0065x - 0.0102$	0.26	0.006
Potamogeton spp.	Calcium	$\mathrm{Log}_{10}(y+1) = 0.2123(\mathrm{Log}_{10}(x+1)) - 0.0328$	0.57	<0.001
FL_NRT	Calcium	$(y+1)^{1/2} = 0.0524(x+1)^{1/2} - 0.0915$	0.28	0.005
NFL_RT	Calcium	$\mathrm{Log}_{10}(y+1) = 0.1622(\mathrm{Log}_{10}(x+1)) + 0.0685$	0.37	0.001
NFL_NRT	Calcium	$y = 0.0132x + 0.1371$	0.16	0.039
Ceratophyllum demersum	Magnesium	$(y+1)^{1/2} = 0.2575(x+1)^{1/2} - 0.2407$	0.37	0.001
Elatine minima	Magnesium	$\mathrm{Log}_{10}(y+1) = -0.1707(\mathrm{Log}_{10}(x+1)) + 0.128$	0.40	<0.001
Eleocharis acicularis	Magnesium	$\mathrm{Log}_{10}(y+1) = -0.1226(\mathrm{Log}_{10}(x+1)) + 0.1179$	0.25	0.009
***Isoetes* spp.**	Magnesium	$\mathrm{Log}_{10}(y+1) = -0.1115(\mathrm{Log}_{10}(x+1)) + 0.122$	0.15	0.043
Juncus pelocarpus	Magnesium	$\mathrm{Log}_{10}(y+1) = -0.1292(\mathrm{Log}_{10}(x+1)) + 0.1165$	0.29	0.004
Lobelia dortmanna	Magnesium	$(y+1)^{1/2} = -0.1777(x+1)^{1/2} + 0.4144$	0.24	0.010
Myriophyllum sibiricum	Magnesium	$\mathrm{Log}_{10}(y+1) = 0.1107(\mathrm{Log}_{10}(x+1)) - 0.0375$	0.31	0.002
Myriophyllum tenellum	Magnesium	$\mathrm{Log}_{10}(y+1) = -0.0968(\mathrm{Log}_{10}(x+1)) + 0.0946$	0.17	0.035
Najas flexilis	Magnesium	$\mathrm{Ln}(y+1) = 0.1525(\mathrm{Ln}(x+1)) + 0.0475$	0.19	0.022
Potamogeton amplifolius	Magnesium	$(y+1)^{1/2} = 0.1557(x+1)^{1/2} - 0.0214$	0.24	0.010
Potamogeton richardsonii	Magnesium	$y = 0.0257x - 0.0242$	0.52	<0.001
Potamogeton robbinsii	Magnesium	$(y+1)^{1/2} = 0.2637(x+1)^{1/2} - 0.0856$	0.25	0.007
Potamogeton spirillus	Magnesium	$y = 0.0291x - 0.0319$	0.22	0.015
Potamogeton zosteriformis	Magnesium	$(y+1)^{1/2} = 0.2372(x+1)^{1/2} - 0.1877$	0.42	<0.001
Vallisneria americana	Magnesium	$(y+1)^{1/2} = 0.3598(x+1)^{1/2} - 0.11$	0.45	<0.001
Potamogeton spp.	Magnesium	$(y+1)^{1/2} = 0.3516(x+1)^{1/2} + 0.0668$	0.52	<0.001

APPENDIX V (continued). Regression results of significant species (italics and boldface) and guild—water chemistry relations at the whole lake scale in 53 Wisconsin lakes (26 southeastern and 27 northern). The equations listed represent the best model for each relation. Regressions listed are those of species that occur in ≥ 5% of the quadrats in the respective ecoregion. Guilds are defined in Appendix E. Water chemistry variables are defined in Appendix K.

Macrophyte Species Relative Occurrence	Water Chemistry Variable	Equation	r^2	P
Basal Species	Magnesium	$\mathrm{Log}_{10}(y+1) = -0.2766(\mathrm{Log}_{10}(x+1)) + 0.2862$	0.55	<0.001
NFL_RT	Magnesium	$\mathrm{Log}_{10}(y+1) = 0.2454(\mathrm{Log}_{10}(x+1)) + 0.0792$	0.41	<0.001
Potamogeton richardsonii	Chlorophyll-*a*	$y = 0.0033x + 0.0265$	0.15	0.047
***Chara* spp.**	Color	$\mathrm{Log}_{10}(y+1) = -0.0785(\mathrm{Log}_{10}(x+1)) + 0.1318$	0.21	0.018
Elatine minima	Color	$(y+1)^{1/2} = -0.0922(x+1)^{1/2} + 0.5214$	0.16	0.039
Juncus pelocarpus	Color	$(y+1)^{1/2} = -0.1023(x+1)^{1/2} + 0.6337$	0.26	0.006
Lobelia dortmanna	Color	$\mathrm{Log}_{10}(y+1) = -0.0595(\mathrm{Log}_{10}(x+1)) + 0.0821$	0.15	0.050
***Nitella* spp.**	Color	$\mathrm{Log}_{10}(y+1) = 0.0686(\mathrm{Log}_{10}(x+1)) - 0.0517$	0.17	0.031
Potamogeton pusillus	Color	$(y+1)^{1/2} = 0.0649(x+1)^{1/2} – 0.0575$	0.15	0.049
Potamogeton spirillus	Color	$y = 0.0057x - 0.0215$	0.18	0.028
Potamogeton richardsonii	Secchi	$\mathrm{Log}_{10}(y+1) = -0.0771(\mathrm{Log}_{10}(x+1)) + 0.0596$	0.18	0.026
Brasenia schreberi	Nitrogen	$\mathrm{Log}_{10}(y+1) = 0.2861(\mathrm{Log}_{10}(x+1)) - 0.0318$	0.17	0.038
***Chara* spp.**	Nitrogen	$(y+1)^{1/2} = -1.2383(x+1)^{1/2} + 1.8245$	0.21	0.019
Elatine minima	Nitrogen	$\mathrm{Log}_{10}(y+1) = -0.5106(\mathrm{Log}_{10}(x+1)) + 0.1284$	0.20	0.023
***Isoetes* spp.**	Nitrogen	$(y+1)^{1/2} = -1.7268(x+1)^{1/2} + 2.4716$	0.29	0.005
***Juncus* spp.**	Nitrogen	$\mathrm{Log}_{10}(y+1) = -0.4368(\mathrm{Log}_{10}(x+1)) + 0.1265$	0.19	0.028
Lobelia dortmanna	Nitrogen	$\mathrm{Log}_{10}(y+1) = -0.3626(\mathrm{Log}_{10}(x+1)) + 0.0841$	0.21	0.020
Potamogeton spirillus	Nitrogen	$y = 0.2947x - 0.1021$	0.25	0.010
Basal Species	Nitrogen	$(y+1)^{1/2} = -1.2988(x+1)^{1/2} + 2.1944$	0.19	0.027
Lily Pads	Nitrogen	$\mathrm{Log}_{10}(y+1) = 0.3536(\mathrm{Log}_{10}(x+1)) - 0.0268$	0.17	0.040
Juncus pelocarpus	Phosphorous	$(y+1)^{1/2} = -13.006(x+1)^{1/2} + 13.42$	0.21	0.020
Potamogeton spirillus	Phosphorous	$y = 3.6998x - 0.0173$	0.27	0.007

APPENDIX V (continued). Regression results of significant species (italics and boldface) and guild—water chemistry relations at the whole lake scale in 53 Wisconsin lakes (26 southeastern and 27 northern). The equations listed represent the best model for each relation. Regressions listed are those of species that occur in ≥ 5% of the quadrats in the respective ecoregion. Guilds are defined in Appendix E. Water chemistry variables are defined in Appendix K.

Macrophyte Species Relative Occurrence	Water Chemistry Variable	Equation	r^2	P
		Southeastern Ecoregion		
***Chara* spp.**	Alkalinity	$y = 0.0039x - 0.05$	0.26	0.008
Najas marina	Alkalinity	$(y+1)^{1/2} = 0.0624(x+1)^{1/2} – 0.5901$	0.20	0.023
Stuckenia pectinata	Alkalinity	$(y+1)^{1/2} = 0.0414(x+1)^{1/2} – 0.2153$	0.15	0.048
***Chara* spp.**	Conductivity	$y = 0.0012x + 0.0361$	0.31	0.003
Ceratophyllum demersum	pH	$y = 0.3796x - 3.1661$	0.19	0.026
***Chara* spp.**	pH	$(y+1)^{1/2} = -2.542(x+1)^{1/2} + 8.1627$	0.22	0.016
Myriophyllum spicatum	pH	$y = 0.5209x - 4.2706$	0.22	0.017
Najas marina	pH	$(y+1)^{1/2} = -1.956(x+1)^{1/2} + 5.9168$	0.18	0.030
Potamogeton gramineus	pH	$(y+1)^{1/2} = -1.9673(x+1)^{1/2} + 5.9522$	0.27	0.007
Basal Species	pH	$(y+1)^{1/2} = -1.6563(x+1)^{1/2} + 5.0142$	0.26	0.008
NFL_RT	pH	$y = 0.3165x - 2.0749$	0.23	0.012
***Chara* spp.**	Calcium	$y = 0.0184x + 0.0131$	0.20	0.024
Najas marina	Calcium	$y = 0.0094x - 0.1829$	0.21	0.020
***Chara* spp.**	Magnesium	$y = 0.0186x + 0.029$	0.38	0.001
Najas marina	Magnesium	$(y+1)^{1/2} = 0.1137(x+1)^{1/2} - 0.4172$	0.26	0.008
Stuckenia pectinata	Magnesium	$(y+1)^{1/2} = 0.0682(x+1)^{1/2} - 0.0642$	0.16	0.040
NFL_NRT	Magnesium	$y = 0.012x + 0.3251$	0.23	0.014
Ceratophyllum demersum	Chlorophyll-*a*	$(y+1)^{1/2} = 0.2032(x+1)^{1/2} - 0.2056$	0.34	0.002
Myriophyllum spicatum	Chlorophyll-*a*	$y = 0.0447x + 0.0078$	0.43	<0.001
Najas marina	Chlorophyll-*a*	$(y+1)^{1/2} = -0.1065(x+1)^{1/2} + 0.3871$	0.16	0.046
Vallisneria americana	Chlorophyll-*a*	$(y+1)^{1/2} = -0.123(x+1)^{1/2} + 0.5069$	0.19	0.027

Appendix V (continued). Regression results of significant species (italics and boldface) and guild—water chemistry relations at the whole lake scale in 53 Wisconsin lakes (26 southeastern and 27 northern). The equations listed represent the best model for each relation. Regressions listed are those of species that occur in $\geq$ 5% of the quadrats in the respective ecoregion. Guilds are defined in Appendix E. Water chemistry variables are defined in Appendix K.

Macrophyte Species Relative Occurrence	Water Chemistry Variable	Equation	r^2	P
Exotic Species	Chlorophyll-*a*	$y = 0.0361x + 0.1341$	0.31	0.003
NFL_RT	Chlorophyll-*a*	$\mathrm{Log}_{10}(y+1) = 0.1131(\mathrm{Log}_{10}(x+1)) + 0.1368$	0.28	0.006
Myriophyllum spicatum	Secchi	$\mathrm{Log}_{10}(y+1) = -0.4652(\mathrm{Log}_{10}(x+1)) + 0.3473$	0.33	0.002
Emergent Species	Secchi	$(y+1)^{1/2} = 0.13(x+1)^{1/2} - 0.0904$	0.19	0.028
Exotic Species	Secchi	$\mathrm{Log}_{10}(y+1) = -0.339(\mathrm{Log}_{10}(x+1)) + 0.3048$	0.20	0.023
Najas marina	Nitrogen	$\mathrm{Ln}(y+1) = 0.3529(\mathrm{Ln}(x+1)) - 0.1797$	0.21	0.019
***Chara* spp.**	Phosphorous	$(y+1)^{1/2} = -8.4278(x+1)^{1/2} + 9.2125$	0.18	0.033
Vallisneria americana	Phosphorous	$y = 3.3224x + 0.0055$	0.30	0.004
FL_RT	Phosphorous	$(y+1)^{1/2} = -6.0333(x+1)^{1/2} + 6.5523$	0.17	0.036
NFL_NRT	Phosphorous	$(y+1)^{1/2} = -5.9066(x+1)^{1/2} + 6.7703$	0.21	0.018

APPENDIX W. Regression results of significant near-shore species (italics and boldface) and guild—water chemistry relations in 53 Wisconsin lakes (26 southeastern and 27 northern). Data from only the first four quadrats was used in these analyses. The equations listed represent the best model for each relation. Regressions listed are those of species that occur in ≥ 5% of the quadrats in the respective ecoregion. Guilds are defined in Appendix E. Water chemistry variables are defined in Appendix K.

Macrophyte Species Relative Occurrence	Water Chemistry Variable	Equation	r^2	P
		Regions Combined		
***Chara* spp.**	Alkalinity	$y = 0.003x - 0.0337$	0.60	<0.001
Basal Species	Alkalinity	$(y+1)^{1/2} = -0.0638(x+1)^{1/2} + 0.9501$	0.62	<0.001
Exotic Species	Alkalinity	$(y+1)^{1/2} = 0.0508(x+1)^{1/2} - 0.2229$	0.41	<0.001
FL_NRT	Alkalinity	$(y+1)^{1/2} = 0.0158(x+1)^{1/2} - 0.0136$	0.08	0.045
NFL_RT	Alkalinity	$\mathrm{Log}_{10}(y+1) = 0.0768(\mathrm{Log}_{10}(x+1)) + 0.0275$	0.29	<0.001
NFL_NRT	Alkalinity	$(y+1)^{1/2} = 0.0588(x+1)^{1/2} - 0.0229$	0.63	<0.001
***Chara* spp.**	Conductivity	$y = 0.001x - 0.0215$	0.59	<0.001
Basal Species	Conductivity	$(y+1)^{1/2} = -0.0364(x+1)^{1/2} + 0.9196$	0.57	<0.001
Exotic Species	Conductivity	$(y+1)^{1/2} = 0.0299(x+1)^{1/2} - 0.2127$	0.40	<0.001
NFL_RT	Conductivity	$\mathrm{Log}_{10}(y+1) = 0.0667(\mathrm{Log}_{10}(x+1)) + 0.0165$	0.22	<0.001
NFL_NRT	Conductivity	$(y+1)^{1/2} = 0.033(x+1)^{1/2} + 0.0128$	0.56	<0.001
***Chara* spp.**	pH	$\mathrm{Ln}(y+1) = 1.2352(\mathrm{Ln}(x+1)) – 2.562$	0.43	<0.001
Basal Species	pH	$(y+1)^{1/2} = -1.7439(x+1)^{1/2} + 5.4071$	0.48	<0.001
Exotic Species	pH	$(y+1)^{1/2} = 1.395(x+1)^{1/2} - 3.7904$	0.32	<0.001
NFL_RT	pH	$(y+1)^{1/2} = 0.9027(x+1)^{1/2} - 1.9238$	0.35	<0.001
NFL_NRT	pH	$(y+1)^{1/2} = 1.5033(x+1)^{1/2} - 3.8327$	0.42	<0.001
***Chara* spp.**	Calcium	$y = 0.0163x - 0.0638$	0.55	<0.001
Basal Species	Calcium	$(y+1)^{1/2} = -0.1564(x+1)^{1/2} + 1.0196$	0.57	<0.001
Exotic Species	Calcium	$(y+1)^{1/2} = 0.118(x+1)^{1/2} - 0.2532$	0.34	<0.001
FL_NRT	Calcium	$(y+1)^{1/2} = 0.0481(x+1)^{1/2} - 0.067$	0.11	0.016

APPENDIX W (continued). Regression results of significant near-shore species (italics and boldface) and guild—water chemistry relations in 53 Wisconsin lakes (26 southeastern and 27 northern). Data from only the first four quadrats was used in these analyses. The equations listed represent the best model for each relation. Regressions listed are those of species that occur in ≥ 5% of the quadrats in the respective ecoregion. Guilds are defined in Appendix E. Water chemistry variables are defined in Appendix K.

Macrophyte Species Relative Occurrence	Water Chemistry Variable	Equation	r^2	P
NFL_RT	Calcium	$\text{Log}_{10}(y+1) = 0.0847(\text{Log}_{10}(x+1)) + 0.0653$	0.21	0.001
NFL_NRT	Calcium	$(y+1)^{1/2} = 0.1465(x+1)^{1/2} - 0.0963$	0.60	<0.001
***Chara* spp.**	Magnesium	$y = 0.0145x + 0.0155$	0.62	<0.001
Basal Species	Magnesium	$\text{Log}_{10}(y+1) = -0.149(\text{Log}_{10}(x+1)) + 0.2338$	0.66	<0.001
Exotic Species	Magnesium	$(y+1)^{1/2} = 0.1014(x+1)^{1/2} - 0.1238$	0.41	<0.001
NFL_RT	Magnesium	$\text{Log}_{10}(y+1) = 0.0613(\text{Log}_{10}(x+1)) + 0.1042$	0.21	0.001
NFL_NRT	Magnesium	$\text{Log}_{10}(y+1) = 0.1433(\text{Log}_{10}(x+1)) - 0.0329$	0.61	<0.001
***Chara* spp.**	Color	$\text{Ln}(y+1) = 0.1391(\text{Ln}(x+1)) - 0.1385$	0.15	0.005
Lily Pads	Color	$\text{Log}_{10}(y+1) = 0.0548(\text{Log}_{10}(x+1)) - 0.0248$	0.11	0.015
NFL_NRT	Color	$(y+1)^{1/2} = -0.0988(x+1)^{1/2} + 0.7762$	0.11	0.014
***Chara* spp.**	Nitrogen	$\text{Log}_{10}(y+1) = -0.5045(\text{Log}_{10}(x+1)) + 0.1936$	0.25	<0.001
Basal Species	Nitrogen	$(y+1)^{1/2} = -1.6392(x+1)^{1/2} + 2.5687$	0.43	<0.001
Exotic Species	Nitrogen	$(y+1)^{1/2} = 1.1763(x+1)^{1/2} - 1.3405$	0.23	<0.001
NFL_RT	Nitrogen	$(y+1)^{1/2} = 0.4616(x+1)^{1/2} + 0.0544$	0.09	0.027
NFL_NRT	Nitrogen	$\text{Log}_{10}(y+1) = 0.5043(\text{Log}_{10}(x+1)) - 0.0135$	0.21	0.001
Basal Species	Phosphorous	$(y+1)^{1/2} = -9.6666(x+1)^{1/2} + 10.189$	0.11	0.016
		Northern Ecoregion		
***Chara* spp.**	Alkalinity	$(y+1)^{1/2} = 0.0639(x+1)^{1/2} - 0.1548$	0.43	<0.001
Elatine minima	Alkalinity	$(y+1)^{1/2} = -0.0882(x+1)^{1/2} + 0.7209$	0.30	0.003
Lobelia dortmanna	Alkalinity	$(y+1)^{1/2} = -0.0496(x+1)^{1/2} + 0.4125$	0.18	0.030
Najas flexilis	Alkalinity	$(y+1)^{1/2} = 0.0885(x+1)^{1/2} - 0.0725$	0.31	0.003

APPENDIX W (continued). Regression results of significant near-shore species (italics and boldface) and guild—water chemistry relations in 53 Wisconsin lakes (26 southeastern and 27 northern). Data from only the first four quadrats was used in these analyses. The equations listed represent the best model for each relation. Regressions listed are those of species that occur in ≥ 5% of the quadrats in the respective ecoregion. Guilds are defined in Appendix E. Water chemistry variables are defined in Appendix K.

Macrophyte Species Relative Occurrence	Water Chemistry Variable	Equation	r^2	P
Potamogeton gramineus	Alkalinity	$(y+1)^{1/2} = 0.076(x+1)^{1/2} - 0.1524$	0.27	0.005
Vallisneria americana	Alkalinity	$(y+1)^{1/2} = 0.0896(x+1)^{1/2} - 0.1845$	0.51	<0.001
Potamogeton spp.	Alkalinity	$(y+1)^{1/2} = 0.0792(x+1)^{1/2} - 0.008$	0.37	0.001
FL_NRT	Alkalinity	$(y+1)^{1/2} = 0.0419(x+1)^{1/2} - 0.1374$	0.25	0.008
NFL_RT	Alkalinity	$(y+1)^{1/2} = 0.0739(x+1)^{1/2} + 0.2089$	0.34	0.001
NFL_NRT	Alkalinity	$(y+1)^{1/2} = 0.0514(x+1)^{1/2} + 0.0034$	0.25	0.009
Elatine minima	Conductivity	$\text{Log}_{10}(y+1) = -0.0911(\text{Log}_{10}(x+1)) + 0.2183$	0.21	0.017
Juncus pelocarpus	Conductivity	$\text{Log}_{10}(y+1) = -0.0679(\text{Log}_{10}(x+1)) + 0.1862$	0.19	0.024
Vallisneria americana	Conductivity	$(y+1)^{1/2} = 0.0486(x+1)^{1/2} - 0.1415$	0.43	<0.001
Potamogeton spp.	Conductivity	$(y+1)^{1/2} = 0.0299(x+1)^{1/2} + 0.143$	0.15	0.045
***Chara* spp.**	pH	$(y+1)^{1/2} = 0.8642(x+1)^{1/2} - 2.227$	0.34	0.001
Elatine minima	pH	$\text{Log}_{10}(y+1) = -0.7782(\text{Log}_{10}(x+1)) + 0.783$	0.15	0.048
Najas flexilis	pH	$(y+1)^{1/2} = 1.2087(x+1)^{1/2} - 2.9753$	0.25	0.008
Potamogeton gramineus	pH	$(y+1)^{1/2} = 1.0626(x+1)^{1/2} - 2.7136$	0.23	0.011
Vallisneria americana	pH	$(y+1)^{1/2} = 1.2816(x+1)^{1/2} - 3.2845$	0.46	<0.001
Potamogeton spp.	pH	$(y+1)^{1/2} = 1.1225(x+1)^{1/2} - 2.7195$	0.33	0.002
NFL_RT	pH	$(y+1)^{1/2} = 0.9927(x+1)^{1/2} - 2.169$	0.27	0.006
NFL_NRT	pH	$(y+1)^{1/2} = 0.71(x+1)^{1/2} - 1.7046$	0.20	0.018
***Chara* spp.**	Calcium	$(y+1)^{1/2} = 0.1044(x+1)^{1/2} - 0.1051$	0.35	0.001
Elatine minima	Calcium	$\text{Log}_{10}(y+1) = -0.1098(\text{Log}_{10}(x+1)) + 0.1483$	0.24	0.010
Najas flexilis	Calcium	$(y+1)^{1/2} = 0.1158(x+1)^{1/2} + 0.074$	0.16	0.037
Potamogeton gramineus	Calcium	$(y+1)^{1/2} = 0.1358(x+1)^{1/2} - 0.1248$	0.27	0.006
Vallisneria americana	Calcium	$(y+1)^{1/2} = 0.1495(x+1)^{1/2} - 0.1237$	0.44	<0.001

APPENDIX W (continued). Regression results of significant near-shore species (italics and boldface) and guild—water chemistry relations in 53 Wisconsin lakes (26 southeastern and 27 northern). Data from only the first four quadrats was used in these analyses. The equations listed represent the best model for each relation. Regressions listed are those of species that occur in ≥ 5% of the quadrats in the respective ecoregion. Guilds are defined in Appendix E. Water chemistry variables are defined in Appendix K.

Macrophyte Species Relative Occurrence	Water Chemistry Variable	Equation	r^2	P
Emergent Species	Calcium	$y = 0.012x + 0.0085$	0.23	0.012
Potamogeton spp.	Calcium	$(y+1)^{1/2} = 0.1089(x+1)^{1/2} + 0.1087$	0.22	0.015
FL_NRT	Calcium	$(y+1)^{1/2} = 0.0836(x+1)^{1/2} - 0.1457$	0.31	0.003
NFL_RT	Calcium	$(y+1)^{1/2} = 0.0954(x+1)^{1/2} + 0.3344$	0.17	0.031
NFL_NRT	Calcium	$(y+1)^{1/2} = 0.105(x+1)^{1/2} - 0.0135$	0.31	0.002
***Chara* spp.**	Magnesium	$(y+1)^{1/2} = 0.1264(x+1)^{1/2} - 0.0255$	0.15	0.048
Elatine minima	Magnesium	$(y+1)^{1/2} = -0.2927(x+1)^{1/2} + 0.7326$	0.29	0.004
Juncus pelocarpus	Magnesium	$y = -0.0397x + 0.2695$	0.23	0.011
Lobelia dortmanna	Magnesium	$(y+1)^{1/2} = -0.1565(x+1)^{1/2} + 0.4061$	0.15	0.043
Najas flexilis	Magnesium	$(y+1)^{1/2} = 0.2825(x+1)^{1/2} - 0.0664$	0.28	0.005
Vallisneria americana	Magnesium	$(y+1)^{1/2} = 0.2809(x+1)^{1/2} - 0.1701$	0.44	<0.001
Basal Species	Magnesium	$y = -0.0568x + 0.6163$	0.18	0.026
Potamogeton spp.	Magnesium	$(y+1)^{1/2} = 0.2451(x+1)^{1/2} + 0.0098$	0.31	0.002
NFL_RT	Magnesium	$(y+1)^{1/2} = 0.2218(x+1)^{1/2} + 0.2365$	0.27	0.006
Juncus pelocarpus	Color	$(y+1)^{1/2} = -0.1148(x+1)^{1/2} + 0.7347$	0.30	0.003
***Isoetes* spp.**	Nitrogen	$(y+1)^{1/2} = -2.0065(x+1)^{1/2} + 2.8632$	0.27	0.006
Lobelia dortmanna	Nitrogen	$\mathrm{Log}_{10}(y+1) = -0.3276(\mathrm{Log}_{10}(x+1)) + 0.0835$	0.16	0.041
Lily pads	Nitrogen	$\mathrm{Log}_{10}(y+1) = 0.2637(\mathrm{Log}_{10}(x+1)) - 0.017$	0.18	0.032
FL_RT	Nitrogen	$y = 0.3555x + 0.0605$	0.15	0.050
***Chara* spp.**	Phosphorous	$(y+1)^{1/2} = -9.0329(x+1)^{1/2} + 9.2872$	0.15	0.050
***Isoetes* spp.**	Phosphorous	$(y+1)^{1/2} = -14.328(x+1)^{1/2} + 14.852$	0.15	0.048
Juncus pelocarpus	Phosphorous	$(y+1)^{1/2} = -14.924(x+1)^{1/2} + 15.413$	0.25	0.010

APPENDIX W (continued). Regression results of significant near-shore species (italics and boldface) and guild—water chemistry relations in 53 Wisconsin lakes (26 southeastern and 27 northern). Data from only the first four quadrats was used in these analyses. The equations listed represent the best model for each relation. Regressions listed are those of species that occur in ≥ 5% of the quadrats in the respective ecoregion. Guilds are defined in Appendix E. Water chemistry variables are defined in Appendix K.

Macrophyte Species Relative Occurrence	Water Chemistry Variable	Equation	r^2	P
		Southeastern Ecoregion		
***Chara* spp.**	Alkalinity	$y = 0.0032x - 0.0671$	0.26	0.014
Stuckenia pectinata	Alkalinity	$y = 0.0008x - 0.0513$	0.27	0.006
***Chara* spp.**	Conductivity	$y = 0.001x + 0.0129$	0.26	0.009
***Chara* spp.**	pH	$(y+1)^{1/2} = -2.4939(x+1)^{1/2} + 7.928$	0.23	0.014
Myriophyllum spicatum	pH	$y = 0.3842x - 3.1322$	0.19	0.024
Basal Species	pH	$(y+1)^{1/2} = -1.7283(x+1)^{1/2} + 5.2572$	0.27	0.007
FL_RT	pH	$(y+1)^{1/2} = -2.188(x+1)^{1/2} + 6.8166$	0.25	0.009
***Chara* spp.**	Calcium	$y = 0.0151x - 0.0164$	0.17	0.036
***Chara* spp.**	Magnesium	$y = 0.0143x + 0.0192$	0.29	0.004
Stuckenia pectinata	Magnesium	$\mathrm{Log}_{10}(y+1) = 0.0544(\mathrm{Log}_{10}(x+1)) - 0.0485$	0.20	0.023
Ceratophyllum demersum	Chlorophyll-*a*	$\mathrm{Log}_{10}(y+1) = 0.1877(\mathrm{Log}_{10}(x+1)) - 0.098$	0.35	0.001
Myriophyllum sibiricum	Chlorophyll-*a*	$y = 0.0068x + 0.0124$	0.16	0.043
Myriophyllum spicatum	Chlorophyll-*a*	$y = 0.0303x + 0.0392$	0.33	0.002
Vallisneria americana	Chlorophyll-*a*	$\mathrm{Log}_{10}(y+1) = -0.0786(\mathrm{Log}_{10}(x+1)) + 0.0859$	0.18	0.031
Exotic Species	Chlorophyll-*a*	$y = 0.0265x + 0.1047$	0.25	0.010
NFL_RT	Chlorophyll-*a*	$(y+1)^{1/2} = 0.0661(x+1)^{1/2} + 0.5842$	0.21	0.018
***Nymphaea* spp.**	Color	$\mathrm{Log}_{10}(y+1) = 0.09(\mathrm{Log}_{10}(x+1)) - 0.0542$	0.15	0.049
Lily Pads	Color	$\mathrm{Log}_{10}(y+1) = 0.0947(\mathrm{Log}_{10}(x+1)) - 0.0567$	0.15	0.047
FL_NRT	Color	$\mathrm{Log}_{10}(y+1) = 0.1785(\mathrm{Log}_{10}(x+1)) - 0.1292$	0.21	0.019
Myriophyllum spicatum	Secchi	$\mathrm{Log}_{10}(y+1) = -0.3454(\mathrm{Log}_{10}(x+1)) + 0.2669$	0.27	0.007

APPENDIX W (continued). Regression results of significant near-shore species (italics and boldface) and guild—water chemistry relations in 53 Wisconsin lakes (26 southeastern and 27 northern). Data from only the first four quadrats was used in these analyses. The equations listed represent the best model for each relation. Regressions listed are those of species that occur in ≥ 5% of the quadrats in the respective ecoregion. Guilds are defined in Appendix E. Water chemistry variables are defined in Appendix K.

Macrophyte Species Relative Occurrence	Water Chemistry Variable	Equation	r^2	P
Vallisneria americana	Secchi	$(y+1)^{1/2} = 0.2852(x+1)^{1/2} - 0.2992$	0.20	0.023
Exotic Species	Secchi	$\mathrm{Log}_{10}(y+1) = -0.2902(\mathrm{Log}_{10}(x+1)) + 0.2521$	0.19	0.026
NFL_RT	Secchi	$\mathrm{Log}_{10}(y+1) = -0.1487(\mathrm{Log}_{10}(x+1)) + 0.2705$	0.16	0.045
***Chara* spp.**	Phosphorous	$(y+1)^{1/2} = -8.9861(x+1)^{1/2} + 9.6859$	0.21	0.018
NFL_NRT	Phosphorous	$(y+1)^{1/2} = -6.4893(x+1)^{1/2} + 7.2666$	0.19	0.024

Appendix X. Range of environmental conditions across which each species occurred. For each species, mean, standard error (S. E.) about the mean, and range of each variable were calculated only for lakes in which the respective species was found (N represents the number of lakes).

		Alkalinity		Conductivity		pH	
	N	Mean± (S.E.)	Range	Mean± (S.E.)	Range	Mean± (S.E.)	Range
Brasenia schreberi	20	38.2 (6.57)	5-116	96.0 (16.53)	14-313	7.82 (0.16)	6.45-9.03
Calla palustris	5	44.2 (3.77)	32-55	117.4 (15.19)	93-176	8.14 (0.09)	7.99-8.45
Ceratophyllum demersum	33	101.1 (10.32)	24-203	272.7 (29.71)	51-599	8.42 (0.08)	7.55-9.23
Chara spp.	50	88.6 (8.78)	5-203	244.2 (25.26)	14-647	8.27 (0.09)	6.45-9.23
Dulichium arundinaceum	7	28.7 (6.96)	5-55	61.6 (14.41)	14-117	7.67 (0.27)	6.45-8.45
Elatine minima	18	32.2 (9.87)	4-192	101.0 (28.54)	14-536	7.70 (0.17)	6.45-8.61
Eleocharis acicularis	40	74.0 (9.97)	5-203	196.6 (27.13)	14-647	8.11 (0.10)	6.45-9.03
Eleocharis palustris	12	55.8 (15.86)	6-192	140.0 (41.77)	17-536	8.10 (0.19)	6.62-8.87
Elodea canadensis	39	77.7 (9.60)	8-203	220.5 (28.36)	22-599	8.24 (0.09)	6.90-9.23
Equisetum fluviatile	5	49.6 (14.01)	8-92	104.0 (28.19)	22-188	8.09 (0.34)	6.90-9.02
Eriocaulon aquaticum	19	25.9 (3.74)	4-58	79.1 (12.37)	14-179	7.67 (0.15)	6.45-8.61
Heteranthera dubia	23	99.6 (12.65)	25-201	283.2 (41.17)	60-647	8.39 (0.09)	7.52-9.23
Isoetes spp.	26	32.5 (5.12)	4-136	92.9 (14.71)	14-376	7.75 (0.12)	6.45-8.61
Juncus effusus	5	32.4 (15.33)	5-92	83.2 (29.78)	14-188	7.61 (0.41)	6.45-9.02
Juncus pelocarpus	24	30.1 (3.43)	4-64	77.8 (9.30)	14-176	7.79 (0.13)	6.45-8.61
Lemna minor	18	93.3 (14.29)	22-192	242.3 (40.34)	50-536	8.31 (0.12)	7.28-9.03
Lemna trisulca	6	106.2 (19.38)	48-168	323.3 (82.15)	103-647	8.42 (0.09)	8.21-8.77
Lobelia dortmanna	14	22.1 (3.53)	4-42	77.8 (3.53)	14-179	7.60 (0.18)	6.45-8.61
Megalodonta beckii	13	49.5 (8.12)	25-140	134.2 (29.94)	60-472	8.07 (0.09)	7.52-8.63
Myriophyllum sibiricum	32	94.8 (10.48)	22-203	264.2 (31.96)	50-647	8.38 (0.08)	7.28-9.23
Myriophyllum spicatum	25	129.8 (10.51)	12-203	364.7 (30.41)	80-647	8.56 (0.08)	7.41-9.23
Myriophyllum tenellum	22	28.2 (3.22)	4-55	81.6 (10.35)	14-179	7.77 (0.13)	6.45-8.61
Najas flexilis	47	91.8 (9.02)	6-203	252.9 (26.21)	17-647	8.31 (0.08)	6.62-9.10
Najas gracillima	5	17.6 (3.88)	8-30	52.6 (14.75)	22-103	7.47 (0.28)	6.90-8.55

Appendix X (continued). Range of environmental conditions across which each species occurred. For each species, mean, standard error (S. E.) about the mean, and range of each variable were calculated only for lakes in which the respective species was found (N represents the number of lakes).

		Alkalinity		Conductivity		pH	
	N	Mean± (S.E.)	Range	Mean± (S.E.)	Range	Mean± (S.E.)	Range
Najas marina	12	156.7 (7.09)	122-201	432.0 (29.68)	311-647	8.59 (0.06)	8.09-8.92
Nitella spp.	22	62.7 (12.65)	8-203	174.8 (35.66)	22-647	7.99 (0.11)	6.90-9.02
Nuphar variegata	25	55.3 (9.53)	6-184	147.3 (27.70)	17-472	7.96 (0.12)	6.62-9.02
Nymphaea spp.	36	86.5 (10.41)	5-203	236.7 (29.27)	14-599	8.25 (0.10)	6.45-9.10
Polygonum amphibium	5	44.2 (18.00)	22-116	95.2 (33.90)	50-230	8.20 (0.34)	7.28-9.03
Pontederia cordata	10	39.4 (4.58)	16-64	113.3 (12.23)	60-176	8.05 (0.12)	7.36-8.61
Potamogeton amplifolius	35	73.5 (8.91)	12-192	204.9 (26.38)	50-599	8.27 (0.09)	7.28-9.03
Potamogeton crispus	7	144.3 (12.64)	95-192	408.0 (43.29)	205-536	8.80 (0.10)	8.52-9.23
Potamogeton epihydrus	11	24.1 (3.25)	8-36	79.4 (13.75)	22-179	7.63 (0.16)	6.90-8.61
Potamogeton foliosus	23	69.0 (11.53)	8-184	189.6 (34.73)	22-599	8.17 (0.12)	6.90-9.02
Potamogeton friesii	12	87.9 (16.45)	24-167	210.3 (42.65)	51-436	8.32 (0.13)	7.71-8.92
Potamogeton gramineus	32	85.0 (11.10)	22-203	222.8 (32.28)	50-647	8.29 (0.07)	7.28-9.03
Potamogeton illinoensis	21	129.3 (11.05)	24-203	356.1 (36.48)	51-647	8.56 (0.07)	7.71-9.02
Potamogeton natans	16	96.2 (14.89)	23-203	238.8 (39.92)	51-535	8.41 (0.13)	7.52-9.03
Potamogeton praelongus	12	98.3 (19.03)	22-201	265.7 (60.20)	50-599	8.40 (0.14)	7.28-8.99
Potamogeton pusillus	20	46.0 (9.49)	6-167	127.7 (26.67)	17-472	7.88 (0.04)	6.62-8.79
Potamogeton richardsonii	17	43.1 (5.34)	23-116	105.5 (12.15)	51-230	8.11 (0.10)	7.52-9.03
Potamogeton robbinsii	22	36.6 (2.76)	12-64	91.4 (8.38)	25-176	8.00 (0.09)	7.26-8.61
Potamogeton spirillus	17	35.7 (7.06)	5-140	115.9 (25.04)	14-472	7.85 (0.14)	6.45-8.63
Potamogeton strictifolius	21	84.6 (13.91)	8-203	228.5 (39.04)	22-599	8.23 (0.13)	6.90-9.02
Potamogeton zosteriformis	31	78.7 (10.03)	16-201	208.0 (27.10)	50-528	8.27 (0.09)	7.28-9.10
Ranunculus aquatilis	8	108.1 (18.52)	42-192	328.1 (66.40)	103-599	8.47 (0.12)	8.09-8.99
Ranunculus flammula	6	23.5 (6.30)	5-42	65.7 (24.18)	14-176	7.46 (0.34)	6.45-8.55
Riccia fluitans	5	114.2 (36.27)	16-184	341.8 (102.34)	103-647	8.00 (0.25)	4.36-8.79

Appendix X (continued). Range of environmental conditions across which each species occurred. For each species, mean, standard error (S. E.) about the mean, and range of each variable were calculated only for lakes in which the respective species was found (N represents the number of lakes).

		Alkalinity		Conductivity		pH	
	N	Mean± (S.E.)	Range	Mean± (S.E.)	Range	Mean± (S.E.)	Range
Sagittaria cristata	16	67.0 (13.71)	4-171	201.3 (45.51)	21-599	8.22 (0.18)	6.90-9.02
Sagittaria latifolia	7	23.0 (4.18)	23-55	115.6 (17.24)	51-176	8.09 (0.10)	7.69-8.45
Sagittaria rigida	5	28.0 (3.79)	16-36	85.8 (14.02)	51-131	7.91 (0.24)	7.36-8.61
Schoenoplectus acutus	8	104.5 (25.48)	16-203	263.3 (61.57)	71-461	8.24 (0.15)	7.36-8.70
Schoenoplectus pungens	9	124.6 (15.04)	22-168	362.3 (61.18)	50-647	8.63 (0.19)	7.28-9.02
Schoenoplectus tabernaemontani	9	101.9 (22.23)	22-201	247.4 (58.27)	50-528	8.49 (0.16)	7.28-8.87
Sparganium angustifolium	13	32.5 (9.77)	4-140	102.9 (33.49)	17-472	7.69 (0.18)	6.62-8.63
Sparganium fluctuans	7	36.6 (7.38)	8-64	94.1 (14.65)	22-136	7.76 (0.19)	6.90-8.30
Spirodela polyrrhiza	8	118.1 (21.01)	44-184	315.5 (64.67)	93-535	8.40 (0.10)	7.99-8.79
Stuckenia pectinata	24	140.5 (7.92)	58-203	383.0 (27.19)	125-647	8.65 (0.06)	8.03-9.10
Typha latifolia	6	82.7 (29.53)	22-201	205.8 (79.42)	50-528	8.33 (0.23)	7.28-8.96
Utricularia resupinata	5	16.6 (6.62)	5-42	68.0 (31.44)	14-176	7.21 (0.27)	6.45-8.09
Utricularia vulgaris	14	107.9 (19.61)	8-203	292.1 (57.26)	22-647	8.14 (0.18)	6.90-8.92
Vallisneria americana	40	83.1 (9.72)	8-203	230.5 (28.16)	22-647	8.25 (0.08)	6.90-9.02

Appendix X (extended). Range of environmental conditions across which each species occurred. For each species, mean, standard error (S. E.) about the mean, and range of each variable were calculated only for lakes in which the respective species was found (N represents the number of lakes).

		Chlorophyll-*a*		Color		Secchi	
	N	Mean± (S.E.)	Range	Mean± (S.E.)	Range	Mean± (S.E.)	Range
Brasenia schreberi	20	6.80 (1.30)	1.12-21.09	12.3 (1.53)	5-30	2.40 (0.19)	1.07-3.81
Calla palustris	5	7.78 (3.94)	1.44-21.09	10.8 (1.77)	5-15	2.49 (0.59)	1.07-3.75
Ceratophyllum demersum	33	6.40 (0.94)	1.12-21.09	9.8 (1.17)	5-30	2.59 (0.19)	0.91-5.03
Chara spp.	50	6.04 (0.78)	1.10-26.91	9.9 (0.84)	5-29	2.57 (0.14)	0.91-5.03
Dulichium arundinaceum	7	9.20 (3.89)	1.67-26.91	13.1 (1.81)	5-20	2.31 (0.39)	1.07-3.50
Elatine minima	18	5.72 (1.42)	1.36-26.91	11.1 (1.34)	5-20	2.49 (0.20)	1.07-3.81
Eleocharis acicularis	40	5.81 (0.88)	1.12-26.91	10.4 (0.97)	5-29	2.57 (0.16)	0.91-5.03
Eleocharis palustris	12	8.11 (2.36)	1.44-26.91	11.7 (1.63)	5-20	2.18 (0.23)	1.07-3.50
Elodea canadensis	39	6.51 (0.98)	1.12-26.91	10.9 (1.01)	5-30	2.46 (0.93)	1.07-5.00
Equisetum fluviatile	5	12.11 (4.97)	2.72-26.91	12.0 (2.77)	5-19	2.06 (0.48)	1.07-3.35
Eriocaulon aquaticum	19	5.08 (1.38)	1.12-26.91	11.6 (1.33)	5-25	2.71 (0.20)	1.07-3.81
Heteranthera dubia	23	7.06 (1.54)	1.44-26.91	9.2 (1.18)	5-25	2.65 (0.25)	1.07-5.03
Isoetes spp.	26	6.35 (1.22)	1.12-26.91	11.9 (1.26)	5-29	2.37 (0.18)	0.91-3.81
Juncus effusus	5	4.31 (0.65)	2.50-5.90	13.0 (3.75)	5-25	2.63 (0.32)	1.67-3.50
Juncus pelocarpus	24	6.10 (1.30)	1.12-26.91	10.9 (1.14)	5-25	2.50 (0.19)	1.07-3.81
Lemna minor	18	6.77 (1.38)	1.44-21.09	12.4 (1.77)	5-30	2.58 (0.23)	1.07-5.03
Lemna trisulca	6	8.00 (2.80)	1.67-21.09	11.6 (1.50)	6-15	2.40 (0.39)	1.07-3.50
Lobelia dortmanna	14	4.49 (0.83)	1.36-12.02	10.7 (1.51)	5-25	2.51 (0.23)	1.50-3.81
Megalodonta beckii	13	7.86 (2.31)	1.12-26.91	12.4 (2.15)	5-30	2.49 (0.30)	1.07-3.81
Myriophyllum sibiricum	32	5.71 (0.92)	1.12-21.09	9.5 (1.13)	5-29	2.61 (0.18)	0.91-5.00
Myriophyllum spicatum	25	5.39 (0.96)	1.12-20.70	8.5 (0.96)	5-20	2.72 (0.22)	1.20-5.03
Myriophyllum tenellum	22	5.18 (1.04)	1.12-21.09	10.8 (1.15)	5-25	2.55 (0.19)	10.7-3.81
Najas flexilis	47	6.05 (0.82)	1.12-26.91	10.0 (0.88)	5-29	2.58 (0.15)	0.91-2.03
Najas gracillima	5	4.23 (0.81)	2.72-7.10	14.0 (2.70)	5-20	2.50 (0.26)	1.83-3.35

Appendix X (continued). Range of environmental conditions across which each species occurred. For each species, mean, standard error (S. E.) about the mean, and range of each variable were calculated only for lakes in which the respective species was found (N represents the number of lakes).

		Chlorophyll-*a*		Color		Secchi	
	N	Mean± (S.E.)	Range	Mean± (S.E.)	Range	Mean± (S.E.)	Range
Najas marina	12	3.40 (0.36)	2.11-6.01	6.5 (1.25)	5-20	3.25 (0.32)	1.90-5.03
Nitella spp.	22	4.19 (0.93)	1.12-21.09	11.1 (1.46)	5-29	2.76 (0.23)	0.91-5.03
Nuphar variegata	25	6.69 (1.25)	1.12-26.91	12.2 (1.28)	5-30	2.45 (0.20)	1.07-5.03
Nymphaea spp.	36	6.79 (1.06)	1.12-26.91	10.9 (1.14)	5-30	2.56 (0.18)	0.91-5.03
Polygonum amphibium	5	6.73 (2.78)	2.50-17.40	12.2 (4.28)	5-25	2.40 (0.19)	1.80-2.85
Pontederia cordata	10	5.59 (2.01)	1.44-21.09	11.0 (1.98)	5-25	2.51 (0.32)	1.07-3.75
Potamogeton amplifolius	35	6.96 (1.07)	1.12-26.91	11.4 (1.19)	5-30	2.41 (0.16)	0.91-5.00
Potamogeton crispus	7	5.30 (1.07)	2.15-9.60	9.3 (2.31)	5-20	2.59 (0.50)	1.20-5.00
Potamogeton epihydrus	11	5.80 (1.36)	1.36-14.50	17.0 (2.55)	6-30	2.21 (0.20)	0.91-3.35
Potamogeton foliosus	23	7.16 (1.48)	1.12-26.91	11.2 (1.23)	5-29	2.45 (0.24)	0.91-5.03
Potamogeton friesii	12	5.97 (1.63)	1.44-21.09	8.3 (1.25)	5-16	2.30 (0.31)	1.07-5.00
Potamogeton gramineus	32	5.87 (1.06)	1.12-26.91	9.1 (0.97)	5-25	2.65 (0.17)	10.7-5.03
Potamogeton illinoensis	21	5.36 (1.18)	2.11-21.09	7.1 (0.79)	5-16	2.81 (0.24)	1.07-5.03
Potamogeton natans	16	5.81 (1.23)	1.12-17.40	10.1 (1.89)	5-30	2.56 (0.21)	1.07-4.40
Potamogeton praelongus	12	6.92 (1.95)	2.63-21.09	9.8 (1.65)	5-20	2.42 (0.23)	1.07-4.00
Potamogeton pusillus	20	7.03 (1.17)	1.12-21.09	14.4 (1.63)	5-30	2.28 (0.19)	0.91-3.81
Potamogeton richardsonii	17	8.00 (1.86)	1.12-26.91	11.9 (1.66)	5-29	2.24 (0.25)	0.91-3.81
Potamogeton robbinsii	22	6.87 (1.16)	1.12-26.91	12.5 (1.63)	5-30	2.34 (0.20)	0.91-3.81
Potamogeton spirillus	17	6.84 (1.76)	1.12-26.91	12.2 (1.77)	5-29	2.53 (0.23)	0.91-3.81
Potamogeton strictifolius	21	7.04 (1.60)	1.36-26.91	11.2 (1.48)	5-29	2.40 (0.24)	0.91-5.00
Potamogeton zosteriformis	31	6.15 (1.07)	1.12-26.91	11.0 (1.30)	5-30	2.62 (0.20)	0.91-5.03
Ranunculus aquatilis	8	8.56 (2.78)	2.09-21.09	12.0 (1.74)	5-20	2.39 (0.34)	1.07-3.75
Ranunculus flammula	6	5.26 (1.25)	2.09-10.40	9.3 (2.33)	5-20	2.59 (0.38)	1.50-3.75
Riccia fluitans	5	6.00 (1.55)	2.32-11.03	14.2 (4.14)	6-29	2.62 (0.68)	0.91-5.03

Appendix X (continued). Range of environmental conditions across which each species occurred. For each species, mean, standard error (S. E.) about the mean, and range of each variable were calculated only for lakes in which the respective species was found (N represents the number of lakes).

		Chlorophyll-*a*		Color		Secchi	
	N	Mean± (S.E.)	Range	Mean± (S.E.)	Range	Mean± (S.E.)	Range
Sagittaria cristata	16	6.40 (1.57)	1.36-21.09	10.1 (1.30)	5-20	2.55 (0.19)	1.07-3.81
Sagittaria latifolia	7	7.09 (2.88)	1.67-21.09	13.0 (3.13)	5-30	2.76 (0.38)	1.07-3.75
Sagittaria rigida	5	10.20 (4.38)	3.15-26.91	16.2 (3.69)	6-29	1.58 (0.26)	0.91-2.13
Schoenoplectus acutus	8	7.32 (2.28)	2.20-21.09	9.5 (1.52)	5-15	2.29 (0.42)	1.07-5.03
Schoenoplectus pungens	9	5.95 (1.94)	2.11-20.70	9.0 (1.98)	5-20	2.78 (0.31)	1.55-4.40
Schoenoplectus tabernaemontani	9	5.07 (1.13)	1.67-12.02	10.0 (1.86)	5-20	2.94 (0.30)	1.98-4.40
Sparganium angustifolium	13	7.61 (2.21)	1.36-26.91	12.2 (1.98)	5-29	2.15 (0.27)	0.91-3.81
Sparganium fluctuans	7	9.25 (3.31)	2.67-26.91	14.4 (3.01)	6-29	1.89 (0.36)	0.91-3.35
Spirodela polyrrhiza	8	7.78 (2.29)	1.67-21.09	10.8 (1.61)	5-15	2.52 (0.48)	1.07-5.03
Stuckenia pectinata	24	5.63 (0.94)	2.11-20.70	8.1 (0.93)	5-20	2.66 (0.22)	1.20-5.03
Typha latifolia	6	5.78 (3.07)	1.67-21.09	10.8 (2.60)	5-20	2.91 (0.47)	1.07-4.00
Utricularia resupinata	5	3.18 (0.46)	2.09-4.87	12.0 (2.30)	5-19	2.91 (0.39)	1.83-3.75
Utricularia vulgaris	14	4.82 (1.32)	1.67-21.09	10.5 (1.51)	5-20	2.83 (0.28)	1.07-5.03
Vallisneria americana	40	5.88 (0.94)	1.12-26.91	10.5 (1.09)	5-30	2.60 (0.16)	0.91-5.03

Appendix X (extended). Range of environmental conditions across which each species occurred. For each species, mean, standard error (S. E.) about the mean, and range of each variable were calculated only for lakes in which the respective species was found (N represents the number of lakes).

		Nitrogen		Phosphorous	
	N	Mean± (S.E.)	Range	Mean± (S.E.)	Range
Brasenia schreberi	19	0.57 (0.04)	0.38-1.04	0.019 (0.002)	0.006-0.040
Calla palustris	4	0.43 (0.03)	0.38-0.51	0.017 (0.004)	0.006-0.025
Ceratophyllum demersum	32	0.03 (0.06)	0.32-1.63	0.028 (0.004)	0.006-0.141
Chara spp.	49	0.76 (0.15)	0.32-1.63	0.124 (0.003)	0.006-0.141
Dulichium arundinaceum	7	0.56 (0.07)	0.38-0.81	0.016 (0.003)	0.006-0.025
Elatine minima	18	0.52 (0.04)	0.32-1.08	0.016 (0.002)	0.006-0.030
Eleocharis acicularis	39	0.68 (0.04)	0.32-1.36	0.021 (0.002)	0.006-0.071
Eleocharis palustris	12	0.58 (0.06)	0.38-1.08	0.017 (0.002)	0.006-0.030
Elodea canadensis	38	0.70 (0.05)	0.32-1.39	0.020 (0.002)	0.006-0.054
Equisetum fluviatile	5	0.49 (0.04)	0.43-0.64	0.019 (0.004)	0.006-0.030
Eriocaulon aquaticum	19	0.52 (0.03)	0.32-0.81	0.015 (0.002)	0.006-0.030
Heteranthera dubia	22	0.74 (0.07)	0.32-1.36	0.020 (0.003)	0.006-0.054
Isoetes spp.	25	0.52 (0.03)	0.32-1.06	0.018 (0.003)	0.006-0.071
Juncus effusus	5	0.52 (0.04)	0.38-0.64	0.017 (0.001)	0.012-0.020
Juncus pelocarpus	23	0.50 (0.03)	0.32-0.81	0.016 (0.002)	0.006-0.030
Lemna minor	17	0.76 (0.08)	0.38-1.36	0.023 (0.003)	0.006-0.054
Lemna trisulca	6	0.80 (0.16)	0.38-1.32	0.028 (0.007)	0.006-0.054
Lobelia dortmanna	14	0.51 (0.04)	0.32-0.81	0.015 (0.002)	0.006-0.030
Megalodonta beckii	12	0.54 (0.08)	0.32-1.39	0.019 (0.004)	0.006-0.045
Myriophyllum sibiricum	32	0.74 (0.06)	0.32-1.39	0.023 (0.003)	0.006-0.071
Myriophyllum spicatum	25	0.90 (0.06)	0.49-1.39	0.023 (0.002)	0.006-0.053
Myriophyllum tenellum	21	0.50 (0.03)	0.32-0.81	0.015 (0.008)	0.006-0.030
Najas flexilis	46	0.78 (0.05)	0.32-1.63	0.025 (0.003)	0.006-0.141
Najas gracillima	5	0.56 (0.07)	0.37-0.73	0.020 (0.003)	0.013-0.030

Appendix X (continued). Range of environmental conditions across which each species occurred. For each species, mean, standard error (S. E.) about the mean, and range of each variable were calculated only for lakes in which the respective species was found (N represents the number of lakes).

		Nitrogen		Phosphorous	
	N	Mean± (S.E.)	Range	Mean± (S.E.)	Range
Najas marina	12	1.05 (0.07)	0.63-1.39	0.025 (0.004)	0.006-0.053
Nitella spp.	22	0.61 (0.05)	0.32-1.27	0.020 (0.003)	0.006-0.071
Nuphar variegata	24	0.65 (0.06)	0.32-1.39	0.023 (0.003)	0.006-0.054
Nymphaea spp.	35	0.75 (0.05)	0.38-1.39	0.022 (0.002)	0.006-0.071
Polygonum amphibium	5	0.58 (0.09)	0.37-0.83	0.015 (0.002)	0.006-0.020
Pontederia cordata	9	0.47 (0.02)	0.38-0.57	0.017 (0.003)	0.006-0.025
Potamogeton amplifolius	34	0.69 (0.05)	0.32-1.39	0.022 (0.002)	0.006-0.071
Potamogeton crispus	7	0.91 (0.11)	0.56-1.32	0.028 (0.005)	0.015-0.054
Potamogeton epihydrus	11	0.60 (0.06)	0.32-1.06	0.022 (0.006)	0.006-0.071
Potamogeton foliosus	22	0.66 (0.07)	0.32-1.63	0.027 (0.006)	0.006-0.141
Potamogeton friesii	11	0.66 (0.09)	0.32-1.36	0.020 (0.003)	0.006-0.041
Potamogeton gramineus	31	0.69 (0.05)	0.32-1.39	0.019 (0.002)	0.006-0.053
Potamogeton illinoensis	21	0.88 (0.64)	0.43-1.39	0.022 (0.003)	0.006-0.053
Potamogeton natans	15	0.79 (0.07)	0.38-1.36	0.020 (0.002)	0.006-0.040
Potamogeton praelongus	12	0.72 (0.08)	0.37-1.32	0.021 (0.003)	0.006-0.041
Potamogeton pusillus	19	0.63 (0.07)	0.32-1.39	0.026 (0.004)	0.006-0.071
Potamogeton richardsonii	16	0.53 (0.05)	0.32-1.06	0.017 (0.004)	0.006-0.071
Potamogeton robbinsii	21	0.54 (0.04)	0.32-10.6	0.018 (0.003)	0.006-0.071
Potamogeton spirillus	17	0.59 (0.08)	0.32-1.39	0.020 (0.004)	0.006-0.071
Potamogeton strictifolius	20	0.72 (0.06)	0.43-1.36	0.023 (0.003)	0.006-0.071
Potamogeton zosteriformis	30	0.72 (0.06)	0.37-1.36	0.022 (0.003)	0.006-0.071
Ranunculus aquatilis	8	0.73 (0.12)	0.40-1.32	0.024 (0.005)	0.006-0.054
Ranunculus flammula	6	0.45 (0.06)	0.32-0.69	0.017 (0.004)	0.006-0.030
Riccia fluitans	5	0.99 (0.11)	0.57-1.27	0.038 (0.012)	0.006-0.071

Appendix X (continued). Range of environmental conditions across which each species occurred. For each species, mean, standard error (S. E.) about the mean, and range of each variable were calculated only for lakes in which the respective species was found (N represents the number of lakes).

		Nitrogen		Phosphorous	
	N	Mean± (S.E.)	Range	Mean± (S.E.)	Range
Sagittaria cristata	16	0.67 (0.07)	0.32-1.32	0.020 (0.003)	0.006-0.054
Sagittaria latifolia	7	0.52 (0.06)	0.38-0.81	0.017 (0.004)	0.006-0.032
Sagittaria rigida	5	0.62 (0.11)	0.48-1.06	0.024 (0.012)	0.006-0.071
Schoenoplectus acutus	8	0.66 (0.10)	0.42-1.27	0.022 (0.005)	0.006-0.053
Schoenoplectus pungens	9	0.99 (0.11)	0.64-1.63	0.034 (0.014)	0.006-0.141
Schoenoplectus tabernaemontani	9	0.81 (0.13)	0.37-1.32	0.025 (0.005)	0.006-0.054
Sparganium angustifolium	13	0.60 (0.08)	0.32-1.39	0.023 (0.005)	0.006-0.071
Sparganium fluctuans	6	0.58 (0.10)	0.44-1.06	0.026 (0.010)	0.006-0.071
Spirodela polyrrhiza	7	0.84 (0.15)	0.38-1.39	0.032 (0.005)	0.018-0.053
Stuckenia pectinata	24	0.93 (0.05)	0.46-1.36	0.024 (0.003)	0.006-0.054
Typha latifolia	6	0.82 (0.21)	0.38-1.63	0.038 (0.021)	0.006-0.141
Utricularia resupinata	5	0.51 (0.06)	0.38-0.73	0.017 (0.004)	0.006-0.030
Utricularia vulgaris	14	0.84 (0.09)	0.38-1.39	0.025 (0.004)	0.006-0.053
Vallisneria americana	39	0.72 (0.05)	0.32-1.63	0.024 (0.004)	0.006-0.141

Appendix X (extended). Range of environmental conditions across which each species occurred. For each species, mean, standard error (S. E.) about the mean, and range of each variable were calculated only for lakes in which the respective species was found (N represents the number of lakes).

		Calcium		Magnesium	
	N	Mean± (S.E.)	Range	Mean± (S.E.)	Range
Brasenia schreberi	20	10.02 (1.58)	1.3-30.1	3.73 (0.84)	0.4-18.2
Calla palustris	5	13.80 (1.14)	11.0-16.2	2.48 (0.59)	1.1-3.8
Ceratophyllum demersum	33	20.55 (1.74)	4.2-40.1	2.59 (0.19)	0.9-5.0
Chara spp.	50	17.92 (1.51)	1.3-40.1	14.66 (1.85)	0.4-41.1
Dulichium arundinaceum	7	7.79 (2.13)	1.3-16.0	2.26 (0.49)	0.4-4.2
Elatine minima	18	8.18 (1.83)	1.3-34.3	4.37 (2.18)	0.4-41.4
Eleocharis acicularis	40	15.29 (1.69)	1.3-34.7	11.74 (2.10)	0.4-41.1
Eleocharis palustris	12	12.47 (2.48)	1.5-34.3	8.31 (3.57)	0.7-41.1
Elodea canadensis	39	16.65 (1.68)	1.7-40.1	12.18 (2.04)	0.9-41.1
Equisetum fluviatile	5	12.04 (3.11)	1.7-18.0	5.36 (2.44)	0.9-14.8
Eriocaulon aquaticum	19	7.19 (1.09)	1.3-16.2	2.55 (0.37)	0.4-6.9
Heteranthera dubia	23	20.45 (2.07)	6.0-40.1	16.79 (2.99)	2.2-41.1
Isoetes spp.	26	8.52 (1.19)	1.3-27.9	3.36 (0.70)	0.4-19.1
Juncus effusus	5	7.88 (2.70)	1.3-17.6	4.64 (2.59)	0.4-17.8
Juncus pelocarpus	24	8.36 (1.02)	1.3-18.0	2.75 (0.31)	0.4-6.9
Lemna minor	18	19.26 (2.25)	5.8-34.7	14.99 (3.19)	2.0-41.1
Lemna trisulca	6	24.57 (3.05)	14.6-32.4	15.08 (5.20)	3.3-36.2
Lobelia dortmanna	14	6.41 (1.18)	1.3-16.2	2.21 (0.33)	0.4-4.3
Megalodonta beckii	13	13.09 (1.78)	6.0-29.9	5.37 (1.87)	2.2-27.7
Myriophyllum sibiricum	32	19.44 (1.81)	4.2-40.1	15.45 (2.26)	2.0-37.4
Myriophyllum spicatum	25	24.69 (1.79)	5.0-40.1	23.23 (2.35)	1.7-41.1
Myriophyllum tenellum	22	8.06 (0.98)	1.3-16.2	2.55 (0.25)	0.4-4.3
Najas flexilis	47	18.52 (1.55)	1.5-40.1	15.20 (1.93)	0.7-41.1
Najas gracillima	5	5.42 (1.43)	1.7-8.6	1.94 (0.45)	0.9-3.4

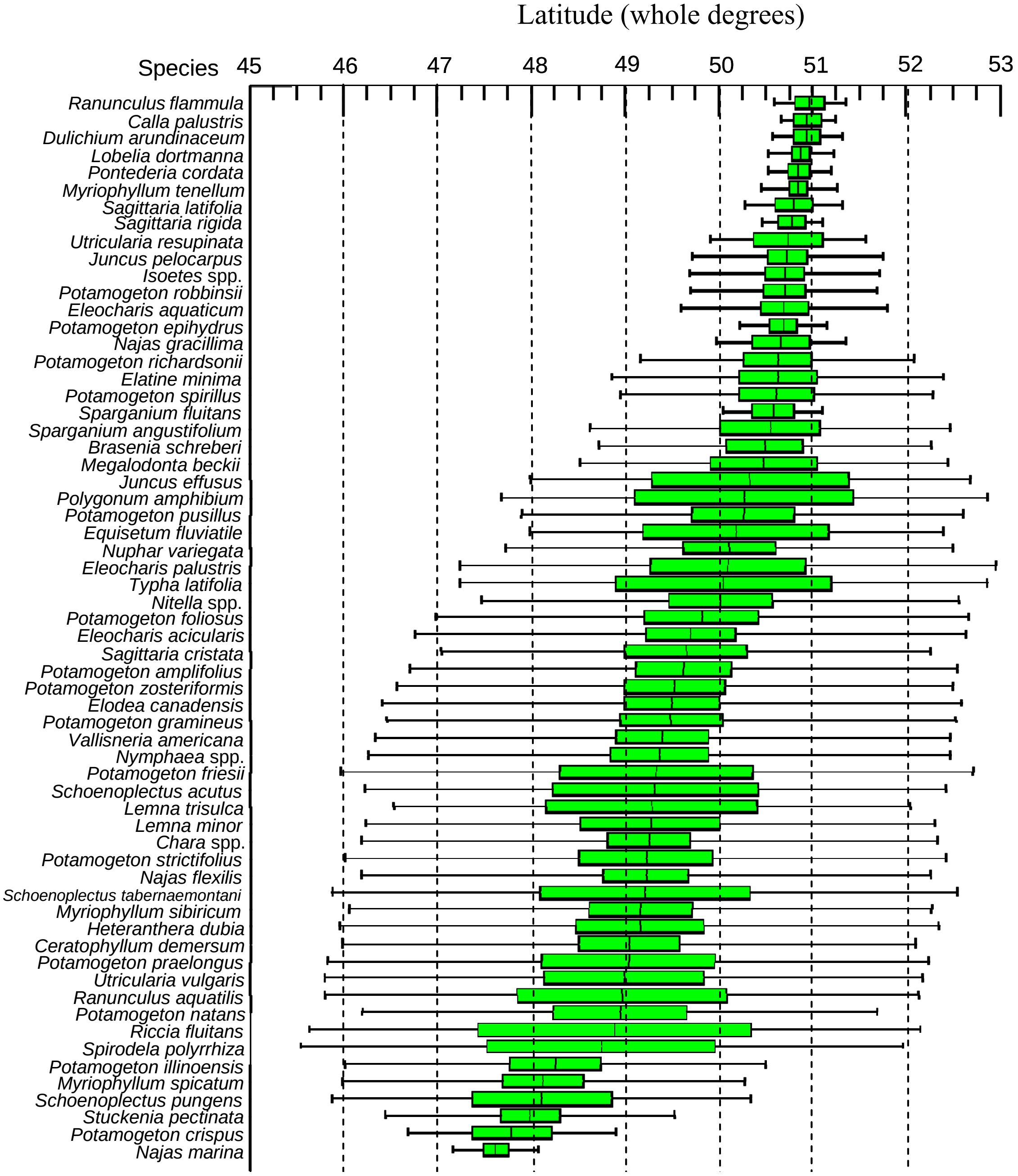
Appendix X (continued). Range of environmental conditions across which each species occurred. For each species, mean, standard error (S. E.) about the mean, and range of each variable were calculated only for lakes in which the respective species was found (N represents the number of lakes).

		Calcium		Magnesium	
	N	Mean± (S.E.)	Range	Mean± (S.E.)	Range
Najas marina	12	29.11 (1.60)	21.0-40.1	30.13 (1.95)	18.6-40.1
Nitella spp.	22	13.71 (2.15)	1.7-34.7	9.64 (2.67)	0.9-36.3
Nuphar variegata	25	13.20 (1.93)	1.5-34.7	7.08 (1.79)	0.7-34.5
Nymphaea spp.	36	17.93 (1.78)	1.3-40.1	14.03 (2.15)	0.4-37.4
Polygonum amphibium	5	9.04 (2.19)	5.8-17.6	5.56 (3.17)	2.0-18.2
Pontederia cordata	10	12.29 (1.29)	6.1-18.0	3.56 (0.26)	2.2-4.9
Potamogeton amplifolius	35	15.69 (1.49)	4.2-34.3	11.36 (1.98)	1.7-41.1
Potamogeton crispus	7	26.46 (2.36)	15.6-34.3	26.53 (3.30)	14.7-41.1
Potamogeton epihydrus	11	5.90 (0.73)	1.7-9.5	2.80 (0.54)	0.9-7.6
Potamogeton foliosus	23	14.92 (2.00)	1.7-34.7	10.45 (2.37)	0.9-34.5
Potamogeton friesii	12	17.57 (2.54)	5.8-31.5	13.96 (3.86)	2.4-34.1
Potamogeton illinoensis	32	17.98 (1.91)	5.8-40.1	13.15 (2.40)	1.9-41.1
Potamogeton gramineus	21	24.86 (1.85)	5.8-40.1	22.90 (2.59)	2.4-37.4
Potamogeton natans	16	18.60 (2.32)	5.9-34.4	15.40 (3.22)	1.9-36.3
Potamogeton praelongus	12	19.98 (3.32)	5.8-40.1	15.90 (3.88)	2.0-37.4
Potamogeton pusillus	20	11.23 (2.04)	1.5-31.5	5.62 (1.72)	0.7-27.7
Potamogeton richardsonii	17	10.57 (1.14)	4.2-18.0	4.41 (0.92)	1.9-18.2
Potamogeton robbinsii	22	9.66 (0.91)	2.6-18.0	3.41 (0.33)	1.1-7.6
Potamogeton spirillus	17	9.47 (1.59)	1.3-29.9	4.38 (1.50)	0.4-27.7
Potamogeton strictifolius	21	16.97 (2.35)	1.7-34.4	14.26 (3.01)	0.9-41.1
Potamogeton zosteriformis	31	16.77 (1.69)	4.2-40.1	12.26 (2.13)	2.0-37.4
Ranunculus aquatilis	8	23.51 (2.81)	12.8-34.3	17.58 (4.65)	3.3-41.1
Ranunculus flammula	6	6.53 (2.24)	1.3-16.2	2.02 (0.57)	0.4-4.3
Riccia fluitans	5	22.28 (6.54)	4.2-34.7	21.79 (6.86)	3.4-36.2

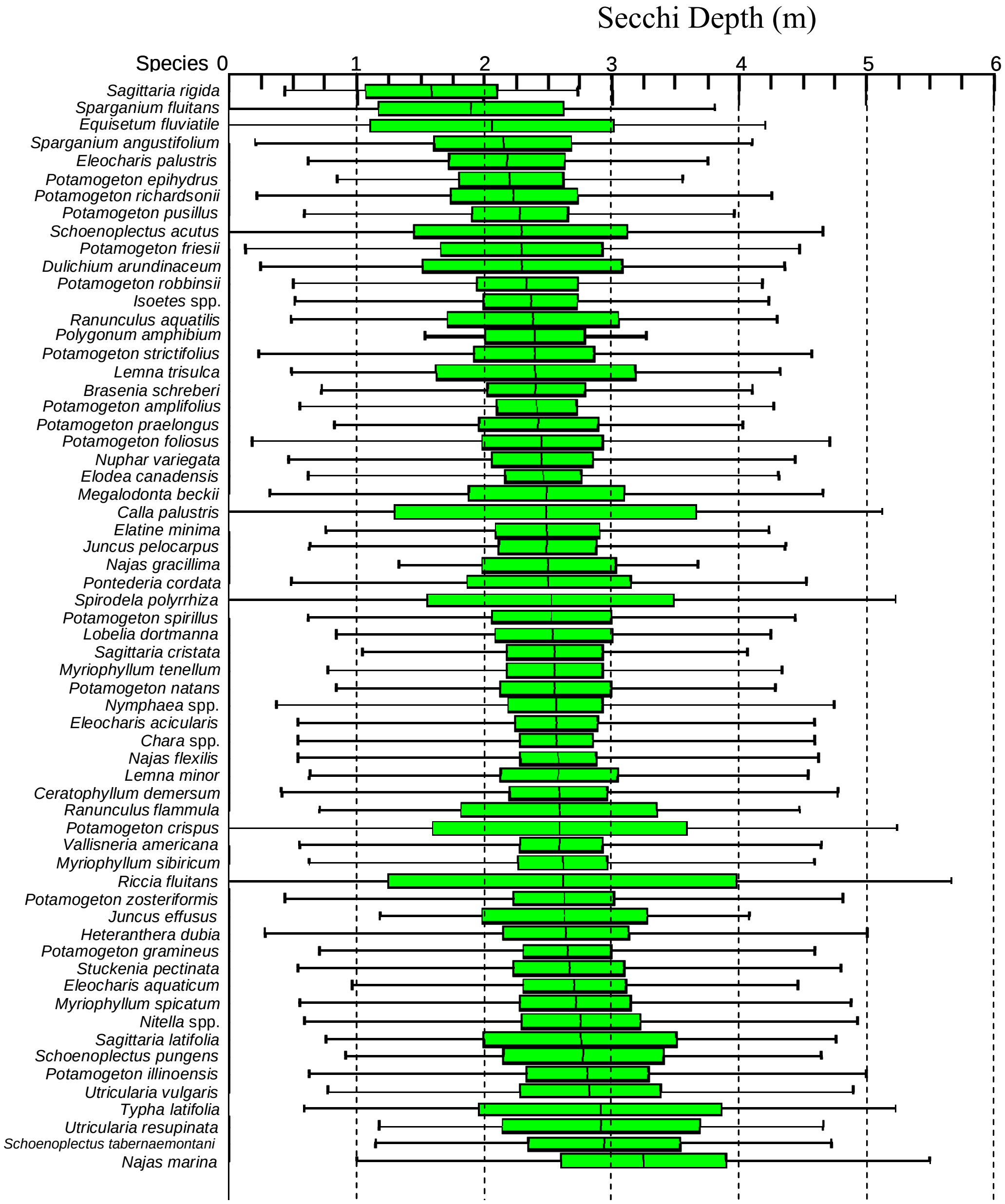
Appendix X (continued). Range of environmental conditions across which each species occurred. For each species, mean, standard error (S. E.) about the mean, and range of each variable were calculated only for lakes in which the respective species was found (N represents the number of lakes).

		Calcium		Magnesium	
	N	Mean± (S.E.)	Range	Mean± (S.E.)	Range
Sagittaria cristata	16	14.61 (2.46)	1.5-30.7	9.76 (2.69)	0.5-30.8
Sagittaria latifolia	7	12.70 (1.42)	5.9-6.2	3.56 (0.32)	1.9-4.3
Sagittaria rigida	5	6.84 (0.82)	4.2-8.6	3.87 (0.93)	2.4-7.6
Schoenoplectus acutus	8	21.61 (3.81)	8.1-34.7	13.31 (5.12)	3.1-36.3
Schoenoplectus pungens	9	23.21 (2.68)	5.8-32.4	23.99 (3.43)	2.0-36.2
Schoenoplectus tabernaemontani	9	20.36 (3.92)	5.8-40.1	16.29 (4.50)	2.0-37.4
Sparganium angustifolium	13	7.65 (2.14)	1.5-29.9	4.37 (2.01)	0.5-27.7
Sparganium fluctuans	7	9.26 (2.05)	1.7-18.0	3.94 (0.77)	0.9-7.6
Spirodela polyrrhiza	8	24.56 (3.22)	11.2-34.7	18.80 (4.65)	3.3-34.5
Stuckenia pectinata	24	26.53 (1.33)	13.1-40.1	24.88 (2.03)	4.9-41.1
Typha latifolia	6	18.38 (5.29)	5.8-40.1	12.92 (6.31)	2.0-37.4
Utricularia resupinata	5	6.08 (2.85)	1.3-16.2	2.02 (0.77)	0.4-4.3
Utricularia vulgaris	14	20.82 (3.29)	1.7-34.7	18.92 (4.06)	0.9-36.3
Vallisneria americana	40	17.29 (1.64)	1.7-34.7	13.53 (2.09)	0.9-41.1

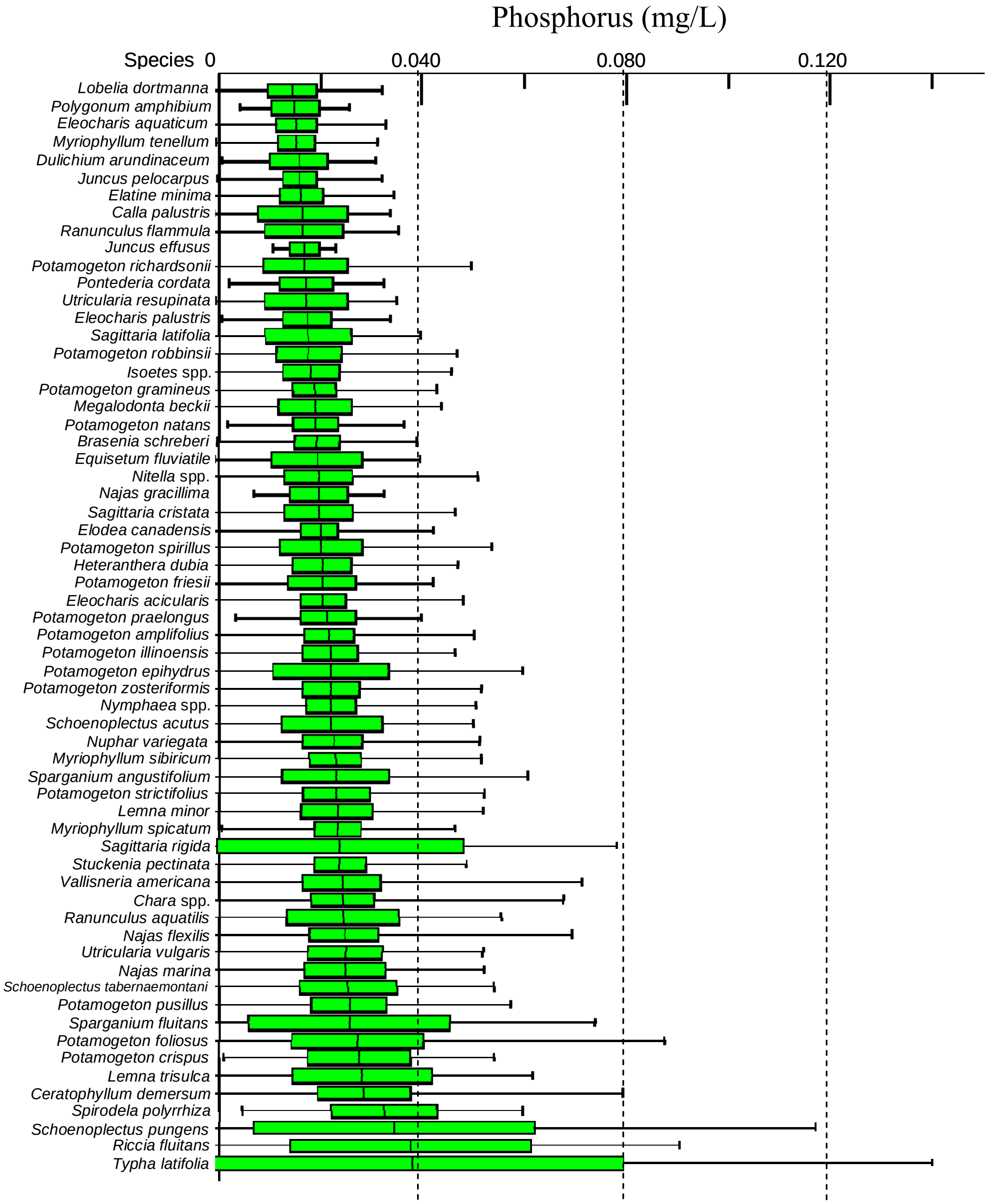
Appendix Y. Latitude tolerances of individual macrophyte species occurring in five or more of the 53 Wisconsin lakes sampled. The center vertical bar in each box represents the mean. Boxes around the mean represent two standard errors about the mean and horizontal lines represent two standard deviations about the mean.



Appendix Z. Water clarity tolerances of individual macrophyte species occurring in five or more of the 53 Wisconsin lakes sampled. The center vertical bar in each box represents the mean. Boxes around the mean represent two standard errors about the mean and horizontal lines represent two standard deviations about the mean.



Appendix AA. Phosphorus tolerances of individual macrophyte species occurring in five or more of the 53 Wisconsin lakes sampled. The center vertical bar in each box represents the mean. Boxes around the mean represent two standard errors about the mean and horizontal lines represent two standard deviations about the mean.



APPENDIX AB. Canonical correspondence analysis biplot of 53 Wisconsin study lakes relative to environmental factors on CCA axes 1 and 2.