A Quantitative Survey of the Submersed Macrophytes in Devil's Lake, Sauk County, with a Historical Review of the Invasion of Eurasian Watermilfoil, *Myriophyllum spicatum* L.

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Abstract. *Quantitative surveys of the aquatic macrophytes of Devil's Lake, Devil's Lake State Park, Sauk County, were conducted July 29–31, 1987, in an effort to assess historical changes in the lake's macrophyte community. Above-ground biomass and frequency of occurrence data were obtained from 28 transects spaced 200 m apart. Biomass samples (0.1 m^2 quadrats) were collected and frequencies of occurrence (0.8 m^2 quadrats) were recorded at 5 m intervals along transects from shore to a water depth of 9 m. Macrophytes occupied 78% of the 0–9 m littoral zone at an average biomass of 187 g/m^2 (within vegetated areas).* Potamogeton robbinsii *Oakes and* Elodea canadensis *Michx. were dominant, accounting for almost half of the 39,000 kg of total plant biomass.* Myriophyllum spicatum *L., an introduced species that accounted for an additional 22% of the total biomass, formed three distinctive surface canopy beds 25–50 m wide by up to 300 m long in water 1.5–3.0 m deep. Milfoil distribution increased dramatically between 1979 and 1987 but showed some indication of declining in 1988 and 1989. Native macrophytes also increased in abundance and distribution. Mechanisms responsible for the growth dynamics of milfoil in Devil's Lake were not identified, but climatic fluctuations and insect disturbances may be significant.*

Devil's Lake State Park, Sauk County, has a rich and diverse flora that has received attention by botanists since the mid-nineteenth century (Lange 1984). However, most botanical collections were of terrestrial species, and relatively little is known about the aquatic flora of Devil's Lake (exceptions include Baker 1975; Lillie 1986). Recently, the Wisconsin Department of Natural Resources (WDNR) conducted a series of limnological investigations to identify possible causes and mechanisms responsible for deteriorating water quality (Lillie and Mason 1986; Lillie 1986; WDNR 1988). Because some rooted submersed macrophytes can effectively translocate nutrients from sediments to the surrounding water column (Barko and Smart 1980; Nichols and Keeney 1976; Prentki 1979; Smith and Adams 1986), changes in the abundance or community composition of submersed macrophytes may influence lake water quality (Landers 1982; Carpenter 1983; Carpenter and Lodge 1986). Consequently, the WDNR conducted macrophyte surveys in Devil's Lake in 1984 and 1987. Specific objectives of these surveys were: (1) to document the composition,

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standing crop biomass, and distribution of the submersed macrophytes in Devil's Lake and (2) to compare current distributions with available historical data. These data, compiled and summarized in this paper, represent a significant contribution to the knowledge of the flora of Devil's Lake and should serve as the basis for monitoring future long-term changes in the lake's aquatic plant community. Likewise, the documented history of the introduction, expansion, and growth dynamics of *Myriophyllum spicatum* L. in Devil's Lake may provide information useful in the management of this exotic invasive species.

Methods

Devil's Lake is a relatively small (151 ha), moderately soft water (total alkalinity 22 mg/L), thermally stratified (maximum depth 14 m), seepage lake with generally very good water quality (Lillie and Mason 1986). Surveys of the submersed macrophytes of Devil's Lake were conducted July 30–August 1, 1984 and July 29–31, 1987. Methods employed in the 1984 survey were described earlier (Lillie 1986) and were generally similar to those used in 1987 as described here. In 1987, macrophyte surveys were conducted via SCUBA along 28 transects spaced 200 m apart around the shoreline (Fig. 1). Two diveteams, consisting of one diver and two topside assistants each, were required to complete the field collections. Presence or absence of all macrophyte species were recorded from 644 (646 in 1984 survey) circular quadrats (0.8 m^2) spaced at 5 m intervals (linear distance) along each transect from shore to a water depth of 9 m. These data were used to compute frequencies of occurrence for each macrophyte species. Divers also visually classified total macrophyte, aboveground, standing crop biomass at each quadrat as either absent, rare, sparse, or dense. Above-ground biomass samples were collected for dry weight determinations from a representative number of each subjective biomass class (i.e. rare, sparse, or dense) by harvesting all plant shoots and stems within 0.1 m^2 quadrats (three-sided aluminum frame) at the sediment-plant interface (Table 1). In some dense stands, sampling intervals were extended to 10 m (linear distance); standing crop data were interpolated for intermediate quadrats. Biomass samples were collected from every fourth sparse and rare quadrat beginning with the first encounter of each day of field collections. All samples were bagged, labeled, placed in a iced-cooler, and transported to the laboratory where they were sorted by species and dried at 106°C for 48 hours. A spikerush, *Eleocharis acicularis* R. & S., was harvested with roots intact. Because it was not possible to distinguish between *Potamogeton illinoensis* Morong and *Potamogeton amplifolius* Tuckerm. in the field, data for these two species were combined (*P. illinoensis* was the more common species based on laboratory examinations). Likewise, *Nitella* spp. and filamentous algae (*Cladophora* spp.) were often physically intertwined and impossible to separate; hence data for these taxa were also combined.

Taxonomy was based on Fassett (1972) and Voss (1972). Voucher specimens were prepared and taxonomy verified by T. Cochran and H. Iltis of the University of Wisconsin-Madison Herbarium and, in the case of pondweeds, by S. G. Smith of the University of Wisconsin-Whitewater.

Average dry weight biomass for each plant taxon was computed for each 1.5-m depth interval along each transect. Average biomass was multiplied by the area of each representative cell (inshore and offshore boundaries of cells were defined by water depth limits; lateral boundaries were defined by common boundaries half-way between adjacent transects. (See Fig. 1 to obtain areal-weighted biomass values.) These values were summed to derive estimates of total standing crop of each taxon by transect, region, depth zone, and entire lake. For purposes of discussion, results will be presented in terms of these four areas, or combinations thereof.

Inasmuch as this method of calculating standing crop biomass did not permit an un-

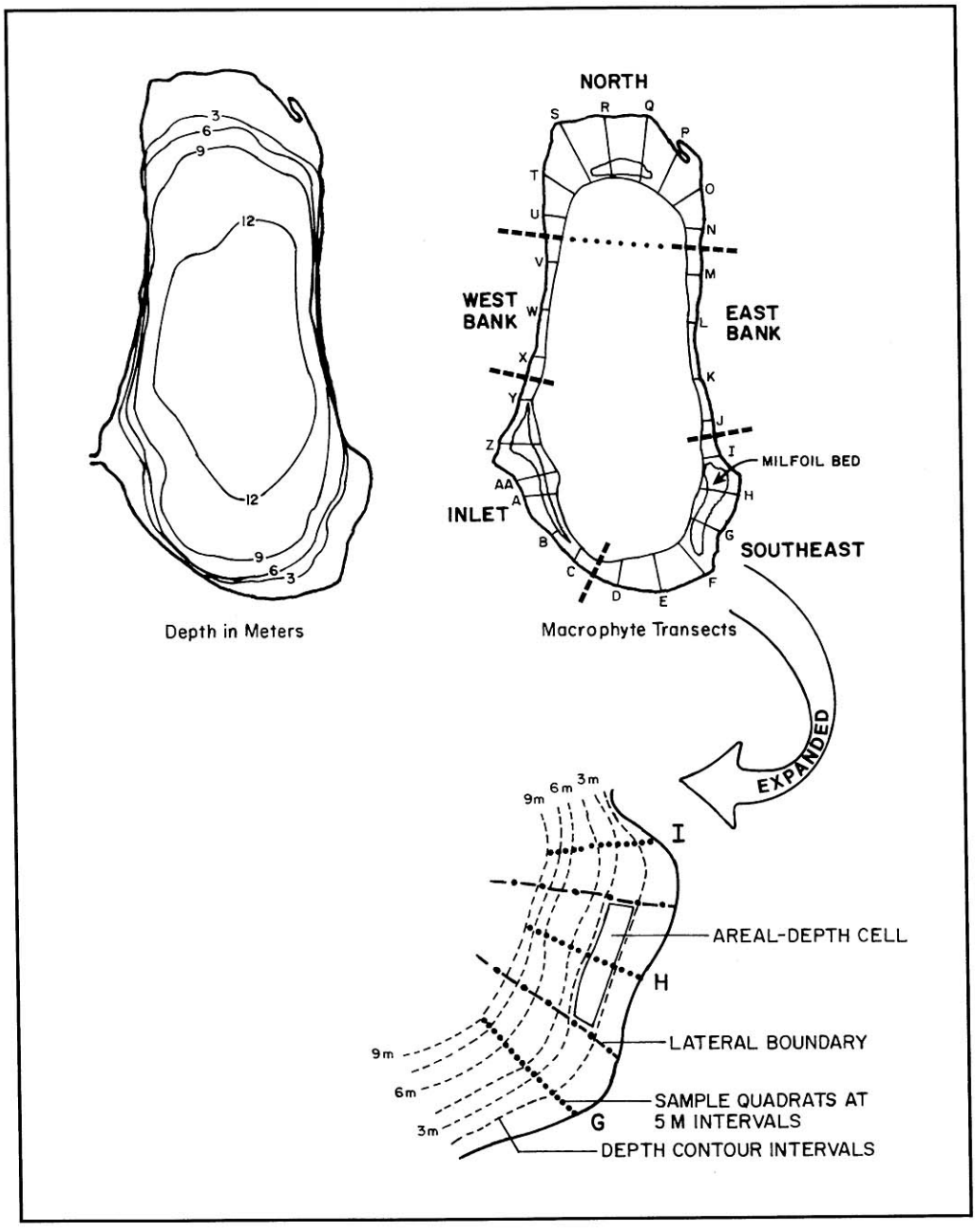

Fig. 1. Hydrographic map of Devil's Lake, Sauk County, Wisconsin with accompanying maps depicting the locations of macrophyte survey transects and boundaries used in estimating plant biomass (see text for further explanation).

biased computation of variance (values were interpolated for intermediate quads and unsampled sites; a few cells contained only 1 quadrat), a second estimate of total standing crop was made using only the data from the rare, sparse, and dense quads that were actually sampled (see Table 1). Average biomass of each subjective plant-biomass class

Table 1. Distribution of biomass samples by visual biomass class. Data represent the percent of quadrats in each visual biomass class within which plants were collected for dry weight measurements.

Visual Biomass Class	*1984*	*1987*
"Dense"	79%	84%
"Sparse"	4	24
"Rare"	1	25
"None"*	-	-
All vegetated sites	47	61
All quadrats	56	68

*by definition - No plants; total biomass zero; no collection necessary.

was multiplied by the area occupied by each class (based solely on frequency of occurrence) to derive estimates of standing crop for each region. This latter method of calculation overestimated standing crop biomass by about 33% but permitted an estimation of biomass variance. Coefficients of variation of total standing crop using this second method of calculation were 6.8% and 6.3% for 1984 and 1987 data, respectively. These variances may be roughly applied to the more accurate areal-weighted biomass data.

Actual dry-weight biomass data were compared with the subjective plant-biomass classes as assigned by divers to derive objective plant-biomass classification (Table 2). Dense stands of macrophytes were defined as areas with standing dry-weight crops exceeding 30 g/m^2; sparse biomass ranged from 15 to 29 g/m^2, and quads classed as rare had < 15 g/m^2. A fifth class, very dense, was arbitrarily set at > 99 g/m^2.

Aerial photographs were taken each summer from 1984 to 1989 and, in conjunction with ground-truth measurements, snorkeling surveys, and the transect data, were used to map the distribution of macrophytes.

Subtle differences in the placement of transects and water level changes occurring between the 1984 and 1987 surveys influenced sample sizes and areas surveyed (see Table 3). These differences compromised the validity of detailed statistical analyses of biomass data between regions and depth-zones between years but did not seriously affect direct comparisons of summary data for each species. Changes in frequencies of occurrence of the major species were evaluated using chi-squared tests. Plant associations and community structure of the 1987 data were explored uti-

Table 2. Plant biomass distribution in Devil's Lake based on (A) subjective plant classification assigned by divers (visual estimates) and (B) objective dry weight biomass measurements (quantitative). Data represent percent of total quadrats in each classification. 1984 N = 646; 1987 N = 644.

(A):	*Subjective Relative Plant Biomass Classification*	*Year* 1984	1987
	"Dense"	48%	51%
	"Sparse"	23%	19%
	"Rare"	12%	13%
	"Absent"	17%	17%

(B):	*Objective Plant Biomass Classification*	*Biomass (g/m^2)*	*Year* 1984	1987
	Very Dense	> 99	29%	29%
	Dense	30-99	14	19
	Sparse	15-29	26	14
	Rare	1-15	14	21
	Absent	0	17	17

lizing principal component analysis, Pearson correlation coefficients, and similarity indices. The degree of association between species was based on common co-occurrences (Marvan and Komarek 1978) adjusted for random chance co-occurrence. The later analysis was more informative than chi-squared tests in elucidating plant associations.

Results and Discussion

General distribution in 1987

Macrophytes occupied 78% of the 0–9 m littoral zone of Devil's Lake at an average dry weight biomass of 83 g/m^2 (Table 3). Dense macrophyte stands covered 21 ha (48–51% by frequency of occurrence; see Table 2) at an average biomass of 187 g/m^2. Another 16 ha of lake bottom was sparsely vegetated (14–19% frequency of occurrence). Ninety-eight percent of the total biomass of submersed vegetation in Devil's Lake (39,000 kg dry wt) was contained in dense beds. Eighty-five percent of the total plant biomass was confined to water less than 4.5 m deep; virtually no plants grew at depths deeper than 9 m. Highest average total biomass (313 g/m^2) within a particular depth-region zone was in the 1.5–3 m Inlet region. Sixteen species of plants were recorded (Table 4). *Potamogeton robbinsii* Oakes and *Elodea canadensis* Michx. were dominant in water less than 4.5 m deep, and a mixture of *Nitella* spp. and filamentous algae (mostly *Cladophora* spp.) was dominant in deeper water. *Myriophyllum spicatum* L. was less common but still comprised 22% of the lake's total biomass (Table 5). *Ceratophyllum demersum* L., *Vallisneria americana* Michx., *Potamogeton diversifolius* Raf., and a mixture of *Pota-*

Table 3. Regional macrophyte distribution within 0-9 m depth in Devil's Lake during 1987. Comparable data for 1984 are given in ()s (recomputed from Lillie 1984[e]).

Parameter	*Inlet*	*North*	*Southeast*	*Total*
Bottom area* in hectares	10.3 (9.4)	22.3 (21.1)	14.7 (15.0)	47.4 (45.5)
Densely Vegetated area** in hectares	5.2 (4.3)	10.1 (9.8)	5.7 (7.2)	21.0 (21.4)
Coverage[a] % of total area	50 (46)	45 (47)	39 (48)	44 (47)
Standing Crop[b] in thousands of kg	15.3 (10.0)	12.7 (12.3)	11.1 (11.9)	39.2 (34.2)
Average Biomass[c] g/m^2	148 (106)	57 (58)	76 (79)	83 (75)
Average Stand Biomass[d] g/m^2	289 (257)	132 (140)	188 (177)	187 (174)

* excludes 2.9 ha of unvegetated, steeply–sloped, rocky, bottom area adjacent to the east and west shorelines. Differences between 1984 and 1987 bottom areas arise from slight positional differences in placement of transects and subsequent definition of cell boundaries.

**frequency of occurrence of quadrats with total biomass > 30 g/m^2 within each regional depth zone multiplied by the total area within the zone.

[a] total densely vegetated area divided by total bottom area within region.

[b] average total dry wt biomass (g/m^2) within each transect-depth zone (cell) multiplied by the area of each cell; products summed within each region; data represent all vegetation.

[c] total standing crop dry wt biomass within region divided by total area; data represent all sites, including unvegetated areas within regions.

[d] sum of dry wts of all quadrats with biomass > 30 g/m^2 within a region divided by number of quadrats.

[e]Data in Lillie 1986 were computed using WDNR's 1955 hydrographic map; these data were recomputed and are summarized for this publication using the more detailed hydrographic base map prepared from depth soundings made in January 1985 (see Lillie and Mason 1986).

Table 4. Macrophyte community composition of Devil's Lake (1987) listed in order of relative importance.

Taxa	*Freq. of Occurrence*		*Relative Importance*		*Rank*
	*Absolute** %	*Relative* %	*Abundance (% Biomass)*	*Value (IV)*** *(as %)*	*Order*[a]
Potamogeton robbinsii Oakes	34.1	18.3	34.5	26.4	1 (1)
Elodea canadensis Michx.	34.6	18.5	15.5	17.0	2 (3)
Myriophyllum spicatum L.	19.0	10.2	21.5	15.8	3 (2)
Nitella & Cladophora (mixed)	32.1	17.2	12.0	14.6	4 (6)
Ceratophyllum demersum L.	18.1	9.7	8.4	9.0	5 (5)
Vallisneria americana Michx.	9.0	4.8	2.6	3.7	6 (8)
Potamogeton diversifolius Raf.	8.3	4.4	1.1	2.8	7 (10)
Potamogeton illinoensis Morong mixed with *Potamogeton amplifolius* Tuckerm.	8.2	4.4	0.8	2.6	8 (4)
Others/unidentified**	5.7	3.1	0.7	1.9	9 (14)
Eleocharis acicularis (L.) Rostk. & Schmidt	4.0	2.1	1.5	1.8	10 (7)
Najas flexilis (Willd.) R. & S.	5.5	3.0	0.6	1.8	11 (12)
Isoetes echinospora Durieu	4.0	2.1	0.5	1.3	12 (9)
Chara sp.	2.0	1.1	0.1	0.6	13 (13)
Potamogeton crispus L.	2.0	1.1	0.1	0.6	14 (11)
Megalodonta[b] *beckii* (Torr.)	0.1	tr.	tr.	0.1	15 (–)

* Absolute frequency of occurrence based on presence/absence at 601 quadrats within 0–9 m (excludes rocky, unvegetated, east and west quartzite-talus slopes); Relative Abundance represents % of total dry wt biomass; IVs computed by averaging Relative Frequency of Occurrence and Relative Abundance.
**Others include *Ranunculus* spp., *Potamogeton pusillus* sensu lato, and *P. gramineus.*
[a]*( )s indicate 1984 ranking.*
[b]now *Bidens beckii* Torr.

mogeton illinoensis and *Potamogeton amplifolius* (hereafter referred to as *P. ill/amp.*) were also relatively common. Biomass distribution of most taxa was depth dependent (Figs. 2 and 3). Based on depth distribution, co-occurrences (Fig. 4), and visual observations, four relatively distinct communities were distinguishable. A diverse assemblage of relatively small, short-stemmed plants consisting of *Najas flexilis* (Wild.) R. & S., *E. acicularis, Potamogeton crispus* L., *P. diversifolius, Chara* spp., *Isoetes echinospora* Durieu, and *V. americana* comprised the shallow-water community. A mixture of *P. robbinsii* and *E. canadensis,* with lesser amounts of *P. ill/amp.* and *V. americana,* formed a distinct community at 2–3 m. *Myriophyllum spicatum,* often accompanied by *C. demersum* at edges of beds, formed very dense beds at the outer edge of the littoral shelf in 2.5–3.5 m (the lake bottom descends sharply beyond this point). A mixture of *Nitella* spp. and *Cladophora* spp. formed the deep-water community.

Distribution of major taxa in 1987

Potamogeton robbinsii, or Robbin's pondweed, was the dominant macrophyte in Devil's Lake, accounting for 34% of the total standing crop biomass. Dense stands, averaging 173 g/m^2, occupied 7.2 ha (18% of all quadrats sampled). *Potamogeton robbinsii* was distributed in relatively broad, primarily monotypic, distinct bands at 1.5–4.5 m adjacent to the North and Southeast shorelines (Fig. 2 and Appendix A). However, highest average stand biomass (280 g/m^2) was located in shallow water (1–3 m) adjacent to the Inlet region. Frequency of occurrence (56–70%) was similar in all three regions. The

largest areal distribution of *P. robbinsii* (2.8 ha) was in scattered beds located off the North shore. *Potamogeton robbinsii* was most commonly associated with *E. canadensis* (Fig. 4). At the time of the survey, *P. robbinsii* appeared to be at the peak of its growth, with strong, well-rooted plant stems. *P. robbinsii* harbored many aquatic fauna, particularly large numbers of dragonfly and caddisfly larvae. Despite its extensive distribution and dense growths, *P. robbinsii* was relatively unnoticed by the average park user due to the plant's low growth form (<1 m height) and moderately deep-water habitat (the beds in the Inlet region were an exception). *Potamogeton robbinsii* has a much narrower ecological niche than that of *C. demersum* or *M. spicatum* (Pip 1988), and hence its dominance in Devil's Lake reflects the relatively low concentration of inorganics present.

Elodea canadensis, or waterweed, was equally as common but less abundant than *P. robbinsii* (16% of total plant standing crop), ranking second in overall relative importance. Where abundant (4.0 ha), *Elodea* stand biomass averaged 142 g/m^2. *Elodea* formed weakly continuous patches (relatively irregular clumps less than 10 m across) with average biomass up to 152 g/m^2 in the North and Inlet regions. *Elodea* co-occurred primarily with *P. robbinsii* and *C. demersum* (Fig. 4). *Elodea* leaves were very short and confined to the margins of the stems (<1.5 m in length), which were weakly rooted. Very dense stands of *Elodea* may interfere with fishing, but generally the plant does not create a problem in Devil's Lake.

Myriophyllum spicatum, or milfoil, comprised 21.5% of the total standing crop. While less extensive in coverage than *P. robbinsii* or *E. canadensis* (only 3.1 ha of dense beds), average milfoil stand biomass (270 g/m^2) was more than 50% higher than either competitor. A maximum biomass of 1100 g/m^2 was recorded at 1 quadrat. Milfoil distribution was concentrated in three distinct beds, 50 m wide by 300 m long, located 50–70 m directly offshore from high-recreation-use areas (Fig. 2). Average biomass in the Southeast and Inlet beds were identical (314 g/m^2) and higher than that of the North bed. Milfoil beds generally were confined to 1.5–3 m with deeper extensions to 4.5 m in the Southeast and Inlet beds (Appendix A). Frequencies of occurrence were highest in the Inlet region (60–73%) and lowest in the North bed (15–21%). Milfoil was commonly associated with *C. demersum* (Fig. 4); however, biomass was not significantly correlated within milfoil beds

Table 5. Regional distribution, average biomass, and total standing crop of the five major plant taxa in Devil's Lake. Total biomass (kg dry wt*) estimates include sparsely vegetated sites. Average densities (g/m^2; = sum of dry weights/number of quads) and distributional area are given for densely vegetated sites only (i.e., those quads with biomass in excess of 30 g/m^2).

Taxa	*Inlet*			*North*			*Southeast*			*All Regions*			
	Dist Area ha**	Aver. Biomass g/m^2	Total Mass 10^3k	Dist. Area ha	Aver. Biomass g/m^2	Total Mass 10^3k	Dist. Area ha	Aver. Biomass g/m^2	Total Mass 10^3k	Dist. Area ha	Aver. Biomass g/m^2	Total Mass 10^3k	# Quads
P. robbinsii	2.0	280	6.5	2.8	127	3.3	2.4	139	3.7	7.2	173	13.5	116
E. canadensis	1.5	146	2.2	2.1	152	3.6	0.5	66	0.2	4.0	142	6.1	62
M. spicatum	1.0	314	3.2	0.7	106	0.7	1.5	314	4.5	3.1	270	8.4	52
Nitella/Cladoph.	1.1	55	0.9	3.0	84	2.6	1.5	49	1.2	5.6	69	4.7	72
C. demersum	0.6	160	1.1	0.7	136	1.0	0.4	232	1.2	1.7	168	3.3	31

* derived by multiplying average biomass (g/m^2) within each transect-depth zone cell by the area of each cell; products summed to derive total biomass within each region.

** sum of totals exceeds that given in Table 3 due to overlap between species.

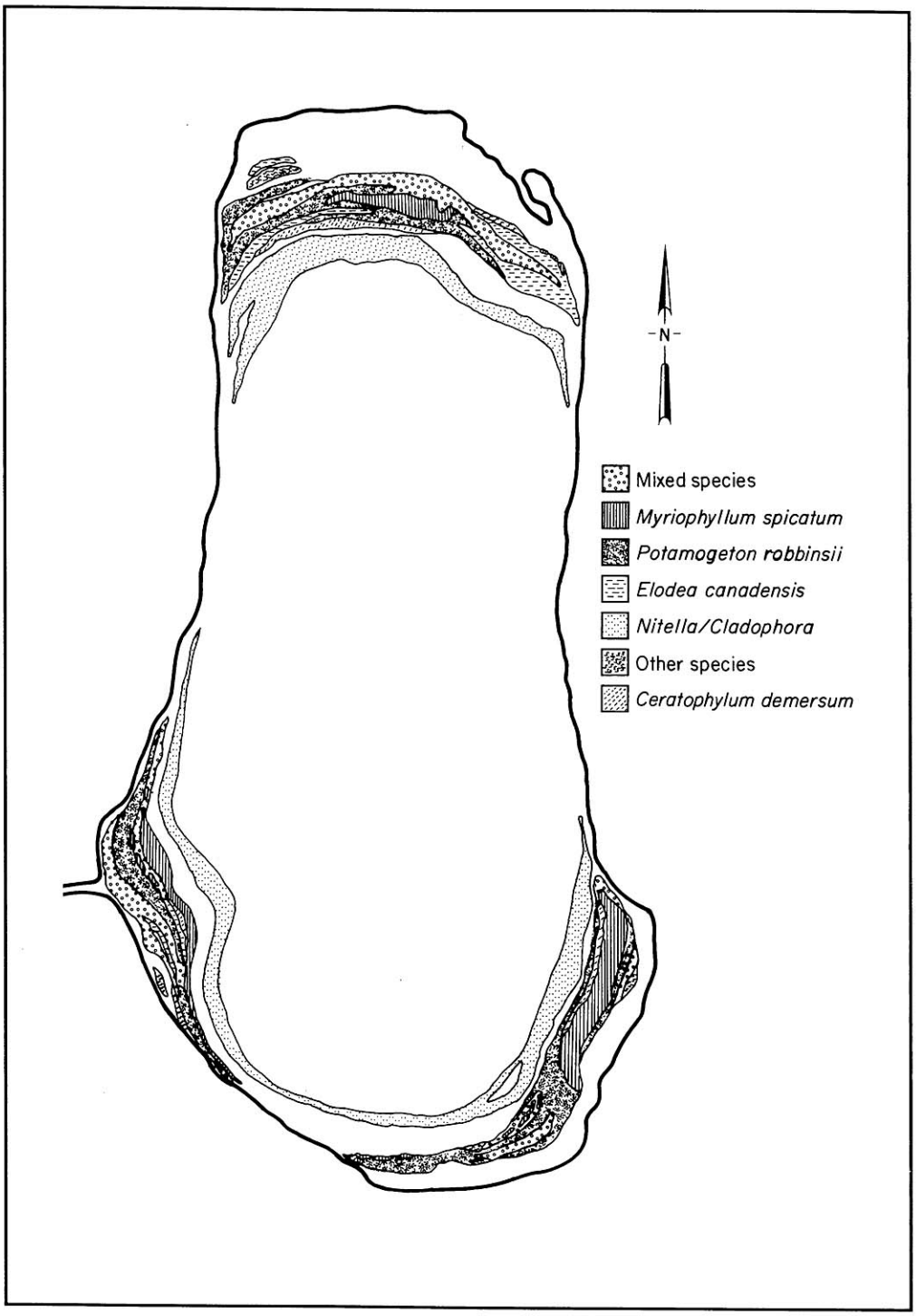

Fig. 2. Generalized distributional map of submersed macrophytes in Devil's Lake. The map denotes areas dominated by particular species; other species may be present as well, but in lesser amounts.

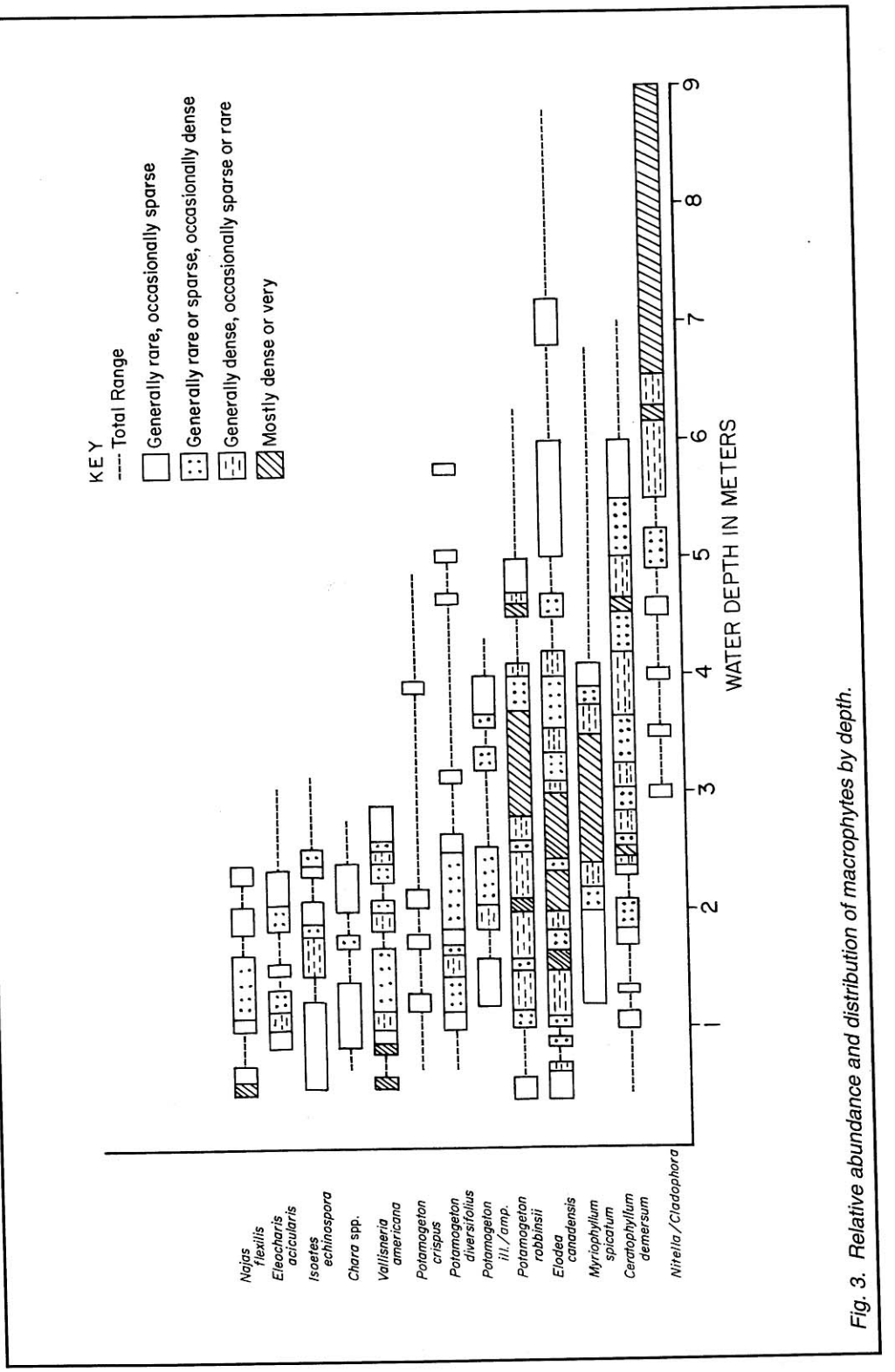

Fig. 3. Relative abundance and distribution of macrophytes by depth.

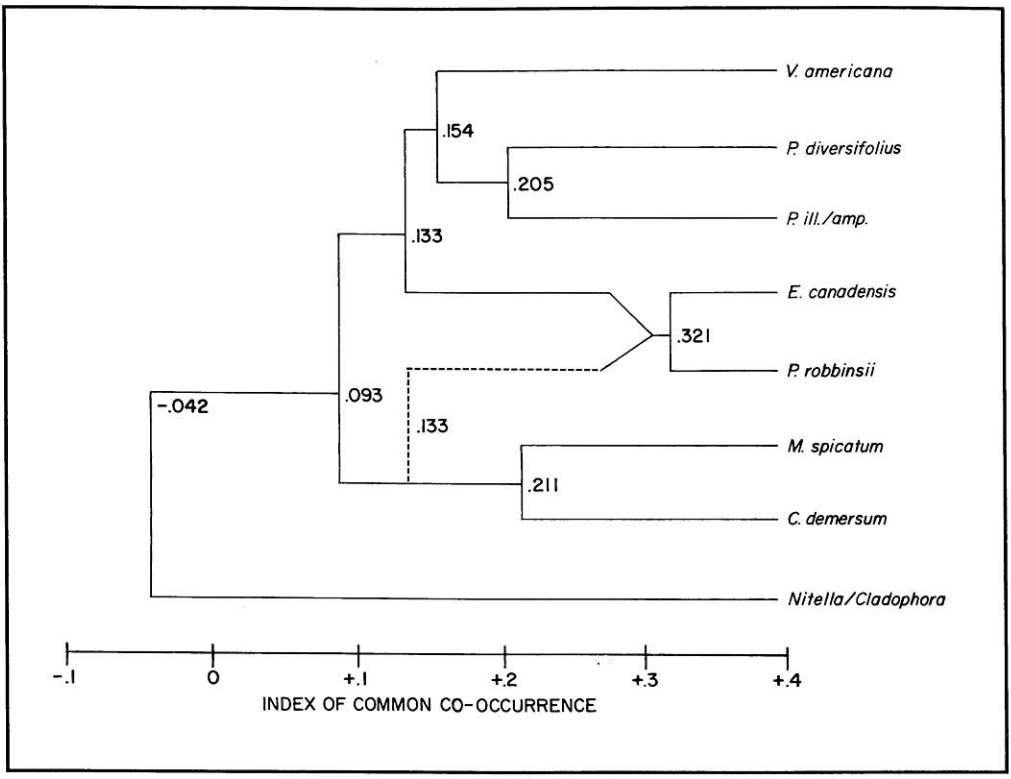

Fig. 4. Plant associations of the more abundant plant taxa based on common co-occurrence.

($p>.05$). Milfoil biomass was inversely related to *E. canadensis* biomass within milfoil beds ($p=.05$), but the standing crop of *P. robbinsii* (the other species from inhabiting similar depths) was not significantly affected ($p>.50$). Milfoil stems often exceeded 3 m in length, and dense stands formed nearly impenetrable masses at the lake's surface. As such, the beds created a severe nuisance to all users and a particularly dangerous threat to swimmers. Other than small beds of *P. ill/amp* and *Ranunculus* spp., milfoil was the only submergent plant in Devil's Lake that was commonly visible from shore.

Nitella spp., a muskgrass or member of the Characeae, and *Cladophora* spp., a filamentous green algae, formed the dominant deep-water community accounting for 12% of the total standing crop in Devil's Lake (82% of the biomass of all plants at 4.5–9 m). Distribution was continuous to patchy, with highest biomass (84 g/m^2) off the North shore in 7.5–9 m where frequencies of occurrence were close to 90% (Appendix A). Few macrophytes were associated with the *Nitella/Cladophora* community. Because these plants grow in relatively deep water and their stems are narrow and weak, they do not present a nuisance to people fishing on the lake. Most filamentous algae problems in Devil's Lake are due to other algae that develop on plants or other substrates in shallower water. Little is known of the fauna associated with the deep-water *Nitella/Cladophora* community in Devil's Lake.

Ceratophyllum demersum, or coontail, had a total standing crop of over 3,000 kg that was relatively evenly distributed among all three regions. Average stand biomass was relatively high (168 g/m^2), approaching that of milfoil in the Southeast bed. The irregular distribution of coontail in Devil's Lake (Fig. 3, Appendix A) may be related to this species' close association with milfoil (Fig. 4); coon-

tail and milfoil were most strongly correlated at the margins of milfoil beds ($p = .008$). While coontail develops rootlets, it does not become firmly attached to the sediments. Hence, coontail may drift about until it becomes entangled within the inner and outer edges of the milfoil beds.

The distributions of the remaining, less common species were primarily patchy. *Vallisneria americana, P. diversifolius, P. ill/amp., P. crispus,* and *I. echinospora* were commonly found at 1.5–4.5 m mixed with *P. robbinsii* and *E. canadensis*. Interspecific competition between many of these ecologically similar species was reduced via spatial (depth) separation or by virtue of life-form structure (see Pip 1988). The rosulate quillwort, *I. echinospora,* was almost exclusively restricted to a very narrow band between 1.5–2.1 m. *Potamogeton ill/amp.* occasionally formed relatively dense beds with plant stems reaching to the lake surface. Other plants were of relatively short stature and formed a varied understory. *Najas flexilis, Chara* spp., *E. acicularis,* and *Ranunculus* spp. formed the bulk of the shallow-water community that undoubtedly received a great deal of human disturbance. *Eleocharis acicularis* was extremely short and often formed contiguous, grass-like mats in the interstitial spaces on the lake bottom between the larger macrophytes. *Megalodonta beckii* (Torr.) (= *Bidens beckii* Torr.) is a relatively rare plant in Devil's Lake (only found in one biomass quadrat) and could easily be mistaken for milfoil or coontail. This species was confined to a few widely scattered patches in 3–4.5 m off the North shore.

Historical Perspective

Milfoil invasion

The pattern of invasion of Eurasian watermilfoil in other lakes has been characterized as one of introduction, rapid expansion, subsequent die-off, and resurgence, not necessarily to previous maxima (Carpenter 1979; Nichols and Shaw 1986). While the invasion and subsequent expansion of milfoil in Devil's Lake have been fairly well documented (Lillie 1986), it has not been possible to identify the mechanism responsible for the introduction nor the exact year that the introduction occurred. Best estimates place the time of the infestation around the early 1960s (Lillie and Mason 1986), although Meier and Ensign (1967) make no mention of milfoil in their field notes during two fish survey seine hauls of the Southeast beach area during 1967. Baker (1975) described milfoil (possibly misidentified as *M. verticillatum*) in the Southeast bed area during a 1974 SCUBA survey as "very scattered, at 1.2 to 4.5 m depth contributing little to the population of the total community." The distribution and area of the three milfoil beds changed dramatically from 1979 to 1983 based on rake-survey data (Southeast bed shown in Fig. 5a) collected by the WDNR (Bale and Molter 1979, 1980, 1981; Schlesser et al. 1982; Molter and Schlesser 1983). In 1979, the North milfoil bed was quite extensively developed, while the Southeast bed was just becoming established. The Inlet bed appeared to be slightly smaller than at present (referring to 1987). By 1983, the Inlet bed was similar or slightly larger than at present, and the North-shore bed extended slightly farther to the west than its present distribution. The Southeast bed extended considerably farther to the west along the south shoreline, but it was much less abundant along its northern extension than at present. Despite a significant decrease in frequency of occurrence of milfoil between 1984 and 1987 ($p<0.05$), the general configuration of the three milfoil beds remained relatively stable. Transect data suggest that the North-shore milfoil bed decreased in both size and average biomass; the Inlet bed biomass increased 140%, primarily due to increases in both size and stand biomass within the 1.5–4.5 m zone; and the Southeast bed remained stable except for a moderate increase in biomass.

Aerial photography suggests that the distribution of milfoil in the Inlet bed expanded

75% from 1984 to 1987, the Southeast bed expanded very slightly, and the North-shore bed declined slightly (Table 6, Fig. 5b). However, during the 1987 survey, tops of milfoil stems were 0.5 and 1 m below the lake surface at the Inlet and North beds, respectively, and at the surface in the Southeast bed. Because milfoil growth had not reached the surface at the North and Inlet beds, other submersed plants may have been mistaken for milfoil; thus milfoil distribution may have been overestimated in those two beds. Biomass estimates presented in Table 5 are believed to be the more accurate, suggesting that milfoil biomass increased by approximately 20% between 1984 and 1987.

While the transect data (1984 and 1987) suggest an overall increase in milfoil biomass (frequency of occurrence decreased), changes in biomass within individual beds were asynchronous; the Inlet bed expanded and the North-shore bed contracted. It appears that the North-shore milfoil bed reached a peak in size in 1983 or 1984 and then experienced a gradual die-off. The expansion of the Inlet bed in 1987 may have represented a reestablishment following a period of decline experienced in the early 1980s. The size of the Southeast bed increased substantially from 1974 to 1984 and then remained relatively stable through 1987. However, continued aerial photography and snorkeling surveys revealed a dramatic die-off of milfoil in the northern half of the Southeast bed between 1987 and 1988 (Fig. 5b). Part of this bed recovered in 1989, but the major portion of the bed remained unvegetated (except for some very scattered sparse growths of native species). While such asynchronous variations in milfoil have been observed in other lakes (Carpenter 1979), the mechanism responsible for these fluctuations has not been clearly identified.

While historical records of milfoil invasions in some lakes suggest that milfoil outcompetes and displaces native macrophytes (Nichols and Mori 1971; Adams and Prentki 1982), some data suggest that milfoil invades disturbed areas or denuded sediments (Keast 1984). While milfoil now occupies areas in Devil's Lake that were formerly occupied by *E. canadensis* and *P. robbinsii*, the historical record is inadequate to determine whether milfoil aggressively displaced the native species or whether milfoil simply filled the void created when the native species succumbed to some other disturbance (Lillie 1986). Of particular note in this respect is the recent report by Devil's Lake State Park staff of an unusual amount of native macrophytes accumulating along the park's beaches during the summer of 1989. Further investigations by the author revealed that an enormous number of caddisfly *(Trichoptera: Leptoceridae)* larvae had constructed their cases from *Elodea* plant fragments. Whether the large masses of free-floating *Elodea* resulted from the mechanical fragmentation by the caddisfly larvae or from increased wave-action intensity accompa-

Table 6. Estimated distributional coverage (ha) of *Myriophyllum spicatum* in Devil's Lake 1984–1989 based on aerial reconnaissance photography.

Bed Location	*1984*	*1985 (*)*		*1986*	*1987*	*1988*	*1989*
Southeast	1.3	1.4	(1.6)	1.3	1.5	0.5	0.7
North	1.1	0.8	(0.8)	0.9	1.0	0.6	0.4**
Inlet	0.7	1.1	(1.2)	0.9	1.3	0.7	0.9
Totals	3.1	3.4	(3.6)	3.1	3.8	1.8	2.0**

*based on ground-truth data collected August 1985.

**much of the North shore milfoil bed was hand-harvested on 24 September 1988 by teams of SCUBA-divers.

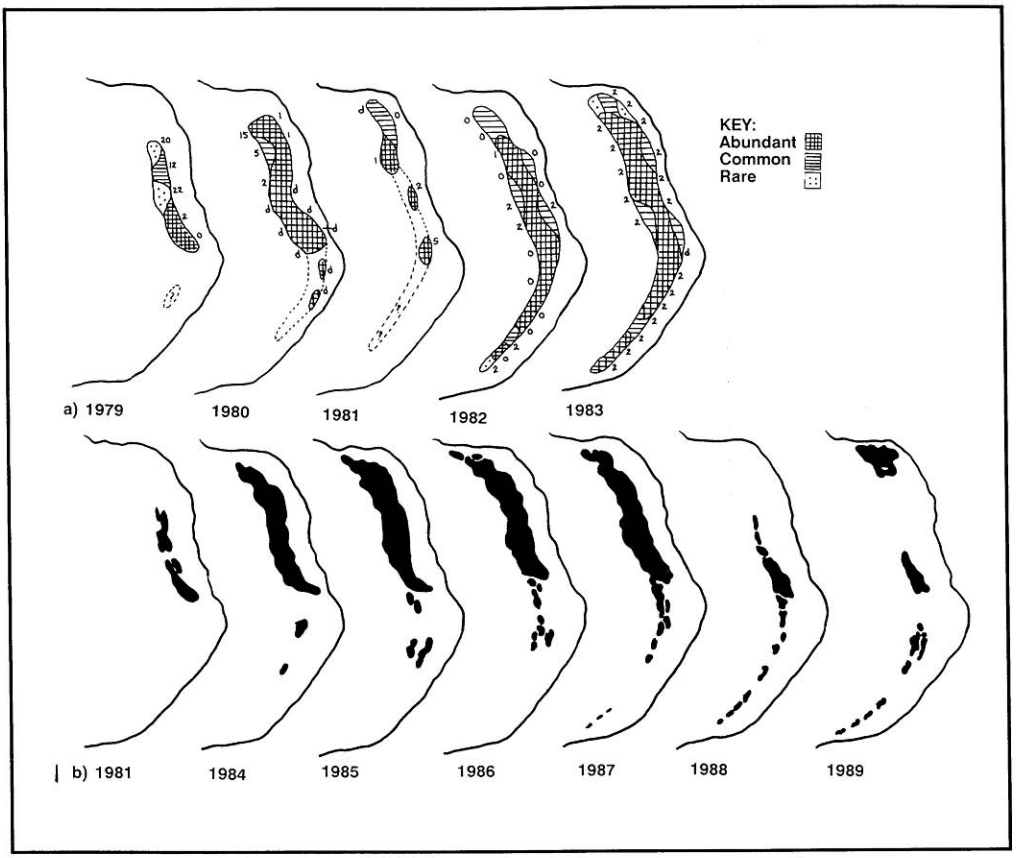

Fig. 5.(a) Generalized configuration and extent of SE milfoil bed based on summer WDNR rake surveys 1979–83 (unpublished WDNR studies—Bale and Molter 1979, 1980, 1981; Schlesser et al. 1982; Molter and Schlesser 1983). Numbers indicate distance (cm) from lake surface to top of plant beds (d = deep, not measured).
(b) Configuration and extent of SE milfoil bed based on aerial photography taken in mid-summer 1981, 1984–1989.

nying a moderately severe drop in lake water level (0.75 m since 1984) was not determined. However, it was clear that large areas formerly occupied by *Elodea* were rapidly becoming denuded. Whether milfoil invades these areas in the future remains to be seen.

Native plant community

In addition to the recent changes in *Elodea* noted above, other changes have occurred in the native plant community of Devil's Lake. Biomass of *P. robbinsii* and *P. ill/amp.* decreased and *E. canadensis, C. demersum,* and *Nitella/Cladophora* biomass increased during the short period from 1984 to 1987. Excluding the deep-water *Nitella/Cladophora* community, the combined standing crop of all native plants increased only 4% from 1984 to 1987. *Nitella/Cladophora* biomass doubled and frequency of occurrence increased significantly during the same time span. Coverage (area) of dense macrophytes (all species combined) differed very slightly from 1984 to 1987 based on visual observations by divers and biomass measurements (Table 2). Total standing crop increased 15–16% during the same period (including milfoil). With the exception of a possible decline in *Elodea* and an increase in coontail, the distributions and biomass of native species

in the Southeast bed during 1984 and 1987 were generally similar to that described by Baker (1975) in his 1974 survey (Baker's 1974 survey was restricted to only the Southeast area; no other quantitative biomass data exist for other beds or other years). The rake-surveys conducted by the WDNR during 1979–1983 documented an increase in the distribution of *E. canadensis* from 1979 to 1982 (down slightly in 1983), and a decline in the distribution of *P. robbinsii* from 1979 to 1983. Apparent fluctuations in distribution and relative abundance of *Nitella* and filamentous algae may have resulted from changes in sampling methodology.

Prior to the 1974 Baker survey, only a few scattered records exist. Perhaps most important are comments from WDNR fish management surveys: 1967 — "Aquatic vegetation, primarily *Anacharis (=Elodea) canadensis,* was growing profusely in the area (Southeast) of the lake seined." *Potamogeton robbinsii* was also listed as common (Meier and Ensign 1967); and 1945 —"There is a weed bed (North shore) that apparently is a feeding spot for perch," and "there is little vegetation" (Wis. Cons. Dep. 1945). While it may be safely assumed that the first of these comments refers to plants hauled up in the seines, the basis for the latter and other records is less certain. Many comments simply may reflect casual observations made from shore or boat, perceptions that may be grossly inaccurate. However, the consensus of opinion among people who have trolled the lake on a regular basis for many years is that submersed vegetation has increased greatly during the past 30 years. Other subjective observations, such as the milfoil expansion and the water lily disappearance off the entrance to the North shore boat landing, have been substantiated by hard data. This data further supports the short-term scientific record and conclusion that submersed vegetation has increased substantially in Devil's Lake during the last 30 years.

Acknowledgments

Data collections and processing of macrophytes were accomplished through the combined efforts of the following individuals whose efforts are hereby acknowledged and thanked: G. Wegner, G. Quinn, P. Garrison, D. Soltis, D. Marshall, B. Dhuey, S. Claas, T. Penniston, and I. Marx. Statistical advice and review were provided by G. Lange and P. Rasmussen. Editorial reviews of earlier drafts were provided by J. Mason, D. Knauer, and K. Lange. The editorial assistance of D. Mears and drafting by R. Burton are also appreciated. Special thanks is due J. Madsen and an anonymous reviewer for several helpful review comments and suggestions. Funding for this study was provided by the Bureau of Water Resources Management and the Bureau of Research, Wisconsin Department of Natural Resources.

Appendix A: Part 1

Total plant biomass (kg) distribution of major plant species in Devil's Lake by year, region and depth (in meters).

		DEPTH ZONES						
Species	*Region*	*0-1.5*	*1.5-3*	*3-4.5*	*4.5-6*	*6-7.5*	*7.5-9*	*SUM*
ALL PLANTS								
1984	Inlet	3,842	5,214	549	114	97	137	9,953
	North	684	7,277	2,982	714	272	342	12,270
	SE	448	6,818	2,701	884	758	328	11,938
								34,161
1987	Inlet	6,482	5,959	1,958	36	70	814	15,319
	North	759	5,496	3,187	890	665	1,736	12,733
	SE	286	5,895	3,449	429	491	593	11,143
								39,195
M. spicatum								
1984	Inlet	15	896	421	50	11	0	1,393
	North	128	1,756	14	0	0	0	1,898
	SE	63	3,231	84	210	0	0	3,588
								6,879
1987	Inlet	0	1,815	1,362	0	2	0	3,220
	North	10	734	4	0	0	0	748
	SE	19	3,131	1,306	10	5	0	4,471
								8,439
P. robbinsii								
1984	Inlet	2,614	3,220	0	2	7	0	5,843
	North	15	4,172	1,495	18	28	0	5,728
	SE	76	3,044	2,005	103	1	0	5,229
								16,800
1987	Inlet	3,790	2,553	130	16	0	0	6,489
	North	24	1,765	1,462	50	0	0	3,301
	SE	12	1,828	1,804	82	4	0	3,730
								13,520
E. canadensis								
1984	Inlet	767	718	5	12	5	0	1,507
	North	121	343	852	447	1	0	1,764
	SE	97	395	168	47	26	0	733
								4,004
1987	Inlet	1,304	872	18	0	0	1	2,195
	North	285	1,885	1,425	20	11	0	3,626
	SE	76	143	20	1	5	3	248
								6,069
C. demersum								
1984	Inlet	4	128	63	36	0	1	232
	North	1	67	379	155	25	8	635
	SE	0	44	360	67	32	31	534
								1,401

cont.

Appendix A: Part 1

Species	*Region*	*DEPTH ZONES* 0-1.5	1.5-3	3-4.5	4.5-6	6-7.5	7.5-9	*SUM*
1987	Inlet	8	661	444	19	4	0	1,136
	North	21	136	255	566	2	0	980
	SE	3	665	298	229	0	0	1,195
								3,311
Nitella-Cladophora community								
1984	Inlet	0	0	0	0	71	137	208
	North	2	0	0	66	217	334	619
	SE	0	1	1	459	700	297	1,458
								2,285
1987	Inlet	0	0	0	0	64	812	876
	North	0	1	12	248	652	1,736	2,649
	SE	0	0	0	101	477	591	1,169
								4,694

Appendix A, Part 2

Frequency of occurrence (% quadrats present*) of major plant species in Devil's Lake by year, region, and depth (meters)..

Species	*Region*	*0-1.5*	*1.5-3*	*3.4-5*	*4.5-6*	*6-7.5*	*7.5-9*	*SUM*
ALL PLANTS								
1984	Inlet	84%	92%	77%	71%	73%	71%	81%
	North	69	99	94	95	97	83	91%
	SE	45	95	97	83	87	96	85%
1987	Inlet	89	98	82	50	61	96	89%
	North	56	95	94	91	92	93	88%
	SE	42	97	97	93	95	87	87%
M. spicatum								
1984	Inlet	24	49	77	29	14	0	31%
	North	50	42	20	0	0	0	30%
	SE	21	65	39	8	0	0	32%
1987	Inlet	0	60	73	0	6	0	26%
	North	8	21	15	0	0	0	11%
	SE	15	41	50	7	9	0	26%
P. robbinsii								
1984	Inlet	52	62	0	7	9	0	30%
	North	7	68	69	26	12	0	42%
	SE	10	60	81	12	4	0	38%
1987	Inlet	67	56	11	25	0	0	34%
	North	23	59	58	9	0	0	33%
	SE	15	59	70	27	4	0	36%
E. canadensis								
1984	Inlet	56	67	15	7	4	0	33%
	North	37	56	74	37	3	0	43%
	SE	14	25	52	25	17	0	23%
1987	Inlet	56	56	11	0	0	4	31%
	North	51	73	79	26	3	0	47%
	SE	19	25	30	7	14	7	19%
C. demersum								
1984	Inlet	20	20	54	43	0	5	20%
	North	2	12	29	63	38	8	18%
	SE	0	15	39	42	30	22	21%
1987	Inlet	15	47	27	38	11	0	24%
	North	13	12	51	52	3	0	17%
	SE	4	13	50	27	0	0	15%
Nitella-Cladophora community								
1984	Inlet	0	0	0	0	50	71	19%
	North	2	1	3	26	84	83	19%
	SE	0	2	3	58	74	96	29%
1987	Inlet	0	0	0	0	56	96	27%
	North	0	1	12	87	92	93	35%
	SE	0	0	0	53	91	87	29%

*allocation of quadrats by regions and years:
1984 (I=134, N=289, SE=182) total N = 605;
1987 (I=137, N=278, SE=186) total N = 601.

Appendix A, Part 3

Mean dry weight biomass (g/m²) distribution of major plant species in Devil's Lake by year, region, and depth zones (in meters).

Species	*Region*	*0-1.5*	*1.5-3*	*3-4.5*	*4.5-6*	*6-7.5*	*7.5-9*	*Avg.*
TOTAL PLANTS								
1984	Inlet	164	281	63	17	7	6	106
	North	11	116	174	43	12	11	58
	SE	13	157	154	71	48	13	79
1987	Inlet	254	313	210	4	5	33	148
	North	12	85	175	50	26	50	57
	SE	8	137	213	33	32	23	76
M. spicatum								
1984	Inlet	<1	48	48	7	<1	0	15
	North	2	28	<1	0	0	0	9
	SE	2	74	5	17	0	0	24
1987	Inlet	0	95	146	0	<1	0	31
	North	<1	11	<1	0	0	0	3
	SE	<1	73	81	<1	<1	0	30
P. robbinsii								
1984	Inlet	111	173	0	<1	<1	0	62
	North	<1	66	87	1	1	0	27
	SE	2	70	115	8	<1	0	35
1987	Inlet	149	134	14	2	0	0	54
	North	<1	27	80	3	0	0	15
	SE	<1	43	111	6	<1	0	25
E. canadensis								
1984	Inlet	33	39	<1	2	<1	0	16
	North	2	5	50	27	<1	0	8
	SE	3	9	10	4	2	0	5
1987	Inlet	51	46	2	0	0	<1	21
	North	5	29	78	1	<1	0	16
	SE	2	3	1	<1	<1	<1	2
C. demersum								
1984	Inlet	<1	7	7	5	0	<1	2
	North	<1	1	22	9	1	<1	3
	SE	0	1	21	5	2	1	4
1987	Inlet	<1	35	48	2	<1	0	11
	North	<1	2	14	32	<1	0	4
	SE	<1	15	18	18	0	0	8
Nitella-Cladophora community								
1984	Inlet	0	0	0	0	5	6	2
	North	<1	<1	<1	4	9	11	3
	SE	0	<1	<1	37	44	12	10
1987	Inlet	0	0	0	0	4	33	8
	North	0	<1	<1	14	25	50	12
	SE	0	0	0	8	31	23	8

* derived by summing total kg in each cell (transect by depth) and dividing by total area in each region.

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